A Qualitative Model of Plant Growth Based on Exploitation of Resources

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Abstract

Understanding how plants extract resources and use them to support growth has important implications for understanding subsequent processes, including population dynamics of plants, competition for limiting resources by different species, and population dynamics of herbivores and predators. Here, we develop and discuss a qualitative model of plant growth based on exploitation of resources. We also discuss some further model improvements that should allow the model to be expanded to investigate how food chains and food webs are ultimately limited by resource supply.

1 Introduction

The fundamental process supporting virtually all life on Earth is the capture of resources by green plants. Understanding how this process occurs has important implications for understanding subsequent processes, including dynamics of plant populations, competition for limiting resources by different species, and population dynamics of species supported by this basic process, i.e., consumers like herbivores and predators.

In his highly influential monograph, Tilman [1982] described plant population growth (*dN/dt*) as a function of the amount of resources (*R*) available and the depletion of resources by plant populations. He considered

$$dN/dt = N[rR/(R + k)] - mN, \qquad \text{(eq. 1)}$$

$$dR/dt = a(S - R) - (dN/dt + mN)Y, \qquad \text{(eq. 2)}$$

where r is the maximum growth rate of the plant, k is the level of R where $dN/dt = 0.5r$, a is the rate of resource supply, S is the amount of resources the system can hold, Y expresses the resource needs per individual plant (i.e., Y converts N into units of R), and m is the mortality rate of the plant. An equilibrium will be reached between the extraction of resources by plants and the resource supply rate. At equilibrium (when $dN/dt = dR/dt = 0$), the level to which the plant population reduces resources via its growth is termed R^*. From Figure 1, it can be seen that R^* is determined by the balance of plant growth rate and mortality rate m.

2 Our Conceptual Model

The basic theory described above forms one of the most important foundations for the study of plant populations, communities, and ecosystems. In investigating the consequences of this theory for multi-species systems, Tilman

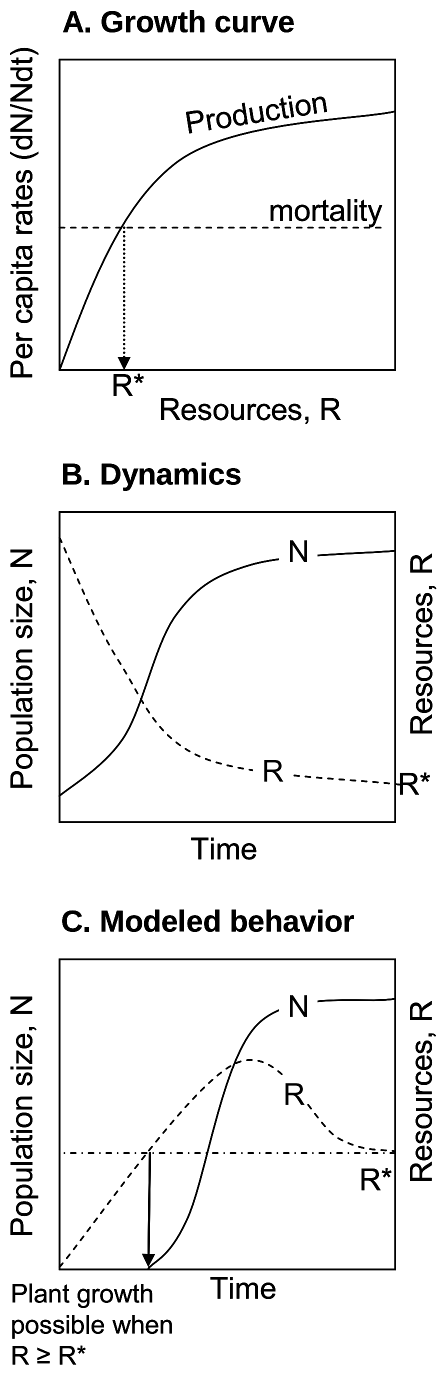

Figure 1. A. Plant growth as a function of resources. B. Dynamics of plant population and resources over time. C. Our model system: expected dynamics when resources and plant population both start from zero. (A and B from Figure 10 in Tilman 1982.)

