SOIL CARBON AND NUTRIENT CYCLING ACROSS COVER TYPES IN SOUTHERN APPALACHIAN HARDWOOD FORESTS

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Abstract

Appalachian mixed hardwood stands along south facing slopes of the Ridge and Valley physiographic province were used to determine fine scale soil respiration (R_s) and nutrient dynamics among four distinct cover types, white oak (WO, *Quercus alba* L.)*,* scarlet oak (SO, *Quercus coccinea* Muech.)*,* chestnut oak (CO, *Quercus montana* Wild.) and a pine-oak co-dominant cover (PO, *Pinus spp.* and *Quercus spp.* (primarily *Pinus pungens* Lamb. and *Q. montana*)). Null hypotheses were that: (1) R_s and its relationship to environmental drivers would not differ among the cover types, (2) water and nutrient use efficiencies (WUE and NUE) would not differ among the cover types, and (3) litter decomposition would not differ among the diverse cover types. In 0.02 ha plots, replicated four times, R_s and associated variables (e.g., soil temperature and moisture) were measured. Measurements occurred in three sub-sample locations per plot, from July 2014 - December 2015. In each plot, foliage from two trees of the dominant species were collected to determine WUE using $\delta^{13}C$ isotope discrimination. Nutrient (N, P and K) content of this fresh foliage was compared with that of litterfall to determine NUE. Litterbags, collected over a one and half year period were used to determine decomposition rate constants for each dominant species. Soil temperature and moisture explained 71% of the variability in R_s. Although only slight, there were statistically significant differences in the R_s models due to cover type. At the same soil temperature, the PO cover type had the highest R_s while the SO, WO cover types had the lowest R_s. WUE, and NUE varied among cover types. SO

had significantly greater WUE than the other species, including Table mountain pine, which had the highest NUE. Higher elevation cover types (i.e., PO and CO) ad greater decomposition rate constants. Among the factors driving decomposition, soil C: N ratio had the strongest correlation to decomposition. Correlations between decomposition and productivity variables of total above ground biomass, total stand biomass, and aboveground net primary production also exist. In conclusion, carbon and nutrient cycling varies across the level of cover type within the southern Appalachian hardwood forests. Future efforts to focus on carbon and nutrient dynamics in the context of land use or global change should consider these finer-scale differences.

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Chapter One: Introduction

1.1   Background

Native hardwood forests contribute considerably to the total productivity of the forests of the

southern United States. Yet, less is known on the fundamental factors controlling their carbon

and nutrient cycles, which are important components of productivity. This is largely because

changes in water availability, transpiration, productivity, and species composition often vary

over short distance. Globally, biogeochemical processes are driven by climate and the quality

and quantity of substrate, which themselves are highly variable over time and space (Reichstein

et al., 2003). Thus, understanding spatial dynamics of the drivers and responses of forest

ecosystems is relevant at multiple spatial scales.

1.1.2 Soil Respiration

Carbon dioxide (CO_2) in plants is fixed through the process of photosynthesis. Resulting

photosynthate is partitioned to the various parts of the plant. Partly, the portion partitioned to

the roots is respired through root respiration and is one component of total soil respiration (R_s).

Soil respiration is also fueled by litter inputs in which CO_2 is released during decomposition and

nutrients are mineralized for plant growth. R_s is influenced by many factors, some of which

work independently while others are reported to have interactive effects as they drive R_s.

1.1.2.1 Temperature as independent driver of R_s

 Temperature drives R_s with R_s increasing as temperature increases (Davidson et al., 1998).

Changes in temperature influence the activity microbial enzymes differently (Katterer et al.,

1998). At the global scale, temperature influences R_s, where warming increases R_s (Reich and Schlesinger, 1992). Davidson et al. (1998) reported an exponential function relating CO_2 fluxes to soil temperature, and that temperature accounted 80% of R_s variability as well in seasonal and diel variation in soil CO_2. Wildung et al. (1975) found temperature was better correlated with Rs in fall, winter and early spring and soil moisture was well correlated when temperature is above 6^oC. In one study, a 1% increase in mean annual temperature (MAT) led to a 10% loss in organic carbon, when MAT was 5^oC; whereas the same increase in a 30^oC MAT region would lead to carbon losses of only 3% (Kirshchbaun, 1994). Thus, areas of the globe with relatively low temperatures appear more sensitive to changes in temperature. The amount of organic C and N is closely associated with climate factors (i.e., soil moisture and soil temperature) as associated to R_s. Kucera and Kirkham (1971) found soil Carbon loss was highly correlated with temperature in Missouri prairie, which according to Toland and Zak (1994) is due to the effect of temperature on microbial enzymes. Soil C fluctuates with changes in temperature (Trumbore et al., 1996). Birch (1960) showed that change in organic gel is due to drying that increases surface area for effective growth and the development of the microbial population. Mathes and Schriefer (1985) showed soil respiration follows soil temperature pattern. DeForest et al. (1991) showed that temperature explains 50 to 80% of the variations in soil respiration, including mineral and litter respiration, although they vary by their C residence time.

Understanding the complex and often interactive drivers of R_s is particularly critical in the diverse landscapes found in southern Appalachian hardwood forests. Changes in species composition, which occur over relatively short distances, could have large impacts on litter quality, decomposition and R_s. Changes in elevation and aspect have direct influences on R_s in

the sense that the sites facing direct solar radiation experiences higher soil temperatures, which will increase R_s.

1.1.2.2 Soil moisture as driving factor of R_s

Soil moisture also influences R_s by changing soil oxygen, substrate, and mineralization, (Davidson et al., 1998; Reichstein et al., 2003; Oberbauer et al., 1992; Linn and Doran 1984). Orchard and Cook (1983) used a range of water potentials and found the range from -0.01 to -0.02MPa caused a 10% decrease in microbial activities and 5 MPa caused 40-time increase in microbial activities. Mayer et al. (1982) found net nitrogen mineralization linearly related to moisture content (%). Adu and Oades (1978) found flush of CO_2 twice because of disruption in soil aggregates resulting in easier access of microbes to carbon as source of energy. Optimal soil moistening increases bacterial population and soil respiration (Lund and Goksoyr (1980). CO_2 production declined, as water content falls below field capacity. The temperature effect on R_s occurs only when sufficient soil moisture permits microbial activities (Davidson et al., 2000). Maximum soil respirations is often associated with intermediate water contents, with higher or lower values decreasing R_s (Oberbauer et al., 1992; Linn and Doran 1984).

Martin and Bolstad (2009) reported that landscape positions, topography and soil textures have influences on moisture infiltration rates, surface flow and soil water residence all of which can impact R_s. Temperature and moisture together affect by plant density, thickness of forest floor and site wetness by moderating microclimates (Binkley and Fisher, 2013).

1.1.2.3 Interdependence of temperature and moisture content as factors for soil respiration

 Soil temperature and soil moisture often do not affect R_s independently. A study by Wildung et al. (1975) found the interaction between temperature and moisture accounted for 70% of variation in R_s .Optimum R_s was found at moisture content 6-10% and temperature of 15°C (Wildung et al 1975). Many other studies reported soil CO_2 flux as a function of soil temperature - soil water content interaction (Kucera and Kirkham, 1971; Grahammer et al., 1991; Norman et al., 1997; DeForest et al., 2008; Pangle and Seiler, 2002).

 1.1.2.4   Substrate and vegetation as Rs drivers

Substrate plays an important role as source of energy for microbial activities as they influence R_s. Foliar carbohydrate partitioned to the roots becomes accessible to soil microbes as a source of energy (substrates) to influence R_s. Foliar clipping or defoliation reduces, CO_2 efflux by 21-49% (Bremer et al., 1998), and grazing reduces CO_2 by 20 to 37% in a pasture and annually estimate of defoliation reduces R_s by 17 to 18% (Bremer et al., 1998). Similarly, litter fall contributes greatly to R_s (DeForest, et al., 2009; Raich, and Nadelhoffer, 1989; Raich and Tufekcioglu, 2000).

Plant biomes influences soil respiration rates differently through their effects on soil microclimate and structure, quantity and quality of detritus, and litter fall (Raich and Tufekciogul, 2000). Findings have shown coniferous forests have lower rates of R_s than the adjacent broad-leaved forests growing on the same soils (Raich and Tufekciogul, 2000), grassland have 20% higher R_s than forest stands (Raich and Tufekcioglu, (2000). However, Raich and Schlesinger (1992) found R_s was associated with NPP. Plants control heterotrophic activities

through carbon supply and soil N mineralization by the microbes improve plant productivity. Webster (2000) found highly productive aspen (*Populus tremula* L.) had greater R_s than less productive jack pine (*Pinus banksiana* Lamb.) stands of the same age. Raich and Nadelhoffer (1998) found productive Hawaiian forest stands have higher aboveground net primary productivity (NPP) and R_s than least productive stands. This was reported differently in other findings where, R_s in Lower Michigan and boreal Alaska were similar although they differed widely in their above ground production (Ruess et al., 1996; Jurik et al., 1991). In contrast, Reiners (1968) reported a poor correlation between R_s and plant productivity. Elsewhere, sites without vegetation have less impact on annual soil CO_2 emission because R_s is a net flux driven from different processes (Raich and Tufuckcioglu 2000).

