“*Like most mathematicians, he [Alfred Lotka] takes the hopeful biologist to the edge of a pond, points out that a good swim will help his work, and then pushes him in and leaves him to drown.”*
- Charles Elton

University of Alberta

Modelling Early Plant Primary Succession on Mount St. Helens

by

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This thesis is dedicated to my parents, Normand and Joan, who taught me the importance of learning.

Abstract

Understanding the mechanisms that control the rate and trajectory of primary succession can lead to insights for ecosystem rehabilitation. Proposed mechanisms include life history traits and nutrient limitation. To explore how these mechanisms can drive successional dynamics, I devised a stoichiometric ecosystem-level model that considered the role of nitrogen and phosphorus limitation in plant primary succession in conjunction with life history traits. This model was applied to the plant community on Mount St. Helens to check the validity of the mechanisms. The results show the competitive hierarchy of plants at the local scale can be explained by nutrient limitation and plant stoichiometry. At regional scales, life history traits interact with local processes to shape community structure and successional dynamics. At all scales, the presence of *Lupinus lepidus*, a nitrogen-fixer, significantly altered community dynamics and succession. This study suggests that primary succession can be examined within the framework of ecological stoichiometry.

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Chapter 1

Introduction

Ecosystems are subject to natural and anthropogenic disturbances that can severely alter their functioning and composition (Walker & del Moral 2003). In some cases, the disturbance is so severe that even the soil itself is removed or buried under a new, barren substrate. These disturbed ecosystems are subsequently colonized by pioneering species that can best cope in these new conditions. The pioneers along with abiotic factors alter the environment and may allow new species to arrive in the ecosystem. These new species may subsequently displace the pioneers, alter the environment themselves and perhaps allow additional species to enter the ecosystem. This phenomenon of a changing composition of the ecological community is known as *ecological succession*.

The concept of ecological succession predates the science of ecology by nearly a half-century, if not more (Clements 1916, Walker & del Moral 2003, Egerton 2009). It is one of the most investigated natural phenomena in ecology, with a simple Web of Science search turning up 4819 papers on the subject (March 14th, 2009). Its study requires knowledge of fields such as soil science, biogeochemistry, biochemistry, physiology, population, community and ecosystem ecology and evolutionary biology (Walker & del Moral 2003). It was noted over forty years ago that understanding ecological succession could lead man to end his conflict with nature (Odum 1969). Modern researchers are applying knowledge gleamed from successional studies to help restore ecosystems damaged by human activities (Walker et al. 2007).

Hence, it is peculiar that a monograph on *primary succession* has been published only six years ago on the subject (Walker & del Moral 2003). Yet understanding primary succession, which is the transition between a barren substrate to an established ecological community, is vital to our efforts to reclaim the barren roads, mines and man-made deserts for future generations (Walker & del Moral 2003).

Thankfully, much progress on primary succession has recently occurred due to researchers turning the tragic disaster of the eruption of Mount St. Helens into our best case study of primary succession (Dale et al. 2005). Large strides have been made in identifying potential mechanisms of primary succession (Wood & del Moral 1987, del Moral & Bliss 1993, Chapin et al. 1994, del Moral et al. 2005). Nonetheless, the importance of these mechanisms has been difficult to ascertain due to limitations in time, in manpower, in financial resources and in experimental methods.

One way to approach this problem is to develop mathematical models that isolate potential mechanisms and to see if those mechanisms are capable of creating the patterns seen in nature (Haefner 2005). These mechanistic models have been applied to single populations and a predator-prey system on Mount St.

Helens (Bishop 1996, Fagan & Bishop 2000, Fagan et al. 2005), but none have been tried at the community or ecosystem level. The only model to explicitly consider succession on Mount St. Helens was phenomenological model that had poor predictive power (Childress et al. 1998).

In this introduction, I will attempt to give the necessary background on successional theory, on the empirical research accomplished on Mount St. Helens and on community and ecosystem models for reader comprehension. I follow these 'introductions' with a conceptual ecosystem model for primary succession on Mount St. Helens that ties all three elements together into a unified whole. Finally, I lay out the contents of the main chapters of the thesis, indicating which parts of the conceptual model are being explored.

1.1 An Introduction to Ecological Succession

1.1.1 *Controversies Over Definition*

The description of ecological succession above seems to lead to a simple definition of the phenomenon. One can easily see what ecological succession *is*; one may deduce that the definition must flow from what is observed to be the case. However, just because one can see something does not mean one can define it in a simple way (Wittgenstein 1969). Therefore how to define ecological succession is fraught with dangers, but one must have some definition in order to use the concept and communicate about it with others.

If one gathered all the definitions that have been proposed for ecological succession, one would find that they are grouped into two broad categories: ones that imply that succession is directional and goes towards a *climax* (Clements 1916, Odum 1969, Ricklefs & Miller 2000, Chapin et al. 2002) and those who claim that succession is simply any change in community composition (Gleason 1917, 1926, 1927, Cooper 1926, Tansley 1935, Whittaker 1975, Walker & del Moral 2003). The climax of ecological succession is a permanent biological community (i.e. it will not be replaced by another community) that has reached equilibrium with all other factors (Tansley 1935). The difference between the two viewpoints is neither trivial nor semantic.

The first view treats ecological succession holistically, focusing on the community and the ecosystem as a whole (Walker & del Moral 2003). The community treated by the holists is composed of species that strongly interact with one another and are dependent for the functioning of the community (Clements 1916, Tansley 1935). This holism also places biotic interactions as the main drivers of succession, with abiotic factors acting as constraints on the rate and trajectory of succession (Clements 1916, Odum 1969). In its most extreme form, it treats whole communities as organisms and compares the development of the community through succession as equivalent to the development of an embryo to an adult organism (Clements 1916).

The alternative view looks at succession through the lens of reductionism: the whole can be understood from the sum of its parts (Walker & del Moral 2003). Here, the parts are individual organisms, population and species that are interacting with each other and their environment. The community, for the reductionists, is composed by species that may or may not interact with one another and are not necessarily dependent on each other for their survival (Gleason 1917, 1926, 1927, Whittaker 1975). Abiotic factors play a much larger role in this view for they can change the trajectories of succession by filtering out certain species from the process (Walker & del Moral 2003). Since abiotic factors can be distributed heterogeneously in space and time and in stochastic fashion, there need not be a single climax community in an area, but numerous climaxes or cyclical climaxes could occur (Whittaker 1975). In fact, some reductionists deny there are ecological communities that are assembled in non-random fashion (Gleason 1917, 1927). Such randomly assembled communities could be described as neutral within the framework developed by Hubbell (2001) if the species have no particular functional role.

The debates over which side is ultimately correct still rage on today (Walker & del Moral 2003), but an operational definition is clearly needed for this thesis. I will therefore use the reductionistic definition given by Walker & del Moral (2003) that ecological succession is the change in community composition over time. The main benefits to this definition are its simplicity and lack of directionality, which may not exist in primary succession (del Moral et al. 2005, del Moral 2007). It also allows us to focus on the mechanisms of succession without getting too caught up about where they necessarily lead.

1.1.2 *Mechanisms of (Primary) Succession*

Over the years, numerous mechanisms for succession have been proposed (Tansley 1935, Connell & Slatyer 1977, Pickett et al. 1987, del Moral & Bliss 1993, Walker & del Moral 2003, del Moral et al. 2005). One can divide them by origin (abiotic or biotic), by place in community (autogenic or allogenic), by function (facilitation, inhibition or tolerance) or by occurrence during succession (nudation, migration, ecesis, competition, reaction in classic Clementsian terms) or all of the above (Clements 1916, Tansley 1935, Connell & Slatyer 1977, Pickett et al. 1987, Walker & del Moral 2003). Since succession is a temporal phenomenon, it is natural to consider the mechanisms and their associated processes from beginning to end.

Nudation is the disturbance that removes or alters the original community (Clements 1916, Pickett et al. 1987). If the disturbance leaves the soil, the seed bank and perhaps some organisms, then the community undergoes secondary succession (Whittaker 1975, Ricklefs & Miller 2000). If the soil is removed and/or bare substrate is exposed with no biological remnants, then one would see primary succession (Whittaker 1975, Ricklefs & Miller 2000). The disturbance is usually considered to be allogenic, which are processes external of the community in question, and abiotic, though biotic processes can cause disturbances (Walker & del Moral 2003). Examples of disturbance include hurricanes, floods, volcanic eruptions, landslides, herbivory, mines and roads (Walker & del Moral 2003).

The disturbance is followed by the migration phase, which is associated with the dispersal of organisms and the initial physical amelioration the substrate, if needed (Walker & del Moral 2003, del Moral et al. 2005). In primary succession, physical amelioration by erosion, physical and chemical weathering, freeze-thaw cycles and nutrient deposition are key processes (del Moral & Bliss 1993, Walker & del Moral 2003, del Moral et al. 2005). Without them, there would be no 'safe sites' that could allow for organisms to establish on the substrate and succession could not proceed (Houle 1997, Jumponnen et al. 1999). Dispersal of propagules to the newly disturbed site is dependent on the dispersal mechanisms of each organism, their isolation from the site and stochastic events (del Moral & Bliss 1993).

Following the migration phase is the ecesis, which is concerned with the establishment, growth and longevity of the colonizers from the migration phase (Walker & del Moral 2003). The pioneers will modify the substrate and their microenvironments at this stage, which is usually proscribed to the reaction phase (Walker & del Moral 2003). The main characteristic that is associated with establishment and vigorous growth of plants during primary succession is large seeds, which have the most difficulty in reaching the site during the migration phase (Wood & del Moral 1987, Wood & Morris 1990,Titus & del Moral 1998a). Plant species can also benefit by associating with symbionts that can access limiting resources, but the symbionts can be parasitic or provide no benefit if nutrient levels are too low (Titus & del Moral 1998bc).

The competition period is no longer considered to only have competition occurring as it did for Clements (Clements 1916, Pickett et al. 1987, Walker & del Moral 2003). Instead, numerous biotic processes such as herbivory, allelopathy (inhibition of other organisms by release of chemicals by focal organisms) and disease combine with competition to determine which species will form the 'mature' community from the 'immature' community (Walker & del Moral 2003, del Moral et al. 2005). Some of these processes are associated with the idea of inhibition (Connell & Slatyer 1977). Species can inhibit other species from displacing them through resource competition or allelopathy (Connell & Slatyer 1977).

The final period of succession for a community is the reaction phase or the further development of the formerly disturbed site by the organisms (Walker & del Moral 2003). The processes that dominate this phase occur within the community (autogenic) and are biotic (Clements 1916, Tansley 1935, Pickett et al. 1987). The organisms modify the abiotic environment by adding organic material to the soil and by developing organic structures that can alter abiotic processes (Walker & del Moral 2003). These modifications can lead to new species being able to invade the current community, which is called facilitation (Connell & Slatyer 1977).

While this summary of mechanisms and processes is not exhaustive, it does touch upon all the main mechanisms currently under investigation by ecologists (Walker & del Moral 2003). Due to the endeavours of these ecologists, some details about the importance of each mechanism have been partially fleshed out in succession theory.

1.1.3 *Notes on Current Successional Theory*

Successional theory is, since the reductionists have become the dominant force in ecological research, derived from observations and experiments that are then generalized in some form (Walker & del Moral 2003). Most of this theory is highly conceptual, is rarely given mathematical articulation, qualitative and may be community or ecosystem specific (Connell & Slatyer 1977, Pickett et al. 1987, Walker & Chapin 1987, Matthews 1992, Callaway & Walker 1997). Still, this body of theory can point to mechanisms that should be further explored in primary succession.

A general point in successional theory is that if succession is driven by facilitation, then succession will be fairly deterministic and predictable (Odum 1969, Connell & Slatyer 1977, Pickett et al. 1987). Facilitation matters most in severe environments with high abiotic stress (Walker & Chapin 1987, Callaway & Walker 1999). Since severe environments increase the importance of facilitation and succession driven by facilitation is considered predictable, then it follows that succession in severe environments would be predictable. This reasoning would imply that primary succession, with its severe environmental stress, would be highly predictable.

However, the successional theory that has been developed for primary succession suggests that it is highly *unpredictable* and perhaps stochastic (del Moral 1999, del Moral 2000, Walker & del Moral 2003). This suggestion is due to the idea that allogenic processes dominate in early succession and are highly variable over the landscape (Matthews 1992). This idea is well supported by the experimental literature (Houle 1997, Jumponnen et al. 1999).

Both stochastic events and facilitation are predicted to play large roles in primary succession and both mechanisms have support in the literature (Walker & Chapin 1987, Callaway & Walker 1999). The inherent difficulty with the mechanisms is that they lead to different conclusions about the possibility of predicting primary succession. Reconciling these two mechanisms within a coherent framework remains an open problem for ecologists.

One of the few mechanistic approaches to succession given mathematical articulation is Tilman's resource-ratio hypothesis (Tilman 1985). The idea behind it is that over time, the relative resource supply will change and community composition will change for certain species will be competitively dominant only for some ranges of supply (Tilman 1985). Tilman proposed that this should occur for light and nitrogen, for nitrogen becomes more abundant as succession progresses and light becomes less abundant. Grassland experiments refuted this hypothesis for early colonizers were not competitively dominant for nitrogen, which goes against the predictions of the hypothesis (Tilman & Wedin 1991b).

Other theoretical predictions such as insect herbivory being less important than mammal herbivory during primary succession, seed arrival being critical during colonization then diminishing afterward, the presence of symbionts being critical throughout succession and competition being somewhat unimportant have met with mixed results (Walker & Chapin 1987, Chapin et al. 1994,Titus & del Moral 1998bc, Bishop 2002, Gill et al. 2006). These facts indicate that much work is left to do on the theoretical side of succession.

1.2 An Introduction to Mount St. Helens

1.2.1 *The Eruption and the New Environment*

On May 18th 1980, the north-face of Mount St. Helens collapsed and a massive lateral eruption followed after two months of high geological activity (Swanson & Major 2005). The force of the blast, the debris avalanche, the mudflows and the pyroclastic flows the eruption unleashed devastated the old-growth conifer forest that occupied most of the northern slope of Mount St. Helens (Swanson et al. 2005, Swanson & Major 2005). New surfaces were laid down and the hydrology was greatly perturbed, creating a new landscape (Swanson & Major 2005). In a flash of creative destruction the old world gave way to the birth of a new world, but the relics of the past still play an important role for the rebirth of the ecosystem.

In many locations, individuals survived the devastation due to being located south of the blast zone, to good fortune and the snowpack (del Moral 1983, del Moral et al. 2005). In these locations, which are known as refugia, recovery was much quicker and species composition was and is different compared to more affected sites (del Moral et al. 2005). Where there is a lack of refugia, such as the Pumice Plain and the Plains of Abraham, the situation is much different.

The Pumice Plain was formed by the pyroclastic flows of the May 18th eruption and subsequent pyroclastic flows that expunged most organisms and created a new bare substrate. This substrate was poor in nitrogen, low in clay, lacked structure and had low water potentials at the surface (del Moral & Clampitt 1985, Reynolds & Bliss 1986, Wagner & Walker 1986, del Moral & Wood 1993). It was also fairly isolated from surviving vegetation, making an ideal location for the study of primary succession (del Moral et al. 2005).

1.2.2 *Previous Studies of Primary Succession on Mount St. Helens*

Two major books (Keller 1986, Dale et al. 2005) and more than a hundred journal articles have been written on the ecological recovery on Mount St. Helens. The sheer amount of information involved makes any short summary woefully incomplete. My focus will be on articles that investigated processes and factors related to plant primary succession, with special attention paid to those that manipulate these processes. The processes are ordered by their occurrence in succession, which is outlined in section 1.1.2.

The earliest phase of plant primary succession involves the arrival of seeds from surrounding vegetation and the physical amelioration of the substrate (del Moral & Bliss 1993, Walker & del Moral 2003). Ever since the major eruption on Mount St. Helens, researchers have looked at plant cover and set up seed traps to see which species are capable of reaching the disturbed habitats (del Moral 1983a, Wood & del Moral 1987, Wood & del Moral 1988, del Moral & Bliss 1993, del Moral & Wood 1993, Wood & del Moral 2000, del Moral et al. 2005). Plants with small, wind-dispersed seeds such as asters like the invasive hairy cat's ear (*Hypochaeris radicata*) are commonly found in the seed rain while species with larger seeds like the prairie lupine (*Lupinus lepidus*) are much rarer (del Moral et al. 2005).

This result would imply that many species without small, wind-dispersed seeds would suffer from dispersal limitation (del Moral et al. 2005). However, long distance dispersal events have occurred on the Pumice Plain for the prairie lupine, which has relatively large seeds that are explosively dehisced only a few meters (Bishop 2002). The long dispersal events have been attributed to snow melts and strong winds, which indicates that even large seeds can overcome dispersal limitation (Bishop 2002). Therefore, dispersal limitation is a limiting-factor for some species, though it can be overcome on occasion.

The physical and chemical qualities of the substrate have been followed with great interest for nearly thirty years (e.g. del Moral & Clampitt 1985, Wagner & Walker 1986, Chapin & Bliss 1988, Halvorson et al. 1991ab, Halvorson & Smith 1995, Tsuyuzaki et al. 1997, Fagan et al. 2004, Halvorson et al. 2005, Gill et al. 2006, Titus 2008, Halvorson & Smith 2009). As the years have progressed, there has been some improvement in the physical landscape with erosion and weathering creating microsites more suitable for colonization (del Moral et al. 2005). Similarly, more organic material and nitrogen have accumulated within the soil, improving substrate fertility (Halvorson & Smith 2009). Other properties of the soil such as pH, phosphorus and soil moisture content have not changed over time, though the values for these properties can vary up to two orders of magnitude (del Moral & Clampitt 1985, Wagner & Walker 1986, Chapin & Bliss 1989, Tsuyuzaki et al. 1997, Fagan et al. 2004, Titus 2008, Halvorson & Smith 2009). Despite this amelioration, much of the Pumice Plain and other primary successional landscapes contain sparse vegetation and few late successional species, indicating that more physical amelioration is required (del Moral et al. 2005, Titus 2008).

When the seeds arrive on the landscape, the question is no longer about dispersal, but rather about establishment, growth and survivorship. The environmental conditions most closely linked to seedling establishment and growth are soil moisture, substrate heterogeneity and nutrient availability (Wood & del Moral 1987, Chapin & Bliss 1989, Wood & Morris 1990, del Moral & Bliss 1993, Tsuyuzaki et al. 1997, Titus & del Moral 1998a). Species with life history traits such as high seed mass, high tolerance for water and nutrient stress and vigorous early growth were able succeed in the harsh conditions of the primary successional habitats (Wood & del Moral 1987, Chapin & Bliss 1989, Wood & Morris 1990, del Moral & Bliss 1993, Braatne & Bliss 1999). The lack of symbionts such as *Frankia* and mycorrhizae can reduce seedling growth and survival for certain species as they allow greater uptake of nutrients, though their presence is not always beneficial (Titus & del Moral 1998bc, Allen et al. 2005, Seeds & Bishop 2009). For many species, it is the lack of the necessary life history traits or lack of symbionts that prevent them from colonizing, not dispersal limitation (Wood & Morris 1990, Tsuyuzaki et al. 1997, Seeds & Bishop 2009).

After the establishment of plant species, numerous processes including herbivory, disease and competition reduce or eliminate certain species from the community. Plant competition on Mount St. Helens seems to be driven by belowground competition as most plants receive full sunlight (Titus 2008). Experiments that added phosphorus and/or nitrogen altered community composition, suggesting that competition for these two resources could drive successional dynamics (Gill et al. 2006). Insect herbivores have also been altering community composition by voraciously consuming the nutrient-rich prairie lupine (Bishop 1996, Bishop 2002, Fagan et al. 2004, Bishop et al. 2005). These two processes are tightly linked by the facilitative effects of the prairie lupine (Morris & Wood 1989, Halvorson et al. 1991b, Halvorson et al. 1992, Gill et al. 2006).

The prairie lupine is capable of facilitating other species by providing nitrogen through its ability to fix nitrogen as a legume (Morris & Wood 1989). The lupine provides its greatest benefit to other plants when it dies and releases its nitrogen (Morris & Wood 1989, Halvorson et al. 1992, Halvorson et al. 2005, Halvorson & Smith 2009). Lupines can therefore allow nitrogen-limited species to colonize Mount St. Helens and can shift the competitive balance in the community, which can lead to alternative successional trajectories (del Moral & Rozzell 2005, Gill et al. 2006). Furthermore, increased herbivory may allow for more nitrogen cycling and less nitrogen-limitation, though too much herbivory could prevent lupines from colonizing nitrogen-poor areas (Bishop 2002, Bishop et al. 2005).

The running thread through all these steps is that the nutrient supply and the ability of plants to access these nutrients are key in understanding the successional patterns seen on Mount St. Helens. This insight will lead us to consider models that link communities to ecosystems through nutrients in section 1.3, but first I will consider what modelling techniques have been tried already on Mount St. Helens.

1.2.3 *Previous Models for Mount St. Helens*

Considering the vast literature on primary succession in general and Mount St. Helens in particular, it comes as a surprise that so few models have been proposed for succession on Mount St. Helens (Childress et al. 1998, del Moral 1999, del Moral & Jones 2002). Childress et al. (1998) used community composition data to create matrices of transition probabilities in order to see how well Markovian matrix models can predict primary succession. The results showed that the matrix models failed miserably at prediction except when allowed to change the transition matrix at each time step. This result led the authors to conclude that considerations of biotic and abiotic processes are needed to predict primary succession (Childress et al. 1998).

The only other model that has been applied to plant succession is a stochastic simulation model called SIMCOM (del Moral 1999). The model simulates the colonization of model plots by using frequency data of plants from real plots. The probability that a species is selected to colonize a plot is based on the frequency data and the cover of each species in the model plot was randomly selected, though no mention is made of the random distribution the cover value was chosen from (del Moral 1999). While the results of the model seem in good agreement with the data and may support the idea that colonization is random in primary succession, the presentation of the model leaves many questions about the assumptions made to obtain these results (del Moral 1999). The modelling procedure used in del Moral & Jones (2002) was similar to SIMCOM.

Three other models concerning the population dynamics and spread of the prairie lupine represent the totality of the modelling efforts on the plant community of Mount St. Helens (Bishop 1996, Fagan & Bishop 2000, Fagan et al. 2005). All three suggest that the prairie lupine can be adversely impacted by herbivory and the latest two indicate that the herbivores could slow or stop the spread of the lupines (Bishop 1996, Fagan & Bishop 2000, Fagan et al. 2005).

Of course, modelling communities can be difficult if one follows the population dynamics and interactions of each individual species over space and time. One way of reducing the complexity involved is to focus on functional groups or groups of species with similar ecological roles or characteristics (Hooper & Vitousek 1997). The three main groups of species representative of the early colonizers on the Pumice Plain were nitrogen-fixing legumes, asters and grasses (del Moral & Clampitt 1985). For my work, I have chosen one species to represent each group in the model. The species chosen were species that have been present on the Pumice Plains since the earliest years of recovery.

1.2.4 *Species of Interest*

Lupinus lepidus var. *lobbi*: prairie lupine

The prairie lupine was the first species to establish on Pumice Plain in 1981 and managed to form colonies over an area of three kilometres squared (Fagan & Bishop 2000, Bishop 2002, Bishop et al. 2005). The lupine is a native, small (maximum radius of 45cm), wintergreen and prostate (maximum high 15cm) nitrogen-fixing legume with a shallow tap root (Braatne & Bliss 1999, Bishop 2002). It has a short-life span with individuals rarely living past five years and can reach reproductive maturity in one growing season (Braatne & Bliss 1999, Bishop 2002). An individual plant can produce hundreds of seeds, which are dispersed short distances by explosive dehiscing of the fruit (Bishop 2002). The seeds of the lupine are relatively short-lived and can remain in the seed bank for up to three years (Bishop 1996, Fagan et al. 2005). The population growth of the lupines was high early on during primary succession (λ=11.6), though this rate of reproduction has not been maintained (Fagan & Bishop 2000).

The lupine is tolerant to low nutrient availability and adult lupines experience little stress from the low soil moisture found in the substrates during the summer droughts (Braatne & Chapin 1986, Braatne & Bliss 1999). The seedlings, on the other hand, can be negatively affected by drought conditions (Braatne & Bliss 1999). The seedlings also experience high mortality within high-density patches of lupines, indicating the importance of intraspecific competition (Bishop 2002). The lupines suffer from insect herbivory, which is the main cause of lupine mortality (Bishop 1996, Fagan & Bishop 2000, Bishop 2002, Bishop et al. 2005). There is evidence that the herbivores prefer lupines on the edge of the colonies, which may be related to differences in nutrient content compared to lupines in the core of the colonies (Bishop 2002, Fagan et al. 2004).

The prairie lupine has done poorly in competition experiments in the alpine meadows of the Cascade Mountains and is considered to be a stress tolerator in the terms of Grime's triangle (del Moral 1983bc, del Moral et al. 1985). It prefers dry, disturbed habitats in full sunlight, making the Pumice Plain an ideal habitat for it (del Moral 1983c). There is some evidence that the prairie lupine reduces the water content of the soil, but it is not known if this will inhibit the establishment of other species (Titus 2008). Its potential for facilitative effects has already been considered in section 1.2.2.

Hypochaeris radicata: hairy cat's ear

Hypochaeris is an invasive perennial aster with origins in Morocco (Ortiz et al. 2008). Its growth form is a rosette with leaves of a maximum length of 25cm and stems that can grow to 60cm tall (Turkington & Aarssen 1983). *Hypochaeris'* roots are fibrous, though it also develops a deep taproot (Turkington & Aarssen 1983). During the winter months, it can persist either as an evergreen, die back to the basal rosette or act as a true hemicryptophyte (it dies back to perennating buds at ground level) depending on the temperature regime (Turkington & Aarssen 1983). *Hypochaeris* is able to go from newly germinated seedling to a reproductive state in two months, though they usually reproduce during the second growing season (Turkington & Aarssen 1983, Fone 1989, Doi et al. 2006).

Hypochaeris can reproduce both vegetatively and sexually, though is self-incompatible for sexual reproduction (Turkington & Aarssen 1983, Pico et al. 2004, Ortiz et al. 2006). Vegetative reproduction occurs by the splitting of shoots and only occurs for large plants with more than two shoots (Doi et al. 2006). The amount of seeds produced through sexual reproduction by a single individual can be in the thousands (Turkington & Aarssen 1983). Each seed has a feathery pappus that allows for long-distance wind dispersal (Turkington & Aarssen 1983, Soons et al. 2004). There is no evidence of seed dormancy for the species and seedlings have been known to emerge throughout the growing seasons (Doi et al. 2006). The longevity of the seeds within the seed bank is believed to be short with germination rates greatly decreasing over time (Turkington & Aarssen 1983).

Hypochaeris is found in many climates, diverse substrates and soils with vastly differing chemical composition (Turkington & Aarssen 1983). It possesses some shade-tolerance, but grows best with ample access to light (Fenner 1978). Its deep taproot gives it some degree of drought-resistance, though to what extent has not been quantified (Turkington & Aarssen 1983). It is also believed that *Hypochaeris* is autotoxic and this autotoxicity results in a pattern of isolated individuals within grasslands (Turkington & Aarssen 1983). *Hypochaeris* is responsive to nutrient additions on Mount St. Helens, though it does not benefit from additional phosphorus due to its associations with mycorrhizea (Titus & del Moral 1998b, Gill et al. 2006). Sources of mortality on the Pumice Plain are not known, though there is some evidence of herbivory by mammals due to the high nutritional qualities of *Hypochaeris* (Turkington & Aarssen 1983).

Hypochaeris is believed to be a good competitor within grasslands and can competitively displace many species (Turkington & Aarssen 1983). Some of its competitive ability has been attributed to allelopathy, though the allelopathy has not been conclusively demonstrated (Turkington & Aarssen 1983). Other researchers maintain, based on sowing experiments and population models, that *Hypochaeris* is not a competitive species *sensu* Grime's triangle, but rather a fugitive species reliant on constant disturbance to remain in the plant community (de Kroon et al. 1987).

Agrostis scabra: tickle grass

Agrostis is a native, perennial bunchgrass with a fibrous root system and is an early successional species found in alpine meadows, prairies and beaches across North America (Watson 1989, Tilman & Wedin 1991abc, Matthews 1992b). It can grow as tall as 130cm, though it is usually 15 to 100cm in length (Matthews 1992b). It is hemicryptophyte and sometimes sheds it leaves and grows new ones during the growing season (Tilman & Wedin 1991c, Matthews 1992b). *Agrostis* can produce tens of thousands of seeds and these seeds are dispersed by inflorescences that break off of the plant and are blown by the wind in a manner similar to tumbleweed (Watson 1989, Tilman & Wedin 1991, Matthews 1992b). *Agrostis* generally reproduces only sexually, though there is some evidence of vegetative reproduction (Matthews 1992b).

Agrostis is mildly drought-tolerant, shade-intolerant and is tolerant of acidic, contaminated and nutrient poor soils (Watson 1989, Matthew 1992, Archambault & Winterhalder 1995). While it can be grazed by herbivores, it is considered to be a poor source of protein and somewhat unpalatable (Matthews 1992b). It also should be noted that *Agrostis* species are used on golf courses and can tolerate mowing (Watson 1989). There is some evidence that grazing may even be beneficial to *Agrostis*, hence herbivory-induced mortality seems unlikely (Matthews 1992b).

Agrostis is a poor competitor for light and nitrogen in grasslands (Tilman & Wedin 1991abc, Wedin & Tilman 1993). Its poor competitive ability for nitrogen may be linked to minimal investment in belowground biomass (Tilman

& Wedin 1991a). With its massive investment in reproduction and lack of competiveness, *Agrostis* fits very well within Grime's triangle as a fugitive species (Archambault & Winterhalder 1995). On the Pumice Plain, there is evidence that *Agrostis* does worse in terms of biomass and cover when *Hypochaeris* is present in the community (Fagan et al. unpublished manuscript). This effect may be due to differences in competitive ability for nitrogen (Gill et al. 2006).

Other functional groups not considered

Bryophytes, shrubs and trees were not considered for the purposes of this study. Trees have barely begun to colonize the Pumice Plain and their arrival will most likely occur during late primary succession, which is not considered here (Titus 2008). Certain parts of the Pumice Plain are being colonized by shrubs such as *Salix* and *Alnus*, but their cover and range is limited and their spread is much more recent (del Moral & Jones 2002). Bryophytes have drastically increased their cover in recent years on the Pumice Plain and there is some evidence they are facilitated by the prairie lupine (del Moral & Rozzell 2005, Titus 2008). However, they were not present in any significant number till 1992 and their overall impact on succession is still uncertain (del Moral & Jones 2002, Titus 2008). Until more is known about the physiology of the bryophytes and how they compete with vascular plants, we can only speculate on their effects on the community.

1.3 An Introduction to Stoichiometric Community/Ecosystem Models

1.3.1 *A Brief History of Community and Ecosystem Models*

The development of mathematical models for ecology, be it at the population, community or ecosystem level is relatively recent (Kingsland 1995). The first scientist to attempt to comprehensively model nature at all scales was the chemist Alfred Lotka (1925). Lotka created the field of *ecological stoichiometry*, the study of the balance of energy and chemical substances in ecological interactions and processes (Sterner & Elser 2002), and made great strides in modelling population dynamics (Lotka 1925). He sought to unify all these fields under the rubric of physical biology, but ecologists subsequent to him branched off into two directions (Kingsland 1995). They either studied populations and communities, creating the fields of population and community ecology, or they studied ecosystems and founded ecosystem ecology (Kingsland 1995).

Population and community ecologists such as Elton, MacArthur, Rosenzweig and Levins focused on pair-wise interactions between species such as competition and predation and took a bottom-up approach to ecology (Elton 1927, Rosenzweig & MacArthur 1963, MacArthur & Levins 1967). Their models involved few species and a limited role for environmental conditions (e.g. Rosenzweig & MacArthur 1963). The discovery of chaotic dynamics in simple population models by May lead to the realization that these models may not be able to predict the destinies of real communities, leading some to question the value of mathematical modelling in ecology (May 1974, Peters 1991). During the same period, ecosystem ecologists were having a similar crisis.

Ecosystem ecologists such as Lindeman and the Odum brothers focused on the flows of energy and material between trophic levels and the ecosystem by treating them as black boxes (Lindeman 1942, Odum 1953). This top-down view of ecology spawned compartmental models and lead to the development of systems ecology and many useful mathematical tools (Hagen 1992). The research program suffered major setbacks after their major project, the International Biology Program (1968-1974), failed to achieve its ambitious goals of revolutionizing ecology (Hagen 1992). The main flaw in the program was the reliance on systems theory, which could simply not keep up with the complexities of the models created to reflect ecosystem processes (Hagen 1992).

The successes and failures of these two approaches have led ecologists to seek ways of reunifying or at least reconnect the two branches of ecology by focusing on the common currencies of energy and elements (Sterner & Elser 2002, Brown et al. 2004). The hope is to be able to scale up from individual cells to the biosphere and back down again, allowing us to examine ecological interactions across a variety of scales (Sterner & Elser 2002, Brown et al. 2004). This thesis will use the conceptual framework of ecological stoichiometry as laid out by Sterner & Elser (2002). Many other models have followed this framework and provide us with clues on how to investigate primary succession on Mount St. Helens.

1.3.2 *Stoichiometric Population, Community and Ecosystem Models*

Stoichiometric models differentiate themselves from non-stoichiometric models by explicitly considering the balance of two or more chemical substances within the organisms or populations under study (Sterner & Elser 2002). For example, traditional trophic food chain models consider the transfer between and balance of carbon (biomass or energy) within each trophic level (e.g. Rosenzweig & MacArthur 1963, Hastings & Powell 1991, Jansen 2001). One can make such a trophic chain stoichiometric by considering amounts of two chemical substances, say carbon and phosphorus, within all trophic levels or by imposing stoichiometric constraints (e.g. Andersen et al. 2004, Cherif & Loreau 2009).

The addition of stoichiometric elements to these models can alter model outcomes. Take the Rosenzweig-MacArthur predator-prey model as an example (Rosenzweig & MacArthur 1963). It was noted that if one increased the ‘carrying capacity’ of the prey to a certain level, i.e. the prey was able to extract more energy from its environment, then the model predicted oscillations in prey and predator biomass (Rosenzweig & MacArthur 1963, Rosenzweig 1971). When stoichiometric constraints are added to the model by introduction of a limiting nutrient, two new behaviours occur: the oscillations can still occur, but require a much higher ‘carrying capacity’ than the non-stoichiometric model or the predator could not survive if the prey was insufficiently nutritious in terms of the limiting nutrient (Andersen et al. 2004).

Numerous stoichiometric models have been constructed to analyze flexible stoichiometry and nutrient uptake in algae (Legovic & Cruzado 1997, Klausmeier et al. 2004, De Leenheer et al. 2006, Klausmeier et al. 2007), competition for limiting resources (Daufresne & Hedin 2005, Cherif & Loreau 2007, Li & Smith 2007, Revilla & Weissing 2008, Grover 2009), trophic dynamics (Grover & Holt 1998, Grover 2002, Grover 2003, Andersen et al. 2004, Grover 2004, Cherif & Loreau 2009), phytoplankton marine community composition and succession (Litchman et al. 2006) and ecosystem-level properties like nitrogen fixation and stoichiometry (Rastetter et al. 1997, Rastetter et al. 2001, Wang et al. 2007, Ballantyne et al. 2008, Houlton et al. 2008). These studies have greatly extended previous theory in all these fields and have spurred experimentalists to test their predictions (Chrzanowski & Grover 2008). One study that is particularly relevant to the plant community on Mount St. Helens is Daufresne & Hedin's (2005) work on nutrient cycling by plants and resource competition.

Daufresne & Hedin's model is an extension of the non-stoichiometric models of Tilman (1980, 1982) to include (fixed) stoichiometry and to allow nutrients within organic matter to be recycled back into the soil. Using classical methods of resource competition theory, the authors were able show that recycling could alter competitive outcomes between the plants (Daufresne & Hedin 2005). Plants may either promote coexistence by recycling relatively more of the nutrient that least limits them or promote exclusion by recycling relatively more of the nutrient that most limits them (Daufresne & Hedin 2005). They also demonstrated that within the regime where only with recycling could there be coexistence between the competitors, it was possible to have stable oscillations of the competitors' biomass (Daufresne & Hedin 2005). They suggested that these oscillations might allow for more than two species to coexist on two limiting nutrients, thereby giving another mechanism to explain biodiversity (Daufresne & Hedin 2005).

The results from their study are highly relevant to Mount St. Helens, for the recycling of nitrogen by the prairie lupine can alter the trajectory of succession (del Moral & Rozzell 2005). In addition, the studies on trophic dynamics are also relevant for insect herbivores seem to prefer the more nutrient-rich lupines to other plant species (Fagan et al. 2004). Finally, studies have shown that different plants on Mount St. Helens are limited by different nutrients and this result may be due to their stoichiometry (Gill et al. 2006). Therefore, a modelling approach that includes stoichiometry would be most beneficial for understanding the mechanisms that drive primary succession on Mount St. Helens.

1.4 A Conceptual Ecosystem Model of Primary Succession on Mount St. Helens

To recapitulate, there is a lack of mechanistic models of primary succession and this deficit is negatively impacting the applicability of successional theory (section 1.1). Mount St. Helens provides a wonderful case study for primary succession and many mechanisms have been observed and experimented upon, but no attempt has been made to explore these mechanisms with models (section 1.2). Models that link community and ecosystem ecology through stoichiometry have given many new insights into both fields (section 1.3). Since nutrient limitation is a key mechanism for primary succession on Mount St. Helens, a stoichiometric model of primary succession could provide new knowledge on the subject (section 1.3).

All models are abstractions of reality that focus on a few processes or variables while neglecting many more (Levins 1966). The more variables and parameters added to the model to capture 'reality', the less able one is to tease out what processes are most important in driving the behaviour of the model (Levins 1966). One can also greatly limit the scope of the model by tailoring it to only correspond to the system of study, which can give us useful quantitative predictions for the system, but the results would have no generality (Levins 1966).

Here, I propose a model that maximizes, in the terms of Levins (1966), generality and realism. The model is tailored to be general enough to apply to other primary successional habitats and tries to capture the mechanisms in operation. The main drawback is the predictions made are mostly qualitative (Levins 1966). Despite this, the results from this model will allow for greater understanding of primary succession, on Mount St. Helens or elsewhere.

The conceptual ecosystem model for primary succession focuses on the interactions between the soil, the plants, the detritus and the over the landscape (Figure 1.1). The model can be extended to include other trophic levels as needed.

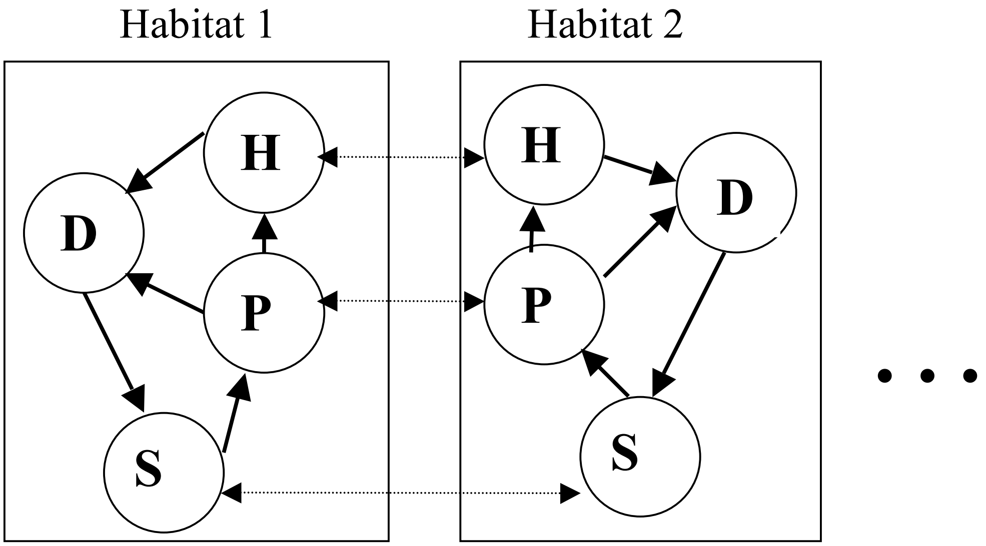

Figure 1.1: Coarse scale ecosystem model for primary succession. Nutrients flow (represented by thick one-headed arrows) from the soil (**S**) to the plant community (**P**) to the herbivores (**H**). Certain portions of plant and herbivore biomass will enter the detritus (**D**). Soil organisms and microorganisms utilize the nutrients in the detritus and eventually release them back into the soil, allowing plants to uptake them. Soil nutrients from one location can diffuse (represented by dotted double-headed arrows) to other locations on the landscape and herbivores as well as plants can disperse across the landscape to other habitats. The ellipsis represents numerous more habitats that are linked to habitat 1 and habitat 2 through diffusion and dispersal.

At the landscape level, one could see differing habitats or physical features that support their own communities and ecological processes (Figure 1.1). One habitat may be more fertile and support species of plants and animals that are less capable of tolerating a severe environment, while another may be devoid of a critical nutrient. Over time, the interactions between organisms and the abiotic environment on the infertile site may lead to an increase in the relative nutrient content in the soil, allowing species from the more fertile habitat to invade. This invasion would change the composition of the community and would be classified as succession.

The landscape level is a bit too coarse to achieve a fine understanding of how the mechanisms of nutrient limitation and nutrient cycling would bring about this successional change. One would need to descend to the finer scale of the local habitat and the physiology of the organisms to accomplish this goal (Figure 1.2).

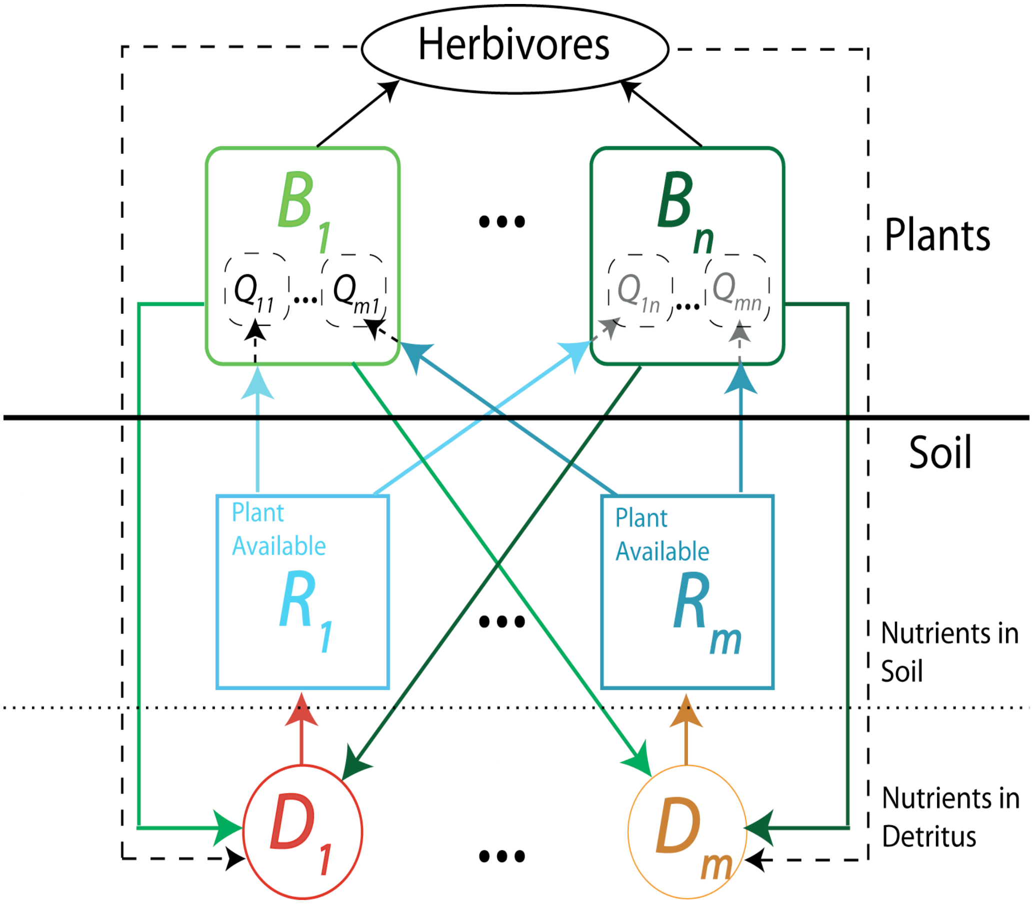

Figure 1.2: Fine scale ecosystem model of primary succession. Here, the flows of nutrients are explicitly followed between and within the soil, the detritus, the plants and the herbivores. Each plant has a biomass, B, which is composed of by the stores of elemental nutrients Q. Plant available nutrients, R, and nutrients in the detritus, D, are located within the soil. The representation of the herbivores as a single compartment is simply to limit the amount of arrows on the diagram.

The fine scale model allows consideration of plant and herbivore stoichiometry, the stoichiometry of the soil and the stoichiometry of the detritus. It can provide insights into the competitive abilities of plants based on their physiological characteristics. It can also result in the derivation biologically important values such as the minimum amount of nutrient a plant needs to survive in its environment.

By combining the insights gained at the fine and coarse scales, many qualitative predictions can be made about the rates and trajectories of primary succession. For example, if one plant is vital for the acceleration of recovery of vascular plant cover, but is very limited in its dispersal, one may see a 'travelling wave' solution in the landscape with this vital plant at the edge of the wave and other species following it (Levine et al. 2006).

Despite the numerous simplifications already made in creating this conceptual model, the model is still highly complex and many years would be needed to fill out every aspect. In my thesis, I have managed to solve some of the questions this model proposes, but much is left to future work.

1.5 Outline of Thesis

With the introduction completed, I can now turn to body of the thesis. In Chapter 2, I study the fine scale ecosystem model with attention given only to the soil, detritus and plants by using ordinary differential equations. I demonstrate that the model equations give rise to a simple graphical representation and competitive relationships between plants can be easily described. I follow the general analysis of the model by parameterizing it with data collected on Mount St. Helens and from the literature. I test the models ability to predict competitive outcomes between the prairie lupine, the hairy cat's ear and the tickle grass (*Agrostis scabra*) seen in experiments (e.g. Gill et al. 2006) and to determine how stressful the nutrient conditions are on Mount St. Helens for plants.

In Chapter 3, I study the coarse scale model by considering the same species in Chapter 2 in a spatial environment. The mathematical model used is an individual-based model that keeps track of patch occupancy. Each plant's ability to colonize a patch is dependent on the presence of other plants, the quality of the patch and the dispersal distance of its seeds. The model is simulated numerous times and over a variety of parameter ranges and initial conditions to see how succession over the landscape proceeds.

In Chapter 4, I synthesize the results from the previous two chapters and piece together the lessons learned for primary succession. I also consider what needs to be done in order to complete the conceptual framework laid out in Chapter 1.

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Chapter 2

A Stoichiometric Model for Plant Primary Succession on Mount St. Helens

2.1 Introduction

The bare substrates that are left behind from large disturbances, such as a volcanic eruption or the retreat of a glacier, are usually poor in some elemental nutrients (Wood & del Moral 1987, Matthews 1992, Chapin et al. 1994, Walker & del Moral 2003, Vitousek 2004). The lack of fertile sites can inhibit plants from colonizing the landscape and can delay ecological recovery (del Moral & Bliss 1993, Walker & del Moral 2003). Species that can overcome low nutrient conditions and ameliorate substrate fertility, like nitrogen-fixers, can accelerate succession and ecosystem recovery through facilitation (Connell & Slatyer 1977, Pickett et al. 1987, Walker & Chapin 1987, Callaway & Walker 1997). Conversely, they also can arrest succession by inhibiting the establishment of other plant species through competition and other means (Pickett et al. 1987, Walker & Chapin 1987, Walker & Vitousek 1991, Chapin et al. 1994).

The outcome between the facilitative and inhibitory effects of early colonizers must be determined if the successional trajectories of the community is to be predicted (Connell & Slatyer 1977, Pickett et al. 1987). The insights gained from these studies can then be applied to ecological restoration, for managers would know to avoid early successional species that have net inhibitory effects on later successional species (Walker & del Moral 2003).

On Mount St. Helens, the current substrate laid down by the pyroclastic flows of the May 18th 1980 eruption and subsequent eruptions was, and is, poor in nitrogen (del Moral & Clampitt 1985, Halvorson et al. 1991a, Halvorson & Smith 1995, Fagan et al. 2004, Halvorson et al. 2005, Titus 2008, Halvorson & Smith 2009). One of the earliest colonizers of this substrate was a small, nitrogen-fixing legume called the prairie lupine (*Lupinus lepidus*; del Moral & Clampitt 1985, Halvorson et al. 1991b, Braatne & Bliss 1999, Bishop 2002). As a nitrogen-fixer, the lupine can create ‘islands’ of fertility in the barren landscape that can support nitrogen-limited organisms (Halvorson et al. 1991a, Halvorson et al. 1992, del Moral & Bliss 1993, Halvorson & Smith 1995, Tsuyuzaki et al. 1997, del Moral & Rozzell 2005). However, these beneficial effects seem to be overshadowed by suppression of seed germination and other inhibitory effects found when the lupine is still alive (Morris & Wood 1989). The presence of these contradictory effects raises many questions.

What is, therefore, the net outcome of these facilitative and inhibitory effects of the lupine on subsequent colonizers of lupine-patches? Does the trajectory of succession change if lupines are present? Does an increase in local lupine mortality result in an increase of the facilitative effect? Some of these questions have been addressed by observational and experimental studies, but the results are often contradictory (del Moral & Rozzell 2005, Titus 2008).

In this work, I hypothesize that the facilitation and inhibition of the various species in the plant community occurs through resource competition (Tilman 1980, 1982). The resources I focus on are the elemental nutrients, nitrogen and phosphorus, which have been shown to limit lupine and other colonists' growth (Gill et al. 2006). The reasons for only considering nitrogen and phosphorus include the lack of light competition (Titus 2008), the lack of evidence for biologically significant differences in pH for barren and colonized areas on the Pumice Plain (Tsuyuzaki et al. 1997, Halvorson et al. 2005, Titus 2008, Halvorson & Smith 2009, but see Ugolini & Dahlgren 2002) and the relative abundance of other nutrients in comparison to nitrogen and phosphorus (Wagner & Walker 1986, Gill et al. 2006, Titus 2008, Halvorson & Smith 2009).

There is some evidence for competition for water, though many species on Mount St. Helens are well adapted to drought conditions (Braatne & Chapin 1986, Chapin & Bliss 1988, Chapin & Bliss 1989, Braatne & Bliss 1999, Titus 2008). As no experiments have been done to see if increased soil water content will alter community composition over time, it remains an open question if competition for water structures communities. There could also be some allelopathy on Mount St. Helens as some species (e.g. *Hypochaeris radicata*) are believed to be allelopathic (Turkington & Aarssen 1983). While allelopathy is not considered in the main results, some consideration is given on how one could model allelopathy and resource competition within Appendix 2.C.

To test the hypothesis and to answer the questions above, I develop a general stoichiometric-explicit ecosystem model that follows flows of nutrients from and between the soil, the plants and the detritus. The properties of the general model such as the existence and the stability of steady states are analyzed mathematically. Many of these results can be expressed by using graphical techniques that were first derived for classical resource competition theory (Tilman 1980, 1982). I utilize these graphical methods to show the results of competition between species.

I follow my analysis of the general model by parameterizing it with field data collected at Mount St. Helens and other data found within the literature. I then utilize the techniques derived from the analysis of the general model to see whether or not *Lupinus lepidus* facilitates the colonization of the other species. Furthermore, I investigate the possibility that the presence of the lupines may change the competitive outcome between the other species, causing a change in successional trajectory. I also investigate whether increased lupine mortality increases or decreases its facilitative effects.

The main theoretical results of my chapter are the discovery of non-equilibrium dynamics in the model caused by the presence of recycling and that traditional graphical analysis fails to predict competitive outcomes between species under certain parameter regimes (Figures 2.7, 2.8). Another key theoretical result is the discovery of areas of bistability where the community can be composed by one species or two other species (Figure 2.11, 2.12).

Overall, the combination of variable stoichiometry and nutrient recycling can lead to rich dynamics unseen when one or the other is not included.

