

Resource Competition among Plants: From Maximizing Individuals to Community Structure

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Abstract

Evidence indicates that natural systems worldwide are threatened by increasing economic activity, suggesting a need for improved understanding of how ecosystems and economies interact. The model of plant community structure developed here is designed to be both biologically reasonable and adaptable to economic models. The model begins with individual plants maximizing their net intake of light energy in a competitive environment, and the individual's success determines whether the population of its species increases or decreases. This bridging model yields numerous testable predictions, and it provides a link between individual plant behavior and community structure. The driving force behind the dynamics of community structure is resource competition in which individual plants respond to a "price" they pay when accessing light, while simultaneously the collective responses of all plants determine the price. Competition for light is well defined and determined by the value of the price. The parameters in the maximization problem that are species dependent determine what species can coexist. Water is added as another resource in the plant's maximization problem, which forces the plant to optimally allocate photosynthate to roots versus shoots. The maximization framework permits relatively easy integration with economic models.

keywords: individual optimization, resource competition, integration with economics, plant communities

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1 Introduction

If ecology is the study of the structure and function of nature (Odum, 1971), then over time ecologists will have less and less to study. This unfortunate state of affairs is supported by growing evidence cited in popular and scientific publications about the decline of natural systems. (Peters, 1991; Perrings et al., 1995; Arrow et al., 1995; Grime, 1997; Daily, 1997; Barrett and Odum, 2000) The primary cause of decline is the increasing per capita resource consumption of increasing numbers of *Homo sapiens*. Most of this consumption is directly attributable to economic activity, so an important step to reversing the decline of natural systems is to understand more about how natural and economic systems interact. There is a need to integrate better ecology and economics.

This paper offers a new model of resource competition in plant communities that is designed to be both biologically reasonable and adaptable to economic models. The major difference between the theory presented here and most other theories of population dynamics is what underpins the population update equations. Most other theories take the update equations as their starting point. The equations include state variables for species populations and they are formed by assuming that the changes in a population depend on the populations of other species in the community and on resource availability.

In the model herein, the theory starts with the individual plant choosing its biomass. The central postulate is that the individual plant behaves consistently: that is, it will consistently choose the same biomass when confronted with the same constraints, where the constraints are determined by resource availability and the choices of other individuals. Consistent behavior is made operational by assuming the plant chooses its biomass in order to maximize its net energy flow, where net energy is the difference between incoming light energy and outgoing energy lost to respiration. The optimum amount of biomass is where the marginal energy gain from growing

another unit of biomass equals the marginal energy loss to respiration from that unit. The success of the individual in processing energy efficiently determines the species growth rate in the update equation.

The plant lives in a community comprised of identical plants in its own species and of plants in other species. The community occupies a fixed space, and as plants grow more biomass and/or become more numerous, the space fills up. As the space fills, each new unit of biomass grown becomes less effective in absorbing energy owing to shading from other plants. The loss in effectiveness is labeled the shading energy loss (SEL) and it represents the “price” the plant must pay to obtain energy. No single plant has any control over the SEL because it is assumed to have no control over its neighbors; yet the value of the SEL depends on the aggregate action of all plants. Specifically, SEL is determined by equating the sum of all plants optimum biomasses, or their “demands” for biomass, to the supply of space. When there are few plants in the space, SEL is zero and there is no competition. As plant biomasses and populations increase, however, SEL turns positive and the greater the aggregate biomass demands, the greater is SEL and the more intense is the competition.

Populations change according to the success of the plants in storing net energy, and their optimum net energy is inversely related to SEL. Thus, when there is no competition and SEL is zero, net energies are positive and the populations grow. When there is competition SEL turns positive and net energies fall. If they fall below zero, populations shrink. The interaction between the plants’ demands and the supply of space tend to move net energies to zero and to a steady state.

If one species’ plants have positive net energies while another species’ plants have negative net energies, the former species will eventually drive out the latter species. Which species will dominate can be predicted based on the parameters in their net energy function.

Basically, species that respire relatively little per unit of their biomass, or species that absorb more energy per unit of their biomass, will be dominant. Also, any number of species can coexist if their ability to respire and absorb are offsetting.

If water is added to the model as an additional resource, each plant must decide how to allocate its biomass between roots and shoots. The choice is again determined by marginal energy losses and gains, but now there is a marginal gain and loss for both roots and shoots. At the optimum the ratio of marginal gains to losses from roots is equal to the ratio of marginal gains to losses from shoots.

To place this new approach in perspective and relate it to economic systems, consider that there are many ways to divide either economic or ecological theory into two parts, and one way is macro versus micro. Macro models deal with aggregate measures wherein little attention is paid to how changes in the system are determined by the actions of the individuals that form the aggregates. Micro models deal with individual measures wherein little attention is paid to how the individual actions lead to aggregate results. Both model types play important roles in our understanding of human and natural systems; however, neither type suitable for the task of integration envisioned here. The micro style models are narrow while the threats to natural systems are broad. The macro style models are too aggregated to appreciate how individual behavior leads to collective outcomes that were never intended.

General equilibrium (GE) models used in economics combine the micro and macro style; both individual behavior and aggregate outcomes are included. General equilibrium theory has been referred to as the most important development in economics in the twentieth century (Sandler, 2001). Combining macro and micro models does not come without cost, and GE models do employ restrictive assumptions or make omissions. For our purposes, the most important omission in the economic GE models is their failure to address ecological

consequences of economic activity. The point then is to develop a GE style model of an ecosystem, in this case a plant community, which can be integrated with an economic GE model. The ecosystem model is a bridging model in that it begins with an individual and works up to communities of plant populations. The behavior of individual plants will lead to outcomes that may not be in the best interest of the individual, but such is the way of competition. The theory is not applied to any specific community; therefore, it omits many species and site-specific characteristics observed in real communities.

In the next section, the model is introduced using a single plant species. Section 3 contains multi species interactions, and lays out necessary conditions for species coexistence. An invasive species is also discussed in Section 3, followed by the introduction of additional resources in Section 4. Section 5 is a discussion of the model's limitations and its potential for integration with economic models, and Section 6 is a brief conclusion.

2 One Plant Species

2.1 Maximization and Competition

What is the plant maximizing? If we observe the plant's strategy at a given point in time, the individual plant is postulated to be maximizing net energy intake per unit time. However, this strategy can be interpreted as a means to maximize fitness as well. I will start with a given point in time, and then explain how the energy maximizing strategy relates to fitness in subsection 2.4.

Energy is singled out as a resource for several reasons, although other resources will be introduced roughly along the lines of Tilman (1980, 1985) in Section 4. As long ago as Cowles (1899), light has been referred to as one of the main limiting resources in succession (along with nitrogen), and the importance of energy efficiency has its roots in Lotka's "maximum power principle" (1922). Huston and Smith (1987, p. 174) state that: "...light competition provides the clearest and most important example of the complexity of competitive ability for a single

resource.” According to Herendeen (1991) energy has been the most frequently chosen maximand in ecological maximization models, and energy maximization by the individual as adopted below is closely aligned with Hannon (1973, 1976) and expanded to multiple species in Tschirhart and Crocker (1987), Crocker and Tschirhart (1992) and Tschirhart (2000). Closely related to energy maximization is maximizing exergy (Mejer and Jorgensen, 1979) or maximizing energy (Odum, 1983), although these goals are carried out at a more aggregate level than the individual. Finally, Grover (1997, p. 207) refers to light as “...a somewhat special resource” relative to nutrients and water in that it does not follow mass balance constraints, and it is an essential resource to almost all primary producers. Light energy is special in the context of the model because it is the plant’s “income” that is used to grow biomass for the purpose of obtaining energy, or for obtaining other resources as in Section 4 where belowground biomass is introduced.

Postulating that plants behave consistently and making this behavior operational using maximization techniques may be useful simply because numerous testable hypotheses emerge (Peters, 1991), but motivation for using the approach also rests with its explanatory power. In particular, the approach presents mechanisms through which: 1) more efficient resource use by an individual leads to greater success, and 2) interactions among individuals lead to observed dynamics in plant communities. Regarding 1), maximization is a precise and compact method for deriving the implications of efficient resource use. (Efficiency is formally defined in Section 3.) Thus, if efficiency leads to greater success, then the implications derived from a maximization model can explain why plants adopt observed strategies.

Regarding 2), a point highlighted by Huston and Smith (1987), combining individual maximization with resource competition permits an explicit representation of the link between the success of the individual and the ultimate community structure. The role of competition has

not been developed to the point of showing precisely how it influences community structure (Peters, 1991); however, in this model competition is well defined and is central for predicting species abundance and coexistence.

2.2 The Individual Plant

All plants in a species are assumed to be identical so the analysis is carried out for the representative plant. (See Schoener (1986) on this assumption as opposed to using an average individual.) In addition, only the mature plant is modeled, no earlier stages of growth are considered; although relaxing this assumption and incorporating age structure is discussed in Section 5. A plant belonging to species i maximizes net energy flow that is measured in power units (e.g., Watts (W)) and given by:

$$R_i = (e_i - e_0)x_i - f_i(x_i) - \beta_i \quad (1)$$

In (1), x_i is the plant's size or biomass (in gm units) and it is the choice variable: other things equal, the greater the biomass the greater the exposure to light energy. The e_i is the flow of solar energy fixed by the plant for each unit of the plant's biomass (W gm^{-1}), and it varies across species based on leaf cell structures (Asner and Wessman, 1997). Within a species, however, e_i is assumed to be a constant. This is not to ignore light-mediated plant responses such as heliotropic leaf movement (Ehleringer and Forseth, 1980) or varying leaf size (Mooney, et al., 1977); but as long as all plants in the species mediate similarly, the advantage of the mediation is competed away so that effectively the e_i can be treated as a constant. The notion of an adaptation being competed away will be explained further below. The e_0 (W gm^{-1}) is the shading energy loss the plant incurs to fix energy from the sun. All plants incur this loss in competing for access to light, and each plant takes e_0 as a constant; but as described below e_0 varies and may be zero depending on the simultaneous behavior of all plants. Thus, $(e_i - e_0)$ is an example of what Bendoricchio and Jorgensen (1997) indicate is needed in modelling ecosystems

- a parameter that addresses how ecosystems change their properties to meet changing environmental conditions.

