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Successional Changes in Leaf Nutrient Concentrations of Woody and Herbaceous Species

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Successional Changes in Leaf Nutrient Concentrations

of Woody and Herbaceous Species

(TITLE)

BY

Daniel Walter Kuchta

THESIS

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Abstract

Leaf nutrient concentrations are an example of a functional trait, a trait that can be used to understand community dynamics by observing how plants interact with their environment. I explored how leaf nutrient concentrations were affected over successional time by environmental changes. The majority of prior research on functional traits focuses on either woody or herbaceous species, but not both life forms simultaneously. To address this, I also explored the successional changes to leaf nutrient concentrations, separating the plant community into woody and herbaceous species.

Healthy, mature leaves were taken from 122 taxa of woody and herbaceous species in a mesic successional community located in New Jersey, USA. Leaf nutrient concentrations of C, N, P, K, Ca, and Mg were determined for the community using abundance-weight trait values. All of the nutrients except leaf Mg produced temporal patterns that became stable later in succession, but had different values between life forms. For example, leaf K concentrations remained fairly constant throughout succession, but were always higher in herbaceous species. The exception to this pattern was that the concentration of leaf N in herbaceous species increased later in succession rather than remaining stable.

My study identified that a strong pattern in leaf nutrient concentrations exists over succession, mostly driven by changes in life form. However, the overall community approach masks trajectories of individual life forms within the

community, which indicates that succession is acting differently on the leaf nutrients of herbaceous and woody species.

Dedications

To my wife Sara, for dealing with me to be away for the last three summers as I completed my degree. I could not have done this without your patience and support.

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Introduction

Succession, a fundamental process of community assembly, is the change in species composition in an ecological community over time (Walker & Wardle, 2014). Succession is centered on the behavior of species assemblages over time that result in a change in the species composition and architecture of a community. Interactions of organisms with each other and the physical environment drive succession. Three general factors that drive succession are variation in site availability and conditions, species availability, and species performance (Pickett, et al., 2011). Site availability refers to site's history of disturbance and resource availability (Meiners, et al., 2015). Species availability refers to a species' ability to disperse to a site or survive a disturbance (Noble & Slatyer, 1980). This includes landscape factors and the ability of a species to disperse its seeds. Finally, species performance involves the mechanisms by which species interact with each other and sort themselves out based on their ecological traits (Meiners, et al., 2015).

A shift towards the study of functional ecology has been a major focus for ecologists in recent years. Functional ecology is based on the ecological attributes, or traits, that a species possesses, rather than a traditional focus on the taxonomic identity of the individual species (Meiners, Pickett, & Cadenasso, 2015). A mechanistic understanding of the community dynamics can be developed through analyzing the responses of functional traits to the environmental factors of the community (McGill, et al., 2006). Therefore, species with more similar traits are more likely to have similar roles or function in the

community (Kleyer, et al., 2012). Suites of core functional traits common to all plant species can be used to describe regenerative processes and physical characteristics of a plant (Diaz, et al., 2004, McGill, et al., 2006, Wright, et al., 2005). These functional traits include leaf size and thickness, seed mass and height, specific leaf area, and woodiness. These, and other traits, can be used to understand the composition of species within an ecosystem, and how plant species use the resources that are available to them (Garnier, et al., 2004). While succession is rarely predictable for the species that will colonize or dominate a site, it can be predictable for the types of functional traits that the species exhibit (Prach & Walker, 2011, Fukami, et al., 2005). Therefore, a functional approach to succession may yield better generalizations about the interactions within a plant community that regulate community assembly.

Leaf nutrient concentrations (LNC) are key functional traits of plants, reflecting both the physical and physiological function of leaves. Each leaf nutrient is associated with different processes, allowing separation of leaf functions. The majority of N and P in leaves are found in metabolically critical molecules like proteins, ribosomes, and nucleic acids (Wright et al., 2005). Leaf N is strongly linked to a plant's photosynthetic ability, while leaf P is also related to a plant's photosynthetic ability (Evans, 1989, Reich, et al., 2009). Similarly, Mg is essential to plants for the formation of chlorophyll (Hermans, et al., 2010). The main roles of K within plants is as an activator for many enzymes in the cell, and to control transpiration via the opening and closing of stomata (Evans & Sorger, 1966, Wright et al., 2005). As the primary function of leaves is photosynthetic,

these nutrients should be critical in identifying important functional variation among species during succession.