1.1.3   Water use efficiency

The species distribution of mixed forest is influenced by topography (i.e., slope and aspect), soil, and disturbance history (Elliot et al., 1997). For instance, soil moisture as influenced by slope and aspect have a significant influence on the forest composition. The effect of aspect influences the distribution of the species, xeric taxa, pines and ericaceous shrubs dominate the southwestern slopes at high ridges while the mesic species such as white oak are found in the lower elevation of the sites (McEvoy et al., 1980). Differences in N cycling patterns (e.g., mineralization and nitrification rates), in   also influence species composition (Gilliam et al., 2001; Fabio et al., 2009).

Forest productivity and water use are highly coupled. Tian et al. (2010) examined net primary productivity (NPP), evapotranspiration (ET) and water use efficiency (WUE) in southern United

States forests and found in years that as ET decreased, WUE and NPP increased. When water stress occurs, plants respond by increasing WUE (Hsiao, 1974).

Plants have different abilities in using their available moisture. Plants, which have higher carbon gain per unit of water loss, have a great water use efficiency. Water use efficiency (WUE) is commonly estimated by stable carbon Isotope discrimination (Guy and Holowachuk, 2001). Principally the plants discriminate against the heavier isotopes of carbon ($\delta^{13}C$) during CO_2 fixation under normal pressure gradient between the atmospheric CO_2 and intercellular CO_2 compositions. The amount of discrimination changes when plants become moisture stressed (O'Leary 1981). In C_3 plants, discrimination is mainly due to the amount of photosynthetic carboxylation enzyme and the ratio of CO_2 intercellular to atmospheric partial pressure controlled by stomata conductance (Farquhar et al., 1989). Carbon isotope discrimination ($\delta^{13}C$) differ in sites with arid areas having $\delta^{13}C$ values of -20 to -26‰, higher rainfall area have $\delta^{13}C$ values of -27 to-34 ‰ and the wetter sites have similar values as in higher rainfall areas in the range of -26 to -34 ‰ (O'Leary 1988; 1992; Ehleringer and Cooper, 1988; DeLucia and Schlesinger, 1991). Plants in drier sites often have higher WUE as compared to wetter sites. In generally term, $\delta^{13}C$ values increase from wettest to driest sites and the mean yields (stem volume) are positively correlated to $\delta^{13}C$. However, some studies found higher WUE plants in moderate elevations (Guy and Holowachuk, 2001).

 Evergreen trees have lower $\delta^{13}C$ discrimination than deciduous species at any given altitude (Marshall and Zhang, 1994). For example, *Thuja plicata* (western red cedar), had lower mean discrimination than *Larix occidentalis* (western larch) a deciduous conifer, meaning the evergreen to have higher water use efficiency (Marshal and Zhang, 1994; Farquhar and

Richards, 1984). CO_2 assimilation and isotopic composition ($\delta^{13}C$) compared between conifer (*Pinus pinaster* Ait.) , a drought avoiding species and Oak (*Quercus petaea* Matt.) ,a drought tolerant species and the result was that *Pinus pinaster* had a negative relationship between Ci/Ca ratio (intercellular CO_2 concentration/ ambient CO_2) and $\delta^{13}C$ suggesting stomata was a factor in WUE, while in oak the relationship was positive suggesting non stomata was a driving factor in WUE (Picon et al., 1996).

Plants with higher WUE often have better production in water limiting conditions and have exorbitant production in favorable moisture conditions (Guy and Holowackuk, 2001). Water use efficiency and biomass production are closely associated (Livingstone et al., 1999). Studies have also found that *Acacia koa* Gray $\delta^{13}C$ increased with elevation from -30.2 to -26.8 ‰ and in a greenhouse, the seedlings of *Acacia koa* Gray $\delta^{13}C$ increased from -27.7 to -24 ‰ as water supply decreased (Ares and Fownes, 1999).

1.1.4 Nutrient use efficiency

Plants survive and grow, even in environments where resources are limited, by reusing nutrients to fix more biomass. The basic strategy, known as reabsorption or retranslocation, involves withdrawing nutrients from senescing leaves prior to abscission (Clark 1977, Turner 1977; Vitousek, 1982). Findings have shown nutrient use efficiency inversely relates to nutrient concentration (Vitousek, 1982). Poor resource sites transfer less N from vegetation to the forest floor because plants on such sites often retranslocate their N internally. As a result, litter in such stands has a longer residence time due to its inherently poor quality (i.e., high C:N ratio) as compared with litter found in resource rich stands (Fassnacht and Gower, 1999). For

instance, conifers have higher NUE than hardwoods, and conifers generally have lower quality

litter (Fassnacht and Grower, 1999). Similarly, longer leaf/needle lifespan, as in the evergreen

forests commonly found on poor sites, have low nutrient content (especially N content), low

litter quality, and longer C and N residence times (Fassnacht and Grower, 1999). Elliott and

White, (1994) showed that plants with higher NUE strategies tolerate nutrient stress on sites of

low soil fertility through phenotypic adjustment to compete effectively with other species. Birk

and Vitousek (1986) showed NUE was correlated with decreasing N availability. Pastor et al.

(1984) found red pine (*Pinus resinosa* Ait.) had high N and P use efficiencies on sites with lowest

N. The ability to retain nutrients before senescing differs by the nutrient, the species, and the

site. A measure of this reabsorption is referred to as nutrient reabsorption efficiency (NRE). NRE

has been established for many nutrients (Vergutz et al., 2012). With the exception of Ca, the

NRE for many other nutrients (e.g., C, N, P, K and Mg) typically decrease with an increase in

nutrient status (Vergutz et al., 2012; Arts and Chapin, 2000; Kobe et al., 2005). Nitrogen NRE is

higher in deciduous than in evergreen species, and in trees relative to shrubs (Yuan and Chen,

2009; Vergutz et al., 2012), while P NRE is higher in graminiods and evergreen trees than in

deciduous species (Arts, 1996; Yuan and Chen, 2009).

1.1.5. Litter decomposition

One of the most important process perpetuating forest ecosystems is litter decomposition. It

controls the availability of nutrients and the releases of CO_2 to the atmosphere (Bragazza et al.,

2007). Decomposition mainly is controlled by factors of climate, litter chemistry and

decomposer microorganisms whereby litter chemistry dominates in favorable climatic

conditions (Couteaux et al., 1995). Catabolizing complex organic structures in poor quality litter

requires enzymatic activities driven by higher activation energies from increasingly high temperatures (Couteaux et al., 1995; Hobbies, 1996; Murphy et al., 1998). Principally decomposition in broadleaf litter is usually faster initially than needle litter, which then decline eventually at the end of the decomposition period where differences between litter types have fewer visible differences (Prescott et al., 2000). Cornelissen (1996) showed deciduous litter decomposed twice as fast as evergreen. Cole and Rapp (1981) reported the turnover in temperate deciduous forests was four times faster than temperate coniferous. Other studies found inconsistency in decomposition and mineralization between broadleaf litter and conifer needles (McClaugherty et al., 1985; Grower and Son, 1992). Taylor and Parkinson (1988) showed trembling aspen (*Populus tremuloids Mixhx*.) litter decomposed more rapidly than pine, except under very dry and cold conditions where pine decomposes faster than aspen. Mixing needle and broadleaf litter was found to hasten the decomposition rates (Fyles and Fyles, 1993; Taylor et al., 1989; McTienan, 1997).Other studies found no effect of mixed litter on decomposition rates of the species (Klemmedson, 1992; Rustard and Cronan, 1988). Perry et al. (1987) associated the initial faster rate of decomposition to higher litter nutrient concentration, low lignin and polyphenols concentrations.

Keeping climatic factors constant, litter from nutrient rich stands would favor faster decomposition rates. Experiments using different nutrient fertilizers independently and in mixture, showed that the control treatment (without fertilization) had a lower decomposition rate constant (k value) of 0.0027 and where N and P were added the k valued increased to 0.0069 (Rejmankove and Sirova, 2007). This suggests higher litter nutrient contents and concentrations stimulates higher decomposition rates. However, in uncontrolled climatic

conditions litter from the drier sites decomposed faster than wetter sites, despite lower litter chemistry (Ozalp et al., 2007). Importantly, in water tupelo (*Nyassa aquatic* L.) litter biomass contributes greatly to the total above ground NPP compared to stem wood biomass in rates of 63% litter to 37% stem to total biomass (Ozalp et al., 2007). Others found litter mass was 34 - 60% of the total biomass (Conner, 1994; Clawson et al., 2001).