When applied to the plant community on Mount St. Helens, the model successfully predicts the observed competitive hierarchy found in the plant community (Figure 2.11). Furthermore, the model supplies additional evidence that the overall effect of *Lupinus* on other species is facilitative and can be explained through nitrogen additions (Figure 2.14). The results suggest that stoichiometry combined with nutrient cycling and nutrient limitation can aid in predicting the qualitative behaviour of plant succession.

2.2 Model Development & Parameterization

This section is divided into three parts. The first part (2.2.1) is the derivation of the mathematical model from a conceptual model of a plant-soil-detritus ecosystem. The second part (2.2.2) lists and explains the assumptions needed to create the mathematical model. The assumptions listed are key to the functioning of the model and the effects of their violation are discussed within the discussion. The third and final part (2.2.3) explains how the model was parameterized from field data and the available literature. A helpful guide to the notation of this chapter is included in Appendix 2.A.

2.2.1 *Model Derivation*

Let us begin by describing a hypothetical ecosystem that has n plant species that can possibly be limited by m nutrients. I will keep track of the biomass of each species j in order to know if it will persist or not in the ecosystem and I denote this value by B_j. Since I am dealing with nutrients that can be limiting, I also need to follow the available amount of nutrient i in the soil, which will be the variable R_i. The amount of nutrient i within species j will determine whether or not that nutrient is limiting, though only if I compare its relative abundance with all other possible limiting nutrients. Therefore, I require the amount of nutrient i per unit of biomass of species j, which I express as Q_{ij}. Finally, I need to keep a tally of all the nutrients that are in the detritus, so for each nutrient i I have a detritus variable D_i. Note that, by having just one detritus variable per nutrient i, I assume that the decomposition rate of the dead material is the same for all species, but there is no loss of generality by making this assumption (Daufresne & Hedin 2005). The flows of nutrients between the various compartments (detritus, available and plant) can be illustrated in a diagram (Figure 2.1):

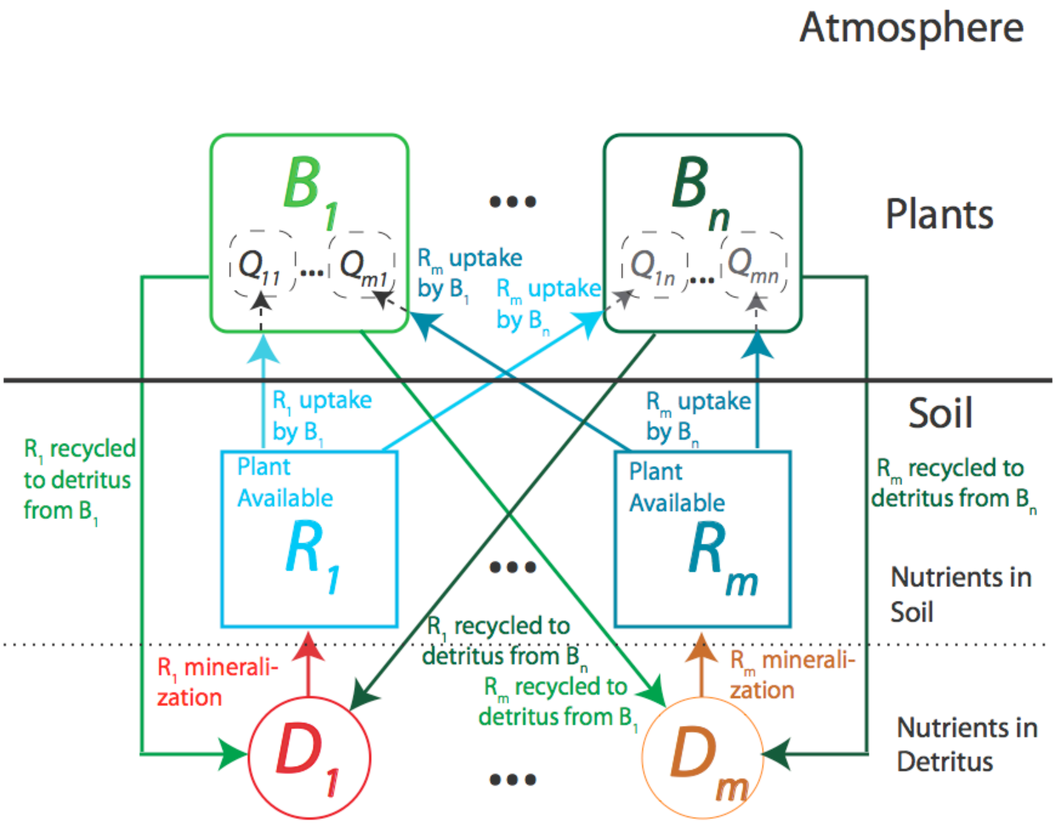

Figure 2.1: Generalized flow diagram for an *n* plant species, *m* nutrient ecosystem. Each plant uptakes available nutrients, *R*, from the soil and brings the nutrients into its internal stores, *Q*. These internal stores provide material to create more plant biomass *B*. When plant biomass perishes, the nutrients within that biomass go into the detritus, *D*. The nutrients within the detritus are mineralized over time and go back into available nutrients. The ellipses indicated that there are numerous species between 1 and *n* and numerous nutrients between 1 and *m*.

This diagram reveals a modelling challenge: for large n and m, the number of variables becomes unmanageable from a mathematical point of view. The number of variables is equal to $n + 2m + nm$, so if I have three plants and three nutrients, I will have 18 variables to consider. A commonly used assumption for simplification is constant yield (i.e. constant stoichiometry; Grover 1992). This assumption would mean that all the Q_{ij} variables would be constants. A veritable mountain of scientific research has been amassed on these constant yield models and their validity (e.g. Tilman 1980, 1982, Huisman & Weissing 1995, Grover 1997, Huisman & Weissing 2001, Craine 2005, Daufresne & Hedin 2005, Miller et al. 2005, Wilson et al. 2007). Overall, constant yields models serve as good approximations of the more realistic models if the community is near steady state (Grover 1992). If I make this assumption, then the equations that would describe the dynamics of the model system are:

$$
\begin{aligned}
\underbrace{\frac{dR_i}{dt}}_{\text{Rate of Change in Plant Available Nutrient i}} &= \underbrace{a_i\left(S_i - R_i\right)}_{\text{Supply Without Plants}} - \underbrace{\sum_{j=1}^{n} q_{ij} H_j B_j}_{\text{Total Plant Uptake}} + \underbrace{\delta_i D_i}_{\text{Gain of Available Nutrient i from Mineralization}} \\
\underbrace{\frac{dB_j}{dt}}_{\text{Rate of Change in Biomass of Plant j}} &= \underbrace{\left(H_j - m_j\right)}_{\text{Net Plant Growth}} B_j \\
\underbrace{\frac{dD_i}{dt}}_{\text{Rate of Change of Nutrient i Within the Plant Detritus}} &= \underbrace{\sum_{j=1}^{n} \zeta_{ij} q_{ij} B_j m_j}_{\text{Amount of Nutrient i Entering the Plant Detritus From Dead Plants}} - \underbrace{\delta_i D_i}_{\text{Loss of Plant Detritus Nutrient i From Mineralization}} \\
\underbrace{H_j}_{\text{Plant j's Growth Function}} &= H_j(R_1, \ldots, R_i, \ldots, R_m) = \min\left\{\frac{h_{ij}(R_i)}{q_{ij}}\right\}
\end{aligned}
\tag{2.1}
$$

$i = 1, 2, \ldots, n$ where n is the number of plant species

$j = 1, 2, \ldots, m$ where m is the number of limiting nutrients

The above equations describe the rates of change of available nutrients, of plant biomass and of nutrients in the detritus. The equation dealing with the dynamics of available nutrients has three main components: the supply of available nutrients without plants, the uptake of available nutrient by plants and the addition of available nutrients from the mineralization of organic nutrients within the plant detritus. Supply without plants is determined by a_i, the dilution rate of nutrient i, and by S_i, the amount of nutrient i becoming available to plants from non-plant sources. Plant uptake of nutrient i is a function of plant j biomass, the growth function of plant j, H_j, and amount of nutrient i per unit biomass of plant j, q_{ij}. Total plant uptake is the sum of each plant species uptake. Gains from the mineralization of organic nutrients within the plant detritus depend on the mineralization rate, δ_i, and amount of organic nutrients within the plant detritus.

The dynamics of plant j biomass are simply a function of gross growth and mortality, m_j. The dynamics of nutrients within the plant detritus are determined by how much nutrients within dead plant material is recycled in the ecosystem and how much is lost to mineralization. The portion of nutrient i from the dead material of plant j that is recycled is denoted by ζ_{ij}.

The growth function H_j obeys Liebig's law of the minimum, i.e. the nutrient that is least available relative to all others determines the growth rate of the plant. Within the growth function, there are functions describing the growth of the plant for each nutrient i and these are denoted by h_{ij}. The h_{ij} functions are considered to be strictly increasing functions with increasing available nutrient and have a constant maximum growth rate at infinite nutrient levels.

Others have analysed this model (Eq. 2.1) previously (Daufresne & Hedin 2005). The novel results from their analysis include changes in coexistence conditions at equilibrium due to the presence of recycling, the possibility that species could gain competitive advantages by differential recycling and the existence of oscillatory dynamics produced by the addition of recycling under certain conditions (Daufresne & Hedin 2005). However, there are some shortcomings to using this model framework for natural ecosystems.

A major problem for the model is the estimation of parameters (Grover 1997). The Monod function, the most used growth function that satisfies the properties of h_{ij}, has its parameters estimated through laboratory population growth data (Grover 1997). The estimates for the parameters can vary widely due to changes in environmental conditions and lead to inconclusive predictions of the model (Grover 1997) In addition, it is relatively rare to have appropriate data for natural plant communities as most researchers use measures such as relative cover rather than biomass (e.g. Wood & del Moral 1988).

A further complication involves the assumption of constant yield (Grover 1997). The inclusion of a variable stoichiometry, which gives rise to a variable-yield model with nutrient storage, can alter the predictions of the model (Grover 1992, Grover 1997, Klausmeier et al. 2004, Revilla & Weissing 2008). For example, variable yield models decouple nutrient uptake from growth, so competitive ability is a function of uptake parameters and plant composition parameters, which can lead to alternative competitive hierarchy than those derived from fixed yield models (Grover 1997, Revilla & Weissing 2008).It is also more difficult (i.e. requires narrower parameter ranges) to have oscillations when organisms have nutrient storage versus when they do not (Revilla & Weissing 2008). Since plants due show variable stoichiometry (e.g. Sterner & Elser 2002), predictions from a fixed stoichiometry model may not apply to actual plant communities.

2.2.1.1 *Including Variable Internal Nutrients and Uptake Rates*

To avoid these difficulties, I allow the stoichiometries to vary, which implies that the internal nutrient concentrations, Q_{ij}, can vary. In addition, I will also explore the possibility that uptake rates depend on the internal concentration of nutrients within the plant. There is evidence that plants uptake more nutrients when internal stores are deficient (e.g. Barber 1995) and this may alter model predictions.

Implementing these changes, the model equations become:

$$\frac{dR_i}{\underbrace{dt}_{\substack{\text{Rate of Change}\\ \text{of Nutrient i}\\ \text{in Soil Solution}}}} = \underbrace{\underbrace{I_i}_{\textit{Influx}} - \underbrace{\phi_i R_i}_{\textit{Efflux}}}_{\text{Supply without Plants}} \underbrace{- \omega \sum_{j=1}^{n} h_{ij}(R_i) g_{ij}(Q_{ij}) B_j}_{\text{Total Plant Uptake}} + \underbrace{\omega \delta_i D_i}_{\text{Mineralization}}$$

$$\frac{dQ_{ij}}{\underbrace{dt}_{\substack{\text{Rate of Change}\\ \text{of Internal Nutrient i}\\ \text{Concentration in Plant j}}}} = \underbrace{h_{ij}(R_i) g_{ij}(Q_{ij})}_{\text{Concentration}} - \underbrace{\mu(Q_{1j},\ldots,Q_{ij},\ldots,Q_{nj}) Q_{ij}}_{\text{Dilution}}$$

$$\frac{dB_j}{\underbrace{dt}_{\substack{\text{Rate of Change}\\ \text{of Plant Biomass j}}}} = \left[\underbrace{\mu(Q_{1j},\ldots,Q_{ij},\ldots,Q_{nj})}_{\text{Growth}} - \underbrace{m_j}_{\text{Mortality}} \right] B_j \qquad \textbf{(2.2)}$$

$$\frac{dD_i}{\underbrace{dt}_{\substack{\text{Rate of Change}\\ \text{of Nutrient i in Plant Detritus}}}} = \underbrace{\sum_{j=1}^{n} m_j B_j Q_{ij} \zeta_{ij}}_{\text{Recycling}} - \underbrace{\delta_i D_i}_{\text{Mineralization}}$$

$$\mu(Q_{1j},\ldots,Q_{ij},\ldots,Q_{nj}) = \mu_{\infty,j} \min\left(1 - \frac{Q_{\min,1j}}{Q_{1j}},\ldots,1 - \frac{Q_{\min,ij}}{Q_{ij}},\ldots,1 - \frac{Q_{\min,nj}}{Q_{nj}} \right)$$

The equation governing the dynamics of the plant detritus remains the same as in Eq. 2.1 except q_{ij}, a constant, is replaced by Q_{ij}, a variable (see Table 2.1 for list of variables and parameters). The biomass equation is also similar, but the growth function is now a function of Q_{ij} and has two new parameters: the maximum growth rate at infinite internal nutrients, $\mu_{\infty,j}$, and the minimum amount of internal nutrients to maintain the plant, $Q_{\min,ij}$. The new equation describing the dynamics of the internal nutrients has a concentration component and a dilution component. As plant *j* uptakes nutrient *i*, the amount of that nutrient per unit biomass within plant *j* increases (concentration). When plant *j* grows and adds more biomass, the amount of nutrients per unit biomass decreases (dilution).

The uptake function itself has changed from Eq. 2.1. Here, it is composed of two functions $h_{ij}(R_i)$, which is a strictly increasing function of R_i that is equal to zero at $R_i = 0$ and equal to $V_{max,ij}$ as R_i approaches infinity, and $g_{ij}(Q_{ij})$, which is a strictly decreasing function of Q_{ij} that is equal to one at $Q_{ij} = Q_{\min,ij}$ and is equal to zero at $Q_{ij} = Q_{\max,ij}$ with $Q_{\max,ij} < 1$. The two new parameters are the maximum uptake at infinite available nutrient and the maximum amount of nutrient *i* in plant *j*, respectively. The reason $Q_{\max,ij}$ must be less than one is that no plant is solely composed of any one element. The specific forms used when I parameterize the model with the Mount St. Helens data are:

$$h_{ij}(R_i) = \frac{V_{\max,ij} R_i}{K_{ij} + R_i},\ g_{ij}(Q_{ij}) = \frac{Q_{\max,ij} - Q_{ij}}{Q_{\max,ij} - Q_{\min,ij}} \qquad \textbf{(2.3)}$$

These functional forms represent Michaelis-Menten kinetics for nutrient uptake with a half-saturation constant K_{ij} and linearly decreasing function of internal nutrient concentration. The g_{ij} function attempts to incorporate into the model the fact that plants modify their nutrient uptake depending on their nutrient status (Barber 1995, Newberry et al. 1995).

Table 2.1: List of variables and parameters with their units for the stoichiometric model (Eq.. 2.2)

Variables	Meaning	Units
R	Plant available nutrients in soil solution	mol nutrient/L
Q	Nutrient concentration within plant	mol nutrient/mol C
B	Plant dry biomass	mol C
D	Nutrients in the detritus	mol nutrient
Parameters	**Meaning**	**Units**
$V_{\max}$	Maximum uptake rate at infinite R	mol N/(day x mol C)
K	Half-saturation constant	mol nutrient/L
μ	Maximum growth rate at infinite Q	1/day
$Q_{\min}$	Minimum nutrient concentration within plant	mol nutrient/mol C
$Q_{\max}$	Maximum nutrient concentration within plant	mol nutrient/mol C
m	Mortality constant	1/day
I	Influx of plant available nutrients from non-plant sources	mol N/(day x L)
φ	Efflux rate constant of plant available nutrients	1/day
ζ	Proportion of dead plant material entering the detritus	dimensionless
δ	Mineralization rate constant for nutrients in detritus	1/day
ω	Conversion factor for nutrients entering the soil solution from the detritus. Takes into account soil moisture levels.	1/L

The available nutrient equation has the same three elements as Eq. 2.1, but the supply without plants is written in different way and there is an additional parameter associated with the mineralization. The supply without plants is now defined by the influx of nutrient *i* from non-plant sources, I_i, and the efflux rate of nutrient *i* from the plant available nutrient compartment, φ_i. One can transform the supply rate in Eq. 2.1 into the form found in Eq. 2.2 by letting $a_i = \varphi_i$ and $a_iS_i = I_i$. The reason for using form found in Eq. 2.2 is due to using net mineralization rates that are in mol nutrient/time. The additional parameter in the mineralization, ω, is a conversion factor from mol nutrient to mol nutrient/L as available nutrients do not have the same units as the plant detritus. It should be noted that I_i is also dependent on water content and changes if ω changes. This relationship will be used during parameterization.

The internal nutrient equation needs a slight modification when it is being used to describe a nitrogen-fixer for nitrogen-fixers can utilize atmospheric nitrogen for growth. In such a case, I need to add an additional term to the concentration component of the equation:

$$\frac{dQ_{ij}}{dt} = \underbrace{\left(h_{ij}\left(R_i\right) + f_{ij}(R_i)\right)g_{ij}(Q_{ij})}_{\text{Concentration}} - \underbrace{\mu(Q_{1j},...,Q_{ij},...,Q_{nj})Q_{ij}}_{\text{Dilution}}$$

$$\begin{aligned}&\text{Properties of } f_{ij}\\ &1.\ \text{If } R_i' > R_i,\ \text{then } f_{ij}(R_i) > f_{ij}(R_i')\\ &2.\ f_{ij}(0) = F_{\max,ij} = \text{constant}\\ &3.\ \lim_{R_i\to\infty} f_{ij}(R_i) = 0\end{aligned} \qquad \textbf{(2.4)}$$

The fixation function, f_{ij}, is a strictly decreasing function of available nutrient for nitrogen-fixers reduce their fixation rates with increasing soil nitrogen (Lee et al. 2003). The maximum fixation rate occurs when no nutrient is present in the soil and approaches zero for infinite amount of available nutrient. For the purposes of the parameterized model, I note that lupines are known to maintain relatively constant nitrogen assimilation that is independent of soil nitrogen content (Gladstones et al. 1998, Lee et al. 2003). Therefore, the concentration component of the internal nutrient equation can be defined as a constant value. I assume this value is equal to $V_{\max,ij}$.

2.2.2 *Model Assumptions*

There are numerous assumptions made within this model concerning the variables and the parameters. This section delves into what assumptions were made and why they were taken. The consequences of violations of key assumptions are considered in the discussion.

Many key assumptions have been made about how nutrients are made available for plants within the soil. Here is a list of the major assumptions of the model:

1. Plants can only obtain nutrients from the soil solution in inorganic forms.
2. The nutrients within the soil solution are considered to be well-mixed, i.e. the plant available nutrient concentrations are identical everywhere in the area considered.
3. Nutrients within the soil are primarily located in the first ten centimetres of the soil.
4. The amount of water within the soil remains constant over time.
5. Plants have a fixed shoot:root ratio in terms of allocation of biomass.
6. Plants have a constant percentage of carbon within plant biomass.
7. Plants have fixed nutrient uptake parameters.
8. Plants suffer from continuous mortality during the growing season.
9. Plants grow vegetatively and sexual reproduction is ignored.
10. The detrital community converts the nutrients in dead plant material into plant available nutrients at a constant rate that is proportional to the total amount of dead plant material.
11. Plants compete through the reduction of belowground resources.

The first assumption is common one for physiological models of plant growth (Nye & Tinker 1977, Barber 1995). This is why the units for plant available nutrients are listed with moles of nutrient per litre in Table 2.1. While it does occur that plants uptake organic nutrients (e.g. Schimel & Bennett 2004), no work has been to quantify how much would be taken up by the plants on Mount St. Helens.

The validity of the second assumption depends on the ionic forms of the nutrients, the elemental identity of the nutrient, soil properties and the amount of overlap in the rooting systems (Huston & DeAngelis 1994, Barber 1995). As phosphorus may only be well-mixed in regions close to the root systems, I consider a fairly small area for plant competition ($1m^2$) in order to minimize the violation of the assumption.

The third assumption is made based on the empirical results of others on Mount St. Helens (Halvorson et al. 2005, Halvorson & Smith 2009). For other primary successional habitats, the location of nutrients within the soil profile may differ and this assumption can easily be relaxed.

The fourth assumption is made for simplicity and analytical tractability for water levels in primary successional soils can vary drastically over time and space (del Moral & Bliss 1993). However, I do vary the amount of water within the soil within relevant ranges and factor the changes of this range into the results.

Concerning the fifth assumption, experimental studies of the allocation to roots and to shoots for species on Mount St. Helens seem relatively constant after early growth (Halvorson et al. 1991b, Titus & del Moral 1998). However, it is true that there can be large variations in allocation as seen in *Lupinus* and where data is available for allocation, it is factored into the model (see Table 2.B in Appendix 2.B).

For the sixth assumption, experimental studies have noted that while there is some variation of carbon content within species, the variation is relatively small compared to variation in nitrogen and phosphorus (Halvorson et al. 1991b, Fagan et al. 2004, Gill et al. 2006). In addition, carbon should not be a limiting resource due to the lack of shading in plant communities on the volcano (Titus 2008).

While the seventh assumption is not true, the model attempts to address this failing by allowing uptake to depend on the nutrient status of the plant, which seems to be a main mechanism in changing the uptake parameters (Newberry et al. 1995). Therefore, the parameters may be constant, but the uptake is not.

The eight and ninth assumptions are made for simplicity and analytical tractability. With these assumptions, it is possible to ignore the stochasticity surrounding mortality events, the possibility of genetic differentiation within the species and life-history characteristics such as seed dispersal and seed size. Many of these assumptions are addressed in the next chapter of the thesis.

The tenth assumption is a gross simplification of the complex community dynamics involved (e.g. Cherif & Loreau 2009) in the detrital community, but can serve as a first-order approximation that will be refined in future studies. For example, one can refine the model by considering when the detrital community releases nutrients to the plant available pool rather than take nutrients from that pool (e.g. Wang et al. 2007). Once again, the simplification is motivated by concerns about understanding model properties and mathematical tractability.

The eleventh and final assumption indicates that factors such as allelopathy, competition for light and other potential mechanisms for competition are not considered here. Of these other factors, allelopathy seems the most likely to occur since *Hypochaeris radicata* may be allelopathic (Turkington & Aarssen 1983). I give a brief example of how to integrate allelopathy into the model and why there are no density-dependent terms in the model in Appendix 2.C.

2.2.3 *Model Parameterization*

Obtaining usable parameters values from the available data also involved making certain assumptions. For example, some values for nutrient uptake are in terms of fresh biomass and others are in dry biomass. Since the stoichiometry of plants is based on dry biomass, I need to convert nutrient uptake parameters into terms of dry biomass. Such a procedure is not trivial, as conversions are impacted by a variety of factors (Westlake 1963). Other parameters, such as the maximum growth rate at infinite internal nutrients or the influx of phosphorus must be estimated indirectly by using some assumptions. The steps taken for each parameter that needed some sort of conversion or indirect derivation is described in Appendix 2.B.

Much of the data on the parameters was presented in the form of point estimates, minimizing the amount of statistical work needed. I did need to estimate the phosphorus uptake parameters of *Hypochaeris* by utilizing a data set from Longeran & Asher (1967) and I used a non-linear regression to determine $V_{\max}$ and K.

It must be noted that not all parameters could be found for the species of interest. In many cases, I could only find measurements for related species. The lack of species-specific data is a common problem for ecologists and should not prevent us from making qualitative predictions if related species are similar in functional type. Hopefully models such as these will spur ecologists to obtain better physiological data on species so that more accurate model predictions can be made.

With all these assumptions, simplifications and caveats, I managed to parameterize the model (Table 2.2). Certain parameters were left as free parameters due to a lack of data regarding their values. Other parameters have large ranges of values for estimates provided by various authors vary widely. Fortunately, the parameters that matter most in competitive ability are also the best known as will be seen in the results.

Table 2.2: Values used and ranges of values for parameters in the model
a) *Lupinus lepidus* physiological parameters

Parameters	Value Used*	Range	Source
$V_{\max,NL}$	7.05×10^{-4}	$5.93\text{-}7.05 \times 10^{-4}$	Halvorson et al. 1992[a]
$V_{\max,PL}$	2×10^{-3}	$1.5\text{- } 2 \times 10^{-3}$	Esteban et al. 2003[b]
K_{NL}	1.15×10^{-4}	$1.15\text{-}1.19 \times 10^{-4}$	Dunabin et al. 2002[c]
K_{PL}	1.57×10^{-5}	$1.57\text{-}1.67 \times 10^{-5}$	Esteban et al. 2003[b]
$Q_{\max,NL}$	0.04507	--	Fagan et al. 2004
$Q_{\max,PL}$	0.00187	--	Fagan et al. 2004
$Q_{\min,NL}$	0.02525	--	Fagan et al. 2004
$Q_{\min,PL}$	0.000816	--	Fagan et al. 2004
$\mu_{\infty,L}$	0.218	--	Halvorson et al. 1991b
m_L	--	0.001-0.03	Braatne & Bliss 1999, Bishop 2002[d]

* Value used means that these values were used for all figures were simulations were used.

a Based on average nitrogen accumulation by *Lupinus lepidus* over whole growing season (hundred days).

b Data from *Lupinus albus*.

c Data from *Lupinus angustifolius and Lupinus pilosus*.

d Value based on 30% yearly mortality if no growth occurs.

Table 2.2 continued

b) *Hypochaeris radicata* physiological parameters

Parameters	Value Used	Range	Source
$V_{\max,NH}$	0.1272	0.0707-0.1272	Van de Djik et al. 1982
$V_{\max,PH}$	3.48×10^{-4}	--	Longeran & Asher 1967[a]
K_{NH}	7×10^{-6}	$0.7 - 1.9 \times 10^{-5}$	Van de Djik et al. 1982
K_{PH}	7.312×10^{-7}	--	Longeran & Asher 1967[a]
$Q_{\max,NH}$	0.050934	--	Fagan et al. unpublished data set
$Q_{\max,PH}$	0.00170	--	Mamolos et al. 1995[b]
$Q_{\min,NH}$	0.011548	--	Fagan et al. unpublished data set
$Q_{\min,PH}$	0.00113	--	Mamolos et al. 1995[b]
$\mu_{\infty,H}$	0.3518	0.2527-0.3518	Fenner 1978, Van de Djik et al. 1982
m_H	--	0.001-0.03	Tsuyuzaki et al. 1997[c]

a Data from *Hypochaeris glabra*. Parameters are derived from fitting using non-linear least squares.

b Assuming constant value for %C of 40.74.

c Data for seedling mortality. No data for adult mortality.

Table 2.2 continued

c) *Agrostis Scabra* physiological parameters

Parameters	Value Used	Range	Source
$V_{\max,NA}$	0.01834	0.01605-0.01834	Rachmilevitch et al. 2006
$V_{\max,PA}$	1.87×10^{-3}	$1.46\text{-}1.87 \times 10^{-3}$	Newberry et al. 1995[a]
K_{NA}	1.5×10^{-5}	$1.5 – 3.0 \times 10^{-5}$	Barber 1995[b]
K_{PA}	3.7×10^{-6}	$1.47 – 3.7 \times 10^{-6}$	Mouat 1983[c]
$Q_{\max,NA}$	0.03766	--	Bishop et al. unpublished data set
$Q_{\max,PA}$	0.003296	--	Newberry et al. 1995[a]
$Q_{\min,NA}$	0.004499	--	Bishop et al. unpublished data set
$Q_{\min,PA}$	0.0004301	--	Newberry et al. 1995[a]
$\mu_{\infty,A}$	0.140	0.120-0.140	Rachmilevitch et al. 2006
m_A	--	0.001-0.02	None

a Data from *Agrostis capillaris*.

b Data from non-*Agrostis* grass species such as *Fescue*.

c Data from *Agrostis tenuis*.

Table 2.2: continued

d) Nutrient and detritus dynamics parameters

Parameters	Value Used	Range	Source
I_N	--	$(5.95\text{-}10.2 \times 10^{-4}, 4.03\text{-}31.1 \times 10^{-6}) \times \omega$	Halvorson & Smith 2009, Gill et al. 2006[a]
I_P	--	$1.00\text{-}8.67 \times 10^{-4} \times \omega$	Halvorson & Smith 2009, Fagan et al. 2004[b]
ϕ_N	1	10^{-12} - 1	Free Parameter
ϕ_P	1	10^{-12} - 1	Free Parameter
ζ_{NL}	--	[0,1[	Free Parameter
ζ_{PL}	--	[0,1[	Free Parameter
ζ_{NH}	--	[0,1[	Free Parameter
ζ_{PH}	--	[0,1[	Free Parameter
ζ_{NA}	--	[0,1[	Free Parameter
ζ_{PA}	--	[0,1[	Free Parameter
δ_N	--	10^{-12}-1	Free Parameter
δ_P	--	10^{-12}-1	Free Parameter
ω	--	[0.04-0.5]	Titus 2008

a Data within parenthesis are in mol N/day and therefore need to be converted into mol N/(L x day), which is done by multiplying the values by the ω parameter. The first range is for data collected in 2005 by Halvorson & Smith (2009), the second for data collected in 2002 by Gill et al. (2006).

b Data are in mol P/day and therefore need to be converted into mol P/(L x day), which is done by multiplying the values by the ω parameter. Range is based on data from Halvorson & Smith (2009) and from Fagan et al. (2004).

2.3 Results

The results are divided into two main sections, with the first section (3.2.1) dealing with the general model with non-specified functional forms and the second exploring the parameterized model (3.2.2). The general model section is structured by first checking important model properties (3.2.1.1) such as positive invariance and is followed by analysing the case of one, two or three or more species (3.2.1.2-3.2.1.4) competing for two nutrient resources. Using the tools developed from the general model section, I explore the behaviour of the parameterized model (3.2.2) to see if it matches qualitative predictions found on Mount St. Helens.

2.3.1 General Model

2.3.1.1 General Properties

All mathematical models of biological phenomena need to be carefully specified in order to capture behaviour that is biologically relevant. In general, biological variables must remain within value ranges that are valid for real organisms, populations and ecosystems. For example, a model that allowed for negative biomass would not be biologically appropriate.

For the purposes of this model, it is required that all biological variables be positive if their initial values are positive for all time (i.e. positive invariance) and there must be an upper limit to the amount of nutrients within the system for all time (i.e. boundedness). Furthermore, certain variables need not only be positive, but also remain within a narrow range of values for all time.

In other words, it is required that R_i, B_j and D_i must be non-negative for all nutrients *i* and all species *j* for all time if their initial values at time 0 are non-negative. For Q_{ij}, it is required that its value remain between $Q_{\min,ij}$ and $Q_{\max,ij}$ for all nutrient *i* and all species *j* for all time if their initial values were initially between those values.

For boundedness, I must introduce a new quantity which represents the total amount of nutrient *i* within the ecosystem and label this quantity T_i. The total amount of nutrient *i* within the ecosystem is the sum of the amount nutrient *i* in the soil solution, the amount of nutrient *i* within all the plants and the amount of nutrient *i* within the plant detritus. The mathematical expression for T_i is:

$$T_i = \underbrace{k}_{\substack{\text{Water Content}\\ \text{of Soil}}} R_i + \sum_{j=1}^{n} B_j Q_{ij} + D_i \qquad \textbf{(2.5)}$$

Within the boundedness condition, there is a new quantity T_i, which is simply the total amount of nutrient *i* within the ecosystem. As long as this variable is always less than some constant θ, then the total amount of nutrient *i* within the ecosystem is bounded. The boundedness of T_i subsequently implies the boundedness of the other variables since Q_{ij} are always positive and the product of B_jQ_{ij} must be finite if T_i is finite. Therefore, there would be upper limits to all the model variables. Such a result makes biological sense for no organism has infinite biomass nor does any ecosystem have infinite amount of nutrients.

The model presented in Eq. 2.2 is both positively invariant and bounded, making it suitable for the biological system of interest. The proofs of theses properties are in Appendix 2.E for the positive invariance and Appendix 2.F for the boundedness. Both proofs are suitable for a system with *n* plants and *m* resources. These results will be helpful for investigating characteristics of the one, two and three plant species case with two nutrients.

In addition, the above results imply that all solutions of the model will eventually be attracted to a global attractor (Zhao 2003, Theorem 1.1.3). A global attractor is a subset of the metric space to which any solution within the metric space will be attracted (Zhao 2003). Knowing what the global attractor of a model is greatly enhances one's understanding of the model. For example, Li & Smith (2007) proved that for a single species with two nutrients with nutrient storage, but no recycling, that all solutions must converge to the plant steady state if it exists. Therefore, the complete behaviour of the model is known and a definite statement can be made about possible outcomes. Such model predictions can then be definitively tested by experiments, as no other outcomes would be possible.

Without knowing the global attractor, the behaviour of the model can only be partially characterized through local stability analyses and numerical simulations, which may miss important properties of the model. Unfortunately, the identity of the global attractor for my model is not known. Hopefully, my model may be of interest to those with greater understanding of mathematical analysis and they will be able to solve what I could not.

2.3.1.2 One Species, Two Nutrients

Even when considering a simple ecosystem with only one species and two nutrients, there are seven coupled ordinary differential equations governing the dynamics of the nutrients and plant biomass:

$$
\begin{aligned}
\underbrace{\frac{dR_1}{dt}}_{\substack{\text{Rate of Change of}\\ \text{Nutrient 1 in Soil}\\ \text{Solution}}} &= \underbrace{I_1 - \phi_1 R_1}_{\substack{\text{Supply of Nutrient 1}\\ \text{Without Plant}}} \underbrace{-\,\omega h_1(R_1) g_1(Q_1) B}_{\substack{\text{Uptake of Nutrient 1 by}\\ \text{Plant}}} + \underbrace{\omega \delta_1 D_1}_{\substack{\text{Gain of Nutrient 1}\\ \text{From Mineralization of}\\ \text{Plant Detritus}}} \\
\underbrace{\frac{dR_2}{dt}}_{\substack{\text{Rate of Change of}\\ \text{Nutrient 2 in Soil}\\ \text{Solution}}} &= \underbrace{I_2 - \phi_2 R_2}_{\substack{\text{Supply of Nutrient 2}\\ \text{Without Plant}}} \underbrace{-\,\omega h_2(R_2) g_2(Q_2) B}_{\substack{\text{Uptake of Nutrient 2 by}\\ \text{Plant}}} + \underbrace{\omega \delta_2 D_2}_{\substack{\text{Gain of Nutrient 2}\\ \text{From Mineralization of}\\ \text{Plant Detritus}}} \\
\underbrace{\frac{dQ_1}{dt}}_{\substack{\text{Rate of Change of}\\ \text{Internal Nutrient 1}\\ \text{Concentration in}\\ \text{Plant}}} &= \underbrace{h_1(R_1) g_1(Q_1)}_{\substack{\text{Gain of Nutrient 1}\\ \text{from uptake}}} - \underbrace{\mu_\infty \min\left(1 - \frac{Q_{\min,1}}{Q_1}, 1 - \frac{Q_{\min,2}}{Q_2}\right) Q_1}_{\text{Dilution of Nutrient 1 due to growth}} \\
\underbrace{\frac{dQ_2}{dt}}_{\substack{\text{Rate of Change of}\\ \text{Internal Nutrient 1}\\ \text{Concentration in}\\ \text{Plant}}} &= \underbrace{h_2(R_2) g_2(Q_2)}_{\substack{\text{Gain of Nutrient 2}\\ \text{from uptake}}} - \underbrace{\mu_\infty \min\left(1 - \frac{Q_{\min,1}}{Q_1}, 1 - \frac{Q_{\min,2}}{Q_2}\right) Q_2}_{\text{Dilution of Nutrient 2 due to growth}} \\
\underbrace{\frac{dB}{dt}}_{\substack{\text{Rate of Change of}\\ \text{Plant Biomass}}} &= \underbrace{\left(\mu_\infty \min\left(1 - \frac{Q_{\min,1}}{Q_1}, 1 - \frac{Q_{\min,2}}{Q_2}\right) - m\right) B}_{\text{Net Growth of Plant Biomass}} \\
\underbrace{\frac{dD_1}{dt}}_{\substack{\text{Rate of Chage of}\\ \text{Nutrient 1 in Plant Detritus}}} &= \underbrace{\zeta_1 m Q_1 B}_{\text{Gain of Nutrient 1 from Plant Mortality}} - \underbrace{\delta_1 D_1}_{\text{Loss of Nutrient 1 from Mineralization}} \\
\underbrace{\frac{dD_2}{dt}}_{\substack{\text{Rate of Chage of}\\ \text{Nutrient 1 in Plant Detritus}}} &= \underbrace{\zeta_2 m Q_2 B}_{\text{Gain of Nutrient 1 from Plant Mortality}} - \underbrace{\delta_2 D_2}_{\text{Loss of Nutrient 1 from Mineralization}}
\end{aligned}
\tag{2.6}
$$

One slight change in terms of notation from Eq. 2.2 is that since there is only one plant species within the ecosystem, the plant identity subscript is dropped. Furthermore, each variable has a number in the subscript indicating the identity of the nutrient, be it nutrient 1 or nutrient 2.

A simple ecosystem such as presented in Eq. 2.6 can only have two biologically relevant steady states. One steady state has no plant biomass, which will be labelled E^0, and one steady state has positive plant biomass, E^1. Furthermore, the E^1 steady state can be further subdivided depending whether the plant is most limited by nutrient 1 at steady state (E_1^1) or by nutrient 2 (E_2^1). For my purposes, I will consider the case where nutrient 1 is most limiting, for the results apply to nutrient 2 by replacing 1 by 2 in the subscripts.

The values of the variables for each steady state are found in Table 2.3. Some of the values can be expressed with an implicit function of the variable in question. It is shown in Appendix 2.G that these values are unique. This result implies that the steady states are of biological interest and not a mathematical artefact of the model.

It is important to note that despite the appearance of ω within the denominator for the steady state value of B in E^1, the value of B is independent of water content, except when water content is so large as to make I_i less than $\phi_i R_i^1$ (Table 2.3). This fact is due to I_i being a linear function of ω, which means that a change in water content alters both I_i and ω in such a way that the value B at steady state remains the same unless I_i becomes too small and the numerator becomes negative.

The conditions for the existence of the steady states are simple. E^0 always exists and E^1 exists if and only if (assuming nutrient 1 is most limiting) the level of nutrients within the soil solution at the no plant steady state and therefore within the plant are sufficient to enable positive growth of the plant species. However, the condition for existence does not indicate whether or not the plant will establish, just that it can. To know if the plant will or will not establish, one must look at the stability conditions of the steady states.

The stability considered here is the local asymptotic stability of the steady state, which indicates whether or not solutions will return to the steady state if they are slightly perturbed. The local stability is derived by linearizing around the steady state, which generates a Jacobian matrix whose eigenvalues determine the local asymptotic stability. If all of the real parts of the eigenvalues of the Jacobian are negative, then the steady state is locally stable. Otherwise, the linearization does not indicate a return the steady state and the steady state may not be locally stable.

The main result is that if E^1 exists, then E^0 is unstable and E^1 is locally stable and if E^1 does not exist, then E^0 is locally stable. Furthermore, if E^1 exists, then it is locally stable. The Jacobian matrix and derivations for the stability conditions are located in Appendix 2.H. These results mean that if a plant is able to invade the no-plant steady state, then it will establish itself with positive biomass.

It does not mean that all solutions of the model for given parameter values will tend towards either E^0 or E^1. To prove this, one needs to show that E^0 is the global attractor when E^1 does not exist and E^1 is the global attractor when E^1 does exist. Based on numerical results and proofs for similar (though not identical) models (e.g. Li & Smith 2007), I conjecture that E^1 is the global attractor when it exists and E^0 is the global attractor when E^1 does not exist. A rigorous proof of this conjecture would guarantee that if a plant is able to invade the no-plant steady state, the ecosystem will go to a plant steady state.

While the previous results are heavily mathematical, they can be given a simple visual presentation using graphical techniques originally developed by Tilman (1980, 1982). Graphical representation takes place in the nutrient 1-nutrient 2 plane where the zero-net growth isocline of the species of interest and the supply point of the nutrients determine the conditions for existence of E^1 (Figure 2.2).

Table 2.3: Steady states for the variables in Eq. 2.6. The superscript on the variables indicates the steady state from which the value is derived. The subscript on the variable indicates the nutrient. See Table 2.1 for descriptions of the variables.

	Steady States	
Variable	E^0	E^1
Q_1	$h_1(R_1^0)g_1(Q_1^0)$ $-\mu_\infty(Q_1^0 - Q_{\min,1}) = 0$	$\dfrac{\mu_\infty Q_{\min,1}}{\mu_\infty - m}$
R_1	$\dfrac{I_1}{\phi_1}$	$h_1^{-1}\left(\dfrac{\mu_\infty(Q_1^1 - Q_{\min,1})}{g_1(Q_1^1)}\right)$
B	0	$\dfrac{I_1 - \phi_1 R_1^1}{(1-\zeta_1)\omega m Q_1^1}$
D_1	0	$\dfrac{\zeta_1 B^1 Q_1^1 m}{\delta_1}$
Q_2	$h_2(R_2^0)g_2(Q_2^0)$ $-\mu_\infty\left(1 - \dfrac{Q_{\min,1}}{Q_1}\right)Q_2^0 = 0$	$h_2\left(\dfrac{I_2 - (1-\zeta_2)\omega m Q_2^1 B^1}{\phi_2}\right)g_2(Q_2^1)$ $-mQ_2^1 = 0$
R_2	$\dfrac{I_2}{\phi_2}$	$\dfrac{I_2 - (1-\zeta_2)\omega m B^1 Q_2^1}{\phi_2}$
D_2	0	$\dfrac{\zeta_2 B^1 Q_2^1 m}{\delta_2}$

The zero-net growth isocline or ZNGI represents the level of nutrients at which gross growth is equal to mortality, once the internal plant nutrient concentration equilibrates with soil solution nutrients. When dealing with essential nutrients like nitrogen and phosphorus, the ZNGI will be determined by the steady state value of that nutrient in soil solution when it is limiting, resulting in an L-shaped ZNGI (Figure 2.2). The steady state values for the soil nutrients derived from the model are equivalent to Tilman's *R**, which is the nutrient level at which plant growth stops (Tilman 1980). I use *R** values to describe outcomes competition between plants for nutrients, though the model results are not reliant on classical resource competition theory.

Finding the *R** values and hence the ZNGI is straightforward. First, one sets dB/dt to be equal to zero and it is assumed that only one nutrient is limiting. If it is assumed that nutrient 1 is limiting, then:

$$0=\frac{dB}{dt}=\mu_\infty\left(1-\frac{Q_{\min,1}}{Q_1}\right)B-mB$$

$$0=\mu_\infty\left(1-\frac{Q_{\min,1}}{Q_1}\right)-m,\ B\neq 0$$

$$Q_1^*=\frac{\mu_\infty Q_{\min,1}}{\mu_\infty-m}$$

The next step is to set dQ_1/dt equal to zero and to solve for R_1^*, which gives you the value in right-hand column of Table 2.3 for R_1. The procedure is similar to find R_2^* and with both values one can construct the ZNGI.

The supply point of nutrients is the amount of nutrients at steady state with no plants. In the model, this supply point would be $\left(I_1/\phi_1, I_2/\phi_2\right)$ in the nutrient 1-nutrient 2 plane (Figure 2.2). With knowledge of the supply point and the ZNGI, one can easily determine whether or not a particular plant species could establish in a particular environment. If the supply point is to the left and/or below the ZNGI, then net plant growth is negative in this environment and the plant cannot establish (Figure 2.2). If the supply point is above and to the right of the ZNGI, then the plant has positive net growth in the environment and can establish itself (Figure 2.2).

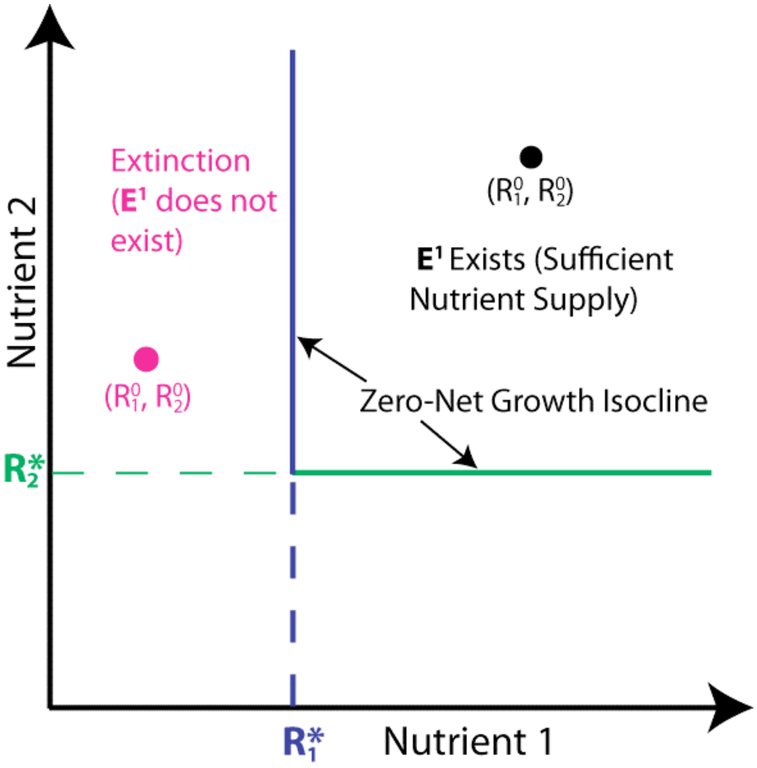

Figure 2.2: Graphical representation of the conditions of existence for E^1 in the general model**.** The black dot represents a supply point that provides sufficient amount of nutrients in order to let E^1 to exist. The pink dot represents a supply point that provides insufficient amount nutrients to allow E^1 to exist, which means the no plant can persist. The zero-net growth isocline or ZNGI divides the nutrient 1-nutrient 2 plane into areas of sufficient and insufficient supply. The ZNGI is determined by the *R** value of each nutrient for the species.

Furthermore, the graphical method allows one to find the values of R_1 and R_2 at the steady state determined by the supply point. These values can be derived from the knowledge that at the steady state, the uptake of the nutrients by the plant must equal the supply. In addition, this point must lie on the ZNGI or there would be no steady state. Finally, it is known from the analysis of the model that only one set of values for R_1 and R_2 will satisfy the condition that uptake will equal supply.

An example is provided in Figure 2.3. The key to finding the steady state is to know the consumption vector ***c*** and the recycling vector ***r*** of the species along its ZNGI and the supply vector ***u*** for the nutrients. To find these vectors, one rewrites the equations for dR_1/dt and dR_2/dt in vector form:

$$\begin{pmatrix} \dfrac{dR_1}{dt} \\ \dfrac{dR_2}{dt} \end{pmatrix} = \begin{pmatrix} I_1 - \phi_1 R_1 - \omega h_1(R_1) g_1(Q_1) B + \omega \delta_1 D_1 \\ I_2 - \phi_2 R_2 - \omega h_2(R_2) g_2(Q_2) B + \omega \delta_2 D_2 \end{pmatrix}$$

One then evaluates the vector equation at steady state and sets all the variables to their values at E^1:

$$\begin{pmatrix} 0 \\ 0 \end{pmatrix} = \begin{pmatrix} I_1 - \phi_1 R_1^1 - \omega h_1(R_1^1) g_1(Q_1^1) B^1 + \omega \zeta_1 m Q_1^1 B^1 \\ I_2 - \phi_2 R_2^1 - \omega h_2(R_2^1) g_2(Q_2^1) B^1 + \omega \zeta_2 m Q_2^1 B^1 \end{pmatrix}$$

The vector on the right hand side can be divided into three vectors, with the first describing the nutrient supply, the second describing nutrient uptake and the third describing nutrient recycling:

$$\begin{pmatrix} 0 \\ 0 \end{pmatrix} = \begin{pmatrix} I_1 - \phi_1 R_1^1 \\ I_2 - \phi_2 R_2^1 \end{pmatrix} + \begin{pmatrix} -\omega h_1(R_1^1) g_1(Q_1^1) B^1 \\ -\omega h_2(R_2^1) g_2(Q_2^1) B^1 \end{pmatrix} + \begin{pmatrix} \omega \zeta_1 m Q_1^1 B^1 \\ \omega \zeta_2 m Q_2^1 B^1 \end{pmatrix} \tag{2.7}$$

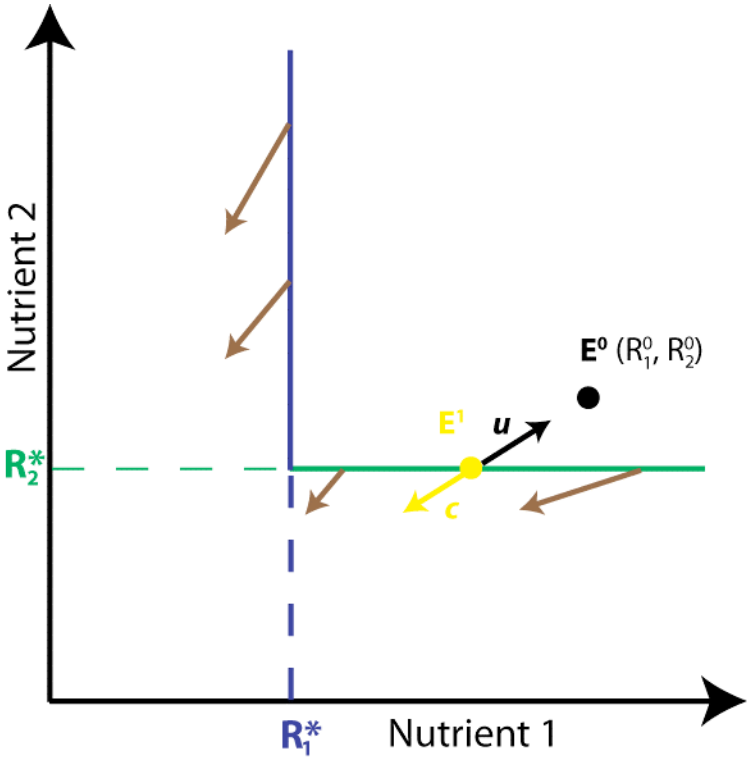

Figure 2.3: Using the graphical method to find E^1. The steady state (the yellow dot) will be located where the supply vector u (the black arrow) will be equal to the consumption vector c (the yellow arrow). The possible consumption vectors (the brown arrows) along the ZNGI (blue-green L-shaped line) change in magnitude and direction depending on location, which is different than in classical resource competition models.

I call these vectors as ***u***, ***c*** and ***r***:

$$u = \begin{pmatrix} I_1 - \phi_1 R_1^1 \\ I_2 - \phi_2 R_2^1 \end{pmatrix}, c = -\begin{pmatrix} h_1(R_1^1)g_1(Q_1^1) \\ h_2(R_2^1)g_2(Q_2^1) \end{pmatrix}\omega B^1, r = \begin{pmatrix} \zeta_1 Q_1^1 \\ \zeta_2 Q_2^1 \end{pmatrix}\omega m B^1 \qquad \mathbf{(2.8)}$$

When there is no recycling, ***r*** will be equal to zero and at E^1, the consumption vector will have to cancel out the supply vector, which implies that ***c*** + ***u*** = 0 (Eq. 2.7). Therefore, the point in the plane at which ***c*** + ***u*** = 0 is true will be E^1. It should be noted that unlike classical resource competition models (e.g. Tilman 1980), the slope and magnitude of the consumption vector can change along the ZNGI since ***c*** is dependent on internal nutrient concentrations (Figure 2.3).

