Root Stage Distributions and their Importance in Plant-Soil Feedback Models

A Dissertation Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Tyler Poppenwimer

December 2020

Acknowledgements

Throughout the writing of this dissertation I have received a great deal of support and assistance.

I would like to acknowledge the support of the National Institute for Mathematical and Biological Synthesis, an Institute supported by the National Science Foundation through NSF Award #DBI-1300426.

I would like to acknowledge the support of the National Institute for Mathematical and Biological Synthesis Graduate Student Award which allowed me to purchase a much-needed laptop computer.

I would like to thank the staff of the Ecology and Evolutionary Biology Department who helped organize my conference travel and have always been there to help navigate the bureaucracy of the graduate school.

I would also like to thank my advisors Lou Gross and Joe Bailey for their invaluable feedback and phenomenal support. Without your expertise, constant encouragement and thoughtful discussion this dissertation would never have been complete.

In addition to my advisors, I would like to thank the other members my committee, Colleen Iversen and Hamparsum Bozdogan, for their ongoing support, feedback, and encouragement throughout my time in graduate school.

I would like to thank my great colleague Megan Rúa for her constant input, penchant for grounding me in what is actually feasible in graduate school, and for always being a great conference partner.

In addition, I would like to thank my parents for always being there to support me even when things were rough.

Finally, I would like to thank my wife Tabitha, for her constant and continuous patience, support and, encouragement.

Abstract

Roots are fundamental to PSFs, being a key mediator of these feedbacks by interacting with and affecting the soil environment and soil microbial communities. However, most PSF models aggregate roots into a homogeneous component or only implicitly simulate roots via functions. Roots are not homogeneous and root traits (nutrient and water uptake, turnover rate, respiration rate, mycorrhizal colonization, etc.) vary with age, branch order, and diameter. Trait differences among a plant's roots lead to variation in root function and roots can be disaggregated according to their function. The impact on plant growth and resource cycling of changes in the distribution of roots in different functional stages is poorly understood largely due to the difficulty of manipulating below-ground processes experimentally. An unresolved question is whether the findings of many PSF models arise due to their simplifying assumptions about plant root structure.

This dissertation assesses the impact of root heterogeneity on simulated whole-plant growth and determines the effects of plant allocation strategy, resource availability, and soil microbial community interactions on the spatio-temporal behavior of root stage distributions of simulated plants. An additional objective is to determine the importance of root heterogeneity within PSFs and assess whether PSF model assumptions about roots bias the resulting implications on plant growth.

To investigate these objectives, a model is developed to simulate growth of a single perennial woody plant and incorporates explicit root structure and function. A model plant is disaggregated into above-ground photosynthetic capable biomass (ABG) and below-ground resource acquiring biomass (roots), with roots having distinct consecutive stages and associated costs and benefits. Growth and ageing feedbacks are incorporated whereby roots acquire soil resources, which are used by ABG biomass to produce photosynthate, which is allocated to maintenance and production of biomass. This framework is used for three successive models with increasing levels of complexity.

Table of Contents

List of Tables

List of Figures

Chapter 1

Theory and analysis of how different abiotic and biotic factors affect the patterns of community assemblies is fundamental to community ecology. Explication of these patterns will provide greater accuracy and precision of projections for species distributions as well as insights on how community assemblages could change under alternative future conditions. Most work on plant community assemblages and their associated evolutionary pressures is biased towards aboveground dynamics, often neglecting below ground ecology (Bever, 2003). Empirical evidence suggests that changes in soil properties and the dynamics of below ground communities in response to plants and the successive impact of these changes on plant performance (collectively called plant-soil feedbacks, PSFs) are a key mechanism of plant community and evolutionary dynamics (Van der Putten *et al*., 2013).

Roots are fundamental to PSFs, being one of the key mediators of these feedbacks by interacting with and affecting the soil environment and soil microbial communities (Kardol *et al*., 2015). The chemical and hydrological properties of soil can be modified by roots through the input and removal of chemical compounds (Read *et al.*, 2003; Inderjit *et al*., 2011). Roots are the primary vector by which root symbionts (mycorrhizal fungi, beneficial rhizobia, etc.) and root pathogenic communities interact with the plants (Mangla & Callaway, 2008; Van der Putten *et al*., 2013). Roots can modify soil microbial communities through their exudates (Shi *et al*., 2011; Hu *et al*., 2018) and soil microbial communities likewise alter root properties and their growth patterns (Bray *et al*., 2003; Schroeder & Janos, 2004; Wu *et al*., 2012; Chen *et al*., 2016).

Unfortunately observing and manipulating below ground dynamics experimentally is difficult and even more so for mature perennial wood plants. Studies that explore belowground dynamics of perennial woody plants often focus on saplings and to our knowledge there are few studies, if any, that attempt to examine the entire root system and associated below ground dynamics of mature perennial woody plants. Forest studies do not usually differentiate between individual mature plants, leading to a spatially-averaged view of belowground dynamics. Furthermore, estimates of rates of root turnover and/or production are difficult to obtain in both lab and field settings; many methods can provide misleading results or produce widely varying estimates for the same species (Tierney & Fahey, 2002). The difficulty of manipulating below-

ground processes experimentally enhances the importance of exploring below-ground processes using models to advance the theoretical foundations (Pierret *et al*., 2016; Ryan *et al*., 2016).

Though theoretical models been fundamental in identifying potential novel consequences of PSFs for a wide variety of plant community and evolutionary dynamics, they nevertheless make a surprising assumption (Van der Putten *et al*., 2013). The earliest models defined the PSF relationship as the process by which a plant alters their soil community and the soil community in turn alters the growth rate of the plant (Bever *et al*., 1997). This conceptual framework has been expanded upon and used to analyze species coexistence (Bever *et al*., 1997; Kulmatiski *et al*., 2008), invasion success (Levine *et al*., 2006), multitrophic interactions (Meyer *et al*., 2009), modifications to community assembly (Jiang & DeAngelis, 2013), dominant plant allocation strategy (Farrior *et al*., 2013), and the prevalence of plant traits (Ke *et al*., 2015). However, despite their important findings, many PSF models make a simplifying assumption about plant root structures. Within most individual and community level PSF models, roots are typically only simulated via functions of nutrient and/or water acquisition, or if the plant is disaggregated, as a single homogeneous component.

Roots are not homogeneous (Guo *et al*., 2008a; McCormack *et al*., 2012), and have been classified by age, diameter, branch order, etc. A variety of root life history traits have been correlated with age, branch order, and diameter: 1) root respiration is negatively correlated with root age (Bouma *et al*., 2001; Wells & Eissenstat, 2002; Volder *et al*., 2005; Ceccon *et al*., 2016) and diameter (Makita *et al*., 2012); 2) nutrient uptake rate is negatively correlated with root age (Bouma *et al*., 2001; Wells & Eissenstat, 2002; Volder *et al*., 2005) and diameter (Pregitzer *et al*., 1998); 3) root lifespan is positively correlated with branch order (Guo *et al*., 2008a) and diameter (Wells & Eissenstat, 2001; Gill *et al*., 2002; Joslin *et al*., 2007) and; 4) mycorrhiza colonization rates are negatively correlated with branch order (Guo *et al*., 2008b). The heterogeneity of traits among roots of different sizes, ages, and branch orders indicates that the function of roots is likewise heterogeneous.

A functional classification for roots has been employed wherein roots were categorized into mainly resource acquiring or transport capable roots. Under this classification, the percentage estimate of net primary productivity used in fine root production and turnover was reduced by 30 percent suggesting that separating roots into functional classes can improve our

capability to analyze ecosystem properties (McCormack *et al*., 2016). A functional classification scheme can be further refined by using a more continuous view of root function with multiple root stages having varying cost/benefit ratios related to their functions. For example, the rate of resource acquisition (water and nutrients) is often highest in early stage roots – younger, thinner, lower branch order – and decreases in later stage roots – older, thicker, higher branch order (Bouma *et al*., 2001; Eissenstat & Volder, 2005; Volder *et al*., 2005). In contrast, transport capacity is often lowest in early stage roots and increases for later stage roots (Pregitzer, 2002; Guo *et al*., 2008b; Valenzuele-Estrada, *et al*., 2008; McCormack *et al*., 2016). It is possible to categorize an entire plant's root system into distinct stages with each stage having various functions and cost/benefit ratios. Categorizing a plant's entire root system by functional stage and considering the distribution of roots in those different stages could improve our understanding of root processes, the factors impacting these processes, and foster a more whole-plant perspective.

A variety of abiotic and biotic factors affect root growth processes such as root turnover and production; two process which plants may be viewed as controlling the stage distribution of roots (Bouma *et al.*, 2001; Eissenstat & Volder, 2005). Soil resource heterogeneity and interactions with and the effects of soil microbial communities have been observed to alter root growth patterns. Under alternative spatial arrangements of resources, root systems display morphological and physiological plasticity (Hutching, & Kroon, 1994; Hodge, 2004; Hodge, 2006; Neatrour *et al*., 2007). Furthermore, many root systems proliferate into regions of high resource availability, increasing the production of new roots (Pregitzer *et al.*, 1993; Hodge *et al.*, 2000; Hodge, 2004). However, this initial benefit of root proliferation into these high availability regions may be outweighed by senescence after patch depletion and the overproduction of roots in those high availability patches (Fransen & De Kroon, 2002). Consequently, the distribution of different root stages may depend on resource heterogeneity and root foraging behavior.

Root interactions with soil microbial communities and the impact of soil microbial communities on the soil environment likewise alters root stage distributions. Soil microbial communities can directly alter root growth rates (Bray *et al*., 2003; Gronberg *et al*., 2011;), morphology (Schroeder & Janos, 2004; Chen *et al*., 2016), foraging patterns (Chen *et al*., 2016;

Chen *et al*., 2018) and architecture (Gronberg *et al*., 2011; Wu *et al*., 2012). Additionally, there is evidence that the growth rate of certain root types may be enhanced or diminished through interactions with soil microbial communities (Gronberg *et al*., 2011). Soil microbial communities indirectly alter root stage distributions by modifying resource availability. Nitrogen fixing bacteria grant roots access to otherwise inaccessible pools of nitrogen (Wes *et al*., 2002) and phosphate solubilizing communities increase availability of phosphorus (Zaidi *et al*., 2009). However, soil microbial communities may compete with root for access to resources which reduces resource availability to plants (Bardgett *et al*., 2003).

Understanding the factors impacting root stage distributions and analyzing the subsequent effects of changes to root stage distributions on plant-growth, resource cycling, and root turnover could elucidate potential mechanisms by which plants respond to abiotic and biotic changes and alter the soil environment. Variations in the distribution of roots in different stages could result in changes to the functions provided by the plant's root system. These changes in the functions of a plant's root system can subsequently alter plant growth, success, and root growth patterns. Perturbations in plant growth processes can impact the plant's ability to alter the soil environment which can subsequently change root growth processes, thereby altering the distribution of roots in different stages. An unresolved question is the impact of abiotic and biotic factors on root stage distributions and the subsequent effects on plant growth, success, and growth. Similarly, the impact of changes in root stage distributions on the functions of a root system and the subsequent effects of these changes on the plant's ability to alter soil properties is unknown.

The objective of this dissertation is to assess the impact of root heterogeneity on simulated plant growth, success, and root growth patterns and to determines the effects of plant allocation strategy, resource availability, and soil microbial community interactions on the spatio-temporal behavior of the root stage distributions of simulated plants. An additional objective is to determine the importance of root heterogeneity within PSFs and assess whether PSF theoretical model assumptions about roots bias the resulting implications for plant growth.

To investigate these objectives, this dissertation is focused on development of a model framework for single plant growth simulation that incorporates explicit root structure and function. A model plant is disaggregated into above-ground leaves, stems, and other supporting

structure biomass (ABG biomass) and below-ground resource acquiring and transport capable biomass (roots), with root biomass having distinct consecutive stages and associated costs and benefits. Growth and ageing feedbacks are incorporated whereby roots acquire soil resources, which are then used by ABG biomass to produce photosynthetic output, and then allocated to maintenance and to new ABG biomass and root biomass. This framework is used for three successive models with increasing levels of complexity.

The first model (Chapter 2) using examined the impact of root stage distributions on plant growth under very simplified assumptions of root growth. The model assumed direct and unlimited access to all resources and made the common assumption that the sole function of roots is resource acquisition. The objective of this model was to determine the viability of the root-stage distribution framework and act as a starting point and provides baseline results for the more complicated models.

The subsequent model (Chapter 3) incorporated transport capacity as a root function to examine the impact of incorporating the two root functions or resource acquisition and transport capacity. This model utilized a spatially explicit 2D soil environment with discrete but continuously connected cells. Within each cell, root biomass can grow and expand to produce a root network through which resources and photosynthate are transported. Soil resources are heterogeneously arrayed with availability impacting both the foraging pattern of the root network and resource acquisition rate of root biomass in a cell. This model assumes that soil resource availability is a static environmental variable that does not change in response to root/plant growth. The objective of this model is to explore the impacts of the root transport capacity and resource availability on the spatial and temporal stage distribution of roots and overall plant growth.

The third, and most complex, model (Chapter 4) incorporated the direct and indirect impact of soil microbial communities on plant growth and root stage distributions. Soil microbial communities directly impact modeled plant growth by increasing or decreasing the resource acquisition rate through root biomass and by siphoning off photosynthetic output during transport. Indirect impacts of the soil microbiota arise through their ability to increase or decrease resource availability throughout the soil environment. Additionally, resource availability responds to root acquisition, decreasing as roots acquire resources, ensuring that soil

microbial communities have an impact on the foraging pattern, root stage distribution, and growth of the simulated plant. Soil resource availability also has natural replenishment and leeching that affects the availability. The model objective is to assess the impact of soil microbial communities on plant growth and the spatial and temporal stage distribution of roots.

A summary and comparison of the implications of the three models (Chapter 5) points out the limitations associated with the assumptions of each of the models. A discussion of how these models may be applied and expanded is provided along with suggestions for the how empirical efforts might be undertaken to assess the main results of the models.

Chapter 2

Summary

- Roots are important mediators of plant-soil feedbacks, but theoretical models often aggregate them as a single component or implicitly incorporate them. Roots are not homogenous and root stages have varying costs and benefits for the plant. Studying impacts on whole plant growth of alternative root stage distributions and factors affecting these is complicated. Complexity arises from the multiplicity of interactions and experimental intractability.
- We developed a stage-based root population model with feedbacks between root resource acquisition and photosynthate production to simulate growth and ageing. An exhaustive parameter search allows examination of alternative root stage distribution assumptions on whole plant growth.
- The model results indicate: plant size is only positively correlated with the percent of root biomass in the earliest root stage; low photosynthate allocation to root maintenance produces the largest plants; and photosynthate production parameters and allocation to new root growth are the strongest predictors of plant size.
- Modeled plant growth is enhanced if root distributions are skewed towards the earliest stage, arising from the common assumption that a root system's function is resource acquisition. The common assumption encourages simplified root perspectives emphasizing fine roots which is insufficient to adequately project whole plant growth or simulate developed root systems.

Introduction

Plant-soil feedbacks (PSFs), the changes in soil properties in response to plants and the successive impact of these changes on plant performance, are a key mechanism used to describe many aspects of plant community and evolutionary dynamics (Van der Putten *et al.*, 2013). Plants can alter the chemical and hydrological properties of soil (Read *et al.*, 2003) and the composition of soil microbial communities (Kourtev *et al.*, 2003; Callaway *et al.*, 2004). Such changes in soil properties then impact the performance of the plant and its abilities to alter the soil properties (Van der Putten *et al.*, 2013). PSFs have been used to examine plant coexistence,

invasion success, trait selection, and other plant community dynamics across a wide variety of ecosystems and scales (Klironomos, 2002; Kardol *et al*., 2007; Schweitzer *et al*., 2014; Van Nuland *et al*., 2016). The impact of PSFs are not limited to plants and have been employed to explore below-ground systems including soil resource cycling, soil carbon sequestration, and soil microbial community dynamics (Hawkes *et al*., 2005; Drake *et al*., 2011; Wardle *et al*., 2012).

While the above- and below-ground elements of PSF have been documented empirically, most individual and community level PSF theoretical models focus explicitly on the above-ground portion of the plant often excluding the below-ground portion and its interactions with soil microbial communities (Bever, 2003). When plants are disaggregated into components and roots are explicitly modeled, roots are frequently simulated as a single homogenous element whose function is resource allocation (Bever *et al*., 1997; Levine *et al*., 2006; Jiang & DeAngelis, 2013; Ke *et al*., 2015). One approach to analyze the impact of this common root perspective among PSF models, is to develop a stage-based root demographic model, with varying cost/benefit ratios for different root stages and feedbacks between root acquired resources, photosynthate production, and biomass growth. Such a model has not been developed previously.

Theoretical models have been fundamental in identifying potential novel consequences of PSFs for a wide variety of plant community and evolutionary dynamics (Van der Putten *et al.*, 2013). The earliest models defined the PSF relationship as the process by which a plant alters their soil community and the soil community in turn alters the growth rate of the plant (Bever *et al*., 1997). When applied in a two-plant species coexistence model, positive feedback leads to a loss of plant diversity while negative feedbacks enhance plant diversity.(Bever *et al*., 1997). Such a conceptual framework regarding feedbacks has been extended to analyze dynamics for coexistence models incorporating more than two plants (Kulmatiski *et al*., 2008). Models have since suggested PSFs can increase invasion success (Levine *et al*., 2006), disrupt multitrophic interactions (Meyer *et al*., 2009), modify community assembly (Jiang & DeAngelis, 2013), and shift the prevalence of plant traits (Ke *et al*., 2015).

An unresolved question is whether the important findings of these and other PSF models arise due to their simplifying assumptions on plant structure since roots are not explicitly incorporated. Only one of the PSF models (Meyer *et al*., 2009) explicitly incorporates roots,

simulating them as a single element. However, roots are not homogenous (Guo *et al*., 2008a; McCormack *et al*., 2012). Observationally, roots have most commonly been classified by age, branch order, and diameter and these classification schemes have been correlated with many root life history traits. Branch order and diameter positively correlate with root lifespan (Guo *et al*., 2008a; McCormack *et al*., 2012). Respiration rate is negatively correlated with root diameter in several tropical tree species (Makita *et al*., 2012). Differences among roots can also impact their function such as how nutrient and water uptake rate are negatively correlated with root age in citrus and apple trees (Wells & Eissenstat, 2002).

A functional classification scheme for roots has been employed to better project ecosystem properties through the separation of roots into stages based on their role within the root system (McCormack *et al*., 2015). This functional classification scheme explored estimates of net primary productivity (NPP) in ecosystems dominated by perennial plants. By categorizing fine roots into two categories of mainly uptake capable or transportive roots the percentage estimate of NPP used in fine root production and turnover was reduced by 30 percent. These results suggest the separation of roots into functional classes can improve our capability to analyze ecosystem properties. Such a functional classification can be further refined using a more continuous view of root function. The rate of resource acquisition (water and nutrients) in early stage roots – younger, thinner, lower branch order – is often higher than in later stage roots – older, thicker, higher branch order (Bouma *et al*., 2001; Eissenstat & Volder, 2005; Volder *et al*., 2005). Thus, categorizing a plant's entire root system by functional stage, and considering the distribution of roots in different stages, could improve understanding of many root processes and foster a more whole-plant perspective on individual plant growth.

It has been suggested that overall plant growth is initially enhanced by maintaining a larger proportion of early stage roots with this proportion decreasing over time (Helmisaari *et al*., 2002). Root turnover and production are two process through which plants may be viewed as controlling the stage distribution of roots (Bouma *et al.*, 2001; Eissenstat & Volder, 2005). Estimating turnover and/or production and their effects on root distribution changes are difficult to obtain in both lab and field settings. Some methods may even provide misleading results or produce widely varying estimates for the same species (Tierney & Fahey, 2002). Consequently, it is difficult to determine the impacts of trade-offs in senescence scheduling of various stage

roots, its subsequent effects on root stage distribution, and how plant fitness and the individual growth components that impact plant fitness, respond. The difficulty of manipulating below-ground processes experimentally enhances the importance of exploring below-ground processes using models to advance the theoretical foundations (Pierret *et al.*, 2016; Ryan *et al.*, 2016).

To better analyze impacts on the plant soil system arising from the heterogeneous nature of root systems, we developed a stage-based root population model with feedbacks between root resource acquisition, above-ground photosynthetic production and subsequent root production and turnover. To our knowledge, no model has examined the effects of individual plant root demography on projections of plant growth, resource cycling, plant community dynamics, soil microbial community dynamics, or plant soil feedbacks. As noted above, many observational studies have demonstrated different life histories among different root stages (branch order, age, diameter, etc.). The proposed model simulates a single perennial woody plant over its entire lifetime with time steps representing a growing season. The plant is separated into above-ground photosynthetic capable biomass (leaves) and below-ground resource acquiring biomass (roots). The roots are categorized into distinct successive stages each with their own resource acquisition rate, maintenance cost, and initial transition rate. The transition rate describes the fraction of root biomass that transitions between stages and the biomass that does not transition senesces. The leaves produce photosynthate using the resources acquired by the roots which is then allocated, based on the plant's allocation strategy, to new root growth, new leaf growth, and root maintenance. The amount allocated to root maintenance and the difference between this amount and the maintenance cost can alter the transition rate for each root stage. The amount allocated to new root and leaf growth produces new Stage 1 root biomass and new leaf biomass respectively. Our model can: 1) examine the effects of root stage distributions on carbon cycling, overall uptake, and whole-plant growth; 2) be applied to identify circumstances in which root demography significantly impacts plant growth and below-ground interactions; 3) suggest experiments and observations; and 4) build linkages between individual plant characteristics and below-ground ecosystem processes.

Description

The model description format we utilize here follows the Overview, Design Concepts and Details (ODD) Protocol developed and updated by Grimm and colleagues (2010). This protocol has been argued as effective to enhance the reproducibility of models, their simulation, and their analysis, a key concern in current science (Stodden *et al.*, 2014).

MODEL OBJECTIVE

We developed a model to analyze the effects of different root stage distributions on the above- and below-ground growth of an individual perennial woody plant over its lifetime. An objective of this model is to determine the effects of different plant allocation strategies on the long-term behavior of root stage distributions and whether these tend towards stable patterns, either static or periodic cycles, or have non-periodic fluctuations.

PLANT COMPONENTS

Plant

The mathematical formulation of a plant consists of coupled differential equations for two main plant components: 1) above-ground photosynthetically capable biomass (leaves); and 2) below-ground resource acquiring biomass (roots). Such a component-based approach to whole plant growth has been applied in many contexts (McGraw, 1983; De Reffye *et al*., 1997; Prusinkiewicz, 1998). This model specifically incorporates heterogeneity in the root component.

Above-ground

In our model, the above-ground biomass (leaves) convert acquired resources into photosynthate which is used by the plant to produce additional leaf and root biomass and maintain a portion of the current root biomass. The leaf biomass is composed of a single stage. The benefit of leaves is their ability to produce photosynthate using the resource acquired by roots. Our model assumes there is no cost associated with maintaining leaf biomass and leaf turnover rate remains unchanged throughout a simulation. New leaf biomass is produced dependent upon the plant allocation strategy and the amount of photosynthate produced in the previous time step.

Below-ground

In the model, below-ground biomass (roots) acquire resources which are used by the leaves to produce photosynthate. Root biomass, R_n is separated into distinct successive stages with early stage roots representing young, thin, fine roots and later stage roots representing old, thick, coarse roots. Root benefits are modeled as the ability to acquire soil resources while their cost is measured in photosynthate needed to maintain the initial turnover rate for a given stage. The turnover rate of roots in each stage may change during the simulation dependent on the root maintenance cost and the plant allocation strategy. New root biomass production is dependent on the plant allocation strategy and the amount of photosynthate produced in the previous step.

Each root stage has its own resource acquisition rate, maintenance cost, and initial turnover rate (**Fig. 1**). The resource acquisition rate describes the amount of below-ground resources (water and nutrients) per unit biomass a stage will acquire during a single time step. This rate is highest in earlier stages and continuously decreases towards later stages, based on physiological root data indicating reduced water and nutrient acquisition rates with root age and increase in woody biomass (Bouma *et al*., 2001; Wells & Eissenstat, 2002; Volder *et al*., 2005). The maintenance cost describes the amount of photosynthate per unit biomass a stage requires to maintain the initial turnover rate. The cost follows a similar trend as resource acquisition rate, as data indicate that root respiration rate decreases with root age (Bouma *et al*., 2001; Wells & Eissenstat, 2002; Volder *et al*., 2005; Makita *et al*., 2012; Ceccon *et al*., 2016). The initial transition rate describes the fraction of root biomass that will transition if the maintenance cost is exactly met (transition is defined to be one minus the turnover rate). The transition rate is lowest for earlier stages (high turnover rate) and continues to increase towards later stages (low turnover rate) (Bouma *et al*., 2001; Joslin *et al*., 2006; Yao *et al*., 2006; Guo *et al*., 2008a; McCormack *et al.*, 2012).

ENVIRONMENT

There is no spatially explicit soil environment included in this model. The plant is assumed to have direct and unlimited access to all soil resources (water and nutrients). Similarly, the plant is assumed to have direct and unrestricted access to sunlight needed to produce photosynthate.

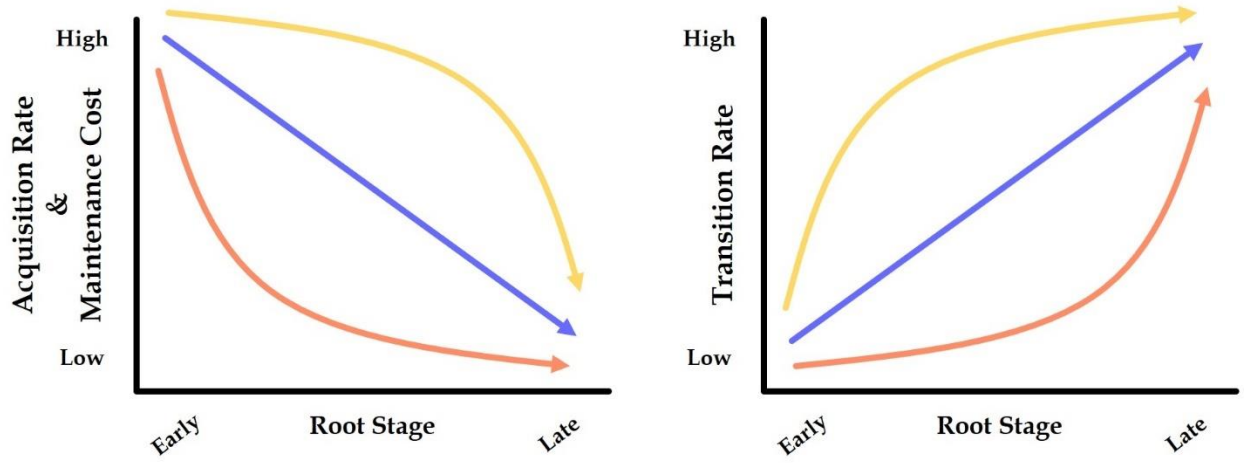

Figure 1: The qualitative relationship between root stage and function.
The qualitative relationship between root stage and resource acquisition rate, maintenance cost, and transition rate. The resource acquisition rate and maintenance cost are measured per unit of root biomass in each stage. The transition rate represents the fraction of root biomass in each stage that will transition if the maintenance cost of the roots in that stage is met. Transition rate is defined as one minus the turnover rate.

ORDER OF EVENTS

The model utilizes individual time steps representing one growing season for the plant (assumed to represent one year). At the start of a time step (growing season) the plant uses photosynthate stored from the previous time step to produce new root and leaf biomass. Following this, the roots acquire soil resources which are in turn used by the leaves to produce photosynthate. The photosynthate is then allocated according to the plant's allocation strategy. The allocation strategy does not change within a simulation and allocates photosynthate to new leaf growth, new root growth, and root maintenance. The amount of photosynthate allocated to root maintenance alters a stage's initial transition rate. If the maintenance allocation is more than a stage's cost, then a larger fraction of root biomass will transition to the consecutive stage. Conversely, if allocation to maintenance is less than a stage's cost, a smaller fraction of root biomass will transition to the next stage. The remaining photosynthate (allocated to new leaf and root growth) is stored for use in the following time step (growing season). After storing photosynthate, the growing season ends (**Fig. 2**).

GROWTH AND AGEING

Growth and ageing of each root stage arises from photosynthate allocation and thus is part of a feedback cycle whereby roots acquire resources which are then used by the leaves to produce photosynthate. Photosynthate is allocated to new root growth, root maintenance, and new shoot growth. Photosynthate allocated to root maintenance is used in the time step in which it was produced (**Fig. 3**).

Photosynthate, P_i, produced during time step i is determined by a rectangular hyperbola with variables of leaf biomass, L_i, and acquired soil resources, N_i, and parameters α, β, and γ (**Eq. 1**). The parameters α increases or decreases the photosynthate produced while β and γ alter the importance to photosynthate production of acquired soil resources and leaf biomass respectively.

$$P_i = \frac{\alpha N_i L_i}{\beta R_i + \gamma L_i} \quad \text{Eq. 1}$$

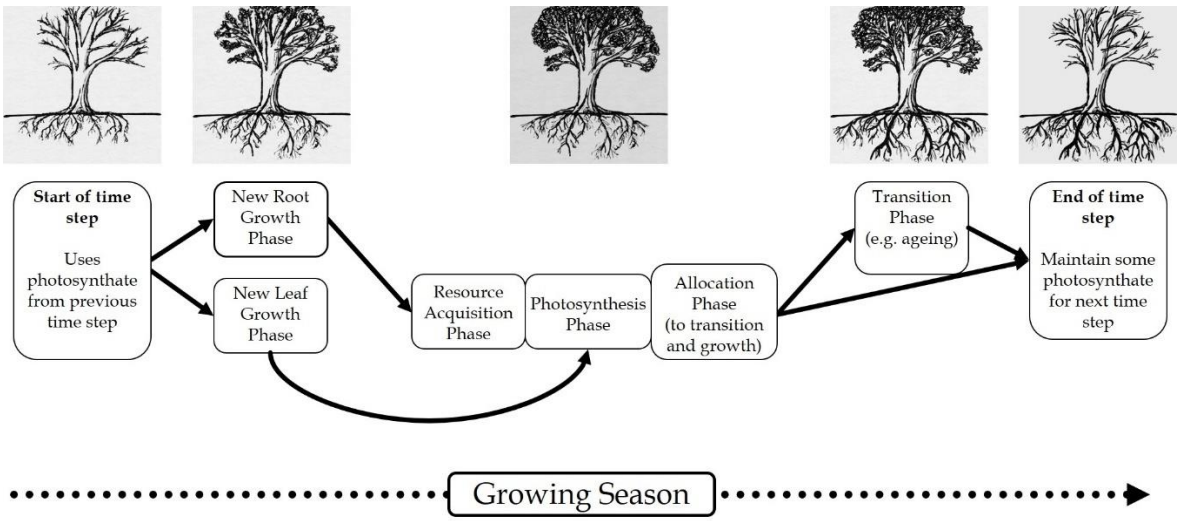

Figure 2: Order of Events for Model 1.
The order of events for one time step (assumed to represent one growing season). At the beginning of a time step, photosynthate from the previous time step is used to produce new root and leaf biomass. The roots acquire resources which are used by the leaves to produce photosynthate. This photosynthate is allocated to new root growth, new leaf growth, and root maintenance. The photosynthate allocated to root maintenance is used in the current time step and determines the new transition rate for each stage of roots. Based on this updated transition rate, root biomass transitions between the stages (biomass that does not transition senesces). Photosynthate allocation to new root and leaf growth is stored for the following season.