While N, P, Mg, and K are important to physiological process of plants, Ca and C are important to adding physical structure to the plant. Calcium provides structure for cell walls and membranes (White & Broadley, 2003). Carbon, the largest single, non-water, component of leaves provide the physical structure for leaves, allowing leaves to grow larger and persist for a longer time (Navas et al., 2010). Plants with larger leaves, and higher concentrations of C, have more access to sunlight and water, while the rate of photosynthesis is slowed (Kikuzawa & Ackerly, 1999). These leaves are better equipped for surviving hot, dry conditions when turgor pressure is not sufficient to support leaves. Higher concentrations of C would lead to higher leaf C:N, investing more of the plant's resources to structural processes (Navas et al., 2010). Leaf nutrient concentrations also impact ecosystem level processes. High investment in leaf structural traits, often expressed as a high leaf C:N ratio, decreases the decomposition rate of leaves in litter (Freschet, et al., 2012). Higher concentrations of leaf N, or a lower C:N ratio, make plants more susceptible to losing their leaves to herbivores (Haukioja, et al, 1985). These leaf nutrient traits can be a useful proxy for identifying successional changes within a community.

The general trend for mesic successional communities is to shift from predominantly herbaceous species to predominantly woody species, causing an overall shift in functional traits over time (Meiners, Pickett, & Cadenasso, 2015). Plant traits, including leaf nutrient concentrations, differ between the two life

forms. Herbaceous plants do not have permanent above ground structures, which allows them to resprout often and spread clonally much more commonly than woody species. On the other hand, woody species have strong permanent structures designed to survive environmental stressors (Klimešová, 2016).

Woody plants tend to have a relatively higher concentration of C, while herbaceous plants tend to have higher levels of the other nutrients (Foulds, 1993; Navas et al., 2010), reflecting their potential growth rates. Most studies of plant traits center on either woody or herbaceous species, not both. Since many traits differ between the two life forms, doing a study on both life forms simultaneously is challenging (Meiners, Pickett, & Cadenasso, 2015) as differences between woody and herbaceous species may mask important variation within each life form.

I used 41 years of vegetation data from the Hutcheson Memorial Forest Center in New Jersey, USA to study changes in leaf nutrient concentrations in a successional plant community. During the transition from agricultural fields to closed canopy forest, I addressed these questions regarding the leaf nutrient concentrations: 1) Do leaf nutrient concentrations change with succession? 2) Do changes in leaf nutrient concentrations over succession differ between woody and herbaceous species? and 3) Does combining woody and herbaceous species obscure important successional variation within each group?

Methods

Study site

The Buell-Small Succession Study (BSS) is a long-term study of plant succession that began in 1958, and is still active today. It takes place at the Hutcheson Memorial Forest Center (HMFC), in the Piedmont region of Somerset County, New Jersey. HMFC contains 26 hectares of old-growth forest with 30 hectares of fields surrounding the forests (Meiners, Pickett, & Cadenasso, 2015). The Piedmont region of New Jersey has an average temperature between 10.5°C to 12.2°C with an average precipitation between 101.6 cm and 116.8 cm. (Piedmont Landforms, 2008).

The BSS fields are abandoned agricultural fields that lie next to the old-growth forest (Figure 1). At the time of abandonment, the forest was composed of a tall canopy of a variety of mature oak species (*Quercus* spp.), and a subcanopy layer of dogwood trees (*Cornus florida*) which served as a source for later successional species. The BSS contains ten fields, which either contained row crops or hay prior to abandonment (Table 1). Fields were abandoned in pairs from 1958 to 1966 and either contained litter from its final crop or were plowed to bare ground. Each field is subdivided into 48 smaller plots, measuring 2.0 m long by 0.5 m wide (Meiners, Pickett, & Cadenasso, 2015). The plots were surveyed every year in late July from abandonment until 1979. From 1980 to the present, each field is surveyed every other year. During sampling, each species that is present in the plot is recorded, as well as the percentage of the plot that is covered by that species. If a species overhangs a plot, the percentage to which it

overhangs is estimated and recorded. The percentages of bare ground, lichen, litter, and moss are also recorded (Meiners, Pickett, & Cadenasso, 2015). The BSS fields provide the long-term context for my leaf nutrient study.

Sampling and plant trait analysis

Healthy, mature leaves were collected over a three-year period from HMFC from 124 taxa of plants, with most of the specimens collected in 2010. Samples contained 43 woody species and 81 herbaceous species. Samples were taken from healthy individuals growing under optimal environmental conditions for each species. Leaves were dried at 60°C for 48 hours and stored dry until processed. Ten or more leaves were collected of an individual species if possible, and treated as a single species value. The leaves were sent to the University of Georgia Stable Isotope Lab (Athens, GA) for chemical analysis of the leaf nutrients. Leaf C and leaf N were analyzed with Micro-Dumas Combustion. Leaf P was analyzed through continuous flow calorimetric analysis. Leaf K, Ca and Mg concentrations were obtained by flame absorption spectrophotometry.