[1982] used a primarily graphical approach. Our goal was to go a step further and create a qualitative model that captures the dynamics of this basic system.

However, to better investigate the causal processes of the effects of resources on plant growth and of plant growth on resource levels, we extend the system depicted in Figure 1B to the one depicted in Figure 1C. Starting with a system where resources and the plant population start at zero but with some resource supply, we expect the resource level to increase steadily until there are enough resources to allow plant growth to occur. The plant population should then start using resources, which should cause resource levels to decrease. Eventually, both resources and the plant population should reach some equilibrium values.

We abstracted from the parameters of eqs. 1 and 2 and formulated a conceptual model that includes the essential causal processes and controlling parameters that would lead to the behavior seen in Figure 1C. These essential ingredients are:

Resource supply: this process describes the amount of resources flowing into the system. Eq. 2 includes this concept as the first term after the equal sign, which describes the flows in a chemostat (a laboratory device with constant inflow and outflow). However, we will take a more general approach considering only the inflow of resources and extraction by plants.

Primary production: this models the conversion of resources into plants, where resources are removed from the resource pool and added to plant material. This process is the first term in eq. 1 and the second term in eq. 2.

Plant mortality: Plants die at a constant per capita rate, as depicted in the mN term in eq. 1. Because resources are lost from populations by other processes in addition to death, we consider *metabolism* as a more general loss of material from the plant population.

R^*: this sets the level at which plant growth can occur as well as the equilibrium level of resources in the presence of plants, and thus is a fundamental controller of the equilibrium values obtained by the system.

3 Our Qualitative Model

We used the concepts specified in our conceptual model to develop a qualitative model that we could simulate. Here we describe all the building blocks of our qualitative plant-resource model. These building blocks, or model primitives, are used to specify the model and are assembled by the simulator based on relevance to the scenario to be modeled. This follows the compositional modeling approach [Falkenhainer & Forbus 1991].

To create the model, we used the HOMER qualitative model-building environment [Bessa Machado & Bredeweg 2001]. HOMER is a graphical tool for creating qualitative models that can be simulated by the GARP qualitative reasoning engine [Bredeweg 1992]. We inspected simulation results using VisiGARP [Bouwer & Bredeweg 2001].

3.1 Entity hierarchy

Entities are the objects that take on behavior in a model. The entity hierarchy contains types and subtypes. This construct is useful when defining general behavior of types that one wants to be inherited and further specified by subtypes. We consider primarily two types of entities: *Environment*s and *Population*s.

Environments are places where populations live. They also have properties like resource inflow and availability (specified below). Different subtypes of *Environment* might be specified that have certain combinations of properties. We might think of *Deserts*, *Forests*, *Oceans*, etc.

Populations are collections of similar organisms. They might be further classified into different functional types or species. Functional types are useful if we want to infer a trophic relationship between two populations that co-occur in the same environment.

3.2 Configuration definitions

A configuration definition specifies how entities in a simulation are related. This relation is used by model fragments to specify consequences of entities having that relation. Here, we consider only the following relation.

Lives in: This specifies the consequences of a population living in an environment. For example, we consider that when *Plants* live in an *Environment*, primary production will occur (see below).

3.3 Quantity Spaces

Quantity spaces (QS) define the values quantities can possess. To keep the simulation as clear and uncomplicated as possible, one generally chooses a quantity space with the fewest values possible that also allows depiction of the behavior of interest. We used the following QSs.

Mzp:* Minus-Zero-Plus. This built-in QS is used for derivatives.

Zlmh: Zero-low-med-high. This is the minimum number of values necessary to see the effects of resource limitation (either imposed or emergent) on quantity values, rather than only on rankings (which are inconvenient to visualize) and derivatives. This QS is used for all amounts.

Zp: Zero-plus. This is used for rates in processes, which are either active (*Plus*) or inactive (*Zero*).

3.4 Quantities

Quantities are the properties entities can have. Here, we consider the following quantities that *Populations* and *Environments* can possess.