The energy required for the plant's respiration which includes growth, maintenance and replacement reproduction, is divided into two parts, both measured in Watts: a variable portion, $f_i(x_i)$, that depends on the plant's biomass, and a fixed portion, β_i , that represents energy lost to the atmosphere independent of the biomass. (The former might be energy lost as temperature rises, while the latter might be energy lost even at low temperatures.) The function $f_i(x_i)$ is assumed to be increasing and continuously twice-differentiable. The product $e_i x_i$ in (1) can be thought of as primary production in which case by (1) the primary production is allocated to energy lost in "preying" on the sun, fixed and variable respiration, and net (or stored) energy which is the maximand. (The definitions of all terms used in the model are in an Appendix.)

The first-order necessary condition for a maximum of (1) is:

$$e_i - e_0 - \frac{df_i(x)}{dx_i} = 0 \quad (2)$$

implying that biomass is increased to the point where the net marginal energy fixed from the last unit of biomass equals the marginal respiration loss from that unit. The net marginal energy is the difference between the gross energy from fixing the last unit of energy minus the loss the plant incurs to fix energy. All maximizing plants follow this marginal benefit equals marginal cost rule, and it will be referred to as the *fundamental behavioral rule*.

The second-order sufficient condition for a maximum is:

$$\frac{d^2 f_i(x_i)}{dx_i^2} > 0 \quad (3)$$

implying that $f_i(x_i)$ is strictly convex in x_i . In general, if (3) is satisfied, then by the implicit function theorem, (2) can be used to obtain the plant's biomass demand as a function of the

parameters in the problem. (Varian, 1992.) To be more specific and for analytical tractability and obtaining solutions in the simulations, let

$$f_i(x_i) = \alpha_i x_i^2 \quad (4)$$

for $\alpha_i > 0$. The parameter α_i (W gm^{-2}) converts the plant's biomass to respiration and is species specific. Other things equal, a plant with a lower α_i respire less for each unit of biomass it accumulates. The functional form of (4) clearly satisfies (3), and using (4) in (2) gives the plant's demand for biomass or its demand function:

$$\hat{x}(e_i, e_0, \alpha_i) = \frac{e_i - e_0}{2\alpha_i} \quad (5)$$

Substituting this demand function into the objective function yields the optimum net energy:

$$\hat{R}_i = (e_i - e_0)\hat{x}_i(\cdot) - \alpha_i \hat{x}_i^2(\cdot) - \beta_i \quad (6)$$

(Yamamura (1997) examines plant objective function that differs from (1). He assumes the plant maximizes its sunlight acquisition for a given biomass, and the plant's choice variable is its shape. The results from Yamamura's approach can be used to obtain a function relating energy intake to biomass, thereby obtaining a relationship similar to (6).)

2.3 The Population

The plant is part of a population that occupies an ecosystem of fixed physical size, thus there is a limit on the amount of biomass that the ecosystem's area can contain. If N_i is the i^{th} species population, then this limit is expressed as:

$$N_i a_i x_i \leq A \quad (7)$$

where A (m^2) is the maximum physical area available to the community and a_i is in units of $\text{m}^2 \text{gm}^{-1}$ so that it converts the left side of (7) to an area. (If the model were extended to account for the vertical nature of light then volume would be the constraining measure.) The plants are competing for light by building biomass, although it is space that is in limited supply and A can

be thought of as the resource the plants are competing for. Thus, although light may not follow a mass-balance constraint (Grover, 1997), the space needed to access light does follow a mass-balance constraint given by (7).

Given this framework, and assuming that biomass is measured by total leaf area of a plant, growth happens as follows. If (7) is satisfied as an inequality the plants are not in intraspecies competition for light energy, because their numbers can increase without individuals shading one another. This environment is labeled the noncompetitive state, and the energy loss individuals incur to obtain solar energy, e_0 , is zero. The plants still must expend energy to produce leaves or to open their stomata in low light intensities (Chazdon and Pearcy, 1991) or to hang their leaves in very high intensities (Grime, 1966; Ehleringer and Forseth, 1980), etc., but this expenditure is assumed to be included in the variable respiration function. Each individual will grow to its maximum size when energy is freely available; a size where further growth is undesirable because the marginal energy fixed would be less than the energy lost to respiration.

The competitive state begins when the population increases (as explained in the next subsection) to fill the available area and (7) is satisfied by equality. Individual plants vie for the same space, and SEL, e_0 , turns positive. Conceptually, the value of SEL is obtained as follows. Suppose there is no competition and a plant expends energy (accounted for in $f(x)$) to produce a leaf of one biomass unit. Suppose further that 1 cal min^{-1} of radiant energy strikes the leaf of which 0.8 are absorbed to fix CO_2 . If the same plant produces the same unit biomass in competitive conditions and only absorbs 0.4 cal min^{-1} from the potential 1 cal min^{-1} arriving at the leaf surface, then the SEL incurred is $0.8 - 0.4 = 0.4 \text{ cal min}^{-1}$.

Figure 1 illustrates the process that determines SEL. SEL turns positive and increases as the population increases owing to increased shading. The plant's demand given by (5) is summed over all individuals to obtain the total biomass demand curve. The point where this curve

intersects the vertical curve representing the supply of space is the SEL on the vertical axis. (SEL plays the same role as a market price in an economic model of competition.) SEL changes when the total demand curve in Figure 1 shifts right or left, and these shifts are a result of changing

[Figure 1 about here]

populations as explained in the dynamics. Before proceeding to the dynamics, we can summarize several predictions:

Principle 1 – From (5), for a given population N_i the plant's maximum size is given by its demand: $\hat{x}_i = \frac{e_i - e_0}{2\alpha_i}$. If the solar energy fixed, e_i , increases (decreases) or variable

respiration parameter, α_i , decreases (increases) then the demand curve for the representative plant, hence the market demand shifts rightward (leftward) causing SEL to increase (decrease). Also, an increase (decrease) in population will mean more (fewer) demand curves to add to obtain the market demand curve and SEL will increase (decrease). (Note that in the noncompetitive state the total demand curve on the right must intersect the horizontal axis to the left of A so that SEL is zero.) Because $e_0 = (>) 0$ in the noncompetitive (competitive) state, the maximum size is larger (smaller) in the noncompetitive (competitive) state, implying by (7) that the population is smaller (larger) in the noncompetitive (competitive) state. Moreover, in either state, the maximum size increases with the plant's ability to fix energy per unit of biomass (e_i), decreases with the plant's variable respiration (α_i), and is independent of the plant's fixed respiration (β_i).

2.4 Population Growth

The success of the representative plant as measured by its optimum net energy in (6) determines whether the plant's species reproduces sufficiently to increase its population. In other words, a population increase depends on individuals' abilities to convert energy into offspring (Schoener, 1986). The dynamic growth process proceeds as follows. If the optimum net energy, \hat{R} , is positive, the representative individual channels the energy to reproduction above replacement levels and the population increases. Alternatively, if the optimum net energy is

negative, this subtracts from the energy needed for replacement and the population decreases. It follows that zero optimum net energy implies no change in the population. Thus, the success associated with accumulating energy is made operational here by linking net energy to population changes, and this is the sense of the claim in subsection 2.2 that an individual plant maximizing energy at any point in time is also maximizing fitness over reproductive cycles.

The population is assumed to change according to the adjustment equation:

$$N_i^{t+1} - N_i^t = N_i^t \gamma_i \frac{\hat{R}_i(N_i^t)}{\beta_i} \quad (8)$$

where γ_i is a species-specific growth rate constant, and $\gamma_i \frac{\hat{R}_i(N_i^t)}{\beta_i}$ is the per-capita growth rate.

The idea is that since the optimum net energy in the numerator is energy available for reproduction above replacement levels (and it may be negative), and since the fixed respiration in the denominator is the minimum energy that must be spent by new individuals, then the total number of new individuals is at most $\frac{\hat{R}_i(N_i^t)}{\beta_i}$. Including γ_i allows for interspecies differences in converting net energy to offspring. This interpretation suggests that $\gamma_i \leq 1$, and below I show that $\gamma_i > 1$ yields chaotic oscillations.

Populations change differently in the noncompetitive and competitive states. In the noncompetitive state, each individual earns positive net energy (otherwise the population would never grow) so $\hat{R}_i > 0$. Also, because $e_0 = 0$ in the noncompetitive state, (5) and (6) imply that \hat{x}_i and \hat{R}_i are constants so that by (8) the population experiences a discrete version of exponential growth. In the competitive state, \hat{x}_i and \hat{R}_i are not constants, and the population may increase or decrease.

At some point if the population levels off in the competitive state a steady state is said to

be attained. A steady state is defined by three conditions: the available space is filled, each plant is maximizing its net energy, and net energies are zero. To solve for the steady state, set (1) to zero, and use (2) and (7) as equalities to obtain biomass demand, SEL and population.

Principle 2 – In a steady state, biomass demand, SEL and population are given by:

$$\hat{x}_i^s = \left(\frac{\beta_i}{\alpha_i} \right)^{0.5} \quad \hat{e}_0^s = e_i - 2(\alpha_i \beta_i)^{0.5} \quad N_i^s = \left(\frac{\alpha_i}{\beta_i} \right)^{0.5} \frac{A}{a_i} \quad (9)$$

The results in (9) illustrate that the steady state maximum plant size (which can only be attained in the competitive state because there is exponential growth in the noncompetitive state) depends on the respiration characteristics of the individual plant, and it is independent of the price the plant pays for energy, its ability to fix energy per unit of its size, the species growth rate, and the physical space. The steady-state SEL in the middle equation in (9) is also independent of the species growth rate and the physical space, but does depend on all three individual plant parameters. The steady-state population does depend on ecosystem size as well as the respiration characteristics of an individual plant. In the absence of any other species, the steady-state population can be thought of as the carrying capacity.