The above formulation is only correct when there is no recycling. When there is recycling, the consumption vector must equal the magnitude of the sum of the supply vector with the recycling vector ***r***. The addition of recycling changes the location of E^1 such that the point in the nutrient 1-nutrient 2 plane must satisfy ***c*** + ***u*** + ***r*** = 0 or ***c*** + ***u'*** = 0 where ***u'*** = ***u*** + ***r*** (Eq. 2.7). Recycling also alters the location of the supply point, which may cause a shift in the nutrient that is most limiting (Figure 2.4). However, recycling does not change the conditions for stability or existence in the one-species case. It does, however, play a large role in the two species case.

2.3.1.3 Two Species, Two Nutrients

The behaviour of the model becomes more complex with the addition of an additional species. With two species and two nutrients, there can be as many as four steady states. These steady states are the no-plant steady state (E^0), the plant *x* only steady state (E^x), the plant *y* only steady state (E^y) and the coexistence steady state (E^{xy}). The existence of the no-plant and single plant steady states have already been derived in section 2.3.1.2: the no-plant steady state always exists and the single plant steady states exist if the R_i^* for the species in question are less than R_i^0. The existence of the coexistence steady state requires that at least one point in the nutrient 1-nutrient 2 plane must have zero net growth for both species. In graphical terms, the ZNGIs of plant *x* and plant *y* must intersect (Figure 2.5a).

The crossing of the ZNGIs implies that at the coexistence steady state, the two species must be limited by different nutrients. If the two species were limited by the same nutrient and they did not share the same R^* for that nutrient, then the species with the lowest R^* will lower the nutrient in the soil solution to a level at which the other species cannot persist and no coexistence is possible. Without the crossing of the ZNGIs, one species will always be able to bring one of the nutrients down to a level that the other species will experience negative growth at, which leads to the exclusion of the second species (Figure 2.5b).

Another condition for the existence of the coexistence steady state is that the consumption of nutrients by the two species must be balanced by the supply of nutrients without plants plus the nutrients supplied by recycling. This condition can be translated mathematically into $\boldsymbol{c}_{xy} + \boldsymbol{u} + \boldsymbol{r}_{xy} = 0$, where $\boldsymbol{c}_{xy} = \boldsymbol{c}_x + \boldsymbol{c}_y$ and $\boldsymbol{r}_{xy} = \boldsymbol{r}_x + \boldsymbol{r}_y$ (see Appendix 2.I for details).

This condition limits the possible locations of the supply point in the R_1-R_2 plane that can allow for coexistence as the combined consumption vector of species x and y can only take on certain values without the biomass of one of the species becoming negative. What values the slope of the supply vector can take, which implies the values of the supply point, is determined by the following formula (the derivation of this formula is in Appendix 2.I):

$$\beta_y > \frac{(I_2 - \phi_2 R_2^{xy})}{(I_1 - \phi_1 R_1^{xy})} > \beta_x \qquad \textbf{(2.9)}$$

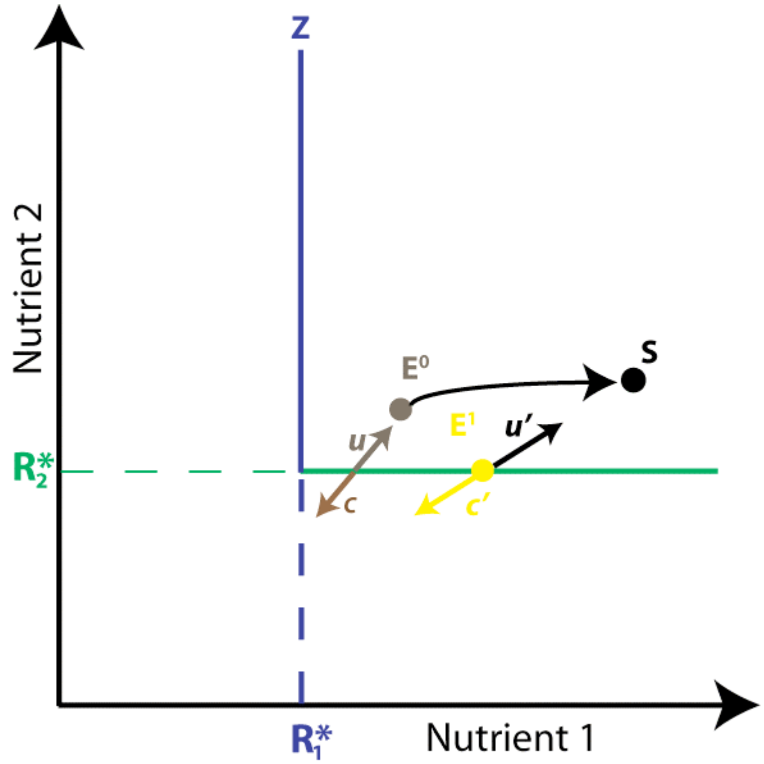

Figure 2.4: Impact of recycling on the one species, two nutrient case of the general model. Adding recycling to the system translates the original supply point (gray dot), labelled E^0 to denote the fact its value is determined by the no-plant steady state, to the right and upwards in nutrient 1-nutrient 2 space (black dot). The shifting of the supply point changes the slope of the supply vector at steady state from ***u*** (grey arrow) to ***u'*** (black arrow). This change in the supply vector alters the slope of the consumption vector at steady state from ***c*** (brown arrow) to ***c'*** (yellow arrow). The net result of this

translation is a change in the steady state values of E^1 (yellow dot), which lies on the ZNGI (Z).

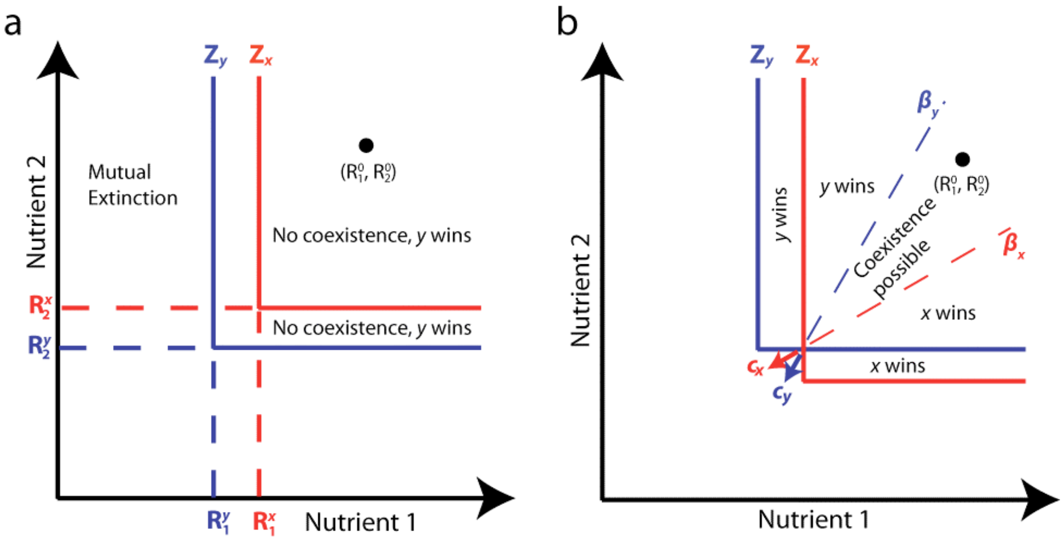

Figure 2.5: Using graphical analysis to determine the competitive outcomes between two species for two limiting nutrients. The relative competitive abilities for each species for each nutrient are determined by the R^* values, which define the ZNGIs (Z_x, Z_y.). (A) Plant *y* has a lower R^* for both nutrient 1 and nutrient 2 and is able to always competitively exclude plant *x*, making coexistence impossible. (B) Plant *y* has a lower R^* for nutrient 1 and plant *x* for nutrient 2, making coexistence possible within a range of ($R^0{}_1$, $R^0{}_2$) values. The area of possible coexistence is determined by the slopes of the consumption vectors (β_x and β_y) at steady state. Outside of this area, one species or the other will competitively exclude the other.

Where β_j is the slope of the net consumption vector of plant species *j* at steady state. The net consumption vector of species *j* is defined to be gross consumption of nutrients plus the amount of nutrients recycled by species *j*, so it is therefore equal to ($\mathbf{c}_j + \mathbf{r}_j$). The value of β_j can be found from this simple expression:

$$\beta_j = \frac{(1-\zeta_{1j})Q^{xy}_{1j}}{(1-\zeta_{2j})Q^{xy}_{2j}} \qquad \textbf{(2.10)}$$

The slope of the net consumption vector of plant *j* can then be interpreted to be equal to the ratio of nutrients lost during the recycling of dead matter of plant *j* at steady state (see Appendix 2.J for derivation of Eq. 2.9). This result indicates that the losses of nutrients by each plant during recycling dictate the possibility of coexistence between the two plants.

The satisfaction of both conditions is needed to permit the existence of the coexistence steady state (Figure 2.5b). However, the satisfaction of these conditions does not guarantee the stability of the steady state, which is vital in determining whether or not coexistence will occur. The derivations of the conditions for the stability of the various steady states for the two species, two nutrient case, when such conditions can be found analytically, are found in Appendix 2.K.

The stability of the no-plant steady state depends, as in the single species case, on the existence of other steady states. If E^x and/or E^y exists, then the no-plant steady state will be unstable. The stability of the single plant steady states, E^x and E^y, depends on the ability of the other species to support positive growth at the level of nutrients at the steady state. For example, E^x is only locally stable if plant *y* cannot maintain positive growth for the nutrient levels at the plant *x* only steady state:

$$\mu_{\infty,y} \min\left(1-\frac{Q_{\min,1y}}{Q_{1y}^x}, 1-\frac{Q_{\min,2y}}{Q_{2y}^x}\right)-m_y < 0 \qquad \textbf{(2.11)}$$

The same condition applies when the steady state with only plant *y*. These conditions for the stability of the two single species steady states make sense when using graphical analysis (Figure 2.5). In Figure 2.5a, E^y is always locally stable, no matter which nutrient is most limiting to it, for plant *x* has negative net growth at those levels of nutrients. In addition, E^x is always locally unstable for plant *y* maintains positive growth at the level of nutrients determined by this steady state. Therefore, plant *y* will always dominate and exclude plant *x* in competition and no coexistence can occur.

In Figure 2.5b, in certain areas of the nutrient 1-nutrient 2 space, E^y is locally stable and E^x is locally unstable and in others the situation is reversed. For example, in the area marked '*y* wins' and E^x exists, plant *x* is most limited at steady state by nutrient 1. A monoculture of plant *x* can be invaded by plant *y* in this region of nutrient 1-nutrient 2 space as plant *y* would have positive growth at that level of nutrients. Plant *y* in this region of nutrient 1-nutrient 2 space will then bring the level of nutrient 1 below that needed for plant *x*, resulting in the exclusion of plant *x*. A similar situation occurs in the areas marked '*x* wins' as plant *x* outcompetes plant *y* for nutrient 2, which is most limiting in that region of nutrient 1-nutrient 2 space. Within the areas of possible coexistence, both steady states may be stable or unstable, depending on the slopes of the consumption vectors.

In classical resource competition theory, if each species consumes relatively more of the nutrient that it is the worst competitor for, then the two single species steady states are locally unstable and the coexistence steady state is stable (Tilman 1980). For the example in Figure 2.5, since plant *y* consumes relatively more of nutrient 2 and plant *x* consumes relatively more of nutrient 1 at the coexistence steady state, then it should be stable according to classical theory. If the situation is reversed such that plant *x* consumes relatively more of nutrient 2 and plant *y* consumes relatively more of nutrient 1 at the coexistence steady state, then the coexistence steady state should be unstable and the two single species steady states would both be stable (Tilman 1980).

The results of classical resource competition theory still hold if stoichiometry is included as long as there is no recycling and there is conservation of mass in the system (Li & Smith 2007, Revilla & Weissing 2008). If recycling is ignored, similar predictions are found in this model as in the previous models even though there is no conservation of mass (Figure 2.6). When recycling is added, the predictions of the model become more complicated.

Recycling can expand or contract the area of coexistence and the relative positions of the consumption vectors by modifying their slopes (e.g. Figure 2.13). It has been shown previously in a resource competition model with fixed stoichiometry that recycling can make an unstable coexistence steady state stable or vice-versa (Daufresne & Hedin 2005). Furthermore, it was demonstrated that it is possible to induce limit cycles when the coexistence steady state can only stable when recycling is present (Daufresne & Hedin 2005).

A key result from the stoichiometric model is that cycles can also occur under the same conditions as in Daufresne & Hedin (2005) (Figure 2.7a). The formation of cycles is dependent on the rate of mineralization, with no cycles or cycles with small magnitudes for faster mineralization and high amplitude cycles for slower mineralization (Figure 2.7b). If the mineralization becomes too slow, then the stabilizing effect of recycling is lost and competitive exclusion will occur (Figure 2.7c).

The cycles are due to changes in the relative internal nutrient concentrations, with the most limiting nutrient becoming less limiting and the least limiting nutrient becoming more limiting. These changes can be dramatic enough to cause the flipping of limiting nutrients for each species over time (Figure 2.8). The switching alters the consumption patterns near the steady state, causing the solution to move away from the steady state even though it may be predicted to be locally stable through numerical local stability analysis as Figure 2.7b is.

Therefore, there are limitations to the predictions garnered from graphical analysis and local stability analysis for this model. These limitations are caused by allowing the uptake rates to be dependent on internal nutrient concentrations of the plant, which can result in consumption vectors near steady state to not go towards steady state, especially when there are delays caused by recycling. Still, the techniques do give insights on what may be expected from the model even if they do not always predict the correct outcome.

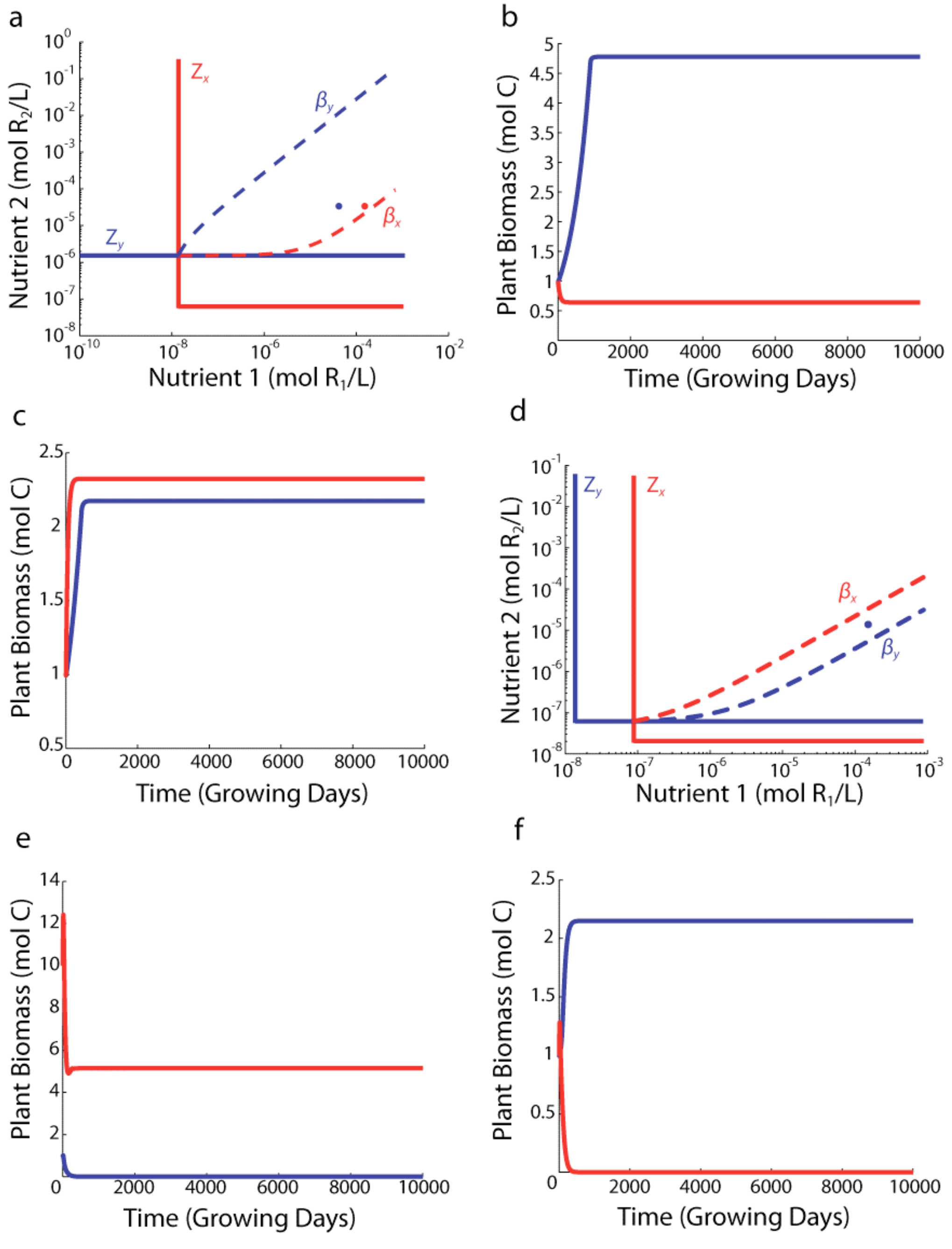

Figure 2.6: Predictions from graphical analysis of stoichiometric model with no recycling using ZNGIs (Z_x and Z_y) and slopes of the consumption vectors (β_x and β_y). **a** Graphical analysis predicts coexistence between plant y (blue) and plant x (red) between β_x and β_y (lines are curved due to log-log scale). Numerical local stability analysis also predicts coexistence between the two species in that area. **b** Numerical simulation of model at the blue supply point in **a**, which shows coexistence between the two species. **c** Numerical simulation of model at red supply point in **a**, which also shows coexistence.

d Graphical analysis and numerical stability analysis predicts bistability in area between β_x and β_y. **e & f** Numerical simulation of model at blue supply point in **d** with different initial conditions. In the first case, plant *x* wins in competition and in the second, plant *y* wins in competition.

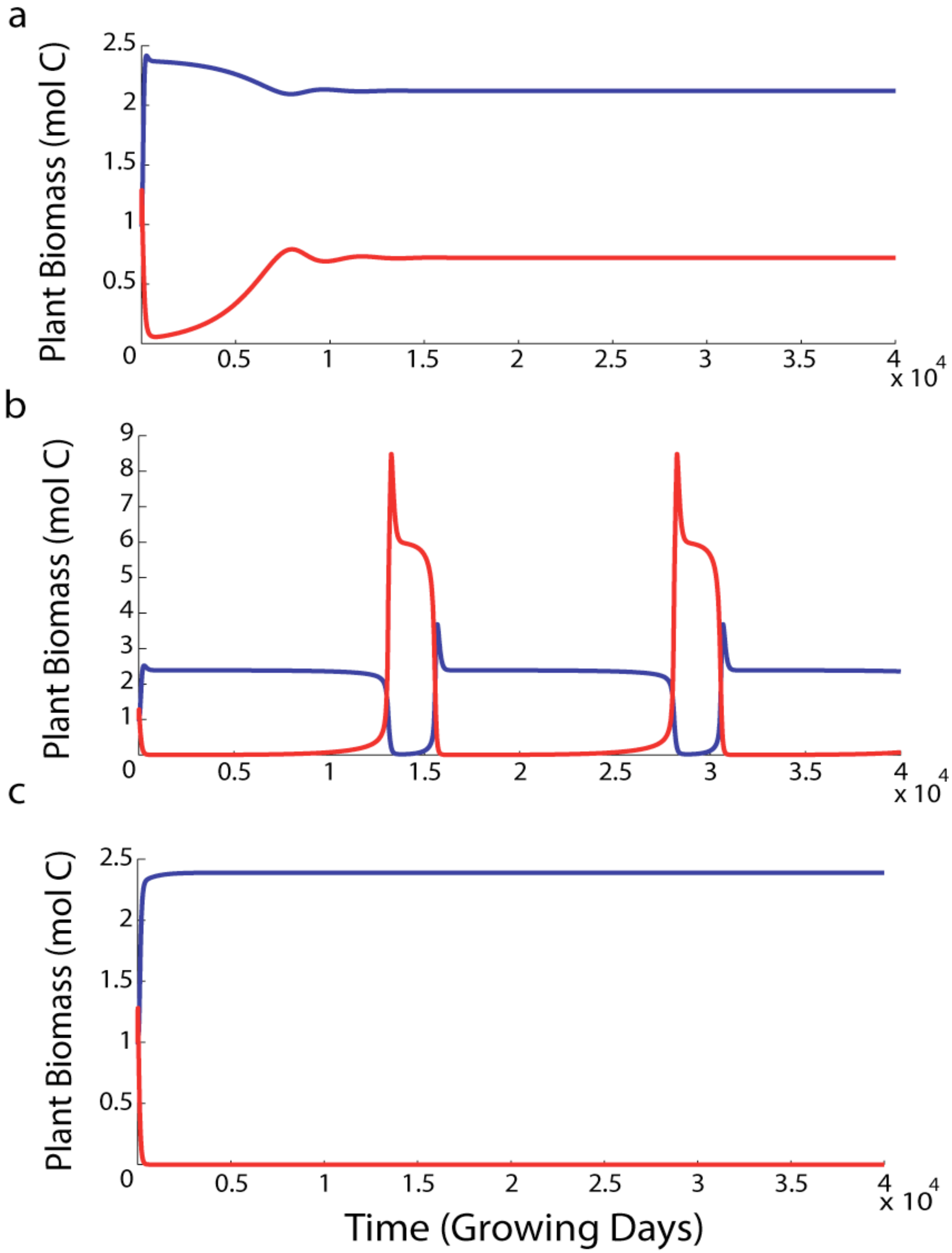

Figure 2.7: The effects of the rate of mineralization on plant biomass dynamics when recycling is needed to allow coexistence. **a** With $d_i = 0.15$, plant biomass tends towards a stable steady state. **b** When $d_i = 0.015$, the steady state is no longer stable and the plant biomass for both species follow a limit cycle. Plant *y* (blue) is very close to going

extinct, hence these cycles demonstrate pseudo-exclusion. **c** When $d_i = 0.0015$, plant *x* (red) excludes plant *y* from the ecosystem.

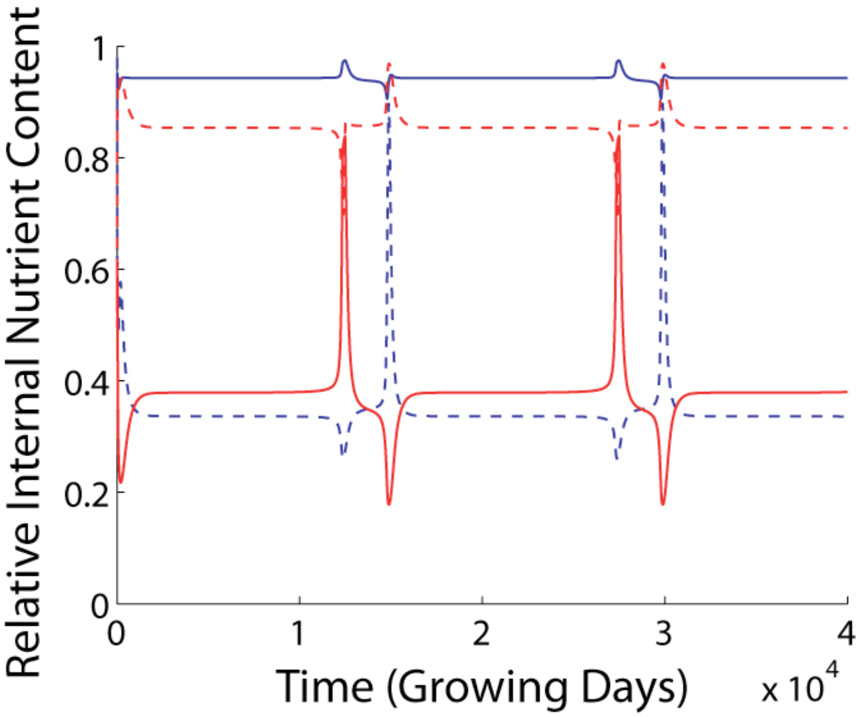

Figure 2.8: Evidence of switching of the limiting nutrient over time. Relative internal nutrient content is an index with values ranging from 0 to 1, with 0 being infinite internal nutrients and 1 being the minimum amount of nutrients possible ($Q_{\min}$). The nutrient with the highest value is most limiting. Nutrient 2 (solid blue line) is usually most limiting for plant *y*, but nutrient 1 (dashed blue line) briefly becomes most limiting at periodic intervals. For plant *x*, nutrient 1 (dashed red line) is normally most limiting except for brief periods where nutrient 2 is most limiting (solid red).

2.3.1.4 Three or More species, Two Nutrients

The case of three or more species competing for two essential limiting nutrients is somewhat similar to the previous cases. With only two essential nutrients, it is generally not possible for three species coexistence steady state to exist. This fact can be derived from the geometric properties of the zero-net growth isoclines.

Each isocline is composed of a vertical line and a horizontal line, which forms an L shape. Two isoclines form a coexistence steady state when the first isocline's vertical line intersects with the second's horizontal line or vice-versa. In order to have a third species at the steady state, it must intersect the steady state with either its vertical line or horizontal line. However, then this third species will then have at least one of its R^* values identical to another species, which means there is no coexistence steady state between the two species. Therefore, there is no coexistence between three species.

It may be possible for non-equilibrium coexistence between three or more species competing for two nutrients when recycling is present (Daufresne & Hedin 2005). However, such behaviour has not been observed during the exploration of the parameter space of this model.

As with the single and two species case, graphical analysis is useful in determining the outcomes of competition of three or more species (Figure 2.9). As with the two species case, the outcomes of competition are dependent on the slopes of the consumption vectors at the steady states (Figure 2.9). It also makes it straightforward to see which steady states are unstable even without considering the consumption vectors. For example, at the potential steady state of plant *y* and plant *z*, plant *x* will have positive growth, indicating that it must be unstable (Figure 2.9).

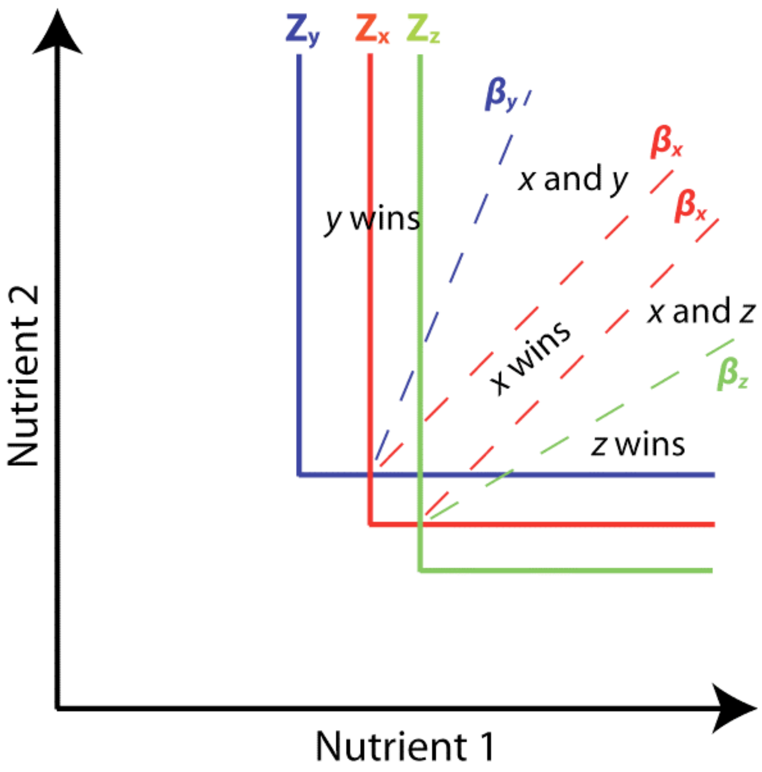

Figure 2.9: An example of using graphical analysis for three species competing for two nutrients. Since the three isoclines (Z_x, Z_y, Z_z) cannot intersect at the same point, there is no possibility for a steady state with all three species. In this example, there are three possible steady states that exhibit two-species coexisting, with two being stable due to the slopes of the consumption vectors (β_x, β_y, β_z) at steady state (the red-blue dot and the red-green dot). The dashed lines defined by these slopes divide R_1-R_2 space into regions of single species dominance and two-species coexistence, with the location of the supply point determining the outcome of competition.

2.3.2 Parameterized Model

The theoretical models outlined above were parameterized with the data from Table 2.2. Based on these parameters, the competitive abilities of the three plants were measured by calculating their *R** values, which serves as a proxy for competitive ability (Table 2.4). Since these values are sensitive to a number of parameters, the effects of the parameters on the *R** values was investigated (Appendix 2.L).

Parameters that reduce *R** values (increase competitive ability) when increasing are the nutrient uptake rates, the growth rate at infinite quota and the maximum internal nutrient concentration. Parameters that increase *R** values when increasing are the half-saturation constants, the mortality rate and the minimum internal nutrient concentration. Due to a lack of estimates for the mortality rate constants, I analyze competitive ability assuming comparable mortality rates between species, with slightly higher rates for *Lupinus* due to herbivory.

Table 2.4: Relative competitive abilities of *Lupinus*, *Hypochaeris* and *Agrostis* for nitrogen and phosphorus

a**)** Assuming m_L=0.003 and $m_H = m_A = 0.00233$

	Lupinus	*Hypochaeris*	*Agrostis*
R^*_N	0[a]	1.49-7.32 x 10^{-9}	8.74 – 20.0 x 10^{-9}
R^*_P	1.97 – 2.8 x 10^{-8}	5.69 – 5.73 x 10^{-9}	8.05 – 26.0 x 10^{-10}

a *Lupinus* can maintain positive growth with no nitrogen being supplied due to its nitrogen fixation.

b) Assuming m_L=0.03 and m_H=m_A=0.029

	Lupinus	*Hypochaeris*	*Agrostis*
R^*_N	0[a]	2.07-10.6 x 10^{-8}	1.41 – 3.40 x 10^{-7}
R^*_P	2.58-3.69 x 10^{-7}	1.04 – 1.22 x 10^{-7}	1.30 – 4.43 x 10^{-8}

a *Lupinus* can maintain positive growth with no nitrogen being supplied due to its nitrogen fixation.

The competitive ranking for *Lupinus*, *Hypochaeris* and *Agrostis* remain the same for low and high mortality rates (Table 2.4). For nitrogen, *Lupinus* is the best competitor, followed by *Hypochaeris* with *Agrostis* being the worst (Table 2.4). For phosphorus, the rankings are inverted with *Agrostis* being the superior competitor and *Lupinus* being the worst. There is no overlap between *R** values for any of the species, signalling that if the assumption of similar mortality rates is true, than the competitive abilities between species are different.

Due to the rankings of competitive abilities, there are three possible two-species coexistence steady states (Figure 2.10, see Appendix 2.D for parameter values for Figures). One of these steady states, the *Agrostis*-*Lupinus* steady state, will always be unstable in the presence of *Hypochaeris*, since *Hypochaeris* can maintain positive growth at the associated nutrient levels. If I ignore recycling, the *Hypochaeris*-*Lupinus* steady state is locally stable if it exists and the *Agrostis*-*Hypochaeris* steady state is unstable (Figure 2.11). In addition, the empirically derived region of nutrient supply is located within both these regions, indicating large potential shifts in community composition depending on the local environment (Figure 2.11).

Furthermore, there is an area within the parameter space where a stable *Hypochaeris-Lupinus* steady state overlaps with the unstable *Agrostis-Hypochaeris* steady state (Figure 2.11). Numerical exploration of this parameter space indicates that the eventual outcome is either a community composed of *Agrostis* alone or composed of *Hypochaeris* and *Lupinus* (Figure 2.12). The outcome is dependent on the initial conditions, indicating that the region is bistable (Figure 2.12).

The nutrient supply levels are sufficient enough to support all three plants. Therefore, the model predicts that all three species should be capable of establishing on Mount St. Helens. Furthermore, the region of supply indicates that *Hypochaeris* should normally outcompete *Agrostis* though it will sometimes depend on chance (Figure 2.12).

Nutrient recycling can affect competitive outcomes between the species on Mount St. Helens (Figure 2.13). Nutrient recycling can allow coexistence between *Agrostis* and *Hypochaeris* as well as a reduction of the space of coexistence between *Hypochaeris* and *Lupinus* (Figure 2.13). However, this effect requires a high discrepancy between the recycling of phosphorus and nitrogen for both species, which may not be biologically reasonable. Furthermore, this effect requires relatively high levels of nitrogen within the soil, which may not always be present (Figure 2.13) Another effect is that *Lupinus* adds more nitrogen than it uptakes from the environment at the steady states observed here, it can allow other species to establish at nutrient supply levels that they could not without *Lupinus* (Figure 2.13). Therefore, *Lupinus* can facilitate the establishment of species even in environments where there is nearly no nitrogen being supplied by any other source. In sum, nutrient recycling is important to consider in the structuring of the community.

In addition to facilitating establishment, *Lupinus* can also promote greater community biomass by supplying nitrogen to *Agrostis* and *Hypochaeris* (Figure 2.14a). While *Hypochaeris* and *Agrostis* can establish themselves in the environment with *Hypochaeris* eventually excluding *Agrostis*, there is little total community biomass (Figure 2.14a). With the addition of *Lupinus*, community biomass would be approximately nine times higher for the parameter values specified (Figure 2.14b). The beneficial effects of *Lupinus* decline as the environment becomes richer in nitrogen and *Lupinus* suffers from greater competition (Figure 2.15).

Increasing *Lupinus* mortality does not increase the biomass of other species (Figure 2.16a). Instead, increased mortality results in the exclusion of *Lupinus* and the elimination of any potential benefit from nitrogen-fixation (Figure 2.16a). Rather, the community as a whole seems to benefit from decreased *Lupinus* mortality, with greater biomass for *Hypochaeris* (Figure 2.16b). It should be noted that the qualitative behaviour of the simulation results for Figures 2.14-2.16 generally hold for other parameter values than those used in the simulations.

The model makes similar qualitative predictions to those found in field experiments on Mount St. Helens (e.g. Gill et al. 2006), though the simulation results are sensitive to the parameter values for the model is attempting to capture transient behaviour of the plant community. Simulating short-term nitrogen, phosphorus and both nutrient additions, I found that *Hypochaeris* is most responsive to nitrogen additions and phosphorus additions resulted in a mild increase to *Lupinus* biomass, in agreement with the experimental results (Figure 2.17a,b,c). The model also predicts that when both nutrients are added, *Hypochaeris* dominates the community, which is also seen in the experiment (Figure 2.17d). However, *Lupinus* did not decline as seen in the experiments, which may indicate that another process other than nutrient limitation is involved (Figure 2.17d). Overall, the community is limited by nitrogen and phosphorus, with phosphorus limiting *Lupinus* and nitrogen limiting the other species.

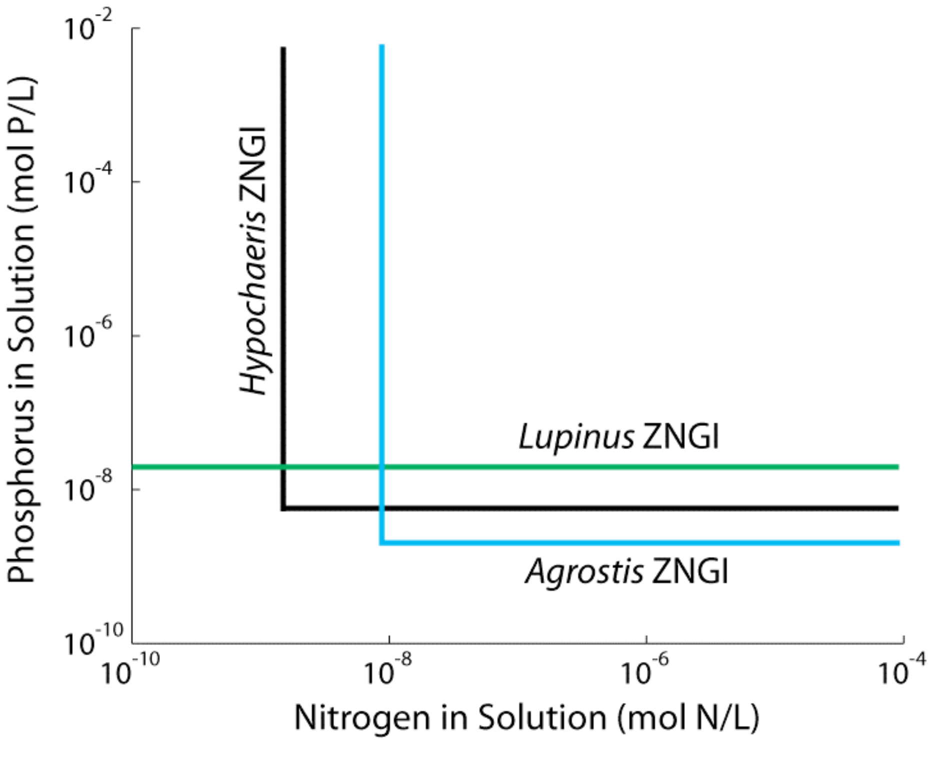

Figure 2.10: Graphical representation of the relative competitive abilities of *Agrostis*, *Hypochaeris* and *Lupinus*. It is assumed that m_L=0.003, m_A=m_H=0.00233. At each intersection of the ZNGIs, there is a potential coexistence steady state. The *Agrostis*-*Lupinus* steady state is unstable in the presence of *Hypochaeris* as *Hypochaeris* can maintain positive growth at that nutrient level. The *Agrostis*-*Hypochaeris* and the *Hypochaeris*-*Lupinus* are both potentially stable.

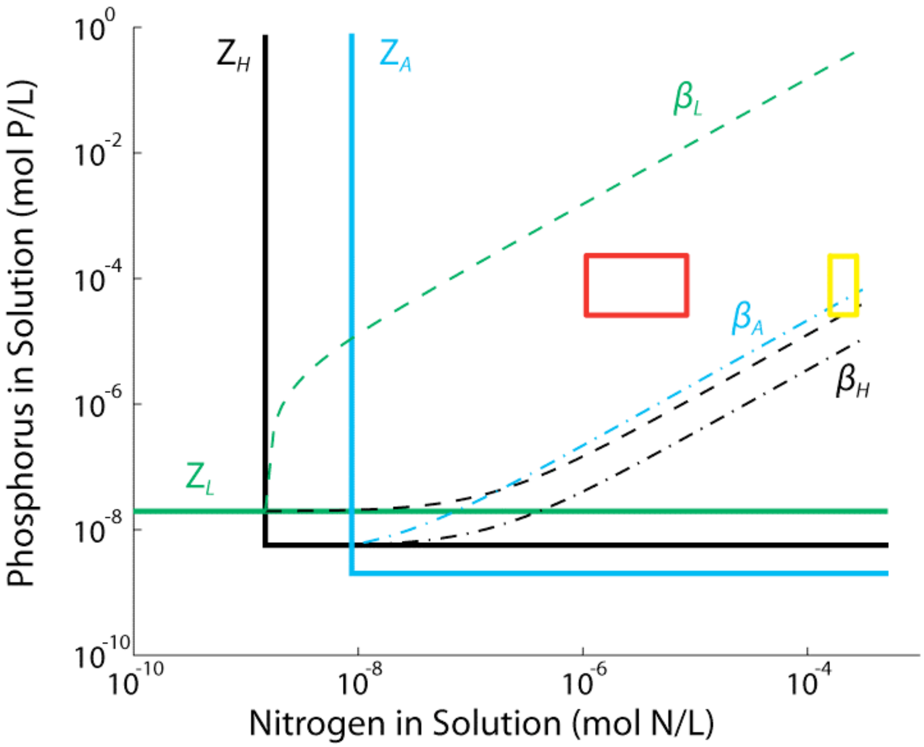

Figure 2.11: Regions of coexistence for *Agrostis*, *Hypochaeris* and *Lupinus* with no recycling. Regions are defined by the slopes of the consumption vectors for *Agrostis* (β_A), *Hypochaeris* (β_H) and *Lupinus* (β_L). The zero-net growth isoclines, Z_j, are the same as Figure 2.10. The amount of water per m^2 is assumed to be 3.75L or approximately 3% of soil weight. The *Hypochaeris*-*Lupinus* steady state, indicated by where Z_L and Z_H cross, is stable for they both consume more of the nutrient that most limits them at steady state as seen from the slopes of the consumption vectors (black dashed line and green dashed line). The *Agrostis*-*Hypochaeris* steady state, indicated by where Z_A and Z_H cross, is always unstable as *Hypochaeris* consumes relatively more nitrogen and *Agrostis* consumes relatively more phosphorus as indicated by the slopes of the consumption vectors (black dashed-dotted line and cyan dashed-dotted line). Hence in the regions defined by their consumption vectors, there is bistability. The yellow box and the red box denote empirically measured supply rates from two different data sets (red box: Gill et al. 2006, yellow box: Halvorson & Smith 2009), assuming daily turnover. For all values in the red box and most values in the yellow box, the community is predicted to be dominated by *Lupinus* and *Hypochaeris*. For the lower values of phosphorus in the yellow box, there is some overlap between *Agrostis*-*Hypochaeris* bistability and *Hypochaeris*-*Lupinus* coexistence regions, indicating that the community may be composed of *Lupinus* and *Hypochaeris* or by only *Agrostis*.

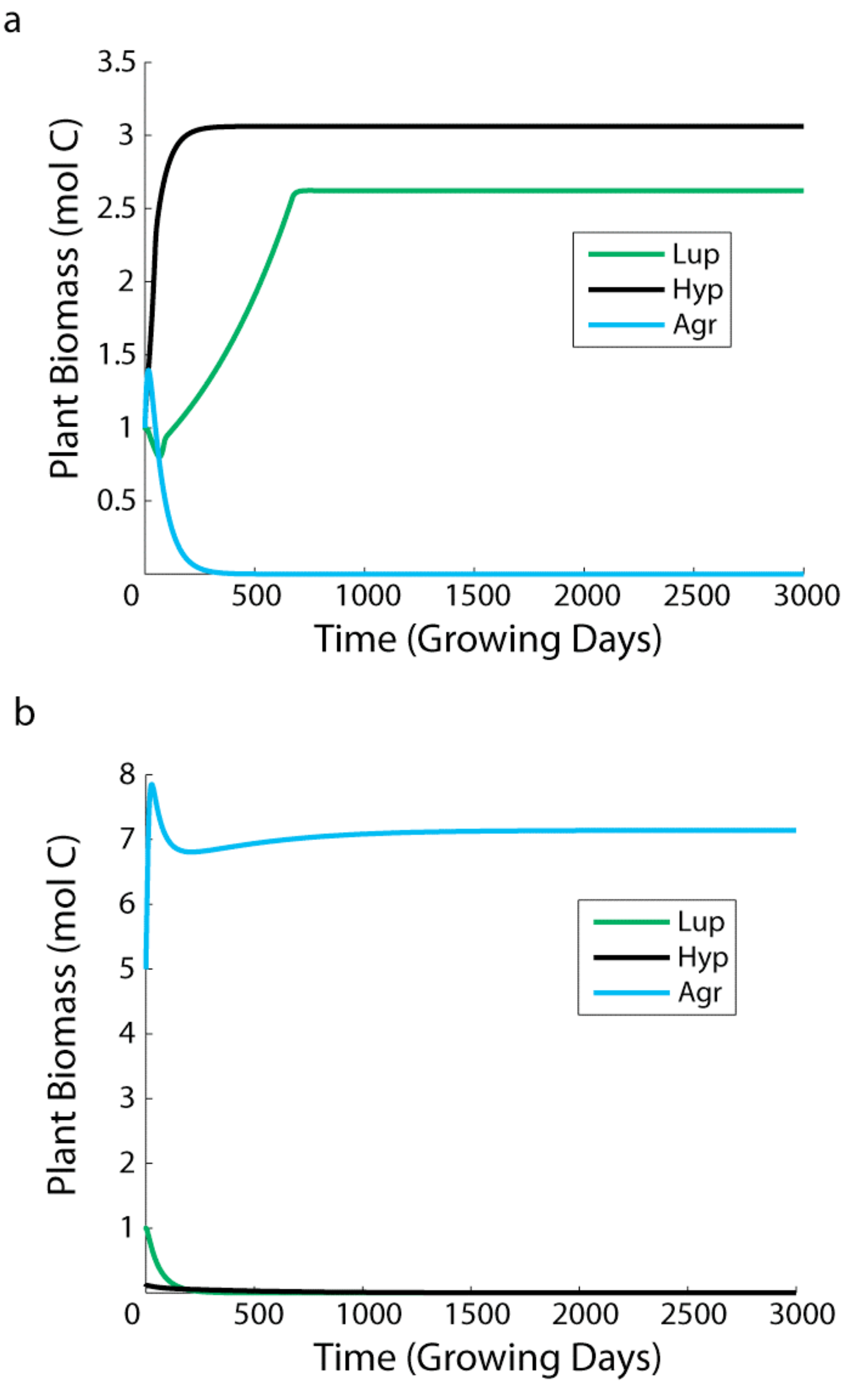

Figure 2.12: Plant biomass dynamics of *Agrostis*, *Hypochaeris* and *Lupinus* in the area of overlap defined in Figure 2.11. The mortality rates have been changed to $m_H = m_A = 0.02$ and $m_L = 0.023$ for better visualization of initial conditions. The area of overlap is the same even with the changes in mortality. Depending on the initial conditions, the community will go towards **a** a monoculture of *Agrostis* or **b** a community of *Hypochaeris* and *Lupinus*, which indicates bistability.

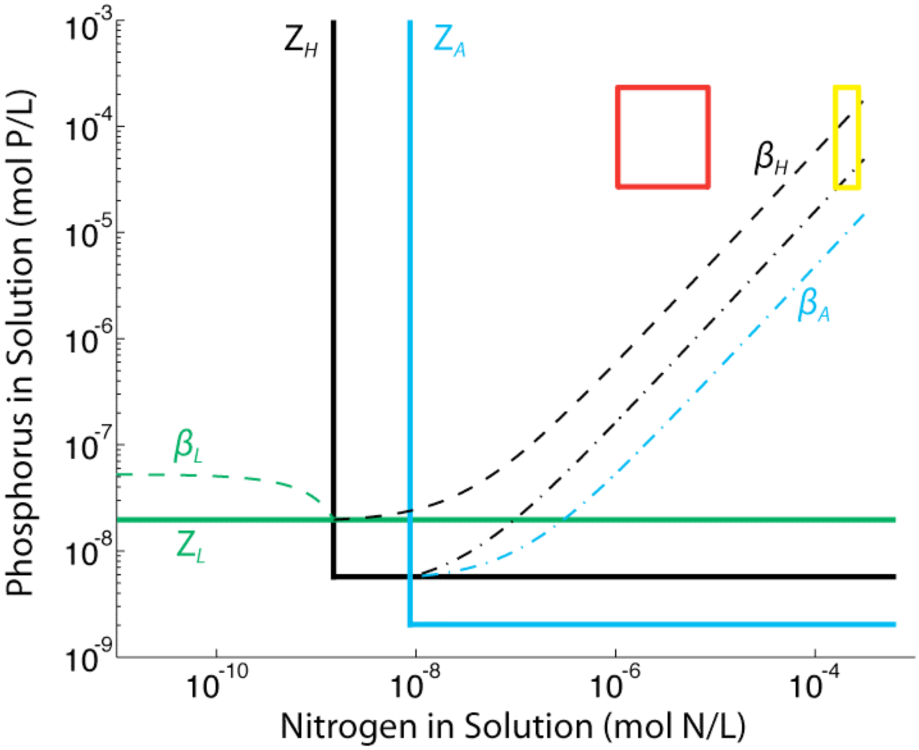

Figure 2.13: Regions of coexistence for *Agrostis*, *Hypochaeris* and *Lupinus* with recycling. The mortality rates and the water levels are the same as Figure 2.11. The recycling of nutrients switched the relative positions of the slopes of the consumption vectors for *Hypochaeris* (black dashed and dashed dotted lines) and *Agrostis* (cyan dashed-dotted line), when assuming very large differences in the recycling of nitrogen and phosphorus (see Appendix 2.D for values). However, the slope of the consumption vector for *Lupinus* (green dashed line) drastically changes with even minor recycling, indicating that *Lupinus* gives more nitrogen to the soil than it uptakes. It also indicates that it could support other species at levels of poor supply of nitrogen. Effects on community composition due to recycling may be large or non-existent, depending on nitrogen supply. Within the yellow box (same box as in Figure 2.11), the community will be composed of *Hypochaeris* and *Lupinus* for high phosphorus and may be composed of either *Agrostis* or *Hypochaeris* for low phosphorus, with *Hypochaeris* dominating intermediate values. Community composition within the red box remains unaltered by recycling.

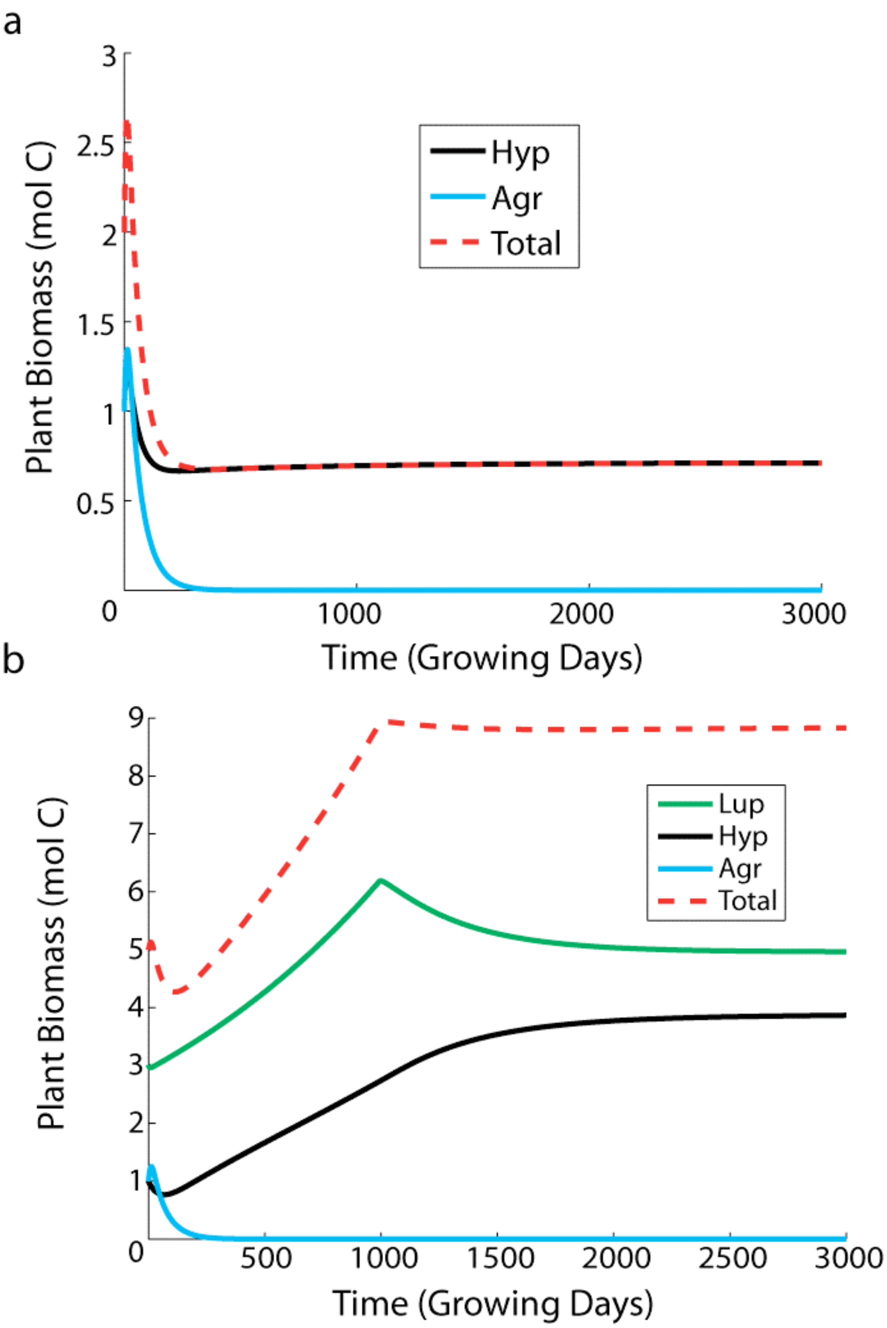

Figure 2.14: Dynamics of plant community biomass with and without *Lupinus* in the community within current levels of nutrient supply. It is assumed that m_L=0.024, m_A=0.02 and m_H=0.02. Total plant community biomass (red dotted line) is approximately nine times higher **b** with *Lupinus* than **a** without and *Hypochaeris* biomass (black line) doubles in the presence of *Lupinus*.