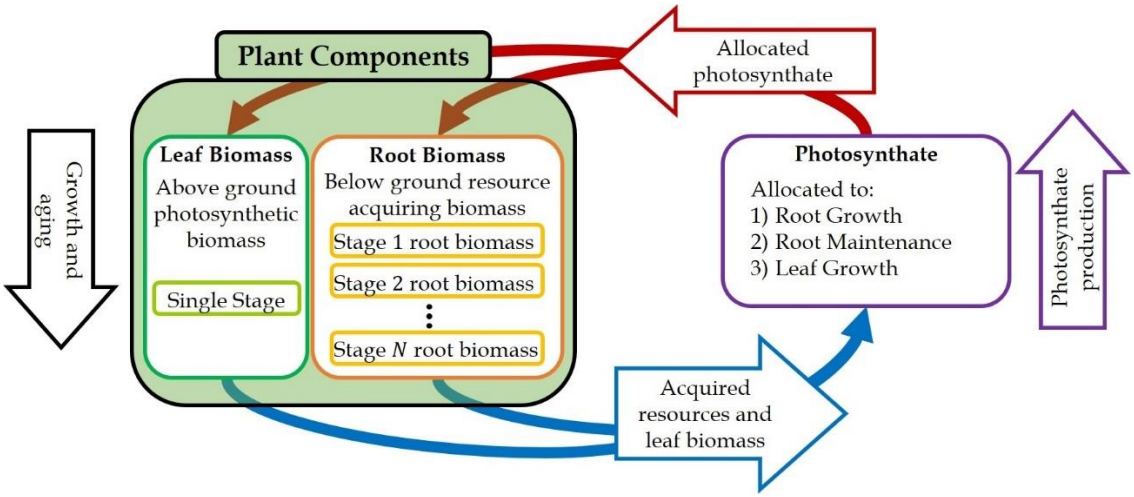

Figure 3: Components of a Simulated Plant.
A simulated plant is composed of leaf biomass (single stage) and root biomass (composed of multiple stages). The roots acquire resources which are used by the leaf biomass to produce photosynthate. This photosynthate is allocated to three components; 1) new root growth; 2) root maintenance; 3) and new leaf growth. Photosynthate allocation to root maintenance is used in the current time step to maintain some of the current root biomass by transitioning a proportion of root biomass in each stage to the subsequent stage. Photosynthate allocation to new root and leaf growth is used in the following time step to produce new Stage 1 root biomass and leaf biomass respectively.

Photosynthate allocated to root maintenance alters the transition rate for each root stage. Although each root stage has an initial turnover rate, this rate can be influenced by the amount of photosynthate allocated to root maintenance. The photosynthate allocated to root maintenance is distributed to each stage based upon the biomass in each stage. If a stage receives an amount of photosynthate equal to its maintenance cost, the transition rate will not change from the stage's initial transition rate. If a stage receives less photosynthate than its maintenance cost, then the stage will have a lower transition rate than its initial rate. In contrast if a stage receives more photosynthate, the stage will have a higher transition rate. The updated transition rate, $T_{i,n}$, during time step i for Stage n is determined by a logistic equation with the stage's initial turnover rate, τ_n, and the stage's difference between photosynthate maintenance allocation $M_{i,n}$ and maintenance cost C_n (**Eq. 2**).

$$T_{i,n} = \frac{1}{1 + e^{\ln\left(\frac{1-\tau_n}{\tau_n}\right)-(M_{i,n}-C_n)}} \quad \text{Eq. 2}$$

The new transition rate determines the percentage of root biomass in each stage that will transition to the consecutive stage. The transition rate for the last stage describes the percentage of biomass that will remain in the last stage. The biomass in each stage that does not transition senesces and is lost from the root system. The transition rate for leaf biomass does not change during a simulation and describes the fraction of leaf biomass that survives to the next time step.

Photosynthate allocated to new root growth and new leaf growth is stored until the following season. New root biomass always starts as Stage 1 biomass. New Stage 1 biomass production is a function of photosynthate allocation, photosynthate produced in the previous time step, and root biomass conversion rate. There is no distinction as to which stage produces the new Stage 1 biomass. For leaf biomass, as there are no stages, new biomass is simply added to the current leaf biomass and is a function of photosynthate allocation, photosynthate produced in the previous time step, and leaf biomass conversion rate.

PARAMETER SPACE SEARCH

A parameter space search was conducted to determine the impact of parameters affecting plant allocation strategy (e.g. allocation of photosynthate to new root growth, new leaf growth and root maintenance), conversion rates of photosynthate to root and leaf biomass, and

photosynthate production on root stage distribution. The range of values used in the parameter space search can be found in (**Table 1**). The set of values used produced approximately 295 million simulations.

INITIALIZATION

Each simulation began with one unit of biomass in each of the five root stages for a total of five units of root biomass. The leaf biomass was set at five units of biomass, so initially each plant has 10 units of biomass. Although biomass from the previous time step is needed to produce new leaf and root biomass at the start of a time step, the initial time step has no previous time step and so the previous step's photosynthate is determined by the initial root and leaf biomass. The leaf turnover rate and allocation strategy are determined by the parameter set used for that simulation which also specifies the relationships between root stage and resource acquisition rate, maintenance cost, and initial transition rate. These relationships are qualitatively described above (early stages: high acquisition and maintenance, low transition; late stages: low acquisition and maintenance, high transition) with a form for each which is linear, concave or convex.

ANALYSIS

A parameter space search was conducted in MATLAB 2018a to analyze the effects of different parameter sets on the model outcomes. The range of values used in the parameter space search can be found in (**Table 1**). The model was run for 100 time steps after which the outputs were analyzed. The outputs include root biomass in each stage, leaf biomass, and time step of death if applicable. The parameter space search was also run for 50 and 200 time steps with no significant differences in the resulting analyses.

Of the 295 million simulated plants, approximately 55 million of the plants had a final total biomass greater than their initial biomass; meaning that approximately 19 percent of simulations resulted in growing plants while the other 81 percent resulted in dying or dead plants. All analyses were conducted on the surviving plants.

Table 1: Parameter Space Search Components.
The parameters, their description, and their values used in the parameter space search.

	Parameter	Description	Range of Values start : step : end
Roots	n	Number of root Stages	5
Root Cost/Benefit Ratio	η_n	Resource uptake functional form for Stage n	linear, convex, concave
	C_n	Maintenance cost functional form for Stage n	linear, convex, concave
	τ_n	Initial transition rate functional form for Stage n	linear, convex, concave
Leaves	T_L	Transition rate for leaf biomass	$0.5 : 0.1 : 1$
Allocation Strategy	G	Percent of photosynthate allocated to new root growth	$0.0\overline{3} : 0.0\overline{3} : 0.9\overline{3}$
	M	Percent of photosynthate allocated to root maintenance	$0.0\overline{3} : 0.0\overline{3} : 0.9\overline{3}$
	S	Percent of photosynthate allocated to new leaf growth	$0.0\overline{3} : 0.0\overline{3} : 0.9\overline{3}$
Conversion Rates	δ_r	Photosynthate conversion rate for root biomass	$0.75 : 0.05 : 1$
	δ_l	Photosynthate conversion rate for leaf biomass	$0.75 : 0.05 : 1$
Photosynthesis Production	α	Multiplicative constant of photosynthesis	$0.6 : 0.2 : 1.4$
	β	Importance of resources in photosynthesis	$0.6 : 0.2 : 1.4$
	γ	Importance of leaf biomass in photosynthesis	$0.6 : 0.2 : 1.4$

Results

Frequency of Root Stage Distributions. Overall, the frequency of root biomass is bimodally distributed for root stages 1 and 5. Of the surviving plants, approximately 75 percent had 50 percent or more of their root biomass contained in Stage 1 with 55 percent having 99 percent or more root biomass in Stage 1. Approximately seven percent of surviving plants had less than one percent of root biomass in Stage 1 (**Fig. 4a**). Over 80 percent of all surviving plants had less than one percent of their root biomass contained in Stages 2, 3, and 4 (**Fig. 4b**). Approximately 20 percent of surviving plants had 50 percent or more of their root biomass contained in Stage 5 with approximately 7 percent of plants having 99 percent or more root biomass in Stage 5 (**Fig. 4b**).

Effects of Root Stage Distribution on Plant Growth. Plant biomass was largest for those with a root stage distribution skewed towards Stage 1 (**Fig. 5a**). The largest plants maintain a root stage distribution with 100 percent of their root biomass in Stage 1. Plants with 100 percent of root biomass in Stage 1 have a mean Log_{10} plant biomass of 17.3 (**Fig. 5b**). Biomass is positively correlated with the percent of root biomass maintained in Stage 1 (**Fig. 5a**) while biomass in all other stages is negatively correlated with the percent of biomass in the stage, with no plants maintaining more than 50 percent of their root biomass in Stage 2, 3 or 4 (**Fig. 5c**).

Frequency of Allocation Strategy. The most frequent proportion of photosynthate allocated to new root growth is centered around $0.36\overline{6}$. The most frequent proportion of photosynthate allocated to root maintenance, is the minimum amount of $0.03\overline{3}$. The frequency of allocation to root maintenance decreases as the proportion allocated to this component increases. The most frequent proportion of photosynthate allocated to new leaf growth is centered around $0.33\overline{3}$. The most frequent proportion of photosynthate allocated to a single component is $0.03\overline{3}$ allocated to root maintenance; approximately 11 percent of all surviving plants used this allocation strategy. The frequency of allocation to a single component is only negatively related with the proportion of photosynthate allocated to root maintenance (**Fig. 6a**).

The most frequent allocation of photosynthate strategies leading to plant survival, occur when allocation to root maintenance is low with the remaining allocation split relatively equally between new root growth and new leaf growth. The least frequent strategies leading to plant survival are those in which allocation to root maintenance is high (**Fig. 6b**).

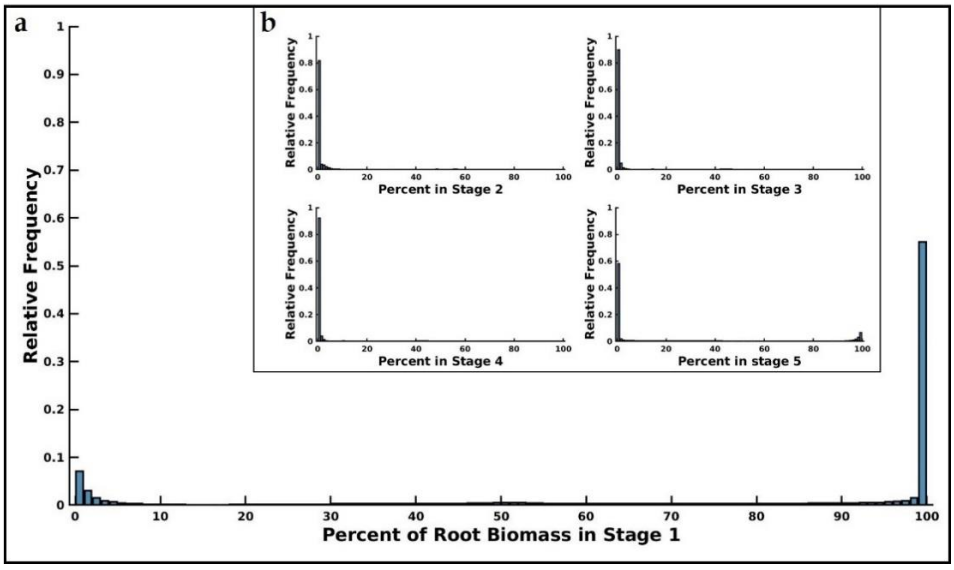

Figure 4: Relative Frequency of Root Stage Distributions.
The relative frequency of the percent of root biomass in Stage 1 (a) and Stages 2, 3, 4, and 5 (b). Bars represents an aggregate of plants within 1 percent span and an inclusive lower and exclusive upper bound; the last bar has an inclusive upper bound. Approximately 56 percent of all surviving plants had 99 percent or more biomass in Stage 1 (a). No surviving plants had more than 60 percent of root biomass in Stages 2, 3, or 4 respectively (b). Approximately 80 percent of surviving plants had less than 50 percent of their root biomass in Stage 5 (b).

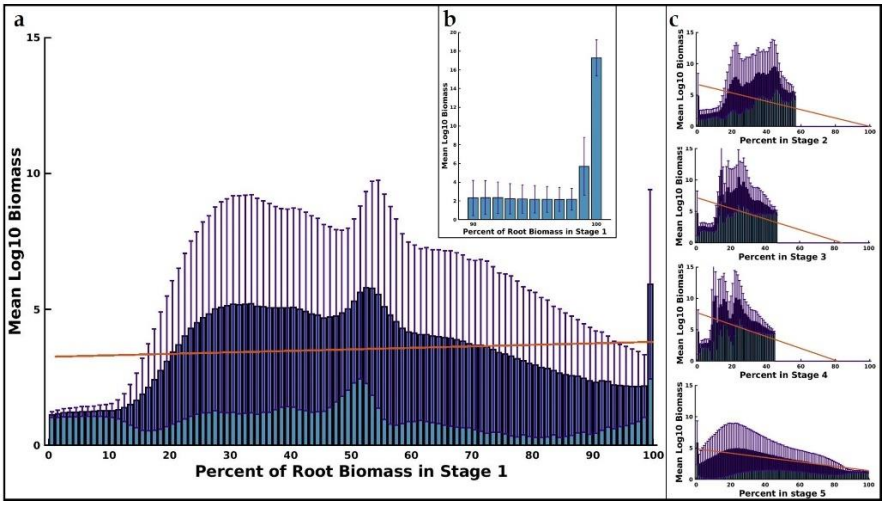

Figure 5: Relationship of Plant Biomass and Root Stage Distribution.
Mean Log10 plant biomass response to the percent of root biomass in Stage 1 (a, b) and Stages 2, 3, 4, and 5 (c) for surviving plants with 1 standard deviation error bars. Teal bars represent mean Log10 plant biomass within a 1 percent span and an inclusive lower and exclusive upper bound; the last bar has an inclusive upper bound (a, c). An exclusive upper bound for the percent of root biomass in Stage 1 adds an additional bar representing those plants with 100 percent of root biomass in Stage 1 (b). The percent of root biomass in Stage 1 is positively correlated to plant biomass (a) and plants with 100 percent of root biomass in Stage 1 have the largest mean Log¬10 plant biomass (b). The percent of root biomass in Stages 2, 3, 4, and 5 are negatively correlated with plant biomass (c).

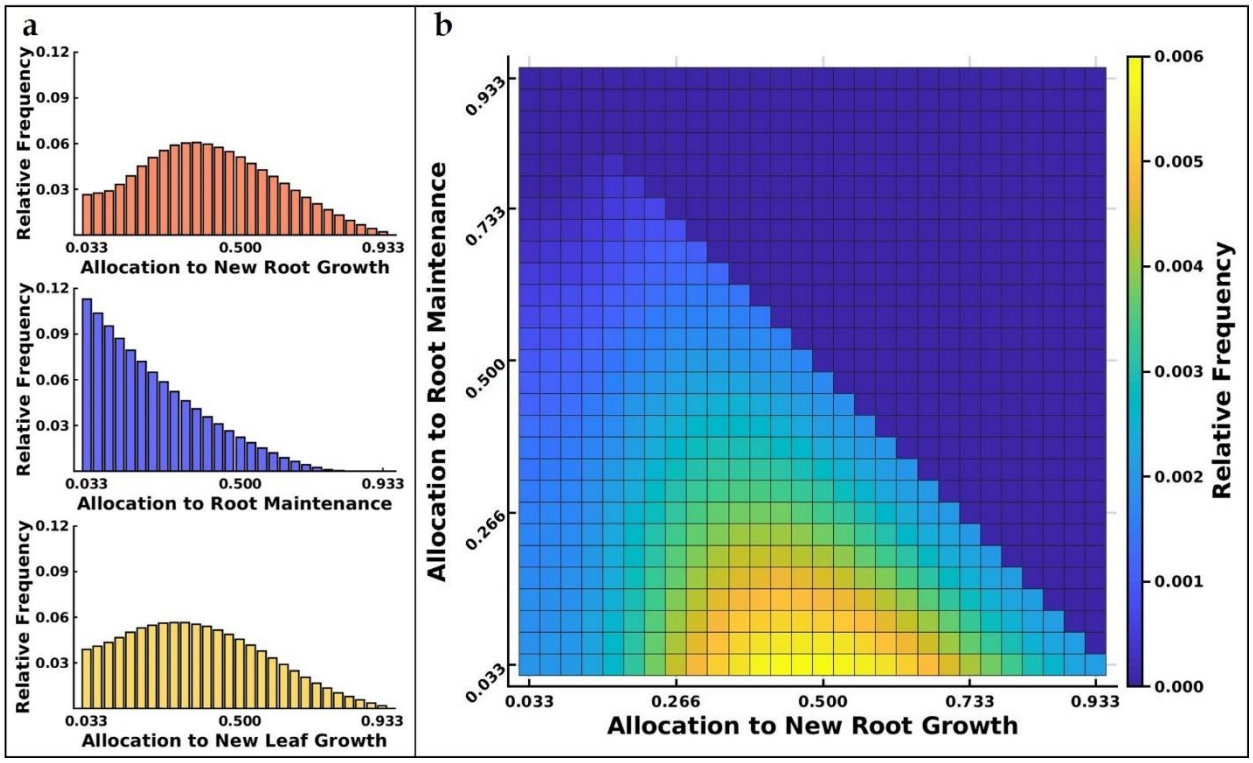

Figure 6: Frequency of Allocation Strategy.

The relative frequency of the proportion of photosynthate allocated to each allocation component, new root growth, root maintenance, and new leaf growth (a), and the allocation strategy employed (b) for the surviving plants. The most frequent proportion allocated to each component occurs at 0.366^{-}, 0.033^{-}, and 0.333^{-} respectively (a). The most frequent allocation strategies have a low proportion allocated to root maintenance and relatively equal proportion allocated to new root growth and new leaf growth (b).

Effects of Allocation Strategy. The proportion of photosynthate allocated to new root growth that leads to the largest plant biomass is centered around 0.400 with a gradual decrease in plant biomass as the proportion allocated increase and decreases. The best fit quadratic equation is $\log_{10} y = -21.46x^2 + 21.20x + 0.35$ and has a maximum at a proportion of 0.494. The proportion of photosynthate allocated to root maintenance that leads to the largest plant biomass is $0.03\overline{3}$ and plant size decreases as the proportion allocated increases. The best fit quadratic equation is $\log_{10} y = -1.06x^2 - 4.84x + 5.76$ and has no maximum within the bounds. The proportion of photosynthate allocated to new leaf growth leading to the largest plant biomass is centered around $0.43\overline{3}$ with a gradual decrease in plant biomass as the proportion allocated increases or decreases. The best fit quadratic equation is $\log_{10} y = -22.17x^2 - 19.22x + 1.41$ and has a maximum at a proportion of 0.434 (**Fig. 7a**).

The allocation strategies producing the largest plants are associated with a low proportion of photosynthate allocated to root maintenance and the remaining proportion split relatively evenly between new root growth and new leaf growth. Plant biomass decreases with allocation strategies heavily skewed towards or away from new root growth or new leaf growth though strategies heavily skewed towards new root growth produce larger plants than one heavily skewed away from new root growth. Plant biomass increases with allocation strategies that are skewed away from root maintenance (**Fig. 7b**).

Regression Tree Analysis. Regression tree analysis indicates the parameters with the largest impact on plant size are those associated with photosynthate production and the proportion of photosynthate allocated to new leaf growth. The strongest predictor of plant size is the multiplicative constant on photosynthate production, $\boldsymbol{\alpha}$, with larger values increasing the amount of photosynthate produced. The other main predictors of plant size are allocation to new root growth, and the effect of acquired soil resources on photosynthate production, $\boldsymbol{\beta}$, with smaller numbers reducing the amount of photosynthate produced (**Fig. 8**).

Discussion

The model results demonstrate how root stage distribution impacts plant size, the proxy used for overall plant success. Plant size is positively correlated with the proportion of root biomass in the earliest stage and negatively correlated with the proportion of biomass in all other

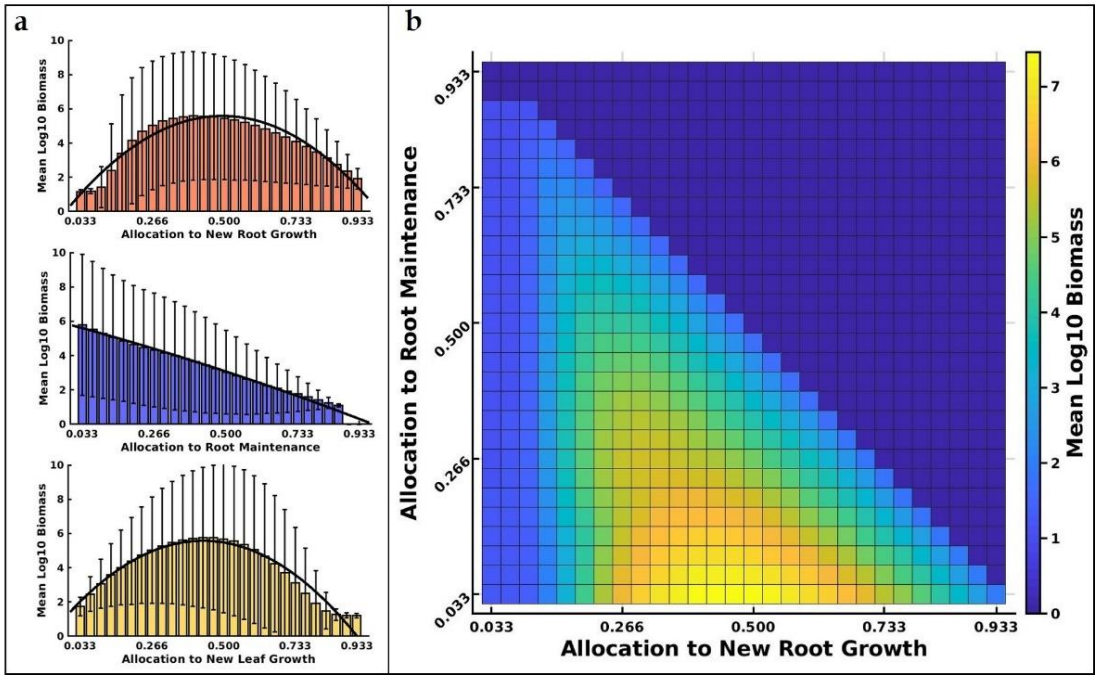

Figure 7: Relationship of Plant Biomass and Allocation Strategy.

Mean Log10 plant biomass response to the proportion of photosynthate allocated to each individual component, new root growth, root maintenance, and new leaf growth with 1 standard deviation error bars (a), and to the allocation strategy employed (b) by the surviving plants. The best fit quadratic equations (black curves) for new root growth and new leaf growth have maximums at approximately 0.49 and 0.43 respectively and the maximum for root maintenance is beyond the bounds (a). The largest plants are associated with low allocation to root maintenance and relatively equal allocation to new root growth and new leaf growth (b).

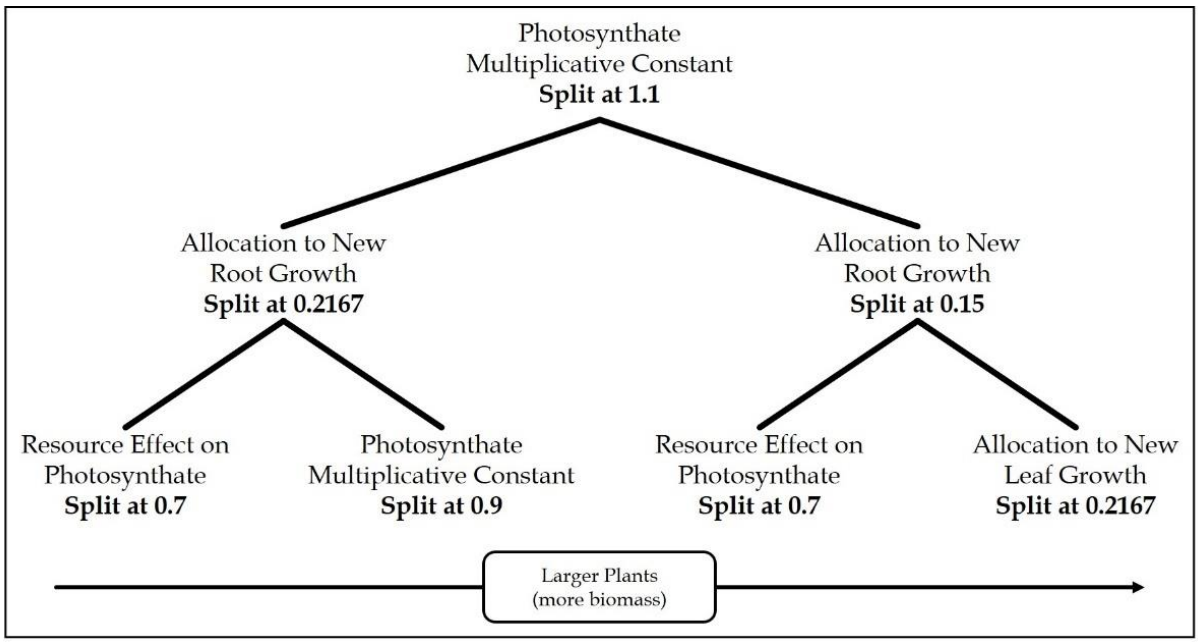

Figure 8: Regression Tree Analysis.
Regression tree analysis of all parameters for surviving plants. The multiplicative constant on photosynthate production, allocation to new root growth, and the importance of acquired resources on photosynthate production are strong predictors of surviving plant biomass.

stages (**Fig. 5**). Furthermore, the results indicate that of the surviving plants, a majority had a root stage distribution with more than 99 percent of root biomass in Stage 1 (**Fig. 4**). Thus, the model suggests only the earliest root stage is important for plant growth. This contrasts to field experiments and observations which indicate a majority of root biomass is not fine root biomass (Hendrick & Pregitzer, 1992; Vogt *et al.*, 1995; Helmisaari *et al*., 2002; Claus & George, 2005). The model developed here provides a means to determine the underlying mechanism that encourages plant growth when a majority of root biomass is in Stage 1.

The model results regarding high amounts of root biomass in the earliest stage roots can be explained by the importance of allocation strategy on plant growth. The allocation strategy describes the proportion of photosynthate allocated to each of the three components, new root growth, root maintenance, and new leaf growth. Strategies too heavily favoring any of the three allocation components produced small plants or those that did not survive. It would be expected that strategies with very little allocation to any of the three allocation components would likewise produce small plants. However, the largest plants are associated with strategies for which allocation to root maintenance is almost at a minimum and allocation to root growth and leaf growth are generally equal. Furthermore, the best fit quadratic equation for allocation to root maintenance has a maximum proportion of less than zero suggesting root maintenance does not confer a benefit for the plant and allocation to maintenance can even be disadvantageous for the plant. The model structure and assumptions lead to the implication that plants derive no benefit from maintaining a developed root system.

The extremely low allocation to root maintenance indicates most of the surviving plants had nearly complete root turnover every growth season. A low proportion of photosynthate to root maintenance results in the photosynthate cost of maintaining root biomass not being met. If the cost of maintaining roots is not met, the transition rate for root biomass moving between stages is decreased and most of the root biomass senesces instead of transitioning. Consequently, a low allocation to root maintenance results in root stage distributions that cannot maintain later stage root biomass because so little root biomass transitions to the later stages.

It may seem detrimental for the plant to have nearly its entire root system turnover every season, but the model assumptions allow the plant to still produce new root biomass in the following season. Photosynthate is stored between seasons and it is only the previous season's

photosynthate that determines the amount of new root growth. Having no root biomass at the end of a season does not constrain the ability of the plant to produce new root biomass in the coming season. Since all new root growth always starts as the earliest stage biomass, a plant's root stage distribution becomes skewed towards the earliest stage. This explains the model result of a highly skewed root stage distribution but does not indicate how the model assumptions lead to the lack of necessity for the plant to maintain later stage roots.

The model makes the common assumption that the only functions of roots are to acquire water and nutrients, collectively called resources in the model, and thus the only benefit a plant gains from its root biomass is the acquisition of resources. The cost associated with maintaining root biomass produces a cost/benefit ratio for each root stage. Although the earliest roots have the highest resource acquisition rate, they also have the highest cost and, depending on the exact stage to function relationship, its cost/benefit ratio could be higher than other stages. However, the ratio for each root stage is irrelevant in this model, because the plant incurs no growth penalty for not paying the cost of maintaining root biomass. The plant can still produce new biomass without any other root stage biomass present. With effectively no cost, the cost/benefit ratio instead becomes a measure of benefit and the stage with the highest benefit is the driving factor in the model. Thus, the earliest stage roots, the stage with the highest resource acquisition rate, is the most important driver of plant growth. Similarly, there is no advantage for the plant to maintain later root stages because all other stages have a lower resource acquisition rate. The assumption has the consequence of making the earliest stage the most important, but also making all other root stages completely irrelevant.

Our main model result provides novel insight about root demographic and its impact on plant allocation strategies because it suggests only including the function of resource acquisition for roots is not sufficient to realistically simulate a developed root system. Furthermore, it suggests that models which only consider fine roots of an entire root system, for which Stage 1 root biomass is representative, do not accurately simulate the growth and ageing dynamics of a root system. Consequently, modeling roots through the singular function of resource acquisition or assuming only fine roots matter ignores the impact of a majority of root biomass on plant growth and the associated root system dynamics.

Modelling roots in such a manner is common practice among many individual and community level plant soil feedback models. For example, Farrior *et al.* (2013) developed a model to predict the dominant plant allocation strategy but only simulated the root system as fine roots and their function was resource acquisition. It is not clear from their model whether, if other root functions were included, the dominant allocation strategy would change. Similarly, addition of other types of roots could lead to very different allocation conclusions. These issues arise in the many other plant growth models discussed in the introduction for which the implications of ignoring additional root functions and root heterogeneity on model allocation results are expected to be considerable.

The model results indicate that to account for observed developed root systems, models should include additional roles for roots beyond resource acquisition and ensure later stage root biomass continues to provide a benefit for the plant. McCormack *et al*. (2015) demonstrate that classifying roots into mainly resource acquisition or transportive can improve our understanding of many root processes. Consequently, transport capacity is a natural function to include. The additional role for roots could ensure later stages continue to provide a benefit as later stage roots – older, thicker, higher branch order, etc. – often have more transport capacity than earlier stage roots (Guo *et al.*, 2008b; Kong *et al.*, 2010). Another assumption that could more realistically simulate observed root systems could be to include a heterogeneous resource environment. The model assumed roots had continued and unrestricted access to resources, but foraging strategy is known to influence fine root demographics (Paula & Pausas, 2011; Li *et al.*, 2012). Consequently, resource foraging could favor plant allocation strategies that maintain a more developed root system. In combination, both a heterogeneous resource environment and a transportation role for roots could sure ensure there is an advantage for maintaining later stage root biomass and a disadvantage for not favoring a developed root system.