The distinction between the plant's biomass demand in (5) and the steady-state biomass demand in (9) can be understood by examining the forces that drive the population to a steady state. Whenever \hat{R}_i is not zero there are demand and supply forces that drive it toward zero: if \hat{R}_i is positive (negative), the population increases (decreases) from (8) which drives up (down) SEL as in Figure 1 which decreases (increases) both the biomass demand and \hat{R}_i . This drive toward $\hat{R}_i = 0$ is the reason why in steady state the plant size does not depend on e_i even though in moving to the steady state the plant's demand does depend on e_i .

To see this, suppose the system is in steady state and an individual plant develops a

successful response to its environment that improves its ability to fix energy so that e_i increases. This plant will then be more successful than its neighbors in terms of net energy intake and biomass. However, I am assuming all plants in a species are identical so the process of how the adaptation spreads through the species, perhaps forming a new species, while interesting, is beyond the scope of this paper. Therefore, I focus on the situation after all plants in the species adapt the same response. Once all individual plants develop the successful response, they attempt to increase their demand and biomass, which would cause their \hat{R}_i to become positive, and their population to grow. However, it is impossible for both the population and biomass to increase from their steady-state values because of the limited space. Thus, in the new steady-state, the biomass and populations will be the same as the original steady state, but in order for the plants to be maximizing net energy and earning zero net energy in the new steady state with the higher e_i , it must be the case that e_0 increases. In essence, the plants' improved ability to fix energy led to upward pressure on their sizes and population; but without additional space to occupy, the improved plants could only compete away their potential growth. (An analogy in economics is when one firm in a competitive industry develops a cost cutting technology. It can earn more profit than its competitors temporarily, but once all the firms in the industry adopt the same technology, all firms' profits move toward equality.)

The stability of the steady state depends on the value of the growth rate constant, γ . In the competitive state from (7) it must be that $x_i = A/N_i a_i$, and substituting this result into (5) yields $e_0 = e_i - 2\alpha_i A/N_i a_i$. Substitute these values for x_i and e_0 into (1) to obtain the optimum $R_i(N_i)$, then substitute the $R_i(N_i)$ into the dynamic adjustment equation, (8). Finally perform a stability analysis (May, 1974) around the steady-state value for population in (9) to find:

Principle 3 – For $0 < \gamma < 1$, the steady-state population is stable; for $\gamma = 1$, the steady state population exhibits stable limit cycles whose amplitudes depend on the starting

populations; and for $\gamma > 1$, the steady state is unstable and chaos results.

Simulations are used to illustrate the single-species dynamics. All simulations were performed using Mathematica v3.0. The procedure is to start with a small population of plants in the noncompetitive state with given parameters and zero SEL, and calculate the plant size and net energy using (5) and (6). Then using the net energy, adjust the population using (8). Population adjustments continue with the same net energy (Because this is the noncompetitive state, the plant size and net energy do not change.) until (7) is satisfied by equality and the competitive state begins. At his point the plant size and net energy are recalculated between each population adjustment.

Figure 2 shows the simulation results. In Panel A, population, plant size and SEL are tracked for 28 periods using the parameters shown in the box. Note that the population grows exponentially through period 12 at which point the competitive state begins and the growth oscillates for about 4 periods before converging to the steady state. On entering the competitive state SEL jumps up from zero and the optimum plant size decreases.

[Figure 2 about here]

In each of Panels B though E, one and only one of the parameters is changed from Panel A's base case, and parameter a_i in (7) is set equal to one for simplicity. In Panel B the incoming energy, e_i , is increased *ceteris paribus*, and at the outset the plant sizes (9.6) are larger than the plant sizes (8.0) in Panel A. However, in the steady state the plant sizes are the same in both Panels as are the populations in accordance with Principle 2. The larger e_i only causes the steady state SEL to increase from 268 to 668. Panels C and D show that the respiration parameters do affect steady state plant size and population, but not SEL. Also, in accordance with Principle 3, Panel E shows how setting the growth rate to one yields limit cycles in which e_i , x_i and N_i

oscillate around their steady-state values from Panel A. Not shown are chaotic results for $\gamma > 1$. When oscillations occur the SEL is moving in the opposite direction of the biomass and population. The former is due to the *law of demand* from (5), and the latter is due to the higher SEL causing net energy to turn negative. Finally, if the initial population is set above the steady-state population (not shown in Figure 2), over time the population falls to the steady state and plant sizes increase in accordance with the self-thinning rule (Yoda et al., 1963; Westoby, 1981).

3 Multiple Plant Species

To introduce a second species, return to the single species in Figure 2 with the parameters shown in Panel A, and suppose ten plants of a second species are present with the ten plants of the first species at the start in period 1. The space constraint is now

$$\sum_{i=1}^2 N_i a_i x_i \leq A. \quad (10)$$

The second species has the parameters shown in Figure 3 that shows the simulations of the two-species interaction. (For simplicity I assume that $a_i = 1$ for all i in a multispecies setting to concentrate on other aspects of community dynamics. The assumption implies each unit of biomass for all species has an equivalent impact on crowding.)

[Figure 3 about here]

The interesting question is what parameter values for the species in this model allow for species coexistence? The answer can be seen in Figure 4 that extends Figure 1 to multiple species. Generally, coexistence of species in a steady state community requires that each plant in each species is maximizing its net energy and the net energies are equal to zero. When this

[Figure 4 about here]

occurs the populations are unchanging and a multispecies steady state is attained. From (9), in a steady state each plant is maximizing net energy and net energy is zero when

$\hat{e}_0^s = e_i - 2(\alpha_i \beta_i)^{0.5}$. If $\hat{e}_0^s > e_i - 2(\alpha_i \beta_i)^{0.5}$ then the plant is earning negative net energy and its species' population is decreasing. Therefore, as competition intensifies with the growth of species populations and \hat{e}_0 increases toward \hat{e}_0^s , any species for whom the term $e_i - 2(\alpha_i \beta_i)^{0.5}$ is below \hat{e}_0^s dies off. In the steady state only the species with the highest $e_i - 2(\alpha_i \beta_i)^{0.5}$ remain. The value of $e_i - 2(\alpha_i \beta_i)^{0.5}$ leads to a definition of efficiency. More efficient plants have greater $e_i - 2(\alpha_i \beta_i)^{0.5}$, implying that more efficient plants exhibits a combination of fixing relatively large amounts of energy per unit of biomass (large e_i), or for a given amount of energy fixed have relatively low variable respiration (α_i), or have relatively low fixed respiration (β_i).

Principle 4. If at the outset of the noncompetitive state there are m species present, then species i , $i \in \{1, \dots, m\}$, will still be present in the steady state community if

$$e_i - 2(\alpha_i \beta_i)^{0.5} \quad (11)$$

is a maximum over all m species; that is, i is the species that earns zero net energy at the highest SEL generated by the demands and supplies in the competition for space. All other potential species earn negative net energy at this SEL and are driven to extinction before steady state.

Principle 5. More than one species will be present in the steady state community if the maximum of (11) over all m species is not unique.

For two species in the steady state community, say i and j , from (9) the population of the i^{th} species no longer has area A to fill but has area A minus whatever area is being filled by species j . Thus,

$$N_i^s = \left(\frac{\alpha_i}{\beta_i} \right)^{0.5} \left[A - \left(\frac{\beta_j}{\alpha_j} \right)^{0.5} N_j^s \right] \quad (12)$$

which makes it clear that a species' steady-state population depends on individual plant parameters in addition to populations of other species, which in turn depend on initial populations and species' growth rates.

Principle 6 – In a multispecies steady state in a community with limited space, the mix of species present depends on the characteristics of the individual plants including the plants' respiration parameters and abilities to fix energy per unit of biomass. The mix of species present depends neither on plant growth rates nor the original species present in the noncompetitive state and their populations. The final populations of the steady state species, however, do depend on the original species present and their populations and growth rates.

See Chapin et al. (1994) for an example of field work consistent with Principle 6.

Figure 5 illustrates the noncompetitive and competitive states for two coexisting species. The parameters are given in the Figure and are consistent with Principle 5; that is, in the steady state

$$e_1 - 2(\alpha_1\beta_1)^{0.5} = e_2 - 2(\alpha_2\beta_2)^{0.5} = 268 \quad (13)$$

After the two populations reach a steady state in Figure 5, a disturbance, for example a human-altered habitat which is a common form of disturbance (Orians, 1986), is assumed to occur that causes the population of species 1 to fall and allows exotic species 3 to invade, then species 3 drives out the original three species. The successful invasive species has $e_3 - 2(\alpha_3\beta_3)^{0.5} > 268$ so that it will be earning positive net energy when the two original species are at zero net energy.

[Figure 5 about here]

4 Additional Resources

Tilman (1980, 1985, 1988) developed the resource-ratio hypothesis that underscores the importance of limiting resources for explaining community structure, and now other resources are introduced here. The plant maximization problem is flexible in that additional resources can

be introduced into a variety of ways; two possibilities are considered. The first possibility is to introduce temperature which is not a resource but does affect respiration, growth and photosynthesis separately from light availability, and it has been shown to be important in determining competitive success (See Chpt. 3 in Grover (1997) for a summary). Because biological processes increase with rising temperatures above freezing, then flatten out before starting to decrease (Ellert and Bettany, 1992), I assume that there is an optimum temperature for each plant and that movements away from the optimum increase energy losses via respiration. Temperature, therefore, enters the individual plant's maximization problem, as opposed to introducing temperature into the more aggregated population adjustment equation as in Pacala and Tilman (1994).

