

## Nutrient fluxes at the landscape level and the $R^*$ rule

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### ABSTRACT

Nutrient cycling in terrestrial ecosystems involves not only the vertical recycling of nutrients at specific locations in space, but also biologically driven horizontal fluxes between different areas of the landscape. This latter process can result in net accumulation of nutrients in some places and net losses in others. We examined the effects of such nutrient-concentrating fluxes on the  $R^*$  rule, which predicts that the species that can survive in steady state at the lowest level of limiting resource,  $R^*$ , can exclude all competing species. To study the  $R^*$  rule in this context, we used a literature model of plant growth and nutrient cycling in which both nutrients and light may limit growth, with plants allocating carbon and nutrients between foliage and roots according to different strategies. We incorporated the assumption that biological processes may concentrate nutrients in some parts of the landscape. We assumed further that these processes draw nutrients from outside the zone of local recycling at a rate proportional to the local biomass density. Analysis showed that at sites where there is a sufficient biomass-dependent accumulation of nutrients, the plant species with the highest biomass production rates (roughly corresponding to the best competitors) do not reduce locally available nutrients to a minimum concentration level (that is, minimum  $R^*$ ), as expected from the  $R^*$  rule, but instead maximize local nutrient concentration. These new results require broadening of our understanding of the relationships between nutrients and vegetation competition on the landscape level. The  $R^*$  rule is replaced by a more complex criterion that varies across a landscape and reduces to the  $R^*$  rule only under certain limiting conditions.

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### 1. Introduction

A major advance in ecosystem ecology has been the recognition of mechanisms that lead to self-organization of vegetative patterns on the wetland landscapes (e.g., Rietkerk et al., 2004; Larsen et al., 2007; Givnish et al., 2008). These mechanisms include biologically driven positive feedbacks. One important feedback is the ability of patches of high density vegetation to accumulate nutrients from other parts of the landscape, which increases the growth rates of vegetation in these patches, which further increases their ability to accumulate nutrients (Wetzel et al., 2005). Thus a self-reinforcing pattern of patches with high biomass and high soil nutrient concentrations can emerge in an oligotrophic landscape matrix.

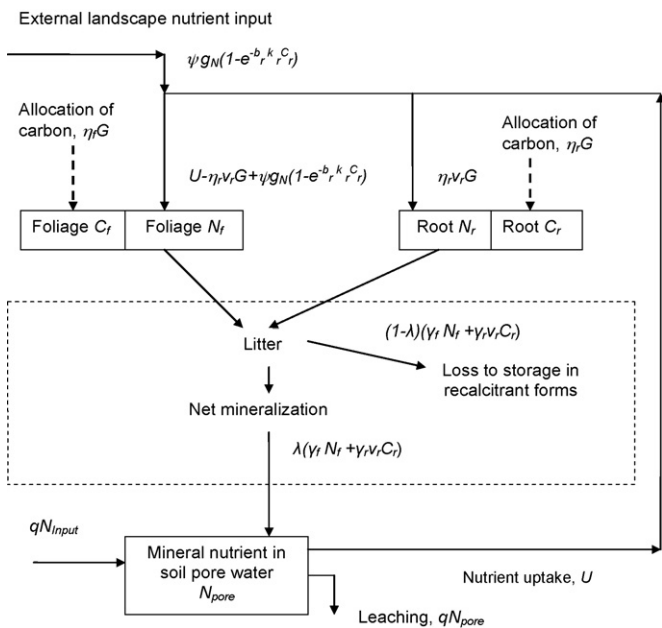
Such patterns of vegetation and nutrient distribution are observed in wetland ecosystems such as the Everglades. In the Everglades, measurements of the limiting nutrient, phosphorus in available form in soil pore water, show one to two orders of magni-

tude differences between sawgrass prairie and adjacent hardwood hammock tree islands (Ross et al., 2006 see their Fig. 3b). Thus, these tree islands are hotspots for phosphorus concentration in an ecosystem that is otherwise oligotrophic, with especially low phosphorus concentration. Because self-organizing landscapes, such as bogs and marshes having patches of dense vegetation (e.g., tree islands) in a matrix of less dense vegetation, are common in many parts of the world (Wetzel, 2002), these types of nutrient patterns may also be common in nature.

Possible explanations have been proposed for the accumulation of phosphorus in tree islands relative to surrounding marsh. Relatively high biomass productivity is favored on these islands by slightly higher elevation than the marsh, but that productivity is amplified by one or more of the following positive feedbacks. (i) Tree islands have higher evapotranspiration than the surrounding marsh, and thereby pull in water and phosphorus from the surrounding marsh (Ross et al., 2006). (ii) Tree islands can serve as nesting places for colonial wading birds, which deposit nutrients (in guano) gained from foraging in the marsh (e.g., Oliver and Legovic, 1988). (iii) By projecting above the surrounding marsh, tree islands might be able to capture relatively more airborne nutrients as dry deposition (Lowman and Rinker, 2004). All three processes might reasonably be expected to capture new nutrients from external sources at rates proportional to the amount

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**Fig. 1.** Schematic of model used in this paper. It is a modified version of the G'DAY model (Comins and McMurtrie, 1993), with the details of litter decomposition and soil processes omitted, but an available soil pore water nutrient pool added. The foliage and root compartments have separate variables for carbon and nutrient. Nutrient fluxes are represented by solid lines and carbon fluxes by dashed lines.