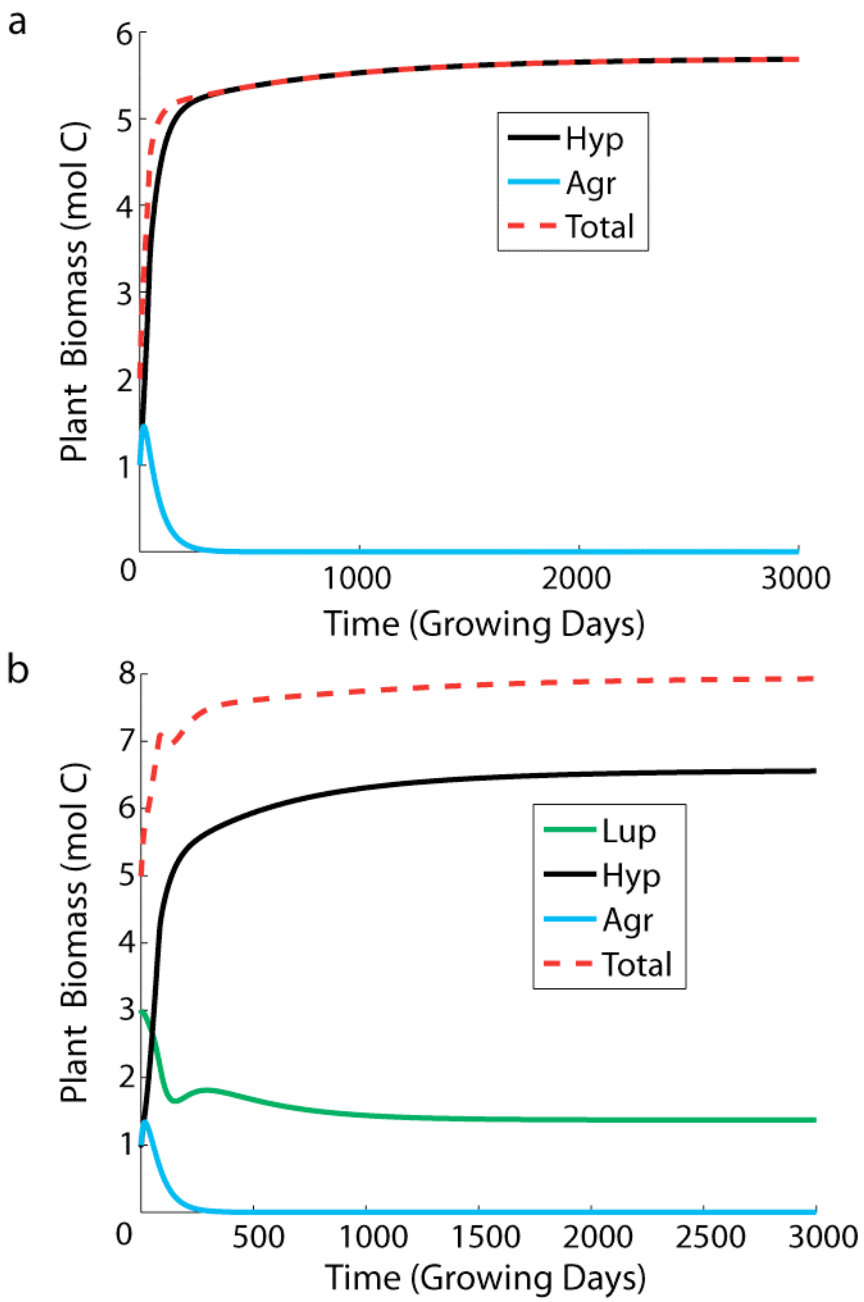

Figure 2.15: Dynamics of plant community biomass with and without *Lupinus* in the community with approximately eight times the current levels of nitrogen supply. Total plant community biomass (red dotted line) is mildly higher **b** with *Lupinus* than **a** without and *Hypochaeris* biomass (black line) is little affected by the presence of *Lupinus*.

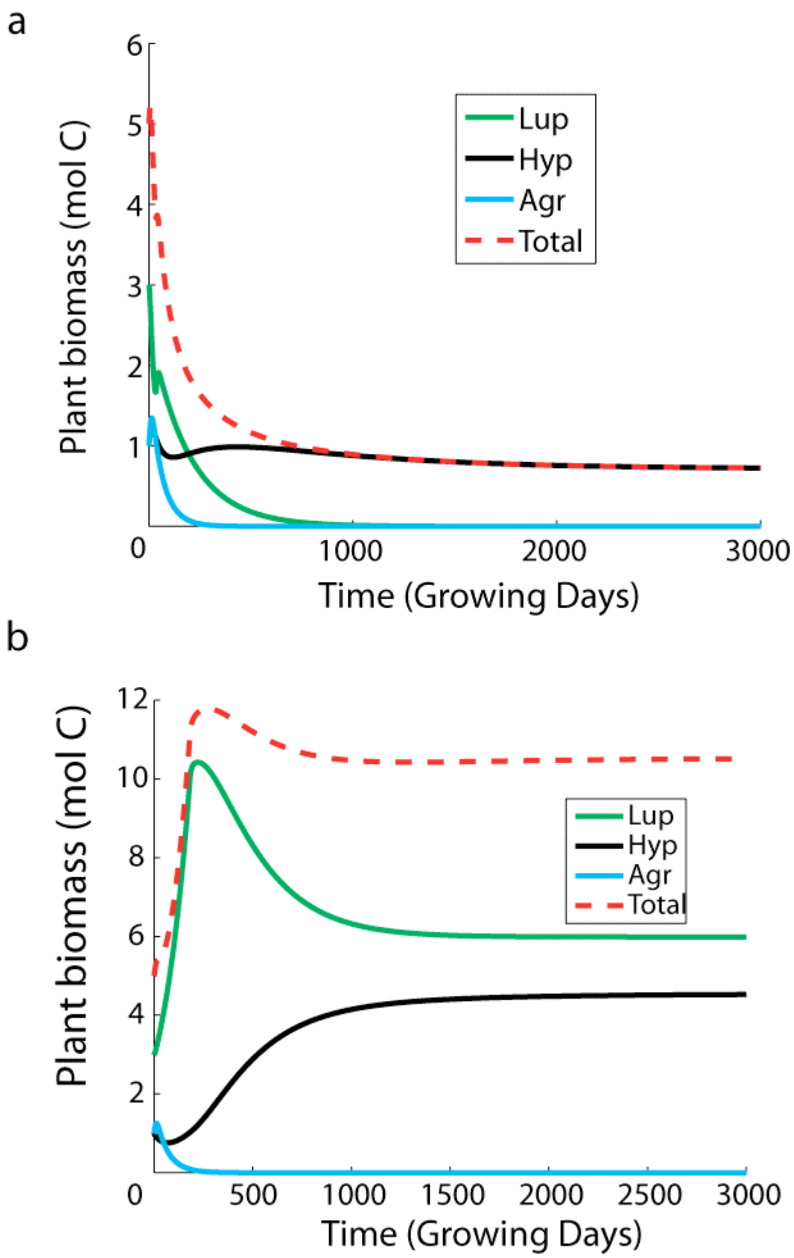

Figure 2.16: The effect of altering *Lupinus* mortality on plant community biomass. **a** Increasing *Lupinus* mortality to m_L=0.03 results in the exclusion of *Lupinus* and a decrease in both total plant biomass and *Hypochaeris* biomass compared to Figure 2.14b. **b** Decreasing *Lupinus* mortality to m_L =0.018 results an increase in total plant biomass and a slight increase in *Hypochaeris* biomass compared to Figure 2.14b.

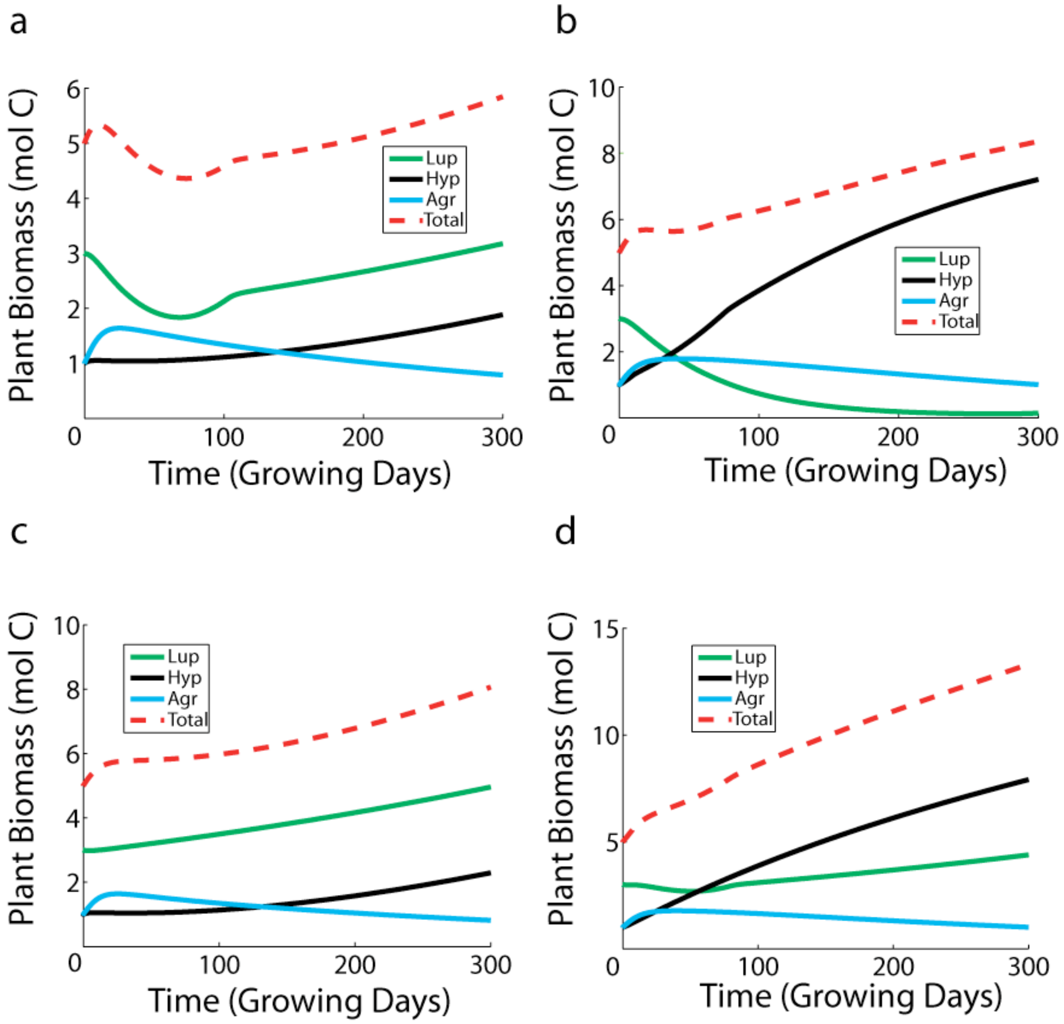

Figure 2.17: Simulation of the effects of short-term nitrogen and phosphorus additions on the dynamics of plant community biomass. **a** Control simulation shows *Lupinus* dominant with low levels of *Hypochaeris* and *Agrostis*. **b** Nitrogen addition simulation shows *Hypochaeris* becoming dominant with decline of *Lupinus*. **c** Phosphorus addition simulation shows increase in *Lupinus* biomass. **d** Nitrogen and phosphorus addition simulation show increase in *Hypochaeris* biomass with a slight increase in *Lupinus* biomass compared to **a**. Total plant biomass in order of highest to lowest is **d>b>c>a**, though **b** and **c** are very close in biomass.

2.4 Discussion

Developing a mechanistic underpinning to the study of plant primary succession is key for any potential application of its theory to ecological restoration (Walker & del Moral 2003). Various mechanisms and processes have been invoked in conceptual models for primary succession, such as competition, herbivory, dispersal ability and others (Pickett et al. 1987, Walker & Chapin 1987). However, it is exceedingly rare that the mechanisms invoked are then explored within a mechanistic model to see if they can give rise to the patterns observed in nature (Chapter 1, Walker & del Moral 2003).

In this chapter, I developed a mechanistic model (Figure 2.1, Eq. 2.2) to determine if nutrient limitation, nutrient cycling and ecological stoichiometry can explain some of the patterns observed in plant primary succession. The properties of the model were explored and it was discovered that many of the results can be expressed using graphical analysis developed by Tilman (1980) and extended by others (Daufrense & Hedin 2005, Figures 2.2-2.6). The results indicate that even with only two nutrients and two competitors, a variety of complex community dynamics such as population cycles can arise due to nutrient cycling (Figures 2.7-2.8).

The model was then parameterized with data from Mount St. Helens to see if its predictions matched expectations found in the field observations and field experiments. The model successfully predicted that *Lupinus* is outcompeted for phosphorus and that *Hypochaeris* out competes *Agrostis* for nitrogen (Table 2.4). The model also indicated that *Lupinus* has a net facilitative effect on other species on Mount St. Helens due to its capacity to add nitrogen into the nitrogen-poor substrate (Figures 2.14-2.16). In addition, the model predicted the qualitative response of the plant community had in nutrient-addition experiments in the field (Figure 2.17). These results indicate that ecological stoichiometry, nutrient limitation and nutrient cycling can explain much of the observed patterns on Mount St. Helens for early plant primary succession.

2.4.1 *Comparisons with Previous Hypotheses*

One hypothesis that is widely held by ecologists on Mount St. Helens and is not supported by the model is that increased mortality of *Lupinus* should make nitrogen more available to other species and increase their growth within the immediate area (Bishop 2002). In fact, the model predicts that decreased *Lupinus* mortality would benefit other plants (Figure 2.16). The difference could be explained by two factors.

First, inputs of nitrogen by *Lupinus* usually occur in the field when it dies for it releases little nitrogen when alive (Halvorson & Smith 2009). Furthermore, mortality normally occurs in large pulses (Braatne & Bliss 1999). A low mortality rate may mean very few dead *Lupinus* in an area and none of the nitrogen that has been fixed becoming available to other plants. Since the model explored here assumes there is always some nitrogen entering the soil from *Lupinus* mortality due to averaging over the growing season, the negative effects of lower mortality could be masked.

Second, *Lupinus* do not only add nitrogen to the soil when it dies, but carbon as well (Halvorson & Smith 2009). There is evidence that soil microorganisms on Mount St. Helens can be severely carbon-limited and such limitation would result in nitrogen-limitation since these organisms would not be in sufficient number to break down the organic nitrogen (Halvorson et al. 2005, Halvorson & Smith 2009). In the model, such a positive effect by *Lupinus* would increase the nitrogen input parameter, I_N, and would result in higher plant biomass for other species (Figure 2.15). Therefore, a positive effect of higher *Lupinus* mortality may be ignored.

Nevertheless, lower *Lupinus* mortality would mean that more nitrogen would be fixed. When *Lupinus* plants would perish, a larger amount of nitrogen would be added compared to a situation with nearly no *Lupinus* surviving to a large size when there is very high mortality (Bishop 2002). It seems likely that the model is capturing this aspect of *Lupinus* mortality and therefore does support some hypotheses made by others.

One intriguing result from the model is the overlap areas of possible coexistence in Figure 2.11. Such an overlap indicates that all three species can potentially become dominant or at least be present in the community and presents a case for alternative successional trajectories. Depending on the initial conditions, the composition of the community is either a monoculture of *Agrostis* or an assemblage of *Hypochaeris* and *Lupinus* plants (Figure 2.12). Since initial conditions are dependent on variable abiotic and biotic factors such as substrate quality, moisture content, nutrient content, temperature, seed rain and nurse plants, it is appropriate to say the outcome will be partially stochastic.

This result is in line with the view that early primary succession is dominated by stochastic events since highly variable abiotic factors will control establishment of species (Walker & Chapin 1987, Walker & del Moral 2003, del Moral et al. 2005). This view implies that early primary succession will therefore be highly unpredictable until conditions improve and biotic factors such as competition and predation become important (Matthews 1992, del Moral et al. 2005). However, there is some predictability in the result, such as the fact that *Lupinus* would not dominate by itself and *Agrostis* and *Hypochaeris* cannot coexist without large differences in nutrient recycling that have not been observed. In addition, many of the other results successfully predicted the observed outcomes on Mount St. Helens, indicating that good predictions based from mechanistic modelling can be obtained even in stochastic environments.

2.4.2 *Validity of Assumptions*

The application of the model was only possible due to a number of simplifying assumptions (section 2.2.2). The most important assumptions were that the nutrients were well distributed within the soil and that water content was constant. Both of these assumptions are certainly violated on Mount St. Helens since diffusion of mineral nutrients is highly dependent on water content and water content fluctuates wildly over time and space (Barber 1995, Titus 2008). When water content is very low, nutrients such as phosphorus will be highly localized and species located only a few centimetres away from one another could experience very different environments (Caldwell et al. 1987, Barber 1995). By restricting the domain of interaction to only one squared meter, I hoped that the rooting systems of the plant species would overlap and thus remove some of the effects of spatial heterogeneity. Nevertheless, considering the spatial scales of nutrient movement is key in order to determine if competition will occur or not (Huston & DeAngelis 1994, Barber 1995).

Furthermore, the water levels will also play a role in the mineralization of organic nutrients as saturated soils may lack sufficient oxygen for aerobic mineralization and drought can decrease decomposition rates of organic material (Barber 1995, Chapin et al. 2002). Because of this, my assumption that I_i scales linearly with the amount of water may not be valid and could result in different predictions.

Other assumptions such as constant mortality rate, lack of sexual reproduction and limited spatial scale are all addressed in the subsequent chapter of the thesis for they are certainly unrealistic (e.g. Bishop 2002, Fagan et al. 2005). The key point is that even with all these assumptions of potentially dubious value, the mechanisms of nutrient cycling, nutrient limitation and stoichiometry were able to qualitatively predict many features found in the plant community on Mount St. Helens. This result gives me hope that a mechanistic approach will be successful in developing predictions for primary succession.

2.4.3 *Final Remarks*

While this study is limited in scope with a focus only on the plant community at a local scale with only three functional groups represented, it clearly demonstrates the potential for ecological stoichiometry and nutrient limitation to give useful predictions on plant primary succession in particular and succession in general. Expansion of the scope of the model to create a more general primary for primary succession will be needed for creating a general theoretical framework. Refinement of the model for applications is also needed to include the fact that plants need to disperse and other life-history traits impact survival.

Appendix

2.A *Table of Notation*

Due to the complexity of the notation used in this chapter, I have provided a guide to the meaning of the various symbols strewn about the text that are not included in Table 2.2.

Table 2.A Notational guide for the second chapter of the thesis

Symbol	Meaning
i	Place holder for a nutrient
j	Place holder for a plant species
n	Number of species in the model
m	Number of nutrients or resource in the model
Q_{ij}	Variable for plant species j and nutrient i
E	Steady state of the model
E^0	No-plant steady state for n species model
E^1	One plant steady state for one species model
E^x	One plant steady state for two species model
E^{xy}	Two plant steady state for two species model
R_1^0	Variable at no-plant steady state for n species model
R_1^1	Variable at one plant steady state for one species model
R_1^x	Variable at one plant steady state for two species model
R_1^{xy}	Variable at two plant steady state for two species model
$\mathbf{J}$	The Jacobian matrix
$\boldsymbol{c_x}$	The consumption vector of species x
$\boldsymbol{r_x}$	The recycling vector of species x
$\boldsymbol{u}$	The supply vector of nutrients for the ecosystem
β_x	Slope of consumption vector of species x

2.B *Calculations of Parameters*

Within this section, I present the assumptions and calculations needed to derive the parameter values found in Table 2.2. The parameters can be broken into two broad categories: biological parameters (Table 2.2a,b,c) and environmental parameters (Table 2.2d). I will accordingly treat them separately within this section for they require different assumptions and calculations for their derivations.

The biological parameters can be divided into kinetic parameters, plant stoichiometry and vegetative growth/mortality. The data for plant stoichiometry and vegetative growth are frequently presented in standardized forms (C:nutrient ratios of dry weight and relative growth rates, respectively), kinetic uptake parameters can be expressed in terms of root length, root surface area, root dry weight, root fresh weight, total dry weight or total fresh weight (e.g. Van de Djik et al. 1982, Dunbabin et al. 2002, Esteban et al. 2003). For the model, I seek to convert the kinetic uptake parameters into moles of nutrient per mole of carbon per day. Due to this requirement, I cannot use the data in the literature involving root length and root surface area for relationships between these properties and root weight have not been worked out for the chosen species. I therefore rely on parameters that indicate the weight of the plant or the roots.

The conversion of the kinetic parameters also required making assumptions about the amount of carbon is in the plants' dry biomass, the ratio of fresh weight to dry weight and the ratio of shoot biomass to root biomass. For plant carbon and shoot:root ratios, there is a great deal known for the species considered here (Table 2.A). The percentage of dry biomass in vascular plants can be very difficult to quantify (Westlake 1963). The only species with a percentage of dry weight calculated is *Hypochaeris*, though some information is known about the relative water content of *Lupinus* and *Agrostis*. The values range from ten to twenty percent, but a value of fifteen percent was chosen for all the species for simplicity.

Table 2.B: Assumed values of physiological properties of the study species.

Lupinus lepidus		
Property	Value	Source
% C	41.5	Halvorson et al. 1992
Shoot:root (biomass)	1.52 (young) -7.3 (adult)	Halvorson et al. 1992
% dry (biomass)	15	Braatne & Bliss 1999
Hypochaeris radicata		
Property	Value	Source
% C	40.74	Fagan et al. unpublished manuscript
Shoot:root (biomass)	1.0	Titus & del Moral 1998
% dry (biomass)	15	Van de Djik 1981b
Agrostis scabra		
Property	Value	Source
% C	41.56	Bishop et al. unpublished data set
Shoot:root (biomass)	3.0	Tilman & Wedin 1991
% dry (biomass)	15	None

Using the data within the table, one can now convert uptake kinetic parameters into a usable form. For example, the data obtained from Esteban et al. 2003 for $V_{\max,PL}$ were initially in mol arsenate (an analog of P) per gram fresh weight of root per hour. The gram of fresh weight is equivalent to 0.15 grams of dry weight and a gram of dry root is equivalent to 0.120-0.397 grams of dry plant biomass and hence I have 0.0181-0.0595 grams of dry plant biomass per fresh gram of root. Furthermore, I then need to convert it into grams of carbon, multiplying the above range by 0.415 and dividing the result by 12 to obtain the moles of carbon. Finally, I multiply the above values by 24 to convert the timescale into days. Similar conversions were done for the other $V_{\max}$ parameters.

The only $V_{\max}$ parameter not taken directly from a point estimate in the literature is $V_{\max,NL}$. Instead, I calculated it by considering the amount of nitrogen per gram of biomass accumulated by a single lupine over the growing season and dividing that amount by the number of days in the growing season. This estimate likely underestimates the maximum amount of nitrogen that a lupine is capable of assimilating in a day for I am using the average daily amount of nitrogen assimilated.

The other kinetic parameters, the half-saturation constants, needed no special conversions for they are already in a usable form. The only note concerning these parameters is that they are, except for K_{NH}, drawn from related species and functional groups.

The stoichiometric parameters were generally available for the species used here, though phosphorus content of *Agrostis scabra* is not known and information from *Agrostis capillaris* was used instead. The values taken for $Q_{\max}$ and $Q_{\min}$ represented the maximum and minimum values found for those parameters in the available data. Therefore, there are no ranges associated with their values as measurement error is rarely reported for calculations of C:nutrient ratios.

The growth parameters used in the model cannot be measured directly, as it assumes the possibility of an infinite concentration of nutrients within the plants. Instead, one can use maximum relative growth rates (RGRs) of the plants to indirectly determine the parameter of interest. If I assume no mortality, I have the following formula relating the maximum RGR to the model parameters:

$$RGR_{\max} \approx \mu_{\infty,j} \min\left(1-\frac{Q_{\min,1j}}{Q_{\max,1j}}, 1-\frac{Q_{\min,2j}}{Q_{\max,2j}}\right)$$

$$\Leftrightarrow \frac{RGR_{\max}}{\min\left(1-\frac{Q_{\min,1j}}{Q_{\max,1j}}, 1-\frac{Q_{\min,2j}}{Q_{\max,2j}}\right)} \approx \mu_{\infty,j}$$

The above derivation shows that the theoretical maximum growth rate of plant *j* is approximately the maximum RGR divided by one minus the largest value of the ratio between the minimum concentration and maximum concentration of a nutrient within plant *j*. As data is available for the RGRs and plant stoichiometry, the theoretical maximum growth rates are easily calculated with the formula and some scaling of the RGRs.

The mortality parameter is another parameter that cannot be directly measured in the field, for it encompasses all losses of plant material due to herbivory, mortality, seasonal die back of aboveground parts and many others. In addition, plant mortality has varied dramatically from year to year on Mount St. Helens, which makes it difficult to assign simple constant value for mortality (Braatne & Bliss 1999, Bishop et al. 2005). Therefore, I utilize a large range of possible mortality rates for the model, though I generally set mortality rates to be similar between species, with *Lupinus* having slightly higher rates due to herbivory.

Environmental parameters, detritus parameters and recycling parameters are relatively sparse for Mount St. Helens. For the nitrogen input parameter, I used the rates of net nitrogen mineralization in barren soil found in 2002 and 2005 (Gill et al. 2006, Halvorson & Smith 2009). These rates differ greatly and indicate the heterogeneity in nitrogen supply on Mount St. Helens. I derived the phosphorus input into the soil by assuming that only 0.5% of plant available phosphorus is in the soil solution at anytime and the turnover rate is approximately a day (Barber 1995). Both these parameters depend on the water content of the soil, which has a range determined by field data (Titus 2008). The loss rates of phosphorus and nitrogen within the soil solution are not known and are considered free parameters. However, it seems likely that mineral nitrogen and phosphorus have close daily turnover rates, so I show most of my results with the loss rates being equal to one.

The rate of mineralization of nitrogen and phosphorus from plant material is not known except for *Lupinus* leaf tissue (Gill et al. 2006), though the average nitrogen atom in dead plant material may take two years to become available again (W. Fagan, pers. comm.). Due to the paucity of data, these parameters are also treated as free parameters.

The parameters concerning the recycling of nutrients are also poorly understood. While it is believed that phosphorus and nitrogen are tightly cycled in terrestrial environments, immature terrestrial communities such as those on Mount St. Helens may experience higher degrees of nutrient loss due to lack of substrate (Chapin et al. 2002). With no data to work with, I allow these parameters to freely vary.

2.C *Considering Allelopathy and Density-Dependence in the Model*

The above model formulations ignore the potential of allelopathy in controlling competitive interactions between plant species. This separation of resource competition from allelopathy has been questioned by researchers for allelopathic chemicals can alter nutrient supply and nutrient uptake (Inderjit & del Moral 1997). While these effects are certainly important in the structuring plant communities, no work has been done in investigating the potential for allelopathy on Mount St. Helens. Hence, it is not possible to specify specific functions or parameterize a model that takes into account both resource competition and allelopathy for this system.

Nevertheless, I can propose a general formulation of how one could fit allelopathy into the above modelling framework by looking at previous work on competition and allelopathy. Most models of competition and allelopathy express competition with Lotka-Volterra equations and assume constitutive expression of the allelopathic chemical that depends solely on plant density/biomass (e.g. Dubey & Hussein 2000). A few models use resource competition and slightly more complicated expressions for the excretion of allelopathic chemicals (de Freitas & Fredrickson 1978, Grover 1997). There are no models that explicitly treat allelopathy and resource competition in a stoichiometric fashion.

In terms of modelling allelopathy in the system, I must consider its impacts on i) the plant's stoichiometry, ii) the plant's growth, iii) the plant's ability to uptake nutrients and iv) the ability of the detritus to recycle nutrients. If I add in a variable A_j, which represents the concentration of the allelopathic chemical excreted by plant *j* in the soil, I can represent the impacts of allelopathy in a new model:

$$\begin{aligned}
\frac{dR_i}{dt} &= \underbrace{\underbrace{I_i}_{\textit{Influx}} - \underbrace{\phi_i R_i}_{\textit{Efflux}}}_{\text{Supply Without Plants}} \; \underbrace{- \omega \sum_{j=1}^{n} h_{ij}(R_i, A_1, \ldots, A_n) g_{ij}(Q_{ij}) B_j}_{\text{Total Plant Uptake}} + \underbrace{\omega_i \delta_i D_i}_{\text{Mineralization}} \\
\frac{dQ_{ij}}{dt} &= \underbrace{h_{ij}(R_i, A_1, \ldots, A_n) g_{ij}(Q_{ij})}_{\text{Concentration}} - \underbrace{\mu(Q_{1j}, \ldots, Q_{ij}, \ldots, Q_{nj}, A_1, \ldots, A_n) Q_{ij}}_{\text{Dilution}} \\
&\quad \pm \underbrace{a_{ij}(Q_{ij})}_{\substack{\text{Relative Concentration} \\ \text{or Dilution Due} \\ \text{to Allelopathy}}} \\
\frac{dB_j}{dt} &= \left[\underbrace{\mu(Q_{1j}, \ldots, Q_{ij}, \ldots, Q_{nj}, A_1, \ldots, A_n)}_{\text{Growth}} - \underbrace{m_j}_{\text{Mortality}} - \underbrace{a_j}_{\text{Loss of Carbon due to Allelopathy}} \right] B_j \\
\frac{dD_i}{dt} &= \underbrace{\sum_{j=1}^{n} m_j B_j Q_{ij} \left(\zeta_{ij}(A_1, \ldots, A_n) \right)}_{\text{Recycling}} - \underbrace{\delta_i D_i}_{\text{Mineralization}} \\
\frac{dA_j}{dt} &= \underbrace{a_j B_j}_{\substack{\text{Production of Allelopathic} \\ \text{Chemical}}} - \underbrace{k_j(A_j)}_{\text{Loss of Allelopathic Chemical}}
\end{aligned} \tag{2.C}$$

The inclusion of allelopathy in the growth, uptake and recycling terms of the model may play an important role in determining competitive outcomes, especially if autoinhibition dominates (de Freitas & Fredrickson 1978). However, the role it plays will be determined by its functional relationship and that remains to be discovered.

Another factor I did not consider was density-dependence in the growth or the mortality terms of the model. This exclusion is due to the idea that if a mechanism is causing density-dependence, that mechanism should be explicitly considered in the mechanistic framework of resource competition. For example, take the logistic equation as a model of density dependence for a plant that exhibits density-dependence:

$$\frac{dB}{dt} = r\left(1 - \frac{B}{K}\right)B$$

Where B is the biomass of the plant, K is the 'carrying capacity' and r is the 'intrinsic growth rate'. How can one derive the carrying capacity and the intrinsic growth rate? One could be looking for the mechanisms that control growth in the plant population. Now imagine that the plant is limited by a single nutrient and the ecosystem within which it is in is closed to losses or gains of that nutrient. The plant uptakes the nutrient according to the law of mass action and loses the nutrient in proportion to its biomass. The lost nutrient is instantaneously recycled back into the soil nutrients. I could describe the situation with the following system of equations:

$$\frac{dR}{dt} = mB - vBR$$
$$\frac{dB}{dt} = vBR - mB$$

As the system is closed, the total amount of nutrient in the system, S, is a constant that is equal to $S = B + R$. I can reduce the system of equations to one equation by replacing R by S-B in the second equation. The resulting equation is:

$$\begin{aligned}
&\frac{dB}{dt} = vBS - mB - vB^2 \\
&= ((vS - m) - vB)B \\
&= v\left(S - \frac{m}{v} - B\right)B \\
&= v\left(1 - \frac{B}{S - \frac{m}{v}}\right)B = r\left(1 - \frac{B}{K}\right)B \text{ with } v = r,\ K = S - \frac{m}{v}
\end{aligned}$$

I have derived the density-dependence involved in the population from a mechanistic basis of nutrient limitation. Similarly, the density-dependence that is shown in plant populations on Mount St. Helens ought to be derived from mechanisms such as nutrient limitation.

2.D *Parameter Values for Figures*

The parameter values chosen for the figures were picked to maximize graphical clarity and the results from these values are robust across the ranges shown in Table 2.2. Certain parameters are the same for all figures showing simulation results and are listed in Table 2.2 under value used.

Other parameters, such as the stoichiometric parameters, have no ranges attached to them and are always the same. Some parameter values are also listed in the figure captions when they are relevant or can be read off the figure. The easiest way to give the information is to list each figure and indicate parameter values, if appropriate.

Figure 2.6a,b and c: Plant y (blue lines) has the same parameters as *Lupinus* except $V_{LN} = 2.6 \times 10^{-4}$ and plant x (red lines) has the same parameters as *Hypochaeris*. The mortality rate constants are 0.02 for both species. All the parameters involved in the recycling of nutrients are set to zero. The efflux of nutrients is set equal to one for both nutrients.
Figure 2.6d,e and f: Plant y (blue lines) has the same parameters as *Hypochaeris* and plant x (red lines) has the same parameters as *Agrostis*. The mortality rates are 0.02 for both species. All other parameters are the same as the rest of Figure 2.6.
Figure 2.7, 2.8: Plant y (blue lines) has the same parameters as *Hypochaeris* and plant x (red lines) has the same parameters as *Agrostis.* The mortality rates are 0.02 for both species. For the recycling parameters, ω=0.2667 with $\zeta_{1x}=\zeta_{2y}=0.1$, $\zeta_{2x}=\zeta_{1y}=0.653$. The nutrient supply parameters are I_1=1.5185e-4, I_2=1.38e-5, $\phi_1=\phi_2=1$.
Figures 2.11 to 2.13: See Table 2.2 and figure captions.
Figure 2.13: Same as Figure 2.11 with ω=0.2667, $\zeta_{NA}=\zeta_{PH}=0.1$, $\zeta_{PA}=\zeta_{NA}=0.8$, $\zeta_{NL}= 0.001$ and $\zeta_{PL}=0.001$.
Figure 2.14: See figure caption and ω=0.2667, $\zeta_{NA}=\zeta_{PH}=0.1$, $\zeta_{PA}=\zeta_{NA}=0.1$, $\zeta_{NL}=0.2$, $\zeta_{PL}=0.1$, I_N=4.185e-5, I_P=5.38e-5, $\phi_N=\phi_P=1$ and $\delta_N=\delta_P=0.0015$.
Figure 2.15: Same as Figure 2.14 with I_N=33.48e-5.
Figure 2.16: Same as Figure 2.14 with different mortalities for *Lupinus* listed in caption.
Figure 2.17: For **a-d**, see Table 2.2 with ω=0.2667, $\zeta_{NA}=\zeta_{PH}=0.1$, $\zeta_{PA}=\zeta_{NA}=0.1$, $\zeta_{NL}=0.2$, $\zeta_{PL}=0.1$, $\phi_N=\phi_P=1$, $m_L=0.023m_H=0.005$, $m_A=0.004$ and $\delta_N=\delta_P=0.0015$. For **a**, I_N=1.293e-5 and I_P=2.5e-5. For **b**, I_N=12.93e-5 and I_P=2.5e-5. For **c**, I_N=1.293e-5 and I_P=5e-5. For **d**, I_N=12.93e-5 and I_P=5e-5. Nitrogen supply was increased by a factor of ten, but phosphorus only by a factor of two since Gill et al. 2006 most likely underestimated available soil phosphorus and most phosphorus was likely occluded (Gill et al. 2006, Halvorson & Smith 2009).

2.E *Positive Invariance of Model*

In this section, I show for the general model (Eq. 2.2) that any solution that begins within boundaries specified by each species' biology and ecosystem properties will remain within those boundaries. These conditions are that all soil solution nutrients i, all plants' biomass j and all detritus nutrients i are non-negative for all time if the initial conditions are non-negative. For the internal nutrient concentrations for all nutrients i in all plants j, the value must remain within the minimum and maximum values defined by the parameters $Q_{\min,ij}$ and $Q_{\max,ij}$.

To verify that the model is in fact positively invariant, one must check the solutions at the boundary or boundaries to see if the solutions leave the area specified. I can do this by looking at the rate of change at the boundary. I check the boundaries for each variable one at the time and assume the other variables are within the ranges specified above. I start with the variables describing soil nutrients:

$$\left.\frac{dR_i}{dt}\right|_{R_i=0} = I_i + \omega\delta_i D_i > 0$$

At the boundary, the rate of change in soil nutrients increases indicating that R_i remains non-negative if it is initially non-negative. For the variables describing plant biomass:

$$\left.\frac{dB_j}{dt}\right|_{B_j=0} = 0$$

At the boundary, the rate of change in plant biomass is zero, which it must as B_j=0 is a steady state. Therefore, plant biomass is always non-negative if it is initially non-negative. For the variables describing nutrients in the detritus:

$$\left.\frac{dD_i}{dt}\right|_{D_i=0} = \sum_{j=1}^{n} \zeta_{ij} B_j Q_{ij} > 0$$

Similar to soil nutrients, the rate of change in nutrients in the detritus increases at the boundary. Therefore, D_i will remain non-negative if it is initially non-negative. For the variables describing internal nutrient concentrations, there are two boundaries to consider:

$$\left.\frac{dQ_{ij}}{dt}\right|_{Q_{ij}=Q_{\min,ij}} = h_{ij}(R_i) > 0$$

$$\left.\frac{dQ_{ij}}{dt}\right|_{Q_{ij}=Q_{\max,ij}} = -\mu(Q_{1j},\ldots,Q_{\max,ij},\ldots,Q_{mj}) < 0$$

At the lower boundary, $Q_{ij} = Q_{\min,ij}$, the rate of change in internal nutrient concentration is positive. At the upper boundary, $Q_{ij} = Q_{\max,ij}$, the rate of change in internal nutrient concentration is negative. Therefore, internal nutrient concentration remains within these boundaries if it is initially within the boundaries. Since each variable remains within the boundaries specified, then the model is positive invariant.

2.F *Upper Bounds to Model Solutions*

In this section, I demonstrate that the solutions of the general model (Eq. 2.2) must be bounded and no variable within the model can approach an infinite value. Biologically, this result implies that there will be no infinite populations of plants, which is important for biological realism. The simplest way of showing this to be true is to show that the total amount of any nutrient *i* will be bounded within the ecosystem. To start, I define the total amount of nutrient *i* as the sum of the nutrient *i* in soil solution, in all of the plants' biomass and in the plant detritus:

$$\underbrace{T_i}_{\substack{\text{Total Amount of}\\ \text{Nutrient i}}} = \underbrace{kR_i}_{\substack{\text{Amount of}\\ \text{Nutrient i in}\\ \text{Soil Solution}}} + \underbrace{\sum_{j=1}^{n} Q_{ij}B_j}_{\substack{\text{Amount of Nutrient i}\\ \text{in All Plants}}} + \underbrace{D_i}_{\substack{\text{Amount of Nutrient}\\ \text{i in Plant Detritus}}}$$

Where *k* is equal to the total amount of water in the ecosystem considered and is therefore equal to $1/\omega$. To be bounded, T_i must be less than some finite constant, which I will denote by θ, for all time. To show that this is the case, I will examine the rate of change of T_i and demonstrate that each component of T_i must be less than finite constant and thus T_i must be less than the sum of these finite constants.

To begin, it must be noted that R_i is always greater than zero, Q_{ij} must be greater than $Q_{\min,ij}$ and less than $Q_{\max,ij}$ and B_j and D_i must always be equal or greater than zero from 2.E. Therefore, T_i will always be greater than zero and if the amount of nutrient *i* in plants is finite, then the biomass of all the plants must be finite since all Q_{ij} are always greater than zero. The second fact is important as I will now introduce a new variable, U_{ij}, which is defined as the amount of nutrient *i* in plant *j*:

$$U_{ij} = Q_{ij}B_j$$

The use of this new variable helps in simplifying the derivation. The derivative of U_{ij} with respect to time is:

$$\frac{dU_{ij}}{dt} = Q_{ij}\frac{dB_j}{dt} + \frac{dQ_{ij}}{dt}B_j$$
$$\frac{dU_{ij}}{dt} = Q_{ij}\left[\mu\left(Q_{1j},...,Q_{ij},...,Q_{mj}\right) - m_j\right]B_j +$$
$$\left[h_{ij}(R_i)g_{ij}(Q_{ij}) - \mu\left(Q_{1j},...,Q_{ij},...,Q_{mj}\right)Q_{ij}\right]B_j$$
$$\frac{dU_{ij}}{dt} = h_{ij}(R_i)g_{ij}(Q_{ij})B_j - m_jQ_{ij}B_j$$
$$\frac{dU_{ij}}{dt} = h_{ij}(R_i)g_{ij}(\frac{U_{ij}}{B_j})B_j - m_jU_{ij}$$

With this information, I can now take the derivative of the total amount of nutrient *i* within the ecosystem with respect to time:

$$\frac{dT_i}{dt} = k\frac{dR_i}{dt} + \sum_{j=1}^{n}\frac{dU_{ij}}{dt} + \frac{dD_i}{dt}$$
$$= kI_i - k\phi_iR_i - k\omega\sum_{j=1}^{n}h_{ij}(R_i)g_{ij}(\frac{U_{ij}}{B_j})B_j + k\omega\delta_iD_i + \sum_{j=1}^{n}h_{ij}(R_i)g_{ij}(\frac{U_{ij}}{B_j})B_j$$
$$-\sum_{j=1}^{n}m_jU_{ij} + \sum_{j=1}^{n}\zeta_{ij}m_jU_{ij} - \delta_iD_i$$
$$= kI_i - k\phi_iR_i - \sum_{j=1}^{n}(1-\zeta_{ij})m_jU_{ij} \text{ since } k\omega = 1$$

At this point, I introduce another simplification in order to remove the sum in the above equation. I will assume, without loss of generality, that m_j and ζ_{ij} are the same for all species *j* and I let U_i be equal to the sum of U_{ij} for all *j*, giving:

$$\frac{dT_i}{dt} = kI_i - k\phi_iR_i - (1-\zeta_i)mU_i$$

To show that T_i is bounded, I will introduce another quantity, $\overline{T_i}$, which is always larger than T_i and is bounded, hence T_i must be bounded as well. I define $\overline{T_i}$ to be equal to:

$$\overline{T_i} = kR_i + U_i + cD_i$$
$$c = 1+\varepsilon, \varepsilon > 0 \text{ and choose } \varepsilon \text{ such that } (1-\zeta_ic) > 0$$
$$\text{with } \zeta_i < 1$$

Taking the derivative of $\overline{T_i}$ with respect to time gives the following equation:

$$\begin{aligned}\frac{d\bar{T}_i}{dt} &= kI_i - k\phi_i R_i - (1-c\zeta_i)mU_i - (c-1)\delta_i D_i, \delta_i > 0 \\ &\le kI_i - \min\left(\phi_i, (1-c\zeta_i)m, \frac{(c-1)\delta_i}{c}\right)\bar{T}_i\end{aligned} \qquad \textbf{(2.F.1)}$$

Here, *k*, I_i, φ_i and *m* are all fixed positive constants. At this point, one can use the comparison theorem for one-dimensional ordinary differential equations to obtain an upper bound on $\bar{T}_i$. I first present the following differential equation:

$$\frac{d\bar{T}_i}{dt} = kI_i - \min\left(\phi_i, (1-c\zeta_i)m, \frac{(c-1)\delta_i}{c}\right)\bar{T}_i \qquad \textbf{(2.F.2)}$$

The solution to Eq. 2.F.2 is always greater or equal to the solution Eq. 2.F.1 by the comparison theorem. The solution to Eq. 2.F.2 is:

$$\bar{T}_i(t) = \left(\bar{T}_i(0) - \frac{kI_i}{\min\left(\phi_i, (1-c\zeta_i, \frac{(c-1)\delta_i}{c}\right)}\right)\exp\left(-\frac{kI_i}{\min\left(\phi_i, (1-c\zeta_i, \frac{(c-1)\delta_i}{c}\right)}t\right) + \frac{kI_i}{\min\left(\phi_i, (1-c\zeta_i, \frac{(c-1)\delta_i}{c}\right)}$$

The solution to Eq. 2.F.1 must therefore be:

$$\bar{T}_i(t) \le \left(\bar{T}_i(0) - \frac{kI_i}{\min\left(\phi_i, (1-c\zeta_i, \frac{(c-1)\delta_i}{c}\right)}\right)\exp\left(-\frac{kI_i}{\min\left(\phi_i, (1-c\zeta_i, \frac{(c-1)\delta_i}{c}\right)}t\right) + \frac{kI_i}{\min\left(\phi_i, (1-c\zeta_i, \frac{(c-1)\delta_i}{c}\right)}$$

Since the right-hand side is strictly decreasing with time and is finite, $\bar{T}_i$ must be bounded. Since we have proved that $\bar{T}_i$ is bounded, then T_i, which is strictly less than $\bar{T}_i$, must also be bounded. With T_i bounded, then all the other variables that make up T_i are bounded as well. Therefore, the solutions of the general model (Eq. 2.2) are bounded.

2.G *Uniqueness of the Values of Implicitly Defined Variables at Steady States with One Species, Two Nutrients*

In this section I show that for given parameters of the model, there will exist at most one positive value given steady state. The notation used here is the same as found in Eq. 2.6. I begin by examining the implicit functions for Q_1^0 and Q_2^0, which are defined in Table 2.3 as the steady state values of Q_1 and Q_2 at the no-plant steady state, for which the steady state always exists. Q_1^0 must satisfy the following equation (assuming nutrient 1 is limiting):

$$h_1(R_1^0)g_1(Q_1^0) - \mu_\infty(Q_1^0 - Q_{\min,1}) = 0$$

To show that some value of Q_1 must satisfy this equation, I plug in $Q_{\min,1}$ and $Q_{\max,1}$ for Q_1^0 on the left hand side:

$$h_1(R_1^0)g_1(Q_{\min,1}) - \mu_\infty(Q_{\min,1} - Q_{\min,1}) = h_1(R_1^0) > 0$$

$$h_1(R_1^0)g_1(Q_{\max,1}) - \mu_\infty(Q_{\max,1} - Q_{\min,1}) = -\mu_\infty(Q_{\max,1} - Q_{\min,1}) < 0$$

Since $g_1(Q_1)$ is decreasing with increasing Q_1

At $Q_{\min,1}$ and at $Q_{\max,1}$, the left-hand side of the equation must be positive and negative, respectively. This indicates a switching of signs and therefore for some value of Q_1 between $Q_{\min,1}$ and $Q_{\max,1}$, the above equation must pass through zero. However, this does not indicate that there is only one Q_1 value that satisfies the equation. To show uniqueness, I note that both $g_1(Q_1)$ and $-\mu_\infty(Q_1 - Q_{\min,1})$ are monotonically decreasing functions.

In a similar fashion I can show that Q_2^0 exists and is unique when satisfying the following equation:

$$h_2(R_2^0)g_2(Q_2^0) - \mu_\infty(1 - \frac{Q_{\min,1}}{Q_1^0})Q_2^0 = 0$$

Plugging in $Q_{\min,2}$ and $Q_{max,2}$ for Q_2^0 on the left-hand side of the equation gives us:

$$h_2(R_2^0)g_2(Q_{\min,2}) - \mu_\infty(1 - \frac{Q_{\min,1}}{Q_1^0})Q_{\min,2} = h_2(R_2^0) > 0$$

$$h_2(R_2^0)g_2(Q_{\max,2}) - \mu_\infty(1 - \frac{Q_{\min,1}}{Q_1^0})Q_{\max,2} = -\mu_\infty(1 - \frac{Q_{\min,1}}{Q_1^0})Q_{\max,2} < 0$$

One may ask why the second term of the left-hand side falls out in the expression with $Q_{\min,2}$. If nutrient 1 is limiting, then $Q_{\min,1}/Q_1 < Q_{\min,1}/Q_2$. If Q_2 is equal to $Q_{\min,2}$, then Q_1 must be equal to $Q_{\min,1}$ if it is suppose to be limiting.

Therefore the second term must be equal to zero (technically, both nutrients would be limiting in this case). As I have the switching of signs and the monotonic properties of the functions as above, there is only one value of Q_2 that resides in between $Q_{\min,2}$ and $Q_{\max,2}$ that satisfies the equality and it is defined as Q_2^0. Others have proven the above in a more general fashion without the assumption of one nutrient being limiting (Li & Smith 2007, Lemma 9).

The other case of an implicit formulation for variable is Q_2^1. The most intuitive way to show the result is to start with the derivation for the formulation. The derivation begins with setting dR_2/dt, dQ_2/dt and dD_2/dt all equal to zero for they must be if E^1 is a steady state:

$$0 = \frac{dR_2}{dt} = I_2 - \phi_2 R_2 - \omega h_2(R_2) g_2(Q_2) B^1 + \omega \delta_2 D_2$$
$$0 = \frac{dQ_2}{dt} = h_2(R_2) g_2(Q_2) - \mu_\infty \left(1 - \frac{Q_{\min,1}}{Q_1^1}\right) Q_2$$
$$0 = \frac{dD_2}{dt} = \zeta_2 m B^1 Q_2 - \delta_2 D_2$$

I can quickly reduce these three equalities to two by substituting in the value of $D^1{}_2$ for D_2. I also can remove any mention of Q_1^1 by noting that:

$$\mu_\infty \left(1 - \frac{Q_{\min,1}}{Q_1^1}\right) = m$$

After the substitutions, I have:

$$0 = I_2 - \phi_2 R_2^1 - \omega h_2(R_2^1) g_2(Q_2^1) B^1 + \omega \zeta_2 m B^1 Q_2^1$$
$$0 = h_2(R_2^1) g_2(Q_2^1) - m Q_2^1$$

I can further simplify the first inequality by substituting $m Q_2^1$ for $h_2(R_2^1)g_2(Q_2^1)$:

$$0 = I_2 - \phi_2 R_2^1 - \omega m Q_2^1 B^1 + \omega \zeta_2 m B^1 Q_2^1$$
$$= I_2 - \phi_2 R_2^1 - (1 - \zeta_2) \omega m Q_2^1 B^1$$
$$\Rightarrow R_2^1 = \frac{I_2 - (1 - \zeta_2) \omega m Q_2^1 B^1}{\phi_2}$$

This expression for R_2^1 satisfies the condition that if E^1 exists, then $R_i^1 < I_i / \phi_i$ for $i = 1, 2.$ Substituting in the expression derived for R_2^1 into the second equality, I know have:

$$h_2\left(\frac{I_2-(1-\zeta_2)\omega m Q_2^1 B^1}{\phi_2}\right)g_2(Q_2^1)-mQ_2^1=0$$

I know that the equality is violated at $Q_2^1 = Q_{\min,2}$ for $dQ_2/dt > 0$ at $Q_{\min,2}$ from Appendix 2.E, which implies that:

$$h_2\left(\frac{I_2-(1-\zeta_2)\omega m Q_{\min,2} B^1}{\phi_2}\right)-mQ_{\min,2}>0$$

Similarly, I know the equality is violated at $Q_2^1 = Q_{\max,2}$ for $dQ_2/dt < 0$ at $Q_{\max,2}$ from Appendix 2.E, which implies that:

$$-mQ_{\max,2}<0$$

Due to the switching of signs, I know that some value of Q_2 between $Q_{\min,2}$ and $Q_{\max,2}$ must satisfy the equality and due to the monotonicity of the functions, I know only one value will satisfy this equality. Thus, I have shown the uniqueness of Q_2^1 and by association, R_2^1 and D_2^1.

2.H *Jacobian Matrices and Derivation of Stability Criterion*

With the values of the variables at steady state, I can investigate the local stability of this steady state and the conditions for its stability. To do this, I linearize the system of equations around the steady state of interest, which creates a Jacobian matrix. The signs of the eigenvalues of the Jacobian will determine whether the steady state is locally stable or unstable.