1.2   Hypothesis and Objectives

Forest ecosystem of the Ridge and Valley physiographic province vary in moisture, fertility, and stand structure and species composition along a gradient in slope. Often times abrupt changes in species cover types occur over very short distances. Considering these factors raises questions about the controls on carbon and nutrient cycles in this region. Namely, 1) How is soil CO_2 efflux driven by soil temperature and moisture across these cover types? 2) What are the patterns of water use efficiency (WUE) and nutrient use efficiency (NUE) across these cover types. 3) What differences and similarities exists in litter decomposition among these cover types? 4) How do these above measured variables related to changes in productivity?

Our specific hypothesis are:

HO: The relationship of soil CO_2 efflux to abiotic factors will not show any differences among different cover types found in the southern Appalachian Mountains. Our **specific objectives** here are to determine the major environmental drivers of R_s, in this system, develop a predictive model for R_s, and determine whether changes in cover type influence R_s.

HO: Common species found in the southern Appalachian Mountains will not differ in water use efficiency (WUE), nutrient use efficiency (NUE), or nutrient reabsorption efficiency (NRE). Our

specific objectives here are to: 1) determine if a relationship exists between WUE, NUE, and NRE among cover types, 2) determine if changes in litter, above ground and stem biomass production are related to WUE, NUE and NRE in these cover types and 3) determine if foliar tissue nutrition is related to site quality, WUE, NUE and NRE.

HO: With exception of pine species, litter decomposition will not vary among the different species of oak. Our **specific objectives** here are to 1) determine the differences in the litter decomposition rates among three oak cover types and Table mountain pine (*Pinus pungens* Lamb.), a common species found in the mixed-oak pine cover type, 2) determine how chestnut oak litter decomposition varies in other cover type locations and 3) examine how decomposition rates are related to site productivity.

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Chapter 2. Soil CO$_2$ Efflux Across Diverse Cover Types in a Southern Appalachian Hardwood Forest

Abstract

To understand how soil respiration (R$_s$) is driven by abiotic factors and changes in litter and cover types, R$_s$ was measured under four dominant canopy types white oak (WO, *Quercus alba* L.), scarlet oak (SO, *Quercus coccinea* Muech.), chestnut oak (CO, *Quercus montana* Wild.) and pine-oak (PO, *Pinus spp. & Quercus spp.)* in a southern Appalachian mixed oak forest (Virginia). Our hypothesis was that R$_s$ would not differ among the canopy types and a single functional model can be used for all of them. Together with soil temperature and soil moisture, R$_s$ was measured in three sub-sample locations between July 2014 and December 2015 in 0.02 ha plots replicated four times for each canopy type. Across the different canopy types, soil temperature and moisture explained 71.3% of the variability in R$_s$. Although only slight, there were some statistically significant differences in the models due to canopy type. At the same soil temperature, the PO cover type had the highest R$_s$ while the SO and WO cover types had the lowest R$_s$. These trends appear to be related to litterfall, litter decomposition rates and foliar nutrient quality.

2.1   Introduction

Carbon dioxide (CO$_2$) in plants is fixed through the process of photosynthesis and resulting photosynthate is partitioned to the various parts of the plants. A portion of photosynthate partitioned to the roots is respired through root respiration and is one component of total soil respiration (R$_s$). Soil respiration is also fueled by litter inputs in which CO$_2$ is released during

decomposition and nutrients are mineralized for plant growth. R_s is influenced by many factors, some of the factors works independently while others are reported to have interactive effects as they drive R_s. Soil temperature and soil moisture have been reported in many studies (Wildung et al., 1975; Martin and Bolstad, 2005; Davidson et al., 2000; Howard and Howard, 1993), as principal drivers of R_s. The influence of soil temperature on R_s comes mainly from the Q_{10} (activation) of the enzymes in microorganisms during the breakdown of organic substrate (Katterer et al., 1998). Optimal R_s is normally achieved by optimum temperature and moisture, which differ with forest types, altitude and latitude. For example, Lamberty et al. (2004) found the optimum temperature and moisture content in broad leave trees as $35^{\circ}C$ and 37% respectively while in conifers the respective values were $25^{\circ}C$ and 21%.

Fungi and bacteria drive R_s optimally in a temperature range $25^{\circ}C$ to $30^{\circ}C$; however bacteria remain active at temperatures above $30^{\circ}C$, while fungi favor temperatures below $25^{\circ}C$ (Pietikaninen et al., 2005; Lipson et al., 2002; Ley and Schimidt, 2002).

Understanding the complex and often interactive drivers of R_s is particularly critical in the diverse landscapes found in southern Appalachian hardwood forests. Changes in species composition, which occur over relatively short distances, could have large impacts on litter decomposition because of R_s. Changes in elevations and aspects have direct influences on R_s in the sense that the sites facing direct solar radiation experiences higher soil temperatures, which will increase R_s. Similarly, soil moisture is impacted by elevation and aspect. Martin and Bolstad (2009) reported that landscape positions, topography and soil textures have influences on moisture infiltration rates, surface flow and soil water residence all of which can impact R_s. Temperature

and moisture affect by plant density, thickness of forest floor and site wetness by moderating microclimates (Binkley and Fisher, 2013).

Soil mineralization and net primary production (NPP) are correlated to soil respiration. Rustad and Fernandez (1998) showed that elevated soil temperature could increase mineralization and NPP by 40% and 19% respectively. They also reported coniferous forests have lower mineralization and NPP due to lower temperatures that kept carbon in recalcitrant and oxidized forms which would require higher temperatures to breakdown this fixed soil organic carbon (SOC), a scenario which is not the same with other forests (Rustad and Fernandez, 1998; Peterjohn et al., 1994). A similar link between NPP and soil respiration was reported by Reich and Tufekcioglu (2000) for three highly productive Hawaiian forests that provides adequate microbial substrate and have about 30% higher soil respiration as compared to lower productive sites. Jurik et al. (1991) and Ruess et al. (1996) did not find such differences among the forest stands and suggested that local factors such as soil types, inter site habitat variability, species composition or land use history might have obscured correlations that occur across broad geographical scale.

In this study, we examine R_s in common cover types found in the valley and ridge physiographic province of the southern Appalachian Mountains. These cover type changes occur over relatively short distances as slope position, slope percent and aspect change. Our objectives were to determine the major environmental drivers of R_s, in this system, develop a predictive model for R_s, and determine whether changes in cover type and their litter properties influence R_s

2.2   Material and Methods

2.2.1 Experimental design

We examined four common cover types: white oak (WO, *Quercus Alba* L.), scarlet oak (SO, *Quercus coccinea* Muench.), chestnut oak (CO, *Quercus montana* Wild.) and mixed pine-oak (*PO, Pinus spp. & Quercus spp*). Within each of these cover types, four circular, 1/50 ha plots were established. The experiment was designed as a randomized complete block with four replications (Figure 2. 1). The block in this case is time taken during measurements such that all the different cover types were measure at very narrow time, this avoided concentration measuring treatments different time of the day.

2.2.2   Measurements

2.2.2.1 Aboveground Biomass

In each plot, all trees with >5.1 cm diameter at breast height DBH (DBH, 1.37m above ground), were measured for diameter in March 2015 and March 2016. Stem biomass (wood + bark) was estimated by equation $M=aD^b$ where M is mass in kilograms, D is the diameter at breast height in cm**,** a and b were constants established for each species, WO (a=0.1392, b=2.1844), SO (a=0.1434, b=2.2391), CO (a=0.0741, b=2.5226), and Pine (a=0.0751, b=2.3261). To predict the total above ground biomass different constants were used, WO (a=0.2022, b= 2.1666), SO (a=0.1241, b=2.4395), CO (a=0.0907, b= 2.5344) and Pine (a=0.1040, b= 2.3373) (Ter-Makaelian and Korzukhin, 1997).

The site quality was estimated using Forest Site Quality Index (FSQI), which was formulated to predict site quality in the Ridge and Valley terrain, based on aspect, slope percent and slope position; by clinometer slope percent was estimated at two points in each plot. A compass was used to determine aspect. Slope positions was identified at plot installation. FSQI for each plot corresponds to range of site index established in the literature (Carmean, 1975; Meiners et al., 1984).

Litter was collected in each plot from two randomly located litter traps. The litter traps were constructed from 0.16 m^2 laundry baskets lined with nylon screen placed above the dominant understory vegetation. In general, the top of the traps were 0.75 to 1.2 m above the ground. Litter was collected each month, sorted by species and dried at 65°C to constant weight.

2.2.2.2   Soil CO_2 Efflux

A LI-COR 6250 infrared gas analyzer (LI-COR biosciences. Lincoln, NE) with 24.5 cm, diameter chamber was used to measure R_s (Tyree et al., 2014). In each experimental unit (Figure 2.1), three sub-sample points were chosen randomly each time measurements were collected. In total 20 measurement dates occurred between July 2014 and December 2015. Measurements were taken monthly in summer, autumn, and winter. In spring as bud break occurred rapidly, measurements occurred more often. In the same spots where R_s were taken, soil temperature at 10 cm and soil moisture from 0 to 12 cm were also measured. Soil temperature was measured using a digital thermometer (AcuRite 00641, Chaney Instrument Co., and Lake Geneva, WI). Percent volumetric soil moisture was measured using a hydrosense soil-water sensor (Campbell Scientific USA, Logan, UT).