of standing crop biomass of the tree island. Each of these mechanisms would cause an increase in nutrient input that is positively related to the standing crop of vegetation biomass, consistent with the self-organizing processes discussed by Rietkerk et al. (2004) and Givnish et al. (2008). Because of these mechanisms of external nutrient intake, the rate at which nutrients are returned to the local nutrient pool (soil pore water) by decomposing dead biomass can approach, or perhaps even exceed, the amount taken up by the vegetation from that local pool, despite losses due to the fall of litter that is not completely mineralized, but lost to recalcitrant forms. This biomass-density dependent external input does not lead to endlessly growing biomass in such locations, because diffusion and other loss processes eventually balance the biologically driven fluxes. However, these mechanisms do lead to sustained inhomogeneities in the distribution of nutrients and vegetation over the landscape.

Using modeling, we investigated the effect of such biomass-dependent nutrient accumulation mechanisms on the well-known  $R^*$  rule. That rule states that, when consumers exert top-down control on resources, the species that can survive at the lowest levels of a limiting resource will be the best competitor for that resource and will displace all other species (Tilman, 1982). The  $R^*$  rule has received much empirical support; see Wilson et al. (2007) for a review, as well as Miller et al. (2005). However, this support is mostly from studies of microbial systems, primarily bacteria, phytoplankton, and zooplankton.

To examine the effect of local nutrient accumulation, such as occurs on tree islands in a wetland, we used a model in which both solar radiation and a single nutrient are potentially limiting, with the former imposing an ultimate limitation on growth rate. In particular, we modified a well-known model of tree growth and nutrient cycling; the G'DAY model (Comins and McMurtrie, 1993). This model simulates both carbon and nitrogen in tree and soil compartments. We modified the original model by adding an explicit compartment for the limiting nutrient dissolved in soil pore water (Fig. 1). However, to avoid the complexity of soil processes, the seven compartments for litter and soil in the original model were

**Table 1**  
Variables and parameters used in the model. Some values are adapted from Comins and McMurtrie (1993), but the parameters are not fit to a particular system.

| Variables  |                      |
|--|----------------------|
| $C_f, C_r$ : carbon pool for foliage, root ( $\text{kg m}^{-2}$ )                |                      |
| $N_f, N_r$ : nutrient pool for foliage, root ( $\text{kg m}^{-2}$ )              |                      |
| $N_{pore}$ : soil pore water nutrient pool ( $\text{kg nutrient kg}^{-1}$ water) |                      |
| $\eta_f$ : allocation fraction of carbon to root                                 |                      |
| Parameters   | Value(s) or range(s) |
| $\eta_f$ : allocation fraction of carbon to foliage                              | 0.01–0.57            |
| $\psi$ : external landscape nutrient input (assumed constant)                    | 0.001–0.0001         |
| $v_r$ : N:C ratio for root   | 0.008                |
| $\gamma_f$ : senescence rate for foliage ( $\text{yr}^{-1}$ )                    | 0.10                 |
| $\gamma_r$ : senescence rate for root ( $\text{yr}^{-1}$ )                       | 0.30                 |
| $\lambda$ : recycling ratio  | 0.9993               |
| $G_0$ : maximum possible growth rate ( $\text{kg C m}^{-2} \text{yr}^{-1}$ )     | 7.56                 |
| $v_0$ : foliar N:C ratio above where N is non-limiting                           | 0.06                 |
| $g_N$ : maximum possible steady nutrient uptake rate per ground area             | 3.00                 |
| $k_N$ : half-saturation coefficient for N plant uptake                           | 0.01                 |
| $b_r$ : root area per unit C ( $\text{m}^2 \text{kg}^{-1}$ )                     | 1.0                  |
| $b_f$ : foliage area per unit C ( $\text{m}^2 \text{kg}^{-1}$ )                  | 2.0                  |
| $k_f$ : radiation light extinction coefficient                                   | 0.50                 |
| $k_r$ : soil resource extinction   | 0.01                 |
| $q$ : throughput of water ( $\text{kg m}^{-2} \text{yr}^{-1}$ )                  | 0.005                |
| $N_{input}$ : nutrient concentration in input water ( $\text{kg kg}^{-1}$ )      | 0.0025               |

omitted, and mineralization of nutrient from litter was assumed to occur instantaneously, with the released nutrient going straight to the soil pore water, without being processed through all of the litter and soil compartments. It was also assumed that some nutrient could be lost during recycling through loss to the atmosphere or as recalcitrant forms in soil at a rate proportional to litterfall. We examined the  $R^*$  rule for plants that could allocate carbon among photosynthetic biomass (foliage) and nutrient acquiring biomass (fine roots). Structural biomass (wood) was not modeled as an explicit variable, but was assumed to be implicit as some fraction in the allocations to foliage and fine roots. We used the model to explore whether a strategy that leads to minimum  $R^*$  also leads to the maximum possible growth rate of the plant.