Let t be temperature and rewrite the respiration function from (4) as

$$f_i(x_i; t) = \alpha_i x_i^2 [(t - t_i)^2 + 1] \quad (4')$$

The t_i is plant i 's ideal temperature, and when $t = t_i$ the plant's variable respiration is at a minimum. When $t < t_i$ the temperature is below the ideal and when $t > t_i$ the temperature is above the ideal; in either case the squared term in parentheses implies that deviations from the ideal stress the plant and increase respiration.

Principles 4 and 5 that state the conditions for coexistence in a steady state can be extended to include temperature. Solving for steady state values as in (9) but now using (4') instead of (4) yields $\hat{e}_0^s = e_i - 2(\alpha_i \beta_i)^{0.5} [(t - t_i)^2 + 1]^{0.5}$ for species i , and following Principles 4 and 5, m species coexisting in a steady state community requires:

$$e_1 - 2(\alpha_1 \beta_1)^{0.5} [(t - t_1)^2 + 1]^{0.5} = e_2 - 2(\alpha_2 \beta_2)^{0.5} [(t - t_2)^2 + 1]^{0.5} = \dots = e_m - 2(\alpha_m \beta_m)^{0.5} [(t - t_m)^2 + 1]^{0.5} \quad (14)$$

Going through the same maximization problem as above but now using (4'), the plant's demand for biomass from (5) becomes:

$$\hat{x}(e_i, e_0, \alpha_i) = \frac{e_i - e_0}{2\alpha_i[(t - t_i)^2 + 1]} \quad (15)$$

and the steady-state plant size and SEL from (9) becomes:

$$\hat{x}_i^s = \left(\frac{\beta_i}{\alpha_i[(t - t_i)^2 + 1]} \right)^{0.5} \quad \text{and} \quad \hat{e}_0^s = e_i - 2(\alpha_i \beta_i)^{0.5} [(t - t_i)^2 + 1]^{0.5} \quad (16)$$

Thus, temperature affects biomass demand as well as the steady-state plant size and SEL.

The second expression in (16) exhibits a parabolic relationship between temperature and the steady state SEL as displayed in Figure 6. The Figure illustrates the combinations SEL and temperature at which one or more species are in a steady state. Moreover, although there are but two resources (referring to temperature as one resource and access space to light as the other), there is no limit on the number of species that can coexist because any number of parabolas can be drawn through the same point in the e_0-t plane. This follows because the shape and position of the parabolas are determined by the e_i , α_i and β_i in (16), and there are infinite combinations of these parameters giving the same \hat{e}_0^s .

[Figure 6 about here]

As a second possibility for adding resources to the basic competitive model, consider a resource that is captured by the plant's roots. This possibility adds to the plant's problem by requiring it to allocate photosynthate to roots versus shoots. Although plants use a variety of nutrients contained in the moisture that is captured by the roots, I will refer to the second resource simply as water. The maximization framework ensures that the plant is allocating photosynthate optimally between root and shoots to take advantage of varying levels of light access and soil moisture.

Rewrite the i^{th} plant's objective function from (1) as:

$$R_i = (e_i - e_0)(x_i^a \tanh(wx_i^b)) - \alpha_i(x_i^a + x_i^b)^2 - \beta_i \quad (17)$$

where biomass now has aboveground and belowground components denoted by the a and b superscripts, and w is water measured as the percent of the maximum water availability. Note that respiration now depends on both aboveground and belowground biomass in the second term on the right side of (17). Both forms of biomass are treated the same with respect to respiration, although if maintenance respiration is greater for roots than shoots (Amthor, 1984), then a parameter could be appended to reflect this.

The first term on the right side is the total energy as before, but now both aboveground and belowground biomass appear. To interpret this term, consider that for a given water level and a given belowground biomass, more allocation to aboveground biomass implies more energy captured. Also, $\tanh(wx_i^b) \rightarrow 1$ as $wx_i^b \rightarrow \infty$, thus for a given aboveground biomass, more allocation to belowground biomass and/or more water imply more energy captured. This last implication is due to the ability of a plant with a larger root system or with more available water to keep its stomates open and stay photosynthetically active. Water use efficiency varies across plants (Barbour et al., 1999) and, again, a parameter could be appended to reflect this. Resource allocation in this newly formulated problem is a combination of plastic allocation patterns dependent on the environmental conditions, w and e_0 , and genetically predetermined responses dependent on the physiological parameters α_i , β_i and e_i .

Assuming the plant chooses above and belowground biomass to maximize (17), the first-order necessary conditions for a maximum are:

$$\partial R_i / \partial x_i^a = (e_i - e_0) \tanh(wx_i^b) - 2\alpha_i(x_i^a + x_i^b) = 0 \quad (18)$$

$$\partial R_i / \partial x_i^b = (e_i - e_0)x_i^a w \operatorname{sech}(wx_i^b)^2 - 2\alpha_i(x_i^a + x_i^b) = 0 \quad (19)$$

The first term after the first equality in (18) is the marginal energy received by the plant from growing another unit of aboveground biomass, and the second term is the marginal energy lost to

respiration from growing another unit of aboveground biomass. The terms in (19) are similar but for belowground biomass. Basically, both (18) and (19) are marginal benefit (marginal energy received) equal marginal cost (marginal energy lost) conditions reflecting the *fundamental behavioral rule*. Dividing both equations by the marginal cost terms and then combining them yields the condition:

$$\frac{MB_i^a}{MC_i^a} = \frac{MB_i^b}{MC_i^b} \quad (20)$$

The marginal benefit (*MB*)/marginal cost (*MC*) ratio must be the same across biomass types. If they were unequal the plant would not be maximizing: it could acquire more energy by allocating more (less) biomass to whichever biomass type has the greater (lesser) ratio in (20). This result conforms to the multiple limitation hypothesis (Gleeson and Tilman, 1992) that stipulates all resources limit growth simultaneously.

Finally, if the second-order sufficient conditions to the maximization problem are satisfied, then by the implicit function theorem (18) and (19) can be used to obtain the individual's biomass demands as functions of the parameters:

$$x_i^a = x_i^a(e_i, e_0, w, \alpha_i) \quad \text{and} \quad x_i^b = x_i^b(e_i, e_0, w, \alpha_i) \quad (21)$$

The method of comparative statics (Varian, 1992) yields information about the signs of the partial derivatives of these two demands. Of particular interest are:

$$\partial x_i^a / \partial e_0, \quad \partial x_i^b / \partial e_0, \quad \partial x_i^a / \partial w \quad \text{and} \quad \partial x_i^b / \partial w \quad (22)$$

because the signs of these terms yield information about whether there is a positive or negative correlation between resources as described by Gleeson and Tilman (1992). Noting that changes in x^a and x^b are associated with change in light absorption and water uptake, respectively, then we can ask what changes can be expected in absorption and uptake if competition for light becomes more intense, i.e., e_0 increases. Possibilities include:

$$\{\partial x_i^a / \partial e_0 > 0, \partial x_i^b / \partial e_0 > 0\} \quad \text{or} \quad \{\partial x_i^a / \partial e_0 < 0, \partial x_i^b / \partial e_0 < 0\} \quad (23)$$

$$\{\partial x_i^a / \partial e_0 > 0, \partial x_i^b / \partial e_0 < 0\} \quad \text{or} \quad \{\partial x_i^a / \partial e_0 < 0, \partial x_i^b / \partial e_0 > 0\} \quad (24)$$

$$\{\partial x_i^a / \partial e_0 \neq 0, \partial x_i^b / \partial e_0 = 0\} \quad \text{or} \quad \{\partial x_i^a / \partial e_0 = 0, \partial x_i^b / \partial e_0 \neq 0\} \quad (25)$$

For the left-most braced terms in (23), increased competition for light causes the plant to increase both aboveground and belowground biomass in order to increase both light absorption and water uptake. Therefore, there is a positive correlation as both resources are increased simultaneously. The same positive correlation applies for the right-most braced terms in (23) except that light absorption and water uptake are decreased simultaneously. For (24) there is negative correlation, but simultaneity. And for (25) there is what Gleeson and Tilman describe as negative correlation and independent uptake. Which possibility prevails depends on the plant parameters, SEL and water availability, and the current aboveground and belowground biomasses. Similar possibilities apply for changes in water by examining the partials with respect to w .

[Figure 7 about here]

Figure 7 provides simulation results for one plant growing aboveground and belowground biomass with varying water availability. As the percent of water available changes, the roots and shoots change, but not always in the same direction. For example, when water increases from 60% to 80% around period 12, both root and shoot decrease to new steady-state values by period 15. When water increases from 40% to 50% around period 24, root decreases but shoot increases. The first case illustrates positive correlation and the second case illustrates negative correlation. The difference can be attributed to differences in light competition: in case one competition is relatively intense ($e_0 = 350$) while in case two the plant is in the noncompetitive state and there is no competition ($e_0 = 0$). In both cases, the additional water decreases the plant's need to allocate photosynthate to roots; in case one, the plant also allocates

slightly less photosynthate to shoots because competition for light is great and additional shoot biomass will not be very successful in capturing more light; in case two, the plant allocates significantly more photosynthate to shoots because competition for light is small and additional shoot biomass will be very successful in capturing more light. These results are consistent with alternative root/shoot allocation theories and experimental studies (Stuefer, During and de Kroon, 1994; Stuefer, During and Schiering, 1998). An important point here is that one cannot examine the plant's reaction to changes in one resource in isolation, because such resource changes cause the plant to change its allocation which inevitably changes the availability of other resources.

Throughout all these water changes the root to shoot ratio changes and is always moving in the opposite direction of the water change. As water increases the plant can allocate relatively less photosynthate to the less scarce resource. What guides these root/shoot changes is the unchanging equality between the root and shoot marginal benefit/marginal cost ratios according to (20). That is, the maximizing plant over time experiences changes in the marginal benefits and marginal costs associated with allocating photosynthate to roots and shoots, but the plant keeps the marginal benefit/marginal cost ratios equal so that all resources are equally limiting.