2.3   Data Analysis

JMP Pro 11 software was used for analysis of variance and Minitab 17 statistical software was used for multiple linear regression analysis. Subsamples in each plot were averaged and used as the experimental unit. Stand biomass variables were subjected to analysis of variance and treatment means were compared using student t –test. Multiple linear regressions was used to determined environmental and stand variables related to R_s. Data was transformed by natural log for soil respiration and soil moisture content and square root transformation for temperature. Once an overall model was developed the influence of cover types on the slopes and intercepts were examined. Multivariate correlation using JMP determined the correlation between Rs and plant parameters and above ground productivity. The litter weight in grams was converted into kilograms per hectare (metric values) and means compared each month using ANOVA.

2.4   Results

Cover types were accurately delineated as the aboveground biomass of each cover type is largely dominated (71% and above) by their respective species names (Figure 2.2). In the PO stand, 71.7% of the stand biomass is pine (primarily Table mountain pine, *Pinus pungens* Lamb.) and 22.2 % oak (primarily chestnut oak). WO were found on lower foot slope positions and had a FSQI of 11 (site index approximately 74) which was not different from SO. CO higher in elevation and on a shoulder slope had a FSQI of 9 (site index 69) and the pine oak FSQI was 7.5 (site index of 61). Stems per hectare varied from 336 in SO to 863 in the PO. SO had the largest diameter (36.9 cm) and chestnut oak in the PO plots had the smallest diameters (19.7 cm) (Table 2.1).

As expected R_s was higher during warmer growing season months and lower during the colder dormant season months (Figure 2.3a). Rates fell quickly in autumn as leaves came off the trees even while soil temperatures were still high. For example, in both years soil temperatures were still around 14°C in October (Figure 3b) yet R_s dropped sharply. R_s was also lower during the growing season of the second year, which does not appear to be related to temperature (Figure 2.3a and 2.3b). Temperatures in the months of July, August and September in both growing seasons were similar. Soil moisture however was lower in August and September of the second growing season averaging 8% and 3 % respectively, which may have contributed to the lower rates in the second growing season, WO R_s dropped at the end of each growing season sooner than any of the other stands types.

Soil moisture was generally much lower in PO and CO cover types (Figure 2.3c). At times, it was as much as 7 % lower than the SO and WO cover types. Over all dates, soil moisture in the cover types averaged 15.7%, 15.8%, 9.8% and 10.0% for the WO, SO, CO and PO respectively.

The WO cover type dropped litter earlier compared to the other cover types (Figure 2. 4). In October of the first year of observation, litterfall in WO (888 kg/ha) was significant higher than CO (468 kg/ha) and SO (129 kg/ha). The same was true in October of the second year of observation, where WO had significantly higher litterfall mass relative to PO and SO. The slight yearly differences in litter fall peak quantity could be due local factors such as wind and animal disturbance.

In our multiple regressions of all cover types combined, soil temperature alone explains 70.7% of the variation in R_s. Soil moisture were significant if added to the model (Temperature $p>0.001$

and Moisture p >0.024 respectively) but the R^2 only increases to 71.3% when moisture was added.

Although not large, there were statistical differences between cover types when they were modelled separately (Table 2.2 and Figure 2.5). The intercept for PO and SO were significantly lower and higher showing PO was more influenced by the independent variables than SO. A unit change in temperature will have more impact on R_s of PO followed by CO, SO and WO because soil temperature slopes followed the same order of being high in PO and least in WO. The influence of moisture is less on SO, as the estimated soil moisture was significantly lower in SO, although R_s was not influenced significantly by any stand variables (e.g. number of trees/ha, diameter and aboveground NPP)

2.5   Discussion

There were small but statistically significant differences in the R_s response to soil temperature and moisture among the canopy types. PO and CO had the greatest temperature response while WO and SO had a lower temperature response. PO and CO stands are found at higher slope positions, had a lower site quality than either WO, and SO cover types. These R_s response differences in cover types are not due to temperature differences since this is accounted for in the model. It could be that changes in litter decomposition, litter chemistry or soil microbiology may be causing the differences. We found (chapter 4) that both SO and WO had the lowest litter decomposition rates. SO also had the lowest foliar nitrogen concentrations (chapter 3) reflected in higher litter C:N ratio (88.7) as compared to the lower C:N ratio (53.2) in WO litter. Studies have shown that mass loss by R_s is greater from litter with higher nutrient availability

(Gosz et al., 1993; Trofymow, 2002) and litter quality stimulates and increases the release of recalcitrant litter organic materials (Fyles and Fyles, 1993; Biones and Ineson, 1996). Rapid decomposition in the first phase of decomposition is due to labile and soluble nutrient compounds and the slow decomposition in the second phase is associated breakdown of complex compounds, and this ability differs among species (Melillo, 1989).

Overall, soil temperature was a major driver of soil respiration (Figure 2.3a & 2.3c) but a slightly better prediction was achieved with soil moisture added to the model. The influence of moisture on Rs might partially explain the lower R_s rates in second growing season where soil moisture was lower in late summer and R_s was lower. Soil moisture averaged 11% in August and September in the first year and 5.4% in the second year (Figure 2.3c).

Many studies have confirmed that temperature is the major driver of R_s. Davidson et al. (2000) found 80% of the variations in soil respiration was explained by temperature but better explanations of the variations were achieved when soil moisture was incorporated. Moisture is critical to chemical reactions and must be present for decomposition to occur. Reich and Schlesinger (1992) found the power of predicting R_s increased when both temperature and moisture were considered. However, some studies looked at soil temperature and soil moisture as independent factors in driving the soil respiration. Temperature as an independent R_s driving factor was clearly shown when relating higher temperatures of the Tropics to cold temperature zones of Boreal and Tundra. The turnover in the Tropics is high due to higher temperature, which positively influences productivity and higher Rs. Boreal, and Tundra productivity is low due to low turnover as result of low temperature in its effect on R_s (Trumbore et al., 1996; Schlesinger and Andrew, 2000). Some studies considered soil moisture as exclusively

independent driver of R_s (Peterjohn et al., 1994; Christensen et al., 1997; Rustard and

Fernandez, 1998.

There was a sudden sharp drop in soil respiration in September for WO and in October 2014 for

SO, PO and CO when the temperatures were still relatively high at about 14°C (Figure 2.3a and

2.3b) at the time of heavy litter fall. Leaf senescing signals cessation of photosynthesis which

ultimately affects assimilation and henceforth reduction of substrate (carbohydrates) for root

(autotrophic) and microbial (heterotrophic) uses. In both years, R_s in the white oak cover type

began to show a decrease before other oak cover types (Figure 2.3a). We also found white oak

began dropping its foliage earliest at the end of each growing season (Figure 2.4). Reich and

Tufekciogulu (2000) showed that higher allocation of photosynthate to the soil would increase

below ground soil respiration. They also found a positive correlation between R_s and NPP.

Systems, which do not spare photosynthate in storage systems, have higher respiration rates

than those that do since more photosynthates reach the microbes responsible for R_s. Zak et al.

(1994) showed that C limitation to microbial activities support the suggestion that plants

control heterotrophic activities via the control over C supply. Studies have shown that because

of root exudates, the rhizosphere has influence on microbial assimilation and activities, which

increases when the concentration of exudate increases (Whipps and Lynch, 1983). Norton and

Firestone (1991) showed that nearly 57% of the microbial population and activities are

centered on the root periphery from where they benefit directly from the organic materials

produced by the plants as sources of energy to drive the soil respiration. Our study found the

PO had highest R_s and higher litter nutrient use efficiency (chapter 3). Many studies have shown

that habitats with poor soil nutrition produce more organic matter per a unit nutrient than

plants from nutrient rich habitats because of greater nutrient use efficiency (Reich et al., 1989; Vitousek, 1982; 1977; Clark, 1977; Monk 1966.) Perhaps this is related to the higher R_s rates in our PO treatment, which is on low site quality.

2.6   Summary and Conclusions

We found soil temperature and soil moisture explained 71.3% of the variation in R_s in our Appalachian hardwood stands. Temperature alone explained 70.7 % of the variation. Although slight, we did find that cover types significantly influenced the R_s models. The SO and WO cover types had lower R_s at the same temperatures and this decrease likely was related to decreased litter decomposition and earlier litter fall in the WO cover type.

In conclusion, soil respiration is mainly the interactive product of soil temperature and soil moisture. This implies that changes in diurnal, annual and periodical weather pattern could predict the R_s of the cover types differently. Also based on these findings, the total R_s under these cover types could be estimated for the entire Appalachian hardwood forests.