Incorporation of root stage distributions suggests root stage distribution does impact plant growth, with a heavily first stage skewed distribution being most beneficial. Similarly, allocation strategy impacts both root stage distribution and root growth with low allocation to root maintenance being favored. Under the model assumptions, early stage biomass is most important for plant growth. The model's early root stage favorability could be the result of the common single-function view of roots as only resource gatherers. This view increases the importance of

fine roots to the exclusion of all other later stages. Consequently, our results suggest models with resource acquisition as the sole function of roots or an exclusively fine-root perspective may lead to results that are not appropriately realistic to apply to whole-plant growth and be misleading regarding evolutionary implications of various growth strategies.

Chapter 3

Introduction

Roots are key mediators of plant-soil feedbacks (PSF) as roots interact with and affect both the soil environment and soil microbial communities (Kardol *et al.*, 2015). Roots are not homogeneous, and their impact on the soil environment and soil microbial communities may be, in part, dependent on their age, diameter, and branch order (Guo *et al.*, 2008b; Ceccon *et al.*, 2016). Many root traits are correlated with these classifications; 1) root respiration is negatively correlated with root age (Bouma *et al.*, 2001; Wells & Eissenstat, 2002; Volder *et al.*, 2005; Ceccon *et al.*, 2016) and diameter (Makita *et al.*, 2012); 2) nutrient uptake rate is negatively correlated with root age (Bouma *et al.*, 2001; Wells & Eissenstat, 2002; Volder *et al.*, 2005) and diameter (Pregitzer *et al.*, 1998); 3) root lifespan is positively correlated with branch order (Guo *et al.*, 2008a) and diameter (Wells & Eissenstat, 2001; Gill *et al.*, 2002; Joslin *et al.*, 2007) and; 4) mycorrhiza colonization rates are negatively correlated with branch order (Guo *et al.*, 2008b). Consequently, the heterogeneity of traits among roots of different sizes, ages, and branch orders indicates the function of roots is likewise heterogeneous.

Many individual and community level PSF theoretical models tend to ignore the heterogeneity among both root traits and functions, opting instead to incorporate roots through functions that affect plant processes, most often nutrient and/or water acquisition or, if the model plant is disaggregated, as a single homogeneous component (Bever *et al.*, 1997; Rastetter *et al.*, 2001; Levine *et al.*, 2006; Meyer *et al.*, 2009; Farrior *et al.*, 2013; Jiang & DeAngelis, 2013; Ke *et al.*, 2015). Consequently, models may be ignoring a key aspect of below-ground dynamics by not including the heterogeneity of root traits, their functions, and subsequent impact on the abiotic and biotic conditions of the soil environment. However, incorporating roots with varying rates of transition between root sizes, maintenance cost, and rates of resource acquisition may not accurately simulate a developed root system The common individual and community level PSF model assumption that the function of roots is to acquire nutrients and water (we collectively refer to this as resource acquisition) may inadvertently favor fine roots because these roots are responsible for a majority of the acquired resources (Hendricks *et al.*, 1993). Incorporating additional root functions in models could enhance the realism of assumptions about function by ensuring that later stage roots continue to provide a benefit to the plant.

One additional root function that could be incorporated is transport capacity. It has been suggested that fine roots can be categorized into either mainly resource acquiring or transportive roots and doing so improves our understanding of root dynamics (McCormack *et al.*, 2016). Transport capability is often higher in later stage roots – thick, older, woody roots – than in earlier stage roots (Pregitzer, 2002; Guo *et al.*, 2008b; Valenzuele-Estrada, *et al.*, 2008; McCormack *et al.*, 2016). We suggest that incorporating resource acquisition and transport capacity as well as the varying tradeoffs between mainly resource acquiring and transport capable roots can ensure models are not favoring fine roots to the exclusion of all other roots, better capture root dynamics, and provide a more realistic means to assess the impact of roots on integrated whole plant function.

Under alternative spatial arrangements of resources, root systems display morphological and physiological plasticity (Hutching, & Kroon, 1994; Hodge, 2004; Hodge, 2006; Neatrour *et al*., 2007). Consequently, the distribution of different root stages with different rates of resource acquisition and transport capacity and the subsequent long-term impact on whole-plant growth of the dynamics of root stage distribution may depend on resource heterogeneity and root foraging behavior. When encountering regions of high resource availability, many root systems often proliferate into the region, elongating individual roots (Leyser & Fitter, 1998; Zhang *et al.*, 1999), and/or increasing the production of new roots (Pregitzer *et al.*, 1993; Hodge *et al.*, 2000; Hodge, 2004). While proliferation into a region of high availability may confer an initial benefit, this benefit could be outweighed by costs of root maintenance and senescence after patch depletion and the overproduction of roots in those high availability patches (Fransen & De Kroon, 2002). Accurately assessing the distribution of roots in different functional stages and the long-term impact of abiotic factors on this distribution is experimentally and observationally difficult (Pregitzer, 2002; Pierret *et al.*, 2016; Ryan *et al.*, 2016). Due to this difficulty, models that account for root heterogeneity provide a means to compare and assess alternative hypotheses for the detailed impact of roots on plant-soil feedback.

Our objective is to analyze the impact of incorporating two root functions (resource acquisition and transport capacity) on root stage distributions, root growth, and root dynamics in a simulated plant and the impact of resource heterogeneity on root stage distributions and the subsequent long-term impact on whole-plant growth, to address these challenges, we developed a

stage-based root population model with feedbacks between root resource acquisition, above-ground photosynthetic production and subsequent root production and turnover. The model simulates a single woody perennial over its entire lifetime with each time step representing one growing season. The simulated plant is separated into an above-ground photosynthetic capable component (ABG) and a below-ground component (roots). Resources acquired and transported by the roots are used by ABG biomass and the resulting photosynthate is then allocated to root growth, root expansion, root maintenance, and ABG growth.

Root biomass is separated into distinct consecutive stages with each root stage having its own transport capacity, resource acquisition rate, transition rate (turnover), and maintenance cost. Acquisition rate and maintenance are assumed to be relatively higher for early stage roots, and turnover and transport capacity are assumed to be higher for later stage roots. Roots expand into a 2-dimensional soil space composed of individual cells with each soil environment cell having its own resource availability. As the plant grows, root biomass expands into neighboring cells, producing a root network through which acquired resources will be transported from the roots to the ABG biomass and photosynthate will be transported from the ABG biomass to the roots. Our model is useful to 1) examine the impact of incorporating two root functions on root stage distribution and plant root growth; 2) examine the effects of root stage distribution on overall resource uptake and root growth; 3) identify the impacts of alternative resource availability patterns on root stage distribution and the associated effect on root growth; and 4) build linkages between individual plant characteristics and below-ground ecosystem processes. The model we develop is the first to incorporate general properties of root heterogeneity as it impacts these various aspects of plant processes. Although there have been very detailed below-ground models for specific root systems, particularly in an agricultural context (Drouet & Pages, 2003; King *et al.*, 2003; Yang *et al.*, 2004; Bigham & Wu, 2011; Garré *et al.*, 202) these lack the generality needed to investigate key questions about plant-soil feedbacks.

Methods

The model description format follows the Overview, Design Concepts and Details (ODD) Protocol developed and updated by Grimm and colleagues (2010). This protocol is effective in enhancing the reproducibility of models, their simulation, and their analysis, a key concern in current science (Stodden *et al.*, 2014).

MODEL OBJECTIVE

This model explores the effects of different root stage distributions on the above and below ground growth of a perennial woody plant over its lifetime. One objective is to determine the effects of incorporating, resource acquisition and transport capacity on the root-stage distribution, whole-plant growth, and alternative allocation strategies. Another objective is to assess the impact of alternative spatial patterns of soil resource availability on the long term spatial and temporal behavior of root stage distributions and whole-plant growth.

PLANT COMPONENTS

Plant

A simulated plant is composed of above-ground photosynthetic capable biomass, leaves, stems, and supporting structure (called ABG for above-ground biomass) and below-ground soil resource acquiring and transport capable biomass (roots). The plant exists in a 2-dimensional soil environment within which root biomass can grow and expand producing a root network. This biomass of the root network acquires a single soil resource, representing necessary nutrients and water, arrayed heterogeneously throughout the soil environment and transports the acquired resource to the ABG biomass. ABG biomass uses the transported resource to produce photosynthate which is allocated to each component to produce new ABG biomass, new root biomass, expand the root network, and maintain some of the current root biomass. Plants maintain an allocation strategy wherein some proportion of photosynthate is allocated to new root growth, root expansion into the soil environment, root maintenance, and new ABG growth. ABG biomass is represented by a single stage whereas roots are separated into distinct consecutive stages with each stage having a different cost/benefit ratio and initial transition rate to the next stage. Such a component-based approach to whole plant growth has been applied in many contexts (De Reffye *et al.*, 1997; McGraw, 1983; Prusinkiewicz, 1998), though our emphasis is on considering heterogeneity in roots.

Above-ground component (ABG)

The above-ground biomass, leaves, stems, and supporting structure (ABG) converts acquired and transported resource into photosynthate which is then used by the plant to produce

additional ABG and root biomass and maintain a proportion of the current root biomass. ABG biomass is composed of a single stage. The benefit produced by ABG biomass is its photosynthetic capability. The model assumes the cost associated with ABG biomass maintenance is implicit in the amount of photosynthate produced per unit of ABG biomass. If maintenance cost was explicitly included, the amount of photosynthate produced per unit of ABG biomass would increase, but then effectively decrease once the maintenance cost is considered. New ABG biomass production is dependent on the proportion of photosynthesis produced in the previous step allocated to new ABG growth.

Below-ground component

The below-ground biomass (roots) acquire the soil resource, transport the acquired resource to ABG biomass and, transport photosynthate from ABG biomass to the roots. Root biomass (R) is separated into distinct consecutive stages (there are 5 stages denoted with i) with young, thin, fine roots representing early stage roots and old, thick, coarse roots representing later stage roots. Root biomass exists in a 2D soil space composed of cells with each cell having its own root-stage distribution and within which root biomass can expand. There is a limit on the total root biomass allowable in each spatial cell. As root biomass expands into the soil space, more cells become occupied with root biomass and this collection of root-occupied cells produces a root network through which the acquired resource and photosynthate are transported.

Each root stage has its own soil resource acquisition rate (a_i), transport capacity (ρ_i), photosynthate maintenance cost (c_i), and initial transition rate (θ_i) (Figure 9). Soil resource acquisition rate is the amount of a soil resource a unit of biomass in each root stage can acquire in a time step and is high for early stage roots and decreases as root stage increases (though this rate is modified by resource availability). Transport capacity is the amount of the soil resource or photosynthate a unit of biomass in each stage can transport and is low for early stage roots and increases as root stage increases. Photosynthate maintenance cost is the per unit biomass photosynthate cost of maintaining the initial transition rate for each stage and is high for early stages and decreases as the root stage increases. The initial transition rate gives the fraction of root biomass in a stage that will transition to the next consecutive stage during each time step and is low for early stages and increases as root stage increases. The transition rate includes the

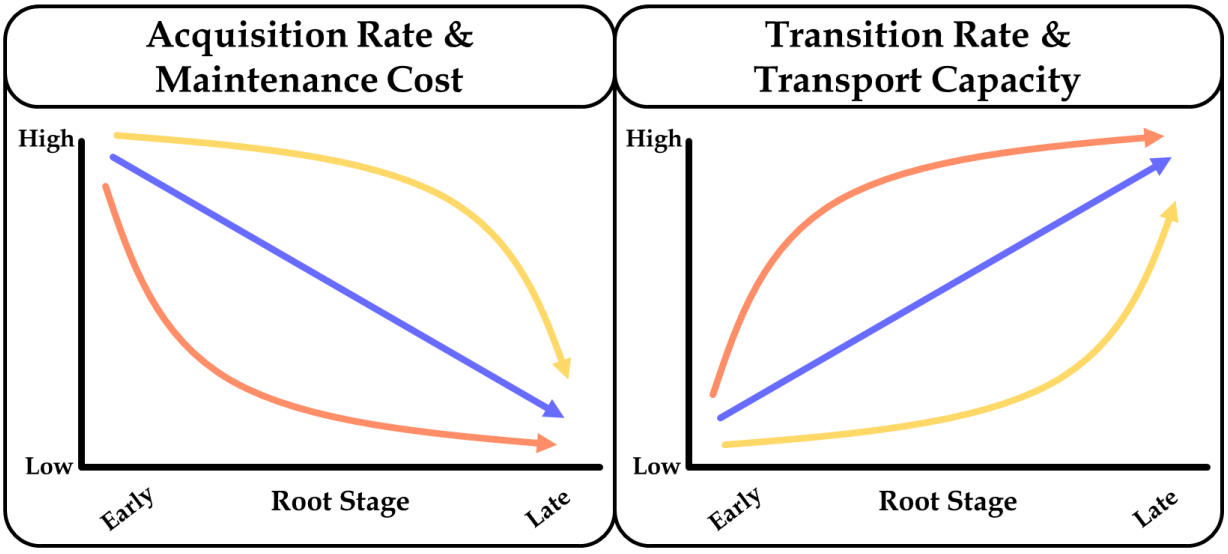

Figure 9. The qualitative relationship between root stage and function
Resource acquisition rate, maintenance cost, initial transition rate, and transport capacity vary across root stage. The exact relationship may be variable, but the qualitative relationship is the same for each root cost/benefit function.

turnover rate of each root stage, as the biomass that does not transition senesces; in this view early stage roots have a high turnover rate and later stage roots have a low turnover rate. The transition rate is modified by the amount of photosynthate allocated to maintenance a root stage receives. Together these four functions of resource acquisition rate, transport capacity, photosynthate maintenance cost, initial transition rate characterize the cost/benefit ratio of each root stage.

ENVIRONMENT

The soil environment consists of a 2-dimensional spatial grid within which the plant's roots can grow and expand. Each cell has a finite amount of space and is characterized by the amount of the single soil resource available and whether the cell is currently occupied by root biomass. A cell occupied by root biomass, a root-occupied cell, is also characterized by the amount of root biomass in each stage and the direction and number of root-occupied cells it is connected to. Adjacency between cells is determined by the Von Neuman Neighbourhood (up, down, left, and right). The connections between root-occupied cells creates a network that is used during the transport of acquired resources from the roots to ABG biomass and of photosynthate from ABG biomass to the roots. A root network can only expand by one cell leftwards, rightwards, or downward at each time step and so the maximum width and depth of the soil environment is constrained by the number of time steps. The root network can expand into a cell that is above a currently occupied cell, but because the central root cell is at the shallowest row in the soil environment, the entire root network cannot expand any further upwards. The width of the modeled soil environment is twice the number of time steps plus the width of the initial root network, and the depth is the number of time steps plus the depth of the initial root network. Furthermore, certain cells are beyond the expansion range of the root network given the constraints on adjacency and the number of time steps and so are not tracked (Figure 10).

The resource availability in each cell alters the total amount of the resource a root-occupied cell can acquire. The amount of the resource available in a cell constrains the amount that is actually available to the root biomass. The root-available amount of the resource is given by Eq. 3 where a_i is the acquisition rate of the soil-resource for root stage i and ψ_λ is the

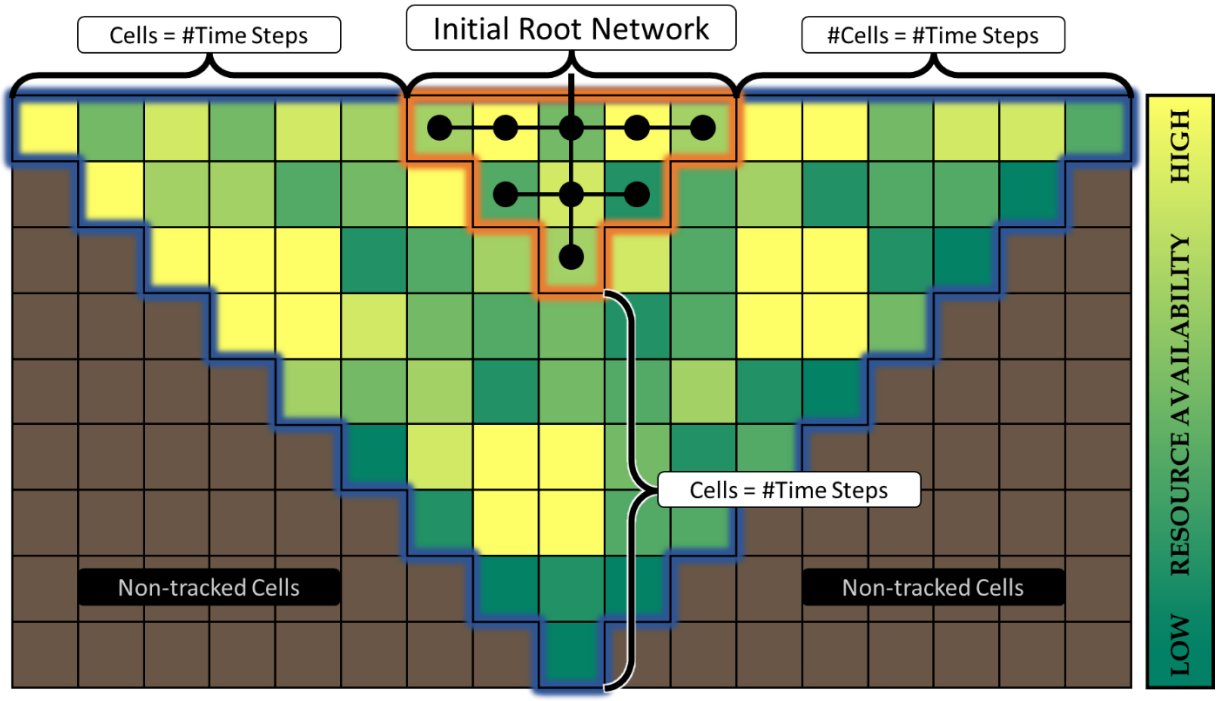

Figure 10. Soil Environment

The soil environment with heat map soil-resource availability (green - yellow) and the initial root network indicated by the orange highlighted cells. Although the environment is a 2-D grid, only a certain portion of the grid is tracked (highlighted in blue) given the expansion and time step constraints of the model.

availability of the resource in root-occupied cell λ and is always less than the actual amount of the resource in a cell.

$$\Psi_\lambda = \frac{\max(a_i) \times \psi_\lambda}{\max(a_i) + \psi_\lambda} \quad \text{Eq. 3}$$

Resource acquisition by a root-occupied cells is the minimum of its acquisition rate and root-available amount. There is no response of resource availability change due to resource acquisition by a root-occupied cell. The pattern of resource availability is established during model initialization and remains the same throughout the simulation.

A simulation is initialized with nine root-occupied cells and the corresponding network connecting them (see initialization for more information). This initial root network is centered on one cell, the central root cell, that is the connection between the entire root network and the above-ground component of the plant. The transport of the resource and photosynthate between ABG biomass must flow through this central root cell and so, any root-occupied cell that is not connected to the central root cell via the root network will completely senesce. As a simulation progresses and the plant grows, root-occupied cells will initially start connected to the root network and therefore to the central root cell.

GROWTH, EXPANSION, AND AGEING

As a simulation progresses, the plant can grow new biomass, expand the root network into unoccupied cells, and will have some of its existing biomass age and senesce. The processes involved in this are dependent on the photosynthate produced by the plant and the allocation strategy of the plant. This dependency creates a feedback whereby roots acquire resources which are used by ABG biomass to produce photosynthate which is then allocated to the growth and ageing processes. This allocation can in turn alter the amount of root and ABG biomass which can alter the amount of photosynthate produced.

Photosynthate Production

Photosynthate production is determined by a rectangular hyperbola using current ABG biomass and amount of each soil resource the central stem of the plant received. The amount of photosynthate, P_t, produced during time step t with ABG biomass, L_t, amount of resource transported to ABG biomass, Ω_t, and parameters α, β, and γ is given by Eq. 4.

$$P_t = \frac{\alpha L_t \Omega_t}{\beta L_t + \gamma \Omega_t} \quad \text{Eq. 4}$$

The parameter α increases or decreases the photosynthate produced while β and γ alter the importance of current ABG biomass and the soil resource respectively.

Allocation Strategy

The plant allocates photosynthate to four components: new ABG growth, new root growth, root expansion, and root maintenance. The proportion of photosynthate allocated to each component, the plant's allocation strategy, is established during initialization and remains the same throughout the simulation. New ABG growth, new root growth, and root expansion add new biomass to the plant with the former adding new ABG biomass, and the latter two adding new root biomass. In contrast, root maintenance determines the amount of root biomass the plant maintains between steps by altering each root stage's transition rate. Only root maintenance uses photosynthate during the time step it was produced, while new ABG growth, new root growth, and root expansion use photosynthate stored from the previous season.

Relative Importance

The relative importance of cells is used when determining the amount of photosynthate each cell is intended to receive during new root growth, root network expansion, and root maintenance. Each cell's relative importance is determined by summing the importance criteria, of the current allocation strategy component, for each cell and then dividing by the total sum across all cells in consideration. For new root growth the importance criteria calculated for each of the root-occupied cells are: 1) the amount resources acquired in the previous step, 2) soil resource availability and, 3) the remaining available space. For root network expansion, the importance criterion calculated for each unoccupied cell immediately adjacent to a root-occupied cell is: 1) soil resource availability. For root maintenance the importance criteria calculated for each of the root-occupied cells are: 1) the amount resources acquired in the previous step, 2) amount of resource lost during transport, 3) amount of photosynthate lost during transport, and 4) and the total maintenance cost of the root biomass in the cell.

Root allocation components

New root growth and root expansion add stage 1 root biomass and root maintenance cost alters the proportion of biomass that transitions from one stage to the next (and therefore the proportion that remains between time steps). The relative importance of each cell under consideration is used to determine the amount of photosynthate each cell intended to receive. Photosynthate is then transported from the ABG biomass to the root-occupied cells via the root network and stage 1 root biomass is grown or transition rate is updated.

For root maintenance, once a cell receives photosynthate, it is partitioned to each root stage based on the maintenance cost of that stage. The updated transition rate, $\Theta_{t,\lambda,i}$, during time step t in root occupied cell λ for root stage i is determined by a logistic equation (Eq. 5) with the stage's initial turnover rate, θ_i, and the received amount of photosynthate, $M_{t,\lambda,i}$ and photosynthate maintenance cost $C_{t,\lambda,i}$. The functional form chosen for transition rate update, guarantees the following behaviour arises; 1) if a stage receives less photosynthate than its maintenance, the transition rate decreases, 2) if a stage receives the same photosynthate as its maintenance cost, the transition rate remains the same and, 3) if a stage receives more photosynthate than its maintenance cost, the transition rate increase.

$$\Theta_{t,\lambda,i} = \frac{1}{1 + e^{\ln\left(\frac{1-\theta_i}{\theta_i}\right) - \left(M_{t,\lambda,i} - C_{t,\lambda,i}\right)}} \quad \text{Eq. 5}$$

The new transition rate determines the percentage of root biomass in each stage that will transition to the consecutive stage. The transition rate for the last stage describes the percentage of biomass that will remain in the last stage. The biomass in each stage that does not transition, senesces and is lost from the root community.

TRANSPORT

A key function of roots is to transport resources acquired by root biomass and of photosynthate produced by ABG biomass. The transport of the resource acquired and photosynthate occurs within the root network with resource transport flowing from the roots to ABG biomass and photosynthate transport flowing from ABG biomass to the roots. Each root-occupied cell has a total transport capacity determined by the amount and stage distribution of root biomass in the cell. A cell's total transport capacity determines the absolute maximum

amount of a resource or photosynthate that can be transported through it. Any amount of resource or photosynthate that is transported through a root-occupied cell that is greater than a cell's total transport capacity is assumed lost (e.g. leached from the root network). Because all transport flows through the central root cell, it is possible to determine the absolute maximum amount of the resource that can be transported and the absolute maximum amount of photosynthate that can flow to the root network. The absolute maximum amount of the resource and photosynthate that can be transported is given by taking the maximum amount of cell space, ζ, and multiplying by the greatest transport capacity across all root stages

$$\rho_{max} = \zeta \cdot \max(\rho_i) \quad \text{Eq. 6}$$

The transport capacity, per unit of root biomass, is assumed to be the same for the soil-resource and photosynthate.

Soil Resource Transport

The transport of acquired soil resource begins from the farthest root-occupied cells (those with the longest path to the central root cell) and flows towards the central root cell. At the start of resource transport, all root-occupied cells that are equally farthest from the central root cell transport the amount of the current resource they acquired to their next closest neighbor in the root network. Upon receiving all neighbor's transported resources, the total transport capacity of the receiving root-occupied cells is applied. Any amount of resource over a root-occupied cells transport capacity is lost from the cell. After the transport capacity is applied, the receiving cells, as well as any other root-occupied cells that are the same distance from the central root cell, transport their acquired resources, and their received resources if applicable, to the next closest neighbor. As a result of this method of transport, the root-occupied cells at confluences between network branches simultaneously receive their neighbors transported resources. This process continues until reaching the central root cell and the resource is then transported to the ABG biomass.

Photosynthate Transport

Transport of photosynthate begins at ABG biomass and flows outward across the root network. Each root-occupied cell is intended to receive some amount of photosynthate. A root-occupied cell may receive less than its intended amount based on its location in the root network,

the total transport capacity of the root-occupied cells "upstream", and the total amount of photosynthate produced. Transport begins when photosynthate is moved to the central root cell which takes as much of its intended amount of photosynthate as possible. After taking its intended amount photosynthate (or as much as possible), the central root cell's transport capacity is applied with any amount over the capacity being lost. The remaining photosynthate is transported to the next root-occupied cell or cells. If a root-occupied cell is the confluence between branches in the root network, the amount of photosynthate transported to the root-occupied cells at the start of the branch is proportional to the sink strength of the intended amount of all root-occupied cells along each branch. Any root-occupied cell that receives photosynthate first takes as much of its intended amount of photosynthate as possible and then its transport capacity is applied. This process continues until all cells have received photosynthate or the amount being moved is reduced to zero.

ORDER OF EVENTS

The model time steps represent one growing season for the plant (assumed to represent one year for the woody plants under consideration). At the start of a time step (growing season) the plant uses photosynthate stored from the previous time step to produce new ABG biomass and new root biomass in already occupied cells. After new ABG and new root growth, the root network further expands into the soil space by occupying immediately adjacent unoccupied cells. Following this, all root-occupied cells acquire the soil resource which is in turn transported to the above-ground portion of the plant using the root network. Once the acquired resources are transported to ABG biomass, photosynthate is produced. This photosynthate is then allocated according to the plant's allocation strategy to new ABG growth, new root growth, root expansion, and root maintenance. The amount of photosynthate allocated to root maintenance is transported to the root-occupied cells at which point, the root biomass of all root-occupied cells transitions and senesces. The remaining photosynthate (allocated to new ABG, root growth, and root expansion) is stored for use in the following time step (growing season). This ends the growing season (Figure 11).

PATCHINESS METRIC

There are a variety of metrics used to quantify the patchiness of spatial patterns of resources, land use, plant coverage etc. on landscapes (Palmer. 2002; Herold *et al.*, 2003). These metrics are usually omnidirectional and viewing the landscape from any direction yields the same metric. Unfortunately, the spatial arrangement of soil resources in the soil environment within which plants grow and expand is not unidirectional; plant directional growth in the soil environment is constrained. Furthermore, the spatial arrangement of soil resources within two soil environments may have the same patchiness metric, but the distances between areas of high/low availability and initial root network may be different within the soil environments. Without accounting for directionality, the metrics would not distinguish between soil environments where high availability patches are far from or close to the initial root network which could have drastic impact on overall root and plant growth. Consequently, the standard metrics of patchiness cannot be used here.

A new patchiness metric was devised for use with this model that accounts for the direction of resource availability and how availability changes across the distance from the central root network. The novel patchiness metric produces two values, 1) the measure of patchiness; the linearity of resource availability and 2) the direction of change in resource availability as the distance from the initial root network increases. Soil environment patchiness ranges between 0 and 1 and soil environment "direction" has no boundaries. The qualitative description of each metric can be found in Table 2. More details about this metric can be found in the supplement.

PARAMETER SPACE SEARCH & EXPERIMENTS

A parameter space search was conducted to determine the impact of alterative plant allocation strategies, soil resource patchiness patterns, and root cost/benefit functions, on overall root growth and root stage distributions. The values used in the parameter space search can be found in table (Table 3). The set of values resulted in 450,000 simulations.

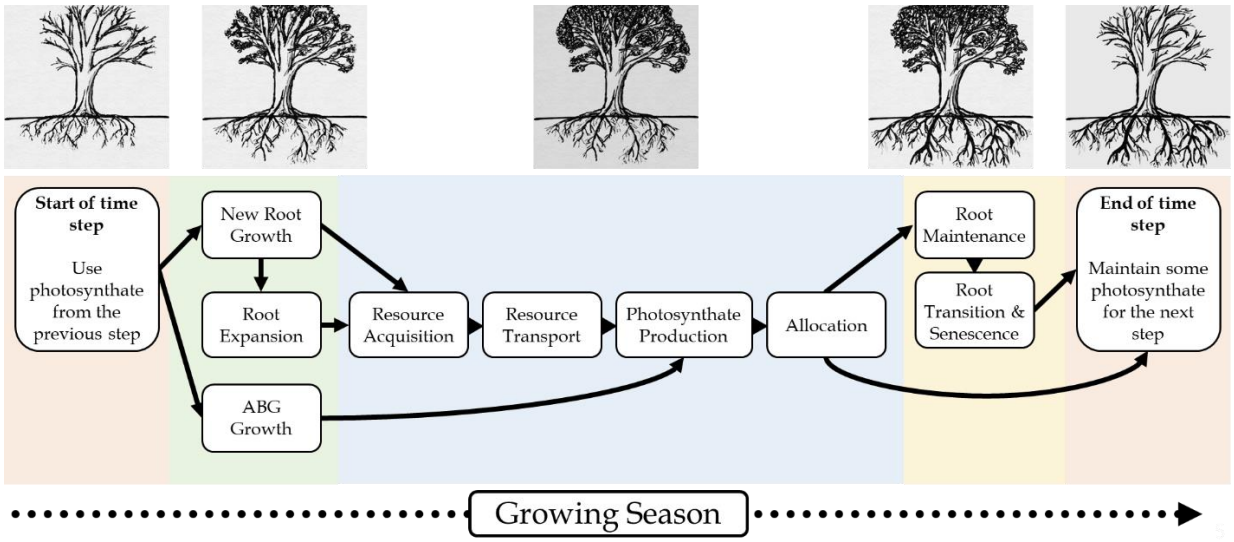

Figure 11. Order of Events
The order of events within a single time step. A time step represents one growing season and starts with new root growth, root network expansion, and ABG growth. After growth, resources are acquired by the roots and then transported to the ABG biomass via the root network. Once the ABG network receives the resources, photosynthate is produced and allocated to the four components. Photosynthate allocated to root maintenance is used to determine the proportion of root biomass in each stage in each root-occupied cell that will transition or senesce.

Table 2. Soil Environment Metrics.
Interpretation of values for patchiness metric and patchiness direction calculated for the soil environment.

Metric	Value	Description
R^2	$R^2 \approx 0$	On average, the availability of soil resources is not linearly uniform and is assumed to be more random
	$R^2 \approx 1$	On average, the availability of soil resources is linearly uniform
Slope	$m \ll 0$	On average, the availability of soil resources decreases with distance from the central root cell (more resources are close to the initial root network)
	$m \approx 0$	On average, the availability of soil resources does not change with distance from the central root cell
	$m \gg 0$	On average, the availability of soil resources increases with distance from the central root cell (more resources are far from the initial root network)

Table 3. Parameter Space Search Values

The parameter ranges and values used for each of the parameters explored within the parameter space search. The numbers correspond to the relative parameter importance estimates in Figure 16.