Data analyses

Percent cover values for all species that leaf nutrient data were available for were used to calculate the relative abundance of each species in each BSS field. This value is the percent abundance for each species relative to all species surveyed. The percent cover of all species all ten BSS fields that were woody plants was also calculated for each successional year. Relative cover values were multiplied by each leaf nutrient concentration to calculate an abundance-

weighted trait value for each field in all years. This was performed first for all 124 species in our study (total community), and then separately for herbaceous and woody species. I only used the first 41 years of data from each field as field ages differed and replication decreased after that age. Trait values were interpolated between years after 1980 when sampling switched to alternate years.

To determine whether succession resulted in changes in leaf nutrient concentrations that differed between woody and herbaceous species, a repeated-measures ANOVA was conducted for each leaf nutrient using Pillai's Trace (Gotelli & Ellison, 2004). As woody species were in very low abundance initially, these analyses started with data from year 5, when woody cover averaged over 1% of the total community. To avoid pseudoreplication with the alternate year sampling, analyses were conducted in 2-year intervals.

These univariate analyses were supplemented with a multivariate analysis to examine successional changes in all nutrients simultaneously. A principal components analysis (PCA) was conducted on the leaf nutrient concentrations of the entire species pool using a correlation matrix. This resulted in two PCA axes that accounted for a total of 69.1% (PC I, 48.4%; PC II, 20.7%) of the variation in the data set. To generate an overall successional trajectory in leaf nutrients, abundance-weighted PC scores were calculated for each field and averaged as was done for the individual nutrients.

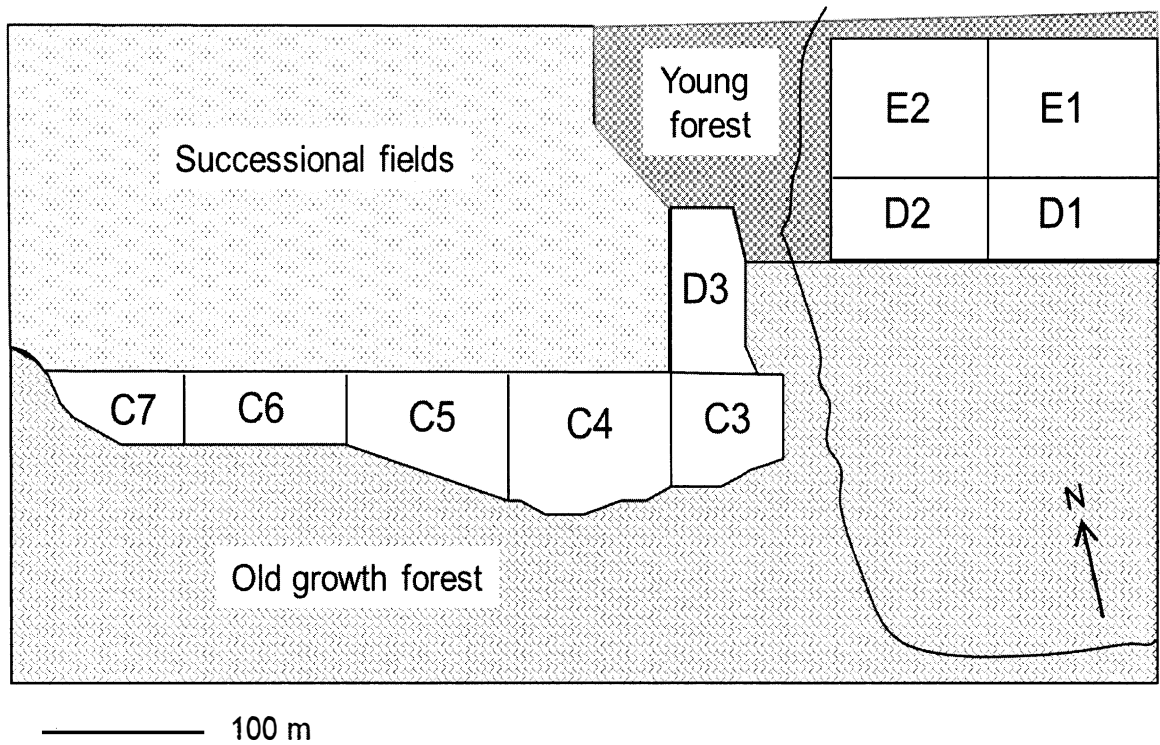


Figure 1: Map of the study site. The abandoned agricultural fields listed comprise the Buell-Small Succession Study (BSS).