2.7   Acknowledgements

2.8   Literature cited

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Table 2.1. Stand characteristics for scarlet oak (SO), white oak (WO), chestnut oak (CO) and pine oak (PO, mixture of pine and oak) cover types; tree diameter, trees per hectare, basal area per hectare (m²/ha), annual litter mass, total biomass, stem biomass and forest site quality index (FSQI)

Cover Type		Diameter at Breast Height (cm)	Trees per ha	Basal Area m²/ha	Litter Mass ton/ha/yr	Total Biomass ton/ha	Stem Biomass ton/ha	Forest Site Quality Index
SO		36.9a	337	36.1	5.13bc	298.8a	162.8a	11a
WO		30.3ab	350	25.2	6.72a	224.4b	88.6b	11a
CO		23.4c	763	32.5	6.06ab	227.9b	179.1a	9ab
PO	Total:	22.2c	863	33.4	4.40cd	147.13c	103. 2b	7.5b
	Pine:	22.8c	688	28.1	3.57d	111.89c	77.9b	
	Oak:	19.7c	175	5.3	0.87e	35.24d	25.3c	

Table 2. 2. Multiple linear regression parameter estimates and adjusted R^2 values for soil CO_2 efflux (R_S) in the form: Ln (R_S) = Intercept + A [sqrt (Soil Temperature)] + B [Ln (Volumetric Soil Moisture)], including the general model with all data (n=960), and cover type-specific models pine-oak (PO), chestnut oak (CO), scarlet oak (SO), white oak (WO)] (n=240). Significant differences (p-value) between parameter estimates for the general model and a cover type-specific model are listed parenthetically below each parameter estimate.