Model Component	#	Description	Range of Values	
			Min	Max
Root Cost/Benefit Ratio	**1**	Maximum per unit maintenance cost	5	10
	2	Maximum per unit biomass transport capacity	10	200
	3	The functional form of relationship between root stage and transport capacity	convex, linear, or concave	
Photosynthesis Production	**4**	Multiplicative constant of photosynthesis	1	10
	5	Importance of resources in photosynthesis	0.1	2
	6	Importance of ABG biomass in photosynthesis	0.1	2
ABG	**7**	ABG transition rate	0.5	1
Allocation	**8**	Proportion allocated to new root growth	0.02	0.94
	9	Proportion allocated to root expansion	0.02	0.94
	10	Proportion allocated to root maintenance	0.02	0.94
	11	Proportion allocated to new ABG growth	0.02	0.94
Soil Availability Pattern	**12**	Soil resource availability patchiness	0	1
	13	Soil resource availability “direction”	≈-900	≈1000

INTIALIZATION

Each simulated plant began with a root network composed of nine root occupied cells (Figure 10), each with one unit of biomass and nine units of above ground biomass. The biomass of the initial root network was distributed such that that $^2/_9$ of root biomass was in stages 1, 2, 3, and 4, and $^1/_9$ of root biomass was in stage 5. The soil environment within which the plant and its accompanying root network will grow used a predetermined soil resource availability pattern with a given patchiness and direction that remained static throughout a simulation. Each cell within the soil space has a maximum capacity of 100 units of root biomass.

The plant's allocation strategy, ABG turnover rate, and the relationships between root stage and resource acquisition rate, and initial transition rate, and transport capacity are all determined by the parameter set used for the simulation.

At the start of a simulation, the initial root and ABG biomass is used to determine the amount of photosynthate produced in the previous step because there was no previous step. This photosynthate is allocated according to the plant allocation strategy and is used to start the first growth phase of a simulation.

ANALYSIS

A parameter space search was conducted in MATLAB 2019a using computing clusters at the University of Tennessee, Knoxville Advanced Computing Facility to analyze the effects of different soil resource availability patterns and parameter sets on the model outcomes. The parameter space search consisted of 450,000 simulations wherein each simulation was run for 50-time steps after which the outputs at the end of a simulation was obtained. The parameter space search conducted using the ACF consisted of 300 jobs each with 1500 parameter sets using between 16 and 24 cores per job submission. Each job took on average approximately 23 hours to complete for a total of 6,900 computing hours.

Prior to this final parameter space search, 8 previous parameter space searches were conducted to narrow the range of values and eliminate parameters that had little to no effect on model outputs. Combined, these 6 initial parameter space searches contained approximately 4.5

million simulations each with a unique parameter set consisting of approximately 65,000 computing hours.

Of the 450,000 simulated plants produced in this parameter space search, approximately 263,000 of the plants had a final total biomass greater than their initial biomass; meaning that approximately 58 percent of simulations resulted in surviving plants. The outputs of each simulation were obtained by averaging the model outputs at the beginning and end of only the last time step. All analyses were conducted using these averaged outputs of the surviving plants using MATLAB 2020a.

Results

PLANT SUCCESS

For the purposes of this model, plant success is defined using two metrics: (i) total plant biomass in the last time step or (ii) root network size in the last time step. Last time step total plant biomass is positively correlated with last time step root biomass and is used as the metric of plant success in lieu of total plant biomass. However, there is no correlation of last time step total plant biomass with last time step root network size and thus we utilize last time step root network size is an alternative metric of plant success since it is not correlated with the first metric.

ROOT STAGE DISTRIBUTION

Of the surviving plants, none had more than 80% of root biomass in the first stage or had less than 25% of root biomass in the first stage. No surviving plant had more than 70% of root biomass in the last stage or had less than 5% of root biomass in the last stage. Of the surviving plants, the most frequent distribution (≈30% of plants) had a root stage distribution with 30-35% of root biomass in the first stage and 50-55% of root biomass in the last stage. The 3 most common root stage distributions, accounting for approximately 65% of surviving plants, maintained 30-40% of root biomass in the first stage and 45-55% of root biomass in the last stage (Figure 12a).

Overall, despite the generality of the model, there were an extremely narrow ranges of root stage distributions maintained by plants that produced the most root biomass or the largest

root network. On average, those plants that maintained root stage distributions outside of the narrow ranges produced much less biomass or much smaller root networks respectively. However, there are different constraints on the root stage distributions that were maintained by plants that produced the most root biomass compared to those plants that produced the largest root networks.

Plants the produced the most root biomass maintained a bimodal root stage distribution with nearly all root biomass balanced between the first and last stage, though the proportion in the last stage was slightly greater than the proportion in the first stage. On average, those plants that maintained a distribution of 40-45% of root biomass in the first stage and 45-50% of root biomass in the last stage produced the most root biomass. The 4 root stage distributions maintained by plants that produced the most root biomass had between 35-45% of root biomass in the first stage and 40-55% of root biomass in the last stage. Of the 4 root stage distributions maintained by plants with the least root biomass, 3 distributions had between 80-90% of root biomass in the first stage and 0-10% of root biomass in the last stage with the other having between 35-40% of root biomass in the first stage and 55-60% of root biomass (Figure 12b).

In contrast to the plants with the most root biomass, the plants with the largest root networks maintained heavily first stage skewed distributions. The plants with the largest root networks maintained a root stage distribution of 80-85% of root biomass in the first stage and 5-10% of root biomass in the last stage. The 4 root stage distributions maintained by plants that produced largest root networks had between 75-90% of root biomass in the first stage and 5-15% of their root biomass in the last stage. The plants that produced smallest root network maintained a root stage distribution of 25-30% of root biomass in the first stage and 30-35% of root biomass in the last stage. However, there was no similarities among root stage distributions maintained by plants that produced the smallest root networks. The root stage distributions maintained by plants with the smallest root networks were, from smallest to largest, 1) 25-30% and 30-35%, 2) 35-40% and 25-30%, 3) 25-30% and 65-70%, and 4) 50-55% and 35-40% in the first and last stages respectively (Figure 12c).

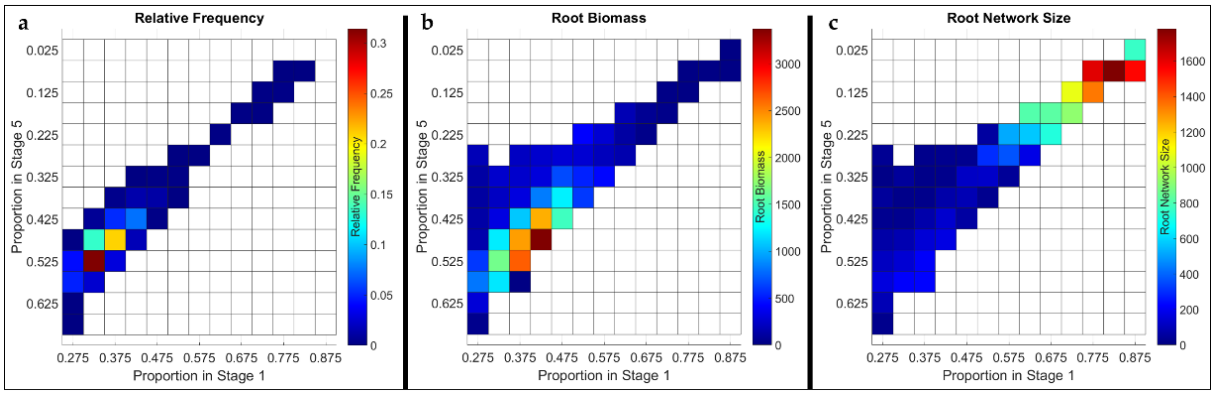

Figure 12. Root Stage Distributions

The relative frequency (a), the units of root biomass (b), and the size of the root network (c), of plants that maintained a given root stage distribution. For surviving plants, the proportion in the first and last stage accounted for a majority of root biomass and so the proportion in these two stages is considered representative of the distribution.

ALLOCATION STRATEGY

The most frequent allocation strategies of surviving plants had a relatively balanced allocation strategy. As allocation strategies became more skewed towards one component, the frequency of the strategy decreased. Similarly, as allocations became more skewed away from one component the frequency of allocations decreased. However, allocation strategies skewed. away from aboveground (ABG) growth remained relatively frequent compared to strategies that were skewed away from the other 3 components (Figure 13a). The allocation strategies used by plants that had the most root biomass slightly favored allocation to root maintenance with relatively balanced allocation to the other 3 components. The 4 allocation strategies used by plants that had the most root biomass allocated between 40-60% of photosynthate too root maintenance. Similarly, those 4 strategies had a balanced allocation to the other components. In contrast, those strategies used by plants that had the least root biomass were skewed away from root maintenance in favor of the other strategies. Similarly, plants with allocation strategies that too heavily favored root maintenance produced very little root biomass (Figure 13b).

The allocation strategies used by plants that produced the largest root networks were heavily skewed away from maintenance. The 4 allocation strategies used by plants with the largest root networks allocated between 0-40% of photosynthate to root maintenance. Furthermore, the allocation strategies used by plants with the largest root networks also favored new root growth or root expansion with the remaining photosynthate being allocated to ABG growth (Figure 13c).

Allocation strategies used by plants that maintained the highest proportion of root biomass in the first stage were heavily skewed away from maintenance. Furthermore, the strategies used by plants with the highest proportion of biomass in the first stage allocated photosynthate to new root growth and/or root expansion in lieu of the other 2 components (Figure 14a). In contrast, those strategies used by plants that maintained the highest proportion of root biomass in the last stage favored root maintenance and limited allocation to new root growth (Figure 14b). However, the variation in the proportion of root biomass the first and last stages for a given allocation strategy was limited with the proportion in the first stage ranges between 0.65-0.78 and the proportion in the last stage ranges between 0.07-0.17. Nevertheless,

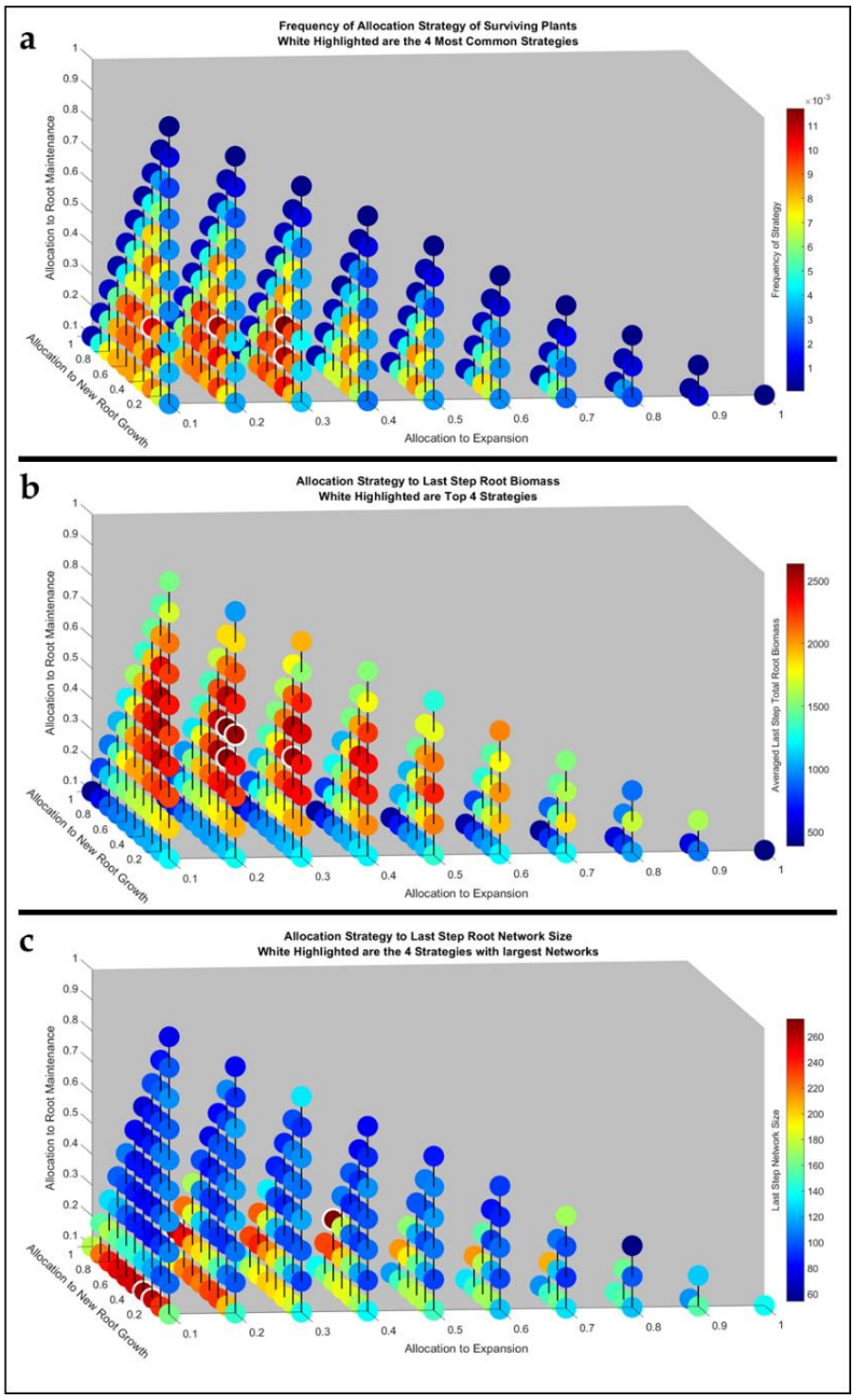

Figure 13. Allocation Strategy and Plant Growth

Allocation to 3 components with allocation to the fourth component found by subtracting allocation from 1. Note that due to the visualization and the discretization of allocation strategies, the sum allocated to all components may appear greater than 1. The frequency of allocation strategies of surviving plants (a), the allocation strategy used by plants that produced differing amounts of root biomass (b), and the allocation strategy used by plants that produced the different size root networks (c).

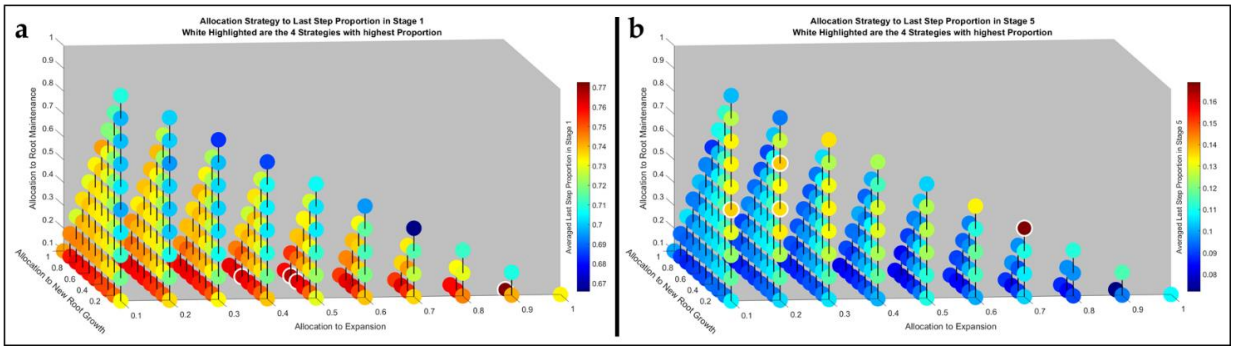

Figure 14. Allocation Strategy and Root Stage Distributions

Allocation to 3 components with allocation to the fourth component found by subtracting allocation from 1. Note that due to the visualization and the discretization of allocation strategies, the sum allocated to all components may appear greater than 1. Allocation strategies used by plants with varying proportions of root biomass in the first stage (a) and allocation strategies used by plants with varying proportions of root biomass in the last stage (b).

the ranges of proportion in the first and last stage indicate that a majority of root biomass was maintained in either of these two stages regardless of the strategy.

MAXIMUM TRANSPORT CAPACITY

Maximum transport capacity is positively correlated with root biomass and network size. There is no correlation between maximum transport capacity and the proportion of biomass in the first or last stage. However, when maximum transport capacity is extremely low, ANOVA analysis (available in the supplement) indicates there is a significant decrease in the proportion of biomass in the first stage and a significant increase in the proportion of biomass in the last stage compared to when maximum transport capacity is higher (Figure 15).

SOIL ENVIRONMENT PATCHINESS and DIRECTION

There is no correlation of soil environment patchiness or soil environment direction with root biomass, network size, nor root stage distribution.

PARAMETER IMPORTANCE ESTIMATION

Parameter importance estimation was conducted using the predictorImportance function (which estimates the predictor importance using an ensemble of decision trees) within MATLAB 2020a. For root biomass, root network size, proportion of biomass in the first stage, and proportion of biomass in the last stage, the most important parameter was maximum transport capacity with a relative importance of 0.47, 0.55, 0.39, and 0.26 respectively. The components of the allocation strategy, when individual relative importance is combined, are the second most important parameter, though allocation to maintenance is consistently higher than the other 3 components. Individually, allocation to maintenance is the second most important parameter for root biomass, size of root network, and proportion of biomass in the last stage, but is third for the proportion of biomass in the first stage. For the proportion of biomass in the first stage, the maximum maintenance cost is the second most important parameter. Of all components, soil environment patchiness ranked consistently low in relative importance and had no importance for proportion in the first or last stage. Similarly, soil environment direction is consistently

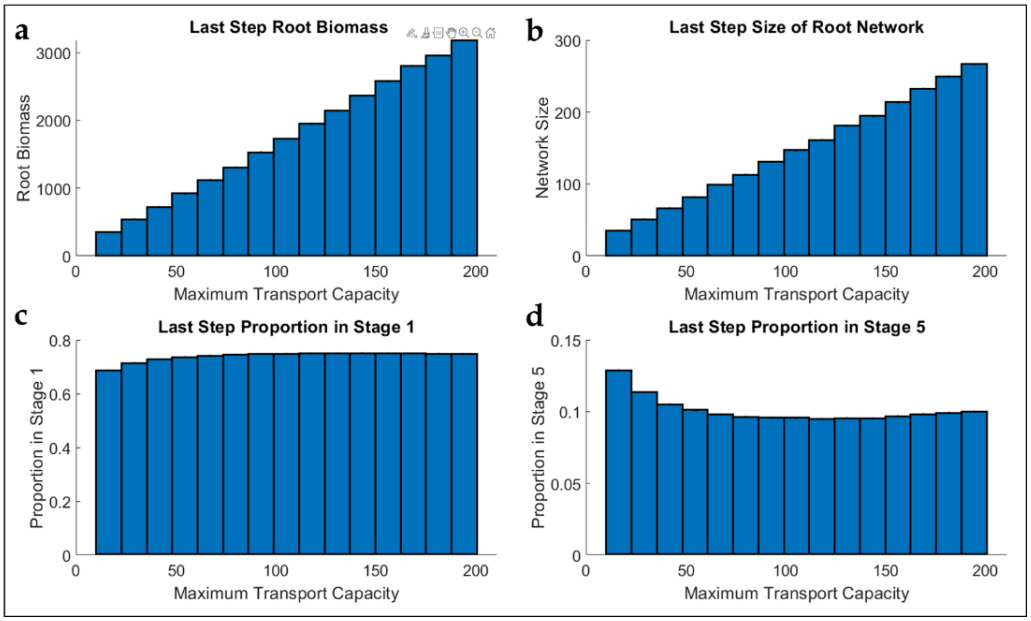

Figure 15. Impact of Maximum Transport Capacity
The relationship between maximum transport capacity (the upper bound of the relationship between root stage and capacity and the per unit transport capacity for the last stage) and root biomass (a), root network size (b), proportion of root biomass in the first stage (c), and proportion of root biomass in the last stage (d).

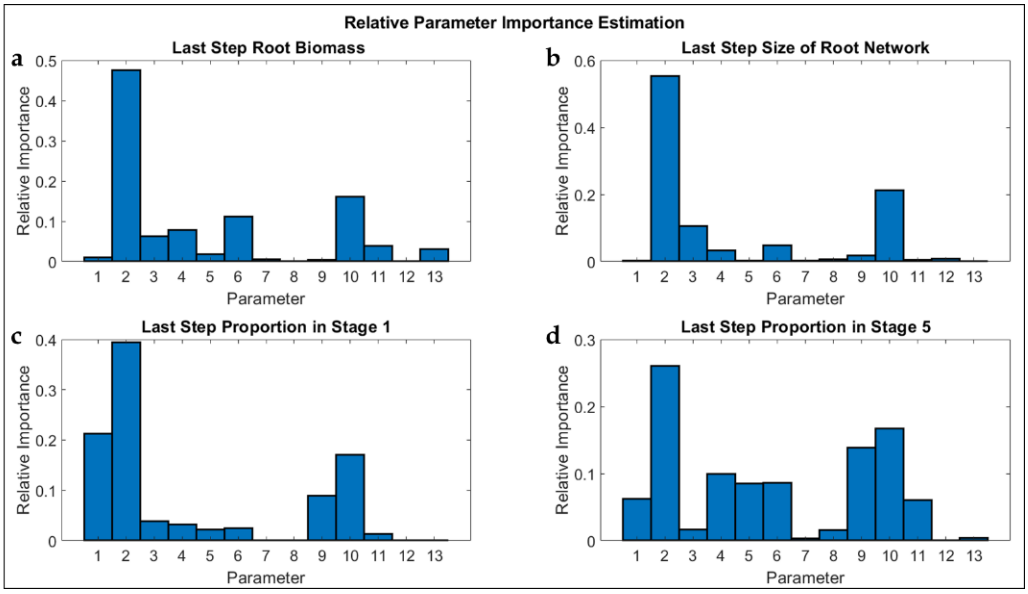

Figure 16. Parameter Importance Estimation
The relative importance of parameters for root biomass (a), root network size (b), proportion of biomass in the first stage (c) and proportion of biomass in the last stage (d). Parameter number 2 is the maximum transport capacity and parameter number 10 is the proportion of photosynthate allocated to root maintenance. The parameters associated with each number can be found in Table 3.

ranked as one of the least important parameters though it is always ranked above soil environment patchiness (Figure 16).

Discussion

The model results suggest root stage distribution impacts root biomass and root network size, our two proxies for plant success. Those plants that maintained less than 45 percent of their root biomass in the first stage and between 40 and 60 percent of biomass in the last stage had the most root biomass (Figure 12a). Similarly, of the surviving plants, the most frequent root stage distributions were skewed towards the last stage with the most common distribution having between 50-55 percent of root biomass contained in the last stage and 35-50 percent of root biomass contained in stage 1 (Figure 12b). These results are consistent with field experiments and observations which have indicated that a majority of root biomass is contained in later stage roots (Hendrick & Pregitzer, 1992; Vogt *et al.*, 1995; Helmisaari *et al.*, 2002; Claus & George, 2005). In contrast, plants that produced expansive root networks maintained root stage distributions that were heavily first-staged skewed. The plants with the largest root networks, maintained a large majority (70+ percent) of root biomass in the first stage and less than 15 percent of root biomass in the last stage (Figure 12c). The differences in root stage distributions maintained by plants that produced the most root biomass or largest root networks may indicate tradeoffs among root stages with certain stages being favored under alternative root growth patterns. Although root stage distribution may impact root biomass, survival, and root network size, the distribution maintained by plants could be a result of the allocation strategies that better supported root growth, survival, or root network expansion.

Within the model, allocation strategies are simulated by the proportion of photosynthate allocated to four components (new root growth, root expansion, root maintenance, and ABG growth). Any amount of photosynthate allocated to one component cannot be allocated to another and represents tradeoffs in the growing strategy of the simulated plants. The impact of these tradeoffs can be seen in the different strategies used by plants that survived, produced the most root biomass growth, grew the largest network, and maintained different root stage distributions (Figure 13). The most frequent strategy of the surviving plants was a relatively balanced allocation to each of the components (Figure 13a) whereas those plants that produced the most root biomass slightly favored root maintenance with a balanced allocation to the other

three components (Figure 13b). Those strategies used by plants with the largest root networks severely limited allocation to root maintenance and favored either new root growth or root expansion (Figure 13c). Allocation strategies used by plants that maintained the largest proportion of first stage biomass limited allocation to root maintenance (Figure 14a) whereas the strategies of plants with the largest proportion of last stage biomass favored maintenance increased maintenance (Figure 14b). These results are consistent with previous work that suggests allocation strategies are key drivers of plant success (Doust, 1989; Schaffer & Fox, 1989; Weiner, 2004) and indicate that tradeoffs in growing strategies produce plants with different growth patterns, and root stage distributions.

Although allocation strategies are key drivers, parameter importance estimation indicates that transport maximum is the largest driver plant performance and root stage distribution. Maximum transport capacity (the upper bound of the relationship between root stage and capacity and the per unit transport capacity for the last stage) was found to be the most important parameter for root biomass, root network size, and root stage distribution (Figure 16). Root biomass and root network are positively correlated with transport capacity (Figure 15a & b) most likely resulting from the increased ability of the root network to transport resources and photosynthate. However, maximum transport capacity is not correlated with the proportion of biomass in the first and last stage (Figure 15c & d). This suggests that although maximum transport capacity is important for plant success it does not alter the relative importance of each root stage within the simulated plant.

It has been suggested that soil resource heterogeneity may alter the relative importance of each root stage resulting from the morphological and physiological changes in root systems in response to soil heterogeneity (Hodge, 2006; Neatrour *et al*., 2007). The changes in root stage distributions are the result of variations in root foraging patterns and root production rates under alternative spatial arrangements of soil resources (Pregitzer *et al.*, 1993; Hodge *et al.*, 2000; Hodge, 2004). Contrary to previous work, the model results suggest there is no effect of soil environment patchiness nor soil environment direction (indicating how availability changes with increasing distance from the initial root network) on root biomass, network size, nor root stage distribution. However, this could be a result of the model assumption that the soil environment is static, and that resource availability does not respond to root resource acquisition.

The morphological and physiological changes in root systems in response to soil resource heterogeneity are not only a result of differences in resource availability in space, but also in time (Fransen & De Kroon, 2002). When a root network encounters regions of high availability, roots proliferate into the region, but only do so until resource availability diminishes. Once resource availability has decreased, root production is slowed and root biomass in that region may senesce (Fransen & De Kroon, 2002). Without a response to resource acquisition by roots, resources will not diminish over time and so the changes to root production may remain. Similarly, the impact of low soil resource availability around the initial root network may be diminished as the resource availability, though low, is infinitely available to the root network and would also not decrease as roots acquire additional resources. This result indicates that including only one the spatial aspect of soil resource heterogeneity may not be enough to assess the impact of soil resource heterogeneity on root stage distribution or metrics of plant success.

The main model results provide insights on the impact of root stage distributions on plant success and suggests that different root stage distributions support alternative plant growth patterns. Plants that survived, produced the most biomass, and produced the largest root networks maintained different root stage distributions. Similarly, plant allocation strategies that lead to plants with more root biomass growth or larger root networks likewise resulted in plants that maintain different root stage distribution. This suggests that plant allocation strategies may alter root stage distributions which may better support alternative growth patterns of the simulated plant. Together, these results indicate that incorporating multiple root stages and allocation strategies may provide a better method of simulating root dynamics and its resulting impact on plant growth patterns.

Future models could benefit from including root stage distributions and various allocations strategies. By incorporating these components, models could better simulate root dynamics and provide a more complete examination of the causal effects of allocation strategies. Without root stage distributions in models, allocation strategies only alter root growth rates which does not capture the connecting impact of variations in root growth rate to changes in root stage distribution and the subsequent changes in plant growth patterns. The model suggests that not only do allocation strategies lead to plants with different growth patterns but also to plants that maintain different root stage distributions. Furthermore, the alterations in roots distributions

due to alternative allocation strategies could impact other plant-soil feedback dynamics such as mycorrhiza colonization rates (Majdi *et al.*, 2001; Guo *et al.*, 2008b), soil resource cycling (Bouma *et al.*, 2001; Wells & Eissenstat, 2002; Volder *et al.*, 2005) which vary by root stage

Overall, the model provides a novel example of how incorporating root stage distributions and allocation strategies provide a more realistic method to simulate root dynamics. Without root stage distributions models may be inadvertently ignoring a key causal effect of various allocation strategies which could have wider implication on other PSF belowground dynamics. The model results also suggest that to accurately simulate the impact of soil resource heterogeneity, both temporal and spatial variations should be incorporated as well as soil resource response to root resource acquisition. This model serves as a reminder that treating key complex dynamics as a homogenous component may be missing essential dynamics.

Chapter 4

Introduction

The interactions between plants and soil microbial communities has long been recognized as a key driver of overall plant growth, productivity, and success (Kulmatiski, *et al*., 2008; Van der Putten *et al*., 2013). Such communities can modify the ability of roots to acquire soil resources, alter the supply of nutrients within the soil, and/or siphon resources from the plant. Nitrogen fixing bacteria fix atmospheric nitrogen providing plants access to an otherwise inaccessible pool of nitrogen (Wes *et al*., 2002). Similarly, phosphate solubilizing communities increase availability of phosphorus by solubilizing phosphates in the soil that were previously unavailable for acquisition (Zaidi *et al*., 2009). Mycorrhizae fungi increase the root acquisition rate of phosphorous (Van Der Heijden *et al*., 2008), nitrogen (Bücking & Kafle, 2015) and water (Augé *et al*., 2004). However, not all microbial communities are beneficial; soil microbial communities may compete with plants for access to resources thereby reducing resource availability to plants (Bardgett *et al*., 2003) or act as pathogens actively siphoning resources and/or photosynthate (Van Der Heijden *et al*., 2008).

The ability of soil microbial communities to alter resource availability and resource acquisition rates underlies their capability to mitigate the impacts of environmental stress on plant growth (Van Der Heijden *et al*., 2008; Miransari, 2010; Bennet & Klironomos, 2018). Under stress conditions mycorrhizae can increase overall surface area of the roots and improve root resource acquisition (Subramanian *et al*., 1995). Similarly, under drought conditions, mycorrhizae can increase the osmotic potential of roots increasing the ability of the root system to acquire water (Augé *et al*., 2004). In contrast, in conditions of abundance of key plant resources, impacts of soil microbial communities on plant growth may be diminished (Schroeder & Janos, 2004; Nilsson *et al*., 2007). Though the impact of soil microbial communities on plant growth varies along environmental gradients (Van Der Heijden *et al*., 2008), they nevertheless provide an alternative method by which plants can tolerate stressful conditions (Bennet & Klironomos, 2018)

The mechanisms through which soil microbial communities impact plant growth or mitigate soil environment stress directly impact root growth patterns. Soil microbial communities alter root growth rates (Bray *et al*., 2003; Gronberg *et al*., 2011;), morphology

(Schroeder & Janos, 2004; Chen *et al*., 2016), foraging patterns (Chen *et al*., 2016; Chen *et al*., 2018) and architecture (Gronberg *et al*., 2011; Wu *et al*., 2012). Furthermore, the growth rate of certain root types may be enhanced or diminished through interactions with soil microbial communities (Gronberg *et al*., 2011). The variations in root growth patterns in response to soil microbial communities can subsequently alter the distribution of roots of different size, age or stage classes.