## 2. Methods: model of tree growth and nutrient cycling

Our model, although inspired by landscape patterns observed in the Everglades, is general, and not intended to apply precisely to any specific ecosystem or any specific limiting nutrient. The conceptual scheme is represented in Fig. 1. The variables of the model are carbon (C), and nutrients (N) in two plant compartments (foliage, subscript  $f$ , and roots, subscript  $r$ ). This would imply four equations, but, because we assume a fixed ratio  $N_r:C_r$ , only one equation is needed for roots. A fourth equation is needed for nutrient in available form in soil pore water ( $N_{pore}$ ). The first three equations, for  $C_f$ ,  $C_r$ , and  $N_f$ , are presented below. They are mass balance equations, in which carbon dynamics of foliage and roots result from the primary production allocated to each compartment, minus the losses from each due to senescence, and the dynamics of the limiting nutrient in foliage is caused by nutrient uptake minus the loss due to senescence (all variables and parameters are defined in Table 1):

$$\frac{dC_f}{dt} = \eta_f G - \gamma_f C_f \quad (1a)$$

$$\frac{dC_r}{dt} = \eta_r G - \gamma_r C_r \quad (1b)$$

$$\frac{dN_f}{dt} = (U - \eta_r \nu_r G) + \psi g_N (1 - e^{-b_r k_r C_r}) - \gamma_f N_f \quad (1c)$$

As noted above, the equation for nutrient bound in roots,  $N_r$ , is omitted, as  $N_r$  is assumed to be in a fixed ratio with  $C_r$ . No seasonality is assumed in this model.

Three key functions in the model are the rate of photosynthesis,  $G$  (carbon fixation), the uptake rate of limiting nutrient  $U$ , and the rate of biomass-dependent input flux of nutrient from outside of the local cycle,  $\psi g_N (1 - e^{-b_r k_r C_r})$ , each of which is described in detail below. The  $U - \eta_r \nu_r C_r$  factor in (1c) represents available nutrient allocated to foliage after subtraction of fixed nutrient allocation to roots to maintain a ratio of  $N_f:C_r = \nu_r$ . Our basic assumption here is that root biomass requires a certain minimum  $N_r:C_r$  ratio, but that root efficiency does not improve with higher ratios. Therefore, the nutrient necessary to achieve this minimum is first allocated; then the remaining nutrient is allocated to foliage, where a higher  $N_f:C_r$  ratio improves photosynthetic performance up to a point. The photosynthetic rate,  $G$ , is assumed to be a function of both the amount of foliage and  $N_f:C_r$  ratio in the foliage:

$$\begin{aligned} G &= \text{net carbon production, or growth per unit time} \\ &= G_0 I(C_f) E(\nu_f) \\ I(C_f) &= \text{light interception factor} \\ &= 1 - e^{-k_f b_f C_f} \\ E(\nu_f) &= \text{rate-limiting effect of low nutrient concentration on growth,} \end{aligned}$$

where

$$\nu_f = N : C \text{ ratio in foliage} = \frac{N_f}{C_f}$$

$$\begin{aligned} E(\nu_f) &= 1 && \text{if } \nu_f > \nu_0 \\ E(\nu_f) &= \nu_f / \nu_0 && \text{if } \nu_f < \nu_0 \end{aligned}$$

$G_0$  is the maximum possible primary production.  $I(C_f)$  is the saturating effect of leaf area index ( $LAI = b_f C_f$ ) on photosynthesis, where  $b_f$  converts carbon per square meter to  $LAI$  and  $k_f$  is the foliage light extinction (Beer–Lambert law) coefficient.  $E(\nu_f)$  represents the assumption that the photosynthetic efficiency of foliage is linearly dependent on the  $N_f:C_f$  ratio below the threshold level  $\nu_0$ . We assume that this carbon can be allocated in arbitrary proportions by the plant among its three components. Two parameters,  $\eta_f$  and  $\eta_r$ , govern the allocation of carbon between foliage and fine root biomass, respectively, including structural material implicitly, where  $\eta_f + \eta_r = 1$ . The constants  $\gamma_f$  and  $\gamma_r$  are senescence (i.e., litterfall) rates.

The function  $U$  represents the nutrient uptake rate of plant-available nutrient, where we assume a saturated response of uptake to soil pore water concentration

$$U = \left( \frac{g_N N_{\text{pore}}}{k_N + N_{\text{pore}}} \right) (1 - e^{-k_r b_r C_r}).$$

Here  $g_N$  is the maximum possible nutrient uptake rate,  $k_N$  is the half-saturation constant, and  $N_{\text{pore}}$  is the concentration of available nutrient in the soil pore water. The second factor represents the saturating effect of root biomass on nutrient uptake, where  $b_r$  is a coefficient of fine root length per unit carbon, and  $k_r$  is a coefficient analogous to the light extinction coefficient  $k_f$ . In Eq. (1c), it is assumed that a fixed ratio,  $\nu_r$ , of  $N_r$  to  $C_r$ , is first allocated to roots; that is, the amount  $\eta_r \nu_r G$ . After allocation to roots, the remaining nutrient goes to foliage.