5 Discussion

To test the model's predictions, plant parameters must be estimated and related to the processes and factors describing vegetation dynamics (Pickett, et al., 1987). Theoretical bounds on parameters can be set based on necessary and sufficient conditions for obtaining a maximum to the plants' net energy problems, and from stability analyses of the dynamics. Parameters within the bounds can be obtained through statistical estimation applied to sample data from well-defined populations and through calibration.

The plant's demand for biomass as a function of SEL can be related to traditional models

that examine shading in general. For example, Raulier and Ung (1997) develop a procedure to estimate total leaf area and apply it to sugar maples (*Acer saccharum* Marsh). When these authors estimate total leaf area (their equation (8)), essentially they are estimating the plant's demand function for biomass given by (5). The two major terms in their equation are: "the potential leaf area, i.e. the leaf area of a crown entirely irradiated by an irradiance equal to that of the top cover" and "the reduction of potential leaf area caused by shading." The first term contains the potential irradiance and the second the reduction in the potential due to transmittance, and these two measures of light are analogous to e_i and e_o , both of which appear in the demand function, (5). A major difference between the model presented here versus Raulier and Ung and other models that examine light and shading is the origin of the demand function. Most models begin by constructing a demand function that relates the leaf area with light variables and parameters. The model herein begins at a more underlying level by postulating that plants maximize their exposure to light. This postulate justifies formulating the plant's objective function, and maximization procedures yield the plant's demand function.

Principle 5 has important implications for the relationship between coexistence and the number of resources. A long-standing principle is that the maximum number of coexisting populations in steady state cannot exceed the number of resources (Levin, 1970; Armstrong and McGehee, 1980). Some authors have noted this result to be too restrictive (Tilman, 1982; Huston and DeAngelis, 1994). In the context of just one population, the principle is the R^* rule (Grover, 1997) where R is a measure of the resource and R^* is the lowest level of the resource at which a population can survive. The rule states that the species with the lowest R^* will exclude all other species in a steady state. In the model herein, there is no similar restriction on the number of coexisting species; as per Principle 5, any number of non-identical species can be present in a steady state. The reason has to do with the dynamic adjustment equation describing net

population growth that is zero in steady state. In approaches that begin with a differential equation for each species, and with only one resource, only one (non identical) species can have the lowest resource requirement. Alternatively, here steady state occurs when the output of the maximization problem yields an $R_i(N_i) = 0$. But R_i depends on the behavioral parameters e_i , α_i and β , and there are infinite combinations of these three parameters yielding $R_i(N_i) = 0$. Plants adapt to find a combination of these parameters that permit their success in the competitive environment.

A limitation of the model is that only resource competition is addressed and other forms of competition are omitted. Beyond this, other forms of interaction are omitted as well such as mutualism and amensalism. Perhaps more important is that only mature plants are considered which omits many interesting issues with respect to plant succession. An important extension, therefore, would be to allow for age structure. This could be done by defining a separate population for each plant at each life stage: thus, N_{ij} is the population of species i in the j^{th} stage. In each stage, each plant maximizes net energy, and the magnitude of the net energies determines how many plants in stage j survive to stage $j + 1$.

One of the intended contributions of this work is to develop a reasonable community model that can be integrated with economic models. To this end, two further steps are needed. First, herbivores and carnivores need to be appended to the plant model. This can be done along the lines of Tschirhart (2000) wherein an example of a six species food web is presented that contains a plant species, two herbivores, and three carnivores. The plant species in the food web is simple compared to the model in this paper, but the method used there for introducing animals applies. For example, adding an herbivore to the i^{th} species representative plant's objective function from (1) gives us:

$$R_i = [e_i - e_0]x_i - \sum_{k=p+1}^m e_b y_{ik} - f^i(x_i) - \beta_i$$

where y_{ik} is the supply of biomass from the i^{th} plant to the k^{th} herbivore summed over m herbivores, and e_b is the energy embodied in a unit of supplied biomass. Herbivores pay an energy price to “capture” plant biomass that is similar to the plants’ SEL. The herbivore also maximizes its net energy where the incoming energy is supplied by the plants and the outgoing energy either goes to respiration or to carnivores, who are in turn maximizing their net energy. Demand and supply interactions between the plants and animals lead to population adjustments along the lines shown in this paper.

The second step toward integration is to take the food web model and combine it with an economic GE model. Extant economic models typically either rely on a circular flow of physical goods which has been criticized justifiably for violating the second law of thermodynamics (Amir, 1979; Georgescu-Roegen, 1971), or they incorporate the ecosystem using highly aggregated logistic growth functions (Woodwell, 1998). The ecosystem model developed above and integrated with an economic model would avoid these shortcomings.

As humans interact with one another in an economy, they also interact with ecosystems, and integration requires identifying the points of contact. Of course, there are many: humans make consumptive and non consumptive use of nonhumans, growing human populations create habitat loss, industries generate toxic wastes, insects pollinate crops and spread disease, and so on. In the plant community model, humans might reduce the habitat by reducing the available space, A , or they might divert water, w , or they might introduce invasive species, or they might use herbicides that alter the plants’ respiration functions, and so on. An integrated model can address these human-ecosystem interactions, all the while tracking how both humans and nonhumans optimally respond to changing conditions. Finnoff and Tschirhart (2001) provide an

example of an integrated model that contains a marine food web studied by Estes et al. (1998) and commercial fishing.

6 Conclusion

The challenging opening sentence in this paper is not unparalleled. “Ecology is a discipline headed toward extinction” if it does not study habitats where human impact is substantial instead of minimal (Tilman, 1997). These admonitions apply as well in reverse: If economics is the study of how human societies allocate scarce resources among competing ends, then over time economists will have less and less to study because there will be fewer of *nature’s* services to allocate. (At some point if natural systems become scarce enough, human societies may become preoccupied simply with replacing nature’s services.) The road to integration runs two ways: ecology needs to integrate more human behavior to be relevant in a contemporary world; economics needs to integrate more of nature’s behavior, and admit more of nature’s services into its work, because these are the foundations of human well being.

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Appendix – Glossary of Symbols

Symbol	Definition	Units	Symbol	Definition	Units
R_i	net energy for a representative (rep) plant in specie i	Watts (W)	r_i	growth rate in logistic function	1/time
e_i	energy flow to rep plant when zero crowding	W gm ⁻¹	K_i	carrying capacity in logistic function	pop
e_0	shading energy loss (SEL)	W gm ⁻¹	\hat{x}_i^s	steady state biomass of rep plant	gm
x_i	biomass of rep plant	gm	\hat{e}_0^s	steady state SEL	W gm ⁻¹
$f_i(x_i)$	variable respiration of rep plant	W	N_i^s	carrying capacity of species i	pop
β_i	fixed respiration of rep plant	W	t	temperature	degrees
a_i	variable respiration parameter for rep plant	W gm ⁻²	t_i	ideal temperature for rep plant	degrees
\hat{R}_i	optimum net energy for rep plant	W	x_i^a	above ground biomass for rep plant	gm
\hat{x}_i	optimum biomass for rep plant	gm	x_i^b	below ground biomass for rep plant	gm
N_i	population	pop	w	water	%
a_i	converts biomass to an area for rep plant	m ² gm ⁻¹	N_{ij}	population of species i in j th life stage	pop
A	area occupied by plant community	m ²	β_{ij}	basal respiration for rep plant in j th life stage	W
N_i^t	population in period t	pop	y_{ik}	supply of biomass from i th to j th species	gm/time
γ_i	growth rate constant	1/time	e_b	energy embodied in a unit of biomass	kcal/gm

Figure 1 – Demand and SEL

The upper graph breaks the plant's objective function, (1), into two parts: 1) the net incoming solar energy per unit of biomass, $(e_i - e_0)x_i$, shown by the four rays from the origin, each for a different SEL; and 2) the fixed and variable respiration shown as the strictly convex curve (from the second-order condition for a maximum) emanating from β_i on the vertical axis. By maximizing (1) the plant is choosing the x_i on the horizontal axis that maximizes (minimizes) the distance between the ray and the curve if the ray lies above (below) the curve. The optimum occurs when the slopes of the ray and curve are equal as per (2). For each ray the optimum x_i is traced down to the horizontal axis on the lower graph and linked to SEL on the vertical axis that gave rise to the x_i . For example, when SEL is e_0 the plant is said to demand x_i' of biomass. The line in the lower left graph is the plant's demand curve for biomass. The negative slope indicates the plant is following the *law of demand*: higher prices imply less is demanded. In the noncompetitive state, SEL is zero and corresponds to the ray shown with the greatest slope. At this price the demand curve cuts the horizontal axis. The price rises in the competitive state, the ray pivots downward, and the plant's demand decreases. SEL is determined in the biomass market shown in the right-side graph. If there are two plants in the market, say i and j , their demand curves are added horizontally to obtain the total biomass demand shown in at the extreme right, and the intersection between the total demand and the market supply of space, A , determines SEL. Thus, the individual plant cannot control SEL but the activity of all plants determines it. One can think of the graphs working together by following the arrows, although the activity is happening simultaneously.

Figure 2 – Single Species Growth

Each panel shows the population, biomass and SEL for one plant species over time and given the parameters shown. In each panel, one parameter is changed relative to Panel A. (Values on the vertical axis are rescaled for easier viewing.)

Figure 3 – Two Incompatible Species

The population of species two grows faster than the population of species one through the noncompetitive state, but when the competitive state begins species two starts a decent toward ultimate extinction while species one begins to climb to a population of 144 which is its steady state value in the single species scenario. In addition, while both species begin at size 8 in the noncompetitive state, when the competitive state commences in period 13 and the price of energy begins to increase to its single species steady state value of 268, both species slowly shrink in size on their way to their steady state values of 6.9 as in Figure 2, although species 2 disappears before actually attaining the steady state.