A variety of root traits are correlated with different root classifications: 1) root respiration is negatively correlated with root age (Bouma et al., 2001; Wells & Eissenstat, 2002; Volder et al., 2005; Ceccon *et al*., 2016) and diameter (Makita *et al*., 2012); 2) nutrient uptake rate is negatively correlated with root age (Bouma et al., 2001; Wells & Eissenstat, 2002; Volder *et al*., 2005) and diameter (Pregitzer *et al*., 1998); 3) root lifespan is positively correlated with branch order (Guo *et al*., 2008a) and diameter (Wells & Eissenstat, 2001; Gill *et al*., 2002; Joslin *et al*., 2007) and; 4) mycorrhiza colonization rates are negatively correlated with branch order (Guo *et al*., 2008b). The variations of traits among roots of different sizes, ages, and branch orders indicates that the functioning of roots is likewise variable. If the distribution of roots in different stages varies in response to interactions with soil microbial communities, the functioning of entire root system is liable to change as well.

Understanding the impact of soil microbial communities on a plant's root stage distribution could elucidate potential mechanisms through which soil microbial communities alter plant growth, success, and productivity. Unfortunately, explication of the impact of soil microbial communities on the root stage distribution of the entire root system of a perennial woody plant is experimentally difficult. Studies that examine the entire root system response to soil microbial of perennial woody plants are often conducted on seedlings or saplings (Weimken *et* al., 2001; Porras-Sorianoa *et al*., 2009; Mangan *et al.*, 2010a; Mangan *et al*., 2010b; Gronberg *et al*., 2011; Seline *et al*., 2011; Razouk & Kajji, 2015; Kannenberg & Phillips 2016). Models exploring plant-soil feedbacks or the impact of soil microbial communities on plant growth tend to ignore the heterogeneity of root functions and traits usually incorporating roots through a single function or, if the model plant is disaggregated, as a single homogeneous component (Bever *et al*., 1997; Levine *et al*., 2006; Meyer *et al*., 2009; Farrior *et al*., 2013; Jiang & DeAngelis, 2013; Ke *et al*., 2015).

We develop a model simulating the growth of a single perennial woody plant over its lifetime with biomass separated into photosynthetic capable above ground (ABG) biomass and below ground resource acquiring and transport capable biomass (roots). The root biomass is separated into distinct consecutive stages with varying cost/benefit ratios. Feedbacks between root resource acquisition, above-ground photosynthetic production and subsequent root production and turnover simulate the growth and aging of the plant. The simulated plant's root system expands into a 2-dimensional soil space composed of individual cells with each soil environment cell having its own resource availability and soil microbial community. The simulated soil microbial communities can alter soil resource availability, root resource acquisition rates, and confer a photosynthate cost on the plant. Soil resource availability is diminished by root resource acquisition and soil microbial communities and is replenished by external resource deposition, soil microbial communities, and root exudates. The model is applied to 1) examine the impact of different soil microbial community structure on root stage distribution and the subsequent effects on plant success and root growth patterns; 2) assess how plant allocation strategy affects root stage distribution; and 3) identify alternative process though which soil microbial communities alter plant growth.

Methods

The model description uses the format outlined in the Overview, Design Concepts and Details (ODD) Protocol developed and updated by Grimm and colleagues (2010). This protocol is effective in enhancing the reproducibility of models, their simulation, and their analysis, a key concern in current science (Stodden *et al.*, 2014).

MODEL OBJECTIVE

This model examines the impact of different root stage distributions on the success, productivity, and growth pattern of a perennial woody plant over its lifetime. One objective is to assess the impact of soil microbial communities on root stage distributions and the successive effects of changes to root stage distributions on plant success, total root growth, and root growth patterns.

PLANT COMPONENTS

A simulated perennial woody plant is composed of above-ground biomass photosynthetic capable and structural support biomass (ABG) and below-ground resource acquiring and transport capable biomass (roots) with each time step representing one growing season. The simulated plant exists in a 2-D soil environment with heterogeneous variable resource availability and static soil microbial communities arrayed homogenously throughout. Within the soil environment, roots can grow and expand producing a root network. The biomass of the root network acquires a single soil resource, representing necessary nutrients and water, interacts with soil microbial communities, and transports the acquired resource back to the ABG biomass. The ABG biomass uses the transported resource to produce photosynthate which is allocated to 1) new ABG growth; 2) new root growth; 3) expansion of the root network; and 4) maintenance of current root biomass. Plants maintain a static allocation pattern in which a proportion of photosynthate that the plant produces is allocated to each of the 4 components. ABG biomass is represented by a single stage and root biomass is separated into distinct consecutive stages with young, thin, fine roots representing early stage roots and old, thick, coarse roots representing later stage roots. Each root stage has its own cost benefit/ratio and initial transition rate (Figure 17) that describes the proportion of root biomass in that stage that will transition to the next stage. A component-based approach to whole plant growth has been applied previously (De Reffye *et al*., 1997; McGraw, 1983; Prusinkiewicz, 1998), though our emphasis is on heterogeneity among roots. For more details about the components of the simulated plant see Chapter 3, Description, Plant Components.

SOIL ENVIRONMENT

The soil environment is composed of a 2-dimension spatial grid of individual cells within which the root network will grow and expand. Each cell is characterized by the amount of resource available and the composition of the soil microbial community. The cells may become occupied by root biomass – a root-occupied cell – after which the cell is additionally characterized by the amount of biomass in each root stage. The adjacency between cells is defined by the Von Neumann neighborhood (up, down, left, right). The root-occupied cells and the connections between them create a root network that is used to transport acquired resources

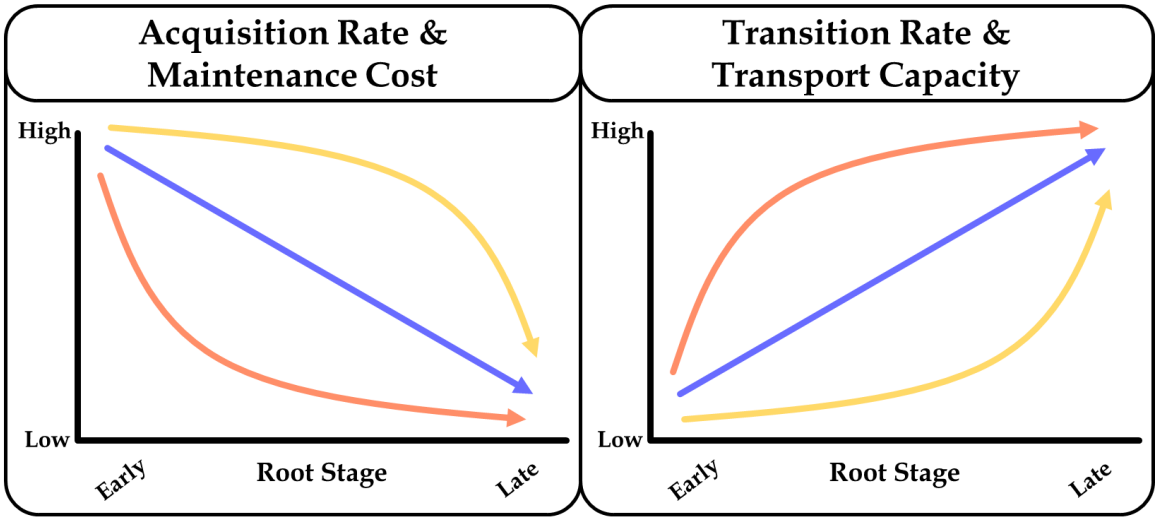

Figure 17. The qualitative relationship between root stage and function
Resource acquisition rate, maintenance cost, initial transition rate, and transport capacity vary across root stage. The exact relationship may be variable, but the qualitative relationship is the same for each root cost/benefit function.

from the roots to ABG biomass and photosynthate from ABG biomass to the roots. Due to constraints in modelling expansion, the root network can only expand by one cell leftwards, rightwards, and downwards during each time step. As such, the maximum width and depth of the soil environment is constrained by the number of time steps. The width of the modeled soil environment is twice the number of time steps plus the width of the initial root network, and the depth is the number of time steps plus the depth of the initial root network. Furthermore, certain cells are beyond the expansion range of the root network, given the constraints on adjacency and the number of time steps, and so are not tracked (Figure 18A).

A simulation is initialized with nine root-occupied cells and the corresponding root network connecting them (see initialization for more details). This initial root network has one root-occupied cell, the central cell, that is the connection between the entire root network and the ABG biomass. The transport of the acquired resource and photosynthate must flow through this central root cell and so any root-occupied cell that becomes disconnected completely senesces as it no longer has access to photosynthate. When a cell becomes occupied, it is connected to an already occupied cell that is connected to the existing root network and so any newly occupied cell is likewise connected to the central root cell.

Resource availability

Each cell has its own resource availability that constrains the total amount of the resource a root-occupied cell can acquire. The amount of resource available to a root-occupied cell (before modification by soil microbial communities) is given by Eq. 3 where where a_i is the acquisition rate of the soil-resource for root stage i and ψ_λ is the availability of the resource in root-occupied cell λ.

$$\Psi_\lambda = \frac{\max(a_i) \times \psi_\lambda}{\max(a_i) + \psi_\lambda} \qquad \text{Eq. 7}$$

This functional form of Eq. 3was chosen to ensure the amount of root-available resource is always less than the actual amount of the resource in the cell, thus representing an inaccessible pool of the resource.

The availability of the resource is modified by root resource acquisition, root exudation, soil microbial communities, and abiotic deposition, leaching, and loss. When a root-occupied

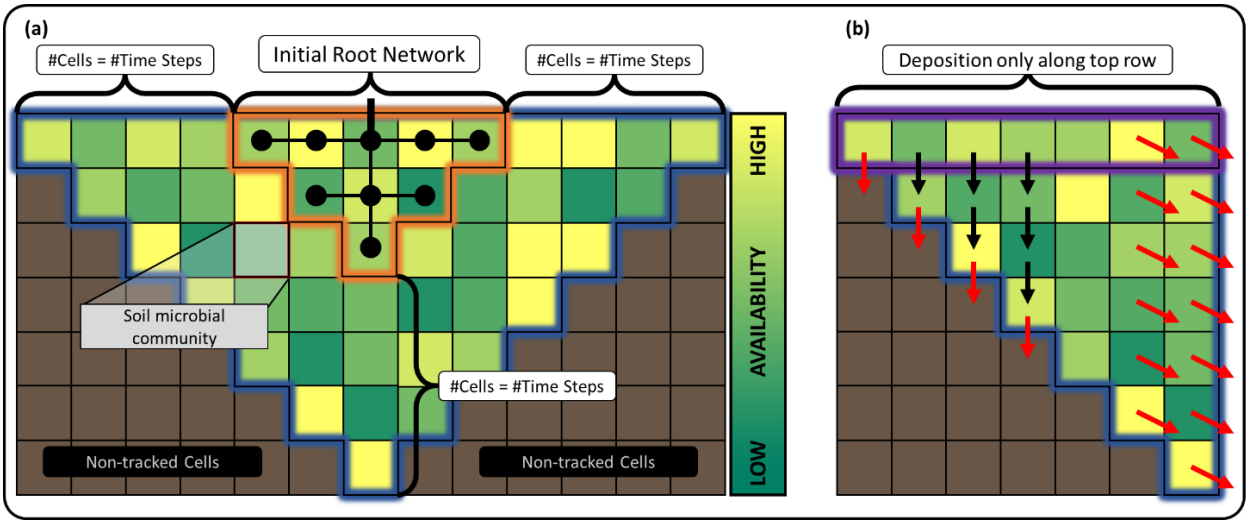

Figure 18. Soil Environment.

The soil environment with heat map of soil-resource availability (green - yellow), the corresponding components, and size of the soil environment (a). Although the environment is a 2-D grid, only a portion of the grid is tracked (highlighted in blue) given the expansion and time step constraints of the model. The abiotic mechanisms that alter soil resource availability (b). Deposition adds resource to the top row, leaching moves a proportion of the resource from one cell to the next, and leaching removes some proportion of the resource from the system. The red arrows indicate a loss of resource.

cell acquires some amount of the resource, this amount is removed from the cell. During transport of the resource (see transport for more details) a root may exude the resource that is beyond its capacity to transport, at which point the amount exuded is added to the availability within the cells. Soil microbial communities can increase or decrease the availability of the resource in a cell by a given proportion depending on the community composition. The availability of the resource is increased by deposition, is moved within the soil environment via leaching, and is removed from the soil environment through loss (Figure 18B).

Soil Microbial Communities

Each cell has a resident soil microbial community that is a static component of the environment. There is ample evidence that soil microbial communities can 1) alter resource availability 2) alter root resource uptake rates, and 3) incur a photosynthate cost upon the roots (Van Der Heijden *et al*., 2008)**.** Consequently, the soil microbial communities within the soil space are modeled by their ability to alter the availability within a cell, alter the root resource acquisition rate, and/or the siphoning of photosynthate from the root biomass (representing the cost of associating with microbes). A soil microbial community can alter any of these three components, though the ability to alter the same component is only modeled as the net change for that component (Table 4). The different behaviors of the soil microbial communities are a result of the different microbial composition of each community. However, within a simulation, the soil space is composed of a homogenous soil microbial community in which the community in each cell has the same effect on resource availability, root acquisition rate, and siphoning. There is no response of soil microbial communities to change in the soil environment or root biomass and the community within a cell remains unchanged during a simulation.

The soil microbial communities that alter resource availability do so by increasing or decreasing the availability in the cell by a given proportion. The alteration of the soil resource availability occurs at the start of a time step, prior to acquisition by roots and prior to photosynthate allocation to new root growth and root expansion. This is done because the relative importance of each root-occupied cell and immediately adjacent cell depends on the availability of the resource in each cell. In having resource availability altered by microbes before photosynthate allocation, the effects of the soil microbial community can be accounted for

Table 4. Soil Microbial Communities

The 30 different soil microbial communities arranged into 6 groups (A-F) with groups A-E grouped by their effect on soil resource availability and organized in by descending effect on resource uptake rate. Group F was included to explore soil microbial communities that had indirect effects or no effect on root biomass.

Group	Community Number	Community Effect on…			Direct / Indirect
		Availability	Uptake	Siphon	
A	1	0.25	0.15	0.05	Both
	2	0.25	0.075	0.05	Both
	3	0.25	0	0.05	Both
	4	0.25	-0.075	0.05	Both
	5	0.25	-0.15	0.05	Both
B	6	0.125	0.15	0.05	Both
	7	0.125	0.075	0.05	Both
	8	0.125	0	0.05	Both
	9	0.125	-0.075	0.05	Both
	10	0.125	-0.15	0.05	Both
C	11	0	0.15	0.05	Direct
	12	0	0.075	0.05	Direct
	13	0	0	0.05	Direct
	14	0	-0.075	0.05	Direct
	15	0	-0.15	0.05	Direct
D	16	-0.125	0.15	0.05	Both
	17	-0.125	0.075	0.05	Both
	18	-0.125	0	0.05	Both
	19	-0.125	-0.075	0.05	Both
	20	-0.125	-0.15	0.05	Both
E	21	-0.25	0.15	0.05	Both
	22	-0.25	0.075	0.05	Both
	23	-0.25	0	0.05	Both
	24	-0.25	-0.075	0.05	Both
	25	-0.25	-0.15	0.05	Both
F	26	0.25	0	0	Indirect
	27	0.125	0	0	Indirect
	28	0	0	0	None
	29	-0.125	0	0	Indirect
	30	-0.25	0	0	Indirect

at the model time step in which the plant allocates photosynthate to root growth. The alteration of soil resource availability occurs in all tracked cells regardless of root occupation.

The soil microbial communities that alter root resource acquisition rate do so by increasing or decreasing the acquisition rate of the root biomass in that cell by a given proportion, though the acquisition rate cannot allocate resources which surpass the availability in the cell. The changes to resource acquisition rate only occur in root-occupied cells.

The soil microbial communities that siphon photosynthate do so by reducing the amount of photosynthate being transported via the root biomass by a given proportion. There are three instances during which photosynthate is transported and so the proportion of photosynthate that is siphoned by a soil microbial community is reduced by $1/3$ to account for the multiple instances when siphoning occurs. Siphoning of photosynthate by the soil microbial community occurs during new root growth, root expansion, and root maintenance. There is no siphoning of the resource being transported by the root biomass.

Resource Deposition, Leaching, and Loss

As a simulation progresses, the amount of the resource within the soil environment will fluctuate due to the biotic mechanisms of resource acquisition by roots and the impacts of the soil microbial community. However, there are abiotic factors that can also affect resource availability, and these effects are incorporated via resource deposition, leaching, and loss. Deposition adds resources to the soil environment, leaching moves resources within the soil environment, and loss removes resources from the modeled soil environment. These abiotic impacts on soil resource availability occur at the end of a time step with deposition occurring first, followed by leaching and loss occurring simultaneously. Deposition adds a given amount of resource, uniformly, to the top row of the soil space (representing the soil that is closest to the surface). Leaching of the soil resource is simulated by moving a proportion of the resource in each cell to the cell one row beneath it. The proportion leached is row (e.g. depth) dependent with shallower rows moving a larger proportion and deeper rows moving a smaller proportion. However, because not all cells are tracked, the proportion of the resource leached in edge cells is lost from the system. The loss of soil resources from the system is simulated by removing a proportion of the resource in each cell from the system. The proportion lost is row dependent

with shallower rows losing a larger proportion and deeper rows losing a smaller proportion (Figure 18B).

GROWTH, EXPANSION, AND AGEING

As a simulation progresses, the plant can grow new ABG and root biomass, expand the root network, and will have some of its existing biomass age and senesce. The processes involved in this are dependent on photosynthate production and the allocation strategy (the proportion of photosynthate allocated to 4 components) of the plant. This dependency creates a feedback whereby roots acquire resources which are used by ABG biomass to produce photosynthate which is then allocated to the growth and ageing processes. The allocation of photosynthate subsequently alters the amount of root and ABG biomass which in turn alters the amount of photosynthate produced in the following time step.

Photosynthate production is dependent on the amount of resource transported to the above-ground component of the plant and the current ABG biomass. The produced photosynthate is then allocated to four components: 1) new ABG growth, 2) new root growth, 3) expansion of the root network via root growth, and 4) root maintenance. New ABG growth adds additional ABG biomass to the already existing biomass. New root growth adds stage 1 root biomass to already root-occupied cells. The expansion of the root network adds stage 1 root biomass to unoccupied cells that are immediately adjacent to root-occupied cells. Root maintenance alters the initial transition rate of the biomass in each stage in each cell. The change to the initial transition rate is dependent on the amount of photosynthate received so that receiving less photosynthate than the maintenance cost reduces the initial transition rate and receiving more photosynthate than the maintenance cost increases the initial transition rate. The proportion of biomass in each stage that does not transition senesces.

During allocation to the 3 root components the relative importance of each cell under consideration is used to determine the amount of photosynthate each cell is intended to receive. However, the amount of photosynthate that a given cell will receive may not be its intended amount due to transport limitations and the amount of photosynthate produced. Each cell's relative importance is determined by summing the importance criteria of the current allocation strategy component for each cell and then dividing by the total sum across all cells in

consideration. For new root growth the importance criteria calculated for each of the root-occupied cells are: 1) the amount resources acquired in the previous step, 2) soil resource availability and 3) the remaining available space. For root network expansion, the importance criterion calculated for each unoccupied cell immediately adjacent to a root-occupied cell is: 1) soil resource availability. For root maintenance the importance criteria calculated for each of the root-occupied cells are: 1) the amount resources acquired in the previous step, 2) amount of resource lost during transport, 3) amount of photosynthate lost during transport and 4) and the total maintenance cost of the root biomass in the cell. For more details about growth, expansion and aging see Chapter 3, Description, Growth, Expansion, and Ageing.

TRANSPORT

Roots transport resources acquired by root biomass and photosynthate produced by ABG biomass through the root network. Resource transport flows from the roots to ABG biomass and photosynthate transport flows from ABG biomass to the roots. Each root-occupied cell has a total transport capacity determined by the amount and stage distribution of root biomass in the cell. The cell's total transport capacity determines the absolute maximum amount of the resource or photosynthate that can be transported through it. Any amount of resource or photosynthate that is transported through a root-occupied cell that is greater than a cell's total transport capacity is exuded. The amount of resource exuded is added to the cell's resource availability. Because photosynthate within the soil environment is not tracked, is not acquired by roots, and is not used by soil microbial communities, the amount of photosynthate exuded is not tracked. If photosynthate is transported through a root-occupied cell containing a soil microbial community that siphons photosynthate, the amount moving through the cell is reduced by the soil microbial community before the cell obtains photosynthate. For more details on the transport of photosynthate and the acquired resource, see Chapter 3, Description, Transport.

ORDER OF EVENTS

The model time steps represent one growing season for the plant which is assumed to represent one year for the perennial woody plants under consideration. At the beginning of a time step (growing season) the soil microbial communities alter the availability of the soil

resource in each cell. The plant then uses photosynthate from the previous season to produce new ABG biomass and new root biomass in already occupied cells. Following new root growth, the root network expands into immediately adjacent unoccupied cells. After new growth has occurred all root cells simultaneously acquire the soil resource which is then transported via the root network to the ABG biomass. The ABG biomass uses the transported resource to produce photosynthate which is then allocated to new ABG growth, new root growth, root expansion, and root maintenance. The amount allocated to root maintenance alters the initial transition rate of the biomass in each root stage in each cell. The root biomass then transitions to the next stage dependent on its update transition rate and any biomass that does not transition senesces. The photosynthate allocated to new ABG growth, new root growth, and root expansion is stored for use in the following time step. At the end of a time step, the abiotic mechanisms that affect resource availability (deposition, leaching, and loss) change the availability throughout the soil environment (Figure 19).

INTIALIZATION

Each simulated plant began with a root network composed of nine root occupied cells (Figure 18 A), each with one unit of biomass and nine units of above ground biomass. The biomass of the initial root network was distributed such that that $^{5}/_{9}$ of root biomass was in stage 1, $^{3}/_{9}$ of root biomass in stage 2 and, $^{1}/_{9}$ of root biomass was in stage 3. This distribution was chosen because the initial root network is assumed to have formed after 3 growing seasons. The central cell grew during the first season, the immediate adjacent cells grew from the central cell during the second growing season, and the edge cells grew from the second season cells during the third growing season. Furthermore, because root biomass must begin as stage 1 biomass which then transitions to later stage, the oldest cell, the central root cell has had 2 growing seasons pass at which point it can have root biomass in stage 3, and so on for the distribution of the other initial root-occupied cells.

The soil environment within which the plant and its accompanying root network will grow uses a predetermined soil resource availability pattern, soil microbial community, and values for deposition, leaching and loss. The availability pattern and the associated values for deposition, leaching and loss were selected such that under static conditions (without roots or

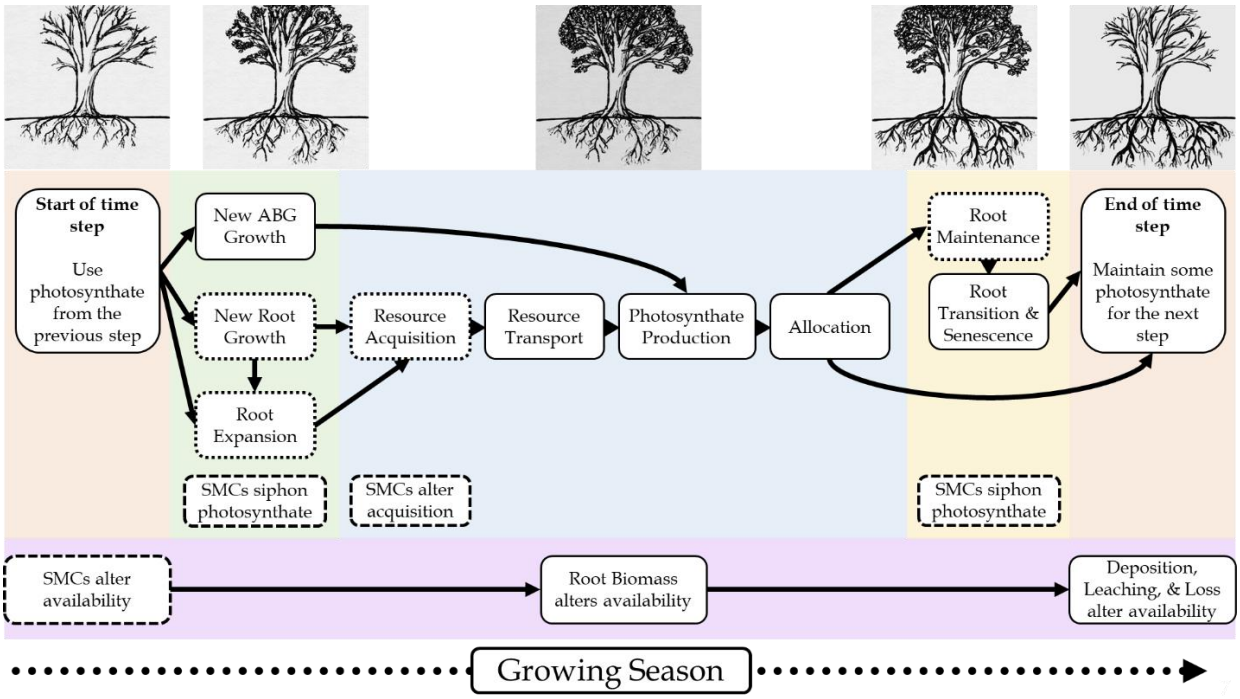

Figure 19. Order of Events.
The order of events within a single time step. A time step represents one growing season. The colored regions represent different segments of the model, 1) orange is start/end, 2) green is growth, 3) blue is plant processes, 4) yellow is aging and senesce, and 5) purple is changes to soil resource availability. The components with the dotted lines represent model processes that are altered by soil microbial communities (SMCs) and the processes included in the dashed line boxes indicate the corresponding effect of the SMCs. However, because the composition of the SMCs, not all model processes and their corresponding effects may occur within a given simulation.

soil microbial communities) the availability remains relatively stable for more than 50 time steps. The soil microbial is arrayed homogenously throughout the soil environment ensuring that each cell has the same community composition with the same effect on resource availability, root resource acquisition rate, and siphoning of photosynthate. Each cell within the soil space has a maximum capacity of 100 units of root biomass.

At the start of a simulation, the initial root and ABG biomass is used to determine the amount of photosynthate produced in the previous step because there was no prior step. This photosynthate is allocated according to the plant allocation strategy and is used to start the first growth phase of a simulation.

PARAMETER SPACE SEARCH & ANALYSIS

A parameter space search was conducted in MATLAB 2019a using computing clusters at the Advanced Computing Facility (ACF) to analyze the effects of alternative plant allocation strategies, soil microbial communities, and root cost/benefit functions, on overall root growth and root stage distributions. The soil microbial communities used in the parameter space search can be found in table (Table 4) and the parameter values can be found in table (Table 5). The parameter space search consisted of 150,000 simulations wherein each simulation was run for 50-time steps after which the outputs for the last time step of each simulation was maintained.

Of the 150,000 simulated plants, approximately 140,000 of the plants had a final total biomass greater than their initial biomass; meaning that approximately 93 percent of simulations resulted in growing plants. All analyses were conducted on the surviving plants using MATLAB 2020a.

The parameter space search conducted using the ACF consisted of 400 jobs each with 375 parameter sets using between 16 and 24 cores per job submission. Each job took on average approximately 20 hours to complete for a total of 8,000 computing hours. Prior to this final parameter space search, 7 previous parameter space searches were conducted to narrow the range of values and eliminate parameters that had little to no effect on model outputs. Combined, these 7 initial parameter space searches contained approximately 3.5 million simulations with each having a unique parameter set and used approximately 80,000 computing hours.

Table 5. Parameter Space Search Values

The parameter ranges and values used for each of the parameters analyzed in the parameter space search. The numbers correspond to the relative parameter importance estimates in Figure 23. Those parameters without numbers were excluded from the parameter importance estimates.

Model Component	#	Description	Range of Values	
			Min	Max
Root Cost/Benefit Ratio	**1**	Maximum per unit resource acquisition rate	50	100
	2	Maximum per unit transport capacity	500	1000
		Maximum initial transition rate	0.8	0.99
Photosynthate Production		Photosynthesis multiplication constant	1	10
	3	Importance of resource in photosynthesis	0.1	1
	4	Importance of ABG biomass in photosynthesis	0.1	1
ABG Biomass	**5**	ABG transition rate	0.5	1
Allocation	**6**	Proportion allocated to new root growth	0.02	0.94
	7	Proportion allocated to root expansion	0.02	0.94
	8	Proportion allocated to root maintenance	0.02	0.94
	9	Proportion allocated to new ABG growth	0.02	0.94
Microbial Community	**10**	Soil microbial community number	1	30

Results

PLANT SUCCESS

For the purposes of this model, plant success is using two metrics: (i) total plant biomass in the last time step or (ii) root network size in the last time step. Last time step total plant biomass is positively correlated with last time step root biomass and is used as the metric of plant success in lieu of total plant biomass. In contrast with the model in Chapter 3, for this model last time step plant biomass is positively correlated with last time step root network size, but last time step root network size is used as a separate metric of plant success to assess other aspects of plant growth and success in the model.

ROOT STAGE DISTRIBUTION

For most surviving plants, the majority of root biomass was maintained in the first and last stages with the 10 most common root stage distributions, accounting for approximately 80% of surviving plants, having between 70-85% of root biomass in the first and last stage. For the surviving plants, the two most frequent distributions (each ≈13% of plants) had a root stage distribution with 50-60% of root biomass in the first stage and 20-30% of root biomass in the last stage. The 10 most common root stage distributions, accounting for approximately 80% of surviving plants, maintained between 30-65% of root biomass in the first stage and 20-55% of root biomass in the last stage. Although, there are plants with root stage distributions having 0-5% of root biomass in the first stage, these are rare and collectively account for less than 2% of surviving plants (Figure 20A).

Plants that produced the most root biomass maintained a bimodal root stage distribution with nearly all root biomass maintained in the first and last stages. The 10 distributions maintained by plants that produced the most root biomass maintained between 75-95% of biomass in the first and last stage. On average, those plants that maintained a root stage distribution of 35-40% of root biomass in the first stage and 50-55% of root biomass in the last stage produced the most root biomass. The 10 distributions maintained by plants that produced the most root biomass had between 30-60% of root biomass in the first stage and 20-55% in the last stage and collectively accounted for approximately 65% of surviving plants (Figure 20B).

Similarly, plants that produced the largest root networks maintained a bimodal root stage

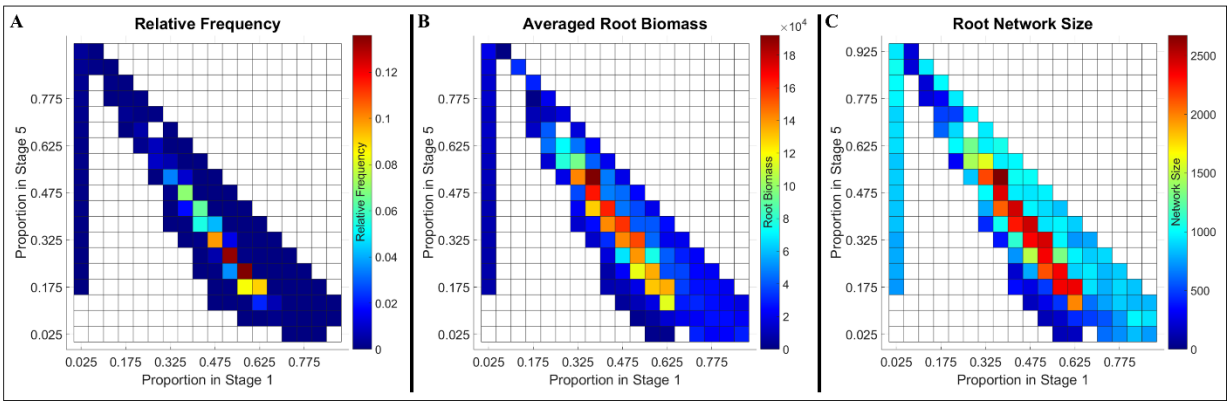

Figure 20. Root Stage Distributions

The relative frequency (A), the units of root biomass (B), and the size of the root network (C), of plants that maintained a given root stage distribution. For surviving plants, the proportion in the first and last stage accounted for a majority of root biomass and so the proportion in these two stages is considered representative of the distribution.

distribution with nearly all root biomass maintained in the first and last stages. The 10 distributions maintained by plants with the largest root networks maintained between 70-95% of biomass in the first and last stage. On average, those plants that maintained a root stage distribution of 35-40% of root biomass in the first stage and 50-55% of root biomass in the last stage produced the largest root network. The top 10 distributions maintained by plants that had the largest root networks had between 30-65% of root biomass in the first stage and 20-55% in the last stage and collectively accounted for approximately 75% of surviving plants (Figure 20).