I begin with the single species case as defined by Eq. 2.6. I start by defining the Jacobian and I arrange it so that the order of the rows is dR_1/dt, dQ_1/dt, dD_1/dt, dB/dt, dR_2/dt, dQ_2/dt and dD_2/dt:

$$\mathbf{J} = \begin{pmatrix} j_{11} & j_{12} & j_{13} & j_{14} & 0 & 0 & 0 \\ j_{21} & j_{22} & 0 & 0 & 0 & 0 & 0 \\ 0 & j_{32} & j_{33} & j_{34} & 0 & 0 & 0 \\ 0 & j_{42} & 0 & j_{44} & 0 & 0 & 0 \\ 0 & 0 & 0 & j_{54} & j_{55} & j_{56} & j_{57} \\ 0 & j_{62} & 0 & 0 & j_{65} & j_{66} & 0 \\ 0 & 0 & 0 & j_{74} & 0 & j_{76} & j_{77} \end{pmatrix}$$

$$j_{11} = -\omega \frac{\partial h_1(R_1)}{\partial R_1} g_1(Q_1)B - \phi_1,\ j_{12} = -\omega \frac{\partial g_1(Q_1)}{\partial(Q_1)} h_1(R_1)B,\ j_{13} = \omega\delta_1$$

$$j_{14} = \omega g_1(Q_1)h_1(R_1), j_{21} = \frac{\partial h_1(R_1)}{\partial R_1} g_1(Q_1),\ j_{22} = \frac{\partial g_1(Q_1)}{\partial(Q_1)} h_1(R_1) - \mu_\infty$$

$$j_{32} = mB\zeta_1,\ j_{33} = -\delta_1,\ j_{34} = mQ_1\zeta_1, j_{42} = \frac{\mu_\infty Q_{\min,1} B}{(Q_1)^2}$$

$$j_{44} = \mu_\infty \left(1 - \frac{Q_{\min,1}}{Q_1}\right) - m,\ j_{54} = \omega h_2(R_2) g_2(Q_2)$$

$$j_{55} = -\omega \frac{\partial h_2(R_2)}{\partial R_2} g_2(Q_2)B - \phi_2, j_{56} = -\omega \frac{\partial g_2(Q_2)}{\partial(Q_2)} h_2(R_2)B,\ j_{57} = \omega\delta_2$$

$$j_{62} = \frac{\mu_\infty Q_{\min,2} Q_2}{(Q_1)^2},\ j_{65} = \frac{\partial h_2(R_2)}{\partial R_2} g_2(Q_2)$$

$$j_{66} = \frac{\partial g_2(Q_2)}{\partial(Q_2)} h_2(R_2) - \mu_\infty \left(1 - \frac{Q_{\min,1}}{Q_1}\right),\ j_{74} = mQ_2\zeta_2,\ j_{76} = mB\zeta_2,\ j_{77} = -\delta_2$$

The general Jacobian (notice that I have not entered in the steady state values for the variables) is block lower triangular:

$$\mathbf{J} = \begin{pmatrix} \mathbf{D}_1 & 0 \\ \mathbf{L} & \mathbf{D}_2 \end{pmatrix}$$

This observation greatly simplifies the work needed to find the eigenvalues of **J**, for the eigenvalues of **J** are the eigenvalues of $\mathbf{D}_1$ and $\mathbf{D}_2$, which are lower dimension than **J**. It should be noted that when all the eigenvalues of **J** evaluated at the steady state have negative real parts, then the steady state will be locally stable. I shall therefore look only at $\mathbf{D}_1$ and $\mathbf{D}_2$ for the remainder of the analysis. I look at $\mathbf{D}_1$ and $\mathbf{D}_2$ evaluated at E^0:

$$\mathbf{D}_1 = \begin{pmatrix} -\phi_1 & 0 & \omega\delta_1 & j_{14} \\ j_{21} & j_{22} & 0 & 0 \\ 0 & 0 & -\delta_1 & j_{34} \\ 0 & 0 & 0 & j_{44} \end{pmatrix} \quad \mathbf{D}_2 = \begin{pmatrix} -\phi_2 & 0 & \omega\delta_1 \\ j_{65} & j_{66} & 0 \\ 0 & 0 & -\delta_2 \end{pmatrix}$$

The procedure for finding the eigenvalues is to take to the determinant of $\mathbf{D}_1$-$\mathbf{I}\lambda$, where λ is the eigenvalue and $\mathbf{I}$ is the identity matrix, and finding the eigenvalues that make the determinant equal to zero. Using this procedure, I found that the eigenvalues of $\mathbf{D}_1$ are j_{44}, $-\delta_1$, $-\phi_1$ and j_{22} and the eigenvalues of $\mathbf{D}_2$ are $-\delta_2$, $-\phi_2$ and j_{66}. All the eigenvalues except for j_{44} are always negative and therefore the stability of E^0 depends on the sign of j_{44}. Inspection of j_{44} at steady state shows that it is negative if the following is true:

$$m > \mu_\infty \left(1 - \frac{Q_{\min,1}}{Q_1^0}\right)$$

This condition for stability can be interpreted as follows: if the plant cannot maintain positive net growth at the internal nutrient content that is determined by the supply of nutrients (note the $h_1(R_1^0)$ term in the equation for Q_1^0 and that R_1^0 is determined by the influx and efflux of plant available nutrient), then the plant will go extinct. I can rewrite the equation to come up with a value of Q_1^0 at which this equilibrium becomes unstable:

$$Q_1^0 < \frac{\mu_\infty Q_{\min,1}}{\mu_\infty - m}$$

When this condition is violated, then it is possible to have net positive growth at the given levels of nutrient supply and the plant will not go extinct. The breaking of this condition also leads to a biologically relevant E^1 coming into existence for it did not exist if the condition remained unbroken.

For the stability of E^1, I look at the eigenvalues of $\mathbf{D}_1$ and $\mathbf{D}_2$ when they are evaluated at E^1, this time starting with $\mathbf{D}_2$. Instead of actually finding the eigenvalues, I use the Routh-Hurwitz criteria to see if they all have negative real parts, which will guarantee the asymptotic local stability of E^1. The elements of $\mathbf{D}_2$ at E^1 are:

$$\mathbf{D}_2 = \begin{pmatrix} j_{55} & j_{56} & j_{57} \\ j_{65} & j_{66} & 0 \\ 0 & j_{76} & j_{77} \end{pmatrix}$$

$$= \begin{pmatrix} -\omega \dfrac{\partial h_2(R_2^1)}{\partial R_2} g_2(Q_2^1) B^1 - \phi_2 & -\omega \dfrac{\partial g_2(Q_2^1)}{\partial Q_2} h_2(R_2^1) B^1 & \omega\delta_2 \\ \dfrac{\partial h_2(R_2^1)}{\partial R_2} g_2(Q_2^1) & \dfrac{\partial g_2(Q_2^1)}{\partial Q_2} h_2(R_2^1) - \mu_\infty & 0 \\ 0 & mB^1\zeta_2 & -\delta_2 \end{pmatrix}$$

To utilize the Routh-Hurwitz criteria, I need to find the coefficients of the characteristic polynomial for $\mathbf{D}_2$. The formula for the characteristic polynomial of a three by three matrix is:

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3$$

Where λ is the eigenvalue of the matrix and the a_i values are the coefficients. All the eigenvalues of $\mathbf{D}_2$ will have negative real part if and only if $a_1>0$, $a_3>0$ and $a_1a_2-a_3>0$. The value of a_1 is equal to the negative of the trace of $\mathbf{D}_2$, which is the sum of the diagonal elements of $\mathbf{D}_2$. The value of a_3 is equal to the negative of the determinant of $\mathbf{D}_2$ and the value of a_2 is equal to the sum of the minors of each element on the diagonal of $\mathbf{D}_2$. Inspection shows that the three terms listed above are all positive and thus the real parts of all three eigenvalues are negative.

The situation for $\mathbf{D}_1$ is a bit more difficult to discern for the Routh-Hurwitz criteria are more complicated. The formula for the characteristic polynomial of $\mathbf{D}_1$ is:

$$\lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4$$

All the eigenvalues of $\mathbf{D}_1$ will have negative real part if and only if $a_1>0$, $a_3>0$, $a_4>0$ and $a_1a_2a_3 - a_1^2a_4 - a_3^2 > 0$. Due to the complexity, I will proceed by evaluating each condition one at a time in order to see if they are satisfied. I start by examining the elements of $\mathbf{D}_1$:

$$\mathbf{D}_1 = \begin{pmatrix} j_{11} & j_{12} & j_{13} & j_{14} \\ j_{21} & j_{22} & 0 & 0 \\ 0 & j_{32} & j_{33} & j_{34} \\ 0 & j_{42} & 0 & 0 \end{pmatrix}$$

$$= \begin{pmatrix} -\omega h_1^{'}(R_1^1) g_1(Q_1^1) B^1 - \phi_1 & -\omega g_1^{'}(Q_1^1) h_1(R_1^1) B^1 & \omega\delta_1 & -\omega m Q_1^1 \\ h_1^{'}(R_1^1) g_1(Q_1^1) & g_1^{'}(Q_1^1) h_1(R_1^1) - \mu_\infty & 0 & 0 \\ 0 & \zeta_1 m B^1 & -\delta_1 & \zeta_1 m Q_1^1 \\ 0 & \mu_\infty \dfrac{Q_{\min,1}}{(Q_1^1)^2} B^1 & 0 & 0 \end{pmatrix}$$

$$\operatorname{sgn}(\mathbf{D}_1) = \begin{pmatrix} - & + & + & - \\ + & - & 0 & 0 \\ 0 & + & - & + \\ 0 & + & 0 & 0 \end{pmatrix}$$

Here, sgn($\mathbf{D}_1$) indicates the sign of the elements in $\mathbf{D}_1$ and can help simplify the analysis of the matrix. For example, all the diagonal elements of $\mathbf{D}_1$ are negative and hence the trace of $\mathbf{D}_1$ will be negative. Since the coefficient a_1 is equal to the negative of the trace of $\mathbf{D}_1$, it will be positive and the first condition of the Routh-Hurwitz criteria is met.

The other coefficients require a bit more algebra for to get at their signs. The fourth coefficient, a_4, is equal to the determinant of $\mathbf{D}_1$, which is equal to the following expression:

$$a_4 = \det(\mathbf{D_1}) = -j_{42} j_{21} (j_{13} j_{34} - j_{14} j_{33})$$

Since j_{42} and j_{21} are positive, a_4 is only positive if $j_{14}j_{33}$ is greater than $j_{13}j_{34}$ since both are positive. This is true as long as ζ_1 is less than one, which is true by definition (see Table 2.2). Therefore, this condition is always met. The third coefficient, a_3, is equal to:

$$a_3 = (-j_{33} j_{22} j_{11} + j_{33} j_{21} j_{12} + \omega j_{33} j_{21} j_{32} - j_{14} j_{21} j_{42})$$

The first term in the expression is positive, the next two terms are negative and the last term is positive. To show that a_3 is positive, it is sufficient to demonstrate the first term is larger than the next two terms:

$$\begin{aligned} &-j_{33} j_{11} j_{22} + j_{33} j_{21} j_{12} + \omega j_{33} j_{21} j_{32} \\ &= -j_{33} (j_{11} j_{22} - j_{21} j_{12} - \omega j_{21} j_{32}) \end{aligned}$$

At this point, I only need to show that the value inside the parenthesis is positive since $-j_{33}$ is positive:

$$j_{11}j_{22} - j_{21}j_{12} - \omega j_{21}j_{32} = -\phi_1 g_1^{'}(Q_1^1)h_1(R_1^1) + \omega(\mu_\infty - \zeta_1 m)h_1^{'}(R_1^1)g_1(Q_1^1)B^1 + \mu_\infty\phi_1 > 0$$

Since the interior of the parenthesis is positive, a_3 is positive and another condition is met. The second coefficient, a_2, is required to be positive in order for the last criterion to be satisfied, though a positive second coefficient does not guarantee that the last criterion is met. The coefficient can be expressed as:

$$a_2 = j_{11}j_{22} + j_{11}j_{33} + j_{22}j_{33} - j_{12}j_{21}$$

The first three terms are positive while the last term is negative. Since the first term is larger in magnitude than the last term as seen in the derivation of the sign of a_3, a_2 must be positive as well. Therefore, the final criterion, $a_1a_2a_3 - a_1^2a_4 - a_3^2 > 0$, can possibly be met. Unfortunately, evaluating this criterion requires knowledge of the magnitudes of the coefficients and it is difficult to determine whether the condition holds for all parameter values that allow for E^1 to exist.

However, I will approach solving this problem by looking at what happens when δ_1 is equal to zero (no recycling) and when it approaches infinity (instant recycling). In both cases, the system of equations reduces to five dimensions from seven, making it easier to apply the Routh-Hurwitz criteria.

Let us first consider the case with no recycling. I introduce a new matrix called **N**, which is the Jacobian matrix for the ecosystem with no recycling evaluated at E^1. The elements of **N** will be a subset of the elements of **J** and are listed below the matrix:

$$\mathbf{N} = \begin{pmatrix} n_{11} & n_{12} & n_{13} & 0 & 0 \\ n_{21} & n_{22} & 0 & 0 & 0 \\ 0 & n_{32} & 0 & 0 & 0 \\ 0 & 0 & n_{43} & n_{44} & n_{45} \\ 0 & n_{52} & 0 & n_{54} & n_{55} \end{pmatrix}$$

$n_{13} = j_{14}, n_{32} = j_{42}, n_{33} = j_{44}, n_{43} = j_{54}$

$n_{44} = j_{55}, n_{45} = j_{56}, n_{52} = j_{62}, n_{54} = j_{65}, n_{55} = j_{66}$

$n_{ik} = j_{ik}$ for the remainder

The eigenvalues of **N** can be obtained by finding the eigenvalues of the each submatrix on the diagonal, which I label $\mathbf{V}_1$ and $\mathbf{V}_2$. Instead of finding the eigenvalues directly, I will use the Routh-Hurwitz criteria to make sure the real part of all eigenvalues is negative. Since $\mathbf{V}_2$ is a two by two matrix, its characteristic polynomial takes on the following form:

$$\lambda^2 + a_1\lambda + a_2$$

For the eigenvalues to have negative real part, a_1 and a_2 both need to be positive. To find their expression, I examine $\mathbf{V}_2$:

$$\mathbf{V_2} = \begin{pmatrix} n_{44} & n_{45} \\ n_{54} & n_{55} \end{pmatrix}, \mathrm{sgn}(\mathbf{V_2}) = \begin{pmatrix} - & + \\ + & - \end{pmatrix}$$

Since a_1 is equal to the negative of the trace of $\mathbf{V}_2$, by inspection of $\mathbf{V}_2$ it can be seen that a_1 must be positive. Also by inspection, the determinant of $\mathbf{V}_2$, which is equal to a_2, must be positive. Therefore, the Routh-Hurwitz criteria are met for $\mathbf{V}_2$ and both eigenvalues have negative real parts.
For $\mathbf{V}_1$, the characteristic polynomial and the Routh-Hurwitz criteria is the same as for $\mathbf{D}_1$ as they are both three by three matrices. I begin by examining the elements of $\mathbf{V}_1$:

$$\mathbf{V_1} = \begin{pmatrix} n_{11} & n_{12} & n_{13} \\ n_{21} & n_{22} & 0 \\ 0 & n_{32} & 0 \end{pmatrix}, \mathrm{sgn}(\mathbf{V_1}) = \begin{pmatrix} - & + & - \\ + & - & 0 \\ 0 & + & 0 \end{pmatrix}$$

The expressions for a_1, a_2 and a_3 in terms of the elements of $\mathbf{V}_1$ are:

$$a_1 = -\mathbf{tr}(D_1^N) = -(n_{11} + n_{22})$$
$$a_3 = -\det(D_1^N) = -n_{13}n_{21}n_{32}$$
$$a_2 = D_{11}^N + D_{22}^N + D_{33}^N = n_{11}n_{22} - n_{12}n_{21}$$

Remembering that the Routh-Hurwitz criteria for a three by three matrix is that $a_1>0$, $a_3>0$ and $a_1a_2-a_3>0$, it is straightforward to meet the first two criteria. By inspection of the sign matrix, a_1 and a_3 must both be positive. The third criterion is a bit more complicated as it involves the magnitudes of the coefficients:

$$
\begin{aligned}
&a_1a_2 - a_3 = -(n_{11}+n_{22})(n_{11}n_{22}-n_{12}n_{21}) + n_{13}n_{21}n_{32} \\
&a_1a_2 = \underbrace{(\omega h_1'(R_1^1)g_1(Q_1^1)B_1^1)^2\mu_\infty}_{>0} \underbrace{-\omega h_1'(R_1^1)g_1(Q_1^1)B_1^1\phi_1 h_1(R_1^1)g_1'(Q_1^1)}_{>0} \\
&+\underbrace{\omega h_1'(R_1^1)g_1(Q_1^1)B_1^1\mu_\infty\phi_1}_{>0} + \underbrace{\phi_1(\omega\mu_\infty h_1'(R_1^1)g_1(Q_1^1)B_1^1 - \phi_1 h_1(R_1^1)g_1'(Q_1^1) + \mu_\infty\phi_1)}_{>0} \\
&\underbrace{-h_1(R_1^1)g_1'(Q_1^1)(\omega\mu_\infty h_1'(R_1^1)g_1(Q_1^1)B_1^1 - \phi_1 h_1(R_1^1)g_1'(Q_1^1) + \mu_\infty\phi_1)}_{>0} \\
&\underbrace{+\omega\mu_\infty^2 h_1'(R_1^1)g_1(Q_1^1)B_1^1}_{>0} \underbrace{-\mu_\infty\phi_1 h_1(R_1^1)g_1'(Q_1^1)}_{>0} + \underbrace{\mu_\infty^2\phi_1}_{>0} \\
&-a_3 = -\omega\mu_\infty m\frac{Q_{\min,1}}{Q_1^1}h_1'(R_1^1)g_1(Q_1^1)B_1^1
\end{aligned}
$$

Every element of a_1a_2 is positive, so if at least one element of a_1a_2 is greater in magnitude than -a_3, then a_1a_2-a_3 must be greater than zero. By inspection, the third to last element of a_1a_2 must always be greater in magnitude than a_3 since μ_∞ is always larger than m, then a_1a_2-a_3 is greater than zero and all the criteria are met. Therefore, all the eigenvalues of **N** have negative real parts, which implies that E^1 is locally stable when there is no recycling. With the lower bound of mineralization rate constant examined, I now proceed to the upper bound where it is infinite, i.e. the recycling is instantaneous. I define a new matrix called **T**, which is the Jacobian for the ecosystem with instantaneous recycling evaluated at E^1. The elements of **T** are nearly identical to **N** with some slight modification to four elements:

$$
\mathbf{T} = \begin{pmatrix}
t_{11} & t_{12} & t_{13} & 0 & 0 \\
t_{21} & t_{22} & 0 & 0 & 0 \\
0 & t_{32} & 0 & 0 & 0 \\
0 & 0 & t_{43} & t_{44} & t_{45} \\
0 & t_{52} & 0 & t_{54} & t_{55}
\end{pmatrix}
$$

$$t_{12} = n_{12} + \omega\zeta_1 mB^1,\ t_{13} = n_{13} + \omega\zeta_1 mQ_1^1$$

$$t_{43} = n_{43} + \omega\zeta_2 mQ_2^1,\ t_{45} = n_{45} + \omega\zeta_2 mB^1$$

$t_{ik} = n_{ik}$ for the remainder

Since **T** is block diagonal like **J** and **N**, I will find its eigenvalues by examining the submatrices along its diagonal, which I label $\mathbf{W}_1$ and $\mathbf{W}_2$:

$$\mathbf{W_1} = \begin{pmatrix} t_{11} & t_{12} & t_{13} \\ t_{21} & t_{22} & 0 \\ 0 & t_{32} & 0 \end{pmatrix}, \operatorname{sgn}(\mathbf{W_1}) = \begin{pmatrix} - & + & - \\ + & - & 0 \\ 0 & + & 0 \end{pmatrix}$$

$$\mathbf{W}_2 = \begin{pmatrix} t_{44} & t_{45} \\ t_{54} & t_{55} \end{pmatrix}, \operatorname{sgn}(\mathbf{W}_2) = \begin{pmatrix} - & + \\ + & - \end{pmatrix}$$

The characteristic polynomials and Routh-Hurwitz criteria for $\mathbf{W}_1$ and $\mathbf{W}_2$ are the same those for $\mathbf{N}_1$ and $\mathbf{N}_2$. The coefficients for the characteristic polynomial of $\mathbf{W}_2$ are:

$$a_1 = -\mathbf{tr}(\mathbf{W_2}) = -(t_{44} + t_{55})$$
$$a_2 = \det(\mathbf{W_2}) = t_{44}t_{55} - t_{45}t_{54}$$

By inspection, both of the coefficients are positive. Since the Routh-Hurwitz criteria for $\mathbf{W}_2$ is that a_1 and a_2 both be positive, both eigenvalues of $\mathbf{W}_2$ have negative real parts. The coefficients for the characteristic polynomial of $\mathbf{W}_1$ are:

$$a_1 = -\mathbf{tr}(\mathbf{W_1}) = -(t_{11} + t_{22})$$
$$a_3 = -\det(\mathbf{W_1}) = -t_{13}t_{21}t_{32}$$
$$a_2 = t_{11}t_{22} - t_{12}t_{21}$$

By inspection, all three coefficients are positive. Therefore, two of the Routh-Hurwitz criteria, namely that $a_1>0$ and $a_3>0$, are met. The last criterion, $a_1a_2-a_3>0$, requires more work:

$$a_1a_2 - a_3 = -(t_{11} + t_{22})(t_{11}t_{22} - t_{12}t_{21}) + t_{13}t_{21}t_{32}$$

$$a_1a_2 = \underbrace{(\omega h_1'(R_1^1)g_1(Q_1^1)B_1^1)^2(\mu_\infty - m\zeta_1)}_{>0}$$

$$\underbrace{-\omega h_1'(R_1^1)g_1(Q_1^1)B_1^1\phi_1 h_1(R_1^1)g_1'(Q_1^1)}_{>0} + \underbrace{\omega h_1'(R_1^1)g_1(Q_1^1)B_1^1\mu_\infty\phi_1}_{>0}$$

$$+\underbrace{\phi_1(\omega(\mu_\infty - m\zeta_1)h_1'(R_1^1)g_1(Q_1^1)B_1^1 - \phi_1 h_1(R_1^1)g_1'(Q_1^1) + \mu_\infty\phi_1)}_{>0}$$

$$\underbrace{-h_1(R_1^1)g_1'(Q_1^1)(\omega(\mu_\infty - m\zeta_1)h_1'(R_1^1)g_1(Q_1^1)B_1^1 - \phi_1 h_1(R_1^1)g_1'(Q_1^1) + \mu_\infty\phi_1)}_{>0}$$

$$\underbrace{+\omega\mu_\infty(\mu_\infty - m\zeta_1)h_1'(R_1^1)g_1(Q_1^1)B_1^1}_{>0}\underbrace{-\mu_\infty\phi_1 h_1(R_1^1)g_1'(Q_1^1)}_{>0} + \underbrace{\mu_\infty^2\phi_1}_{>0}$$

$$-a_3 = -\omega\mu_\infty m\frac{Q_{\min,1}}{Q_1^1}(1 - \zeta_1)h_1'(R_1^1)g_1(Q_1^1)B^1$$

As for matrix $\mathbf{V}_1$, all the elements of a_1a_2 are positive and if any one of those elements is greater that a_3, then a_1a_2-a_3 must be positive. By inspection, the third to last element of a_1a_2 is larger than a_3 since μ_∞ is always larger than m. Therefore, the third criterion is met and all three eigenvalues of $\mathbf{V}_1$ have negative real parts. Since all the eigenvalues of $\mathbf{V}_1$ and $\mathbf{V}_2$ have negative real parts, E^1 is locally stable when recycling is instantaneous.

Therefore at both the upper and lower limits of the mineralization parameter, I find that E^1 is stable if it exists. I will now treat the final Routh-Hurwitz criterion for the matrix $\mathbf{J}$ evaluated at E^1 as a function of the mineralization parameter and I will see if the function never crosses zero for any positive value of this parameter. If this is the case, then the mineralization parameter has no effect on the stability of E^1 and this would imply that E^1 is always stable if it exists independent of the value of δ_1. The function is:

$$
\begin{aligned}
&a_1a_2a_3 - a_1^2a_4 - a_3^2 = \\
&[(1-\zeta_1)j_{14}j_{42}j_{21} + -(j_{11}+j_{22})(j_{22}j_{11} - \omega j_{21}j_{32} - j_{21}j_{12})]\delta_1^3 + \\
&[-2(j_{11}+j_{22})(1-\zeta_1)j_{14}j_{42}j_{21} - (j_{22}j_{11} - \omega j_{21}j_{32} - j_{21}j_{12})^2 - \\
&(j_{22}j_{11} - \omega j_{21}j_{32} - j_{21}j_{12})(j_{11}+j_{22})^2 + \\
&(j_{22}j_{11} - \omega j_{21}j_{32} - j_{21}j_{12})(j_{22}j_{11} - j_{21}j_{12}) + j_{14}j_{42}j_{21}(j_{11}+j_{22})]\delta_1^2 + \\
&[(j_{11}+j_{22})^2(1-\zeta_1)j_{14}j_{42}j_{21} + 2(j_{22}j_{11} - \omega j_{21}j_{32} - j_{21}j_{12})j_{14}j_{42}j_{21} - \\
&(j_{22}j_{11} - j_{21}j_{12})j_{14}j_{42}j_{21} - j_{14}j_{42}j_{21}(j_{11}+j_{22})^2 \\
&-(j_{22}j_{11} - \omega j_{21}j_{32} - j_{21}j_{12})(j_{22}j_{11} - j_{21}j_{12})(j_{11}+j_{22})]\delta_1 + \\
&j_{14}j_{42}j_{21}(j_{11}+j_{22})(j_{22}j_{11} - j_{21}j_{12}) - (j_{14}j_{42}j_{21})^2 = b_1\delta_1^3 + b_2\delta_1^2 + b_3\delta_1 + b_4
\end{aligned}
$$

I will show that each coefficient b_i is greater than zero, thereby demonstrating that the Routh-Hurwitz criteria is always met for any positive value of δ_1. I start with b_4:

Hypothesis: $b_4 > 0$

$$j_{14}j_{42}j_{21}(j_{11}+j_{22})(j_{22}j_{11} - j_{21}j_{12}) - (j_{14}j_{42}j_{21})^2 > 0$$

I note that $j_{14}j_{42}j_{21}$ is present in both terms. I can therefore divide through by $j_{14}j_{42}j_{21}$, though I must alter the signs since $j_{14}j_{42}j_{21}$ is negative. I then have:

$$-(j_{11}+j_{22})(j_{22}j_{11} - j_{21}j_{12}) + j_{14}j_{42}j_{21} > 0$$

The first term is identical to a_1a_2 for the matrix $\mathbf{V}_1$ and the second term is identical to $-a_3$. As I have already shown that a_1a_2-a_3 is positive for $\mathbf{V}_1$, it must also be the case here. Therefore, b_4 is positive. The situation is similar for b_1:

Hypothesis: $b_1 > 0$

$$(1-\zeta_1)j_{14}j_{42}j_{21}-(j_{11}+j_{22})(j_{22}j_{11}-j_{21}j_{12}-\omega j_{21}j_{32})>0$$

The first term here is identical to $-a_3$ for the matrix $\mathbf{W}_1$ and the second term is nearly identical to a_1a_2 with a term missing that does not change the final result. Since I have already shown that a_1a_2-a_3, it must also be the case here. Therefore, b_1 is positive.

These results indicate that as the mineralization parameter approaches either infinity or zero, the Routh-Hurwitz criteria will be satisfied for the full system, just as it was when I assume instantaneous recycling and no recycling. The next two coefficients require using some insights gained from the previous work:

Hypothesis: $b_2 > 0$

$$b_2 = \underbrace{-2(j_{11}+j_{22})(1-\zeta_1)j_{14}j_{42}j_{21}}_{-ve}\underbrace{-(j_{22}j_{11}-\omega j_{21}j_{32}-j_{21}j_{12})^2}_{-ve}$$

$$\underbrace{-(j_{22}j_{11}-\omega j_{21}j_{32}-j_{21}j_{12})(j_{11}+j_{22})^2}_{+ve}+$$

$$\underbrace{(j_{22}j_{11}-\omega j_{21}j_{32}-j_{21}j_{12})(j_{22}j_{11}-j_{21}j_{12})}_{+ve}+\underbrace{j_{14}j_{42}j_{21}(j_{11}+j_{22})}_{+ve}$$

The first two terms of b_2 are negative and as long as the other three terms, which are all positive, are larger, then b_2 would need to be positive. To begin, the second term is smaller in magnitude than the fourth term. This fact can be quickly derived by the fact that if you divide both by $j_{11}j_{22}-\omega j_{21}j_{32}-j_{21}j_{12}$, which is positive, adding the two terms together gives $\omega j_{21}j_{32}$, which is a positive number. If ζ_1 is greater than 0.5, then the following must be true:

$$-2(j_{11}+j_{22})(1-\zeta_1)j_{14}j_{42}j_{21}+j_{14}j_{42}j_{21}(j_{11}+j_{22})>0$$

Even if ζ_1 is less than 0.5, the smallest it can be is zero and so the following must hold:

$$\left|-2(j_{11}+j_{22})(1-\zeta_1)j_{14}j_{42}j_{21}+j_{14}j_{42}j_{21}(j_{11}+j_{22})\right| \le \left|-(j_{11}+j_{22})(1-\zeta_1)j_{14}j_{42}j_{21}\right|$$

Therefore, the magnitude of the remaining negative term is than the one on the right hand side. Adding the third term to the term on the right hand side gives a positive value since, after diving by -(j_{11}+j_{22}), the third term is nearly identical to a_1a_2 for $\mathbf{V}_1$ with one term missing that does not affect the final result and the remaining negative term is identical to $-a_3$. Therefore, b_2 is positive. The final coefficient to investigate is b_3:

Hypothesis: $b_3 > 0$

$$b_3 = \underbrace{(j_{11}+j_{22})^2(1-\zeta_1)j_{14}j_{42}j_{21}}_{-ve} + \underbrace{2(j_{22}j_{11}-\omega j_{21}j_{32}-j_{21}j_{12})j_{14}j_{42}j_{21}}_{-ve}$$

$$\underbrace{-(j_{22}j_{11}-j_{21}j_{12})j_{14}j_{42}j_{21}}_{+ve}\underbrace{-j_{14}j_{42}j_{21}(j_{11}+j_{22})^2}_{+ve}$$

$$\underbrace{-(j_{22}j_{11}-\omega j_{21}j_{32}-j_{21}j_{12})(j_{22}j_{11}-j_{21}j_{12})(j_{11}+j_{22})}_{+ve}$$

As with b_2, two terms are negative and three are positive. Adding the first term and the fourth term together gives a positive number since 1 is always greater than $(1-\zeta_1)$. Furthermore, adding the second term to the third term gives a negative number with a magnitude always less than or equal to:

$$\left|(j_{22}j_{11}-j_{21}j_{32}-j_{21}j_{12})j_{14}j_{42}j_{21}\right|$$

Adding the above expression to the final term and dividing this sum by $(j_{22}j_{11}-j_{21}j_{32}-j_{21}j_{12})$, which is a positive number, results in the final term being exactly $a_1a_2-a_3$ for $\mathbf{V}_1$, which is positive. Therefore, b_3 is positive.

Since all the values of b_3 are non-negative, the polynomial has no real positive roots, is strictly positive and increasing if δ_1 is non-negative. This result implies that δ_1 does not affect the stability of E^1 and it also indicates that if E_1 exists, then it is locally stable. I have therefore extended the results from variable resource storage models with no recycling (Klausmeier et al. 2004) and instantaneous recycling (Ballantyne et al. 2008) to a model with a detritus compartment. I also somewhat generalized the uptake functions for the organisms by allowing it to be affected by the concentrations of nutrients within the plant.

I now know the conditions for the stability of both steady states: E^0 is stable if E^1 does not exist, E^0 is unstable and E^1 is stable if E^1 exists.

2.I *Derivation of a Condition for the Coexistence Steady State*

In this section, I derive one of the conditions for the existence of the coexistence steady state. The derivation comes from the fact that at this steady state, the consumption of nutrients by the organisms must equal the supply of nutrients, with the supply originating from abiotic sources and the recycling of dead plant material. This fact can be translated into a vector formulation such that $\boldsymbol{c}_{xy}$, the consumption vector at steady state, must balance the sum of the abiotic supply vector $\boldsymbol{u}$ and the recycling vector $\boldsymbol{r}_{xy}$. As I know the formulas for these vectors from Eq. 2.7 and 2.8, I can write out the vector equation:

$$u + c + r = 0$$

$$\begin{pmatrix} I_1 - \phi_1 R_1^{xy} \\ I_2 - \phi_2 R_2^{xy} \end{pmatrix} + \begin{pmatrix} -\omega h_{1x}(R_1^{xy}) g_{1x}(Q_{1x}^{xy}) B_x^{xy} - \omega h_{1y}(R_1^{xy}) g_{1y}(Q_{1y}^{xy}) B_y^{xy} \\ -\omega h_{2x}(R_2^{xy}) g_{2x}(Q_{2x}^{xy}) B_x^{xy} - \omega h_{2y}(R_2^{xy}) g_{2y}(Q_{2y}^{xy}) B_y^{xy} \end{pmatrix} +$$

$$\begin{pmatrix} \omega \zeta_{1x} m_x Q_{1x} B_x^{xy} + \omega \zeta_{1y} m_y Q_{1y} B_y^{xy} \\ \omega \zeta_{2x} m_x Q_{2x} B_x^{xy} + \omega \zeta_{2y} m_y Q_{2y} B_y^{xy} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

I only want certain solutions of this vector equation, specifically those that allow for B_x and B_y to be positive. Therefore, I want to solve for these two unknowns with the two equations. The easiest way to solve the system is to rewrite the above equations as:

$$\begin{pmatrix} \omega(-h_{1x}(R_1^{xy}) g_{1x}(Q_{1x}^{xy}) + \zeta_{1x} m_x Q_{1x}) & \omega(-h_{1y}(R_1^{xy}) g_{1y}(Q_{1y}^{xy}) + \zeta_{1y} m_y Q_{1y}) \\ \omega(-h_{2x}(R_2^{xy}) g_{2x}(Q_{2x}^{xy}) + \zeta_{2x} m_x Q_{2x}) & \omega(-h_{2y}(R_2^{xy}) g_{2y}(Q_{2y}^{xy}) + \zeta_{2y} m_y Q_{2y}) \end{pmatrix}$$

$$\begin{pmatrix} B_x^{xy} \\ B_y^{xy} \end{pmatrix} = -\begin{pmatrix} I_1 - \phi_1 R_1^{xy} \\ I_2 - \phi_2 R_2^{xy} \end{pmatrix}$$

The vector equation is now in the familiar form of **Ax=y**, where **A** is a coefficient matrix, **x** is the vector of unknowns and **y** is the vector of known values. If **A** is invertible, i.e. it is a square matrix whose determinant is not equal to zero, one can solve for **x** by multiplying both sides of the vector equation by $\mathbf{A}^{-1}$, the inverse of **A**. One then has $\mathbf{x}=\mathbf{A}^{-1}\mathbf{y}$ and it is then possible to obtain the values of **x**. The determinant of **A** is:

$$\mathbf{A} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} = \begin{pmatrix} c_{1x} + r_{1x} & c_{1y} + r_{1y} \\ c_{2x} + r_{2x} & c_{2y} + r_{2y} \end{pmatrix}$$

$$= \omega \begin{pmatrix} -h_{1x}(R_1^{xy}) g_{1x}(Q_{1x}^{xy}) + \zeta_{1x} m_x Q_{1x} & -h_{1y}(R_1^{xy}) g_{1y}(Q_{1y}^{xy}) + \zeta_{1y} m_y Q_{1y} \\ -h_{2x}(R_2^{xy}) g_{2x}(Q_{2x}^{xy}) + \zeta_{2x} m_x Q_{2x} & -h_{2y}(R_2^{xy}) g_{2y}(Q_{2y}^{xy}) + \zeta_{2y} m_y Q_{2y} \end{pmatrix}$$

$$\det(\mathbf{A}) = a_{11}a_{22} - a_{12}a_{21} =$$
$$\omega^2 \left(-h_{1x}(R_1^{xy}) g_{1x}(Q_{1x}^{xy}) + \zeta_{1x} m_x Q_{1x}\right)\left(-h_{2y}(R_2^{xy}) g_{2y}(Q_{2y}^{xy}) + \zeta_{2y} m_y Q_{2y}\right) -$$
$$\omega^2 \left(-h_{2x}(R_2^{xy}) g_{2x}(Q_{2x}^{xy}) + \zeta_{2x} m_x Q_{2x}\right)\left(-h_{1y}(R_1^{xy}) g_{1y}(Q_{1y}^{xy}) + \zeta_{1y} m_y Q_{1y}\right)$$

The determinant of **A** will not equal to zero as long as the net consumption of the limiting nutrient at steady state for each species is not equal to the net consumption of the non-limiting nutrient at steady state. This condition will be satisfied as long as the species are not both co-limited by the two nutrients at steady state, which is highly unlikely. I therefore assume that the determinant is not zero and I define the inverse of **A** as:

$$\mathbf{A}^{-1} = \frac{1}{\det(\mathbf{A})}\begin{pmatrix} a_{22} & -a_{12} \\ -a_{21} & a_{11} \end{pmatrix}$$

With the inverse in hand, I can now solve the vector equation:

$$\begin{pmatrix} B_x^{xy} \\ B_y^{xy} \end{pmatrix} = -\mathbf{A}^{-1}\begin{pmatrix} I_1 - \phi_1 R_1^{xy} \\ I_2 - \phi_2 R_2^{xy} \end{pmatrix} =$$

$$-\frac{1}{\det(\mathbf{A})}\begin{pmatrix} a_{22}(I_1 - \phi_1 R_1^{xy}) - a_{12}(I_2 - \phi_2 R_2^{xy}) \\ a_{11}(I_2 - \phi_2 R_2^{xy}) - a_{21}(I_1 - \phi_1 R_1^{xy}) \end{pmatrix}$$

$$a_{ij} < 0 \text{ for } i, j = 1,2$$

The possible values of the nutrients at steady state that can give a positive solution to the biomass of the two species depends on if the determinant of **A** is positive or negative. If the determinant of **A** is positive, then:

$$\frac{1}{\det(\mathbf{A})} = \alpha = +\text{ve constant}$$

$$B_x^{xy} = \frac{1}{\alpha}(-a_{22}(I_1 - \phi_1 R_1^{xy}) + a_{12}(I_2 - \phi_2 R_2^{xy}))$$

$$B_x^{xy} > 0 \text{ if } -a_{22}(I_1 - \phi_1 R_1^{xy}) > -a_{12}(I_2 - \phi_2 R_2^{xy}) \Leftrightarrow \frac{a_{22}}{a_{12}} > \frac{(I_2 - \phi_2 R_2^{xy})}{(I_1 - \phi_1 R_1^{xy})}$$

$$B_y^{xy} = \frac{1}{\alpha}(-a_{11}(I_2 - \phi_2 R_2^{xy}) + a_{21}(I_1 - \phi_1 R_1^{xy}))$$

$$B_y^{xy} > 0 \text{ if } -a_{11}(I_2 - \phi_2 R_2^{xy}) > -a_{21}(I_1 - \phi_1 R_1^{xy}) \Leftrightarrow \frac{a_{21}}{a_{11}} < \frac{(I_2 - \phi_2 R_2^{xy})}{(I_1 - \phi_1 R_1^{xy})}$$

$$\therefore \frac{a_{22}}{a_{12}} > \frac{(I_2 - \phi_2 R_2^{xy})}{(I_1 - \phi_1 R_1^{xy})} > \frac{a_{21}}{a_{11}} \text{ for } B_x^{xy}, B_y^{xy} > 0$$

Therefore, the slope of the supply vector must lie in between the slopes of the net consumption vectors of the two species. This result implies that the supply point must also lie between the slopes of the net consumption vectors for otherwise the slope of the supply vector would lie outside the slopes of the net consumption vectors. The result is similar when the determinant is negative, with only the changing the 'greater than' signs with less 'less than' signs. The condition can be rewritten using the components of the consumption and recycling vectors:

$$\frac{c_{2y}+r_{2y}}{c_{1y}+r_{1y}} > \frac{(I_2-\phi_2 R_2^{xy})}{(I_1-\phi_1 R_1^{xy})} > \frac{c_{2x}+r_{2x}}{c_{1x}+r_{1x}}$$

For the sake of simplicity, within the main text I define the slope of the net consumption vectors as β_j.

2.J *Derivation of Eq. 2.9*

The formulation of β_j found in Eq. 2.9 can be derived from the existence conditions of the coexistence steady state. β_j is formally defined as the slope of the net consumption vector of plant *j*, which can be written mathematically as:

$$\beta_j = \frac{c_{2j}+r_{2j}}{c_{1j}+r_{1j}}$$

I note that at steady state, the uptake of nutrients per unit biomass must be equal to the loss of nutrients, which means $h_{ij}(R_i^{xy})g_{ij}(Q_{ij}^{xy}) = m_j Q_{ij}^{xy}$ in order for this condition to be satisfied. I substitute the right-hand side of the expression into the formulation of β_j and I derive Eq. 2.9:

$$\beta_j = \frac{c_{2j}+r_{2j}}{c_{1j}+r_{1j}} = \frac{-h_{2j}(R_2^{xy})g_{2j}(Q_{2j}^{xy})B_j^{xy} + \zeta_{2j} m_j Q_{2j}^{xy} B_j^{xy}}{-h_{1j}(R_1^{xy})g_{1j}(Q_{1j}^{xy})B_j^{xy} + \zeta_{1j} m_j Q_{1j}^{xy} B_j^{xy}} =$$

$$\frac{-m_j Q_{2j}^{xy} B_j^{xy} + \zeta_{2j} m_j Q_{2j}^{xy} B_j^{xy}}{-m_j Q_{1j}^{xy} B_j^{xy} + \zeta_{1j} m_j Q_{1j}^{xy} B_j^{xy}} = \frac{(1-\zeta_{2j})Q_{2j}^{xy}}{(1-\zeta_{1j})Q_{1j}^{xy}}$$

2.K *Stability Conditions for Two Species, Two Nutrient Steady States*

As for the single species case, stability conditions are derived by linearising around the steady state and determining the eigenvalues of the associated Jacobian matrix. The general Jacobian matrix for two species and two nutrients, without assuming *a priori* which nutrient is limiting which species, can be written as:

$$\mathbf{J}=\begin{pmatrix} j_{11} & 0 & j_{13} & 0 & j_{15} & j_{16} & 0 & j_{18} & j_{19} & 0 \\ 0 & j_{22} & 0 & j_{24} & j_{25} & 0 & j_{27} & j_{28} & 0 & j_{2,10} \\ j_{31} & 0 & j_{33} & j_{34} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & j_{42} & j_{43} & j_{44} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & j_{53} & j_{54} & j_{55} & 0 & 0 & 0 & 0 & 0 \\ j_{61} & 0 & 0 & 0 & 0 & j_{66} & j_{67} & 0 & 0 & 0 \\ 0 & j_{72} & 0 & 0 & 0 & j_{76} & j_{77} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & j_{86} & j_{87} & j_{88} & 0 & 0 \\ 0 & 0 & j_{93} & 0 & j_{95} & j_{96} & 0 & j_{98} & j_{99} & 0 \\ 0 & 0 & 0 & j_{10,4} & j_{10,5} & 0 & j_{10.7} & j_{10,8} & 0 & j_{10,10} \end{pmatrix}$$

$$j_{11}=-\omega\sum_{j=x,y}\frac{\partial h_{1j}(R_1)}{\partial R_1}g_{1j}(Q_{1j})B_j-\phi_1,\ j_{13}=-\omega\frac{\partial g_{1x}(Q_{1x})}{\partial(Q_{1x})}h_{1x}(R_1)B_x,$$

$$j_{15}=\omega g_{1x}(Q_{1x})h_{1x}(R_1),j_{16}=-\omega\frac{\partial g_{1y}(Q_{1y})}{\partial(Q_{1y})}h_{1y}(R_1)B_y$$

$$j_{18}=\omega g_{1y}(Q_{1y})h_{1y}(R_1),\ j_{19}=\omega_1\delta_1,\ j_{22}=-\omega\sum_{j=x,y}\frac{\partial h_{2j}(R_2)}{\partial R_2}g_{2j}(Q_{2j})B_j$$

$$j_{24}=-\frac{\partial g_{2x}(Q_{2x})}{\partial(Q_{2x})}h_{2x}(R_2)B_x,\ j_{25}=\omega g_{2x}(Q_{2x})h_{2x}(R_2),\ j_{27}=-\omega\frac{\partial g_{2y}(Q_{2y})}{\partial(Q_{2y})}h_{2y}(R_2)B_y$$

$$j_{28}=g_{2y}(Q_{2y})h_{2y}(R_2),j_{2,10}=\omega_2\delta_2,\ j_{31}=\frac{\partial h_{1x}(R_1)}{\partial R_1}g_{1x}(Q_{1x}),$$

$$j_{33}=\frac{\partial g_{1x}(Q_{1x})}{\partial(Q_{1x})}h_{1x}(R_1)-\frac{\partial\mu\left(Q_{1x},Q_{2x}\right)Q_{1x}}{\partial(Q_{1x})},\ j_{34}=-\frac{\partial\mu\left(Q_{1x},Q_{2x}\right)Q_{1x}}{\partial(Q_{2x})}$$

$$j_{42}=\frac{\partial h_{2x}(R_2)}{\partial R_2}g_{2x}(Q_{2x}),j_{43}=-\frac{\partial\mu\left(Q_{1x},Q_{2x}\right)Q_{2x}}{\partial(Q_{1x})}$$

$$j_{44}=\frac{\partial g_{2x}(Q_{2x})}{\partial(Q_{2x})}h_{2x}(R_2)-\frac{\partial\mu\left(Q_{1x},Q_{2x}\right)Q_{2x}}{\partial(Q_{2x})},\ j_{53}=\frac{\partial\mu\left(Q_{1x},Q_{2x}\right)B_x}{\partial(Q_{1x})}$$

$$j_{54}=\frac{\partial\mu\left(Q_{1x},Q_{2x}\right)B_x}{\partial(Q_{2x})},j_{55}=\mu\left(Q_{1x},Q_{2x}\right)-m_x,j_{61}=\frac{\partial h_{1y}(R_1)}{\partial R_1}g_{1y}(Q_{1y}),$$

$$j_{66}=\frac{\partial g_{1y}(Q_{1y})}{\partial(Q_{1y})}h_{1y}(R_1)-\frac{\partial\mu\left(Q_{1y},Q_{2y}\right)Q_{1y}}{\partial(Q_{1y})},j_{67}=-\frac{\partial\mu\left(Q_{1y},Q_{2y}\right)Q_{1y}}{\partial(Q_{2y})}$$

$$j_{72} = \frac{\partial h_{2y}(R_2)}{\partial R_2} g_{2y}(Q_{2y}),\ j_{76} = -\frac{\partial \mu\left(Q_{1y},Q_{2y}\right)Q_{2y}}{\partial(Q_{1y})}$$

$$j_{77} = \frac{\partial g_{2y}(Q_{2y})}{\partial(Q_{2y})} h_{y2}(R_2) - \frac{\partial \mu\left(Q_{1y},Q_{2y}\right)Q_{2y}}{\partial(Q_{2y})},\ j_{87} = \frac{\partial \mu\left(Q_{1y},Q_{2y}\right)B_y}{\partial(Q_{2y})}$$

$$j_{88} = \mu\left(Q_{1y},Q_{2y}\right) - m_y,\ j_{93} = m_x\zeta_{1x}B_x,\ j_{95} = m_x\zeta_{1x}Q_{1x},\ j_{96} = m_y\zeta_{1y}B_y,$$

$$j_{98} = m_y\zeta_{1y}Q_{1y},\ j_{99} = -\delta_1,\ j_{10,4} = m_x\zeta_{2x}B_x,\ j_{10,5} = m_x\zeta_{2x}Q_{2x},\ j_{10,7} = m_y\zeta_{2y}B_y$$

$$j_{10,8} = m_y\zeta_{2y}Q_{2y},\ j_{10,10} = -\delta_2$$

The values of a few of the entries are dependent on which nutrient is limiting at steady state. If the growth of plant *x* is limited by nutrient 1, then j_{34} and j_{54} are equal to zero. Similarly, if the growth of plant *x* is limited by nutrient 2, then j_{43} and j_{53} are equal to zero. These results equally applied to plant *y* such that if it is limited by nutrient 1 or nutrient 2, then j_{67} and j_{87} are equal to zero or j_{76} and j_{86} are equal to zero, respectively. This fact will be important during the analysis of the Jacobian matrices.

At the no-plant steady state, the Jacobian matrix is:

$$\mathbf{J}_{\mathbf{E}^0} = \begin{pmatrix}
j_{11} & 0 & 0 & 0 & j_{15} & 0 & 0 & j_{18} & j_{19} & 0 \\
0 & j_{22} & 0 & 0 & j_{25} & 0 & 0 & j_{28} & 0 & j_{2,10} \\
j_{31} & 0 & j_{33} & j_{34} & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & j_{42} & j_{43} & j_{44} & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & j_{55} & 0 & 0 & 0 & 0 & 0 \\
j_{61} & 0 & 0 & 0 & 0 & j_{66} & j_{67} & 0 & 0 & 0 \\
0 & j_{72} & 0 & 0 & 0 & j_{76} & j_{77} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & j_{88} & 0 & 0 \\
0 & 0 & 0 & 0 & j_{95} & 0 & 0 & j_{98} & j_{99} & 0 \\
0 & 0 & 0 & 0 & j_{10,5} & 0 & 0 & j_{10,8} & 0 & j_{10,10}
\end{pmatrix}$$

Recalling that the eigenvalues must satisfy **det(J-λI)** = 0, where **I** is the identity matrix, and that one can start taking the determinant from any row or column in the matrix, it is fairly simple to obtain the eigenvalues of this large matrix. Inserting the eigenvalues into the above matrix, I have:

$$(\mathbf{J}_{\mathbf{E}^0} - \lambda\mathbf{I}) =$$

$$\begin{pmatrix}
j_{11}-\lambda & 0 & 0 & 0 & j_{15} & 0 & 0 & j_{18} & j_{19} & 0 \\
0 & j_{22}-\lambda & 0 & 0 & j_{25} & 0 & 0 & j_{28} & 0 & j_{2,10} \\
j_{31} & 0 & j_{33}-\lambda & j_{34} & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & j_{42} & j_{43} & j_{44}-\lambda & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & j_{55}-\lambda & 0 & 0 & 0 & 0 & 0 \\
j_{61} & 0 & 0 & 0 & 0 & j_{66}-\lambda & j_{67} & 0 & 0 & 0 \\
0 & j_{72} & 0 & 0 & 0 & j_{76} & j_{77}-\lambda & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & j_{88}-\lambda & 0 & 0 \\
0 & 0 & 0 & 0 & j_{95} & 0 & 0 & j_{98} & j_{99}-\lambda & 0 \\
0 & 0 & 0 & 0 & j_{10,5} & 0 & 0 & j_{10,8} & 0 & j_{10,10}-\lambda
\end{pmatrix}$$

I note that rows five and eight only have one non-zero entry. Thus, I know that j_{55} and j_{88} are eigenvalues for the matrix for if λ is equal to either of them, the determinant of the matrix is zero. Removing the rows and their associated columns leave us with an eight by eight matrix:

$$\begin{pmatrix}
j_{11}-\lambda & 0 & 0 & 0 & 0 & 0 & j_{19} & 0 \\
0 & j_{22}-\lambda & 0 & 0 & 0 & 0 & 0 & j_{2,10} \\
j_{31} & 0 & j_{33}-\lambda & j_{34} & 0 & 0 & 0 & 0 \\
0 & j_{42} & j_{43} & j_{44}-\lambda & 0 & 0 & 0 & 0 \\
j_{61} & 0 & 0 & 0 & j_{66}-\lambda & j_{67} & 0 & 0 \\
0 & j_{72} & 0 & 0 & j_{77} & j_{77}-\lambda & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & j_{99}-\lambda & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & j_{10,10}-\lambda
\end{pmatrix}$$

As before, I have two rows with only one non-zero entry and if the eigenvalues are equal to the entry, then the determinant is equal to zero. Therefore, j_{99} and $j_{10,10}$ are both eigenvalues of the matrix. Removing these two rows and their associated columns from the matrix results in two more rows (the first two) having only one non-zero entry and j_{11} and j_{22} are also eigenvalues for the matrix. I am left with a four by four matrix:

$$\begin{pmatrix} j_{33}-\lambda & j_{34} & 0 & 0 \\ j_{43} & j_{44}-\lambda & 0 & 0 \\ 0 & 0 & j_{66}-\lambda & j_{67} \\ 0 & 0 & j_{76} & j_{77}-\lambda \end{pmatrix}$$

Since one of j_{34} and j_{43} as well as one of j_{67} and j_{76} must be equal to zero since only one nutrient is limiting, then all the entries on the diagonals (j_{33}, j_{44}, j_{66} and j_{77}) are eigenvalues of the Jacobian. Except for j_{55} and j_{88}, all the eigenvalues of the Jacobian are always negative. For these two eigenvalues, they are only negative if and only if:

$$\mu\left(Q_{1x}^0,Q_{2x}^0\right)-m_x<0 \text{ and } \mu\left(Q_{1y}^0,Q_{2y}^0\right)-m_y<0$$

These conditions are violated if either of the single plant steady states exists, which is similar to the single species case. Therefore, the no-plant steady state is only locally stable if the single plant steady states do not exist.