Biomass: The collective biomass of the entire population, irrespective of the number of individuals. As this is an amount, we use the QS *Zlmh.*

Metabolism: The amount of *Biomass* lost just to keep a population alive. This might be considered as using up energy by metabolizing stored energy reserves, or by excreting waste products. Although this might be considered an amount, we treat it as a rate and use the QS *Zp* because we are not explicitly interested in looking at values of *Metabolism*.

Production rate: This quantity adds to a population's *Biomass* and reduces the amount of *Resource available.* As a rate, it uses the *Zp* QS.

R star: This is the critical resource level (R*, Tilman 1982) below which a plant population cannot grow. This QUANTITYbelongs to a population and is compared to the *Resource available* to determine whether the population will grow under the current conditions. As R* represents a reference to a required amount of resource, we use the QS *Zlmh.*

Resource available: The amount of resource available to plants for primary production. We assume that only the most limiting resource is important to include. This is a quantity of resources that can experience inflows and outflows. As this is an amount, we use the QS *Zlmh.*

Resource inflow: The amount of resource flowing into the *Environment*. We assume that only the most limiting resource is important to include. This inflow might be from the sun, from rain, or from nutrient cycling or weathering. Although this might be considered a rate, because we want to look at effects of limitation of resource inflows on population growth, we use QS *Zlmh*, which allows us to set different inflow amounts.

3.5 Model Fragments

Model Fragments (MFs) contain the information about conditons for and consequences of relations between entities and quantities within entities. The various MFs are assembled by the simulator based on relevance to the simulated scenario, using the compositional modeling approach [Falkenhainer & Forbus 1991]. Subtypes of MFs are indicated by indentation. Subtype MFs inherit all properties of the parent MF.

We use two main types of MFs: static and process. Static MFs depict relationships between entities and quantities that do not involve influences, so cannot give rise to behavior. Process model fragments include influences and can give rise to behavior. We describe the various MFs under these two main types.

3.5.1 Static Model Fragments

An environment: This model fragment specifies that an environment consists of resources: the amount stored in the environment (quantity *Resource available*) and the amount flowing into the environment (e.g., as rain, sunlight, nutrients, etc.; quantity *Resource inflow*). These quantities are specified as being comparable by setting the *Med* points to be equivalent.

Assume constant resource inflow: This MF is built upon the imported MF *An environment*. Here, we specify that quantity *Resource inflow* does not go up or down: its derivative is set to *stable* (0; this simply allows the derivative of this quantity to be known).

Population: Here we specify that all populations consist of quantity *Biomass* and quantity *Metabolism*. An equality relation between the two quantities means that *Biomass* and *Metabolism* always have the same magnitude, and the proportionality assures that they have the same derivative. The correspondence indicates that if the *Biomass* becomes *Zero*, the *Metabolism* will also be *Zero*, because populations without biomass cannot have a metabolism.

*Existing population (*subtype of *Population)*: An inequality condition specifies that *Populations* that have a