This model is a modified version of the model used by Ju and DeAngelis (2009) to investigate the relationship between the  $R^*$  rule and Lotka's Maximum Power Principle. The model has been simplified here to eliminate wood as an independent variable. In

the present model there is an additional term,  $\psi g_N (1 - e^{-b_r k_r C_r})$ , in Eq. (1c) to represent biologically driven fluxes from parts of the landscape external to the tree island being modeled. This term represents an input of nutrient that depends on root biomass, but comes from outside of the local soil water nutrient pool,  $N_{\text{pore}}$ , which is sustained by recycling and an externally controlled rate of input,  $N_{\text{input}}$  (described below). (For simplicity, we assume that this biomass-dependent input of nutrient is entirely governed by root biomass,  $C_r$ , through evapotranspiration. Thus we ignore possible inputs from dry deposition that would increase monotonically with foliar biomass.) The quantity  $\psi$  (where  $\psi > 0$ ), when multiplied by the effect of root mass on uptake, represents the availability of nutrients in the marsh water surrounding the tree island. Here  $\psi$  is assumed to be a constant value, based on the assumption of a steady state of nutrients and biomass across the landscape. Thus we are simulating the effect of higher evapotranspiration of a tree island in pulling in water and capturing nutrients from the regional pool of the landscape. In a wetland like the Everglades, this input of nutrients to a tree island will come at the expense of nutrients in the surrounding marsh. We have assumed that these external inputs go directly into tree growth. However, these nutrients could alternatively be assumed to go directly into soil pore water (i.e., as input to Eq. (1d) below), with no qualitative difference in our final results, as long as this external input depends on a biomass component of the tree.

One further equation is needed for the soil pore water nutrient concentration,  $N_{\text{pore}}$  (our equivalent of Tilman's  $R$ ):

$$\frac{dN_{\text{pore}}}{dt} = q(N_{\text{input}} - N_{\text{pore}}) - U + \lambda(\gamma_f N_f + \gamma_r \nu_r C_r). \quad (1d)$$

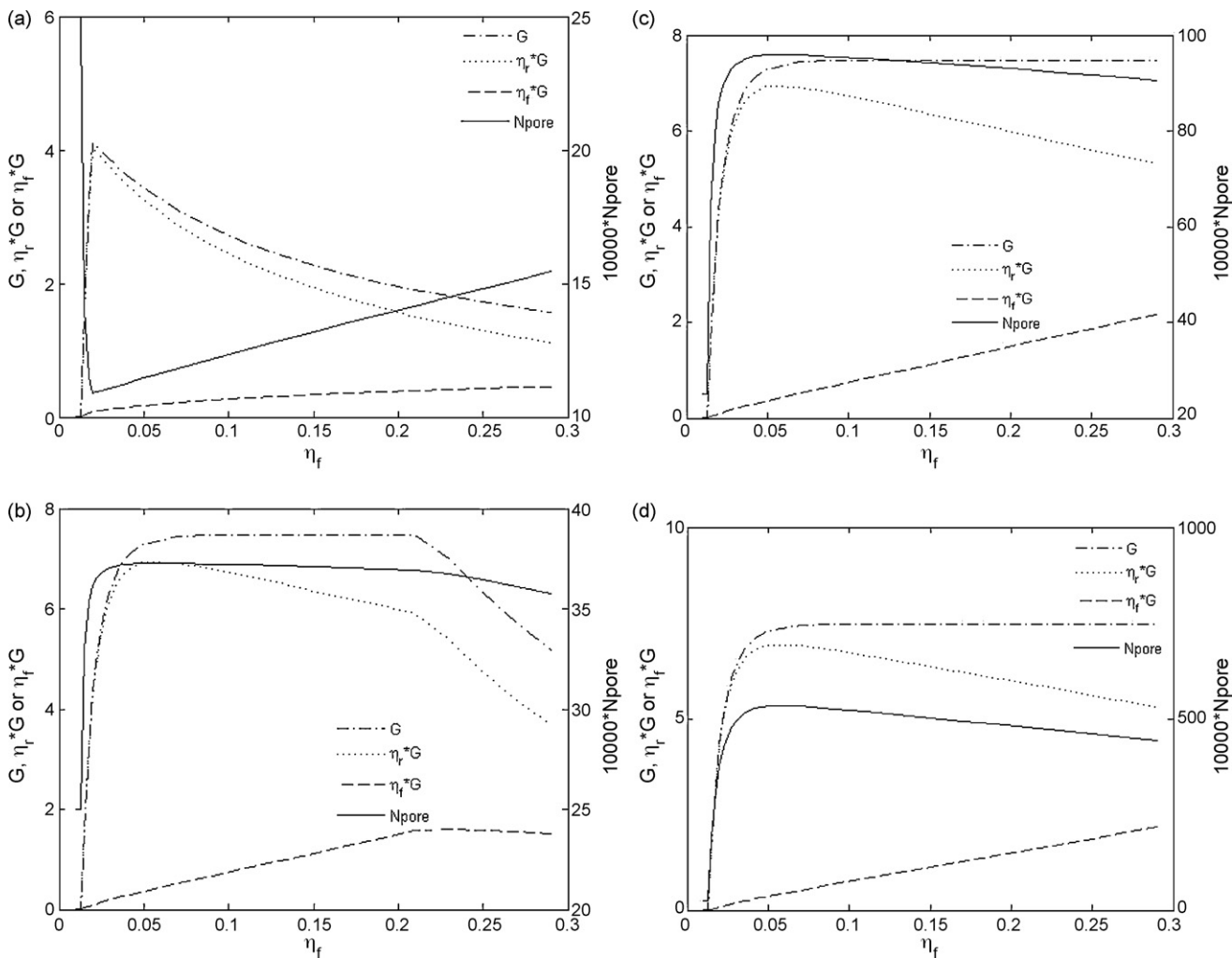
$q$  = input of water through the soil, assumed constant,  $N_{\text{input}}$  = nutrient concentration in input water, assumed constant.