Table 1: Information about the time and the treatment of abandonment in each of the 10 fields in the BSS.

Field	Year abandoned	Season abandoned	Last crop	Mode of abandonment
C3	1958	Fall	Row crop	Leaf litter
D1	1958	Fall	Row crop	Leaf litter
D2	1960	Fall	Row crop	Leaf litter
D3	1960	Spring	Row crop	Bare soil
E1	1962	Fall	Hay	Leaf litter
E2	1962	Spring	Hay	Bare soil
C6	1964	Fall	Hay	Leaf litter
C7	1964	Spring	Hay	Bare soil
C4	1966	Spring	Hay	Bare soil
C5	1966	Fall	Row crop	Bare soil

Results

As is typical of succession in the region, the BSS fields changed from an herbaceous dominated community to a woody dominated community through succession. Year 20 is highlighted as the point where the BSS fields became a predominately woody community. Early in succession, annual herbaceous species like *Ambrosia artemisiifolia* and *Barbarea vulgaris* dominated the community. Grasses such as *Elytrigia repens* and *Agrostis stolonifera* became the dominant herbaceous species a few years into the BSS study. Larger perennial species like *Solidago rugosa* and *Aster pilosus* took over from the grasses as the most dominant herbaceous species around year 10, and continued as the dominant species until around year 20. Years 30-40 are characterized by a dramatic drop in the overall abundance of herbaceous species. At the end of the successional sequence, larger herbaceous species suited for the forest understory such as *Alliaria petiolata* and *Polygonum virginianum* were the most abundant herbaceous species present.

Woody species also showed large compositional variation over time. The first woody species to colonize the BSS were lianas, or woody vines, such as *Lonicera japonica* and *Toxicodendron radicans*. As succession approached year 10, the woody community saw many shrubs begin to grow, with *Rosa multiflora* being the most abundant species. Tall trees later added to the woody dominance of the community such as *Acer rubrum* and *Ailanthus altissima*, resulting in the decline in shrubs.

The total plant community in the HMFC changes from an herbaceous dominant community to a woody dominant community (Figure 2). At year 25, the percent woody cover reaches 80%, and in the following years stays constant (Figure 2). The shift towards woody cover generated similar temporal patterns in leaf nutrient concentrations of all 6 nutrients (Figure 3). The concentrations of all 6 nutrients for the total community remains static starting around year 25 and continuing later in succession (Figure 3). Leaf C and Ca show an increase in concentrations to that point in time, while leaf N, P and K show a decrease in concentrations (Figure 3).

Leaf nutrient concentrations were significantly different for all nutrients except for leaf Mg when separating woody and herbaceous communities (Table 2). Levels of leaf C and leaf Ca were higher in woody species whereas the levels of leaf N, P and K were higher in herbaceous species (Figure 3). Neither a significant life form nor temporal variation was found for leaf Mg (Figure 3).

Leaf N was the only nutrient to show a significant pattern for leaf nutrient concentration for succession (Table 2). The concentration of leaf N in the herbaceous community declined until year 20, and then began to consistently rise again. The concentration of leaf C in herbaceous species follows an opposite pattern, peaking in year 20, with a decline in the following years (Figure 3). The levels of leaf C in woody species stay constant through succession, as the entire community shift towards a higher concentration of leaf C (Figure 3). This change relates to the changes in percent woody cover of the whole community (Figure 2). The change in percent woody cover also translated to an increase in leaf Ca

concentration, and a decrease in leaf N, P and K concentrations (Figures 2 and 3).

The PCA generated two informative axes explaining the variation in the data. Leaf C was negatively correlated axis I of the PCA, while leaf N, K, P and Mg were positively correlated with axis I. Leaf P and K were slightly correlated with axis II of the PCA, while leaf Ca and Mg were negatively correlated with axis II. The mean abundance-weighted PC scores show the trajectories of woody and herbaceous species to be in opposite directions from each other. Herbaceous species displays an initial correlation with higher leaf N, P and K. The nutrient signature shifts toward leaf C during mid-successional years. After about a 10 year transition period starting in year 16, the herbaceous species slowly shifted back towards higher concentrations of leaf N, P and K later in succession. PCA axis II indicates that the herbaceous species are more correlated with leaf P and K early in succession, and shift slightly towards leaf Ca and Mg later in succession. The mean abundance-weighted PC scores for woody species displays an initial reduction of leaf C over time. After about a 7 year transition period starting in year 10, the woody species slowly shifted back towards a correlation with greater leaf C later in succession. PCA axis II indicates that the woody species are more correlated with leaf Ca and Mg than leaf P and K, and that correlation is slightly weaker early in succession (Figure 4).