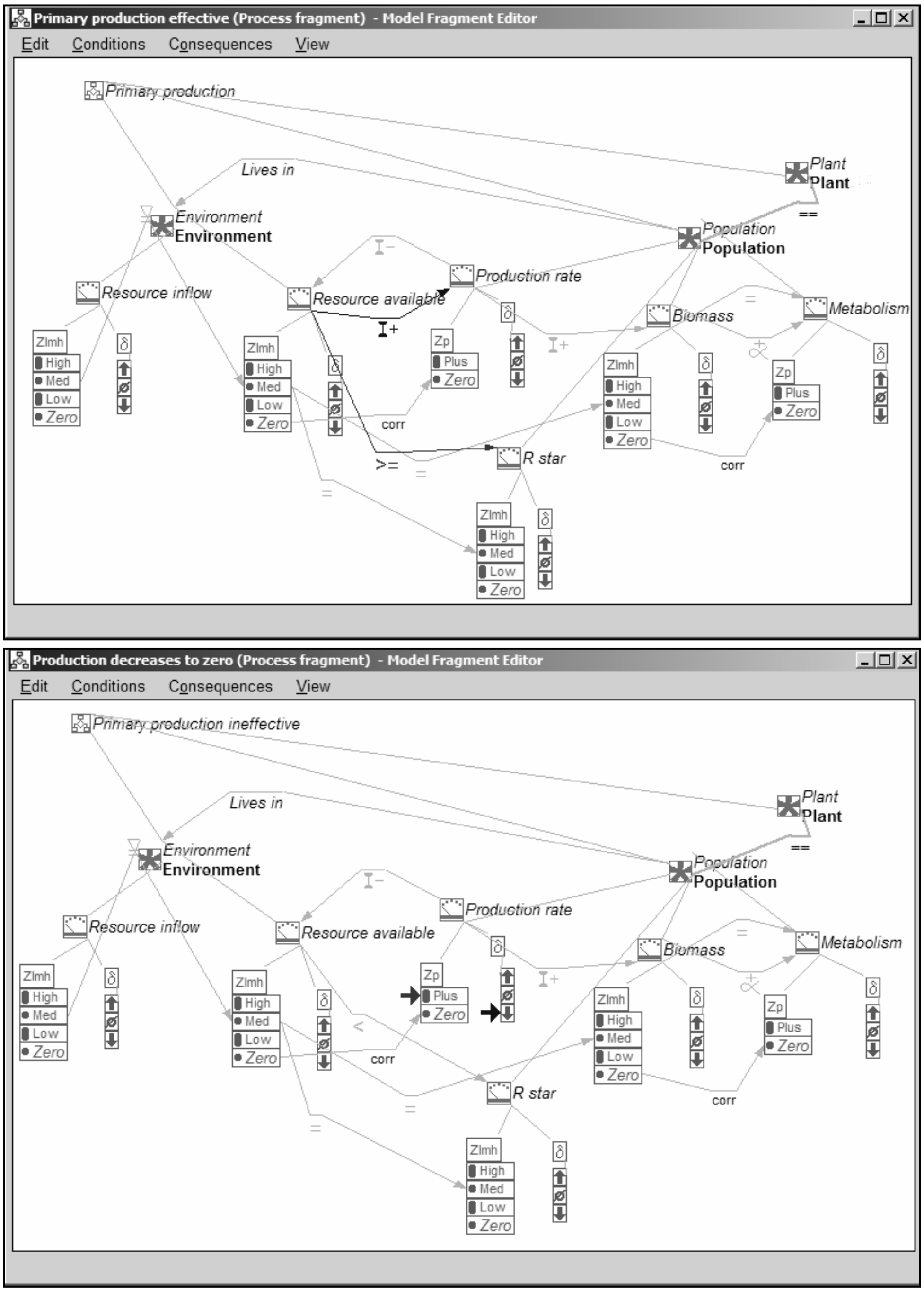

Figure 2. Two model fragments specifying the effects of primary production. The top MF specifies that if *Resource available* ≥ *R star*, then there is a positive influence (I+) of *Resource available* on *Production rate*, meaning it will increase. The bottom MF specifies the reverse: when *Resource available* < *R star* and *Production rate* is plus, then *Production rate* should decrease. This decrease should happen until *Production rate* reaches *Zero*, where another MF (not shown) specifies that it is stable at *Zero*.

Biomass greater than *Zero* will, as a consequence, have a *Metabolism* greater than *Zero*. Other MFs can be built on *Existing population* if it is important that processes not act or only act on populations with biomass greater than zero.

*Nonexisting population (*subtype of *Population):* When *Biomass* = *Zero*, *Metabolism* = *Zero*: *Populations* with no *Biomass*, i.e., that aren't present, don't have a metabolism.

3.5.2 Process Model Fragments

Resource supply: There is a constant inflow of resources into *Resource available*. This is accomplished by importing the MF *An environment* and creating a positive influence from quantity *Resource inflow* to *Resource available*.