The term  $N_{\text{input}}$  represents nutrient that enters the local soil water from the normal processes of water flow through the soil and precipitation. It does not include the extra input of nutrient that occurs through differential evapotranspiration of the tree islands over the surrounding marsh.

The coefficient  $\lambda$  is the fraction of nutrient recycled from decomposing litter; the remainder is assumed to be tied up in recalcitrant forms in the soil (or, if nitrogen, also lost to gaseous forms). If, as is inevitable, there is some loss of available nutrient to recalcitrant compounds in the soil or as gas to the atmosphere occurs during decomposition of litter, then  $0 \leq \lambda < 1$ . However, a sufficiently large input,  $\psi g_N (1 - e^{-b_r k_r C_r})$ , when added to this recycling, can create an 'effective' recycling that is higher.

It is important to clearly distinguish the two sources of nutrients. The rate of nutrient uptake,  $U$ , from the local pore water,  $N_{\text{pore}}$ , increases with the root biomass,  $C_r$ , but the pool size,  $N_{\text{pore}}$ , is limited by the fixed input rate,  $qN_{\text{input}}$  and the leaching rate,  $qN_{\text{pore}}$ . The external nutrient input,  $\psi(1 - e^{-k_r b_r C_r})$ , pulls in nutrients from the surrounding marsh landscape. This addition has the potential to lead to landscape inhomogeneity in soil nutrient concentration and long-term accumulation of nutrients in the tree island. Because of the model's formulation that takes into account finite solar radiation per unit area as well as nutrient leaching, biomass and nutrients in the tree island do not exceed reasonable upper limits, but both greatly exceed levels in the surrounding marsh. The occurrence of both local nutrient cycling within tree islands, and the biomass-dependent capture of external nutrients, is basic to current theories of Everglades landscape patterns (Wetzel et al., 2005), and to theories of patterning in other wetlands (Rietkerk et al., 2004).

We solved the above set of equations numerically at steady state for the growth rate,  $G^*$ , and the soil pore water,  $N_{\text{pore}}^*$ , where the asterisks indicate steady states (see On-line Appendix 1). We examined these steady state values as  $\psi$  was increased from zero. For



**Fig. 2.** Tree growth rate (carbon fixed per unit time),  $G^*$ , carbon flux to roots,  $\eta_r G^*$ , carbon flux to foliage,  $\eta_f G^*$  and soil pore water nutrient,  $N_{\text{pore}}^*$  ( $\times 10^4$ ), as functions of allocation fraction of carbon to foliage,  $\eta_f$ , for four different values of the biomass-dependent external nutrient input,  $\psi$ . (a)  $\psi = 0.000005$ , (b)  $\psi = 0.00001$ , (c)  $\psi = 0.000035$ , and (d)  $\psi = 0.00005$ . Other parameters are  $\lambda = 0.9993$ ,  $q = 0.005 \text{ kg m}^{-2} \text{ yr}^{-1}$ ,  $\nu_r = 0.008$ ,  $\gamma_f = 0.10 \text{ yr}^{-1}$ ,  $\gamma_r = 0.30 \text{ yr}^{-1}$ ,  $G_0 = 7.56 \text{ kg C m}^{-2} \text{ yr}^{-1}$ ,  $\nu_0 = 0.06$ ,  $g_N = 3.00$ ,  $k_N = 0.01$ ,  $b_r = 1.0 \text{ m}^2 \text{ kg}^{-1}$ ,  $b_f = 2.5 \text{ m}^2 \text{ kg}^{-1}$ ,  $k_f = 0.50$ ,  $k_r = 0.01$ , and  $N_{\text{input}} = 0.0025 \text{ kg kg}^{-1}$ .

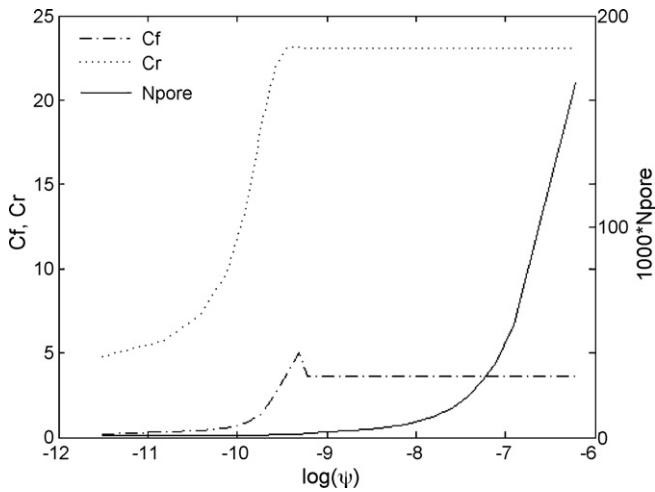
each value,  $\psi$ , we determined, for a given set of parameter values, the maximum value of the steady state growth rate,  $\max(G^*)$ , that exists for some combination of the two allocation parameters  $\eta_f$  and  $\eta_r$ , where  $\eta_f + \eta_r = 1$ . We then examined the relationship between  $\max(G^*)$  and related quantities, and the value of  $N_{\text{pore}}^*$  that is attained at steady state.