Figure 4 – Species Coexistence

In (a) there are representative plants from three species with the same e_i but different respiration parameters α_i and β_i . At the start in the noncompetitive state, $e_0 = 0$ and the highest ray from the origin labeled $e_i - 0$ pertains. All three plants are receiving positive net energy since the ray lies above the respiration curves over at least part of the range of the curves, and each plant chooses an x_i that maximizes the difference between its respiration curve and the ray. Because net energies are positive each species' population grows until the competitive state is entered and e_0 begins to rise. When it reaches e_0' plant three has negative net energy and its population decreases while the populations of species two and one continue to rise. Eventually SEL rises to e_0'' and plant two has negative net energy and a falling population. The steady state community has only species one surviving, an SEL of e_0'' , and the plants earning zero net energy with biomass x_1 . In (b) the species' α_i and β_i parameters are changed. The story begins the same with all three species making positive net energy in the noncompetitive state with their populations increasing. At some point in the competitive state SEL rises to e_0'' at which point species three is driven to extinction. However, species one and two now coexist because at e_0'' both respiration curves are tangent to the lower and final ray so that both plants are making zero net energy, have sizes x_1 and x_2 , and there is no further population growth. In (c) the three plant species now have different e_i , α_i and β_i parameters and all three species are coexisting when SEL rises to e_0' .

Figure 5 – Three Coexisting Species plus an Exotic

Species one and two have parameters that permit coexistence. Each population starts at 10 and grows to a steady-state value. Plant one is the same as the plant shown in Panel A of Figure 2; therefore, its steady state size is the same as when it was the only species present, but its population is different owing to the addition of species two. SEL is also the same as when plant one was alone in steady state; this follows because the price that yields zero net energy is unique to any set of coexisting species by Principles 4 and 5. Plant two is a smaller plant that multiplies faster than plant one. Species 4 is an exotic that is introduced in period 23 following a disturbance that causes the population of species 1 to drop from 48 to 36 allowing a gap which is filled with 10 plants of the invader. Over the next 20 periods the population of the invasive species increases which drives up SEL and forces plants from the original two species to sizes below their steady state values, and to negative net energies yielding falling populations that would ultimately fall to zero. Meanwhile the invasive species is moving to its steady state values of $e_0 = 400$, $x_3 = 7$ and $N_3 = 143$ from (9). What happened in this case is that the invasive species is inferior to the original plants in its ability to fix energy per unit of biomass (i.e., $1800 < 2000$), but is superior with respect to respiration, because what energy it does fix is used more efficiently (α_i is smaller). The growth rate of species three does not contribute to its ultimate success, but rather to the speed with which it drives out the other species. (The values on the vertical axis have been rescaled for easy viewing.)

Figure 6 – Temperature and Light

In the top diagram the parabola shows all the values of e_0 and t for which the plant earns zero net energy and is, therefore, in steady state. The ideal temperature is t and e_{0I} is SEL that would prevail at this temperature: it is the same SEL calculated in the previous section before temperature was not introduced. Any deviation of water availability from tI increases the plant's respiration; therefore, to maintain zero net energy SEL must be lower to offset the water stress. For example, if water availability drops to t' or rises to t'' , then SEL must drop to e_0' to maintain zero net energy. At point a inside the parabola, the plant is enjoying positive net energy and population is increasing. Assuming the temperature does not change from what it is at point a, then the increased population will drive up SEL through demand and supply interactions until the point on the parabola directly above point a is reached and steady state obtains. At point b the plant earns negative net energy, and again if the water level does not change, then population will decrease, SEL will fall, and the plant will move to the parabola and to a steady state. If the water level is t''' , net energy is negative and the plant population will decline to zero if the water level is not reduced. The middle diagram shows two competing species that have different ideal temperatures: species one does better at a lower temperature than species two. Both species must be earning zero net energy to coexist; hence, the only temperature that allows coexistence is t' where the two parabolas intersect. Notice that at point c, where the temperature is t'' , both plants are enjoying positive net energy and both populations are increasing; however, if the temperature remains at t'' , the rising SEL owing to the increasing populations moves plant one above its zero net energy parabola so that its population decreases while plant two population continues to increase until point c' is reached in which case plant one is extinct and plant two is in steady state. The bottom diagram shows four plants all with different ideal temperatures. Along the horizontal axis the plants that are present in a steady state are listed. For any temperature, the species with the highest parabola dominates, because that is the species that can afford the greatest SEL.

Figure 7 – Root/Shoot and Water

Water fluctuates as a percent of its maximum value according to the top piecewise line. The population is a noncompetitive state until period 6 after which it oscillates before reaching the competitive state and a steady state. After 6 periods the steady state is disturbed by an increase in water availability in period 12. After the disturbance, and three more disturbances indicated by the vertical lines, the variables oscillate before converging to the new steady-state values. In period 20, the water supply is so reduced that the population retreats from a competitive to a noncompetitive state as the population plummets. This causes competition to cease as SEL goes to zero. If the water remained at 40%, the population would eventually go extinct. Throughout the 44 periods the plant is following the fundamental behavioral rule by allocating photosynthate to roots and shoots such that the marginal benefit/marginal cost ratios of roots and shoots are always equal. (Values on the vertical axis are rescaled for easier viewing.)