Model	Intercept	A	B	Adj. R^2
General	-3.9948	1.2795	0.1255	0.71
PO	-4.8429	1.5042	0.1581	0.74
	(0.0015)	(<0.0001)	(0.6750)	
CO	-4.3815	1.3365	0.2123	0.72
	(0.1848)	(0.3775)	(0.1397)	
SO	-3.3319	1.1726	0.0133	0.75
	(0.0067)	(0.0077)	(0.0464)	
WO	-3.7245	1.1672	0.1674	0.67
	(0.1840)	(0.0049)	(0.6219)	
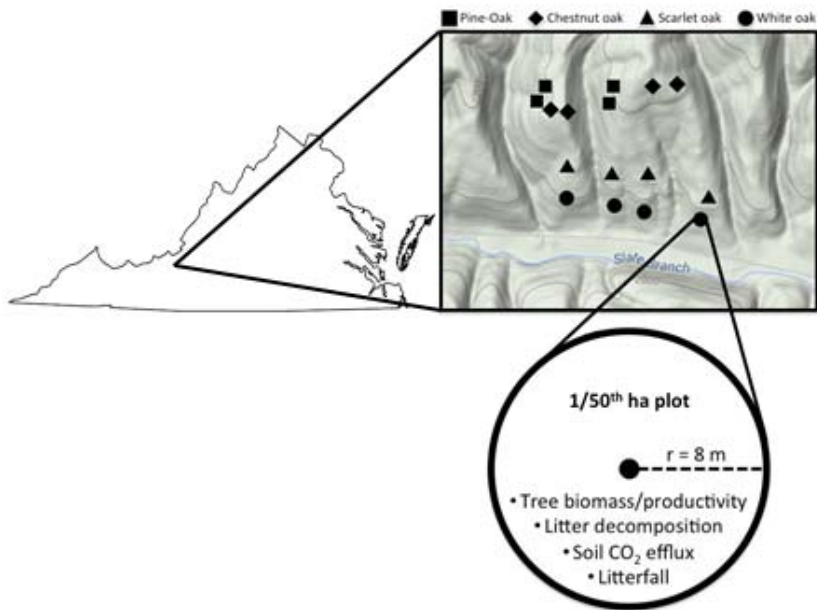
Figure 2.1. Study site location and basic design in the Valley and Ridge Physiographic Province in Montgomery County, Virginia.
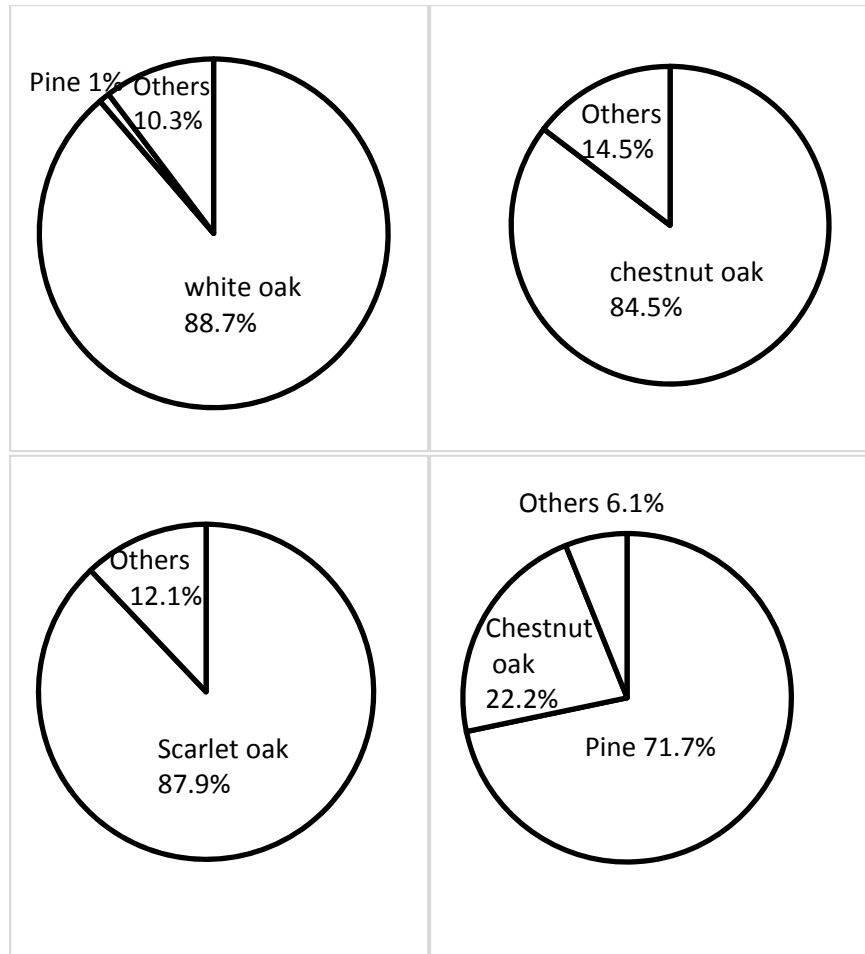
Figure 2. 2. Average species composition in each cover type, white oak (WO), chestnut oak (CO), and scarlet oak (SO) and pine oak (PO, mixture of pine and oak).
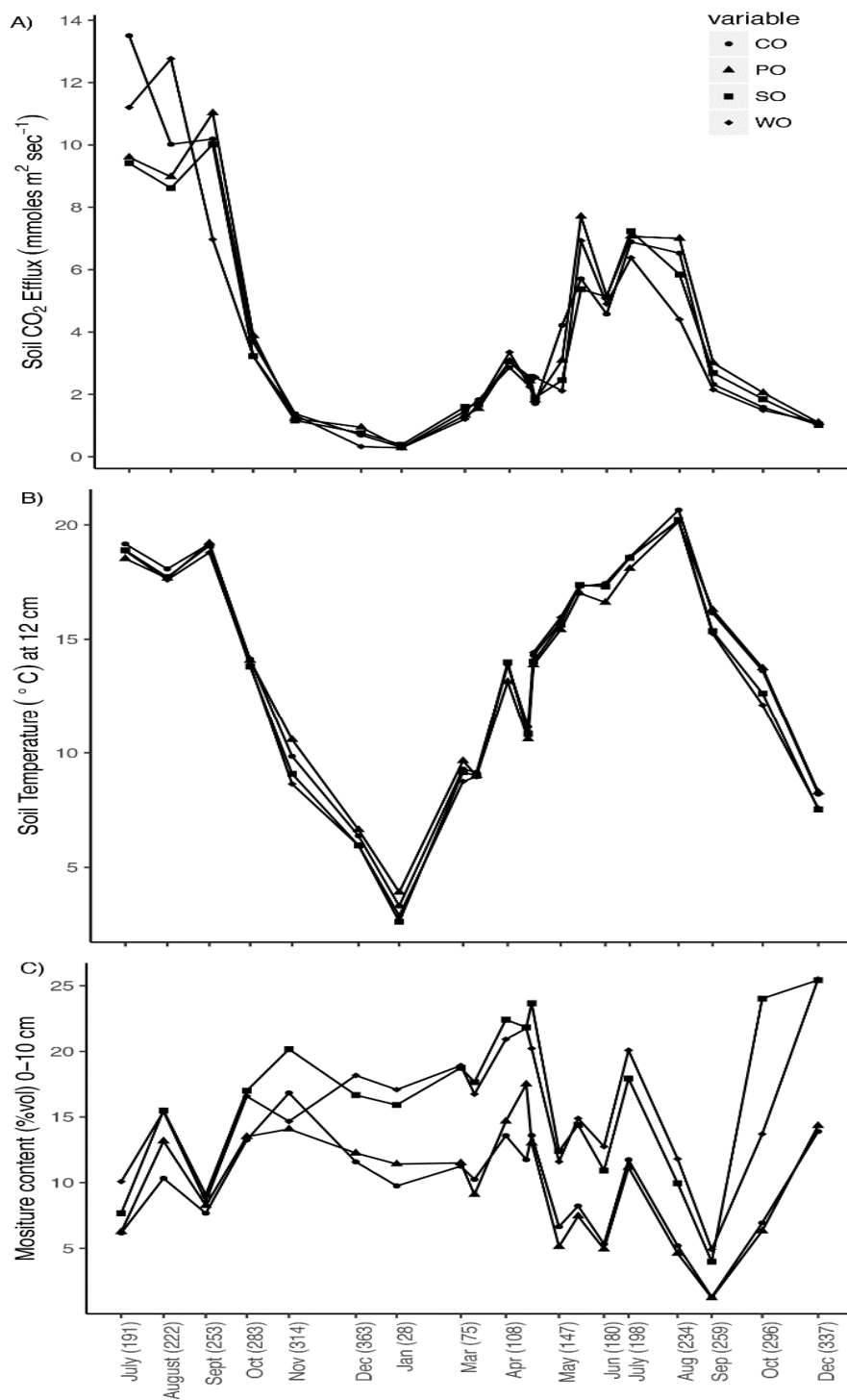
Figure 2.3. Seasonal trend of soil respiration (a), soil temperature (b) and soil moisture (c) for the scarlet oak (SO), white oak (WO), chestnut oak (CO) and pine oak (PO, mixture of pine and oak) from July 2014 to December 2015.
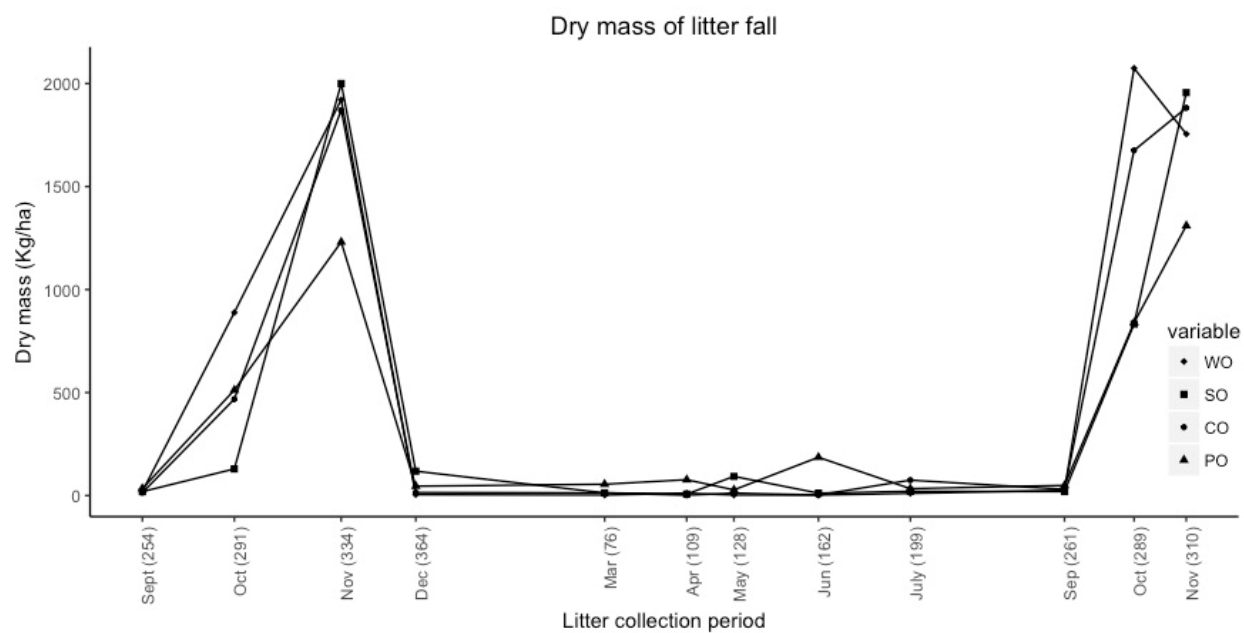
Figure 2.4. Monthly litter fall for white oak (WO), chestnut oak (CO), scarlet oak (SO) and Pine oak (PO, mixture of pine and oak) from two growing seasons.
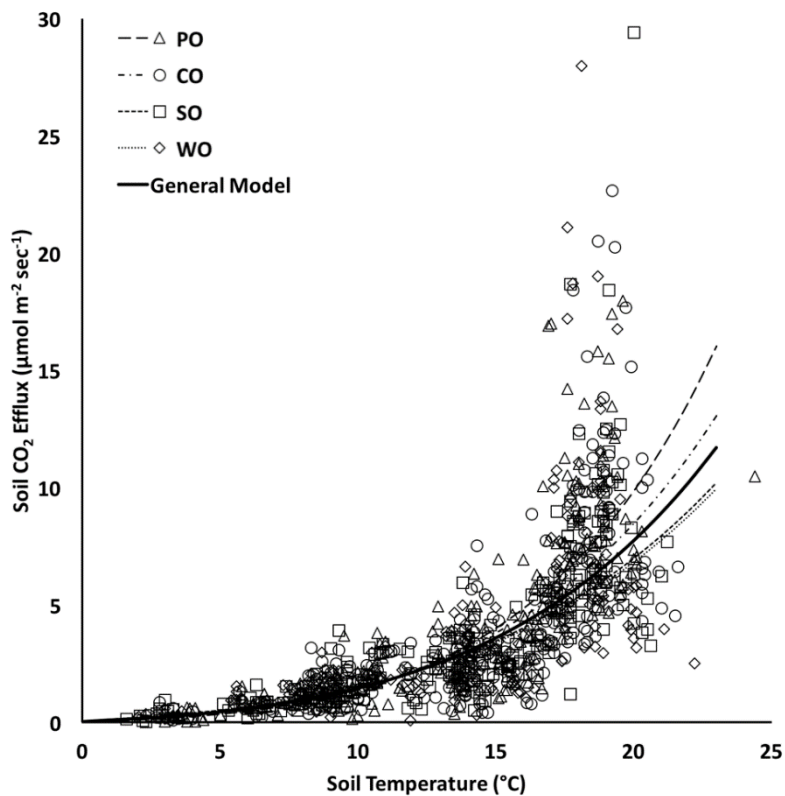
Figure 2.5. Soil respiration in southern Appalachian Mountains (Montgomery County, VA) as influenced by soil temperature for each cover type. Predicted lines were generated using the formulas in table 2.2 while holding soil moisture at the average for the time period, (pine-oak (PO), chestnut oak (CO), scarlet oak (SO), white oak (WO).

Chapter 3. Water use, Nutrient Use, and Nutrient Reabsorption Efficiencies in Diverse Cover Types in a Southern Appalachians Hardwood Forest

Abstract

The southern Appalachian hardwood forest is a diverse mixture of species, which change over relatively short distances due largely to topographic changes in slope position, slope percent soils and aspect. These topographic changes result in large differences in water and nutrient availability. We therefore hypothesized that the water use, nutrient use and nutrient resorption efficiencies (WUE, NUE and NRE) would be strongly related to species composition and position in the landscape. Four replicated plots (0.02 ha) were established in four dominate cover types ranging from lower slope, white oak (WO, *Quercus alba* L), scarlet oak (SO, *Quercus coccinea* Muench.) to higher slope chestnut oak (CO, *Quercus montana* Wild.), pine-oak (PO, *Pinus* spp. and *Quercus* spp). During the middle of the growing season, foliage from two trees of the dominate species per plot were collected from the upper third of the crown. WUE was estimated with this foliage using $\delta^{13}C$ isotope discrimination. Nutrient concentration of this fresh foliage was also determined and compared with litter of the same species collected from litterfall. Nutrient reabsorption efficiency (NRE) was estimated using the difference between fresh foliage and litter. Nutrient use efficiencies (NUE) for each of the dominate species was determined by comparing nutrient contents of foliage, aboveground and stem biomass produced. SO had significantly greater WUE than the other species, including pine. The nutrient contents and concentrations in senesced leaves were related to the growing season concentrations. With the exception of CO, NRE increased with decreasing fresh nutrient contents. Among the oak group, NRE for N, P and K were inconsistent with NUE. We concluded

moisture alone was not the only determinant factor for WUE and NUE in such a slope gradient but other plant adaptive characteristics should have also be involved. We therefore concluded that WUE, NUE, and NRE are important variable, which influences the cover types independently on litter and wood biomass. We also conclude that cover types of SO and CO have higher nutrient resorption ability, which is important for input management decision making, to avoid wasting material if application remained the same as for WO, which has low nutrient resorption ability. We therefore conclude that the cover types from poor sites quality have higher litter turnover because of higher rates of R_s. This implied that majorly growth sources (nutrient) in the drier upper slope and ridges come mainly from decomposition of litter.