The stability of the single plant steady states can also be investigated analytically. I first must assume that the plant is limited by one nutrient at steady state. For this example, I assume that plant x is limited by nutrient 1. With this assumption, the Jacobian matrix evaluated at E^x is:

$$\mathbf{J}_{\mathbf{E}^x}=\begin{pmatrix} j_{11} & 0 & j_{13} & 0 & j_{15} & 0 & 0 & j_{18} & j_{19} & 0 \\ 0 & j_{22} & 0 & j_{24} & j_{25} & 0 & 0 & j_{28} & 0 & j_{2,10} \\ j_{31} & 0 & j_{33} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & j_{42} & j_{43} & j_{44} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & j_{53} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ j_{61} & 0 & 0 & 0 & 0 & j_{66} & j_{67} & 0 & 0 & 0 \\ 0 & j_{72} & 0 & 0 & 0 & j_{76} & j_{77} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & j_{88} & 0 & 0 \\ 0 & 0 & j_{93} & 0 & j_{95} & 0 & 0 & j_{98} & j_{99} & 0 \\ 0 & 0 & 0 & j_{10,4} & j_{10,5} & 0 & 0 & j_{10,8} & 0 & j_{10,10} \end{pmatrix}$$

Three eigenvalues of this matrix are readily available, as j_{88} is the lone non-zero entry in the eighth row and is on the diagonal and therefore must be an eigenvalue in addition to j_{66} and j_{77}, for one of j_{67} and j_{76} is equal to zero due to the fact that only one nutrient is limiting. The matrix that remains is identical to the Jacobian for the single species case, which has only negative eigenvalues as proved in Appendix 2.H. Furthermore, both j_{66} and j_{77} are negative, such that the stability of E^x depends solely on j_{88}. This entry describes the net growth of the plant *y* at the nutrient concentrations at E^x such that plant *y* can invade if j_{88} is positive and cannot invade if it is negative. Mathematically, the stability condition can be defined as:

$$\mu\left(Q_{1y}^{x}, Q_{2y}^{x}\right) - m_y < 0$$

The stability condition for having only plant *y* present at steady state is similar. Due to the complexity of the Jacobian matrix for the coexistence steady state, E^{xy}, no analytic stability conditions were derived.

2.L *R* Derivation for Specified Functional Forms*

In this section, I derive the *R** values for a species by using the specified functional forms as specified in Eq. 2.3. I begin by setting the equations *dB/dt* and *dQ*$_i$*/dt* equal to zero and assume nutrient *i* is limiting:

$$\frac{dB}{dt} = 0 = \left[\mu_\infty\left(1 - \frac{Q_{\min,i}}{Q_i^*}\right) - m\right]B$$

$$0 = \mu_\infty\left(1 - \frac{Q_{\min,i}}{Q_i^*}\right) - m,\ B \neq 0$$

$$Q_i^* = \frac{\mu_\infty Q_{\min,i}}{\mu_\infty - m}$$

$$\frac{dQ_i}{dt} = 0 = \frac{V_{\max,i} R_i^*}{K_i + R_i^*} \frac{Q_{\max,i} - Q_i^*}{Q_{\max,i} - Q_{\min,i}} - \mu_\infty (Q_i^* - Q_{\min,i})$$

$$0 = V_{\max,i} R_i^* \frac{Q_{\max,i} - Q_i^*}{Q_{\max,i} - Q_{\min,i}} - \mu_\infty (Q_i^* - Q_{\min,i})(K_i + R_i^*)$$

$$R_i^*\left(V_{\max,i} \frac{Q_{\max,i} - Q_i^*}{Q_{\max,i} - Q_{\min,i}} - \mu_\infty (Q_i^* - Q_{\min,i})\right) = \mu_\infty K_i (Q_i^* - Q_{\min,i})$$

$$R_i^* = \frac{\mu_\infty K_i (Q_i^* - Q_{\min,i})(Q_{\max,i} - Q_{\min,i})}{V_{\max,i}(Q_{\max,i} - Q_i^*) - \mu_\infty (Q_i^* - Q_{\min,i})(Q_{\max,i} - Q_{\min,i})}$$

*R** values are therefore dependent on the growth rate constant, the half-saturation constant, the mortality rate constant, the maximum uptake rate constant and the minimum and maximum internal concentrations of nutrients inside the plant. Since a plant's competitive ability increases with decreasing *R** values, it is important to know if increasing the value of a model parameter will either increase or decrease the *R** (i.e. decrease or increase competitive ability). The best way to do so is to the take the partial derivatives of *R** with respect to the parameter. To do so, I first rewrite the *R** values with only parameters:

$$R_i^* = \frac{\mu_\infty K_i (Q_i^* - Q_{\mathrm{min},i})(Q_{\mathrm{max},i} - Q_{\mathrm{min},i})}{V_{\mathrm{max},i}(Q_{\mathrm{max},i} - Q_i^*) - \mu_\infty (Q_i^* - Q_{\mathrm{min},i})(Q_{\mathrm{max},i} - Q_{\mathrm{min},i})}$$

$$= \frac{\mu_\infty K_i \left(\frac{\mu_\infty Q_{\mathrm{min},i}}{\mu_\infty - m} - Q_{\mathrm{min},i}\right)(Q_{\mathrm{max},i} - Q_{\mathrm{min},i})}{V_{\mathrm{max},i}\left(Q_{\mathrm{max},i} - \frac{\mu_\infty Q_{\mathrm{min},i}}{\mu_\infty - m}\right) - \mu_\infty \left(\frac{\mu_\infty Q_{\mathrm{min},i}}{\mu_\infty - m} - Q_{\mathrm{min},i}\right)(Q_{\mathrm{max},i} - Q_{\mathrm{min},i})}$$

Next, I take the partial derivatives with respect to each parameter:

$$\frac{\partial R_i^*}{\partial V_{\mathrm{max},i}} = -\frac{\mu_\infty K_i \left(\frac{\mu_\infty Q_{\mathrm{min},i}}{\mu_\infty - m} - Q_{\mathrm{min},i}\right)(Q_{\mathrm{max},i} - Q_{\mathrm{min},i})\left(Q_{\mathrm{max},i} - \frac{\mu_\infty Q_{\mathrm{min},i}}{\mu_\infty - m}\right)}{\left(V_{\mathrm{max},i}\left(Q_{\mathrm{max},i} - \frac{\mu_\infty Q_{\mathrm{min},i}}{\mu_\infty - m}\right) - \mu_\infty \left(\frac{\mu_\infty Q_{\mathrm{min},i}}{\mu_\infty - m} - Q_{\mathrm{min},i}\right)(Q_{\mathrm{max},i} - Q_{\mathrm{min},i})\right)^2}$$

$$\therefore \frac{\partial R_i^*}{\partial V_{\mathrm{max},i}} < 0$$

$$\frac{\partial R_i^*}{\partial K_i} = \frac{\mu_\infty \left(\frac{\mu_\infty Q_{\mathrm{min},i}}{\mu_\infty - m} - Q_{\mathrm{min},i}\right)(Q_{\mathrm{max},i} - Q_{\mathrm{min},i})}{V_{\mathrm{max},i}\left(Q_{\mathrm{max},i} - \frac{\mu_\infty Q_{\mathrm{min},i}}{\mu_\infty - m}\right) - \mu_\infty \left(\frac{\mu_\infty Q_{\mathrm{min},i}}{\mu_\infty - m} - Q_{\mathrm{min},i}\right)(Q_{\mathrm{max},i} - Q_{\mathrm{min},i})}$$

$$\therefore \frac{\partial R_i^*}{\partial K_i} > 0$$

The kinetic parameters have opposite effects on *R** when increasing: the uptake rate decreases *R** and the half-saturation constant increases *R**. Therefore, a plant that minimizes the half-saturation constant and maximizes its uptake rate will be most competitive for the limiting nutrient. Continuing on:

$$\frac{\partial R_i^*}{\partial \mu_\infty} = -\frac{\mu_\infty K_i m^2 Q_{\min,i} V_{\max,i} Q_{\max,i} (Q_{\max,i} - Q_{\min,i})}{(V_{\max,i}(Q_{\max,i} - \frac{\mu_\infty Q_{\min,i}}{\mu_\infty - m}) - \mu_\infty(\frac{\mu_\infty Q_{\min,i}}{\mu_\infty - m} - Q_{\min,i})(Q_{\max,i} - Q_{\min,i}))^2}$$

$$\therefore \frac{\partial R_i^*}{\partial \mu_\infty} < 0$$

$$\frac{\partial R_i^*}{\partial m} = \frac{\mu_\infty^2 K_i m Q_{\min,i} V_{\max,i} (Q_{\max,i} - Q_{\min,i})^2}{(V_{\max,i}(Q_{\max,i} - \frac{\mu_\infty Q_{\min,i}}{\mu_\infty - m}) - \mu_\infty(\frac{\mu_\infty Q_{\min,i}}{\mu_\infty - m} - Q_{\min,i})(Q_{\max,i} - Q_{\min,i}))^2}$$

$$\therefore \frac{\partial R_i^*}{\partial m} > 0$$

The effects of growth rate and mortality meet one's intuitive expectations that a high growth rate and low mortality would allow for better competitive ability, which is the case as higher growth rates decrease *R** and higher mortality rates increase *R**. The last set of parameters is the stoichiometric parameters:

$$\frac{\partial R_i^*}{\partial Q_{\max,i}} = -\frac{\mu_\infty K_i m^2 Q_{\min,i}^2 V_{\max,i}}{(V_{\max,i}(Q_{\max,i} - \frac{\mu_\infty Q_{\min,i}}{\mu_\infty - m}) - \mu_\infty(\frac{\mu_\infty Q_{\min,i}}{\mu_\infty - m} - Q_{\min,i})(Q_{\max,i} - Q_{\min,i}))^2}$$

$$\therefore \frac{\partial R_i^*}{\partial Q_{\max,i}} < 0$$

$$\frac{\partial R_i^*}{\partial Q_{\min,i}} = \frac{\mu_\infty K_i m V_{\max,i}(\mu_\infty(Q_{\max,i}^2 - Q_{\min,i}^2) - m Q_{\max,i}(2Q_{\min,i} - Q_{\max,i}))}{(V_{\max,i}(Q_{\max,i} - \frac{\mu_\infty Q_{\min,i}}{\mu_\infty - m}) - \mu_\infty(\frac{\mu_\infty Q_{\min,i}}{\mu_\infty - m} - Q_{\min,i})(Q_{\max,i} - Q_{\min,i}))^2}$$

$$\therefore \frac{\partial R_i^*}{\partial Q_{\min,i}} > 0$$

The capacity to hold more nutrients and the ability to tolerate lower internal nutrient concentrations both reduce *R** values. Overall, a species with high nutrient uptake rates, a high growth rate and high maximum internal nutrient concentrations combined with a low half-saturation constants, a low mortality rate and low minimum internal nutrient concentrations will be the best competitor for nutrients.

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Chapter 3

Life History Traits, Competition and Stoichiometry: A Spatial Model of Early Plant Primary Succession on Mount St. Helens

3.1 Introduction

The phenomenon of succession poses an important question to ecologists, which many have tried to answer over the years (Clements 1916, Gleason 1927, Odum 1969, Connell & Slayter 1977, Pickett et al. 1987, Walker & Chapin 1987, Walker & del Moral 2003). Can the total development of communities, including rates and trajectories, be predicted at scales relevant for ecosystem rehabilitation? This question spawned two schools of thought, with the holists (e.g. Clements 1916) believing that biotic mechanisms such as competition and facilitation dominate succession and make it deterministic while the reductionists (e.g. Gleason 1927) believed succession to be driven by abiotic mechanisms and therefore highly stochastic (Walker & del Moral 2003). The modern consensus is that no one group of mechanisms can explain the entirety of succession, though life history traits can be used to predict the pattern of succession (Chapin et al. 1994, Chapin et al. 2002, Walker & del Moral 2003). For example, the seed size of the dominant species progressively become larger as succession proceeds, resulting in a pattern of larger seeded species replacing smaller seeded species over time (Chapin et al. 2002).

In early primary succession, the key life history traits are seed dispersal ability, seed germination, vegetative growth and survival (Walker & del Moral 2003). Species with small, wind-dispersed seeds that can reach the bare substrate, germinate, grow rapidly and survive to reproduction should dominate early primary succession (Chapin et al. 1994, Chapin et al. 2002, Walker & del Moral 2003). However, species with small seeds have greater difficulty establishing on stressful primary successional sites than those with larger seeds (Wood & del Moral 1988, Wood & Morris 1990, del Moral & Bliss 1993, Wood & del Moral 2000). Furthermore, even if plants with small seeds do establish, they may have great difficulty producing seed sets due to nutrient limitation (Larcher 2003, Walker & del Moral 2003, Gill et al. 2006). Lastly, species interactions such as competition can help structure the composition of the community even in early primary successional sites, indicating that a focus on only life history traits may result in misleading predictions (Walker & del Moral 2003, Gill et al. 2006).

On the Pumice Plain of Mount St. Helens, the first colonizer was *Lupinus lepidus*, a small, prostrate nitrogen-fixing legume with large seeds and no obvious mechanisms for long-distance dispersal (del Moral 1983, Bishop 2002).

During the first few years of succession, large monocultures of *Lupinus* were established across the Pumice Plain and improved soil conditions within their colonies (Halvorson et al. 1991b, Halvorson & Smith 1995, Halvorson et al. 2005). The colonies were then invaded by herbivores and other colonizing plants such as *Hypochaeris radicata* and *Agrostis scabra*, which greatly reduced their dominance in the community (Bishop et al. 2005, del Moral & Rozzell 2005). The colonies are known to have differing species composition and could be in the midst of diverging in their successional trajectories with neighbouring sites on the Pumice Plain (del Moral & Rozell 2005, del Moral 2007, Titus 2008).

With knowledge of these mechanisms, other authors have made predictions about the possible trajectories and rates of succession on Mount St. Helens and other primary successional habitats (del Moral & Bliss 1993, Chapin et al. 1994, Walker & del Moral 2003, del Moral et al. 2005). However, these predictions are based on conceptual models and empirical work that have difficulties elucidating the relative importance of these mechanisms and how they may interact (Walker & del Moral 2003). To provide a better mechanistic understanding to succession, I have developed a mathematical model that includes life history traits, competition for limiting nutrients and ecosystem stoichiometry within a landscape.

By adding life history traits, the model becomes more biologically realistic compared to the model in Chapter 2. No longer is it assumed that plants act like algae, some green slime vegetatively growing across the Pumice Plain. Nor do the plants continuously lose biomass throughout the growing season at a constant rate and mortality is ever present. Finally, the landscape itself need no longer be a homogeneous pool of nutrients to be accessed and absorbed, but can have some heterogeneous features such as increased or decreased nitrogen and phosphorus supplies at different locations. However, the main reason for the addition of life history traits is to improve model predictions.

The key hypothesis driving this research is that competition for nutrients, plant stoichiometry and nutrient cycling can give key insights to the patterns and rates of primary succession. This hypothesis has been partially validated in Chapter 2 by the good qualitative agreements between field experiments and the model. However, the model made predictions that do not seem to hold, such as a lack of coexistence between *Hypochaeris* and *Agrostis* while they commonly co-occur (e.g. Gill et al. 2006). I hypothesize that the addition of life history traits such as seed dispersal, seed size and others to the basic competition model will allow for *Hypochaeris* and *Agrostis* to coexist in spite of local competitive effects. Such a result would fit well into current theory about colonizer/competitor tradeoffs, with *Agrostis* being the colonizer and *Hypochaeris* the competitor (Tilman 1994). While the original theory has been criticized (Amarasekare 2003), recent theoretical and empirical studies have supported the concept (Calcagno et al. 2006, Hunt & Bonsall 2009).

Another hypothesis, which is more specific to Mount St. Helens, is that herbivory affecting nitrogen-fixers should help increase the biomass of nitrogen-limited species by increasing the nutrient cycling rate (Bishop 2002). The previous model did not support this hypothesis (Chapter 2). It is likely that the assumption of continuous mortality, which is clearly violated by the actual life-cycles of perennial plants such as *Lupinus*, caused the discrepancy. It is therefore predicted that having discrete mortality events will give rise to the effect predicted by others (Bishop 2002).

Both of the specific hypotheses relevant to Mount St. Helens have been borne out in the model (Figures 3.7, 3.11 and 3.14). Competition is important at local scales and becomes more important as nutrient levels increase, but in poor nutrient conditions, poorer competitors with a better suite of life history traits will do better. Such traits include nutrient uptake and plant stoichiometry, validating the previous premise that nutrient limitation, nutrient cycling and stoichiometry matter in primary succession.

3.2 Model Development and Parameterization

In this section, I proceed to derive a spatial model that incorporates the major facets of the biology of the plant community on Mount St. Helens. The key elements include the growing season, which is modelled in a similar way as in Chapter 2, the reproduction of plants at the end of the growing season, mortality events in winter and seed germination and seedling establishment in the spring. Each of these elements includes life history traits that will determine aspects of the competitive ability of the plants and are therefore needed to capture the community dynamics. I follow the derivation by dealing with key assumptions being made within the model and how their validity (or lack thereof) can alter model output. Finally, the last section deals with the parameterization of the model from data.

3.2.1: Model Derivation

When considering the spatial and temporal properties of ecosystems and communities, it is important to choose a model that can appropriately describe the processes of interest (Durrett & Levin 1994). These processes may be continuous in time and space (e.g. nutrient diffusion), continuous in time and discrete in space (e.g. plant growth), continuous in space and discrete in time (e.g. seed reproduction and dispersal) or discrete in both time and space (e.g. plant mortality). Furthermore, the processes can be approximated with deterministic equations or can be described by stochastic models. The choice of model depends on what processes are most important for the problem at hand.

For this chapter, the problem is the spatial distribution of plants on Mount St. Helens over time. Since plants are discrete organisms in space and can form discrete populations, it makes sense to model them in discrete space. Therefore, the spatial structure of the landscape upon which the plants colonize will be a lattice of connected patches (Figure 3.1a). The connections between patches are maintained through the movement of nutrients (Figure 3.1b) and through the dispersal of seeds (Figure 3.1c). The size of each patch is $0.25m^2$, which is the standard unit for measuring plant cover on Mount St. Helens (e.g. del Moral & Bliss 1993). Such an area is large enough to enclose one large plant of all three species considered here, though in rare circumstances a *Lupinus* plant may be larger than $0.25m^2$ (Bishop 2002). The effect of changing patch size is a change in the size of adult plants, though the current patch size gives realistic values for adult plant size.

Some processes involving plants, such as vegetative growth and nutrient uptake, occur continuously throughout the growing season and can be modelled deterministically (Chapter 2). The production of seeds, seed dispersal, plant mortality, seed mortality and seed germination all take place within discrete time frames and can be highly variable (Titus & del Moral 1998, Braatne & Bliss 1999, Bishop 2002). These facts indicate that the growing season should be treated separately from the other events, which has been done in previous models (Fagan et al. 2005).

The general sequence of events for the processes considered here follows the following outline if one starts right after seedling emergence (Figure 3.2):

1. Continuous growing season (~100 days; Halvorson et al. 1992) with vegetative growth, nutrient diffusion and nutrient uptake.
2. Growing season ends. Plants that can reproduce do so. Seeds are dispersed across the landscape.
3. After reproduction, seedlings, adults and seeds suffer mortality from winter and/or herbivory.
4. Spring arrives and seeds germinate. Seedlings compete with one another to lay claim to the patch if it is unoccupied by any adult or by an adult from the same species. Only one seedling or one seedling of each species remains after competition. Enter growing season (event number 1).

The parameters governing the behaviour of the model may change over time and space, for life history traits like mortality and landscape features such as nitrogen levels can vary widely over time and/or space (e.g. Bishop 2002, Titus 2008). In general, I limit changes over time to the scale of one full year or an iteration of the four events listed above. This limitation is in order to ignore seasonality within the growing season, as the other events only occur once each year and therefore can only be changed once each year. Differences between patches are set for the entire time period the model is run, in order to clearly see if those differences can alter patterns seen when no spatial heterogeneity is predetermined.

Each run of the model consists of thirty time iterations, which is the equivalent to thirty years. When considering community dynamics, the initial condition is a single *Lupinus* adult positioned at the centre of the lattice, which corresponds to the single individual found in 1981 on the Pumice Plain (Bishop 2002). The size of the lattice is normally 25 by 25 patches, which is 12.5m by 12.5m, though I did investigate different sizes of the lattice, which had little effect on the results. For each set of parameter values chosen, I run the model for at least 100 runs, unless otherwise indicated, in order to capture the variability inherent in the model. With these general model considerations addressed, I now turn to the specifics of how each event within this model is constructed.

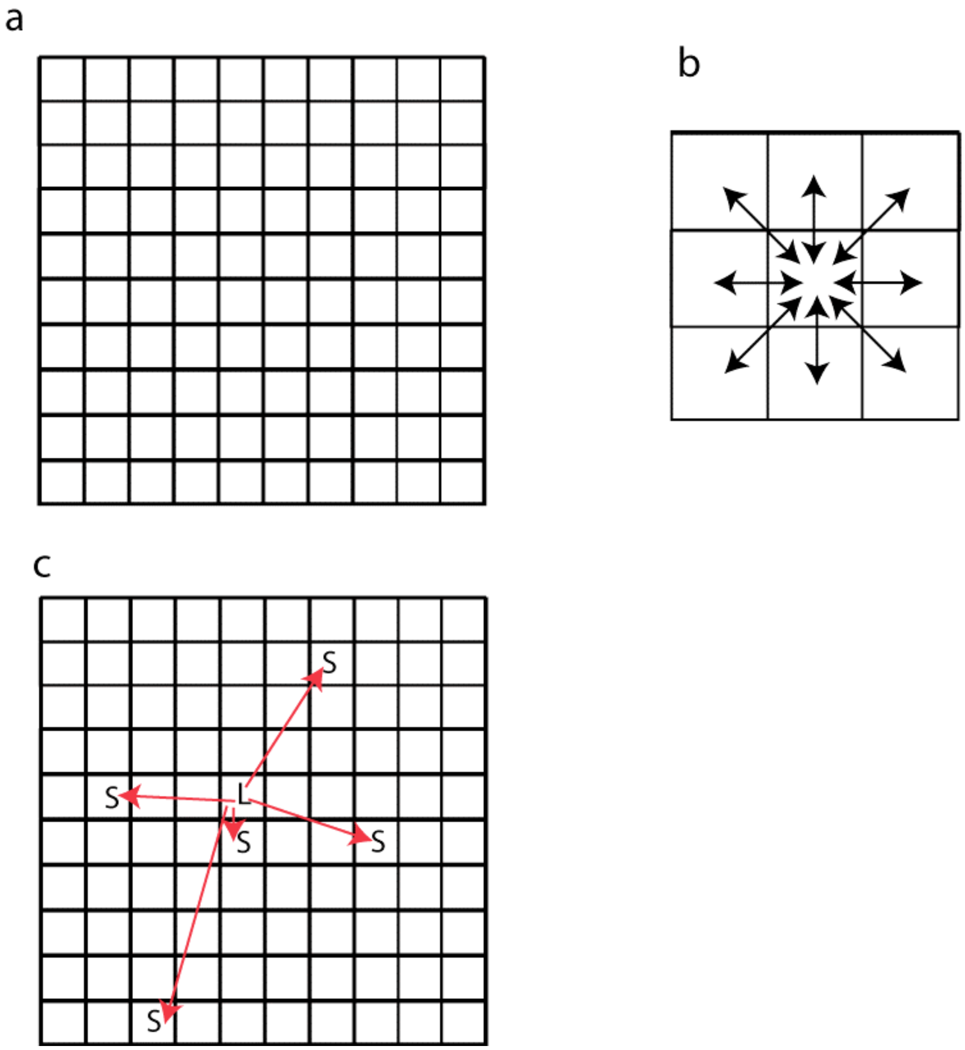

Figure 3.1: Spatial arrangement and connectivity of the model. **a** Patches form a square lattice and are connected through the dispersal of seeds and the movement of nutrients. **b** The connectivity due to the movement of nutrients occurs at a local scale with a maximum of eight neighbours (arrows between patches). **c** The connectivity due to the dispersal of seeds (red arrows, S) can be over long-distance and in any direction from the seed source (L).

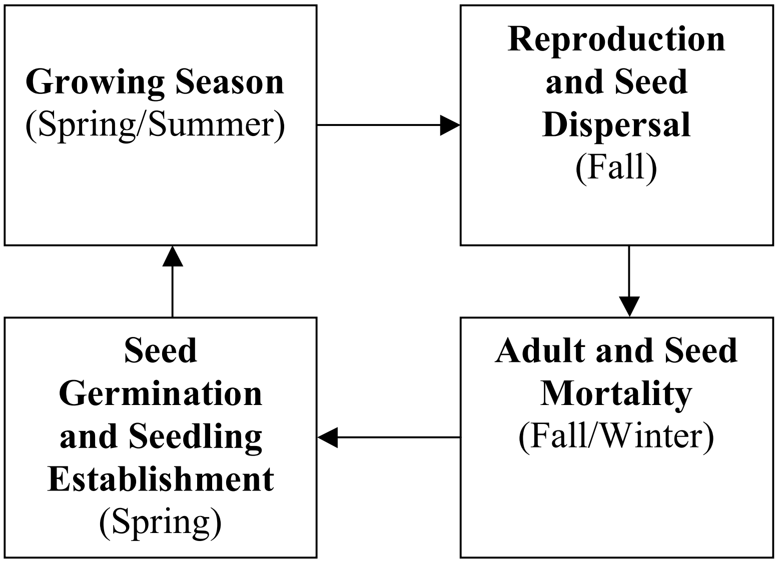

Figure 3.2: Sequence of events in the spatial model. The dynamics of the community during the growing season is determined by a modified version of the well-mixed model that allows for nutrients to be exchanged between spatial subdivisions. The rest of the events in the model occur outside the growing season.

3.2.1.1 *Growing Season*

The growing season (event 1) can be adequately described by coupled ordinary differential equations similar to those used in Chapter 2 (units of variables and parameters are listed in Table 3.1):

$$\underbrace{\frac{dR_{ik}}{dt}}_{\substack{\text{Rate of Change}\\ \text{of Nutrient i in}\\ \text{patch k}}} = \underbrace{I_{ik} - \phi_{ik} R_{ik}}_{\text{Supply without plants}} \underbrace{- \sum_{j=1}^{n} B_{jk} f_{ij}(R_{ik}, Q_{ijk})}_{\text{Plant uptake}} + \underbrace{\omega \delta_{ik} D_{ik} e^{-\delta_{ik} t}}_{\text{Supply from dead tissue mineralization}}$$

$$+ \underbrace{\frac{d_i}{g} \sum_{h}^{g} \left(R_{ih} - R_{ik} \right)}_{\text{Diffusion of nutrients between patches}}$$

$$\underbrace{\frac{dQ_{ijk}}{dt}}_{\substack{\text{Rate of Change of}\\ \text{Nutrient i in plant j}\\ \text{in patch k}}} = \underbrace{f_{ij}(R_{ik}, Q_{ijk})}_{\text{Concentration}} - \underbrace{\mu_j(Q_{1jk}, \ldots, Q_{ijk}, \ldots, Q_{mjk}) Q_{ijk}}_{\text{Dilution}} \tag{3.1}$$

$$\underbrace{\frac{dB_{jk}}{dt}}_{\substack{\text{Rate of Change of}\\ \text{Biomass of plant j in}\\ \text{patch k}}} = \underbrace{\left(\mu_j(Q_{1jk}, \ldots, Q_{ijk}, \ldots, Q_{mjk}) - l_j \right)}_{\text{Net vegetative growth rate}} B_{jk}$$

Where R_{ik} is the concentration of nutrient *i* in the soil solution of patch *k*, Q_{ijk} is the internal concentration of nutrient *i* in plant *j* in patch *k* and B_{jk} is the biomass of plant *j* in patch *k*. D_{ik} is the amount of nutrient *i* within dead plant tissue in patch *k* at the beginning of the growing season and therefore a constant. After the growing season, D_{ik} is updated to reflect the loss of nutrient *i* that occurred during the time period using the following formula:

$$D_{ik}(100) = D_{ik}(0) e^{-100\delta_{ik}} \tag{3.2}$$

In general, the supply of nutrients mostly comes from the mineralization of organic nutrients into inorganic nutrients that are readily available for plant uptake (Chapin et al. 2002). There are also contributions from atmospheric deposition, the weathering of rocks and other abiotic processes, but they are quickly turned into organic forms by soil microorganisms (e.g. Halvorson et al. 2005). Here I separate the mineralization of organic nutrients supplied by dead plant tissue from that supplied by other sources in order to better demonstrate the contributions of plants to the nutrient pool. The parameters associated with the supply of nutrients are the net mineralization rate of bare soil, I_{ik}, the turnover rate, ϕ_{ik} , and the rate of mineralization of the dead plant tissue for nutrient *i* in patch *k*. The other parameter, ω, is a conversion coefficient describing the water content of the soil.

Another way of describing the supply would be to assume that the supply of nutrients follows the total amount of nutrients within the soil (e.g. Tilman 1985). Therefore, the mineralization parameter I_{ik} would be a function of the total amount of nutrient *i* in patch *k*. If this assumption were true, then one would expect the mineralization rate and the pool of inorganic nitrogen to increase with increasing total nitrogen on Mount St. Helens.

Table 3.1: Definitions, units, values and sources of parameters used in the growing season component of the model
a) *Lupinus lepidus* physiological parameters

Parameters	Units	Value (Range)	Definition	Source
$V_{\max,NL}$	mol N/ (mol C x day)	7.05×10^{-4} (5.93-7.05×10^{-4})	Maximum uptake rate for nitrogen	Halvorson et al. 1992[a]
$V_{\max,PL}$	mol P/ (mol C x day)	2×10^{-3} (1.5-2×10^{-3})	Maximum uptake rate for phosphorus	Esteban et al. 2003[b]
K_{NL}	mol N/L	1.15×10^{-4} ($1.15 - 1.19 \times 10^{-4}$)	Half-saturation constant for nitrogen uptake	Dunabin et al. 2002[c]
K_{PL}	mol P/L	1.57×10^{-5} (1.57-1.67×10^{-5})	Half-saturation constant for phosphorus uptake	Esteban et al. 2003[b]
$Q_{\max,NL}$	mol N/mol C	0.04507	Maximum internal nitrogen concentration	Fagan et al. 2004
$Q_{\max,PL}$	mol P/mol C	0.00187	Maximum internal phosphorus concentration	Fagan et al. 2004
$Q_{\min,NL}$	mol N/mol C	0.02525	Minimum internal nitrogen concentration	Fagan et al. 2004
$Q_{\min,PL}$	mol P/mol C	0.000816	Minimum internal phosphorus concentration	Fagan et al. 2004
$\mu_{\infty,L}$	1/day	0.218	Theoretical maximum vegetative growth rate	Halvorson et al. 1991
l_L	1/day	0.005 (0.001-0.01)	Loss of carbon during growing season	Free Parameter

* Value used means that these values were used for all figures were simulations were used.

a Based on average nitrogen accumulation by *Lupinus lepidus* over whole growing season (hundred days).

b Data from *Lupinus albus*.

c Data from *Lupinus angustifolius and Lupinus pilosus*.

d Value based on 30% yearly mortality if no growth occurs.

Table 3.1 continued

b) *Hypochaeris radicata* physiological parameters

Parameters	Units	Value (Range)	Definition	Source
$V_{\max,NH}$	mol N/ (mol C x day)	0.1272 (0.0707-0.1272)	Maximum uptake rate for nitrogen	Van de Djik et al. 1982
$V_{\max,PH}$	mol P/ (mol C x day)	3.48 x 10^{-4}	Maximum uptake rate for phosphorus	Longeran & Asher 1967[a]
K_{NH}	mol N/L	7 x 10^{-6} (0.7 – 1.9 x 10^{-5})	Half-saturation constant for nitrogen uptake	Van de Djik et al. 1982
K_{PH}	mol P/L	7.312 x 10^{-7}	Half-saturation constant for phosphorus uptake	Longeran & Asher 1967[a]
$Q_{\max,NH}$	mol N/mol C	0.050934	Maximum internal nitrogen concentration	Fagan et al. unpublished data set
$Q_{\max,PH}$	mol P/mol C	0.001731	Maximum internal phosphorus concentration	Mamolos et al. 1995[b]
$Q_{\min,NH}$	mol N/mol C	0.011548	Minimum internal nitrogen concentration	Fagan et al. unpublished data set
$Q_{\min,PH}$	mol P/mol C	0.001079	Minimum internal phosphorus concentration	Mamolos et al. 1995[b]
$\mu_{\infty,H}$	1/day	0.3518 (0.2527-0.3518)	Theoretical maximum vegetative growth rate	Fenner 1978, Van de Djik et al. 1982
l_H	1/day	0.005 (0.001 – 0.01)	Loss of carbon during growing season	Free Parameter

a Data from *Hypochaeris glabra*. Parameters are derived from fitting using non-linear least squares.

b Assuming constant value for %C of 40.74.

Table 3.1 continued
c) *Agrostis Scabra* physiological parameters

Parameters	Units	Value (Range)	Definition	Source
$V_{\max,NA}$	mol N/ (mol C x day)	0.01834 (0.01605-0.01834)	Maximum uptake rate for nitrogen	Rachmilevitch et al. 2006
$V_{\max,PA}$	mol P/ (mol C x day)	1.87×10^{-3} (1.46-1.87×10^{-3})	Maximum uptake rate for phosphorus	Newberry et al. 1995[a]
K_{NA}	mol N/L	1.5×10^{-5} ($1.5 – 3.0 \times 10^{-5}$)	Half-saturation constant for nitrogen uptake	Barber 1995[b]
K_{PA}	mol P/L	3.7×10^{-6} ($1.47 – 3.7 \times 10^{-6}$)	Half-saturation constant for phosphorus uptake	Mouat 1983[c]
$Q_{\max,NA}$	mol N/mol C	0.03766	Maximum internal nitrogen concentration	Bishop et al. unpublished data set
$Q_{\max,PA}$	mol P/mol C	0.003296	Maximum internal phosphorus concentration	Newberry et al. 1995[a]
$Q_{\min,NA}$	mol N/mol C	0.004499	Minimum internal nitrogen concentration	Bishop et al. unpublished data set
$Q_{\min,PA}$	mol P/mol C	0.0004301	Minimum internal phosphorus concentration	Newberry et al. 1995[a]
$\mu_{\infty,A}$	1/day	0.140 (0.120-0.140)	Theoretical maximum vegetative growth rate	Rachmilevitch et al. 2006
l_A	1/day	0.005 (0.001 – 0.01)	Loss of carbon during growing season	None

a Data from *Agrostis capillaris*.
b Data from non-*Agrostis* grass species such as *Fescue*.
c Data from *Agrostis tenuis*.

Table 3.1 continued

d) Nutrient dynamics parameters

Parameters	Units	Value (Range)	Definition	Source
I_N	mol N/(L x day)	-- (1.01 x 10^{-6}-2.55 x 10^{-4}) x ω	Influx of plant available nitrogen without plants	Halvorson & Smith 2009, Gill et al. 2006[a]
I_P	mol P/(L x day)	-- (0.25-2.17 x 10^{-4}) x ω	Influx of plant available phosphorus without plants	Halvorson & Smith 2009, Fagan et al. 2004[b]
ϕ_N	1/day	1 (0.1-5)	Efflux of plant available nitrogen without plants	Free Parameter
ϕ_P	1/day	-- (1-5)	Efflux of plant available phosphorus without plants	Free Parameter
d_N	1/day	0.1 (6.06-34.6 x 10^{-7})	Diffusion rate constant of nitrogen	Raynaud & Leadley 2004[c]
d_P	1/day	0.01 (4.8 -106 x10^{-9})	Diffusion rate constant of phosphorus	Raynaud & Leadley 2004[c]
ω	1/L	0.2667 (0.2-2)	Reciprocal of soil water content	Titus 2008

a Ranges of values found on Mount St. Helens in two different studies done in 2002 and 2005.
b Ranges of values found on Mount St. Helens in two different studies done in 2000 and 2005.
c Value used is much greater than the actual ranges of diffusion to show lack of importance of diffusion between patches. Ranges calculated using formula 3 of Raynaud & Leadley (2004) assuming a distance of 0.5m between centres of patches.

Table 3.1: continued
e) Detritus dynamics parameters

Parameters	Units	Value (Range)	Definition	Source
ζ_{NL}	--	0.2 (0-0.99)	Proportion of nitrogen recycled from dead *Lupinus*	Free Parameter
ζ_{PL}	--	0.1 (0-0.99)	Proportion of phosphorus recycled from dead *Lupinus*	Free Parameter
ζ_{NH}	--	0.1 (0-0.99)	Proportion of recycled from dead *Hypochaeris*	Free Parameter
ζ_{PH}	--	0.1 (0-0.99)	Proportion of phosphorus recycled from dead *Hypochaeris*	Free Parameter
ζ_{NA}	--	0.1 (0-0.99)	Proportion of nitrogen recycled from dead *Agrostis*	Free Parameter
ζ_{PA}	--	0.1 (0-0.99)	Proportion of phosphorus recycled from dead *Agrostis*	Free Parameter
δ_N	1/day	0.0035	Mineralization rate of nitrogen from dead plant material	Free Parameter
δ_P	1/day	0.0035	Mineralization rate of phosphorus from dead plant material	Free Parameter

Experimental work has shown that the mineralization rate has fluctuated widely while total nitrogen soil has increased and levels of inorganic nitrogen have remained constant for nearly twenty years, though little is known about why this is occurring (Halvorson et al. 2005, Halvorson & Smith 2009). For example, bare soil on Mount St. Helens seems to have stopped accumulating nitrogen since 1997, yet the net mineralization of the soil has increased (Halvorson & Smith 2009). The lack of an unambiguous relationship between total nitrogen and net nitrogen mineralization prevents describing the nitrogen supply in this fashion.

A potential source or sink for nutrients comes from the diffusion of nutrients between patches. Amount of nutrients entering or leaving a patch through diffusion is determined by the difference of nutrient concentration between patch *k* and patches *h* as well as the diffusion rate constant d_i. The parameter denoted by *g* indicates the size of the neighbourhood of patch *k*. The last component of nutrient dynamics is the uptake of nutrient *i* by all the plants found in patch *k*. The functions describing the uptake of nutrients by plants all have the following form:

$$f_{ij}(R_{ik}, Q_{ijk}) = \frac{V_{\max,ij} R_{ik}}{K_{ij} + R_{ik}} \frac{Q_{\max,ij} - Q_{ijk}}{Q_{\max,ij} - Q_{\min,ij}} \qquad \textbf{(3.3)}$$

Where $V_{\max,ij}$ is the maximum uptake rate, K_{ij} is the half-saturation constant of uptake, $Q_{\max,ij}$ is the maximum internal concentration and $Q_{\min,ij}$ is the minimum internal concentration of nutrient *i* for plant *j*. Biologically, the function means that plants uptake more nutrients in environments with high nutrient levels and when they are impoverished in that nutrient. The nutrients that enter the plant through uptake serve to increase the concentration of that nutrient within the plant while plant growth serves to dilute it (Eq. 3.1). The gross growth functions of all the plants obey Liebig's Law of the Minimum and are described by:

$$\mu_j \left(Q_{1jk}, \ldots, Q_{ijk}, \ldots, Q_{mjk}\right) = \mu_{\infty,j} \min\left(1 - \frac{Q_{\min,1j}}{Q_{1jk}}, \ldots, 1 - \frac{Q_{\min,ij}}{Q_{ijk}}, \ldots, 1 - \frac{Q_{\min,mj}}{Q_{mjk}}\right) \qquad \textbf{(3.4)}$$

Where $\mu_{\infty,j}$ is the theoretical maximum growth rate of plant *j* at infinite internal nutrient concentration and the 'min' within the equation represents the minimum function, i.e. the minimum value within the brackets is always used. The above function indicates that the least abundant nutrient within the plant will control the gross growth rate. The final parameter of note within Eq. 3.1 is l_j, which is the rate at which biomass is lost during the growing season. This rate is used as a proxy for the costs of respiration, root exudates and other losses of biomass encountered by the plant.

Based on the knowledge gleamed from Chapter 2 on which nutrients are limiting for which species on Mount St. Helens, it is possible to reduce the complexity of the model by making a few assumptions. I will assume that phosphorus is always limiting for *Lupinus* and nitrogen is always limiting for *Hypochaeris* and *Agrostis*. I will also assume that the internal nutrient concentration of the non-limiting nutrient will be at the equilibrium value predicted for the parameter values chosen. These assumptions have little to no effect on model output and are made to reduce computing time.

Furthermore, when the assumption that only one plant can grow in a particular patch at a time, then the dynamics of patch *k* simplify greatly:

$$
\begin{aligned}
\underbrace{\frac{dR_k^{\lim}}{dt}}_{\substack{\text{Rate of Change in}\\ \text{the Limiting Nutrient in}\\ \text{Patch k}}} &= I_k^{\lim} - \phi_k^{\lim} R_k^{\lim} - f_k^{\lim}(R_k^{\lim}, Q_k^{\lim})B_k + \omega\delta_k^{\lim} D_k^{\lim} e^{-\delta_k^{\lim} t} \\
&+ \frac{d^{\lim}}{g}\sum_{h}^{g}\left(R_h^{\lim} - R_k^{\lim}\right) \\
\underbrace{\frac{dR_k^{non}}{dt}}_{\substack{\text{Rate of Change in}\\ \text{the Non-Limiting Nutrient in}\\ \text{Patch k}}} &= I_k^{non} - \phi_k^{non} R_k^{non} - f_k^{non}(R_k^{non}, Q_k^{non})B_k + \omega\delta_k^{non} D_k^{non} e^{-\delta_k^{non} t} \\
&+ \frac{d^{non}}{g}\sum_{h}^{g}\left(R_h^{non} - R_k^{non}\right) \\
\underbrace{\frac{dQ_k^{\lim}}{dt}}_{\substack{\text{Rate of Change in}\\ \text{the Limiting Nutrient in}\\ \text{in the Plant in Patch k}}} &= f_k^{\lim}(R_k^{\lim}, Q_k^{\lim}) - \mu_{\infty,k}(Q_k^{\lim} - Q_{\min,k}^{\lim}) \\
\underbrace{\frac{dB_k}{dt}}_{\substack{\text{Rate of Change in}\\ \text{Plant Biomass in Patch k}}} &= \left(\mu_{\infty,k}\left(1 - \frac{Q_{\min,k}^{\lim}}{Q_k^{\lim}}\right) - l_k\right)B_k
\end{aligned}
\tag{3.5}
$$

The dynamics of each patch can now be described with only four equations, rather than the eight needed if one plant of each species can grow within a patch at a time. Nonetheless, both approaches (one plant per patch and one plant per species per patch) will be explored within the modelling framework derived here.

The next three sections are concerned with life history traits of the three plant species under study here. The parameters and units for all life-history characteristics, including dispersal kernels, are listed in Table 3.2. The values for each species are listed in Table 3.3.

3.2.1.2 *Reproduction and Seed Dispersal*

When the growing season ends, the plants enter their reproductive phase (event 2). At this point, the plant has two options: utilize some of the biomass accumulated during the growing season to create reproductive structures and seeds or keep the biomass accumulated and have no reproduction. The option chosen will depend on the size of the plant, which is known as a critical flowering size (Werner 1975). Plants below the threshold do not reproduce while those above it do so. Each species may have its own threshold for flowering and the parameter describing the critical flowering size is denoted as c_{min}.

If a particular plant does have more biomass than the threshold, then the plant will invest a fixed amount of its biomass into reproductive structures, which is denoted by r_a. From the fixed amount allocated to reproductive structures, a certain amount will be allocated to seeds and s_a denotes this value. For example, a plant with biomass 1 mol C might allocate 40% of its biomass to reproduction and 10% of that to seeds. This plant would therefore allocate 4% of its biomass or 0.04 mol C to seed production.

Table 3.2: Parameters used to describe life-history characteristics of the plant species on Mount St. Helens

Symbol	Meaning	Units
m	Non-size dependent probability of mortality	Dimensionless
m_{size}	Size dependent probability of mortality	Dimensionless
c_{size}	Reciprocal of the size needed to halve m_{size}	1/mol C
s_{size}	Seed size	mol C
c_{min}	Minimum plant biomass for reproduction	mol C
s_m	Probability a seed dies during the non-growing season	Dimensionless
s_{g}	Probability a seed germinates	Dimensionless
r_{a}	Proportion of biomass allocated to reproduction	Dimensionless
s_a	Proportion of reproduction biomass allocated to seeds	Dimensionless
b_j	Mean dispersal distance of a seed of species j according to a Laplacian dispersal kernel	Meters
v_H	Location parameter for the Wald dispersal kernel	Meters
λ_H	Scale parameter for the Wald dispersal kernel	Meters

Table 3.3: Life-history parameters for *Agrostis*, *Hypochaeris* and *Lupinus*

a) *Agrostis*

Parameter	Value (Range)	Source
m	0.25 (0.1-0.7)	Free Parameter
m_{size}	0.288 (0.2-0.5)	Free Parameter
c_{size}	10000 (10-10000)	Free Parameter
s_{size}	1.97×10^{-6}	Tsuyuzaki & Miyoshi 2008
c_{min}	0.0683	Free Parameter
s_m	0.5 (0.5-0.99)	Free Parameter[a]
s_g	0.32 (0.32-0.99)	Smyth 1997, Tsuyuzaki & Miyoshi 2008[b]
r_{a}	0.1 (0.1-0.4)	Tilman & Wedin 1991
s_a	0.123 (0.123-0.25)	Rabinowitz & Rapp 1979, Tilman & Wedin 1991
b_{A1}	0.46	Rabinowitz & Rapp 1979
b_{A2}	2.23	Rabinowitz & Rapp 1979

a There is evidence that smaller seeds persist longer, hence the high upper-end of the range (Bekker et al. 1998). In addition, *Agrostis scabra* forms persistent seed banks, which indicates high seed survival year over year (Titus 2008).

b Germination data from two different primary successional sites, with one averaging 32% germination and the other 99%.

b) *Hypochaeris*

Parameter	Value (Range)	Source
m	0.25 (0.042-0.760)	Tsuyuzaki et al. 1997, Becker et al. 2008[a]
m_{size}	0.288 (0.2-0.5)	Free Parameter
c_{size}	10000 (10-10000)	Free Parameter
s_{size}	2.46×10^{-5}	Tsuyuzaki et al. 1997
c_{min}	0.1166 (0.0683-0.1166)	Doi et al. 2006[b]
s_m	0.99 (0.894-0.994)	Roberts 1986, Titus & del Moral 1998[c]
s_g	0.86 (0.647-0.928)	Tsuyuzaki et al. 1997
r_a	0.4 (0.359-0.506)	Doi et al. 2006
s_a	0.1 (0.1-0.14)	Doi et al. 2006
v_H	3.18	Katul et al. 2005
λ_H	3.31	Katul et al. 2005

a Data from locations other than Mount St. Helens is used to provide the full range of values due to a lack of survival analysis for *Hypochaeris*

b Value based on the cover-biomass relationship in Eq. 3.12. The bottom value of the range is used as a null case to see what happens if there was no difference in critical flowering sizes between species.

c Number of seeds surviving based on number of seedlings establishing per 100 seeds sown, since *Hypochaeris* seeds rarely survive more than a year or two.

Table 3.3 continued
c) *Lupinus*

Parameter	Value (Range)	Source
m	0.25 (0.1-0.95)	Braatne & Bliss 1999, Bishop 2002
m_{size}	0.288 (0.2-0.5)	J. Bishop (unpublished data)
c_{size}	10000 (10-10000)	J. Bishop (unpublished data)
s_{size}	1.66×10^{-4}	Halvorson et al. 1991
c_{min}	0.0431 (0.0431-0.0683)	Bishop 1996[a]
s_m	0.78 (0.64-0.92)	Bishop 1996
s_g	0.77 (0.74-0.80)	Bishop 1996
r_{a}	0.18 (0.18-0.26)	Pitelka 1977[b]
s_a	0.27	Pitelka 1977[b]
b_L	2.857	Fagan & Bishop 2000

a Value based on the cover-biomass relationship in Eq. 3.12. The bottom value of the range is used as a null case to see what happens if there was no difference in critical flowering sizes between species.
b Value from *Lupinus variicolor*, a perennial lupine of similar size.

The amount of seeds produced will be the amount of biomass allocated to seed production divided by the amount of biomass required to make a seed, which is denoted by s_{size}. Continuing the above example, if an individual seed weighs 0.001 mol C, then the plant will produce 40 seeds. In addition, there is a fixed amount of the most limiting nutrient for the particular plant within the seeds. This amount is assumed to be higher than that found inside a plant at steady state, such that nutrients need to be transferred from the reproductive tissues to the seeds. This transfer reduces the amount of nutrient inside the reproductive tissues, which are lost to the plant after seed production and enter the detritus.

After the seeds are produced, they must disperse across the landscape according to each species *dispersal kernel*. The dispersal (or redistribution) kernel is a probability density function that describes the dispersal of a population (Neubert et al. 1995). In my case, the dispersal kernel describes the dispersal of the seeds of an individual plant. Each species has its own particular dispersal mechanisms and these mechanisms are factored into the kernels.

The seeds of *Lupinus lepidus* are explosively dehisced and travel fairly short-distances (Bishop 2002). While long-distance dispersal events for *Lupinus* do occur, they are fairly uncommon and require other vectors like runoff due to snowmelts that are not modelled here (Bishop 2002). Others have already modelled *Lupinus* dispersal kernel in one-dimension and used a Laplace or 'double exponential' kernel (Fagan et al. 2005). The formula for the Laplace kernel in one-dimension for the dispersal of an individual seed is:

$$k(x-y)=\frac{1}{2b}\exp\left(-\frac{|x-y|}{b}\right) \tag{3.6}$$

Here, x is the position from the seed source if one treats the seed source as being at position y, $k(x\text{-}y)$ is the probability of the seed being at position x after dispersal and b is the mean seed dispersal distance. For two-dimensions, there is no simple extension of the Laplace kernel (it would be a modified zero-order Bessel function of the first kind; Lewis et al. 2006). Therefore, I model dispersal by using the exponential distribution to generate distances and a uniform distribution from 0 to 2π to pick the direction of the seed travels. The exponential distribution for generating a distance x for a *Lupinus* seed is:

$$k_L(x)=\frac{1}{b_L}\exp\left(-\frac{x}{b_L}\right), x\geq 0 \tag{3.7}$$

Here, $k_L(x)$ is the probability that a *Lupinus* seed travels a distance x and b_L is the mean seed dispersal distance of *Lupinus*. To make use of the distance travelled by the seed and the angle taken from the source for finding the new position of the seed on the lattice, I take the radial coordinates x (the distance) and θ (the angle) and transform them into Cartesian coordinates with $x_1=x\sin(\theta)$ and $x_2=x\cos(\theta)$. The new coordinates of the seed, if the seed was at position (y_1,y_2) before dispersal, would be (x_1+y_1,x_2+y_2).