Figure 3. Two Incompatible Species

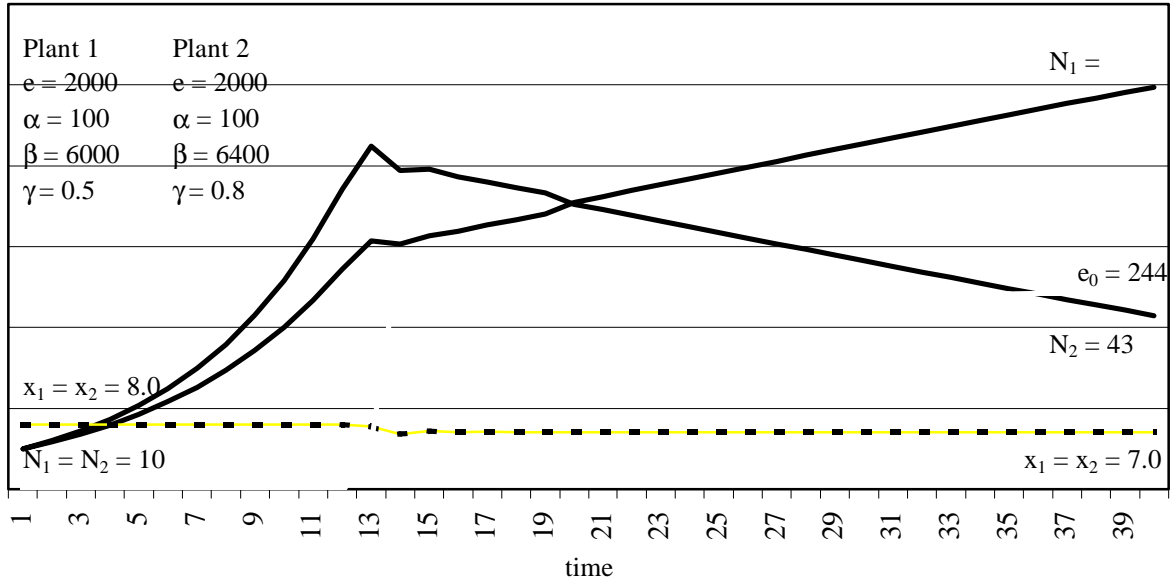


Figure 5 - Two Coexisting Species plus an Exotic

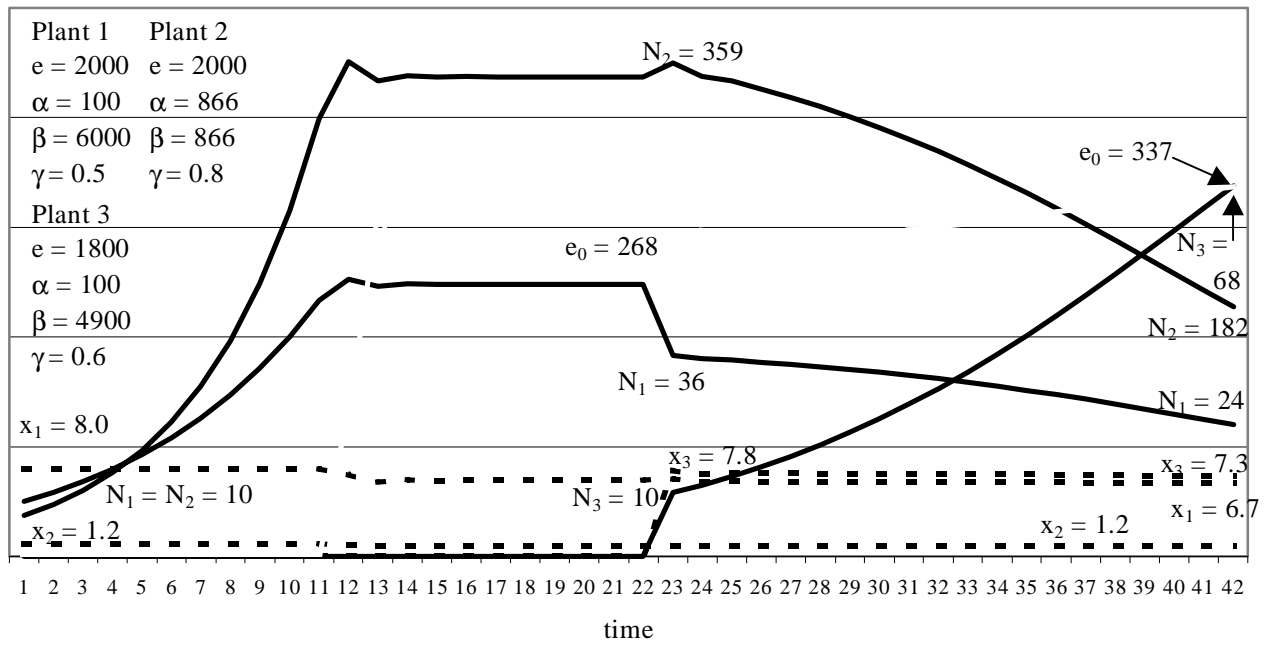
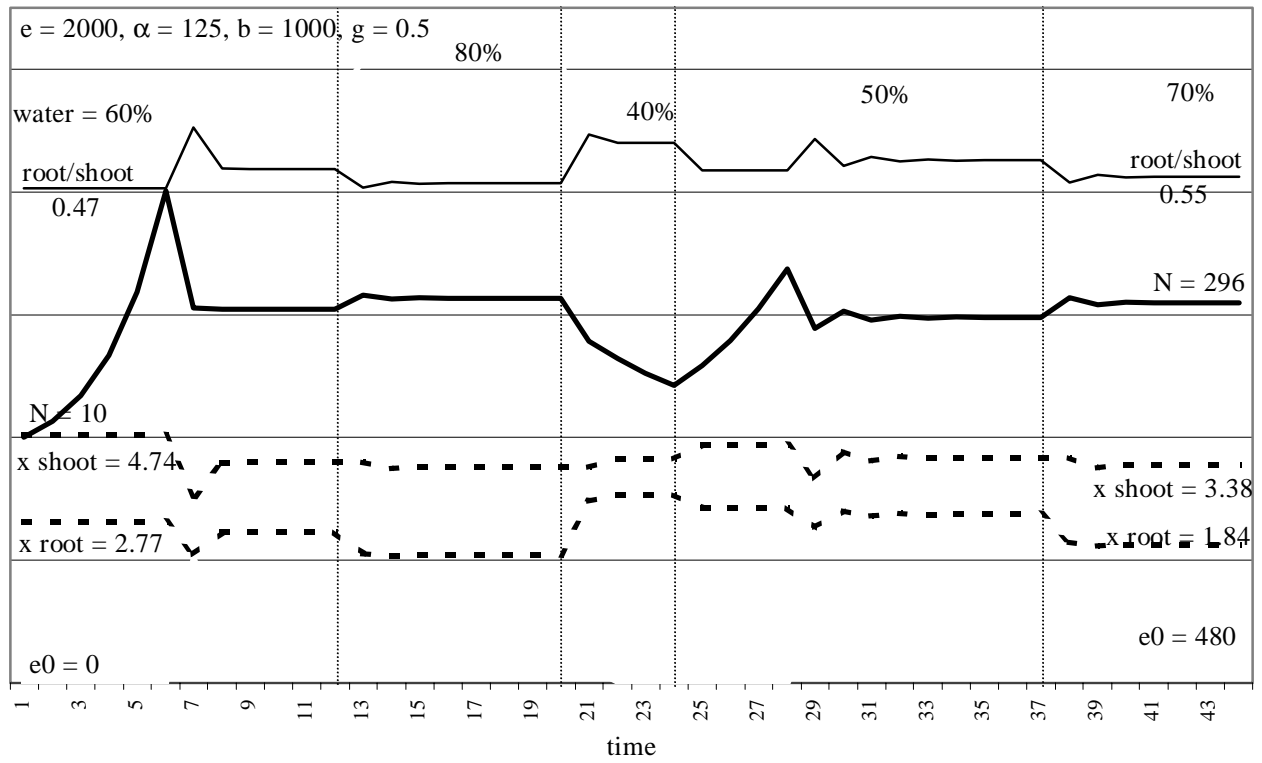
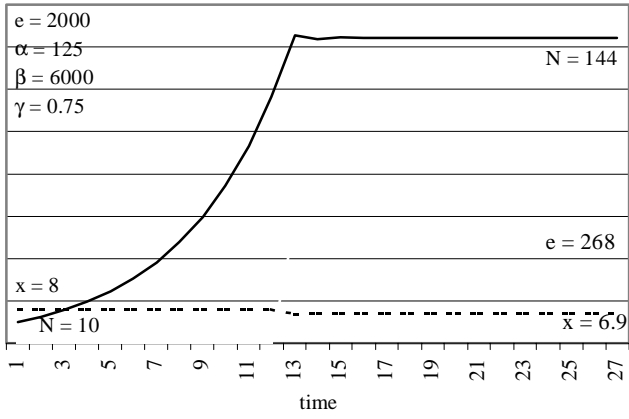