Metabolism: Here we specify that *Metabolism* has the effect of decreasing (negative influence on) *Biomass*. The idea is that populations, even if they are not consuming or receiving energy from anywhere, use up *Biomass* in the course of staying alive. This MF is based on any *Population*, regardless of whether it is existing or not (*Biomass* can be any value, even *Zero*) because the magnitudes of *Biomass* and *Metabolism* are equivalent (see MF *Population*); thus the negative influence acting on a zero quantity does not create a problem.

Primary production: When a plant *Population* (MF) *Lives in* (configuration) *An environment* (MF), primary production can occur. However, the population must be a *Plant* (entity type), which is specified by an identity relation between *Population* and *Plant* (this specifies "if a *Population* is a *Plant*"). The consequences of these conditions are that two Qs are introduced for the *Population: Production rate* and *R star*. *R star* and *Biomass* of the *Population* are defined to be of comparable magnitudes by equality statements between their QS *Med* points and that of the *Environment's* quantity *Resource available*. There can be no production without resources, so when *Resource available* is *Zero,* so is *Production rate* (indicated by a directed correspondence from the *Zero* value in *Resource available* to the *Zero* value in *Production rate*). *Production rate* represents the extraction of resources from the environment for the benefit of the plant. Thus, *Production rate* exerts a negative influence on *Resource available* and a positive influence on *Biomass*.

*Primary production effective (*subtype of *Primary production):* When an environment contains resources in excess of a species' critical resource requirements, the production of a population of that species should increase to take advantage of the surplus resources. Thus this MF specifies that when *Resource available* is greater than or equal to the *R star* for a plant species, *Resource available* positively influences *Production rate.*

*Primary production ineffective (*subtype of *Primary production):* This MF consists only of the condition that *Resource available* of the *Environment* is less than *R star* of the plant *Population.* When resources are below the critical value for the species, the production of that species must decrease because resources are insufficient to maintain an increasing *Production rate*. These consequences are specified in the following subtype MFs.

Production decreases to zero (subtype of *Primary production ineffective*): When *Production rate* of the plant *Population* has the value *Plus*, it must decrease (derivative negative).

Production steady at zero (subtype of *Primary production ineffective*): When *Production rate* of the plant *Population* has the value *Zero*, it cannot decrease further, so it is steady (derivative zero).

3.6 The Scenario

A scenario specifies the system to be simulated. It gives the relevant entitites and starting values of any quantities that cannot be inferred by the simulator by the causal structure contained in the MFs. Here we consider the following scenario to explore the behavior of the model.

A Canadian forest: A *Plant* (labeled *Tree*) *Lives in* an *Environment* (labeled *Black Burn National Park*). The *Tree* has a specifiable beginning *Biomass* and *R star* and *Black Burn National Park* has a specifiable *Resource available* and *Resource inflow.* Other Qs are derived based on the initial values of these Qs.

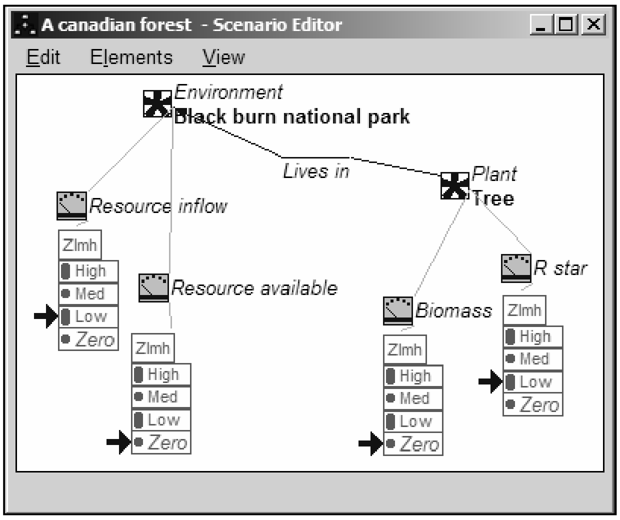

Figure 3. A scenario. This scenario shows *Resource inflow* and *R star* set to *Low*. but other values were also simulated.