The dispersal kernel for *Agrostis scabra* seeds is more complicated than that for *Lupinus* due to two modes of dispersal. The first mode is a short-distance dispersal with seeds falling from the panicle while the second mode involves the panicle breaking off from the culm and rolling like tumbleweed over long-distances (Rabinowitz & Rupp 1979). Both dispersal modes can be adequately modelled by using the exponential distribution for distance and the uniform distribution for the angle taken as described in Eq. 3.7, but an additional modification is required:

$$\begin{aligned} k_A(x) &= pk_{A1}(x)+(1-p)k_{A2}(x) \\ &= p\frac{1}{b_{A1}}\exp\left(-\frac{x}{b_{A1}}\right)+(1-p)\frac{1}{b_{A2}}\exp\left(-\frac{x}{b_{A2}}\right) \end{aligned} \tag{3.8}$$

Here, p is a Bernoulli random variable that can takes on the value of 1 with probability q and the value of zero with probability $(1\text{-}q)$, k_{A1} is the short-distance dispersal kernel of *Agrostis*, k_{A2} is the long-distance dispersal kernel of *Agrostis* and b_{A1} and b_{A2} are the mean seed dispersal distances for short and long-distance dispersal, respectively. This means that each seed is randomly assigned one of the two kernels based on q, which is roughly equal to 0.46 for *Agrostis* (Rabinowitz & Rupp 1979).

The dispersal kernel for *Hypochaeris radicata* seeds has already been modelled by others (Katul et al. 2005). Since *Hypochaeris* seeds have plumes that allow for long-distance transportation by wind, the authors used the inverse Gaussian distribution or Wald distribution as it has a 'fat-tail', i.e. rare long-distance dispersal events can occur (Katul et al. 2005). However, they modelled only the distance that an individual seed travels, so the dispersal kernel is the probability of being distance *x* away from the seed release point:

$$k_H(x) = \left(\frac{\lambda_H}{2\pi x^3} \right)^{1/2} \exp\left(-\frac{\lambda_H (x - v_H)^2}{2 v_H^2 x} \right) \qquad \textbf{(3.9)}$$

Here, v_H is the location parameter and λ_H is the scale parameter of the Wald distribution for *Hypochaeris* and $k_H(x)$ is the probability of a *Hypochaeris* seed travelling a distance *x*. To make the two-dimensional dispersal kernel, I once again used the uniform distribution to obtain an angle for the direction travelled by the seed as I did for *Lupinus* and *Agrostis*.

For each species, the outputs from the continuous distributions are discretized by multiplying the position values by two and rounding them, since the length and width of each patch is 0.5m. This method has proved satisfactory in generating random locations for seeds within the lattice, though it may be possible to use discrete probability density distributions to achieve similar results (Chesson & Lee 2005).

In addition to local reproduction, there are seeds entering the lattice from the seed rain of the surrounding environment (Wood & del Moral 2000). Most of these seeds come from species with wind-dispersal such as *Hypochaeris*, though there are some seeds from grasses (Wood & del Moral 2000). The number of *Hypochaeris* and *Agrostis* seeds entering from the seed rain is modelled with a Poisson distribution with mean equal to 4 for *Hypochaeris* and 1 for *Agrostis*. The mathematical expression for the Poisson distribution is:

$$p(x) = \frac{\lambda^x}{x!} e^{-\lambda}, x = 0, 1, 2, \ldots, \quad \lambda > 0$$

Here, *x* would be the number of seeds deposited into the patch by the seed rain, $p(x)$ is the probability of that many seeds being deposited, the exclamation mark denotes that the number is a factorial and λ is the mean number of seeds deposited.

3.2.1.3 *Adult and Seed Mortality*

After the seeds are dispersed, the plants and their seeds are faced with mortality due to herbivores, seed predators and winter (event 3). Assuming that the death of a plant or a seed is a random event, I use Bernoulli random variables to describe the mortality events. The probability that an individual seed will die during this phase is denoted as s_m, which means the probability that an individual seed survives is 1-s_m, and differs for each species. The probability that an individual plant dies is based on the following function:

$$\Pr(\text{plant dies}) = m + \frac{m_{size}}{1 + c_{size}B} \qquad \textbf{(3.10)}$$

Here, m is the non-size dependent probability of a mortality event, m_{size} is the size dependent probability of a mortality event, c_{size} is the reciprocal of the plant size needed to halve m_{size} and B is the plant's biomass, with each species having its own values for each parameter. The use of a size-dependent mortality term is motivated by the fact that a plant needs to have roots established at least 15cm below the surface in order to survive drought conditions on Mount St. Helens (Braatne & Bliss 1999). Therefore, plants that are small will have increased risk of mortality. The large ranges of values for these terms in Table 3.3 is due to presence of highly stressful events such as droughts and attacks by herbivores (Braatne & Bliss 1999, Bishop 2002).

The nutrients of the dead seeds and plants enter into the detritus compartment according to the recycling parameters ζ_{ij}, which can differ between different species and different nutrients. These nutrients within the detritus are assumed to remain constant until the next growing season, when they are mineralized by the detrital community.

3.2.1.4 *Seed Germination and Seedling Establishment*

After winter, but before the growing season, seeds germinate and seedlings establish (event 4). An individual seed germinates according to a Bernoulli random variable with a probability s_{germ} of a successful germination, which can differ between species. Seeds that do not germinate enter the seed bank and may try again to germinate next year if they survive. The seedlings emerging from the seeds then have to establish within the patch. I have modelled seedling establishment in two ways, depending if only one plant can be in a patch at a time or if one plant of each species can be in a patch at a time.

In the first case, if an adult is present, all seedlings that have emerged lose in competition with the adult and die. The nutrients stored within them enter the detritus compartment in the same way dead seeds and dead adults do (section 3.2.1.3). If only the seedlings of one species emerge in the patch, then one seedling of that species establishes and the others die with their nutrients entering the detritus. If two species or three species have seedlings emerging in the patch, then there is competition between the seedlings. Independent of the type of competition, only a single seedling out of all that emerge in the patch will enter the growing season. The rest of the seedlings perish with their nutrients entering the detritus compartment.

The winner of competition is determined by a binomial (for two species) or a multinomial (for three species) random variable. The probability of one species winning can be symmetric (50% for two species or 33% for three species) or asymmetric. One possible way of implementing the asymmetry is having the probability of one species establishing be equal to the amount of seedling biomass of that species divided by the total biomass of all emerged seedlings. Such a formulation seems reasonable for Mount St. Helens since species with larger seeds are better at establishing than those with smaller seeds if the number of seeds is equal, but this can be counterbalanced by having many more seeds if they are smaller (Titus & del Moral 1998). I use both methods to see if different types of seedling competition alter the patterns of community composition.

In the second case, only if an adult of the same species is present do all the seedlings of the same species perish. Otherwise, one seedling of that species may establish, though it is dependent on the cover of the other two species within patch. The rest of the seedlings that do not establish die and have their nutrients enter the detritus. The probability of seedling of species *x* establishing can be described by the following equation:

$$\begin{aligned}&\Pr\left(\text{Seedling of Species } x \text{ Establishing}\right)=\\&1-(\text{Total Cover of all Species Other than } x)^{\text{Number of Emerged Seedlings}}\end{aligned} \qquad \mathbf{(3.11)}$$

This formulation accounts for the fact that adult plants can negatively impact the growth of seedlings and prevent them from surviving (Morris & Wood 1989). In addition, it also takes into account the multiple chances of at least one seedling out of many establishing somewhere in the patch if the patch does not already have 100% cover. It should be noted that it is possible to have more than 100% cover for a patch as plants can overlap (e.g. Table 1 of del Moral & Rozzell 2005). Cover for each species within the patch is proportional to the biomass of each species and the relationships for each are (data from unpublished data set of Schoenfelder et al.):

$$Lup_{\text{cov}} = 0.467B_L,\ Hyp_{\text{cov}} = 0.281B_H,\ Agr_{\text{cov}} = 0.534B_A \qquad \mathbf{(3.12)}$$

In this formulation, there is no competition between seedlings, only between seedlings and adults. A more complete version with competition between adults and seedlings would require a finer scale model than the one proposed here. However, this formulation is adequate to explore seed inhibition, which has been documented in the plant community (Morris & Wood 1989).

3.2.2 *Model Assumptions*

The model described in section 3.2.1 required certain assumptions within each event of the model in order to create succinct mathematical expressions for the various processes. This section helps clarify what was assumed and notes what justifications there are for making such assumptions. I begin with the assumptions for the spatial structuring of the model and continue in order for each of the events, starting with the growing season.

In making the landscape of Mount St. Helens a two-dimensional lattice, I made the following assumptions about its spatial characteristics:

1. There are no physical barriers that prevent seeds from entering a patch.
2. There are no physical barriers that prevent movement of nutrients between patches, which occurs through diffusion down the concentration gradient.
3. The landscape is flat, i.e. there is no slope which would create a gradient of nutrient flow or make seed dispersal non-isotropic.
4. The boundary condition for seed dispersal is absorbing, i.e. a seed dispersing beyond the boundary is lost.
5. The boundary condition for nutrient diffusion is reflecting, i.e. nutrients do not diffuse to outside of the lattice.

While it is true that physical barriers do exist on many locations of the landscape, a great deal of the Pumice Plain is barren with little to prevent the movement of seeds or nutrients (personal observations). Hence, the first two assumptions seem reasonable especially with the relatively small scales considered here.

The third assumption can approximate some locations on the Pumice Plain where there is little to no slope, but there are some differences in elevation between patches (Tsuyuzaki et al. 1997). However, these differences would be small at the scales considered here (Tsuyuzaki et al. 1997). Therefore, it is likely that this assumption is mildly violated in many locations on the Pumice Plain and should not cause great discrepancies in model outcomes.

Since the lattice is to represent a restricted spatial area of interest, any seeds that leave the area would not be followed and are therefore ignored. It is true that plants that would establish just outside of the area could contribute to the seed rain within the lattice, but then they need to be modelled just like those inside the lattice to know how much they would contribute. Therefore, I simply assume that the area outside of the lattice cannot be colonized and the seeds perish.

For the final assumption regarding spatial features, I once again assume the boundary conditions in order to ignore what is occurring outside of the lattice. Reflecting boundary conditions make more sense than absorbing boundary conditions since it is likely that the areas near the edge patches can have similar nutrient levels.

With regards to the growing season, the following assumptions were made:

1. Plants can only obtain nutrients from the soil solution in inorganic forms.
2. The nutrients within the soil solution in a patch are considered to be well-mixed, i.e. the plant available nutrient concentrations are identical everywhere in the area considered.

3. Nutrients within the soil are primarily located in the first ten centimetres of the soil.
4. Nutrients move between patches only through diffusion.
5. The amount of water within the soil remains constant over time.
6. Plants have a fixed shoot:root ratio in terms of allocation of biomass.
7. Plants have a constant percentage of carbon within plant biomass.
8. Plants have fixed nutrient uptake parameters.
9. Plants grow vegetatively and sexual reproduction is ignored.
10. The detrital community converts the nutrients in dead plant material into plant available nutrients at a constant rate that is proportional to the total amount of dead plant material.
11. Plants compete through the reduction of belowground resources.
12. Plants from one patch do not send biomass into surrounding patches vegetatively.

The justification for most these assumptions are listed elsewhere (section 2.2.2 of thesis). One assumption not dealt with there is that nutrients move only diffusively. This assumption is true for phosphorus, though it is not for nitrogen as mass flow due to water uptake of plants could result in greater movement of nitrogen in the soil (Barber 1995, though see Chapin et al. 2002). However, the form of nitrogen most commonly found on Mount St. Helens is ammonium, which does not move in water as readily as nitrate (Anghinoni & Barber 1990). Therefore, it may be reasonable to only look at diffusion of nutrients between patches. In any case, increasing the diffusion coefficient between patches can approximate the additional effects of mass flow.

Another new assumption needed for the growing season is that plants do not spread vegetatively into other patches, particularly their roots. Since patch size was chosen to be able to contain a large adult plant of any of the species and since most individuals will never reach such a size, it is likely that this assumption would hold if individuals were always located at the centre of patches. Furthermore, the use of well-mixed patches does not amend itself easily to showing overlap in rooting zones, though it can be done (Raynaud & Leadley 2004). If one wanted to follow overlap of roots as plants grow, it would be better to use individual-based models (IBMs) than the model presented here. IBMs were not used here for any such model would be very complex in two dimensional space and ecological stoichiometry.

Only a few assumptions were made for the reproduction of plants and the dispersal of their seeds. The key assumptions for these processes are:

1. The amount of biomass allocated to reproduction and to seeds is fixed.
2. Plants must reproduce if they are larger than the critical size.
3. Plants can transfer enough nutrients from reproductive tissues to seeds to make only biomass the limiting factor for seed production.

The first assumption is used to eliminate the need for a random variable to describe the allocation of biomass, which can be somewhat variable as seen in the values of the constants for *Agrostis* and *Hypochaeris* (Table 3.3b,c). However, the large differences in *Agrostis* are due to very high amounts of nitrogen, which seemed to alter the biomass partitioning of the plant (Tilman & Wedin 1991). Otherwise, the values for allocation do not vary tremendously.

The second assumption is not correct, as plants larger than the critical size may not reproduce at all (Doi et al. 2006). This simplification is made to reduce model complexity and to maximize the amount of reproduction occurring. The model could be adjusted to allow for plants to not reproduce, but more data on the proportion of plants beyond a certain size not reproducing would need to be gathered.

The third assumption helps eliminate the need to consider nutrient levels as well as biomass in determining the number of seeds produced. Since it is true that senescing tissues such as dying flowers can move up to 70% of some of its nutrients back into circulation within the plant (Chapin et al. 2002) and seeds represent such a small percentage of reproductive biomass of these species, it seems likely that the assumption is justified. However, since little is known about the mineral contents of *Agrostis* and *Hypochaeris* seeds, it may be that the senescing tissue would not provide enough nutrients and it would reduce seed production or result in aborted seeds. Still, imposing such a condition would be relatively simple for the model to accommodate.

There is a little to be said about the assumptions made for considering mortality of adult plants and seeds. It is known that mortality events are stochastic, can be made more frequent due to herbivory and other stressors and are influenced by the size of the plants (Bishop 1996, Braatne & Bliss 1999, Bishop 2002). Since the exact functional form of size dependent mortality is not known, I have assumed the relationship in Eq. 3.10 for simplicity.

For seed germination and seedling establishment, the assumption that only one or three plants can establish in a patch needs addressing. It is, of course, not true that only one seedling or adult can establish in a patch. However, in order to model the situation correctly, there would need to be two additional ordinary differential equations for each seedling establishing in the patch, which would soon get out of hand. In order to make the model manageable in terms of analysis and simulation time, I made the above assumption.

3.2.3 *Model Parameterization*

The majority of the parameters estimates listed in Tables 3.1 and 3.3 were obtained from point estimates in the literature or from field data with the sources for particular estimates listed. Since many of the parameter estimates could only be derived from graphs, I used both ImageJ and Adobe Professional's measuring utility to obtain values. Only for a few values were any statistical techniques needed to obtain parameter values or to determine an appropriate functional form. Any estimates requiring such methods in Table 3.1 is listed elsewhere (section 2.2.3).

For the long-distance dispersal kernel of *Agrostis*, I used Matlab's distribution fitting toolbox in order to see which distribution best suited the data found in Rabinowitz & Rapp (1979). I tried numerous distributions including the exponential, gamma, Wald and lognormal distributions and compared their fit using the corrected Akaikie Information Criteria or AICc (de Vries et al. 2006). The AICc indicated that while Wald distribution was the best fitting distribution, the differences were small. I decided to use the exponential distribution since it has only one parameter and its quality of fit was similar to the Wald.

For the functions describing the relationships between plant biomass and plant cover, I fitted a linear regression through the origin to the data set of Schoenfelder et al. (unpublished) after transforming the data into moles of C for the entire plant from grams of aboveground biomass using the assumptions found in Appendix 2.B of my thesis. The quality of fit based on R^2 ranged from 0.3275 to 0.5652.

For the estimation of the size-based mortality parameters for *Lupinus*, I obtained a data set from J. Bishop (unpublished) and used non-linear least squares to determine the parameters. Only seedlings that are smaller than 5cm in diameter are used in the estimation, since the seedlings larger than that size exhibit a pronounced drop-off in survival. This drop-off may be due to size-dependent herbivory (J. Bishop, personal communication) and is not related to the mechanism proposed in Eq. 3.10. Therefore, it is appropriate to ignore the data for larger individuals if one wants to model non-biotic environmental stressors such as drought with Eq. 3.10.

All parameters that lack sufficient data are declared free parameters and I have explored ranges of values that have been suggested to me by biologists in the field or from other studies.

3.3 Results

The results of this chapter are divided into three major sections and one short section. The first section (3.3.1) investigates the importance of nutrient diffusion between patches and the distribution of individual plant species across the spatial domain if only that plant species were around. The second section (3.3.2) explores the formulation of the model where only one plant can occupy a patch at a time, which emphasizes seed dispersal ability and seedling competition. The third section (3.3.3) delves into the formulation of the model where one plant of each species can occupy the patch, which emphasizes local competition between plants and adult inhibition of seedlings. The fourth section (3.3.4) briefly touches upon the sensitivity of the model's outcomes when parameter values are altered within the ranges provided in Table 3.3.

3.3.1 *Nutrient Diffusion and Population Distribution*

A key question that occurs frequently in studies of terrestrial plant communities is the distance at which plants can affect one another in the competition for mineral nutrients (Huston & DeAngelis 1994, Raynaud &

Leadley 2004). For phosphorus, other studies have shown that competition can only occur over very small distances between plants, on the scale of a few millimetres (Cadwell et al. 1987, Barber 1995). However, these studies assume that nutrients move only through diffusion, while bulk movement of solutions in the soil may increase the effective distances of influence of plants (Huston & DeAngelis 1994). For this reason, I used very large diffusion rate constants (compared to those commonly observed, see Table 3.1d) to see if competition between plants in neighbouring patches would occur through the reduction of nutrient levels in the local patches by the plants.

The diffusion of nutrients between patches has nearly no effect on the growth of plants and competitive effects between plants in neighbouring plants are highly unlikely (Table 3.4). In the example in Table 3.4, eight Hypochaeris competitors in a 3x3 lattice surround an Agrostis plant with d_N set to 0.1. If competition was within the patch, *Agrostis* will eventually be excluded by *Hypochaeris* and is immediately impacted by its presence (Table 3.4). However, there is almost no difference between *Agrostis* growing with or without diffusion between patches (Table 3.4). Therefore, competition for nutrients can only occur within patches and not between them, which means the one plant per patch formulation of the model does not incorporate resource competition.

Table 3.4: Effects of nutrient diffusion and within patch competition on a single *Agrostis* plant with eight *Hypochaeris* neighbours or one *Hypochaeris* within the patch. Parameter values used to generate the results are listed in Appendix 3.A.

	Without Diffusion	With Diffusion	Percentage of Without Diffusion	With Competition	Percentage of Without Diffusion
Agrostis Biomass (mol C)	2.9429	2.9426	99.99	0.0110	0.44

The distributions of each plant species are dependent on the seed source, which is in turn dependent on the nutrient levels within the soil. For *Lupinus*, the seed source is solely dependent on the local population and the lupine population exhibits clustering of individuals around the first colonist of the patch (Figure 3.3). The lupine population can be maintained and can expand across the landscape despite the low levels of phosphorus used to generate Figure 3.3.

For *Hypochaeris* and *Agrostis*, the spatial distribution of plants remains random, as would be expected with random seed rain, until soil conditions improve to allow for local reproduction (Figure 3.4). While *Agrostis* is able to have reproductive adults at low nitrogen levels, *Hypochaeris* is not (Figure 3.4). Therefore, the reproductive status of the local populations, which is determined by both the nutrient levels and the individual species growth responses to those nutrient conditions, determines the spatial distribution of individuals.

Herbivory on *Lupinus* was modelled by increasing adult mortality from 0.25 to 0.50 and seed mortality from 0.78 to 0.97 in even years after the tenth year of the simulation for herbivory is cyclical and began in earnest ten years after initial colonization (Fagan & Bishop 2000, Bishop 2002). Herbivory results in a decrease in *Lupinus* cover (Figure 3.5). Average patch occupancy does drop during the years of herbivory, but quickly recovers the next year (Figure 3.5). The loss of cover is primarily due to adult mortality, while the patch occupancy drops due to seed mortality for the most part (Figure 3.5). Even with both effects, only with very high rates of herbivory was any contraction of the spatial extent of *Lupinus* obtained in the model (Figure 3.6).

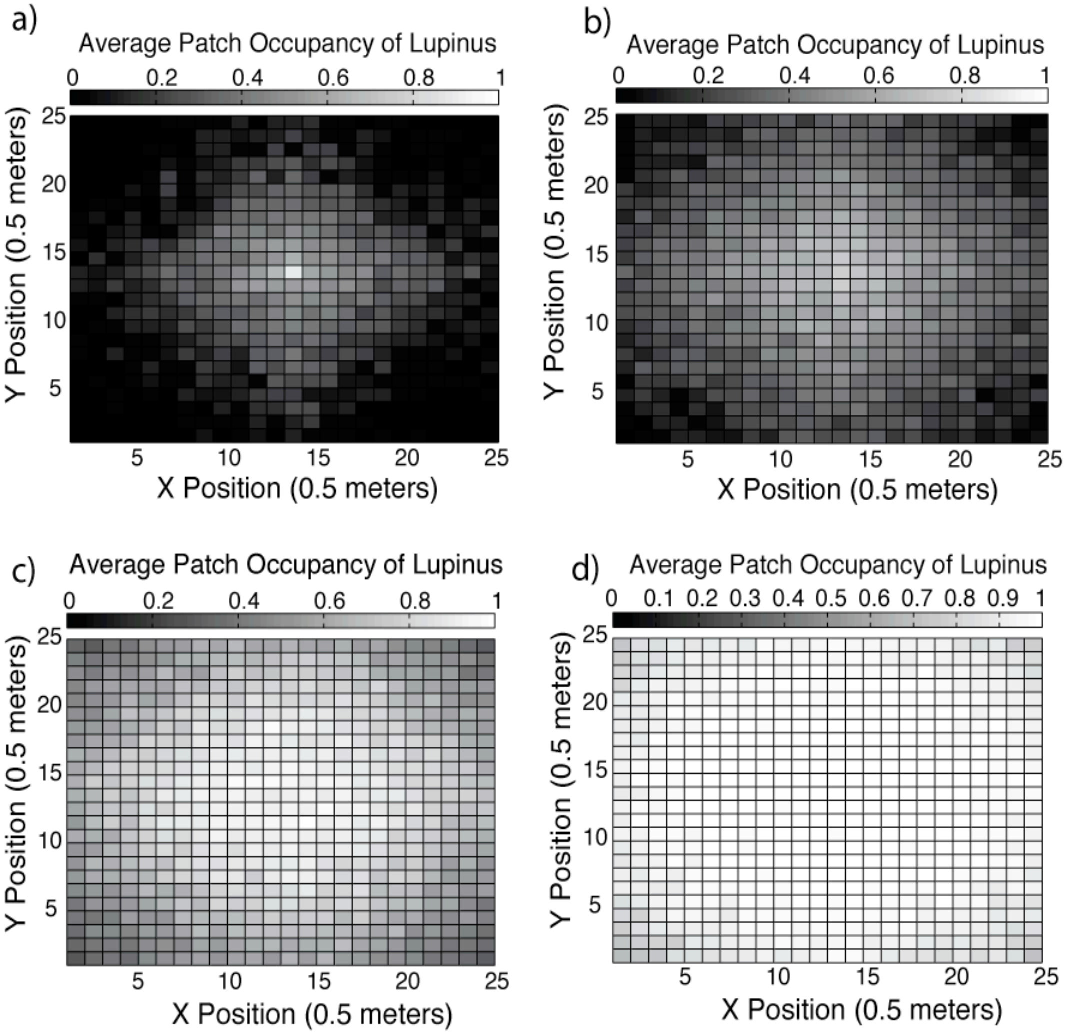

Figure 3.3: The spatial expansion of *Lupinus* from a single adult plant at position (13,13). Using the average patch occupancy for *Lupinus* for one hundred runs of the model, it can be seen that **a** at year two the population is mostly located around the adult plant and expands outward in **b** year four, **c** year six and **d** year eight. After year ten, a Lupinus plant always occupies each patch at the beginning of the growing season.

3.3.2 *One Plant per Patch: Patch Dynamics and Seedling Competition*

In this section, I used two formulations or models of how seedlings compete for patches and establish. In the first case, I assume that all three species have an equal chance of establishing if they have at least one germinated seed. I call this random seedling establishment and I define the model as the OPPRSE model (**O**ne **P**lant per **P**atch with **R**andom **S**eedling **E**stablishment). In the second case, I assume that the probability of establishment for each species is dependent on the total germinated seed weight of each species and of all species combined. I define this model as the OPPSEW model (**O**ne **P**lant per **P**atch with **S**eedling **E**stablishment by **W**eight). The OPPSEW model is likely the most realistic model of seedling competition (Titus & del Moral 1998).

The dynamics of patch occupation is highly dependent on the type of seedling competition used to determine which species will occupy the patch. With the OPPRSE model and low nitrogen, both *Agrostis* and *Lupinus* can maintain high levels of cover (Figure 3.7a). On the other hand, *Lupinus* dominates the biomass with the OPPSEW model and low nitrogen (Figure 3.7b). When nitrogen levels are higher, *Agrostis* biomass increases, though *Lupinus* remains an important contributor to total cover (Figure 3.7c,d). In all cases, *Hypochaeris* has difficulty establishing due to poor seed survival and accumulating less biomass than *Agrostis* at similar nitrogen levels (Figure 3.7).

Increasing *Hypochaeris* seed survival and decreasing *Agrostis* seed survival results in *Lupinus* performing poorly within the OPPRSE model and *Agrostis* performing poorly within the OPPSEW model (Figure 3.8). The poor performance by *Lupinus* in the OPPRSE model is due to a lower probability of occupying a patch, as both *Hypochaeris* and *Agrostis* seeds are likely to be present and low seed production per unit biomass than *Hypochaeris* and *Agrostis*. These two factors combine to greatly reduce *Lupinus*' ability to colonize patches. With the OPPSEW model, *Agrostis* does much worse since its seeds weigh very little and only a fraction survives at the lower seed survival probability.

The changes in cover for the plant species can be explained, in part, by changes in the number of individuals of that species on the lattice (Figure 3.9). The OPPRSE model allows for more *Agrostis* and *Hypochaeris* plants to be present in the lattice and results in higher cover levels for both than in the OPPSEW model (Figure 3.9). Nonetheless, increases in nitrogen levels also play an important role in increasing cover, especially for *Agrostis* (Figure 3.9). It also occurs that cover and number of plants may go in opposite directions due to greater seed competition and higher nutrient levels as time progresses (Figure 3.9c).

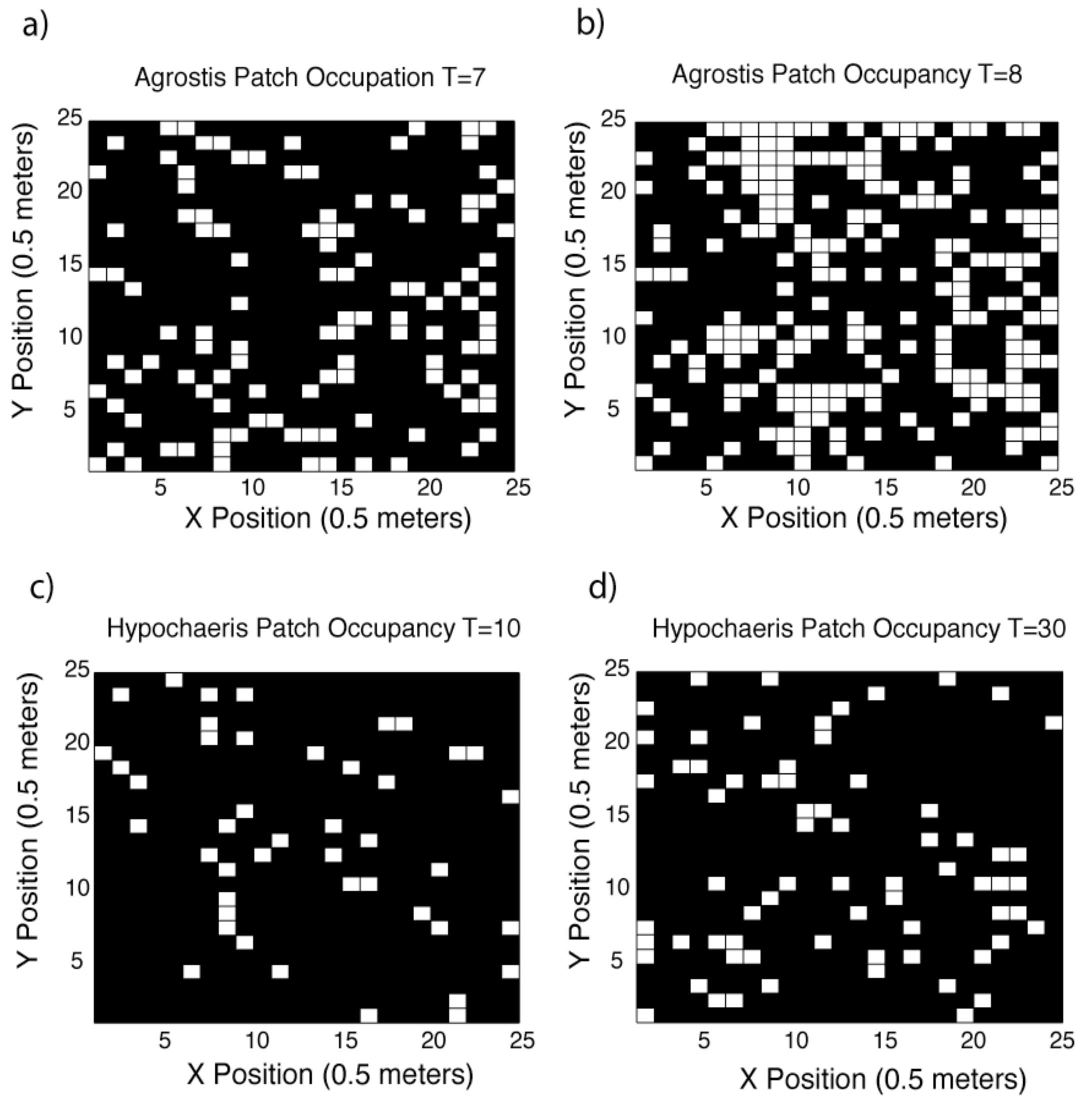

Figure 3.4: Spatial distributions of *Agrostis* and *Hypochaeris* for a single run of the model. Nitrogen increases from 1 x 10^{-7} mol N/L to 3 x 10^{-6} mol N/L by increments of 1 x 10^{-7} mol N/L per year for thirty years. **a** *Agrostis* plants are randomly distributed across the lattice at year seven (T=7) as up to that point no local reproduction occurs. **b** In year eight (T=8), local reproduction has occurred and clustering around reproductive individuals occurs. **c** and **d** No *Hypochaeris* reach reproductive maturity over the thirty-year period, resulting in randomly distributed individuals in the lattice.

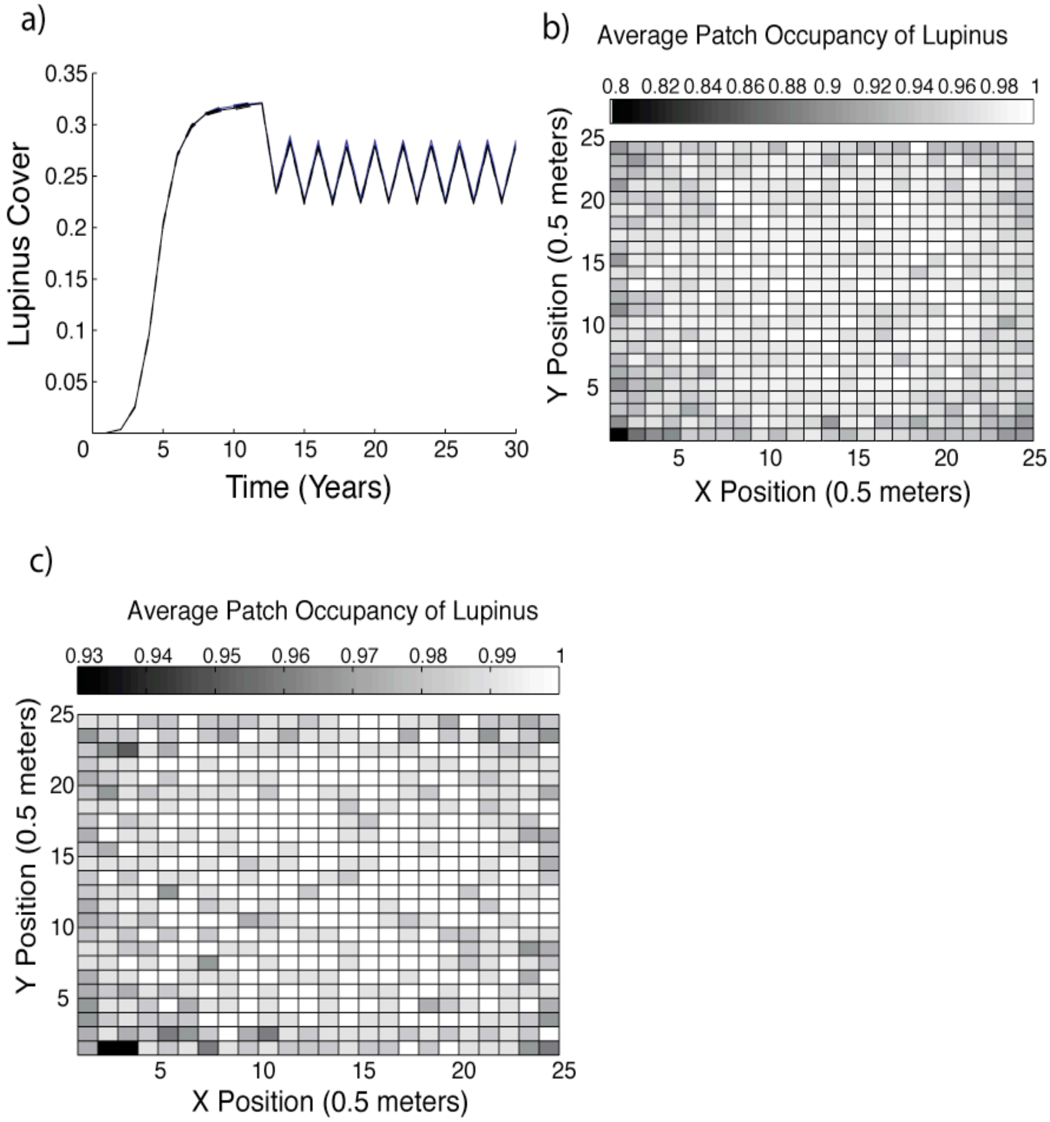

Figure 3.5: The effects of herbivory on *Lupinus*. **a** Herbivory results in the loss of cover by removing adults from the population. The black line, which comprises seed and adult mortality, is indistinguishable from the blue line, which is due solely to adult mortality. **b** Herbivory also reduces the average patch occupancy by *Lupinus* the year following herbivore attacks. Hence in the year above, year 29 of the simulation, patch occupancy is not total everywhere. **c** This reduction in patch occupancy is mostly due to seed herbivory, though adult mortality increases the effect as seen in **b**.

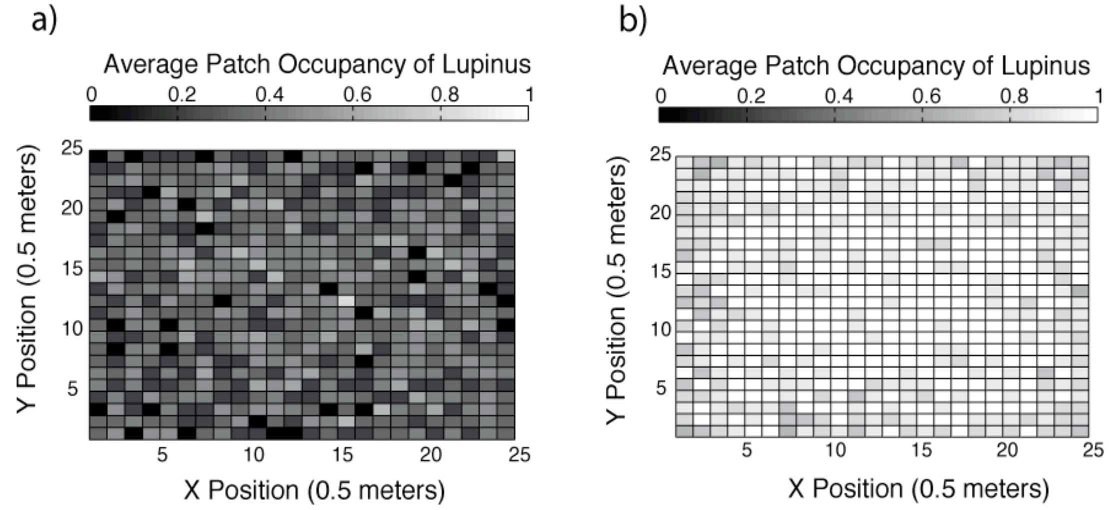

Figure 3.6: Permanent reduction in the extent of the *Lupinus* population due to herbivory. **a** In year 29 of the simulation, the average patch occupancy is very low due to the previous year's herbivory. **b** Though the population does recover in the subsequent year, it does not, on average, reoccupy all the patches as it would at lower herbivory levels. Herbivores are therefore reducing the spatial extent of *Lupinus* even in years when herbivory is not present.

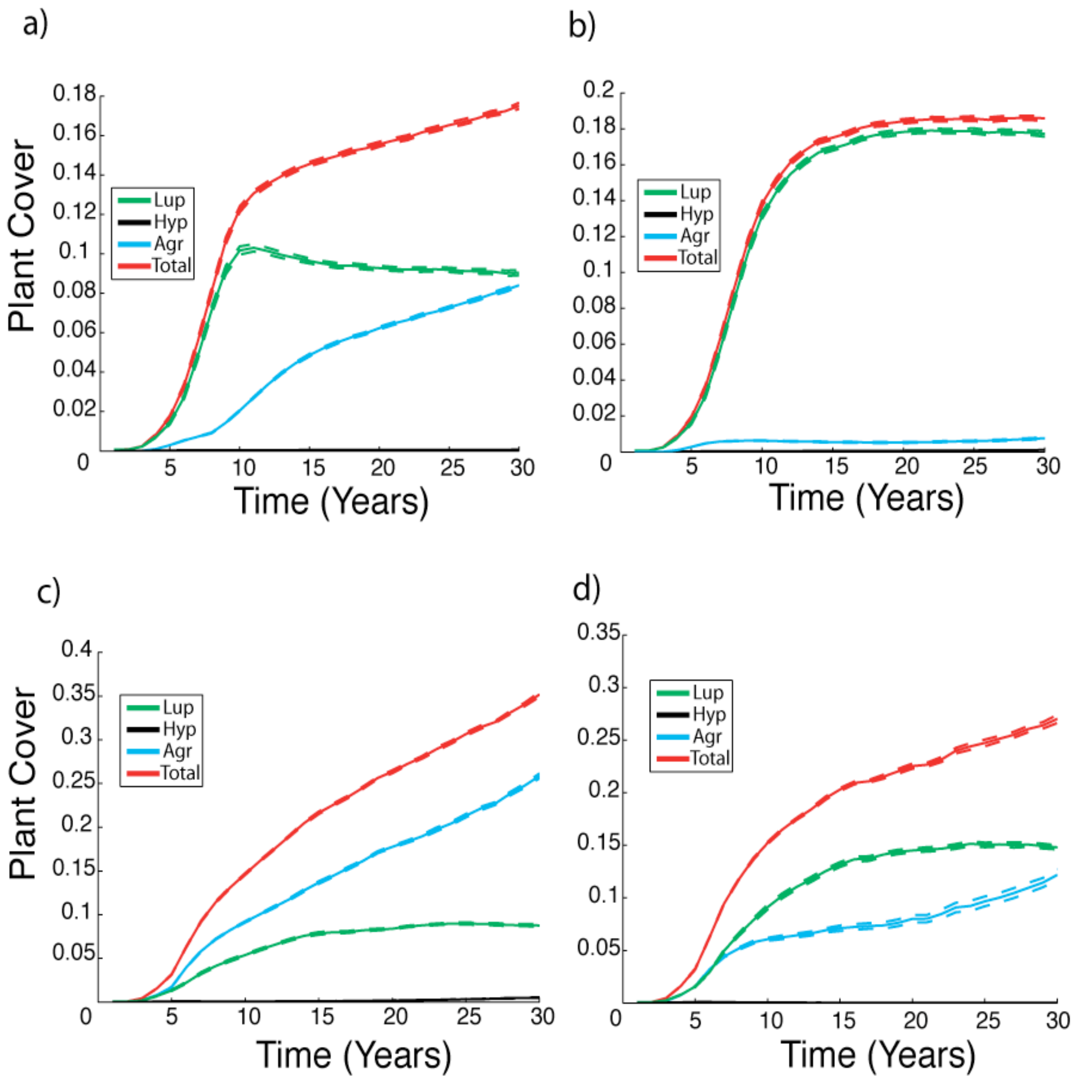

Figure 3.7: Plant cover of each species under different nitrogen levels and different seedling establishment rules. The solid lines represent mean values while the dashed lines represent plus or minus two standard errors. **a** In the OPPRSE model with low nitrogen, *Agrostis* (cyan line) and *Lupinus* (green line) dominate total cover (red line). **b** In the OPPSEW model with low nitrogen, *Lupinus* represents most of the total cover, with some contribution from *Agrostis*. **c** and **d** With higher nitrogen levels, *Agrostis* either dominates cover (**c** OPPRSE) or contributes nearly half of total cover (**d** OPPSEW). In all cases, *Hypochaeris* (black line) accounts for very little of total plant cover.

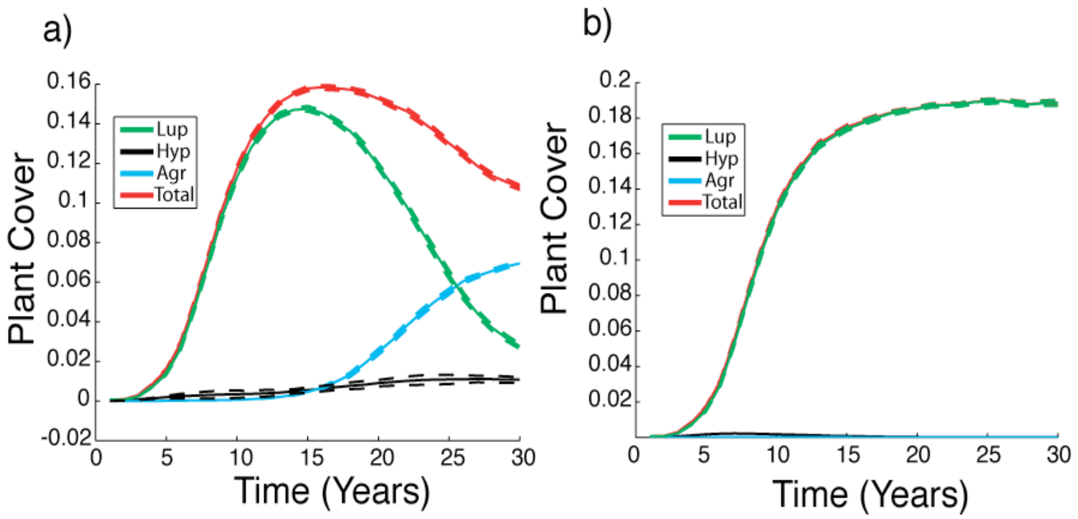

Figure 3.8: The effects of increasing *Hypochaeris* seed survival and decreasing *Agrostis* seed survival. The solid lines represent mean values while the dashed lines represent plus or minus two standard errors. **a** In the OPPRSE model, *Hypochaeris* (black line) does better than previously (Figure 3.7a) and *Lupinus* (green line) suffers a large decline in cover, resulting in an overall decline in total cover (red line). **b** In the OPPSEW model, *Agrostis* does worse due to the lower seed survival and greater seed survival for *Hypochaeris* does little to increase its cover.

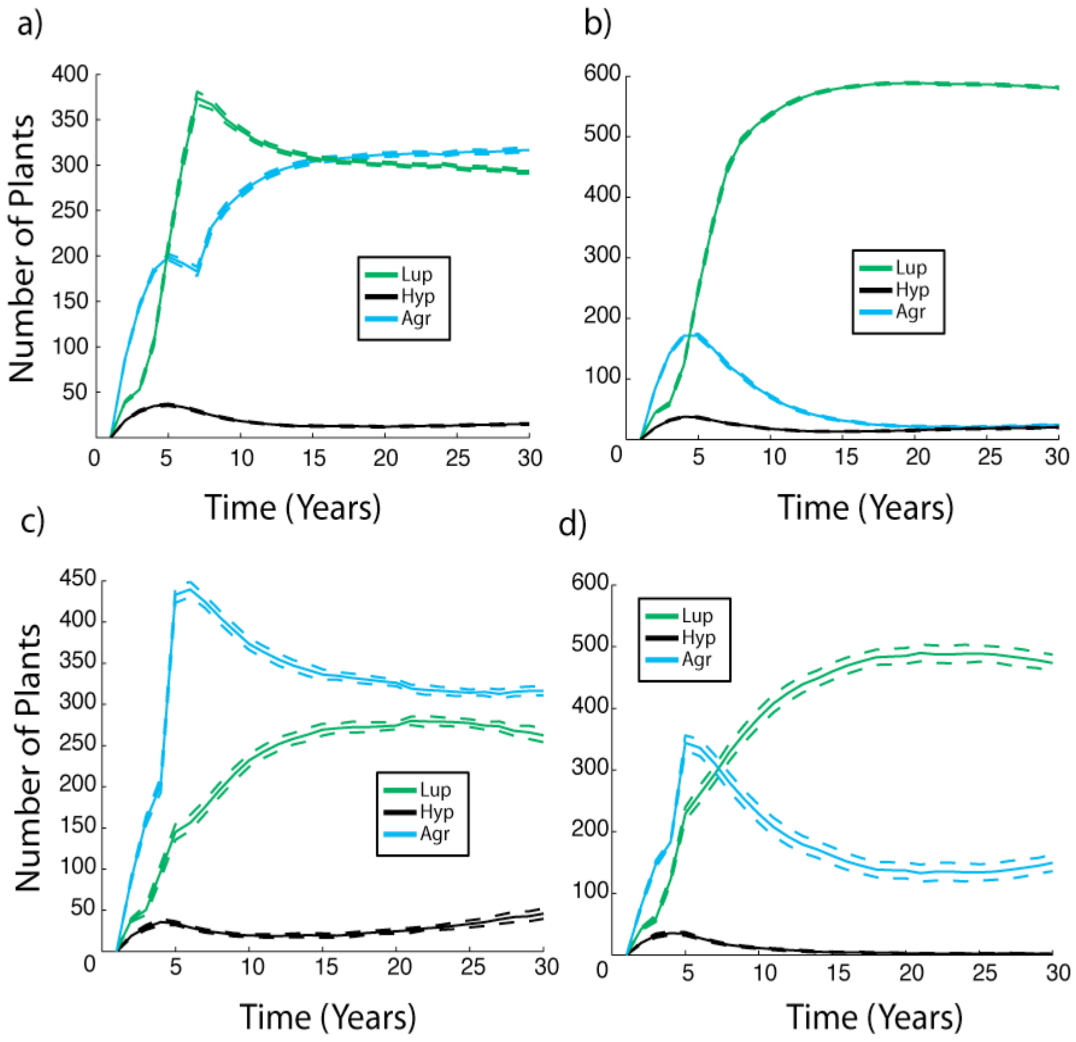

Figure 3.9: The number of plants of each species under different nitrogen levels and different seedling establishment rules. The solid lines represent the mean value and the dashed lines represent plus or minus two standard errors. For **a** and **b**, sample size is 100. For **c** and **d**, sample size is 20. **a** In the OPPRSE model with low nitrogen, *Lupinus* (green line) becomes most numerous after five years, but *Agrostis* becomes numerically dominant after fifteen years as nitrogen levels increase. **b** In the OPPSEW model with low nitrogen, *Lupinus* is always numerically dominant after five years. Note that *Hypochaeris* (black line) has around the same number of individuals as *Agrostis*, but occupies much less space (Figure 3.7b). **c** In the OPPRSE model with higher nitrogen levels, *Agrostis* is consistently numerically dominant, but its dominance is reduced as time progresses. **d** In the OPPSEW model with high nitrogen, *Lupinus* is the numerically dominant species, but *Agrostis* is very common. *Hypochaeris*, on the other hand, is almost driven to exclusion.

The impact of dead *Lupinus* on the seedlings of *Agrostis* and *Hypochaeris* can result in large increasing in seedling biomass (Figure 3.10). For *Agrostis*, the effect is large enough to allow some seedlings to reach reproductive maturity in one growing season when dead *Lupinus* is present (Figure 3.10a). For *Hypochaeris*, the effect of *Lupinus* is more variable, mostly due to the fact that there are simply less *Hypochaeris* seedlings present (Figure 3.10b). However, the mean effect of dead *Lupinus* is positive and large enough to allow *Hypochaeris* seedlings to reproduce in their first growing season (Figure 3.10b).

When herbivory on *Lupinus* is added to the model, the net effect is to increase the cover of *Agrostis* (Figure 3.11). This result can be explained in part by the earlier result showing the large positive response of *Agrostis* seedlings to dead *Lupinus*. This indicates that the additional *Lupinus* mortality due to herbivory greatly increases *Agrostis* seedling size and hence *Agrostis* cover. The fact that *Hypochaeris* does not seem to benefit from the increase in *Lupinus* mortality is due to *Hypochaeris*' poor seed survival, which reduces *Hypochaeris*' ability to establish in dead *Lupinus* patches.

Adding random spatial heterogeneity to the model for nutrient levels in patches and removing nitrogen accumulation does not seem to greatly alter the results, except that *Lupinus* can greatly benefit from patches with higher phosphorus levels (Figure 3.12a). When the spatial heterogeneity is structured in such a way that there are three 'safe-sites' with high nitrogen levels, but the rest of the lattice has poor nitrogen, the cover for *Agrostis* and *Hypochaeris* is much lower (Figure 3.12b). However, the cover at the 'safe-sites' is higher than the other patches when random establishment of seedlings is used (Figure 3.13).

The overall result of this section is that *Hypochaeris* is poorly suited for seed competition while *Agrostis* and *Lupinus* can both compete effectively for patches. The competitive abilities of each species are determined by their life history traits, including stoichiometry, in conjunction with the nutrient status of the environment. In the next section, seed competition is replaced by adult competition for nutrients and adult inhibition of seedling establishment, which can cause substantial differences in results.

3.3.3 *Three Plants per Patch: Adult Competition*

The three plants per patch formulation represents a large change to the competitive dynamics of the model. First of all, seedling establishment becomes a function of the number of germinated seeds and the total cover of other species adults in that patch (Eq. 3.11). Since plant cover can be fairly sparse even with adults present, it is much easier to colonize new patches than in the previous model. Furthermore, the cover levels of each plant will be higher simply because all patches can be, theoretically, colonized by each species even when occupied by other species unless there is 100% cover. Lastly, species are now capable of removing nutrients from other species through resource depletion, which negatively impact a species biomass and reproductive capabilities. These changes should be kept in mind when comparisons are made between results in section 3.3.2 and this section.