3.1   Introduction

 The Appalachian hardwood forest is a mixed species forest within the Ridge and Valley physiographic province. Overall, the over-story composition is approximately 88% hardwood and 12% conifer, with main dominant species being white oak (*Quercus alba* L.), scarlet oak (*Quercus coccinea* Muench.), chestnut oak (*Quercus montana* Wild.), other hardwoods and the conifers (McNab, 1996; Warrillow and Mou, 1999). The species distribution of this mixed forest is influenced by topography (slope, aspect), soil, drainage class and disturbance history (Elliot et al., 1997). Soil moisture regime impacted by slope and aspect have a significant impact on the forest composition. The xeric taxa, pines and ericaceous shrubs dominate the southwestern slopes and high elevation ridges and mesic species such as white oak are in the lower elevation sites (McEvoy et al., 1980). Differences in N mineralization and nitrification rates, N cycling pattern plus other nutrient availability mediated by these site moisture differences also influence the species compositions (Gilliam et al., 2001; Zak et al., 1996; Fabio et al., 2009).

Forest productivity and water use are highly coupled. Tian et al. (2010) examined net primary productivity (NPP), evapotranspiration (ET) and water use efficiency (WUE) in southern United States and found in years that ET decreased, WUE and NPP increased. When water stress occurs, plants respond by increasing WUE (Hsiao, 1974; Waring and Running, 2007). WUE is the amount of CO_2 assimilated per unit of water transpired. WUE is commonly measured by stable carbon isotope discrimination of the foliage or other plant parts (Farquhar and Richards, 1984). Plants discriminate against ^{13}C during photosynthesis both because of slower diffusion of the larger ^{13}C molecule and enzymatic preference for ^{12}C (Garter and Taylor, 1992). Researchers have shown strong relationship between WUE and ^{13}C discrimination with ^{13}C discrimination decreasing when WUE is higher (Garter and Taylor, 1992).

Garter and Taylor (1992) examined δ ^{13}C in mid- summer and before leaf fall in autumn in both temperate deciduous and conifers species and found the δ ^{13}C from autumn leaves were more negative than those from mid –summer in both deciduous and coniferous species implying that better WUE was achieved in summer. Foliage of *Pinus spp*. was found to have a more negative δ ^{13}C values than deciduous trees found in the same location (Garter and Taylor, 1992). Foliar $\delta^{13}C$ varies with topographic position; deciduous leaves from xeric ridge sites had less negative δ ^{13} C values compared to deciduous from mesic site conditions. This is more apparent in the drier years where in xeric ridges less negative foliar $\delta^{13}C$ would be found and no change occurs in mesic valleys (Garter and Taylor, 1992). Species were also found to change their WUE depending on site, red maple (*Acer rubrum* L.) and sourwood (*Oxydendrum arboreum* (L.) DC.) had less negative $\delta^{13}C$ values in a riparian zone than when located on a xeric ridge (Garter and Taylor, 1992).

Nutrient resorption is an important component of nutrient cycling in temperate, deciduous hardwoods and it is a method for conserving limited nutrients by resorbing the nutrients before leaf abscission (Cote et al., 2002; Haag, 1974, Vitousek, 1982). Nutrient reabsorption differs by location and species, and importantly, nutrients resorbed are directly available for plant uptake reducing plant dependency on external nutrient up take from the environment, which fluctuates through time and space (Clark, 1977; Turner, 1977).

Plants generally resorb > 50% of their foliar N and P (Aerts, 1996; Vergutz et al., 2012), these values vary among the species based on adaptive characteristic of retaining tissue nutrient contents. Cote et al. (2002) showed resorption was greater when tissue nutrient concentration was lowest. In general, long living leaves such as needles are mainly associated with nutrient poor sites and short lived leaves are on nutrient rich sites (Beadle, 1966; Monk, 1966; Haag, 1974, and Chapin, 1980) which accounts for better resorption on poor site than on nutrient rich sites. Vitousek (1982) found plants on infertile sites have greater resorption than those in fertile sites, for instance, pine on poor site sites have resorption of 53.5%, 49.2% and 44.3% for N, P and K respectively which was higher than oak resorption values of 23.4%, 24.4% and 25% for the same respective nutrient elements from soil rich sites. Similarly, reports on greater resorption on nutrient poor sites than nutrient richer sites came from many studies (Vitousek, 1982; Aerts and Chapin, 2000; Grime, 1979; Chapin, 1980; Berendse and Aerts, 1987; Aerts, 1990; May and Killingbeck, 1992). This supports the poor site in producing more organic matter than nutrient rich habitats (Vitousek, 1982; Turner, 1977; Clark, 1977; Monk, 1966). Vitousek (1982) and Chapin (1980) showed that NUE for litter and wood are inversely associated to foliage nutrient concentration. Chapin and Kedrowski (1983) found a positive correlation

between leaf mass loss and nutrient resorption from foliage. Other studies found the association of higher nutrient status (leaf concentration) with greater resorption of N and P (Loneragan et al., 1976) but Aert (1996) did not find any evidence of nutritional control on nutrient resorption efficiency.

Nitrogen is closely associated with WUE (Field et al., 1983; Reich et al., 1989). Increases in the rates of N fertilization in both Douglas fir (*Pseudotsuga menziesii Franco*.) and poplar; (Populus x euroamericana (Dole) Guinier) resulted in an increase in WUE, (Field et al., 1983; Reich et al., 1989). Nitrogen is a major component of photosynthetic enzyme, Rubisco, increasing N enlarges the surface area of the enzyme to fix more carbon for the same amount of water transpired (Ripullone et al., 2003; Stitt and Schulze, 1994; Guehl et al., 1995; Farquhar et al., 1982). The increase in WUE in poplar was three times greater than Douglas fir (Ripullone et al., 2003). Perhaps in natural hardwood stands differences in nitrogen use efficiency, resorption efficiency and foliar nitrogen concentration will be related in a similar fashion to WUE.

This study examined water use efficiency (WUE), nutrient use efficiency (NUE) and nutrient resorption efficiency (NRE) in four common cover types found in the valley and ridge physiographic province of the southern Appalachian Mountains. These cover type changes occur over relatively short distances as slope position, slope percent and aspect change. Our overall goal was to determine how WUE, NUE and NRE are related to the distribution of these species, as soil water and nutrient status change site quality. Our specific objectives were 1) To determine if a relationship exists between WUE, NUE, and NRE and cover types, 2) To determine if changes in litter, above ground and stem biomass production is related   to WUE,

NUE and NRE in these diverse cover types and 3) To determine foliar tissue nutrition in relation to site quality, WUE, NUE and NRE.

3.2   Material and Methods

3.2.1 Experimental design

We examined four common cover types in a natural hardwood forest distributed along a southern slope in the Ridge and Valley physiographic province in Montgomery County, Virginia. The cover types were white oak (WO, *Quercus alba* L.), scarlet oak (SO, *Quercus coccinea* Muench.), chestnut oak (CO, *Quercus montana* Wild.) and mixed pine-oak (*PO, Pinus spp. & Quercus spp*). Within each of these cover types, four circular, 1/50 ha plots were established. The experiment was designed as a randomized complete block with four replications (Figure 3.1). The characteristic of the cover types are summarized in Table 3.1.

3.2.2   Measurements

In each plot, all trees >5.1 cm diameter at breast height (DBH, 1.37m above ground), were measured for diameter in March 2015 and March 2016. Stem biomass (wood + bark) was estimated by equation $M=aD^b$ where M is dry mass in kilograms, D is the diameter at breast height in cm, a and b were constants established for each species, WO (a=0.1392, b=2.1844), SO (a=0.1434, b=2.2391), CO (a=0.0741, b=2.5226), and Pine (a=0.0751, b=2.3261). To predict the total above ground biomass, different constants were used, WO (a=0.2022, b= 2.1666), SO (a=0.1241, b=2.4395), CO (a=0.0907, b= 2.5344) and Pine (a=0.1040, b= 2.3373) (Ter-Makaelian and Korzukhin, 1997).

The site quality was estimated using Forest Site Quality Index (FSQI) which was formulated to predict site quality in the Ridge and Valley physiographic province based on aspect, slope percent and slope position (Carmean, 1973; Meiners et al., 1984); Slope percent was estimated at two points in each plot with a clinometer. A compass was used to determine aspect. Slope positions were identified at plot installation. FSQI for each plot corresponds to range of site index established in the literature (Carmean, 1973; Meiners et al., 1984).