### 3. Results

#### 3.1. Numerical results on relating maximum growth rate and nutrient concentration

In [On-line Appendix 1](#) it is demonstrated mathematically that  $N_{\text{pore}}^*$  is closely related to  $\eta_r G^*$  and the nature of that relationship depends on the value of  $\psi$ . For sufficiently small values of  $\psi$ ,  $N_{\text{pore}}^*$  is minimized when  $\eta_r G^*$  is maximized, but when  $\psi$  is large enough,  $N_{\text{pore}}^*$  is maximized when  $\eta_r G^*$  is maximized. It had already been noted by [Ju and DeAngelis \(2009\)](#) that  $N_{\text{pore}}^*$  is minimized when  $\eta_r G^*$ , not  $G^*$ , is maximized. Our new model, however, includes the effect of a biomass-dependent external source of nutrient, the magnitude of which scales with  $\psi$ . When this new parameter,  $\psi$ , increases from zero, it changes the sign of the relationship between  $N_{\text{pore}}^*$  and  $\eta_r G^*$ . To confirm this analytic result, numerical calculations were performed to determine  $G^*$ , and thus

$\eta_r G^*$ , as a function of the allocation strategy parameter  $\eta_f$  (where  $\eta_f = 1 - \eta_r$ ). This was done for several values of the coefficient of external nutrient input,  $\psi$ . For four values of  $\psi$ , values of  $G^*$ ,  $\eta_r G^*$ ,  $\eta_f G^*$ , and  $N_{\text{pore}}^*$  were plotted as functions of  $\eta_f$  ([Fig. 2a–d](#)). Note that, as mathematically predicted, rather than  $G^*$  and  $N_{\text{pore}}^*$  reaching extremal values together, it is the related quantity of carbon flow to roots,  $\eta_r G^*$ , that reaches an extremum together with  $N_{\text{pore}}^*$  for the same value of  $\eta_f$ . According to the  $R^*$  rule, high competitive fitness in a plant is associated with the ability to reduce  $N_{\text{pore}}^*$  (the equivalent in our model to Tilman's  $R^*$ ) to a low value. Thus the expectation is that  $N_{\text{pore}}^*$  would always be minimized at the point where  $\eta_r G^*$ , a measure of plant growth rate, is maximized. However, although the curve for  $\eta_r G^*$  as a function of  $\eta_f$  is concave in all cases (denoting maximization for a particular value of  $\eta_f$ ), the curve for  $N_{\text{pore}}^*$  is convex only for the smallest of the four values of  $\psi$  ([Fig. 2a](#)), and is concave for the larger three values of  $\psi$  ([Fig. 2b–d](#)). This represents a reversal of what is expected from the  $R^*$  rule (i.e., the highest plant fitness, in terms of biomass growth rate, should be associated with the minimum nutrient concentration), whereby now  $N_{\text{pore}}^*$  is maximized when the strategy  $\eta_f$  leads to  $\max(\eta_r G^*)$ . Note that  $G^*$  reaches a flat maximum value of  $G_0$  ( $= 7.56 \text{ kg C m}^{-2} \text{ yr}^{-1}$ ) over much of the range of  $\eta_f$  in [Fig. 2b–d](#). This is because the high nutrient availability allows the growth rate to be maximized.



**Fig. 3.** Values of  $N_{\text{pore}}^*$  ( $\times 10^3$ ),  $C_f^*$ , and  $C_r^*$  at maximum value of  $\eta_r G^*$ , as functions of the biomass-dependent external nutrient input coefficient,  $\psi$ . Other parameter values are  $\lambda = 0.9993$ ,  $q = 0.005 \text{ kg m}^{-2} \text{ yr}^{-1}$ ,  $v_r = 0.008$ ,  $\gamma_f = 0.10 \text{ yr}^{-1}$ ,  $\gamma_r = 0.30 \text{ yr}^{-1}$ ,  $G_0 = 7.56 \text{ kg C m}^{-2} \text{ yr}^{-1}$ ,  $v_0 = 0.06$ ,  $g_N = 3.00$ ,  $k_N = 0.01$ ,  $b_r = 1.0 \text{ m}^2 \text{ kg}^{-1}$ ,  $b_f = 2.5 \text{ m}^2 \text{ kg}^{-1}$ ,  $k_f = 0.50$ ,  $k_r = 0.01$ , and  $N_{\text{input}} = 0.0025 \text{ kg kg}^{-1}$ .

As the coefficient of external nutrient input,  $\psi$ , is increased from zero, the steady state biomasses,  $C_f^*$  and  $C_r^*$ , and available nutrient,  $N_{\text{pore}}^*$ , evaluated at the maximal values of  $\eta_r G^*$ , increase substantially in magnitude, as shown for a specific set of parameters in Fig. 3. The values of  $\psi$  are shown as natural log values on the x-axis. The maximum value  $\psi$  corresponds to a nutrient input of only 0.001 of the saturated uptake of nutrient by the tree island vegetation from its local nutrient source. For values of  $\psi$  close to zero (left end of x-axis), the steady state biomass is very low, corresponding to oligotrophic marsh. For the specific set of parameters used in this specific scenario, roots dominate the biomass. (Other parameter sets can create other patterns.) As  $\psi$  increases, both the two steady state biomass compartments,  $C_f^*$  and  $C_r^*$ , as well as available nutrient,  $N_{\text{pore}}^*$ , increase, the latter increasing by more than an order of magnitude, similar to the differences in these values observed between marsh and tree islands in the Everglades.