Even though the model is generalized, there is a very constrained set of root stage distributions that lead to the highest fitness indicated by total root biomass and root network size. Of the 10 distributions maintained by plants that produced the most root biomass and the 10 distributions maintained by plants with the largest root networks 8 were identical accounting for approximately 57% of surviving plants (Figure 20B and Figure 20C).

ALLOCATION STRATEGY

The most frequent allocation strategies of the surviving plants were those with a relatively balanced allocation to each of the components. The frequency of allocation strategies decreased as the strategy became more skewed towards an individual component. Similarly, the frequency of allocation strategies decreased as the strategy became more skewed away from a single individual component. However, allocation strategies slightly skewed away from aboveground (ABG) growth remained relatively frequent compared to plants that maintained strategies that were skewed away from the other 3 components (Figure 21A).

The allocation strategies maintained by plants with the most root biomass and the largest root networks favored allocation to root maintenance and new root growth with a relatively balanced allocation to the remaining components of root network expansion and ABG growth. Of the 4 allocation strategies used by plants that had the most root biomass and the 4 strategies used by plants that had the largest root networks, 3 were identical. The 4 allocation strategies used by plants that had the most root biomass allocated between 20-50% of photosynthate to root maintenance and 30-50% of photosynthate to new root growth (Figure 21B). The 4 allocation strategies used by plants that had the largest root network allocated between 20-50% of

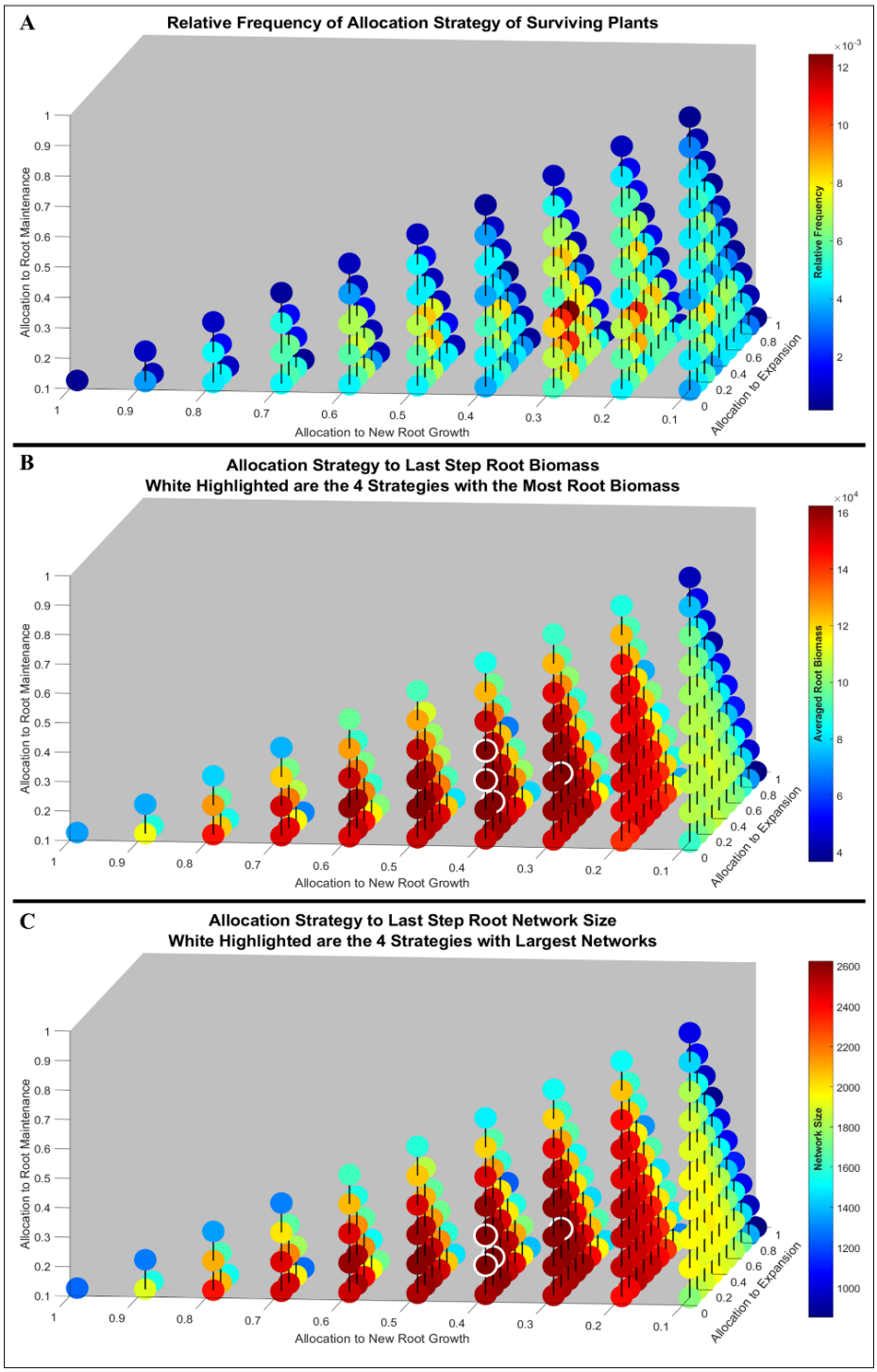

Figure 21. Allocation Strategy and Plant Success

Allocation to 3 components with allocation to the fourth component found by subtracting allocation from 1. Note that due to the visualization and the discretization of allocation strategies, the sum allocated to all components may appear greater than 1. The frequency of allocation strategies of surviving plants (A), the allocation strategy used by plants that produced differing amounts of root biomass (B), and the allocation strategy used by plants that produced different sized root networks (C).

photosynthate to root maintenance and 30-40% of photosynthate to new root growth (Figure 21C).

SOIL MICROBIAL COMMUNITY

There is no significant difference between root biomass produced under different soil microbial communities and there is no significant difference between the root network size under different soil microbial communities.

Within soil microbial groups **C**, **D**, **E** (those that have a neutral affect or decrease availability) ANOVA analysis (available in supplement) indicates there are significant differences in the proportion of root biomass in the first and last stage between the first 3 communities and the last 2 communities within each group (Figure 22). The first three communities in each group greatly increased uptake rate, moderately increased uptake rate, or had no effect on uptake rate while the latter two communities moderately decreased uptake rate or greatly decreased uptake rate. There is a significant effect of soil microbial communities that decrease uptake with aa significantly higher proportion of root biomass maintained in the first stage for groups **C)** 14 and 15 compared to 11, 12, and 13, **D)** for groups 19 and 20 compared to 16, 17, and 18, **E)** for groups 24 and 25 compared to 21, 22, and 23. Similarly, there was a significantly lower proportion of root biomass maintained in the last stage for groups **C)** 14 and 15 compared to 11, 12, and 13, **D)** for groups 19 and 20 compared to 16, 17, and 18, **E)** for groups 24 and 25 compared to 21, 22, and 23. However, the differences between proportions in the first or last stage was small with changes of only 2-3% depending on the soil microbial communities in these groups. For all other groups, there was no significant difference in the proportion of root biomass in the first or last stage under different microbial communities (Figure 22).

PARAMETER IMPORTANCE ESTIMATION

Parameter importance estimation was conducted using the predictorImportance function (which estimates the predictor importance using an ensemble of decision trees) within MATLAB 2020a. The parameters of maximum initial transition rate and photosynthesis multiplication constant were not included in the relative importance estimates because the results were

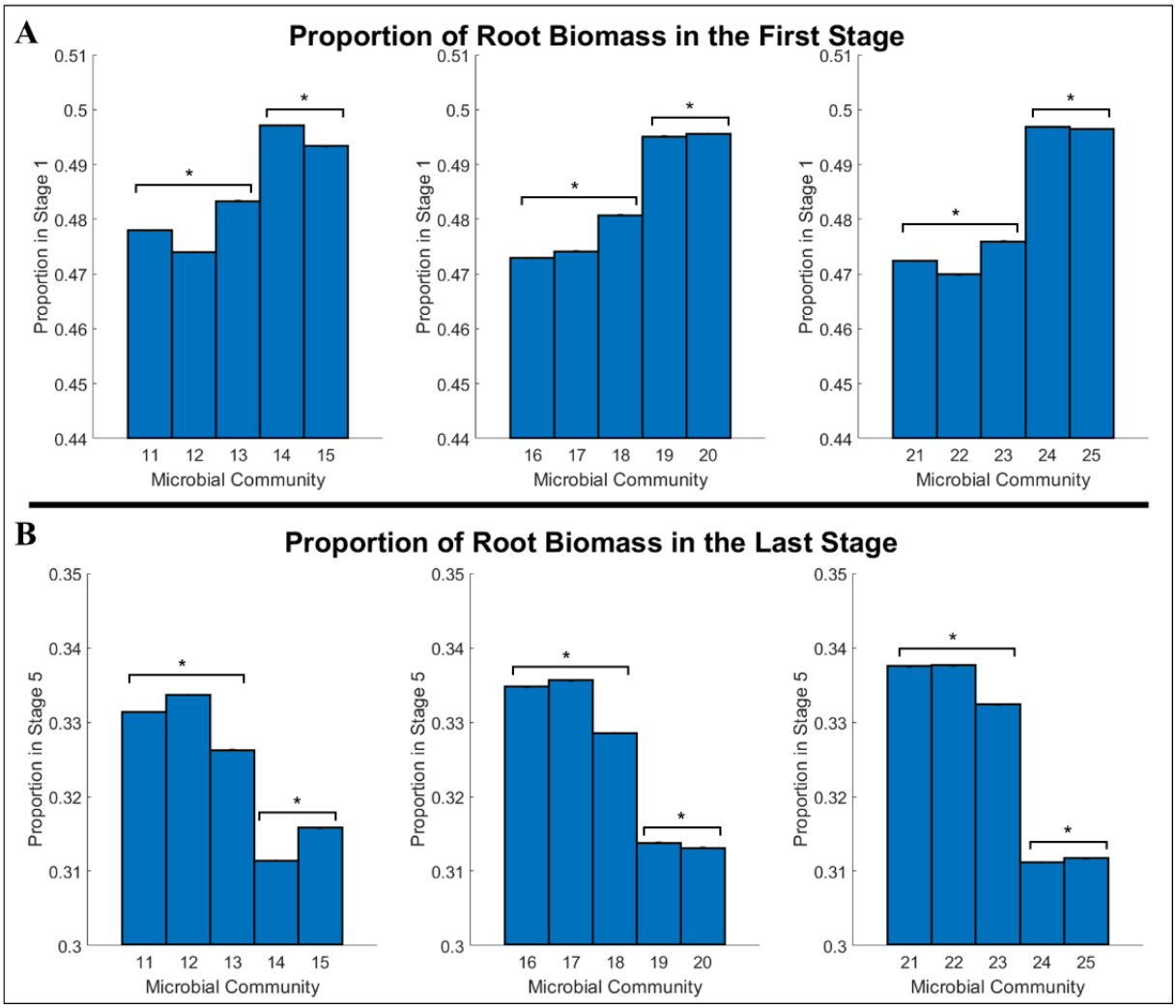

Figure 22. Soil Microbial Communities

The impact of soil microbial communities on the proportion of biomass in the first stage (A), and the last stage (B). Only those soil microbial groups that had significant difference in root stage distributions (groups C, D, and E) are shown. For each group, regardless of the first or last stage, there is a significant difference between the first three communities (large increase to uptake rate, increase to uptake rate, and no effect on uptake rate) compared to the last two communities (decrease uptake rate and large decrease to uptake rate). Note, that the changes in proportion is relatively small with only 2-3% changes depending on soil microbial community.

consistent with expected behavior. The maximum initial transition rate, which determines the proportion of root biomass that survives between steps, was most important for biomass in the first and last stages (0.77 and 0.84 respectively) and photosynthesis multiplication constant, which increases photosynthate production, was the most important for root biomass and root network size (0.35 and 0.38) respectively. Additionally, when included in relative parameter estimates, these parameters limited the ability to examine the relative importance of other parameters.

When those parameters are excluded, the most important parameter for root biomass, proportion of biomass in the first stage, and proportion of biomass in the last stage, was allocation to new root growth with relative importance values of 0.39, 0.69, and 0.67 respectively and the most important parameter. The most important parameter for root network size was allocation to ABG growth with a relative importance of 0.39 though allocation to new root growth was the second most important parameter with a relative importance of 0.36. The components of the allocation strategy are consistently the most important parameters. Allocation to new root growth is by far the important parameter for the proportion of root biomass in the first and last stages while allocation to new root growth and ABG growth are relatively equally important for root biomass and network size. Of all components, soil microbial community had a consistently low relative importance for all output metrics (Figure 23).

Discussion

The results suggest that root stage distribution impacts plant success and despite the very general structure of the model, there are strong constraints on the range of root stage distributions that lead to plant success. Of the top ten distributions that were maintained by plants the produced the most root biomass and largest root network size, there is narrow band of distributions that have between 70-90% of total root biomass in the first and last stages, 65% or less of their root biomass in the first stage, and 55% or less of their root biomass in the last stage. Similarly, of the ten distributions maintained by plants with the most root biomass and the ten distributions maintained by plants with the largest root networks, seven were similar with the other three falling along the same narrow band of distributions. Those distributions that fall

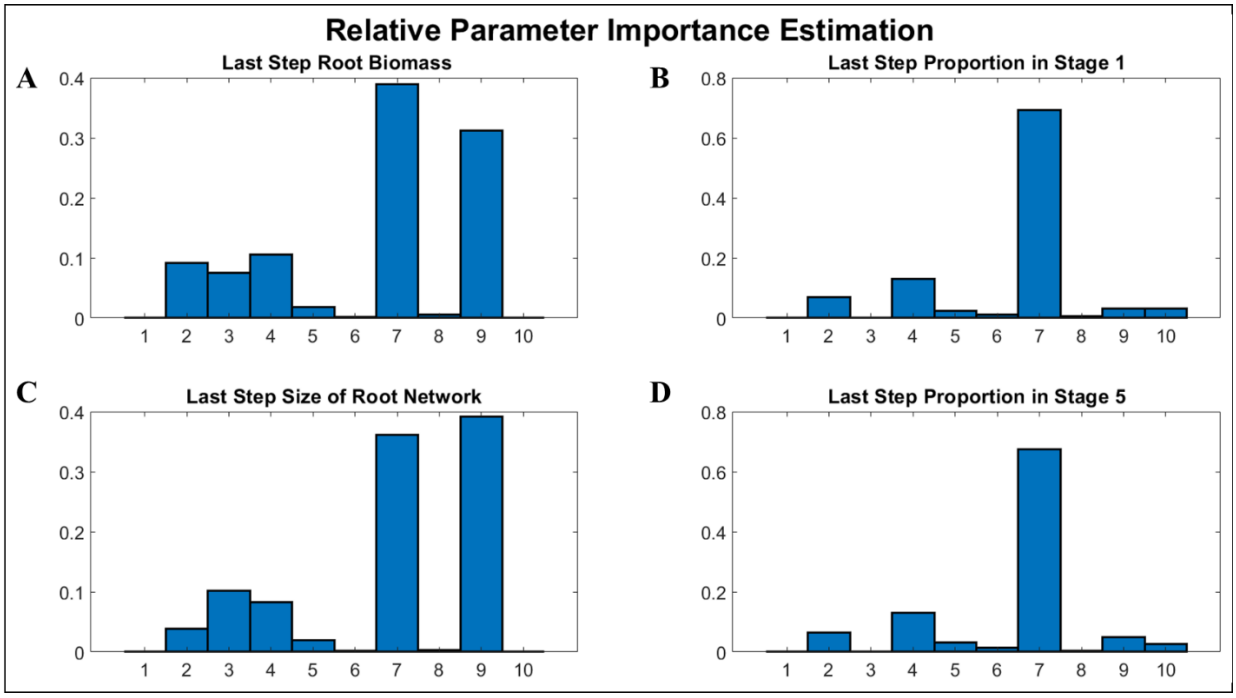

Figure 23. Parameter Importance Estimation

The relative importance of parameters for root biomass (A), root network size (B), proportion of biomass in the first stage (C) and proportion of biomass in the last stage (D). The parameters associated with each number can be found in Table 5.

outside this narrow band of root stage distributions were maintained by plants with much less root biomass and much smaller root networks compared to those within the narrow band. This indicates that only those stages with very high resource uptake rate (first stage) and/or very high transport capacity (last stage) are the most important for the success of the simulated plant.

Although root stage distributions impact plant success, the model results suggest parameter affecting a plant's allocation strategy are the most important ones impacting plant success and root stage distribution. Of the allocation components, allocation to root growth in already occupied cells and ABG growth are most important for plant success. However, strategies with increased allocation to these components are not by themselves ones that lead to plants with more root biomass or larger root networks. Instead, the allocation strategies used by plants with the most root biomass and largest root networks favored relatively balanced allocation strategies with minimal allocation to root network expansion. The plants using strategies that heavily favored any one component were not as successful as plants employing a balanced strategy, indicating that the simulated plants cannot succeed with mainly root biomass or mainly ABG biomass. These results are consistent with previous work that suggests allocation strategies are key drivers of plant success and that plant success is diminished under highly skewed strategies (Doust, 1989; Schaffer & Fox 1989; Weiner, 2004)

As with root stage distributions, the model results suggest there is a narrow set of strategies used by the most successful plants as measured by the final total root biomass and root network size. Of the relatively balanced strategies, those strategies with relatively high allocation to new root growth and/or root maintenance, medium allocation to ABG growth, and minimal allocation to root network expansion, were used by the most successful plants. The strategies that fall outside of this that narrow region were used by plants with much less root biomass and much smaller root networks. In conjunction with the high relative importance of allocation strategy, this suggests that although a variety of allocation strategies may lead to plant survival, plant success is highly dependent on a narrow set of allocation strategies.

It has been suggested that soil microbial communities may affect plant success (Van Der Heijden *et al*., 2008; Miransari, 2010; Bennet & Klironomos, 2018) and root stage distributions (Bray *et al*., 2003; Gronberg *et al*., 2011; Wu *et al*., 2012; Chen *et al*., 2016). In contrast, the model results indicate that soil microbial communities do not affect plant success and have very

little effect on root stage distributions. Regardless of the assumed parameter sets determining how the soil microbial community interacts with roots, there were no significant differences in root biomass or root network size when microbial communities were included. The effects of soil microbial communities had negligible impact on plant success compared to a plant's allocation strategy and root stage distribution. Furthermore, the relative importance of soil microbial communities was consistently low for the metrics of plant success and root stage distributions.

Nevertheless, under certain circumstance soil microbial communities do alter root stage distributions. When simulated plants are grown in soils with microbial communities that do not increase resource availability (groups C, D, and E) there are significant differences in the proportion of root biomass in the first and last stages between those communities that also decrease uptake rate and those that do not. Given the overall model assumption that soil resource availability remained fixed in the absence of root biomass and soil microbial communities, there is a greater reduction in availability when soil microbial communities do not increase resource availability. This suggests that only in environments where soil microbial communities are not actively increasing soil resources do soil microbial communities alter root stage distributions.

Further, the direction of change in the proportion of biomass in the first and last stages is correlated with the effect of the soil microbial communities on plant uptake rate. The proportion of root biomass in the first stage, which has the highest uptake rate, is increased when those soil microbial communities that do not increase resource availability also reduce uptake. This indicates that as the uptake rate is reduced by soil microbial communities, the proportion of root biomass that is needed to acquire resource increases. However, the change in proportion is relatively small (2-3%), indicating that the effects of soil microbial communities are mitigated by other components of the model. These results suggest that the simulated plants can respond to antagonistic soil microbial communities by varying root stage distributions such that the overall success of the plant is not affected.

Future work should continue to explore the impact of antagonistic soil microbial communities on plant success and root stage distributions to determine if weaker or stronger affects produce different results. The plant response was relatively unaffected by those microbial

communities that did not increase soil resource availability. So long as the soil microbial community did not increase availability and decreased resource uptake rate, the proportions of root biomass in the first or last stage were nearly identical. Thus, although reducing resource uptake rate influences root stage distribution, the strength of reduction does not change the plants response. It would be beneficial to simulate a more continuous and wider gradient of affects to explore the different responses of the plants.

Additionally, given that the only significant effects of soil microbial communities occurred when communities did not increase availability, it would be prudent to further explore the effects of soil microbial communities under alternative resource availability patterns. It has been suggested that under different environmental conditions the impact of soil microbial communities could be mitigated or exacerbated (Van Der Heijden *et al*., 2008). The soil resource pattern, deposition amounts, and leaching and loss amounts in each simulation were established such that the availability remained stable in the absence of root biomass and soil microbial communities. However, the soil resource availability could have been too high for soil microbial communities that likewise increased availability to affect plant growth. Under stressful conditions when resource availability is low, it could be possible that there are different impacts of soil microbial communities on plant growth and root stage distributions. Consequently, future work might fruitfully examine the effects of different resource availability patterns and deposition amounts to determine the effects of soil microbial communities under these alternative conditions.

Overall, the model results indicate that root stage distributions and plant allocation strategy are large drivers of plant success. A main result is that these two components of plant growth interact so that that there is a narrow range of root stage distributions and a narrow region of allocation strategies that are maintained and used by plants with the most root biomass and largest root networks. There are strong constraints on simulated plant growth patterns that lead to success despite the wide variety of different growth patterns examined via the parameter space search. Although there is no impact of soil microbial communities on plant success, there is evidence that soil microbial communities that reduce uptake rate do affect root stage distribution. This suggests that plants may be able to mitigate the impact of antagonistic soil microbial communities on growth through a root stage distribution response.

Chapter 5

The model framework developed in this dissertation provides strong evidence that root stage distribution does affect metrics of plant success. The results likewise suggest that the functions of roots, their cost/benefit ratio and a plant's allocation strategy are consistently the largest drivers of root stage distribution. An additional consistent conclusion is that environmental conditions, such as soil resource heterogeneity and soil microbial community composition, do not have a large impact on root stage distribution nor plant success. While these results are important in the theory of plant soil feedbacks (PSF), a plethora of additional research can be done to further investigate the factors influencing root stage distributions and the effects of changes in root stage distributions on plant success. This chapter elaborates on some possible extensions of the models that could provide further evidence of the impacts of root stage distribution on PSFs.

Constructing a small set of distinctly different soil environment resource patterns may provide a more effective and efficient method than the process used here to examine the effects of resource heterogeneity on root stage distributions and plant success. Chapter 3, which examined soil patchiness and direction, used approximately 1,800 different soil resource patterns with varying patchiness metrics between 0 and 1. Although the patchiness metric and patchiness direction attempted to classify each of the patterns the randomness within each pattern may have obfuscated the impact of soil resource heterogeneity. Furthermore, the metrics for the patchiness of the soil resource patterns did not consider the distance of patches from the initial root network so the number of time steps for a root network to reach a given patch could vary for resource patterns that have similar patchiness metrics. A smaller and simpler set of patterns specifically designed to have a given patchiness metric, patchiness direction, and different distances from the patches of varying resource availability may improve the examination of the effects of soil resource heterogeneity on root stage distribution and plant success.

Alternative to choosing a small set of resource availability patterns, another metric of patchiness could be devised that accounts for the typical growth patterns of the simulated root networks. During the beginning time steps, many root networks grow in concentric "rings" (triangular rings due to the spatial constraints of the model) around the central root cell. The small number of immediately adjacent cells and the short path distances between the adjacent

cells and the ABG biomass allows the root network to expand into practically all the adjacent cells. However, there is a time step at which the simulated plant no longer produces enough photosynthate or does not have the transport capacity to occupy all adjacent cells. After this time step, the growth pattern changes and only the most important adjacent cells become occupied. Currently, the patchiness metric does not account for this and instead creates outward flowing paths from the central root cell and records the availability of each cell along the path. The metric could be improved by not only considering the availability along each path, but also the availability of cells in each ring around the initial root network.

As with soil patchiness, it would be beneficial to further explore the effects of soil microbial communities. The results of Chapter 4 suggest that soil microbial communities have only a small impact on root stage distributions and no impact on plant success. However, within groups C, D, and E (those communities that had a neutral or negative affect on availability) there were significant differences in the proportion of root biomass maintained in the first and last stages with communities that decreased resource uptake rate compared to those communities that increased uptake rates. Future work might focus on soil microbial communities that have no effect or negative effects on soil resource availability. Similarly, a larger set of soil microbial communities with effects similar to groups C, D, and E but with a more continuous gradient of effects on soil resource availability and root resource uptake rate could provide a more complete examination of the impact on root stage distributions and plant success.

Another method to examine the effects of soil microbial communities could be to alter the soil environment conditions. It has been suggested that the effects of microbial communities could be exacerbated or lessened by soil resource availability (Van Der Heijden *et al*., 2008; Miransari, 2010; Bennet & Klironomos, 2018). Consequently, alternative soil resource availability patterns could alter the effects of soil microbial communities on root stage distribution and plant success. Similarly, alternative temporal patterns of resource deposition could simulate different future conditions (climate change, fertilization, drought, etc.) providing an experimental platform to explore the effects of soil microbial communities on root stage distributions and plant success. In conjunction with further refinement of the effects of soil microbial communities, these alternative soil resource availability patterns could provide novel hypotheses for the interactive effects with soil microbial communities on root stage distributions.

While the suggestions above may provide methods to further elucidate the effects of soil resource availability patterns and soil microbial communities, a modification that considers these utilizing other metrics than those limited just to the last step of the model is appropriate. The analysis of each model developed in this dissertation was conducted on outputs measured only at the end of a simulation. There could be differences in the temporal behavior of root stage distributions, root growth patterns, and plant growth patterns in response to resource heterogeneity or microbial communities. It has been suggested that for some plants there is a short-term benefit followed by a long-term detriment when roots proliferate into a region of high resource availability (Pregitzer *et al.*, 1993; Leyser & Fitter, 1998; Zhang *et al.*, 1999; Hodge *et al.*, 2000; Hodge, 2004). Measuring root stage distributions and metrics of plant success using the outputs from the end of a simulation may be missing important aspects arising from transients of the plant. Other components of root foraging behavior may likewise produce ephemeral affects that are only measurable for a short time within a simulation.

Analysis of the root network, the distribution of root biomass, and the distribution of root biomass in each stage could provide additional metrics that measure the impact of environmental conditions on root stage distributions and root growth patterns. Unfortunately, the model design is not amenable to analysis using the usually defined and collected branchiness metrics. The "branches" within the root network do not represent a single root, as is required for most branchiness metrics, but instead indicate the amount of root biomass in each of the stages. Consequently, metrics other than branchiness must be utilized to analyze the root network structure.

One method of analysis could be to examine the horizontal and vertical distribution of total root biomass and root biomass in each stage in each soil column or row respectively. This metric could provide an indication of the spread of the root network and where root biomass is concentrated. An additional metric could be to measure the distribution of root biomass and root stage biomass as a function of distance from the central root cell. This metric could be used to determine where most root biomass is concentrated and could indicate the pattern of root network growth. Additionally, analyzing the root network could determine if differences in root network shape lead to differences in root stage distributions.

Although root network metrics could indicate differences in the shapes of the root network, different rooting strategies that favor directional growth may be unable to manifest in the model design. Currently, during the root network expansion phase in the model, there is no preference for vertical or horizontal growth; instead, expansion is solely based on resource availability within each adjacent cell. The model could be altered to reflect different rooting strategies by incorporating different weights for directional expansion. Under this modification, root network expansion would be dependent on resource availability within the adjacent cell and whether the adjacent cell expands the root network vertically or horizontally. Additionally, different weights for directional expansion could be applied to alter the constraints on the growth pattern of the root network. This model alteration could account for vertically or horizontally favored growth within the root network and could be used to examine differences in root stage distributions among different rooting strategies.

Despite model design efforts and the use of parameter space searches to reduce the number of parameters explored there is still a high level of complexity in each model developed here. A general theory of PSF could arise from reducing the complexity of the various models to focus on the factors influencing root stage distributions and the impact of changes in root stage distribution on root growth patterns and plant success. One method to reduce model complexity is to use allometric equations that relate root biomass to ABG biomass. In this model scheme, the ABG biomass transition rate and ABG growth component of the allocation strategy would be reduced to an equation. Reducing the number of allocation strategy components would greatly reduce the complexity of the model and provide a focus since allocation strategy has been shown to be a key driver of plant growth and root stage distributions. In all models developed here, the combined relative importance of each components of a plant's allocation strategy was consistently ranked the most important parameter for all metrics across all measured parameters. Similarly, for each model, the ABG biomass was positively related to root biomass and so reducing the ABG biomass to an allometric equation would not alter the metrics of plant success.

For most surviving plants across all the models, a majority of root biomass was consistently maintained in the first and last stages. This could be a result of the transient nature of the few middle stages, the production of new root biomass always being allocated to first stage biomass, and the accumulating behavior of the last stage. This necessarily focused the

analysis of root distribution on the proportions of root biomass in the first and last stages. Changing the process of new root growth allocation might encourage more realistic root growth and more accurately simulate root stage distributions.

Currently, new root biomass in already occupied cells is always allocated to the first stage biomass. This process could be changed such that new root biomass can be allocated to later stage biomass instead of only the first stage. Under this model process change, the allocation of new root biomass to each stage would be dependent on the distribution of biomass in each stage in an already occupied cell. Not only would this encourage later stage growth, but it would provide the plant with a mechanism to respond to regions of high resource availability in which it may be beneficial to continue producing early stage root biomass.

Furthermore, this process change would have the additional benefit of reducing the amount of root biomass that is needed to increase later stage root biomass. Currently within the models, for any amount of root biomass to reach later stages it must first transition through all previous stages. Because root biomass is reduced during transition, less biomass reaches each subsequent stage. This inevitably means only a very small proportion of first stage biomass ever survives to transition to later stages. Consequently, this process change would also increase later stage root biomass without root biomass needing to transition through earlier stages.

It would be beneficial to evaluate the model using data to determine if the model is accurately simulating realistic root stage distributions. However, model evaluation of root stage distribution is difficult because there are few datasets measuring the root stage distribution of a perennial woody plant over its lifetime. Nevertheless, other datasets are available that could evaluate other components of the model. One method of model evaluation is to compare model projections of above and belowground biomass. Although this would not evaluate the projections of root stage distributions, this comparison would compare the growth and aging components of the model to data to ensure they are realistically capturing plant growth dynamics. Another model evaluation would be to compare projections of root network spread (i.e. vertical and horizontal growth) and root foraging patterns. This would provide an opportunity to analyze the root network expansion component of the model. Regardless of the datasets used to evaluate the model, it is pertinent to continue evaluating model components to increase the confidence in the simulated root stage distributions.