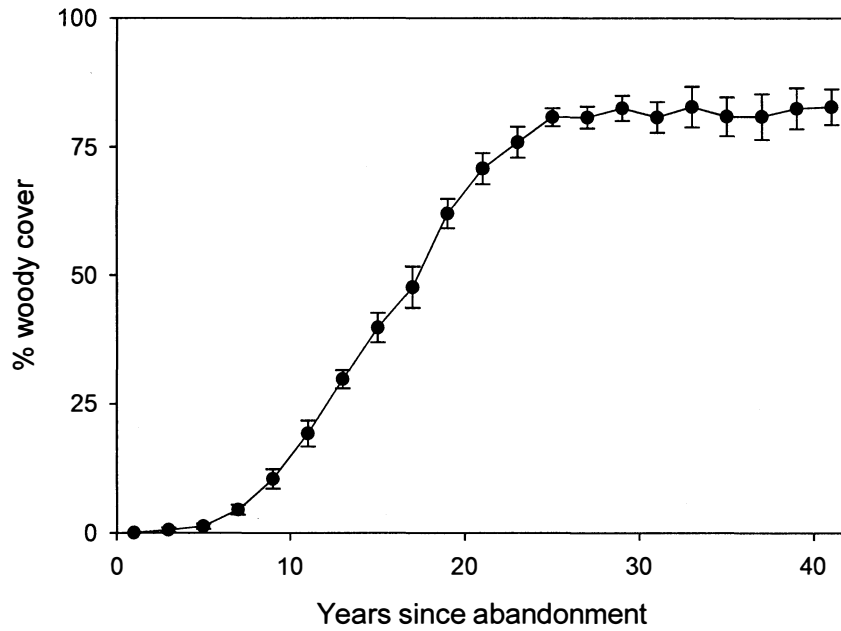


Figure 2: The percent of the BSS fields that were covered by woody species. Error bars represent \pm standard error across the ten fields. For clarity, data points are only plotted for every other year.