### 3.2. Implications for competition between tree species

The above results show that in zones of nutrient accumulation the tree species with a carbon allocation strategy that maximizes growth rate of tree biomass is associated with a maximum in limiting nutrient concentration, not with a minimum, as occurs in zones where nutrients are not being accumulated. This still does not address the basic claim of the  $R^*$  rule, which states that the species that can minimize the limiting nutrient will outcompete all other species. Computer simulations of equations similar to equations (1a–1d) in Ju and DeAngelis (2009) demonstrated that neither the species that minimized  $N_{\text{pore}}^*$  nor the species that maximized plant growth rate, either  $\max(G^*)$  or  $\max(\eta_r G^*)$ , is exactly the fittest in competition with other strategies, though the fittest strategy range always existed somewhere in the vicinity of  $\max(G^*)$ ,  $\max(\eta_r G^*)$ , or  $\max(\eta_f G^*)$ .

To obtain an analytic condition to support this computational finding, we derived, using Eqs. (1a)–(1d), a criterion for invasion of a new plant species into the system occupied by a resident species having different carbon allocation strategies. The criterion for invasion of the resident species, species 1, by an invading species 2 is (see On-line Appendix 2),

$$\eta_r Q_2 W_2 > \gamma_{r2} (\eta_{r2} v_{r2} Q_2 + \gamma_{f2}) \quad (2)$$

where

$$Q_2 = G_{02} k_{f2} b_{f2} \frac{e^{-k_{f1} b_{f1} C_{f1}^*}}{v_{02}} \quad \text{and}$$

$$W_2 = k_{r2} b_{r2} \left( \frac{g_{N2} N_{\text{pore}}^*}{k_{N2} + N_{\text{pore}}^*} + g_{N2} \psi_2 \right) e^{-k_{r1} b_{r1} C_{r1}^*},$$

where the subscript 1 denotes values associated with the resident, species 1, and the subscript 2 denotes values associated with the invading species 2. The exponential terms represent the spatial occupation of the canopy zones and rooting zones by species 1; hence, they represent direct competition for canopy and rooting zone space. If we assume that the parameters  $G_0$ ,  $k_f$ ,  $k_r$ ,  $b_f$ ,  $b_r$ ,  $g_N$ ,  $v_0$ ,  $\gamma_f$ ,  $\gamma_r$ , and  $k_N$  are all the same for both species, then the differences in the strategies depend only on the allocation strategy, and thus only on  $\eta_f$  here, since  $\eta_r = 1 - \eta_f$ . The allocation,  $\eta_{f1}$ , implicit in inequality (2), determines  $C_{f1}^*$ ,  $C_{r1}^*$ , and  $N_{\text{pore}}^*$ . Numerical evaluations of inequality (2) indicate that rather than there being a single optimal  $\eta_{f1}$  that cannot be invaded, there is a narrow contiguous range of values of  $\eta_{f1}$  over which two species can mutually invade each other.

We believe that biomass-dependent horizontal nutrient transport across the landscape, from oligotrophic marsh to tree islands, which results in high concentrations of available nutrients in the soil of the tree islands, results in varying conditions for a new plant species to invade. Ability to invade is governed by conditions that vary spatially, and hence by a criterion more complex than the  $R^*$  rule invasion criterion, which merely specifies that the invading species population be able to reduce  $R^*$  to a lower value than the resident population. Consider two extreme limiting cases for the criterion (2); one for invasion of a plant species in the open marsh area, and one for invasion in the densely vegetated tree island. In the case of the marsh, we might assume that direct competition for space is small, or  $\exp(-k_{f2} b_{f2} C_{f1}^*) \approx 1$  and  $\exp(-k_{r1} b_{r1} C_{r1}^*) \approx 1$ . We also assume  $\psi_2$  is zero. Then, if  $\gamma_{f1}$  is much smaller than the first term on the right hand side of inequality (2), the criterion for invasion reduces to

$$\frac{k_{r2} b_{r2} g_{N2} N_{\text{pore}}}{k_N + N_{\text{pore}}} > \gamma_{r2}. \quad (3)$$

In this extreme case, the invader's success depends only on its ability to survive in the low ambient nutrient concentration that is determined by species 1. Soil pore water nutrient concentration and the ability of the invading plant to extract it must be large enough compared to the root biomass turnover rate for invasion to be possible. This is purely exploitative competition for nutrients. In the opposite extreme, within the tree island, competition for light and space in the rooting zone should be strong, so the two exponential terms in inequality (2) will be small. The soil pore water concentration may be high enough that the Monod function approaches saturation, and  $\psi_2$  is of negligible importance. In this case, the inequality may reduce to

$$\eta_{r2} \left( \frac{G_{02} k_{f2} b_{f2} k_{r2} b_{r2} g_{N2} (1 + \psi_2)}{v_{02}} \right) e^{-k_{f1} b_{f1} C_{f1}^*} e^{-k_{r1} b_{r1} C_{r1}^*} > \gamma_{f2} \gamma_{r2}. \quad (4)$$

Since our assumption is that  $\psi_2 \ll 1$  (that is, uptake of external nutrient is far less than the maximum (saturating) rate of nutrient uptake of local nutrients), this equation could be simplified further. In inequality (4), direct competition plays an important role through the biomass of the resident species,  $C_r^*$  and  $C_f^*$ , and the invading plant must have strong ability to occupy both canopy space and rooting space.