Overall, the model framework developed in this dissertation provides an ideal platform for future explorations of the factors that affect root stage distribution and the impact of changes to root stage distribution on plant growth patterns and success. The suggestions of future directions provided here are all feasible to implement in the overall model framework. Changes in model assumptions could be used to examine the effects of environmental conditions on root stage distributions and the subsequent effect of changes to these distributions. The model framework is designed to be general and can be tailored for specific studies, providing opportunities to examine the unintended consequences of common community and individual level PSF model assumptions on root stage distributions and their subsequent impacts.

References

Augé RM, Sylvia DM, Park S, Buttery BR, Saxton AM, Moore JL, Cho K. 2004. Partitioning mycorrhizal influence on water relations of Phaseolus vulgaris into soil and plant components. *Canadian Journal of Botany* 82: 503–514.

Bardgett RD, Streeter TC, Bol R. **2003**. Soil Microbes Compete Effectively with Plants for Organic-Nitrogen Inputs to Temperate Grasslands. *Ecology* **84**: 1277–1287.

Bennett JA, Klironomos J. **2019**. Mechanisms of plant–soil feedback: interactions among biotic and abiotic drivers. *New Phytologist* **222**: 91–96.

Bever JD, Westover KM, Antonovics J. **1997**. Incorporating the Soil Community into Plant Population Dynamics: The Utility of the Feedback Approach. *Journal of Ecology* **85**: 561–573.

Bever JD. **2003**. Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. *New Phytologist* **157**: 465–473.

Bouma TJ, Yanai RD, Elkin AD, Hartmond U, Flores-Alva DE, Eissenstat DM. **2001**. Estimating age-dependent costs and benefits of roots with contrasting life span: Comparing apples and oranges. *New Phytologist* **150**: 685–695.

Bray SR, Kitajima K, Sylvia DM. **2003**. Mycorrhizae Differentially Alter Growth, Physiology, and Competitive Ability of an Invasive Shrub. *Ecological Applications* **13**: 565–574.

Bücking H, Kafle A. **2015**. Role of Arbuscular Mycorrhizal Fungi in the Nitrogen Uptake of Plants: Current Knowledge and Research Gaps. *Agronomy* **5**: 587–612.

Callaway RM, Thelen GC, Rodriguez A, Holben WE. **2004**. Soil biota and exotic plant invasion. *Nature* **427**: 731–733.

Ceccon C, Tagliavini M, Schmitt AO, Eissenstat DM. **2016**. Untangling the effects of root age and tissue nitrogen on root respiration in Populus tremuloides at different nitrogen supply. *Tree Physiology* **36**: 618–627.

Chen W, Koide RT, Adams TS, DeForest JL, Cheng L, Eissenstat DM. **2016**. Root morphology and mycorrhizal symbioses together shape nutrient foraging strategies of temperate trees. *Proceedings of the National Academy of Sciences* **113**: 8741 LP – 8746.

Chen W, Koide RT, Eissenstat DM. **2018**. Nutrient foraging by mycorrhizas: From species functional traits to ecosystem processes. *Functional Ecology* **32**: 858–869.

Claus A, George E. **2005**. Effect of stand age on fine-root biomass and biomass distribution in three European forest chronosequences. *Canadian Journal of Forest Research* **35**: 1617–1625.

De Reffye P, Fourcaud T, Blaise F, Barthélémy D, Houllier F. **1997**. A functional model of tree growth and tree architecture. *Silva Fennica* **31**: 297–311.

Drake JE, Gallet-Budynek A, Hofmockel KS, Bernhardt ES, Billings SA, Jackson RB, Johnsen KS, Lichter J, McCarthy HR, McCormack ML, et al. **2011**. Increases in the flux of carbon belowground stimulate nitrogen uptake and sustain the long-term enhancement of forest productivity under elevated CO2. *Ecology Letters* **14**: 349–357.

Eissenstat DM, Volder A. **2005**. The Efficiency of Nutrient Acquisition over the Life of a Root. In: BassiriRad H, ed. *Nutrient Acquisition by Plants: An Ecological Perspective*. Springer science & business media, 185-220.

Farrior CE, Dybzinski R, Levin S a, Pacala SW. **2013**. Competition for water and light in closed-canopy forests: a tractable model of carbon allocation with implications for carbon sinks. *The American naturalist* **181**: 314–30.

Fransen B, De Kroon H. **2001**. Long-term disadvantages of selective root placement: root proliferation and shoot biomass of two perennial grass species in a 2-year experiment. *Journal of Ecology* **89**: 711–722.

Gill RA, Burke IC, Lauenroth WK, Milchunas DG. **2002**. Longevity and turnover of roots in the shortgrass steppe: Influence of diameter and depth. *Plant Ecology* **159**: 241–251.

Grimm V, Berger U, DeAngelis DL, Polhill JG, Giske J, Railsback SF. **2010**. The ODD protocol: A review and first update. *Ecological Modelling* **221**: 2760–2768.

Gronberg H, Kaparakis G, Sen R. **2006**. Binucleate Rhizoctonia (Ceratorhiza spp.) as non-mycorrhizal endophytes alter Pinus sylvestris L. seedling root architecture and affect growth of rooted cuttings. *Scandinavian Journal of Forest Research* **21**: 450–457.

Guo D, Mitchell RJ, Withington JM, Fan P-P, Hendricks JJ. **2008a**. Endogenous and exogenous controls of root life span, mortality and nitrogen flux in a longleaf pine forest: root branch order predominates. *Journal of Ecology* **96**: 737–745.

Guo D, Xia M, Wei X, Chang W, Liu Y, Wang Z. **2008b**. Anatomical traits associated with absorption and mycorrhizal colonization are linked to root branch order in twenty-three Chinese temperate tree species. *New Phytologist* **180**: 673–683.

Hawkes C V., Wren IF, Herman DJ, Firestone MK. **2005**. Plant invasion alters nitrogen cycling by modifying the soil nitrifying community. *Ecology Letters* **8**: 976–985.

Helmisaari HS, Makkonen K, Kellomäki S, Valtonen E, Mälkönen E. **2002**. Below- and above-ground biomass, production and nitrogen use in Scots pine stands in eastern Finland. *Forest Ecology and Management* **165**: 317–326.

Hendrick RL, Pregitzer KS. **1992**. The Demography of Fine Roots in a Northern Hardwood Forest. *Ecology* **73**: 1094–1104.

Hendricks JJ, Nadelhoffer KJ, Aber JD. **1993**. Assessing the role of fine roots in carbon and nutrient cycling. *Trends in Ecology & Evolution* **8**: 174–178.

Herold M, Couclelis H, Clarke KC. **2005**. The role of spatial metrics in the analysis and modeling of urban land use change. *Computers, Environment and Urban Systems* **29**: 369–399.

Hodge A, Stewart J, Robinson D, Griffiths BS, Fitter AH. **2000**. Spatial and physical heterogeneity of N supply from soil does not influence N capture by two grass species. *Functional Ecology* **14**: 645–653.

Hodge A. **2004**. The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytologist* **162**: 9–24.

Hodge A. **2006**. Plastic plants and patchy soils. *Journal of Experimental Botany* **57**: 401–411.

Hu L, Robert CAM, Cadot S, Zhang X, Ye M, Li B, Manzo D, Chervet N, Steinger T, van der Heijden MGA, *et al.* 2018. Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota. *Nature Communications* **9**: 2738.

Hutchings MJ, de Kroon H. **1994**. Foraging in plants: the role of morphological plasticity in resource acquisition. *Advances in Ecological Research* **25**: 159-238

Inderjit, Wardle DA, Karban R, Callaway RM. **2011**. The ecosystem and evolutionary contexts of allelopathy. *Trends in Ecology & Evolution* **26**: 655–662.

Jiang J, DeAngelis DL. **2013**. Strong species-Environment feedback shapes plant community assembly along environmental gradients. *Ecology and Evolution* **3**: 4119–4128.

Joslin JD, Gaudinski JB, Torn MS, Riley WJ, Hanson PJ. **2006**. Fine-root turnover patterns and their relationship to root diameter and soil depth in a 14C-labeled hardwood forest. *New Phytologist* **172**: 523–535.

Kannenberg SA, Phillips RP. **2017**. Soil microbial communities buffer physiological responses to drought stress in three hardwood species. *Oecologia* **183**: 631–641.

Kardol P, Cornips NJ, Van Kempen MML, Bakx-Schotman JMT, Van Der Putten WH. **2007**. Microbe-mediated plant-soil feedback causes historical contingency effects in plant community assembly. *Ecological Monographs* **77**: 147–162.

Kardol P, Veen GFC, Teste FP, Perring MP. **2015**. Peeking into the black box: A trait-based approach to predicting plant-soil feedback. *New Phytologist* **206**: 1–4.

Ke P, Miki T, Ding T. **2015**. The soil microbial community predicts the importance of plant traits in plant – soil feedback. *New Phytologist* **206**: 329–341.

Klironomos JN. **2002**. Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* **417**: 67–70.

Kong D, Wu H, Wang M, Simmons M, Lü X, Yu Q, Han X. **2010**. Structural and chemical differences between shoot- and root-derived roots of three perennial grasses in a typical steppe in Inner Mongolia China. *Plant and Soil* **336**: 209–217.

Kourtev PS, Ehrenfeld JG, Häggblom M. **2003**. Experimental analysis of the effect of exotic and native plant species on the structure and function of soil microbial communities. *Soil Biology and Biochemistry* **35**: 895–905.

Kulmatiski A, Beard KH, Stevens JR, Cobbold SM. **2008**. Plant-soil feedbacks: A meta-analytical review. *Ecology Letters* **11**: 980–992.

Levine JM, Pachepsky E, Kendall BE, Yelenik SG, Lambers JHR. **2006**. Plant-soil feedbacks and invasive spread. *Ecology Letters* **9**: 1005–1014.

Leyser O, Fitter A. **1998**. Roots are branching out in patches. *Trends in plant science* **3**: 203–204.

Li HB, Zhang FS, Shen JB. **2012**. Contribution of Root Proliferation in Nutrient-Rich Soil Patches to Nutrient Uptake and Growth of Maize. *Pedosphere* **22**: 776–784.

Lovett Doust J. **1989**. Plant reproductive strategies and resource allocation. *Trends in Ecology & Evolution* **4**: 230–234.

Majdi H, Damm E, Nylund J-E. **2001**. Longevity of mycorrhizal roots depends on branching order and nutrient availability. *New Phytologist* **150**: 195–202.

Makita N, Kosugi Y, Dannoura M, Takanashi S, Niiyama K, Kassim AR, Nik AR. **2012**. Patterns of root respiration rates and morphological traits in 13 tree species in a tropical forest. *Tree Physiology* **32**: 303–312.

Mangan SA, Herre EA, Bever JD. **2010a**. Specificity between Neotropical tree seedlings and their fungal mutualists leads to plant–soil feedback. *Ecology* **91**: 2594–2603.

Mangan SA, Schnitzer SA, Herre EA, Mack KML, Valencia MC, Sanchez EI, Bever JD. **2010b**. Negative plant–soil feedback predicts tree-species relative abundance in a tropical forest. *Nature* **466**: 752–755.

Mangla S, Callaway RM. **2008**. Exotic invasive plant accumulates native soil pathogens which inhibit native plants. *Journal of Ecology* **96**: 58–67.

MATLAB and Statistical ToolBox Release 2018a 2019a 2020a. The MathWorks, Inc. Natick, Massachusetts, United States.

McCormack ML, Adams TS, Smithwick EAH, Eissenstat DM. **2012**. Predicting fine root lifespan from plant functional traits in temperate trees. *New Phytologist* **195**: 823–831.

McCormack ML, Dickie IA, Eissenstat DM, Fahey TJ, Fernandez CW, Guo D, Helmisaari HS, Hobbie EA, Iversen CM, Jackson RB, et al. **2015**. Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytologist* **207**: 505–518.

McGraw JB, Antonovics J. **1983**. Experimental Ecology of Dryas Octopetala Ecotypes: II. A Demographic Model of Growth, Branching and Fecundity. *Journal of Ecology* **71**: 899–912.

Meyer KM, Vos M, Mooij WM, Gera Hol WH, Termorshuizen AJ, Vet LEM, Van Der Putten WH. **2009**. Quantifying the impact of above- and belowground higher trophic levels on plant and herbivore performance by modeling. *Oikos* **118**: 981–990.

Miransari M. 2010. Contribution of arbuscular mycorrhizal symbiosis to plant growth under different types of soil stress. *Plant Biology* 12: 563–569.

Neatrour MA, Jones RH, Golladay SW. **2007**. Response of three floodplain tree species to spatial heterogeneity in soil oxygen and nutrients. *Journal of Ecology* **95**: 1274–1283.

Nilsson LO, Bååth E, Falkengren-Grerup U, Wallander H. **2007**. Growth of ectomycorrhizal mycelia and composition of soil microbial communities in oak forest soils along a nitrogen deposition gradient. *Oecologia* **153**: 375–384.

Palmer JF. **2004**. Using spatial metrics to predict scenic perception in a changing landscape: Dennis, Massachusetts. *Landscape and Urban Planning* **69**: 201–218.

Paula S, Pausas JG. **2011**. Root traits explain different foraging strategies between resprouting life histories. *Oecologia* **165**: 321–331.

Pierret A, Maeght JL, Clément C, Montoroi JP, Hartmann C, Gonkhamdee S. **2016**. Understanding deep roots and their functions in ecosystems: An advocacy for more unconventional research. *Annals of Botany* **118**: 621–635.

Porras-Soriano A, Soriano-Martín ML, Porras-Piedra A, Azcón R. **2009**. Arbuscular mycorrhizal fungi increased growth, nutrient uptake and tolerance to salinity in olive trees under nursery conditions. *Journal of Plant Physiology* **166**: 1350–1359.

Pregitzer KS, Hendrick RL, Fogel R. **1993**. The demography of fine roots in response to patches of water and nitrogen. *New Phytologist* **125**: 575–580.

Pregitzer KS, Laskowski MJ, Burton AJ, Lessard VC, Zak DR. **1998**. Variation in sugar maple root respiration with root diameter and soil depth. *Tree Physiology* **18**: 665–670.

Pregitzer KS. **2002**. Fine roots of trees – a new perspective. *New Phytologist* **154**: 267–273.

Prusinkiewicz P. **1998**. Modeling of spatial structure and development of plants: a review. *Scientia Horticulturae* **74**: 113–149.

Rastetter EB, Vitousek PM, Field C, Shaver GR, Herbert D, gren GI. **2001**. Resource Optimization and Symbiotic Nitrogen Fixation. *Ecosystems* **4**: 369–388.

Razouk R, Kajji A. **2015**. Effect of Arbuscular Mycorrhizal Fungi on Water Relations and Growth of Young Plum Trees under Severe Water Stress Conditions. *International Journal of Plant & Soil Science* **5**: 10.

Read DB, Bengough AG, Gregory PJ, Crawford JW, Robinson D, Scrimgeour CM, Young IM, Zhang K, Zhang X. **2003**. Plant roots release phospholipid surfactants that modify the physical and chemical properties of soil. *New Phytologist* **157**: 315–326.

Ryan PR, Delhaize E, Watt M, Richardson AE. **2016**. Plant roots: Understanding structure and function in an ocean of complexity. *Annals of Botany* **118**: 555–559.

Schaffer WM, Fox GA. **1989**. Plant strategies and the dynamics and structure of plant communities. *Bulletin of Mathematical Biology* **51**: 409–411.

Schroeder MS, Janos DP. **2005**. Plant growth, phosphorus nutrition, and root morphological responses to arbuscular mycorrhizas, phosphorus fertilization, and intraspecific density. *Mycorrhiza* **15**: 203–216.

Schweitzer JA, Juric I, van de Voorde TFJ, Clay K, van der Putten WH, Bailey JK. **2014**. Are there evolutionary consequences of plant-soil feedbacks along soil gradients? *Functional Ecology* **28**: 55–64.

Shi S, Richardson AE, O'Callaghan M, DeAngelis KM, Jones EE, Stewart A, Firestone MK, Condron LM. **2011**. Effects of selected root exudate components on soil bacterial communities. *FEMS Microbiology Ecology* **77**: 600–610.

Stodden V, Leisch F, Peng RD. **2014**. *Implementing reproducible research*. CRC Press, 2014.

Subramanian KS, Charest C, Dwyer LM, Hamilton RI. 1995. Arbuscular mycorrhizas and water relations in maize under drought stress at tasselling. *New Phytologist* 129: 643–650.

Tierney GL, Fahey TJ. **2002**. Fine root turnover in a northern hardwood forest: a direct comparison of the radiocarbon and minirhizotron methods. *Canadian Journal of Forest Research* **32**: 1692–1697.

Valenzuela-Estrada L, Vera-Caraballo V, Ruth L, Eissenstat D. **2008**. Root anatomy, morphology, and longevity among root orders in Vaccinium corymbosum (Ericaceae). *American journal of botany* **95**: 1506–1514.

Van Der Heijden MGA, Bardgett RD, Van Straalen NM. 2008. The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters* **11**: 296–310.

Van der Putten WH, Bardgett RD, Bever JD, Bezemer TM, Casper BB, Fukami T, Kardol P, Klironomos JN, Kulmatiski A, Schweitzer JA, et al. 2013. Plant-soil feedbacks: The past, the present and future challenges. *Journal of Ecology* **101**: 265–276.

Van Nuland ME, Wooliver RC, Pfennigwerth AA, Read QD, Ware IM, Mueller L, Fordyce JA, Schweitzer JA, Bailey JK. **2016**. Plant–soil feedbacks: connecting ecosystem ecology and evolution. *Functional Ecology* **30**: 1032–1042.

Vogt KA, Vogt DJ, Palmiotto PA, Boon P, O'Hara J, Asbjornsen H. **1995**. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. *Plant Soil* **187**: 159–219.

Volder A, Smart DR, Bloom AJ, Eissenstat DM. **2005**. Rapid decline in nitrate uptake and respiration with age in fine lateral roots of grape: Implications for root efficiency and competitive effectiveness. *New Phytologist* **165**: 493–501.

Wardle DA, Jonsson M, Bansal S, Bardgett RD, Gundale MJ, Metcalfe DB. **2012**. Linking vegetation change, carbon sequestration and biodiversity: Insights from island ecosystems in a long-term natural experiment. *Journal of Ecology* **100**: 16–30.

Weiner J. **2004**. Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology, Evolution and Systematics* **6**: 207–215.

Wells CE, Eissenstat DM. **2001**. Marked differences in survivorship among apple roots of different diameters. *Ecology* **82**: 882–892.

Wells CE, Eissenstat DM. **2002**. Beyond the roots of young seedlings: The influence of age and order on fine root physiology. *Journal of Plant Growth Regulation* **21**: 324–334.

West SA, Kiers ET, Simms EL, Denison RF. 2002. Sanctions and mutualism stability: why do rhizobia fix nitrogen? *Proceedings of the Royal Society B: Biological Sciences* **269**: 685–694.

Wiemken V, Laczko E, Ineichen K, Boller T. **2001**. Effects of Elevated Carbon Dioxide and Nitrogen Fertilization onMycorrhizal Fine Roots and the Soil Microbial Community in Beech-SpruceEcosystems on Siliceous and Calcareous Soil. *Microbial Ecology* **42**: 126–135.

Wu Q-S, He X-H, Zou Y-N, Liu C-Y, Xiao J, Li Y. **2012**. Arbuscular mycorrhizas alter root system architecture of Citrus tangerine through regulating metabolism of endogenous polyamines. *Plant Growth Regulation* **68**: 27–35.

Yao S, Merwin IA, Brown MG. **2006**. Root dynamics of apple rootstocks in a replanted orchard. *HortScience* **41**: 1149–1155.

Zaidi A, Khan M, Ahemad M, Oves M. **2009**. Plant growth promotion by phosphate solubilizing bacteria. *Acta Microbiologica et Immunologica Hungarica* **56**: 263–284.

Zhang H, Forde BG. **2000**. Regulation of Arabidopsis root development by nitrate availability. *Journal of Experimental Botany* **51**: 51–59.

Appendices
Appendix 1: Chapter 3

PATCHINESS METRIC

There are a variety of metrics used to quantify the patchiness of spatial patterns of resources, land use, plant coverage etc. on landscapes (Palmer, 2002; Herold *et al.*, 2003). These metrics are usually omnidirectional and viewing the landscape from any direction yields the same metric. Unfortunately, the spatial arrangement of soil resources in the model's 2D soil environment within which plants grow and expand is directional; plant directional growth in the soil environment is constrained. Furthermore, the spatial arrangement of soil resources within two soil environments may have the same patchiness metric, but the distances between areas of high/low availability and initial root network may be different within the soil environments. Without accounting for directionality, the metrics would not distinguish between soil environments where high availability patches are far from or close to the initial root network which could have drastic impact on overall root and plant growth. Consequently, the standard metrics of patchiness cannot be used here.

A new patchiness metric was devised for use with this model that accounts for the direction of resource availability and how availability changes across the distance from the central root network. The novel patchiness metric produces two values, 1) the measure of patchiness; the linearity of resource availability and 2) the direction of change in resource availability as the distance from the initial root network increases. Soil environment patchiness ranges between 0 and 1 and soil environment "direction" has no boundaries. The qualitative description of each metric can be found in Table 2.

The soil environment patchiness value is produced by averaging the linear correlation between cell distance from the central root cell with availability whilst the patchiness direction is produced by averaging the slopes of this linear correlation. The data needed to produce these metrics are obtained by examining the resource availability of cells along paths produced by starting at the central cell going to the cells along the edge of the tracked soil environment. Along a path, the resource availability in each cell and its cell distance from the central root cell are recorded. This data is then used to determine the R^2 value and slope of a least squared

regression line. Multiple paths are formed for a given soil environment and the average R^2 value and average slope become the patchiness metric and patchiness direction respectively.

Paths are formed starting from the central root cell going towards each edge cell. These paths must always take the shortest path available and constantly move away from the central root cell. This constrains each path to have the exact same number of cells and ensures the directionality of the patchiness measures. For edge cells on the left side of the soil environment, paths always go leftwards and downwards (in any combination) and for edge cells on the right of the soil environment, paths always go rightwards and downwards (in any combination). Even with these constraints on path formation, there are multiple paths that can be produced when going from the central root cell to an edge cell. Consequently, multiple paths going to each edge cell are produced to measure the variation in resource availability. However, those edge cells in the corner only have 1 possible path, given the shortest path constraint, and so these cells only have 1 path produced.

After all paths are produced and their availability is recorded, the R^2 value and slope of the least squared regression line for each path is obtained. The R^2 values of each path are averaged to determine the average linear correlation of resource availability with distance from the central root cell. This averaged R^2 value is the soil environment patchiness. Similarly, the slopes of all paths are averaged to determine the average slope of the linear relationship between resource availability and distance from the central root cell. This average slope value is the patchiness direction. Together, these two metrics are used to describe the patchiness of a soil environment.

The soil environment patchiness (R^2) describes the linearity of resource availability and the patchiness direction (slope) describes the change in availability radiating away from the central root cell respectively. An average R^2 value approaching 1 indicates that most of the produced paths have an R^2 value close to 1 signifying a tight correlation between resource availability and distance from the central root cells. Conversely, an average R^2 value approaching 0 indicates that most of the produced paths have an R^2 value close to 0 signifying almost no correlation between resource availability and distance from the central root cells. Slopes that are much greater than 0 indicate that, on average, resource availability increases with distance from the central root cell signifying that resource availability is lower closer to the

initial root network. Slopes that are much less than 0 indicate that, on average, resource availability decreases with distance from the central root cell signifying that resource availability is higher closer to the initial root network (S. Figure 1).

Additionally, the constraints in path formation ensure these metrics are directional. The produced paths radiate outwards from the central root cell and are always move towards the destination edge cell. Therefore, any change in starting position will inevitably alter the set of cells and the order with which those cells are reached along each path. This directionality reflects the constraints on plant growth within the modeled soil environment.

TRANSPORT CAPACITY ANOVA

The results of the following ANOVA tests were obtained using the anova1 and multcompare functions in MATLAB 2020A. Transport capacity was discretized into 15 groups within which the model outputs were averaged. The table beneath the ANOVA results indicate the pair-wise comparisons. The fourth column (Mean Diff) indicates the difference between the estimated group means. The third and fifth columns (Lower95 CI and Upper95 CI) indicate the lower and upper limits for 95% confidence intervals for the true mean difference. The sixth column (p-value) indicates the p-value for a hypothesis test that the mean difference is zero. Any p-values greater than 0.05 are indicated in red.

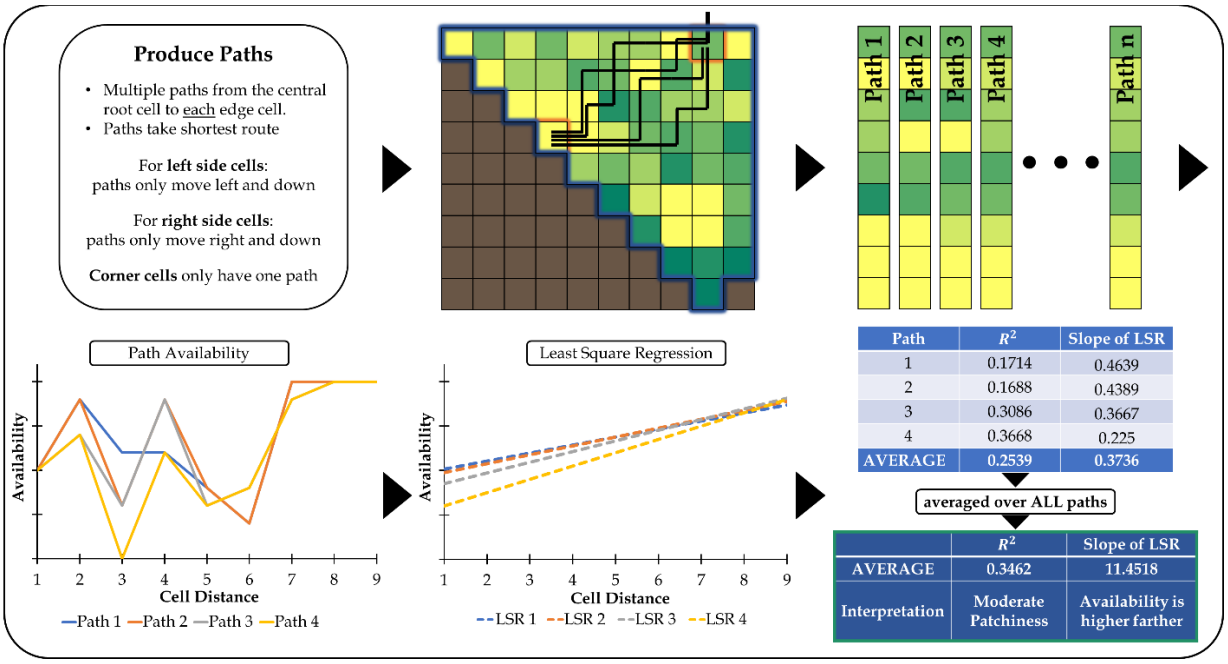

Figure 24 Patchiness Metric
A visualization of how patchiness metrics are determined for an example soil resource availability pattern.

Table 6. Transport Capacity and Root Biomass ANOVA
The results of the ANOVA to measure the differences in the last step root biomass between plants with different maximum transport capacities. Transport capacity was discretized into 15 groups. The first section is the ANOVA results and the second section contains the group comparisons.

Root Biomass					
Source	**SS**	**DF**	**MS**	**F**	**Prob>f**
Groups	207512447267.10	14	14822317661.94	7000.82	0
Error	557382765184.88	263261	2117224.98		
Total	764895212451.96	263275			

Group1	Group2	Lower95 CI	Mean Diff	Upper95 CI	p-value
1	2	-239.60	-190.65	-141.69	0.00
1	3	-421.76	-372.35	-322.94	0.00
1	4	-620.71	-570.94	-521.18	0.00
1	5	-820.49	-770.24	-719.98	0.00
1	6	-1002.65	-952.07	-901.48	0.00
1	7	-1229.02	-1178.36	-1127.70	0.00
1	8	-1427.04	-1376.25	-1325.46	0.00
1	9	-1647.61	-1596.64	-1545.67	0.00
1	10	-1845.13	-1794.07	-1743.01	0.00
1	11	-2064.40	-2013.06	-1961.73	0.00
1	12	-2277.85	-2226.46	-2175.08	0.00

Table 6 continued

1	13	-2503.58	-2452.13	-2400.68	0.00
1	14	-2659.97	-2608.34	-2556.70	0.00
1	15	-2886.26	-2834.01	-2781.76	0.00
2	3	-231.80	-181.70	-131.60	0.00
2	4	-430.74	-380.30	-329.85	0.00
2	5	-630.52	-579.59	-528.66	0.00
2	6	-812.68	-761.42	-710.17	0.00
2	7	-1039.04	-987.71	-936.38	0.00
2	8	-1237.07	-1185.61	-1134.15	0.00
2	9	-1457.63	-1405.99	-1354.36	0.00
2	10	-1655.15	-1603.42	-1551.70	0.00
2	11	-1874.41	-1822.42	-1770.42	0.00
2	12	-2087.86	-2035.82	-1983.78	0.00
2	13	-2313.59	-2261.48	-2209.38	0.00
2	14	-2469.98	-2417.69	-2365.40	0.00
2	15	-2696.26	-2643.36	-2590.46	0.00
3	4	-249.48	-198.60	-147.71	0.00
3	5	-449.26	-397.89	-346.52	0.00
3	6	-631.41	-579.72	-528.03	0.00
3	7	-857.78	-806.01	-754.24	0.00
3	8	-1055.80	-1003.91	-952.01	0.00
3	9	-1276.36	-1224.29	-1172.22	0.00
3	10	-1473.88	-1421.72	-1369.56	0.00
3	11	-1693.14	-1640.72	-1588.29	0.00
3	12	-1906.59	-1854.12	-1801.64	0.00
3	13	-2132.32	-2079.78	-2027.25	0.00
3	14	-2288.71	-2235.99	-2183.27	0.00
3	15	-2514.98	-2461.66	-2408.34	0.00
4	5	-251.00	-199.29	-147.59	0.00
4	6	-433.15	-381.13	-329.10	0.00
4	7	-659.52	-607.41	-555.31	0.00
4	8	-857.54	-805.31	-753.08	0.00
4	9	-1078.10	-1025.69	-973.29	0.00
4	10	-1275.61	-1223.12	-1170.64	0.00
4	11	-1494.88	-1442.12	-1389.36	0.00
4	12	-1708.32	-1655.52	-1602.72	0.00
4	13	-1934.05	-1881.19	-1828.32	0.00
4	14	-2090.45	-2037.39	-1984.34	0.00
4	15	-2316.71	-2263.06	-2209.42	0.00
5	6	-234.33	-181.83	-129.33	0.00

Table 6 continued

5	7	-460.70	-408.12	-355.54	0.00
5	8	-658.72	-606.02	-553.32	0.00
5	9	-879.27	-826.40	-773.53	0.00
5	10	-1076.79	-1023.83	-970.87	0.00
5	11	-1296.05	-1242.83	-1189.60	0.00
5	12	-1509.49	-1456.22	-1402.95	0.00
5	13	-1735.22	-1681.89	-1628.56	0.00
5	14	-1891.61	-1838.10	-1784.58	0.00
5	15	-2117.88	-2063.77	-2009.66	0.00
6	7	-279.18	-226.29	-173.40	0.00
6	8	-477.20	-424.18	-371.17	0.00
6	9	-697.75	-644.57	-591.38	0.00
6	10	-895.27	-842.00	-788.73	0.00
6	11	-1114.53	-1061.00	-1007.46	0.00
6	12	-1327.97	-1274.39	-1220.82	0.00
6	13	-1553.70	-1500.06	-1446.42	0.00
6	14	-1710.09	-1656.27	-1602.44	0.00
6	15	-1936.35	-1881.94	-1827.53	0.00
7	8	-250.98	-197.90	-144.81	0.00
7	9	-471.54	-418.28	-365.02	0.00
7	10	-669.05	-615.71	-562.37	0.00
7	11	-888.31	-834.71	-781.10	0.00
7	12	-1101.76	-1048.10	-994.45	0.00
7	13	-1327.48	-1273.77	-1220.06	0.00
7	14	-1483.88	-1429.98	-1376.08	0.00
7	15	-1710.13	-1655.65	-1601.17	0.00
8	9	-273.77	-220.38	-167.00	0.00
8	10	-471.28	-417.82	-364.35	0.00
8	11	-690.54	-636.81	-583.08	0.00
8	12	-903.98	-850.21	-796.44	0.00
8	13	-1129.71	-1075.88	-1022.04	0.00
8	14	-1286.10	-1232.08	-1178.06	0.00
8	15	-1512.36	-1457.75	-1403.15	0.00
9	10	-251.07	-197.43	-143.79	0.00
9	11	-470.32	-416.43	-362.53	0.00
9	12	-683.77	-629.82	-575.88	0.00
9	13	-909.50	-855.49	-801.48	0.00
9	14	-1065.89	-1011.70	-957.51	0.00
9	15	-1292.14	-1237.37	-1182.60	0.00
10	11	-272.98	-219.00	-165.01	0.00

Table 6 continued

10	12	-486.42	-432.39	-378.37	0.00
10	13	-712.15	-658.06	-603.97	0.00
10	14	-868.54	-814.27	-760.00	0.00
10	15	-1094.79	-1039.94	-985.09	0.00
11	12	-267.69	-213.40	-159.11	0.00
11	13	-493.41	-439.06	-384.72	0.00
11	14	-649.80	-595.27	-540.74	0.00
11	15	-876.05	-820.94	-765.84	0.00
12	13	-280.06	-225.67	-171.27	0.00
12	14	-436.45	-381.87	-327.30	0.00
12	15	-662.70	-607.54	-552.39	0.00
13	14	-210.84	-156.21	-101.57	0.00
13	15	-437.09	-381.88	-326.66	0.00
14	15	-281.06	-225.67	-170.28	0.00

Table 7. Transport Capacity and Root Network Size ANOVA
The results of the ANOVA to measure the differences in the last step root network size between plants with different maximum transport capacities. Transport capacity was discretized into 15 groups. The first section is the ANOVA results and the second section contains the group comparisons.