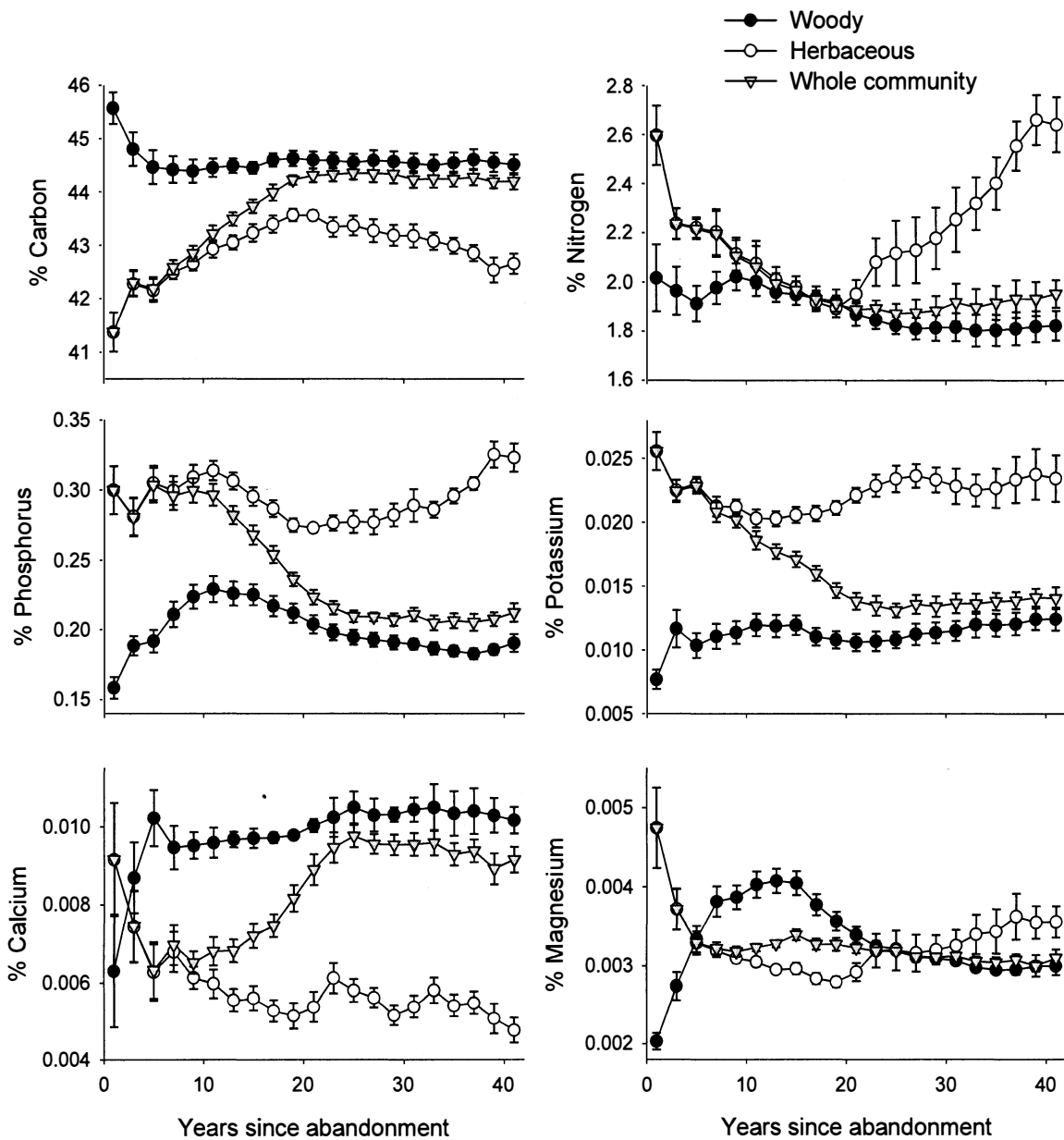


Figure 3: Changes in leaf nutrient concentrations with succession by growth form. Error bars represent \pm standard error across the ten fields. For clarity, data points are only plotted for every other year.

Table 2: Repeated measures analysis of abundance-weighted changes in leaf nutrient concentrations over successional time for herbaceous and woody species (life form). Within-subject effects are multivariate tests using Pillai's Trace. Significant values ($p < 0.05$) are indicated in bold.

Nutrient	Factor	F	P
Carbon	Life form	73.83	<0.0001
	Time	9.53	0.2505
	Form × Time	3.98	0.3777
Nitrogen	Life form	17.91	0.0005
	Time	408.96	0.0024
	Form × Time	379.50	0.0026
Phosphorus	Life form	243.64	<0.0001
	Time	12.65	0.2184
	Form × Time	9.33	0.2527
Potassium	Life form	149.28	<0.0001
	Time	5.10	0.3369
	Form × Time	11.52	0.2283
Calcium	Life form	105.74	<0.0001
	Time	3.02	0.4277
	Form × Time	17.80	0.1847
Magnesium	Life form	2.42	0.1369
	Time	181.53	0.0583
	Form × Time	181.32	0.0584