One can compare the formula for invasion of inequality (2) with that that is derived from the traditional  $R^*$  rule. Demonstration of

the  $R^*$  rule is usually based on a model of two phytoplankton species competing for nutrients:

$$\frac{dR}{dt} = q(R_{\text{input}} - R) - \frac{f_1 R P_1}{k_1 + R} - \frac{f_2 R P_2}{k_2 + R} \quad (5a)$$

$$\frac{dP_1}{dt} = \frac{f_1 R P_1}{k_1 + R} - d_1 P_1 \quad (5b)$$

$$\frac{dP_2}{dt} = \frac{f_2 R P_2}{k_2 + R} - d_2 P_2, \quad (5c)$$

where  $R$  is the nutrient concentration (playing the same role as  $N_{\text{pore}}$  in Eqs. (1c) and (1d)), and  $P_1$  and  $P_2$  are phytoplankton biomasses of the two species. The parameters  $f_1$  and  $f_2$  are maximum nutrient uptake rates,  $k_1$  and  $k_2$  are the half-saturation constants,  $d_1$  and  $d_2$  are the phytoplankton loss rates,  $q$  is the rate of inflow of water,  $R_{\text{input}}$  is the concentration of nutrient solute in this external input, and the  $\gamma_1$  and  $\gamma_2$  factors convert nutrients to biomass. In this case, if species 1 holds the resource level to

$$R_1^* = \frac{k_1 d_1}{f_1 - d_1}$$

then the criterion for successful invasion if the system by species 2 is that

$$\frac{f_2 R_1^*}{k_2 + R_1^*} > d_2. \quad (6)$$

This criterion is similar to the limiting criterion (3), with  $R_1^*$  and  $N_{\text{pore}}$  being equivalent.

#### 4. Discussion

Evidence from experiments using microbial populations suggests the  $R^*$  rule works well in that context. However, this rule is only a special case of a much broader picture at the landscape level. Biologically driven flows of nutrient take place from one part of the landscape to another that are dependent on differences in type and density of vegetation and of primary production. The effect of the  $\psi g_N(1 - e^{-b_r k_r C_r})$  term for such horizontal nutrient flux leads to the surprising effect, shown in Fig. 2, that, for sufficiently large values of  $\psi$ ,  $N_{\text{pore}}^*$  is not minimized for a maximum plant growth rate, but is maximized instead. This occurs in our model for values of  $\psi$  that correspond to less than 0.001 of the uptake of nutrient by the patch of plants from the local nutrient pool. This seems strange at first. Intuitively, it seems that the strategy associated with the fastest growth of plant biomass should drive  $N_{\text{pore}}^*$  to its lowest possible value, since a fraction,  $1 - \lambda$ , of nutrients is continually being lost from the system, and high turnover due to high energy flow should increase this loss rate. The explanation is that our model (Eqs. (1a)–(1d)) allows some capture of nutrients by the plants from outside of the local pool of nutrients  $N_{\text{pore}}^*$ . This capture rate is assumed to be proportional to the root biomass and a constant,  $\psi$ , and, as a result, the strategy with the fastest growth of plant biomass can drive  $N_{\text{pore}}^*$  to its maximal level.

In addition to this reversal of the relationship between  $N_{\text{pore}}^*$  and the maximum flow of energy, the model demonstrates that the traditional  $R^*$  rule does not hold for plants that are capable of carbon allocation strategies. Instead, the criterion for invasion of a plant community varies along vegetation ecotones on the landscape. These results differ from the conclusion of Tilman (1990, page 130) that a single number,  $R^*$ , incorporates the effects of all the traits of a plant on its resource competitive ability. Our inequality for invasion includes not only  $N_{\text{pore}}^*$ , but the effects of allocation by the resident of carbon to foliage,  $C_{f1}^*$  and roots,  $C_{r1}^*$ . At the marsh

end of the ecotone, a condition for invasion similar to Tilman's  $R^*$  rule exists. However, the effects of competition for space, which are related to the sizes of the compartments for foliage,  $C_{f1}^*$  and roots,  $C_{r1}^*$ , of the resident species, become greater towards the tree island end of the ecotone.

The capture of new nutrients from outside the local pool of nutrients is not a hypothetical idea. It is one of the central mechanisms of landscape self-organization (Rietkerk et al., 2004; Larsen et al., 2007; Givnish et al., 2008) that has been proposed to explain landscape patterning within numerous wetland ecosystems, including the Everglades, where patterns of vegetation are accompanied by net movement of nutrients from some parts of the landscape to others. Our model is not intended to be a precise description of the Everglades landscape or any other wetland landscape of marsh and tree islands, but it is intended to more generally illustrate the effect of mechanisms of biomass-dependent movement of nutrients across a landscape, and to show that an understanding of their consequences is crucial for an understanding of biomass and nutrient availability patterns at the landscape level.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2009.10.003.

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