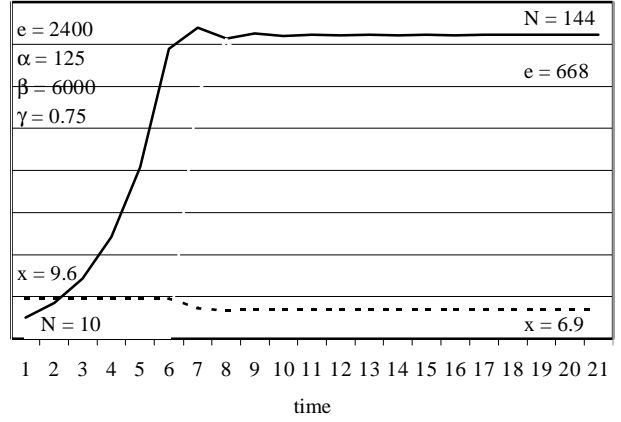
Figure 7 - Root/Shoot and Water



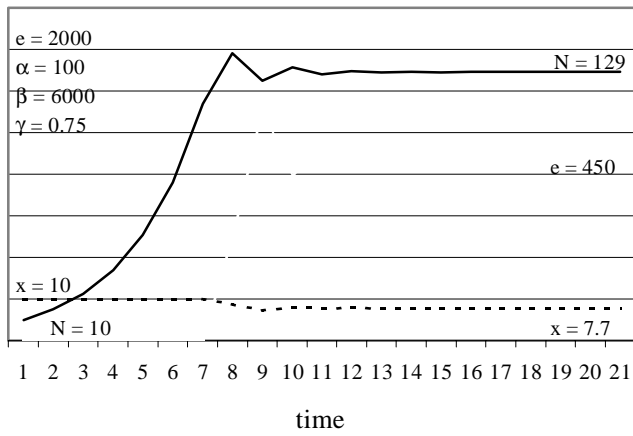
Panel A



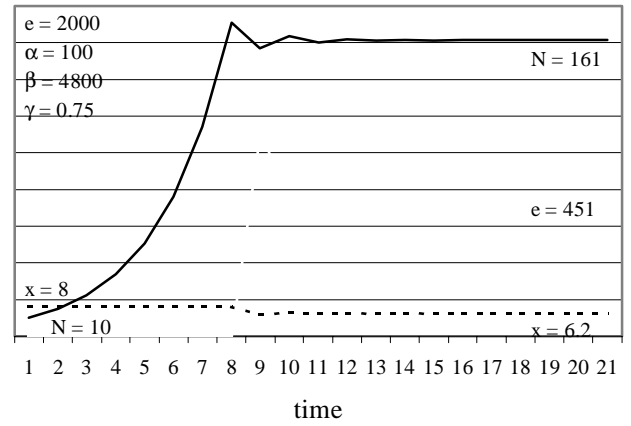
Panel B



Panel C



Panel D



Panel E

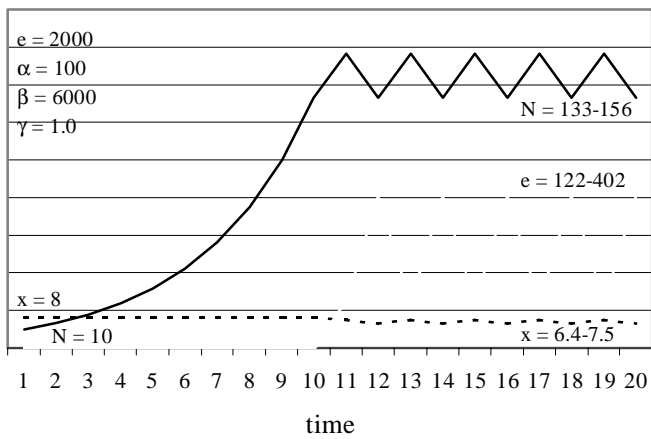


Figure 2. Single Species Growth

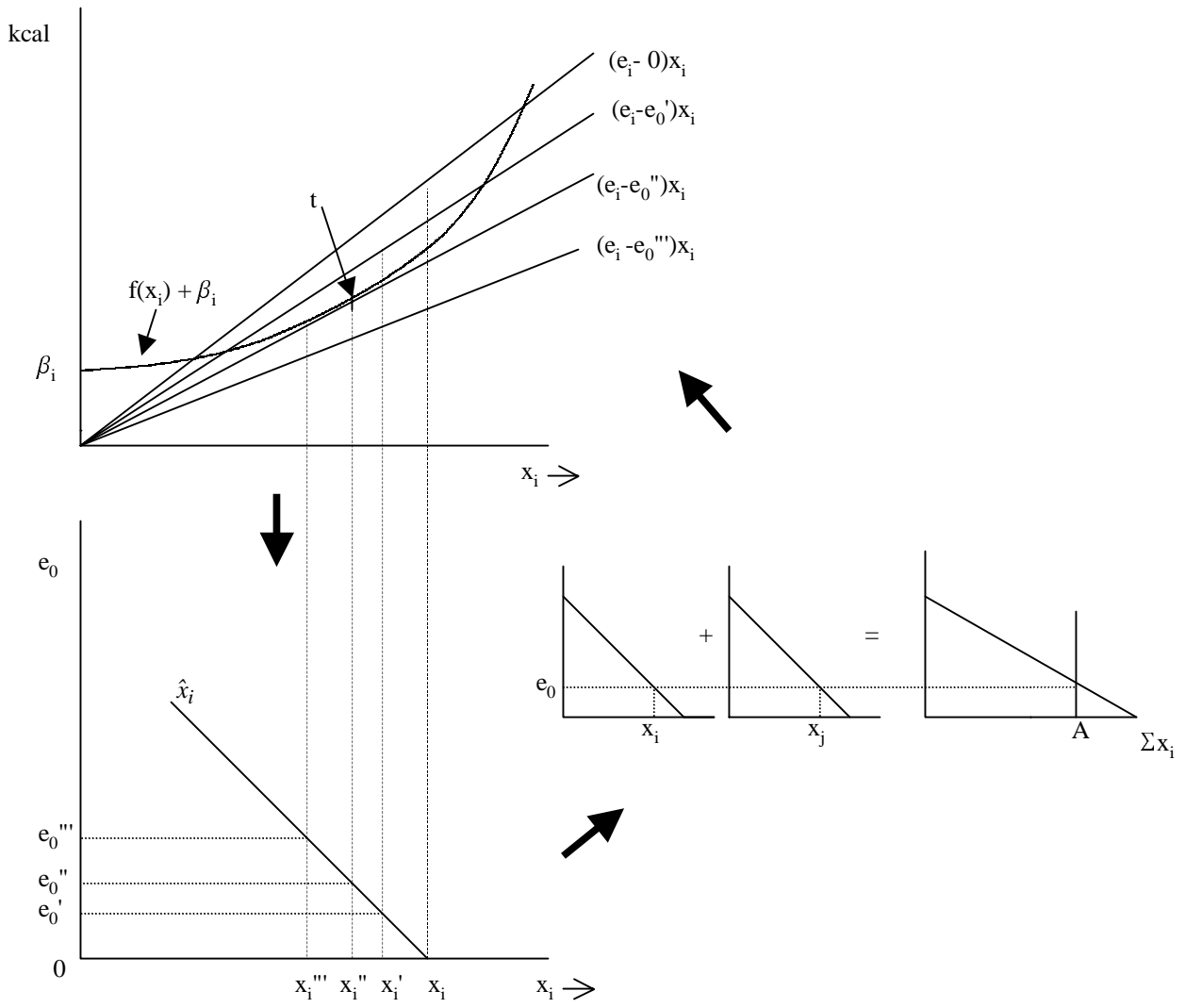


Figure 1 – Demands and SEL

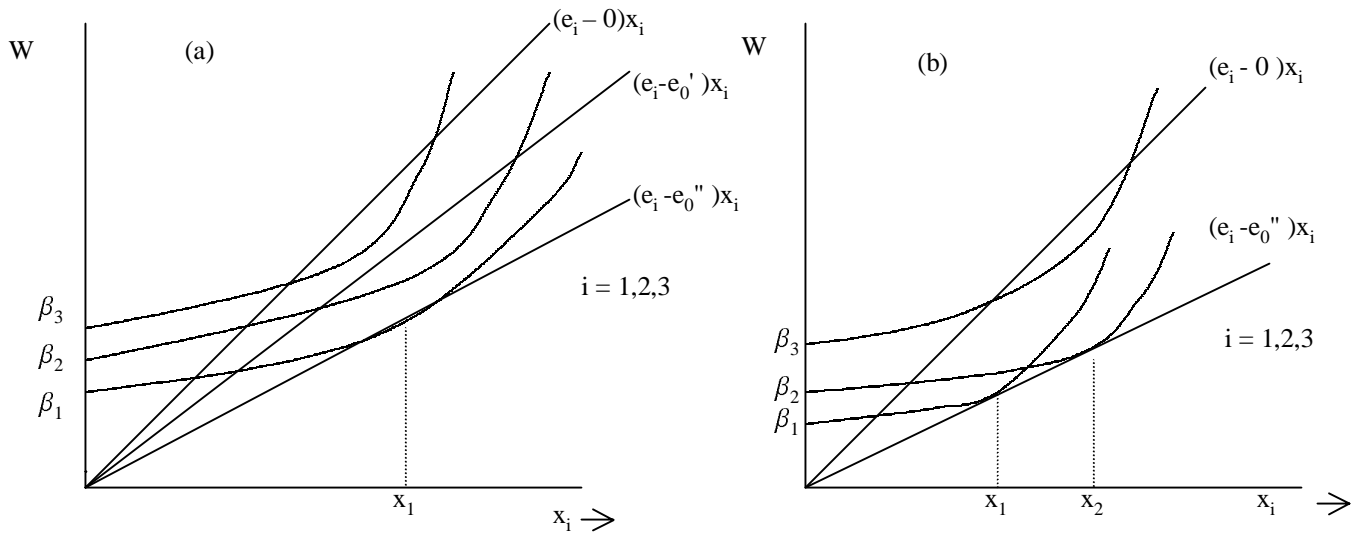
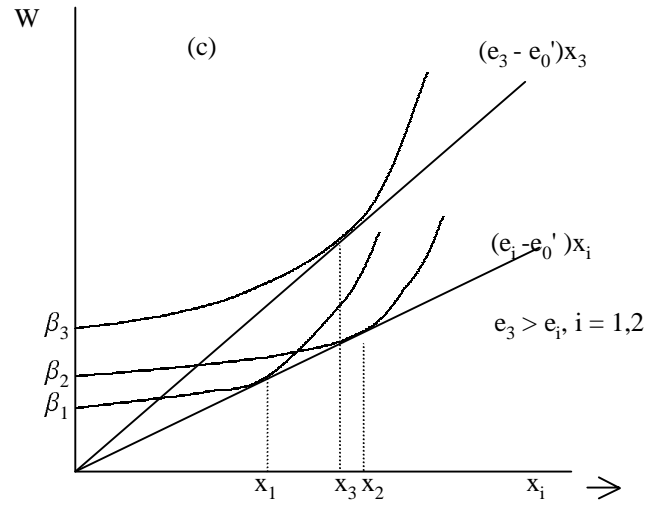


Figure 4 – Species Coexistence



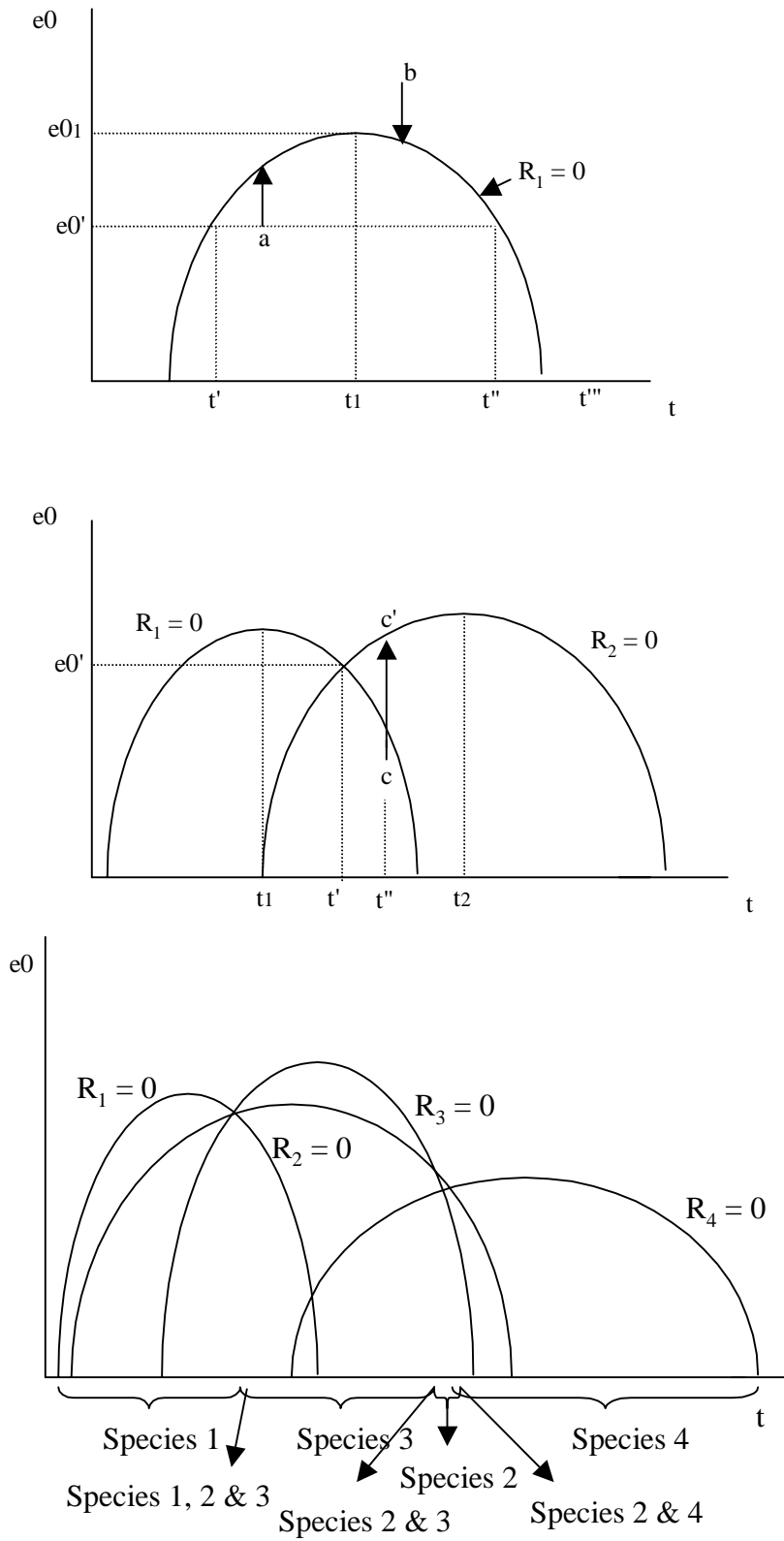


Figure 6 – Temperature and Light