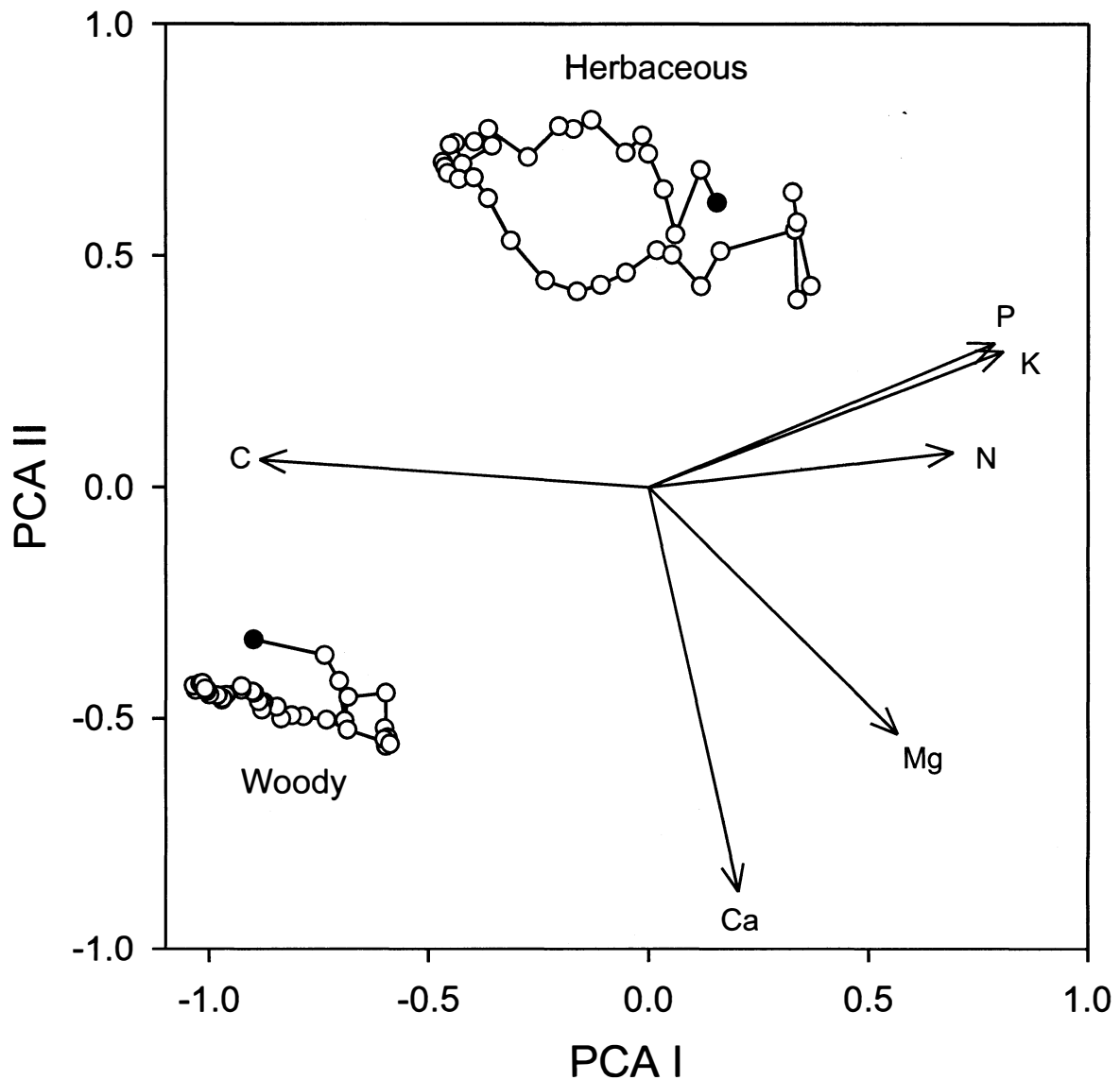


Figure 4: Multivariate changes in leaf nutrient concentration over succession for woody and herbaceous species. Data plotted are the mean abundance-weighted PCA scores of the 10 fields with the first year (age=5) indicated by a filled symbol. Vectors represent the loadings of the individual leaf nutrients in PCA space.

Discussion

When looking at the total (herbaceous and woody) BSS community, all of the leaf nutrient concentrations showed a successional change with the exception of leaf Mg. These temporal changes reflect the change in life form through successional time and the differences in leaf nutrient concentrations between woody and herbaceous species. As the community shifted to woody dominance, leaf nutrient concentrations transition from the herbaceous values to the woody values. Woody species have fundamental differences in leaf nutrient allocations than herbaceous species do, resulting in different strategies for survival (Meiners, Pickett, & Cadenasso, 2015).

Fast growing species which acquire nutrients quickly shift to slow growing, taller species which conserve their nutrients over succession (Garnier et al., 2004, Reich et al., 1995). Plants have a fast rate of growth, and more rapid turnover early in succession, when light and resources are highly available (Tilman, 1987). For example, a successional study of a rain forest in Venezuela found that the leaf life span of species increased temporally with succession. The same study found that specific leaf area decreased temporally, while leaf toughness increased in contrast (Reich et al., 1995). Specific leaf area is the area generated by one gram of dry leaf tissue and is strongly associated with growth rates of species (Westoby, 1998, Wright et al., 2004). Specific leaf area for the HMFC was found to be high in early successional species, and decreased temporally (Duffin, 2015), consistent with the change in leaf nutrient concentrations that I found.

These tradeoffs in plant strategy are characteristic for woody and herbaceous species. Early successional traits are more characteristic of herbaceous species, while later successional traits are more characteristic of woody species, which is reflected in the changes of leaf nutrient concentrations across the whole community. The temporal patterns of leaf nutrient concentrations of the total community reflect the structural transitions of the system. Leaf C and Ca increase until year 20 before remaining constant in the following years. In contrast, leaf N, P and K decrease to around year 20 before remaining constant in the following years. Canopy closure of the fields occurred around this point in time, and is likely responsible for the stabilization of leaf nutrient concentrations as herbaceous species declined. Lianas and shrubs were replaced by trees as the dominant woody life form during the transition to canopy cover. Herbs, vines and shrubs saw a large decrease in abundance once canopy closure took place (Meiners, Pickett, & Cadenasso, 2015). Canopy closure is the critical threshold for the dynamics of the BSS during succession.