4 Results

Figure 4 depicts a simulation resulting from input from the scenario described in section 3.6 and shown in Figure 3. Similar results were obtained for different values of *Resource inflow* and *R star.* Figure 4 contains the state graph (top) of the full simulation and three value histories (bottom) that follow different paths through the state graph. These value histories show the values of all quantities in each state (except those of *Resource inflow* and *R star,* whose values do not change from those in Figure 3).

The first criterion of our conceptual model can be seen in this simulation: tree biomass does not start to increase until resource available exceeds *R** in state 3 (Figure 4: notice that all paths include states 1, 2, and 3). Because the magnitude of the difference between resource inflow and production rate was unspecified, different behaviors can result

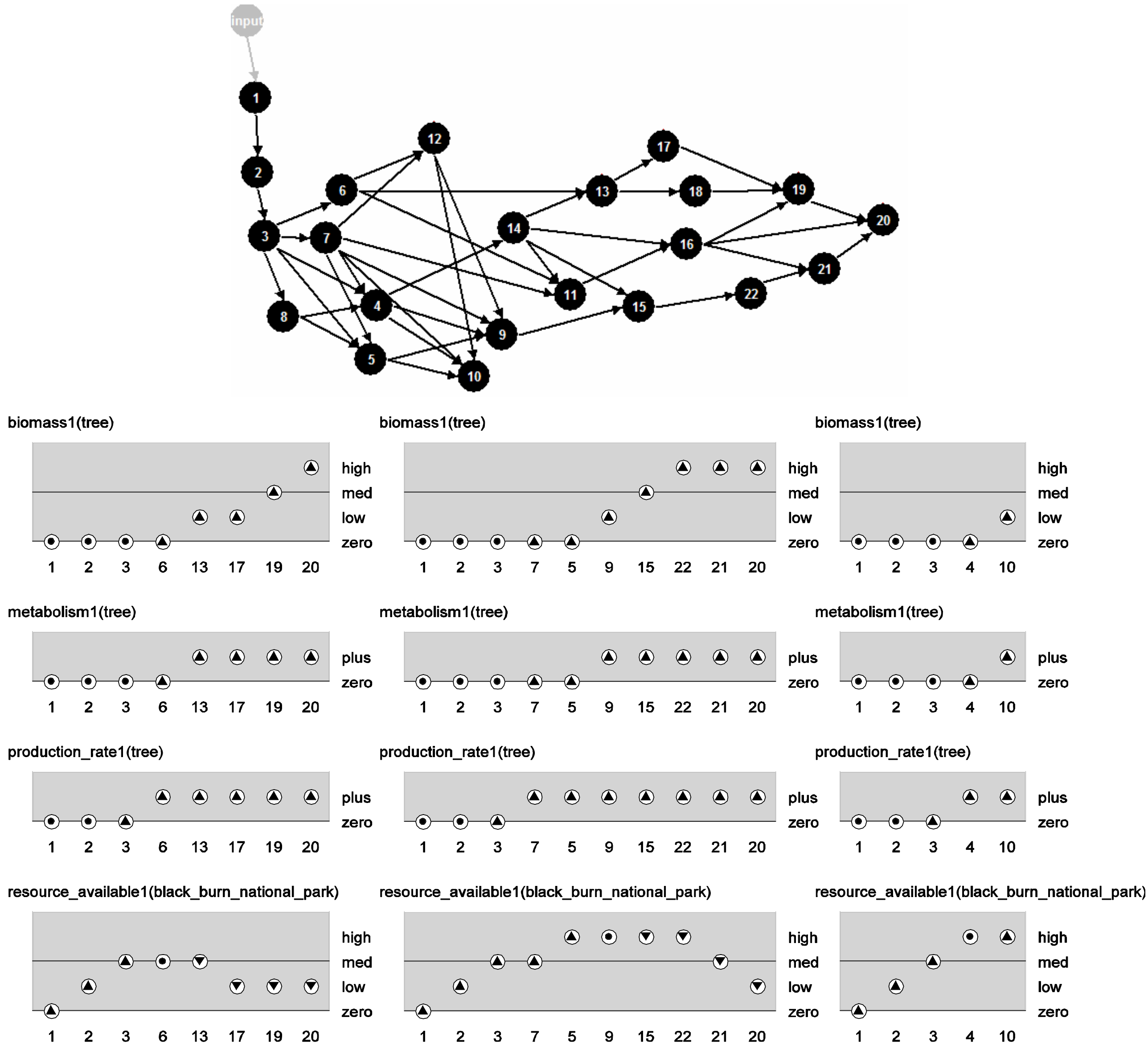

Figure 4. State graph and value histories for three paths resulting from scenario depicted in Figure 3.

from this basic condition. These are seen in the various branching paths that follow from state 3.

The three value-history diagrams at the bottom of Figure 4 demonstrate that our second criterion is met by the qualitative model. In the left pathway of Figure 4, growth is relatively rapid and resources are quickly depleted down to R*, whereas in the middle pathway, growth is slower and resources actually reach high levels before the plant population is large enough to start suppressing them. However, each of these two pathways end in the same state (state 20), with resources low (i.e., equal to *R**) and plant populations high. The other possible end state (state 10) depicts the situation when plant growth is so slow relative to resource inflow that resources cannot be suppressed by the plant population.

The third criterion, that both resources and plant populations eventually reach equilibrium values, was not met by our qualitative model. We see that both states 10 and 20 show all quantities (except resource inflow and *R**, which are constant because no processes directly or indirectly affect them) with increasing or decreasing derivatives, not stable ones as equilibrium implies. Whereas a high value that continues to increase does not indicate a causal inconsistency, the low decreasing value for resources in state 20 should lead eventually to a stable zero value or a stable low value and the low increasing value for tree biomass in state 10 should eventually lead to either a medium value or a stable low value. Thus, we need to further examine the causal structure of our model to resolve inconsistencies that lead to these unexpected behaviors.

5 Conclusions