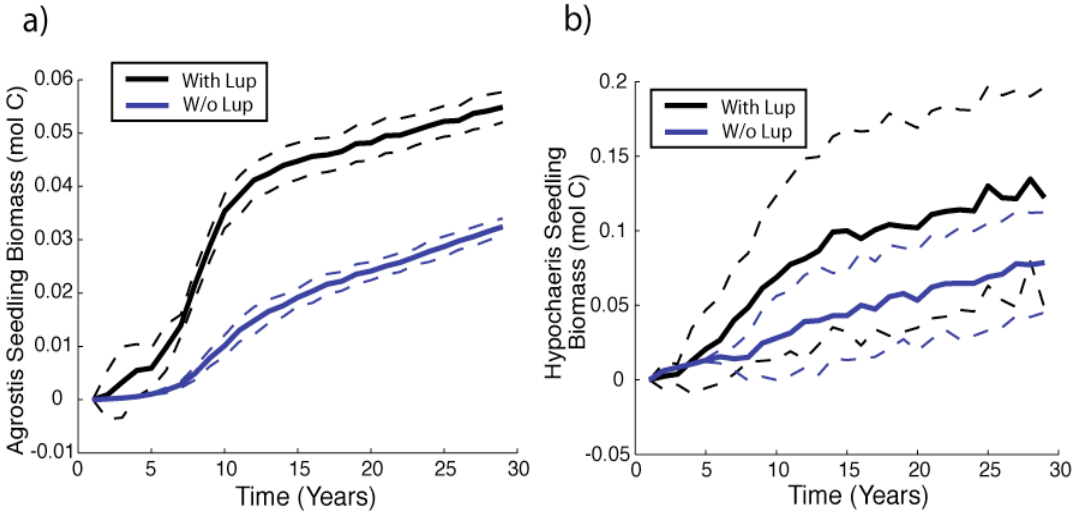

Figure 3.10: The effect of dead *Lupinus* on the growth of seedlings of *Agrostis* and *Hypochaeris*. The solid lines are mean values and the dashed lines are standard deviations. The standard deviations are much larger for *Hypochaeris* due to the lower number of seedlings present in the lattice. **a** *Agrostis* seedlings with dead *Lupinus* (black line) are almost twice the size as those seedlings that do not have a dead *Lupinus* (blue line). **b** *Hypochaeris* seedlings with dead *Lupinus* (black line) are, on average, larger than those without (blue line). Since the critical flowering size of *Hypochaeris* is 0.1166 mol C, many *Hypochaeris* seedlings with dead *Lupinus* should be able to reproduce in their first growing season.

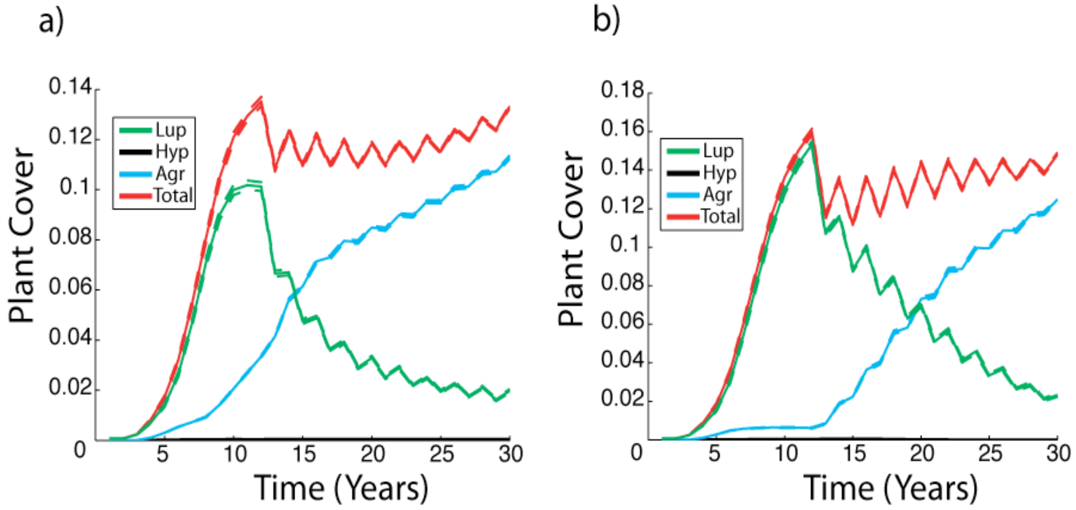

Figure 3.11: The effect of herbivory on plant cover. The solid lines are mean values and the dashed lines are plus or minus two standard errors. **a** and **b** With both OPPRSE (**a**) and OPPSEW models (**b**), *Lupinus* (green line) suffers large declines and *Agrostis* (cyan line) greatly benefits. *Hypochaeris* (black line) does not benefit from the herbivory and total cover (red line) is slightly less than it would be without herbivory (Figure 3.7a,b).

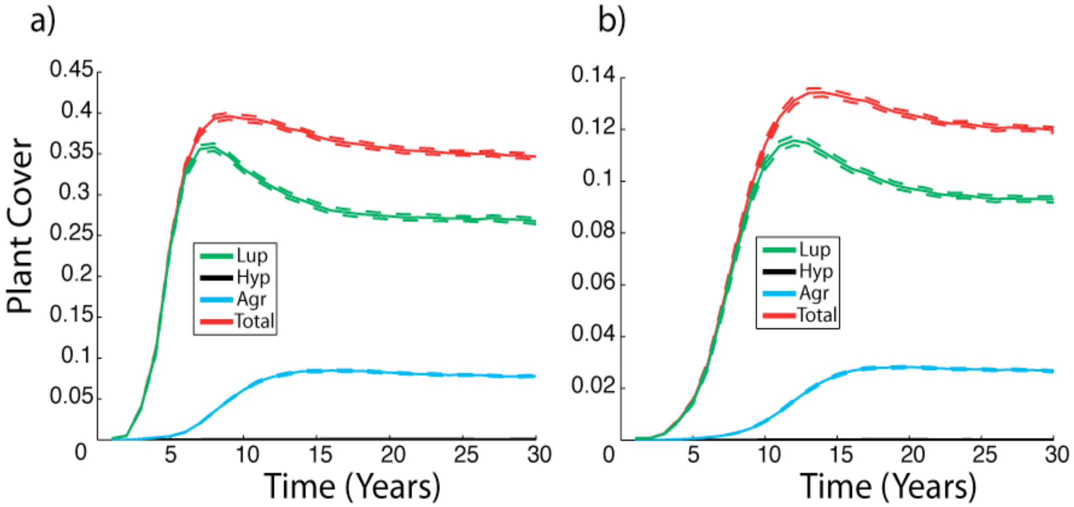

Figure 3.12: The effect of spatial heterogeneity on plant cover with random seedling establishment. The solid lines are mean values and the dashed lines are plus or minus two stand errors. **a** Random spatial heterogeneity with nitrogen values ranging from 10^{-8} to 10^{-6} mol N/L and phosphorus values ranging from 6.817 x 10^{-7} to 6.817 x 10^{-6}. *Lupinus* (green line) biomass is much higher due to areas of high phosphorus content, which increases total cover (red line). *Agrostis* (cyan) biomass is similar to that of Figure 3.7a. **b** The community is dominated by *Lupinus* as nitrogen levels are very low except in three ‘safe-sites’. In both **a** and **b**, *Hypochaeris* (black line) is barely contributes to total cover.

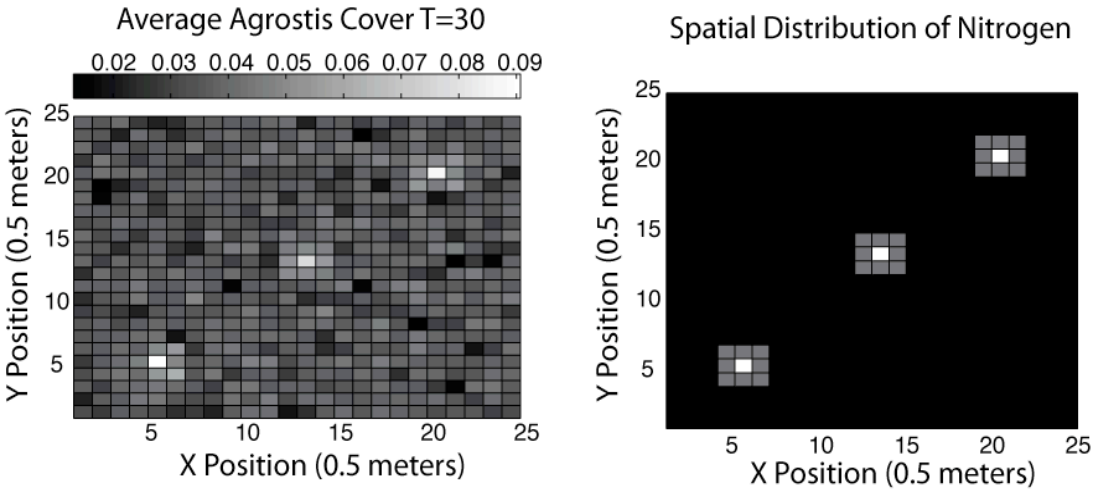

Figure 3.13: Spatial distribution of average *Agrostis* cover at year 30 of the simulation and the spatial distribution of nitrogen. The lighter the colour indicates greater cover or greater nitrogen. The lightest patches in the *Agrostis* cover lattice correspond to the lightest patches in the nitrogen lattice. This result reveals that spatial patterning in nutrient levels should result in some spatial patterning in plant biomass.

In addition to these functional changes, I also decided to allow a small delay between *Lupinus* colonization and the colonization of other species. The motivation for this delay is due to the fact that *Lupinus* was the only species present for a few years on the Pumice Plain (del Moral et al. 2005). This delay does not significantly impact any of the results, but does change the figures in this section.

One general pattern that still holds from the previous section is the relative rankings in plant cover for each species, with *Lupinus* being the most dominant, followed by *Agrostis* and *Hypochaeris* for low nutrient conditions and no herbivory (Figure 3.14a). When herbivory does occur, the benefits to *Agrostis* are minimal compared to the gains found when only one plant could occupy a patch at a time (Figure 3.14b). In fact, the amount of cover for *Agrostis* within the lattice is decreasing in time while both *Hypochaeris* and *Lupinus* are trending upwards (Figure 3.14a,b). This trend towards reduced *Agrostis* cover continues to occur when spatial heterogeneity in resource supply is added randomly or by creating 'safe-sites' with high nitrogen levels (Figure 3.14c,d). The 'safe-sites' within this formulation do not seem to impact plant cover at all, which makes sense as *Lupinus* is present across the lattice and influences soil fertility (Figure 3.14d).

Why does *Agrostis* decline in time within the community, even while nitrogen levels are increasing and therefore should increase the biomass of individual *Agrostis* plants? The answer is the negative effect of *Hypochaeris* on *Agrostis* biomass, as indicated in Table 3.4. Whenever *Hypochaeris* and *Agrostis* co-occur, *Hypochaeris* will reduce *Agrostis* biomass and will eventually displace *Agrostis* from the patch. As time progresses, more and more *Agrostis* plants begin to co-occur in patches containing *Hypochaeris*, which explains the drop in cover despite increases in soil fertility (Figure 3.15).

Nonetheless, the reduction of *Agrostis* cover is slow and all three species coexist at the regional level for all the above scenarios considered (Figure 3.14). Furthermore, all species have fairly significant levels of cover on the lattice, with even *Hypochaeris* reaching nearly 3% average cover in the lattice. These levels of cover for both *Hypochaeris* and *Agrostis* are unlikely to be achieved without *Lupinus* being present, especially in regions with even slower nitrogen accumulation (Figure 3.16).

Without *Lupinus* and slightly poorer nitrogen conditions, *Agrostis* is able to establish a small foothold on the lattice while *Hypochaeris* barely has any cover at all (Figure 3.16a). With phosphorus levels within the ranges reported by Halvorson & Smith (2009), *Lupinus* can achieve very high levels of cover, which may inhibit other species from establishing (Figure 3.16b). However, the net effect of *Lupinus* is a large increase in both *Hypochaeris* and *Agrostis* cover (Figure 3.16b). If herbivory is included, *Agrostis* benefits at the beginning, but *Hypochaeris* does benefit more towards the end of the time period considered (Figure 3.16c).

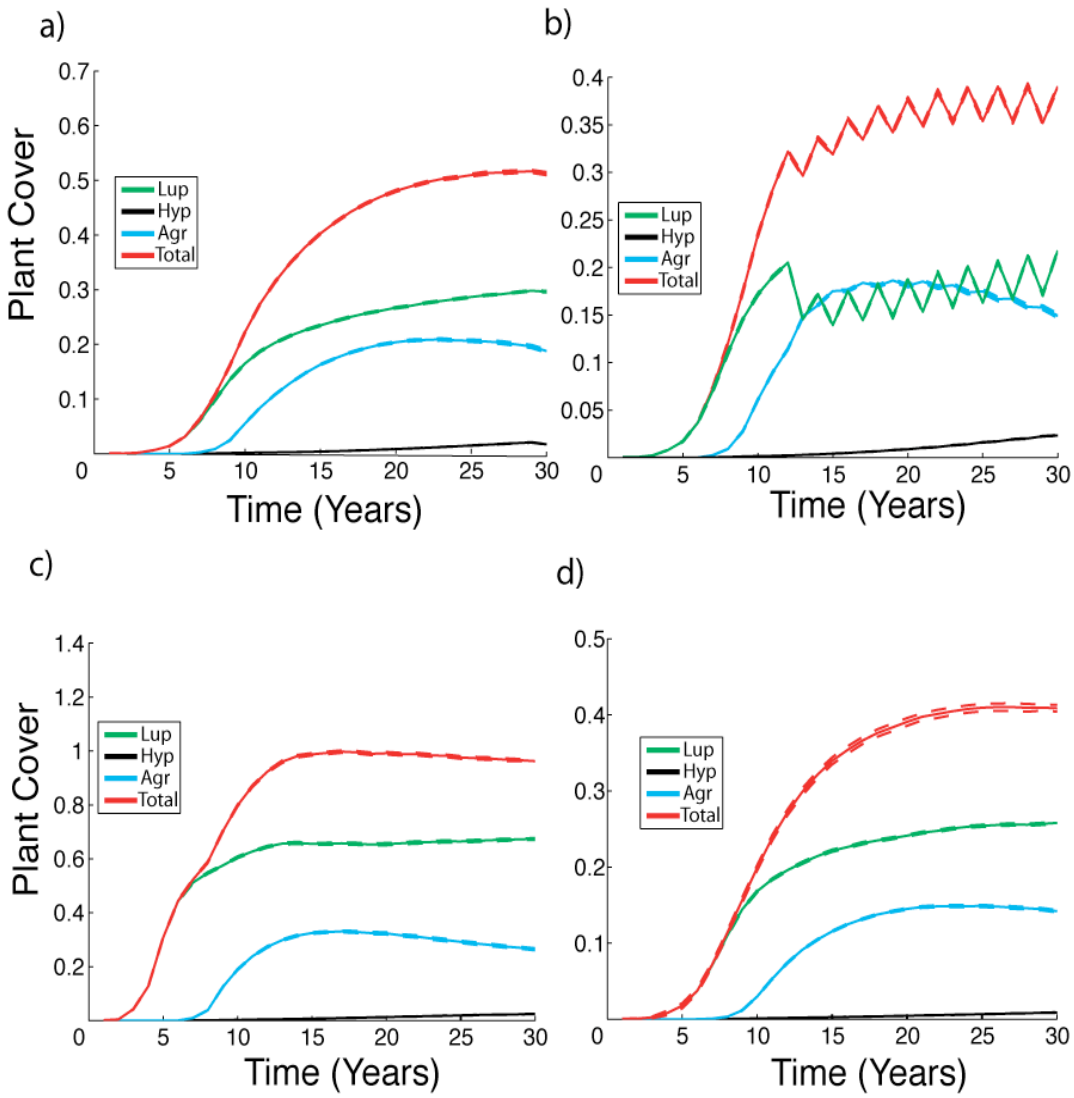

Figure 3.14: Model formulation with within patch competition and adult inhibition of seedling establishment. The solid lines denote mean values while the dashed lines indicate two standard errors around the means. **a** Plant cover of *Lupinus* (green line), *Agrostis* (cyan) and *Hypochaeris* (black line) with the same parameter values as Figure 3.7. As in Figure 3.7a, *Lupinus* and *Agrostis* contribute most to the total cover (red line), though there is more *Hypochaeris* present here. **b** Adding herbivory to the model demonstrates a clear difference with the previous formulation, as *Agrostis* does not benefit from increased *Lupinus* mortality and declines in cover. **c** and **d** Adding spatial heterogeneity does not change the qualitative structure of the community, though there is more cover in **c** due to high phosphorus sites on the lattice to promote *Lupinus* growth.

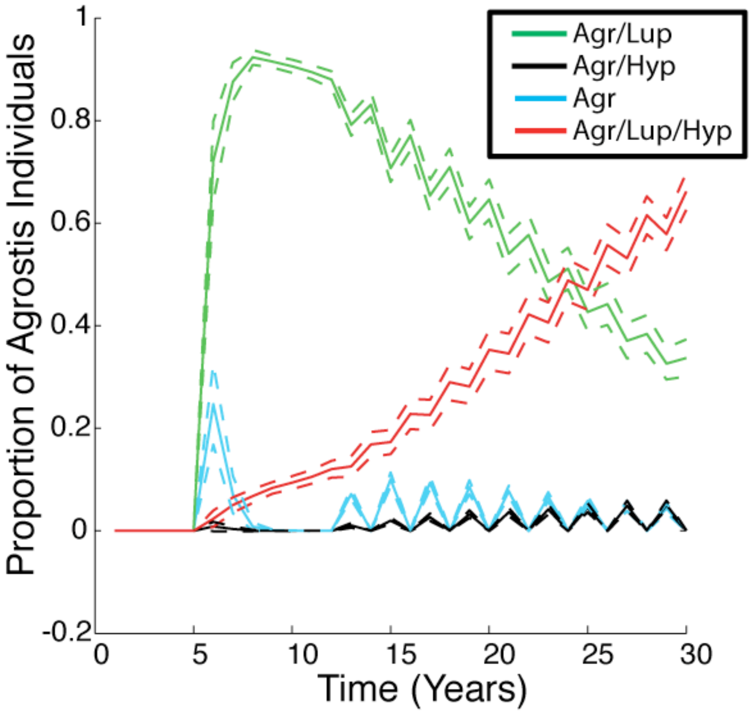

Figure 3.15: Co-occurrence of other species with *Agrostis* over time. The solid lines are mean values and the dashed lines are one standard deviation around the mean. Early on, *Agrostis* is mostly associated with *Lupinus* or is by itself. As time progresses, *Agrostis* becomes increasingly associated with *Hypochaeris* and *Lupinus* as *Hypochaeris* becomes more abundant in the lattice. The net effect of this greater association is a loss of cover for *Agrostis* (Figure 3.14).

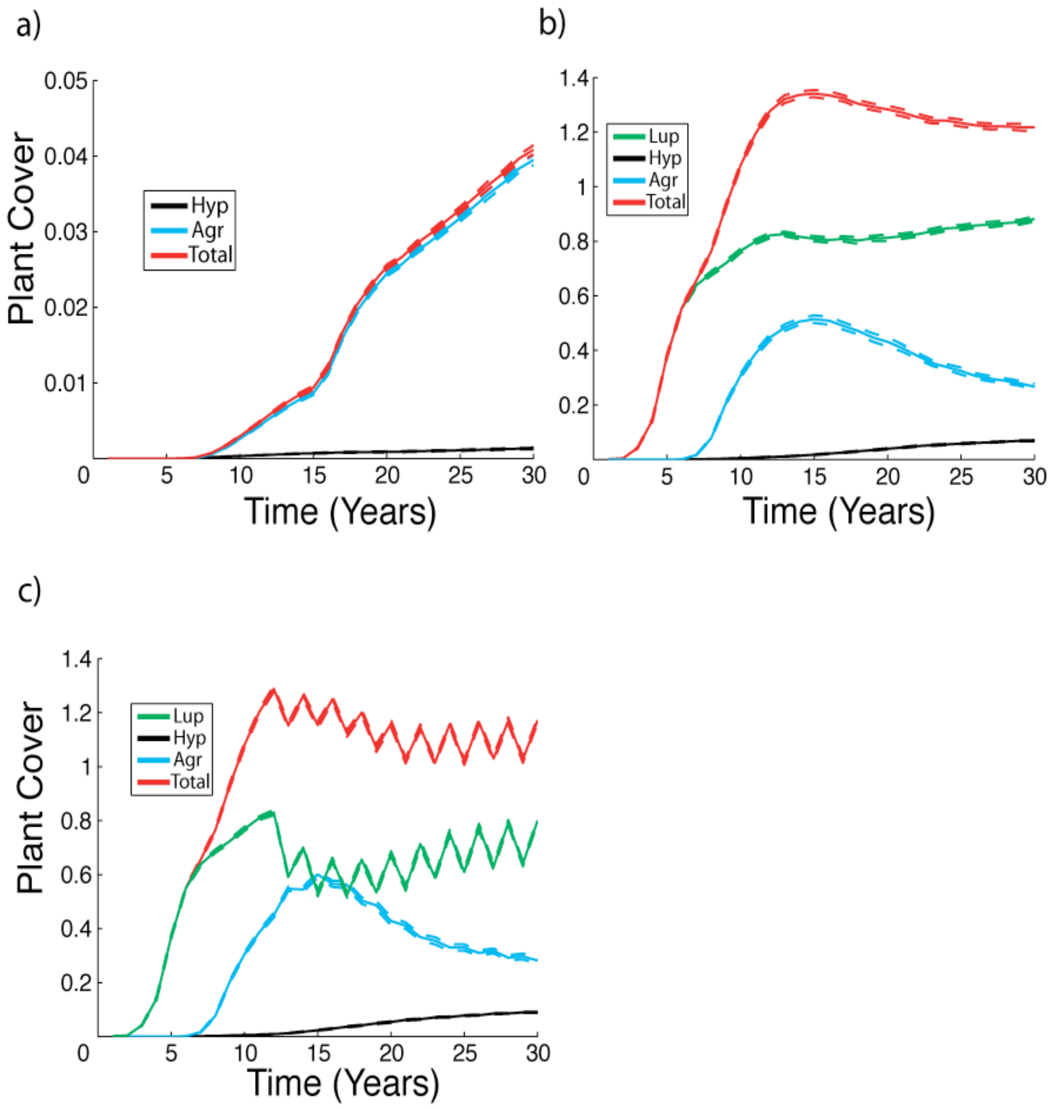

Figure 3.16: The effect of *Lupinus* on the plant community. The solid lines are mean values while the dashed lines are two standard errors around the mean and the sample size is equal to30. **a** Without *Lupinus*, both *Agrostis* (cyan line) and *Hypochaeris* (black line) struggle to establish on the lattice. **b** With the addition of *Lupinus* (green line), the total cover (red line) and the cover of *Agrostis* and *Hypochaeris* greatly increase, despite the fact that increased *Lupinus* cover inhibits other species seedling establishment. **c** Adding herbivory does result in a temporary increase in *Agrostis* cover and a mild increase for *Hypochaeris* cover.

The general results of this section is that *Lupinus* has a large, positive effect on the other two species and *Hypochaeris* does have a negative effect on *Agrostis* at a regional scale, though such an effect can only be seen when nitrogen have accumulated sufficiently to allow for *Hypochaeris* to become common over the landscape.

3.3.4 *Model Sensitivity*

The sensitivity of the model to changes in model parameters is a key determinant in evaluating the validity of the model and can guide other researchers by indicating which parameters are important to study (Haefner 2005). While a full sensitivity analysis of the model would be extremely involved due to the numerous parameters and variables, a partial analysis of some of the life history traits is presented here.

To test model sensitivity, one must use some sort of index to describe how a change one parameter results in changes in model variables. The sensitivity index used here has been termed as a 'global' sensitivity index (Huth & Ditzer 2000, Bampfylde & Lewis, in review) and can be described by the following equation:

$$globalSI(v,p) = \left| \frac{v_{\max} - v_{\min}}{2v_{\text{standard}}} \right| \qquad \textbf{(3.13)}$$

Where v and p are the variable and parameter of interest, $v_{\max}$ and $v_{\min}$ are the maximum and minimum values of the variable over the range of possible p values, respectively, and v_{standard} is the value of the variable for the standard set of parameters. The higher the value of the index, the more sensitive the variable is to the changes of the parameter (Bamfylde & Lewis, in review).

The variables used for the sensitivity index are the average cover levels of each species after thirty years, since cover is traditionally used on Mount St. Helens to estimate amount of a particular plant in the ecosystem (e.g. del Moral & Rozzell 2005). The parameters selected for the sensitivity analysis are adult mortality, loss of carbon during growing season, seed mortality, seed germination (for *Agrostis* and *Hypochaeris*) and allocation to reproduction (for *Lupinus*). The parameters were chosen to capture the different elements in the model such as vegetative growth, mortality and reproduction.

For the single species cases, loss of carbon in the growing season and adult mortality were always most sensitive for all species (Figure 3.17). Only *Hypochaeris* was sensitive to seed mortality and somewhat sensitive to seed germination (Figure 3.17). This likely reflects the difficulty *Hypochaeris* has at establishing a reproductive population on the landscape and any improvements to any life history traits will increase cover. *Lupinus* and *Agrostis* are both able to easily establish on the landscape and hence cover is controlled by growth rates and mortality (Figure 3.17). The slight sensitivity to reproductive allocation for

Lupinus is due to loss of vegetative material associated with higher reproduction (Figure 3.17).

When species interact on the landscape, the sensitivity profiles can differ depending on model structure (Figure 3.18). The three plants per patch model (section 3.3.3) is most sensitive to changes in adult mortality and loss of carbon during the growing season, while both one plant per patch models indicate more sensitivity to seed mortality (Figure 3.18). Furthermore, the three plants per patch model is less sensitive to changes in parameters than the other two models, though the OPPRSE model is only very sensitive in *Hypochaeris* cover with changes to *Hypochaeris* seed mortality (Figure 3.18a,b). In addition, *Agrostis* cover for the OPPSEW model is highly sensitive to a number of parameters when compared to the other models (Figure 3.18c).

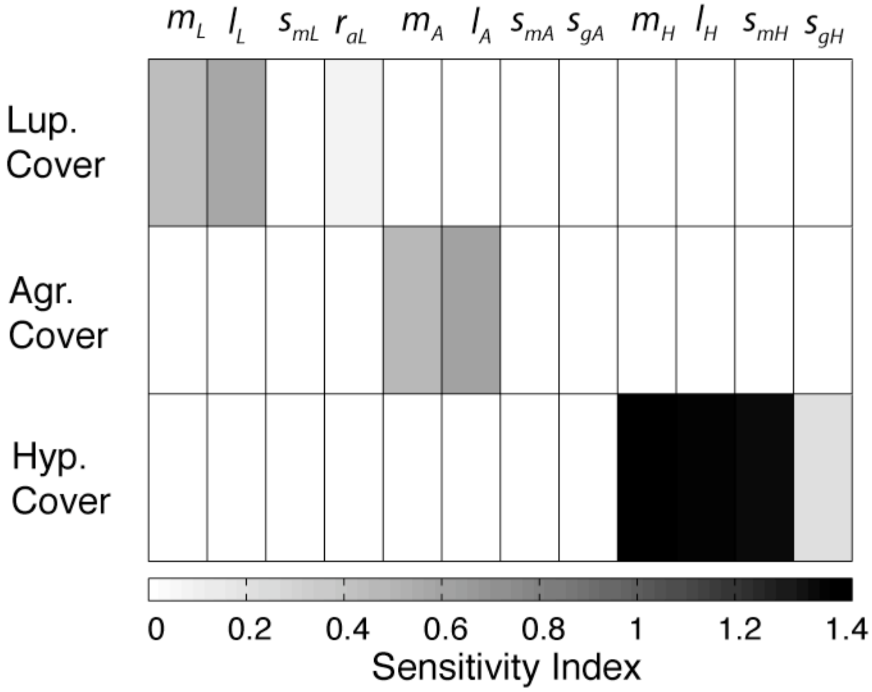

Figure 3.17: Partial sensitivity analysis for the cases where only one species is present on the lattice. The darker the colour of the square, the more sensitive the variable (species plant cover) is to the change of the parameter. The parameters that cause the largest changes in cover for all species are adult mortality and loss of carbon during the growing season. Seed mortality and seed germination of *Hypochaeris* are also important in determining *Hypochaeris* cover.

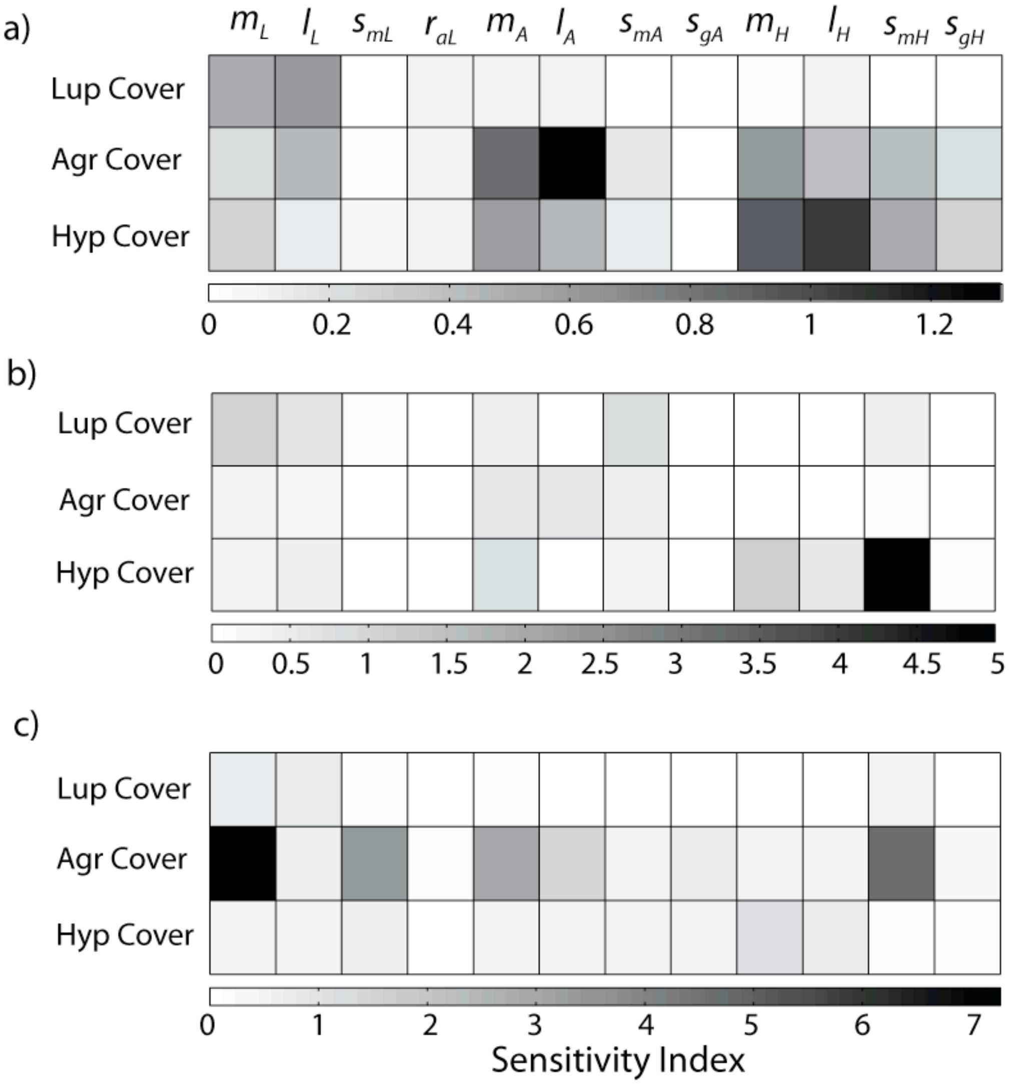

Figure 3.18: Partial sensitivity analysis for the three formulations of the three species model. The darker the colour of the square, the more sensitive the variable (species plant cover) is to the changes of the parameter. **a** The three plants per patch model is fairly insensitive to changes of the parameters (note the scale below the squares). The most important parameters are adult mortality and loss of carbon in the growing season for all species. Seed mortality for *Hypochaeris* also is important for *Agrostis* and *Hypochaeris* cover. **b** The OPPRSE model is also fairly insensitive, except *Hypochaeris* seed mortality has a very large effect on *Hypochaeris* cover. Overall, the pattern is similar to that of **a**, but seed mortality for *Agrostis* and *Hypochaeris* are more important for plant cover of all species. **c** The OPPSEW model is more sensitive to parameter value changes than the previous models, particularly when *Agrostis* cover is considered. The most important parameters are adult mortality for *Lupinus* and *Agrostis* and seed mortality for *Lupinus* and *Hypochaeris*.

3.4 Discussion

Life history traits, nutrient limitation, competition for resources, facilitation and herbivory are commonly invoked mechanisms that can explain the pattern and the rates of succession (Chapin et al. 1994, Chapin et al. 2002, Walker & del Moral 2003). However, how these mechanisms interact and the importance of each mechanism for the development of the plant community is not well known (Walker & del Moral 2003). The only guides for ecologists are conceptual models (e.g. Pickett et al. 1987, Walker & Chapin 1987, Callaway & Walker 1997) that may be overly reliant on previous empirical studies to provide insight into new ecosystems (Walker & del Moral 2003).

In this chapter, I developed a mechanistic model (section 3.2) to see how life history traits interact with nutrient limitation, nutrient cycling, competition and herbivory and how these mechanisms can help explain patterns seen in plant primary succession. The model was parameterized with data for three plant species found on Mount St. Helens and was simulated thousands of times in order to explore the model's behaviour under different assumptions and different parameter regimes.

The model indicates that both life history traits, competitive and facilitative interactions play important roles in the structuring of the primary successional plant community, though the effects of each are dependent on nutrient levels. Furthermore, specific results such as the coexistence of *Hypochaeris* and *Agrostis* were predicted from the model, which indicates that the model is capturing the necessary mechanisms needed to explain field observations. Overall, the model indicates the validity of focusing on nutrient dynamics as a key mechanism in explaining successional dynamics in primary succession.

3.4.1 *Which Life History Traits Matter?*

The addition of life history traits improved both the biological realism and the predictions of my model. However, due to the overall model complexity created by adding all these additional traits, it can be asked which traits where most important. In general, factors such as seed size, seed germination, allocation to reproduction and maximum growth rates are considered to be key life history traits (Chapin et al. 1994, Chapin et al. 2002).

From the results of the model, it seems that seed survival is a key trait for species to have in order to establish themselves in primary successional habitats (Figure 3.8). With poor seed survival, it is unlikely that rare, long dispersal events of seeds will allow for the development of a local population. Even with a steady supply of seeds, *Hypochaeris* has great difficulty establishing itself in the model and on Mount St. Helens in large numbers, except in 'safe-sites' where seed survival is higher (Titus & del Moral 1998, Titus 2008).

Another key trait is the ability to obtain sufficient biomass even at lower nutrient levels, which depends greatly on the stoichiometry of the plant and its nutrient uptake abilities. Since *Agrostis* is capable of maintaining very low levels of nitrogen within its tissue compared to *Hypochaeris*, it is likely that it can maintain superior levels of growth at low nitrogen levels, even though it is a poor competitor for nitrogen (Chapter 2, Tilman & Wedin 1991).

The last trait that could alter model outcomes was seed size. With smaller seed size, *Agrostis* is able to swamp the environment with its long-lived seeds and can allow for quick establishment across the landscape, even though its allocation to reproduction is the lowest of the three species (Table 3.3). However, this benefit became a negative in the OPPSEW model (Figure 3.7). In addition, other factors that may select against smaller seeds, such as drought, were not modelled here and could further reduce the competitive ability of *Agrostis* (Chapin & Bliss 1989, Wood & Morris 1990).

3.4.2 *Model Sensitivity and Structure*

The model proposed in this Chapter relies on parameter estimates that can have large ranges and on assumptions that shape the model's formulation. Two kinds of uncertainty can therefore arise: uncertainty due to parameter values and uncertainty due to model structure (Haefner 2005). To deal with the first kind of uncertainty, I performed a sensitivity analysis for a subset of the model parameters and investigated their effects on model outcomes (section 3.3.4).

The overall sensitivity of the model to changes in parameters investigated is relatively low for two of the formulations, with differences between the minimum and maximum value obtained for the variable being rarely more than twice the value at the standard parameter value (Figures 3.17- 3.18). With the OPPSEW model, the sensitivity of the model was much higher to changes in a number of parameters and the sensitivity profile differed substantially (Figure 3.18c). The parameters resulting in the greatest changes in the model variables were usually adult mortalities for the different species. However, changes seed mortality, particularly *Hypochaeris* seed mortality, can result in large changes in the cover of various species and can alter community composition greatly (Figures 3.8-3.9, 3.18).

The differences found in model sensitivity and model outcomes due to differences in model formulation indicate the uncertainty surrounding the biology of the plant community can result in vastly differing predictions (e.g. Figure 3.8). Such uncertainty in model structure is becoming increasingly important to address as modelling techniques become more common for ecologists to use (Pascual et al. 1997, Wood & Thomas 1999, Stephens et al. 2002). I have tried to use different formulations in order to investigate how such differences may influence model outcomes, but many others could be proposed to investigate the system. The best way to resolve issues surrounding uncertainties with model structure is to gain better knowledge of the mechanisms involved in order to use appropriate mathematical formulations and to test a variety of plausible models (Pascual et al. 1997, Wood & Thomas 1999).

3.4.3 *Possible Improvements and Extensions of the Model*

As with any modelling exercise, there are ways in which the model can be improved in terms of realism, precision or generality, though rarely in all three (Levins 1966). For my part, I will focus on how the model can be improved vis-à-vis the biology of the system.

One possible improvement is to model the nutrient uptake of the plants in a truly spatially explicit way such as in Raynaud & Leadley (2004). With such models, domains of interaction between plants can be precisely defined and hence the possibility of competition can be investigated. However, such models may not be computationally feasible due to the high model complexity involved. Another way of implementing spatial uptake is to have an uptake kernel, similar to the competition kernels proposed by Snyder & Chesson (2004). Such a kernel would depend on the size of the plant, allocation to roots and other factors that impact its range of effect. Such an approach may be mathematically tractable and give greater ability to model competition for resources in space.

Another potential improvement would be to model explicitly the behaviour of the herbivores, which is also an extension of the model to higher trophic levels. Previous work has shown spatially structured herbivory at work on Mount St. Helens (e.g. Fagan et al. 2004, Bishop et al. 2005, Fagan et al. 2005), which would likely result in different predictions than those found here. Furthermore, the herbivory may also be influenced by the nutritional quality of *Lupinus*, which could once again alter the spatial structure of the community (Fagan et al. 2004). While it would be best to explicitly model the herbivores and their behaviour, it may be possible to add rules to the current model to obtain equivalent effects.

A final improvement/extension of the model would be to include a realistic detritus compartment, which involves modelling the soil community. With such a compartment, better understanding of nutrient cycling and nutrient availability becomes possible, even though they can add a great deal of complexity (Cherif & Loreau 2007, 2009). Furthermore, it becomes possible to model plant-soil feedbacks that can alter aboveground community structure (Levine et al. 2006, Cherif & Loreau 2009) Since succession is as much a belowground process as an aboveground one, it is important to consider the detritus community in greater detail (Halvorson et al. 2005).

Appendix

3.A Parameters for Tables and Figures

For all figures and Table 3.4, the values listed under the ‘Value’ column of Table 3.1 are used in the simulations that led to the creation of the figures and Table 3.4. If the values of life history trait parameters are not listed in this Appendix, then they take on the values listed in Table 3.3.

Table 3.4: Model was simulated over a time period of 1000 ‘growing days’ in order to maximize potential differences. Initial plant size was 1 mol C for both *Agrostis* and *Hypochaeris* plants. The loss of carbon parameters, l_A is equal to

0.008/day and l_H is equal to 0.007/day. The influx of nitrogen parameter, I_N, is equal to 3 x 10^{-5} mol N/(day x L).
Figure 3.3: The influx of phosphorus parameter, I_P, is equal to 1.871 x 10^{-6} mol P/(day x L) and phosphorus efflux, φ_P, is equal to 5/day.
Figure 3.4: See caption for changes from Tables 3.1 and 3.3.
Figure 3.5: Same as Figure 3.3 except $\varphi_P = 1$.
Figure 3.6: Same as Figure 3.5 except adult mortality, m_L, due to herbivory is 0.95 and seed mortality, s_{mL}, increases to 0.995.
Figure 3.7: Same as Figures 3.3 and 3.4, except I_N increases from 1 x 10^{-7} mol N/L to 1.2 x 10^{-5} mol N/L by increments of 4 x 10^{-7} mol N/L for **c** and **d**.
Figure 3.8: Same as Figure 3.7a,b except s_{mH} =0.07, s_{mA} =0.01 and s_{gA} =0.95.
Figure 3.9: Same as Figure 3.7.
Figure 3.10: Same as Figure. 3.7a.
Figure 3.11: Same as Figure 3.7a,b.
Figure 3.12: See caption for changes from Tables 3.1 and 3.3.
Figure 3.13: Same as Figure 3.12b.
Figures 3.14-3.15: Same as Figure 3.7a,b.
Figure 3.16: Same as Figures 3.3 and 3.4 except I_N increases from 1 x 10^{-8} mol N/L to 1.2 x 10^{-6} mol N/L by increments of 4 x 10^{-8} mol N/L, ζ_{LN} =0.3 and I_P= 4.871 x 10^{-5} mol P/L.
Figures 3.17-3.18: Same as Figures 3.3 and 3.4.

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Chapter 4

Concluding Remarks

4.1 Approach to Studying Primary Succession: Strengths, Limitations and Applicability

Understanding how an ecosystem recovers after a large-scale disturbance is of growing importance as humans continue to alter ecosystems for various purposes (Walker & del Moral 2003). The phenomenon of ecological recovery from a state with little to no biological remnants to a fully developed ecological community has traditionally been called primary succession or succession on primary areas (Clements 1916). Insights from studies of primary succession after natural disturbances, such as the eruption of Mount St. Helens, have helped ecologists identify key processes that control the trajectory and the rate of succession (Pickett et al. 1987, Walker & Chapin 1987, del Moral & Bliss 1993, Chapin et al. 1994).

However, as indicated by my survey of the literature in Chapter 1, it is a rare thing to see mechanistic models of succession that can be used to explore the importance of and the interactions between the various mechanisms proposed by ecologists. A mechanistic model for succession would need to include facilitation, competition, herbivory and life history traits of the organisms in order to make accurate predictions concerning successional trajectories (Chapin et al. 1994, Chapin et al. 2002). Furthermore, any mechanistic model of succession would need to be able to address processes that function across levels of biological organization and across spatial scales (Walker & del Moral 2003).

Within this thesis, I have developed mechanistic models for plant primary succession by focusing on ecological stoichiometry of the ecosystem (Sterner & Elser 2002). The first model (Chapter 2) treats the ecosystem as a dynamical system, i.e. the ecosystem changes over time and space, which can be analysed with techniques derived from the theory of differential equations (Strogatz 1994). Furthermore, the model postulates that competition at local scales is determined by resource competition, allowing the use of graphical methods and R^* theory developed for classical resource competition models (Chapter 2; Tilman 1980, 1982).

The main strength of this approach is the ability to make predictions about community structure based on plant traits and the dynamics of nutrients. By deriving competitive abilities (R^* values) from plant traits, the model predicts the outcome of competition within the community based upon the nutrient status of the environment. Thus, predictions can be made about the potential success of a newly arrived plant species as long as scientists have knowledge of its traits and the nutrient status of the soil. The predictions from resource competition models have been validated by experimental work on aquatic species in laboratory settings and a few terrestrial field experiments (Dybzinski & Tilman 2007, Wilson et al. 2007).

Despite this strength, there are many limitations to such an approach to primary succession. A major limitation is obtaining usable parameters for the plant traits, for numerous of experiments would be required for each species added to the model. Another limitation to this approach is the difficulty in using a dynamical system to model certain life traits of plants, such as plant mortality and plant reproduction (Chapter 2). While these traits can be incorporated into a mechanistic model of succession (Chapter 3), the powerful analytical techniques from the theory of differential equations can no longer be applied. In addition, competition for resources may only occur on local scales (Huston & DeAngelis 1994, Raynaud & Leadley 2004), may not occur through the reduction of average resources (Inderjit & del Moral 1997, Craine 2005) and may result in poor predictions if allocation of biomass is assumed to be fixed (Dybzinski & Tilman 2007).

Some of these limitations have already been addressed through the elaboration of a spatially-explicit mechanistic model as seen in Chapter 3 or could be addressed by using more elaborate models of plant growth (e.g. Wang et al. 2007) and including other forms of competition such as allelopathy (Grover 1997; Appendix 2.C of Chapter 2). The main stumbling block is obtaining parameters for the models, which requires better communication between theoreticians and experimenters on what to measure and greater funding for basic ecological research.

The application of mechanistic models using ecological stoichiometry has already begun, with models similar to those used in this thesis used for modelling the dynamics of oceanic and aquatic phytoplankton as well as understanding nitrogen fixation and nitrogen limitation in terrestrial ecosystems (Klausmeier et al. 2004, Litchman et al. 2006, Klausmeier et al. 2007, Wang et al. 2007, Houlton et al. 2008). The insights gained from the models proposed in this thesis could also be applied to those systems with some modifications.

Regarding application to other successional habitats, the models developed here can be applied readily to primary successional habitats that have infertile substrates and are colonized by vascular plants. Such habitats are created by volcanic eruptions, rock outcrops, wind erosion (sand dunes), mining and human-made structures such as cities and roads (Walker & del Moral 2003). Glacial moraines, floodplains and landslides are usually richer in nutrients, which would allow succession to quickly proceed into later successional stages and other processes such as light competition would need to be modelled explicitly (Walker & del Moral 2003). Primary successional habitats with significant amounts of lichens and bryophytes can be modelled with my approach, though more needs to be known about the competitive ability of lower plants for mineral nutrients (Bates 2000, Ayres et al. 2006). In general, the models presented here are best suited for modelling early primary succession where competition for light is limited and the life spans of plants are short.

4.2 Summary of Results

By using ecological stoichiometry, I successfully integrated ecosystem processes such as nutrient cycling and nutrient limitation with the community processes like competition and facilitation in Chapter 2. The fine scale model produced in Chapter 2 was capable of predicting the competitive hierarchy observed on Mount St. Helens for the three plant species parameterized. The model also predicted the net facilitative effect of *Lupinus* on the other species as seen on Mount St. Helens and demonstrated good qualitative agreement with nutrient addition experiments. These results indicate that mechanistic models based upon ecological stoichiometry can aid in our understanding of primary succession.

In Chapter 3, I extended the scale of the model developed in Chapter 2 by allowing for explicit space. I also added more biological detail concerning life history traits that many authors deem important for understanding succession (del Moral & Bliss 1993, Chapin et al. 1994, Chapin et al. 2002, Walker & del Moral 2003). The addition of more biological realism further improved model predictions with regards to the plant community on Mount St. Helens. For example, it predicted regional coexistence of *Agrostis* and *Hypochaeris* despite the superior competitive abilities of *Hypochaeris* at local scales, which is seen on Mount St. Helens (e.g. Titus 2008). This prediction results from the superior ability of *Agrostis* to obtain biomass at lower nutrient levels than *Hypochaeris*, resulting in a colonizer/competitor tradeoff that allows coexistence (Tilman 1994).

Combined, the two models act as the first steps in creating a mechanistic and mathematical framework for primary succession. They indicate that life history traits, competition and facilitation all contribute to the community dynamics and community structure in early primary succession. Furthermore, many of the interactions between species and between species and the abiotic environment can be adequately described within the framework of ecological stoichiometry.

4.3 Philosophical Considerations

In Chapter 1, I presented how ecologists have traditionally been split on how succession proceeds. Holists, such as Clements and Odum, viewed succession as a predictable and directional process of community development from bare substrate to a climax community that is dominated by biotic processes (Clements 1916, Odum 1969). Reductionists, such as Gleason and Cooper, viewed succession as an unpredictable and non-directional process dominated by abiotic processes (Gleason 1917, 1926, 1927, Cooper 1926). The majority of ecologists studying succession today view themselves as neo-reductionists and focus on particular processes within a system of study, with emphasis on life history traits, physical gradients and stochastic processes (Walker & del Moral 2003).

The problem of the neo-reductionistic approach is the inability to generalize their empirically derived results to other ecosystems (Walker & del Moral 2003). This failing can be attributed to the lack of an overarching framework to integrate the various processes involved in succession in particular and ecology in general (Walker & del Moral 2003). The lack of a framework is due to discrediting of the top-down approaches to ecology of Clements and others during the twentieth century (Walker & del Moral 2003). However, new frameworks for ecology developed from the bottom-up have been proposed in the past decade and provide hope for generality in ecology (Sterner & Elser 2002, Brown et al. 2004).

One such framework, ecological stoichiometry, proposes that ecological processes and interactions can be explained through the chemical compositions of organisms and their environments (Sterner & Elser 2002). I have used this highly reductionist approach to integrate numerous processes involved in succession. However, though the framework may be reductionistic, my main interest in ecological stoichiometry is to see how community structure and other higher-level phenomena such as nutrient limitation emerge from interactions within the ecosystem. In this way, reductionism leads to holism through the interactions of the parts of the system. Hopefully, such a synthesis will allow the insights from both the holists and the reductionists to be used to help us understand succession and make ecological rehabilitation more efficient.

Also in Chapter 1, I discussed the potential tradeoffs that occur when modelling a complex system. Levins (1966) mentioned how it may not be possible to achieve generality, precision and realism in the same model. Two of the three goals may be achieved at a time, but not all three and each combination leads either to understanding, prediction or control (Haefner 2005). The model in Chapter 2 is intended to be very general at the cost of precision and some realism. The model in Chapter 3 is less general but gains in realism and precision. Still, the emphasis of the models focused on generality in order to foster greater understanding of the processes of succession. Predictive capability and the ability to control ecosystems are secondary concerns for this thesis.

To achieve the amount of realism found in models in this thesis, a good deal of complexity has crept into the model equations. Such complexity can make the model more accurate (Chapter 2 vs. Chapter 3), it comes at the cost of making it difficult understand what will occur if one variable changes, making prediction more difficult (Haefner 2005). Simple models with little realism can allow for good prediction and can be easily used, which is why certain ecologists maintained that simple statistical models are the best way to do ecology (Peters 1991). However, simple models can lead one astray when processes are nonlinear and small changes in one variable can lead to catastrophic changes (Scheffer 1999). It is important for many models of varying degrees of realism, generality and precision to be used in studying ecosystems in order to avoid the pratfalls of any one approach.

4.4 Future Work

The two research chapters have shown the validity of approaching primary succession through the framework of ecological stoichiometry and utilizing mathematical articulation of the mechanisms involved, achieving some of the goals laid out in Chapter 1. However, a great deal more needs to be done to give a full account of primary succession.

Further data collection and parameterization of the models are needed for quantitative predictions to be possible. Many parameters have been estimated by using related species or not estimated at all, which limits the applicability of the model. The key parameters that should be focused on are nutrient uptake rates and loss of biomass due to respiration, adult mortality and seed mortality.

Experimental tests in a controlled setting of competitive abilities for phosphorus and nitrogen are needed to validate the model predictions concerning R^* values. Only in such setting could other effects such as herbivory, water stress and acidity be discounted in explaining the structuring of the community at local scales. In addition, experimental tests of seedling competition is needed to determine the rules of seedling establishment, which has been shown to be important in Chapter 3.

Data on the spatial distribution of plants at fine scales are needed to validate the model output from Chapter 3. While there is data readily available concerning the spatial distribution of plants on Mount St. Helens are large scales (e.g. del Moral & Bliss 1993), the model presented in Chapter 3 has, so far, only been able to model more limited spatial extents. I have tried to obtain such data for my thesis, but discussions are still ongoing and will not be resolved before the end of my degree.

Concerning the models, further mathematical investigation of the models proposed here can allow for more complete understanding of possible model outcomes. In Chapter 2, I was unable to prove the global stability of the steady states for the single-species model and found it difficult to obtain stability criterion for the coexistence steady state of the two species model. While the solutions of these problems are of more interest to the mathematician than the biologist, the results will allow for greater biological understanding. In Chapter 3, a more thorough investigation of the model's sensitivity is needed to examine the validity of model predictions throughout different parameter regimes and to focus attention on the most sensitive parameters.

Explicit consideration of herbivores, detritovores and other trophic groups is necessary for it has been demonstrated in other studies how these groups can alter the ecological stoichiometry of the soil and the structure of plant communities (Bishop 2002, Cherif & Loreau 2009). The addition of more trophic levels will need to be carefully considered, for the mathematical tractability of models becomes lesser as a model becomes more complex and non-linear (Kaplan & Glass 1995).

Other potential extensions of the model include additional plant species, additional resources, more refined modelling of resource exploitation patterns over space by plants, the addition of allelopathy and considerations of longer time scales. All these additions to the model can be comfortably included into the overall conceptual framework developed in Chapter 1. Hopefully, the conceptual framework will help make the study of primary succession more mechanistic and aid us in our quest to understand and predict primary succession.

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