While changes were observed across the entire BSS community, changes within life forms were also observed. Large changes to the leaf nutrient concentrations of all 6 nutrients were observed during the first few years following abandonment of the BSS fields. These changes reflect the initial randomness of which species colonize first, and successional years 1-4 are not included in my analyses as a result. Initial conditions of the 10 BSS fields varied because the mode and time of abandonment differed with each field (Table 1). This led to differences in community assembly early in succession (Li et al.,

2016). Additionally, there would be some randomness with regards to which species were able to reach the abandoned sites initially. These factors, combined with the very low abundance (<1%) of woody species, created very high initial variance in the leaf nutrient concentrations for each life form.

Starting with year 5, similarities are observed for the trajectories of leaf nutrient concentrations of the two life forms, with leaf N and Mg being exceptions. Leaf C, P, K and Ca all show functional equivalence with respect to their leaf nutrient concentrations trajectories (Hubbell, 2005). While individual species do vary in leaf nutrient concentrations, the woody and herbaceous communities reach a functional equivalence (similar successional patterns) for these nutrient concentrations when all species of each life form are studied. This happened despite the overall differences in their base line nutrient concentrations. Only small differences in patterns are observed when looking at leaf C, P, K and Ca over successional time.

In contrast to leaf C, P, K and Ca, the concentrations of leaf N between life forms converge and later diverge from each other, resulting in dramatically different successional patterns. Early successional, short-lived herbaceous species need high allocation of leaf N in order to conduct photosynthesis at a maximum rate (Chapin, 1980). In contrast, clonal, mid-successional herbaceous species like goldenrods (*Solidago* spp.) had lower concentrations of leaf N and would have slower growth rates. Canopy closure around year 20 had a major effect on leaf N concentrations of herbaceous species. In order to persist in the understory of a forest, plants need functional traits adapted for low-light

environments (Landhausser, et al., 1997). The dominant goldenrods in mid-successional years were slowly replaced by herbaceous species with traits more suited for shade tolerance. These late-successional herbaceous species have higher concentrations of leaf N to utilize the limited light available for photosynthesis. Higher leaf N concentrations in the forest understory may be due to plants being able to retain nitrogen longer in low-light environments (Eckstein & Karlsson, 1997). A drawback to having higher leaf N concentrations is that leaves become more palatable to herbivores, a major problem in an environment when resources are limited (Matsuki and Koike, 2006). The woody community had a slight decrease in leaf N concentrations as lianas were replaced by shrubs and trees through succession, as more resources are needed for structural processes of larger woody species. This also reflects the opportunistic, rapid growth of lianas early in succession (Ladwig & Meiners, 2010).

The principle component analysis (PCA) generated a visualization for the overall trajectories of the woody and herbaceous species across all leaf nutrients. This analysis revealed more subtle changes in leaf nutrients within both communities. Herbaceous species showed a trend of towards more leaf C in mid-succession, and then transitioned back towards more leaf N, P and K very slowly. The slow transition is probably due to the high abundance of a few perennial species like goldenrods (*Solidago* spp.) which dominated the fields for over a decade. Canopy closure in the woody species shifted the late-successional herbaceous community back towards higher leaf N, P and K. In contrast to the herbaceous species, woody species had the opposite trajectory in

leaf nutrients over succession. The woody community initially shifted towards more leaf N, P and K, before completing a quicker transition back towards greater leaf C at year 10. Abundances of woody species typically change more slowly than herbaceous species, which causes slower transitions in community assembly (Meiners, Pickett & Cadenasso, 2015). The reversal of the trajectory of leaf nutrient concentrations was slower in the herbaceous species, but the woody species had a much more gradual year to year change.

Conclusions

My study showed large changes in leaf nutrient concentrations over succession, which reflected the shift from a predominantly herbaceous community to a predominately woody community. These successional changes to the total community are generally the same for all of the leaf nutrients, with nitrogen being the exception. A multivariate approach to the data shows that woody and herbaceous species have different approaches to leaf nutrient allocation, and have transitions of leaf nutrient allocation at different times during succession. When the data is combined for the whole community, or for all of the nutrients, many of the individual patterns in leaf nutrient concentrations are obscured. Therefore, more research needs to be devoted to understanding leaf nutrient concentrations of plants.

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