We have developed a qualitative model of resource use by plants that satisfies two of the three criteria specified in our conceptual model and model system. We are confident that future work will lead to a fully closed model that resolves inconsistencies and satisfies all three criteria. Such a model should, instead of explicitly defining *R**, allow it to emerge as the interaction the level of resource where per capita mortality and per capita production are equal (as in Figure 1A). Thus, *R** becomes a prediction, not a parameter, of the model. This approach might involve representing per capita and gross population rates separately.

Such a model will not only be useful for examining the causes and consequences of resource use by plants, but also serve as an important building block for examining important ecological concepts such as competition for resources between different species and consumption of plant material by herbivores and so on up the food chain.

Modeling competition for resources should follow quite naturally from the MFs we have included here: all that is necessary is to describe a scenario where two species live in the same environment. These species might have different *R** values, and in this case, resource competition theory predicts that the species with the lower *R** will competitively displace the species with the higher *R** [Tilman 1982]. We have developed such a scenario, and indeed this prediction does result, but only for systems where one species has an *R** of *Low* and the other an *R** of *High*; in this case, only the species with the lower *R** value can exist, while the other species is never able to obtain enough resources to start growing (the state graph is exactly the same as that depicted in Figure 4, with additional quantities for the second species, all of which stay at *Zero*). However, other combinations of *Resource inflow* and *R** values lead to many states that seem to be inconsistent with the causal structure we are attempting to build.

This study contributes to our efforts to describe basic ecological building blocks from which more complicated systems can be modeled [see Nuttle *et al.* 2004]. Here, we have further refined the foundation of food chains, providing an important link to causal processes important for plant populations that were missing in our previous work. We expect that this refinement will lead to a better representation of what factors limit productivity in food webs, and will help us to investigate important theoretical questions like how resource supply rates affect population dynamics in higher trophic levels.

Acknowledgments

We thank the Department of Biological Sciences at the University of Pittsburgh, USA, for logistical support in the preparation of this manuscript. We also thank three anonymous reviewers for helpful comments that have improved the paper.

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