Root Network Size					
Source	**SS**	**DF**	**MS**	**F**	**Prob>f**
Groups	1353082632.77	14	96648759.48	3400.04	0
Error	7483390461.89	263261	28425.75		
Total	8836473094.66	263275			

Group1	Group2	Lower95 CI	Mean Diff	Upper95 CI	p-value
1	2	-21.38	-15.70	-10.03	0.00
1	3	-36.81	-31.08	-25.36	0.00
1	4	-52.21	-46.44	-40.67	0.00
1	5	-69.32	-63.49	-57.67	0.00
1	6	-83.69	-77.83	-71.97	0.00
1	7	-101.34	-95.47	-89.60	0.00
1	8	-117.51	-111.63	-105.74	0.00
1	9	-131.80	-125.90	-119.99	0.00
1	10	-151.50	-145.58	-139.66	0.00
1	11	-165.10	-159.15	-153.20	0.00
1	12	-184.21	-178.25	-172.30	0.00
1	13	-203.07	-197.11	-191.15	0.00
1	14	-220.30	-214.31	-208.33	0.00
1	15	-237.23	-231.17	-225.12	0.00
2	3	-21.19	-15.38	-9.58	0.00
2	4	-36.58	-30.74	-24.89	0.00
2	5	-53.69	-47.79	-41.89	0.00
2	6	-68.06	-62.12	-56.18	0.00
2	7	-85.71	-79.76	-73.82	0.00
2	8	-101.89	-95.92	-89.96	0.00
2	9	-116.18	-110.19	-104.21	0.00
2	10	-135.87	-129.88	-123.88	0.00
2	11	-149.47	-143.45	-137.42	0.00
2	12	-168.58	-162.55	-156.52	0.00
2	13	-187.45	-181.41	-175.37	0.00
2	14	-204.67	-198.61	-192.55	0.00
2	15	-221.60	-215.47	-209.34	0.00
3	4	-21.25	-15.35	-9.46	0.00
3	5	-38.36	-32.41	-26.46	0.00
3	6	-52.73	-46.74	-40.75	0.00
3	7	-70.38	-64.38	-58.38	0.00

Table 7 continued

3	8	-86.56	-80.54	-74.53	0.00
3	9	-100.85	-94.81	-88.78	0.00
3	10	-120.54	-114.50	-108.45	0.00
3	11	-134.14	-128.07	-121.99	0.00
3	12	-153.25	-147.17	-141.09	0.00
3	13	-172.11	-166.03	-159.94	0.00
3	14	-189.34	-183.23	-177.12	0.00
3	15	-206.26	-200.09	-193.91	0.00
4	5	-23.05	-17.05	-11.06	0.00
4	6	-37.42	-31.39	-25.36	0.00
4	7	-55.07	-49.03	-42.99	0.00
4	8	-71.24	-65.19	-59.14	0.00
4	9	-85.53	-79.46	-73.38	0.00
4	10	-105.22	-99.14	-93.06	0.00
4	11	-118.83	-112.71	-106.60	0.00
4	12	-137.93	-131.81	-125.70	0.00
4	13	-156.80	-150.67	-144.55	0.00
4	14	-174.02	-167.87	-161.73	0.00
4	15	-190.95	-184.73	-178.52	0.00
5	6	-20.42	-14.33	-8.25	0.00
5	7	-38.07	-31.97	-25.88	0.00
5	8	-54.24	-48.14	-42.03	0.00
5	9	-68.53	-62.40	-56.28	0.00
5	10	-88.22	-82.09	-75.95	0.00
5	11	-101.83	-95.66	-89.49	0.00
5	12	-120.93	-114.76	-108.59	0.00
5	13	-139.80	-133.62	-127.44	0.00
5	14	-157.02	-150.82	-144.62	0.00
5	15	-173.95	-167.68	-161.41	0.00
6	7	-23.77	-17.64	-11.51	0.00
6	8	-39.94	-33.80	-27.66	0.00
6	9	-54.23	-48.07	-41.91	0.00
6	10	-73.93	-67.75	-61.58	0.00
6	11	-87.53	-81.33	-75.12	0.00
6	12	-106.64	-100.43	-94.22	0.00
6	13	-125.50	-119.29	-113.07	0.00
6	14	-142.72	-136.49	-130.25	0.00
6	15	-159.65	-153.34	-147.04	0.00
7	8	-22.31	-16.16	-10.01	0.00
7	9	-36.60	-30.43	-24.26	0.00

Table 7 continued

7	10	-56.29	-50.11	-43.93	0.00
7	11	-69.90	-63.68	-57.47	0.00
7	12	-89.00	-82.79	-76.57	0.00
7	13	-107.87	-101.64	-95.42	0.00
7	14	-125.09	-118.85	-112.60	0.00
7	15	-142.02	-135.70	-129.39	0.00
8	9	-20.45	-14.27	-8.08	0.00
8	10	-40.15	-33.95	-27.76	0.00
8	11	-53.75	-47.52	-41.30	0.00
8	12	-72.86	-66.63	-60.39	0.00
8	13	-91.72	-85.48	-79.25	0.00
8	14	-108.94	-102.69	-96.43	0.00
8	15	-125.87	-119.54	-113.22	0.00
9	10	-25.90	-19.68	-13.47	0.00
9	11	-39.50	-33.26	-27.01	0.00
9	12	-58.61	-52.36	-46.11	0.00
9	13	-77.47	-71.22	-64.96	0.00
9	14	-94.70	-88.42	-82.14	0.00
9	15	-111.62	-105.27	-98.93	0.00
10	11	-19.83	-13.57	-7.32	0.00
10	12	-38.93	-32.67	-26.41	0.00
10	13	-57.80	-51.53	-45.26	0.00
10	14	-75.02	-68.73	-62.44	0.00
10	15	-91.95	-85.59	-79.23	0.00
11	12	-25.39	-19.10	-12.81	0.00
11	13	-44.26	-37.96	-31.66	0.00
11	14	-61.48	-55.16	-48.84	0.00
11	15	-78.40	-72.02	-65.63	0.00
12	13	-25.16	-18.86	-12.56	0.00
12	14	-42.38	-36.06	-29.74	0.00
12	15	-59.31	-52.92	-46.53	0.00
13	14	-23.53	-17.20	-10.87	0.00
13	15	-40.46	-34.06	-27.66	0.00
14	15	-23.28	-16.86	-10.44	0.00

Table 8. Transport Capacity and Proportion in Stage 1 ANOVA
The results of the ANOVA to measure the differences in the last step proportion of root biomass in stage 1 between plants with different maximum transport capacities. Transport capacity was discretized into 15 groups. The first section is the ANOVA results and the second section contains the group comparisons.

Proportion in Stage 1					
Source	**SS**	**DF**	**MS**	**F**	**Prob>f**
Groups	87.13	14	6.22	2267.16	0
Error	722.67	263261	0.003		
Total	809.80	263275			

Group1	Group2	Lower95 CI	Mean Diff	Upper95 CI	p-value
1	2	-0.0292	-0.0275	-0.0257	0.0000
1	3	-0.0433	-0.0415	-0.0397	0.0000
1	4	-0.0509	-0.0491	-0.0473	0.0000
1	5	-0.0561	-0.0543	-0.0524	0.0000
1	6	-0.0599	-0.0581	-0.0563	0.0000
1	7	-0.0622	-0.0603	-0.0585	0.0000
1	8	-0.0633	-0.0615	-0.0596	0.0000
1	9	-0.0647	-0.0628	-0.0610	0.0000
1	10	-0.0652	-0.0634	-0.0615	0.0000
1	11	-0.0657	-0.0638	-0.0620	0.0000
1	12	-0.0650	-0.0632	-0.0613	0.0000
1	13	-0.0641	-0.0623	-0.0604	0.0000
1	14	-0.0635	-0.0616	-0.0598	0.0000
1	15	-0.0628	-0.0610	-0.0591	0.0000
2	3	-0.0158	-0.0140	-0.0122	0.0000
2	4	-0.0235	-0.0217	-0.0198	0.0000
2	5	-0.0286	-0.0268	-0.0249	0.0000
2	6	-0.0325	-0.0306	-0.0288	0.0000
2	7	-0.0347	-0.0329	-0.0310	0.0000
2	8	-0.0358	-0.0340	-0.0321	0.0000
2	9	-0.0372	-0.0354	-0.0335	0.0000
2	10	-0.0378	-0.0359	-0.0340	0.0000
2	11	-0.0382	-0.0364	-0.0345	0.0000
2	12	-0.0376	-0.0357	-0.0338	0.0000
2	13	-0.0367	-0.0348	-0.0330	0.0000
2	14	-0.0360	-0.0341	-0.0323	0.0000
2	15	-0.0354	-0.0335	-0.0316	0.0000
3	4	-0.0095	-0.0076	-0.0058	0.0000
3	5	-0.0146	-0.0128	-0.0109	0.0000
3	6	-0.0185	-0.0166	-0.0147	0.0000
3	7	-0.0207	-0.0188	-0.0170	0.0000

Table 8 continued

3	8	-0.0218	-0.0200	-0.0181	0.0000
3	9	-0.0232	-0.0214	-0.0195	0.0000
3	10	-0.0238	-0.0219	-0.0200	0.0000
3	11	-0.0242	-0.0224	-0.0205	0.0000
3	12	-0.0236	-0.0217	-0.0198	0.0000
3	13	-0.0227	-0.0208	-0.0189	0.0000
3	14	-0.0220	-0.0201	-0.0182	0.0000
3	15	-0.0214	-0.0195	-0.0175	0.0000
4	5	-0.0070	-0.0051	-0.0033	0.0000
4	6	-0.0108	-0.0090	-0.0071	0.0000
4	7	-0.0131	-0.0112	-0.0093	0.0000
4	8	-0.0142	-0.0123	-0.0104	0.0000
4	9	-0.0156	-0.0137	-0.0118	0.0000
4	10	-0.0161	-0.0142	-0.0123	0.0000
4	11	-0.0166	-0.0147	-0.0128	0.0000
4	12	-0.0159	-0.0140	-0.0121	0.0000
4	13	-0.0151	-0.0132	-0.0113	0.0000
4	14	-0.0144	-0.0125	-0.0106	0.0000
4	15	-0.0138	-0.0118	-0.0099	0.0000
5	6	-0.0057	-0.0038	-0.0019	0.0000
5	7	-0.0080	-0.0061	-0.0042	0.0000
5	8	-0.0091	-0.0072	-0.0053	0.0000
5	9	-0.0105	-0.0086	-0.0067	0.0000
5	10	-0.0110	-0.0091	-0.0072	0.0000
5	11	-0.0115	-0.0096	-0.0077	0.0000
5	12	-0.0108	-0.0089	-0.0070	0.0000
5	13	-0.0100	-0.0080	-0.0061	0.0000
5	14	-0.0093	-0.0074	-0.0054	0.0000
5	15	-0.0086	-0.0067	-0.0047	0.0000
6	7	-0.0042	-0.0022	-0.0003	0.0056
6	8	-0.0053	-0.0034	-0.0015	0.0000
6	9	-0.0067	-0.0048	-0.0028	0.0000
6	10	-0.0072	-0.0053	-0.0034	0.0000
6	11	-0.0077	-0.0058	-0.0038	0.0000
6	12	-0.0070	-0.0051	-0.0032	0.0000
6	13	-0.0061	-0.0042	-0.0023	0.0000
6	14	-0.0055	-0.0035	-0.0016	0.0000
6	15	-0.0048	-0.0029	-0.0009	0.0001
7	8	-0.0030	-0.0011	0.0008	0.7982
7	9	-0.0044	-0.0025	-0.0006	0.0009

Table 8 continued

7	10	-0.0050	-0.0030	-0.0011	0.0000
7	11	-0.0054	-0.0035	-0.0016	0.0000
7	12	-0.0048	-0.0028	-0.0009	0.0001
7	13	-0.0039	-0.0020	0.0000	0.0407
7	14	-0.0032	-0.0013	0.0007	0.6278
7	15	-0.0026	-0.0006	0.0013	0.9992
8	9	-0.0033	-0.0014	0.0005	0.4876
8	10	-0.0038	-0.0019	0.0000	0.0541
8	11	-0.0043	-0.0024	-0.0005	0.0026
8	12	-0.0036	-0.0017	0.0002	0.1576
8	13	-0.0028	-0.0008	0.0011	0.9798
8	14	-0.0021	-0.0002	0.0018	1.0000
8	15	-0.0015	0.0005	0.0025	0.9999
9	10	-0.0025	-0.0005	0.0014	0.9998
9	11	-0.0029	-0.0010	0.0009	0.9132
9	12	-0.0023	-0.0003	0.0016	1.0000
9	13	-0.0014	0.0005	0.0025	0.9998
9	14	-0.0007	0.0012	0.0032	0.7204
9	15	-0.0001	0.0019	0.0039	0.0793
10	11	-0.0024	-0.0005	0.0015	1.0000
10	12	-0.0017	0.0002	0.0022	1.0000
10	13	-0.0009	0.0011	0.0030	0.8729
10	14	-0.0002	0.0018	0.0037	0.1385
10	15	0.0004	0.0024	0.0044	0.0031
11	12	-0.0013	0.0007	0.0026	0.9977
11	13	-0.0004	0.0015	0.0035	0.3174
11	14	0.0003	0.0022	0.0042	0.0101
11	15	0.0009	0.0029	0.0049	0.0001
12	13	-0.0011	0.0009	0.0028	0.9771
12	14	-0.0004	0.0015	0.0035	0.3240
12	15	0.0002	0.0022	0.0042	0.0134
13	14	-0.0013	0.0007	0.0027	0.9978
13	15	-0.0006	0.0013	0.0033	0.5932
14	15	-0.0013	0.0007	0.0027	0.9986

Table 9. Transport Capacity and Proportion in Stage 5 ANOVA
The results of the ANOVA to measure the differences in the last step proportion of root biomass in stage 5 between plants with different maximum transport capacities. Transport capacity was discretized into 15 groups. The first section is the ANOVA results and the second section contains the group comparisons.

Proportion in Stage 5					
Source	**SS**	**DF**	**MS**	**F**	**Prob>f**
Groups	23.07	14	1.65	559.51	0
Error	775.21	263261	0.003		
Total	798.28	263275			

Group1	Group2	Lower95 CI	Mean Diff	Upper95 CI	p-value
1	2	0.013	0.015	0.017	0.000
1	3	0.022	0.024	0.026	0.000
1	4	0.026	0.028	0.030	0.000
1	5	0.029	0.031	0.032	0.000
1	6	0.030	0.032	0.034	0.000
1	7	0.031	0.033	0.035	0.000
1	8	0.031	0.033	0.035	0.000
1	9	0.032	0.034	0.036	0.000
1	10	0.031	0.033	0.035	0.000
1	11	0.032	0.033	0.035	0.000
1	12	0.030	0.032	0.034	0.000
1	13	0.029	0.031	0.032	0.000
1	14	0.028	0.030	0.032	0.000
1	15	0.027	0.029	0.031	0.000
2	3	0.007	0.008	0.010	0.000
2	4	0.011	0.012	0.014	0.000
2	5	0.013	0.015	0.017	0.000
2	6	0.015	0.017	0.019	0.000
2	7	0.016	0.018	0.020	0.000
2	8	0.016	0.018	0.020	0.000
2	9	0.017	0.018	0.020	0.000
2	10	0.016	0.018	0.020	0.000
2	11	0.016	0.018	0.020	0.000
2	12	0.015	0.017	0.019	0.000
2	13	0.013	0.015	0.017	0.000
2	14	0.012	0.014	0.016	0.000
2	15	0.011	0.013	0.015	0.000
3	4	0.002	0.004	0.006	0.000
3	5	0.005	0.007	0.009	0.000
3	6	0.007	0.009	0.011	0.000
3	7	0.007	0.009	0.011	0.000

Table 9 continued

3	8	0.007	0.009	0.011	0.000
3	9	0.008	0.010	0.012	0.000
3	10	0.008	0.010	0.011	0.000
3	11	0.008	0.010	0.012	0.000
3	12	0.006	0.008	0.010	0.000
3	13	0.005	0.007	0.009	0.000
3	14	0.004	0.006	0.008	0.000
3	15	0.003	0.005	0.007	0.000
4	5	0.001	0.003	0.005	0.000
4	6	0.003	0.005	0.007	0.000
4	7	0.003	0.005	0.007	0.000
4	8	0.003	0.005	0.007	0.000
4	9	0.004	0.006	0.008	0.000
4	10	0.004	0.006	0.008	0.000
4	11	0.004	0.006	0.008	0.000
4	12	0.002	0.004	0.006	0.000
4	13	0.001	0.003	0.005	0.000
4	14	0.000	0.002	0.004	0.077
4	15	-0.001	0.001	0.003	0.962
5	6	0.000	0.002	0.004	0.145
5	7	0.000	0.002	0.004	0.003
5	8	0.001	0.003	0.005	0.001
5	9	0.001	0.003	0.005	0.000
5	10	0.001	0.003	0.005	0.000
5	11	0.001	0.003	0.005	0.000
5	12	-0.001	0.001	0.003	0.589
5	13	-0.002	0.000	0.002	1.000
5	14	-0.003	-0.001	0.001	0.935
5	15	-0.004	-0.002	0.000	0.068
6	7	-0.001	0.001	0.003	0.999
6	8	-0.001	0.001	0.003	0.990
6	9	-0.001	0.001	0.003	0.510
6	10	-0.001	0.001	0.003	0.958
6	11	-0.001	0.001	0.003	0.855
6	12	-0.002	0.000	0.002	1.000
6	13	-0.004	-0.002	0.000	0.148
6	14	-0.005	-0.003	-0.001	0.000
6	15	-0.006	-0.004	-0.002	0.000
7	8	-0.002	0.000	0.002	1.000
7	9	-0.001	0.001	0.003	0.995

Table 9 continued

7	10	-0.002	0.000	0.002	1.000
7	11	-0.002	0.000	0.002	1.000
7	12	-0.003	-0.001	0.001	0.904
7	13	-0.004	-0.002	0.000	0.003
7	14	-0.005	-0.003	-0.001	0.000
7	15	-0.006	-0.004	-0.002	0.000
8	9	-0.001	0.001	0.003	0.999
8	10	-0.002	0.000	0.002	1.000
8	11	-0.002	0.000	0.002	1.000
8	12	-0.003	-0.001	0.001	0.791
8	13	-0.005	-0.003	-0.001	0.001
8	14	-0.006	-0.004	-0.002	0.000
8	15	-0.007	-0.004	-0.002	0.000
9	10	-0.002	0.000	0.002	1.000
9	11	-0.002	0.000	0.002	1.000
9	12	-0.004	-0.002	0.000	0.138
9	13	-0.005	-0.003	-0.001	0.000
9	14	-0.006	-0.004	-0.002	0.000
9	15	-0.007	-0.005	-0.003	0.000
10	11	-0.002	0.000	0.002	1.000
10	12	-0.003	-0.001	0.001	0.628
10	13	-0.005	-0.003	-0.001	0.000
10	14	-0.006	-0.004	-0.002	0.000
10	15	-0.007	-0.005	-0.003	0.000
11	12	-0.004	-0.002	0.001	0.416
11	13	-0.005	-0.003	-0.001	0.000
11	14	-0.006	-0.004	-0.002	0.000
11	15	-0.007	-0.005	-0.003	0.000
12	13	-0.003	-0.001	0.001	0.583
12	14	-0.004	-0.002	0.000	0.008
12	15	-0.005	-0.003	-0.001	0.000
13	14	-0.003	-0.001	0.001	0.958
13	15	-0.004	-0.002	0.000	0.096
14	15	-0.003	-0.001	0.001	0.964

Appendix 2: Chapter 4

SOIL MICROBIAL COMMUNITY ANOVA

The results of the following ANOVA tests were obtained using the anova1 and multcompare functions in MATLAB 2020A. Each ANOVA analysis was conducted within each soil microbial community group though only the results of communities C, D, E are included here. The table beneath the ANOVA results indicate the pair-wise comparisons. The fourth column (Mean Diff) indicates the difference between the estimated group means. The third and fifth columns (Lower95 CI and Upper95 CI) indicate the lower and upper limits for 95% confidence intervals for the true mean difference. The sixth column (p-value) indicates the p-value for a hypothesis test that the mean difference is zero. Any p-values greater than 0.05 are indicated in red.

Table 10. SMC and Proportion in Stage 1 ANOVA
The results of the ANOVA to measure the differences in the last step proportion of root biomass in stage 1 between plants with different soil microbial communities. Only those soil microbial community groups that had significant difference are included.

PROPORTION IN STAGE 1					
Group C					
Source	**SS**	**DF**	**MS**	**F**	**Prob>f**
Groups	1.83	4	0.46	28.24	1.95e-23
Error	377.80	23884	0.02		
Total	379.63	23888			
Group D					
Source	**SS**	**DF**	**MS**	**F**	**Prob>f**
Groups	2.30	4	0.57	33.14	1.33e-27
Error	407.40	23530	0.02		
Total	409.65	23534			
Group E					
Source	**SS**	**DF**	**MS**	**F**	**Prob>f**
Groups	3.32	4	0.83	45.39	4.86e-38
Error	431.02	23573	0.02		
Total	434.33	23577			

Table 11. SMC Group C and Proportion in Stage 1 ANOVA
The group comparison results of the ANOVA to measure the differences in the last step proportion of root biomass in stage 1 between plants with different soil microbial communities. The soil microbial communities included here are in group C.

Soil Microbial Group C					
Group1	**Group2**	**Lower95 CI**	**Mean Diff**	**Upper95 CI**	**p-value**
1	2	-0.003	0.004	0.011	0.554
1	3	-0.013	-0.005	0.002	0.244
1	4	-0.026	-0.019	-0.012	0.000
1	5	-0.023	-0.015	-0.008	0.000
2	3	-0.017	-0.009	-0.002	0.003
2	4	-0.030	-0.023	-0.016	0.000
2	5	-0.027	-0.019	-0.012	0.000
3	4	-0.021	-0.014	-0.007	0.000
3	5	-0.017	-0.010	-0.003	0.001
4	5	-0.003	0.004	0.011	0.595

Table 12. SMC Group D and Proportion in Stage 1 ANOVA
The group comparison results of the ANOVA to measure the differences in the last step proportion of root biomass in stage 1 between plants with different soil microbial communities. The soil microbial communities included here are in group D.

Soil Microbial Group D					
Group1	**Group2**	**Lower95 CI**	**Mean Diff**	**Upper95 CI**	**p-value**
1	2	-0.009	-0.001	0.006	0.992
1	3	-0.015	-0.008	0.000	0.033
1	4	-0.030	-0.022	-0.015	0.000
1	5	-0.030	-0.023	-0.015	0.000
2	3	-0.014	-0.007	0.001	0.106
2	4	-0.028	-0.021	-0.014	0.000
2	5	-0.029	-0.021	-0.014	0.000
3	4	-0.022	-0.014	-0.007	0.000
3	5	-0.022	-0.015	-0.007	0.000
4	5	-0.008	0.000	0.007	1.000

Table 13. SMC Group D and Proportion in Stage 1 ANOVA
The group comparison results of the ANOVA to measure the differences in the last step proportion of root biomass in stage 1 between plants with different soil microbial communities. The soil microbial communities included here are in group E.

Soil Microbial Group E					
Group1	**Group2**	**Lower95 CI**	**Mean Diff**	**Upper95 CI**	**p-value**
1	2	-0.005	0.003	0.010	0.897
1	3	-0.011	-0.004	0.004	0.711
1	4	-0.032	-0.024	-0.017	0.000
1	5	-0.032	-0.024	-0.016	0.000
2	3	-0.014	-0.006	0.002	0.192
2	4	-0.035	-0.027	-0.019	0.000
2	5	-0.034	-0.027	-0.019	0.000
3	4	-0.028	-0.021	-0.013	0.000
3	5	-0.028	-0.020	-0.013	0.000
4	5	-0.007	0.000	0.008	1.000

Table 14. SMC and Proportion in Stage 5 ANOVA
The results of the ANOVA to measure the differences in the last step proportion of root biomass in stage 5 between plants with different soil microbial communities. Only those soil microbial community groups that had significant difference are included.

PROPORTION IN STAGE 5					
Group 3					
Source	**SS**	**DF**	**MS**	**F**	**Prob>f**
Groups	1.769	4	0.44	19.03	1.21e-15
Error	543.30	23884	0.02		
Total	545.07	23888			
Group 4					
Source	**SS**	**DF**	**MS**	**F**	**Prob>f**
Groups	2.303	4	0.58	23.71	1.35e-19
Error	571.33	23530	0.02		
Total	573.63	23534			
Group 5					
Source	**SS**	**DF**	**MS**	**F**	**Prob>f**
Groups	3.457	4	0.86	33.89	3.01e-28
Error	601.15	23573	0.0255		
Total	304.61	23577			

Table 15. SMC Group C and Proportion in Stage 5 ANOVA
The group comparison results of the ANOVA to measure the differences in the last step proportion of root biomass in stage 5 between plants with different soil microbial communities. The soil microbial communities included here are in group C.

Soil Microbial Group C					
Group1	**Group2**	**Lower95 CI**	**Mean Diff**	**Upper95 CI**	**p-value**
1	2	-0.011	-0.002	0.006	0.951
1	3	-0.003	0.005	0.014	0.479
1	4	0.011	0.020	0.029	0.000
1	5	0.007	0.016	0.024	0.000
2	3	-0.001	0.007	0.016	0.129
2	4	0.014	0.022	0.031	0.000
2	5	0.009	0.018	0.026	0.000
3	4	0.006	0.015	0.023	0.000
3	5	0.002	0.010	0.019	0.008
4	5	-0.013	-0.004	0.004	0.622

Table 16. SMC Group D and Proportion in Stage 5 ANOVA
The group comparison results of the ANOVA to measure the differences in the last step proportion of root biomass in stage 5 between plants with different soil microbial communities. The soil microbial communities included here are in group D.

Soil Microbial Group D					
Group1	**Group2**	**Lower95 CI**	**Mean Diff**	**Upper95 CI**	**p-value**
1	2	-0.010	-0.001	0.008	0.999
1	3	-0.003	0.006	0.015	0.292
1	4	0.012	0.021	0.030	0.000
1	5	0.013	0.022	0.030	0.000
2	3	-0.002	0.007	0.016	0.173
2	4	0.013	0.022	0.031	0.000
2	5	0.014	0.023	0.031	0.000
3	4	0.006	0.015	0.024	0.000
3	5	0.007	0.015	0.024	0.000
4	5	-0.008	0.001	0.009	1.000

Table 17. SMC Group E and Proportion in Stage 5 ANOVA
The group comparison results of the ANOVA to measure the differences in the last step proportion of root biomass in stage 5 between plants with different soil microbial communities. The soil microbial communities included here are in group E.

Soil Microbial Group E					
Group1	**Group2**	**Lower95 CI**	**Mean Diff**	**Upper95 CI**	**p-value**
1	2	-0.009	0.000	0.009	1.000
1	3	-0.004	0.005	0.014	0.523
1	4	0.017	0.026	0.035	0.000
1	5	0.017	0.026	0.035	0.000
2	3	-0.004	0.005	0.014	0.500
2	4	0.017	0.026	0.035	0.000
2	5	0.017	0.026	0.035	0.000
3	4	0.012	0.021	0.030	0.000
3	5	0.012	0.021	0.030	0.000
4	5	-0.009	-0.001	0.008	1.000

Vita

Tyler Poppenwimer was born in Falls Church, Virginia though he only lived there for three years. After which he moved to Puerto Rico for three years until finally moving to Mildenhall in the UK. After graduating high school, he attended The College of Wooster and received a Bachelor of Arts in Biology and Mathematics. During his undergraduate degree he studied abroad with the School for International Training in Australia where he discovered his passion for using mathematical and computational tools to study biology. After returning, he worked on his Independent Study "Generalist and Specialist Pollination Syndromes: When are they Favored?" and presented this work at the NIMBioS Undergraduate Research Conference. While there he recognized his passion for theoretical ecology and evolution and decided to attend graduate school. He chose to attend the University of Tennessee, Knoxville to pursue a Doctor of Philosophy degree in Ecology and Evolutionary Biology and a concurrent Master of Science degree in Statistics. His research interest includes using models to study plant-soil feedbacks with a focus on root dynamics and the exploring the impacts of varying spatial temporal scales on plant community assembly. After graduation, he will start his new position as a postdoc in the Tel Aviv University in Tel Aviv Israel. He is incredibly grateful for all the support from his wife, parents, and friends as he begins his new career.