Two dominate/co-dominate trees were chosen in each plot except in PO were four trees were chosen two each from pine and oak, from which sample foliage was removed by shotgun from the upper one third of the crown. Ten to 20 leaves from oak or needles from Table mountain pine (*Pinus pungens* Lamb.) were sampled and packed separately in paper bags. In each plot, two 0.16m^2 litter traps were randomly fixed at various heights above the ground depending on surface vegetation. This was intended to avoid interference by understory vegetation. The litter was later sorted by species and the leaf litter for the dominant species in each cover type selected for analysis. The samples then were oven dried at 65°C to constant dry weight and milled to pass through a number 20 stainless steel mesh screen. The milled foliar samples were divided for isotopic analysis and foliar nutrient concentration analysis.

 The dry milled foliage and litter samples were kept in a desiccator prior to weighing. Samples (between 1.55mg to 1.75mg) were then sealed in aluminum capsules for analyses in a stable isotope ratio mass spectrometer (IsoPrime100, Isoprime Ltd., UK) (Boutton and Yamaski, 1996) for δ ^{13}C, and percent total C and N. The δ ^{13}C values were expressed relative to the Pee Dee Belemnite international standards (Craig, 1953; Farquhar et al., 1989).

For determination of P, K and other nutrients, the milled dry green foliage and leaf litter were weighed into separate ignition tubes and ashed in a muffle furnace at 500°C for 18 hours. To the ashed material in the test tube, ten ml of N HCl was added and sealed at the top with aluminum foil and left for 24 hours. Then 40ml of deionized H_2O was added and centrifuged for thorough mixing and left to settle for 1 hour. This solution was then transferred into a scintillation vial and filled to a final volume of 50ml. An atomic absorption spectrometer (AAS4129M, Electronics Corporation of India Limited, Hyderabad, India) was used to determine the concentration of P, K and other nutrients. Total nutrient contents were then calculated using the ppm concentrations (from fresh foliage and litter) and total foliage collected.

Nutrient resorption efficiency (NRE) and nutrient use efficiency (NUE) for each of the cover types was determined following the equations modified from Cote et al. (2002):

$$NRE = \left(\frac{[Nutrient\ in\ Foliage - Nutrient\ in\ senesced\ leaf]}{Nutrient\ in\ foliage} \right) * 100$$

$$NUE = \frac{litter\ or\ wood\ produced\ (\frac{kg\ C}{ha})}{nutrient\ (\frac{kg\ nutreint}{ha})}$$

The weight of litter was obtained from the litter basket collections. Nutrient concentration of litter was converted into kilogram per hectare by (kg/ha) which then was used in the calculation of NRE and NUE. The wood produced (kg/ha) was determined by transforming diameter values using the equations adapted from Ter-Makaelian and Korzukhin, 1997.

3.3   Statistical Analysis

WUE, NUE, and NRE were analyzed using Analysis of Variance in the JMP11 statistical package. The multivariate analysis using JMP 11 was used for the correlations between WUE, NUE, NRE, and productivity. The correlation between NRE, NUE and WUE and the respective nutrients concentrations were determined by multivariate analysis using JMP 11.

3.4   Results

Cover types varied in different carbon and nutrient cycling metrics. Overall SO had less negative $\delta^{13}C$ (-28.6), followed by the pine (-29.3) while the values of other oaks were not significantly different (Table 3.2). Among oaks, SO had lower foliar N (1.75), P (0.095), and K (0.57) concentrations, although overall pine had lowest nutrient concentrations (Table 3. 2). SO (162.8 Mg/ha) and CO (179.2 Mg/ha) had higher stem biomass compared to other cover types (Table 3. 1). Among the oak groups SO and CO did not show differences in their aboveground biomass with respective values of 298.8 ton/ha and 227.9 ton/ha (Table 3.1). SO was on better site quality (FSQI 11) while pine was in the poorest site quality (Table 3. 1).

Nitrogen use efficiencies varied among the cover types, one unit of N in pine cover type fixed more litter biomass (342.5) and same unit size fixed lowest mass in WO (111.2) while other oaks have insignificant differences among themselves (Table 3.3). Nitrogen use efficiency in wood biomass have wider gap among the cover types , one unit of N in SO fixed higher wood biomass (1084.5) and the lowest was fixed in WO (77.2) cover types, similarly a unit of SO fixed more stem biomass (550.8) and lowest was in WO (57) while other cover types remained at intermediate levels (Table 3.3). With exception of pine the resorption efficiency of N, followed

the gradient with lowest value being in WO (55.9%) and the highest values was in CO (71%) and oak in pine (72%) (Table 3.3). An inconstant pattern existed between litter N concentrations and NRE. The lowest percent of litter N corresponded to higher N resorption, for instance Oak in pine had senesced litter N value of 0.06g (litter nutrient content) and NRE was 72%, which was the highest while WO with content of 0.58g had the lowest resorption efficiency value. The behavior of CO was slightly different; it had higher resorption at moderate litter concentration. The only productivity variables that was differentiate SO (3.55 ton/ha) and CO (6.72 ton/ha) was NPP_{ST} but otherwise both cover types did not show any differences in the entire productivity variable (Table 3.1).

Foliar phosphorus contents in WO (0.084g) and CO (0.066 g) were not significantly different but differences occurred in their senesced litter concentration (Table 3.4). Oak in Pine had the lowest senesced litter concentration (0.002g) but has the highest value in PNRE (82.2%) (Table 3.4). PNRE among the oaks increased from WO to CO along the gradient (Table 3.4). One kg of P in pine produced the high litter mass (7053.5kg). The PNUEL in CO (3968.1kg) was significantly lower than CO in Pine (5116.5kg) (Table 3.4). SO and CO had similar productivity with exception in their NPP_{ST} (Table 3.1).

K resorption efficiency was higher in Pine (78.8%) while K resorption was similar among all the Oaks and lower than pine (Table 3.5). One kg of K in pine fixed more litter biomass (1200.9kg) which is moderately significant from SO (500.1 kg) but highly significant from other cover types (Table 3.5). One kg of K fixes high stem biomass in both Pine (1339.2 kg) and SO (1519.75 kg) but the difference was apparent in $KNUE_{AB}$ where SO had significant higher value then pine and

highly significant from other cover types (Table 3.5). The concentration of K in green and in

senesced in both WO and CO were not significantly different but highly different from other

cover types (Table 3.5).

Changes in litter quantity were mainly driven by nutrient use efficiency of N, P and K in   both

aboveground and stem wood productivity (Table 3.6). Litter production and Nitrogen Use

Efficiency in aboveground biomass ($NNUE_{AB}$) was association by a correlation of -0.5080

(p=0.0222) and with stem biomass production ($NNUE_{ST}$) the correlation was -0.5024 (p=0.0240).

Phosphorus use efficiency in both aboveground biomass ($PNUE_{AB}$) and in stem biomass

($PNUE_{ST}$) have significant influences on litter production shown by respective correlations of -

0.5403 (p=0.0139) and – 0.5042 (p= 0.0234). Similarly, $KNUE_{AB}$ and $KNUE_{ST}$ have influence on

litter production. WUE and NUEL (litter use efficiency) were not association with any of the

productivity variables (Table 3. 6). There was no strong association between resorption

efficiencies and productivity variables (Table 3.6).

The influence of litter chemistry on water use efficiency was mainly from potassium

concentration signified by correlation of -0.4789 (p=0.0326) (Table 3.7). Litter nutrient use

efficiency (NUEL) was driven by the concentrations of the three nutrient elements of N, P, and K

as shown by the significant correlations, N = -0.9956 (p=0.0001), P= -0.8914 (p= 0.0001) and K=

-0.6843 (p=0.0009). Among other productivity parameters only stem nitrogen use efficiency

(NUE_{ST}) was significantly correlated (-0.5153 p= 0.0201) to P concentration (Table 3.7).

Potassium use efficiency is influenced by all the elements both, in stem ($KNUE_{ST}$) and

aboveground biomass ($KNUE_{AB}$) were strongly correlated to to N, P and K concentrations (Table

3. 6). Among the resorption efficiencies, KRE was tightly correlated to the concentration of all the elements (Table 3.7).

3.5 Discussion

WUE, NUE and NRE are strategies for plants to overcome changes in water and nutrients status (Aerts, 1990; May and Killingbeck, 1992) and vary by cover types. We found SO cover type was significantly better in WUE than other cover types. According to studies, such outstanding cover type in WUE should normally be associated with dry peak slopes as WUE increases with increasing gradient (Elliot et al., 1997; Friend et al., 1989). This was not the case in this study, CO and PO in the upper slope gradient were lower in WUE compared to SO in mid gradient. Uniquely SO WUE was higher than WO although they shared same site quality. We then explored the factors which drives the efficiency of SO in WUE to establish a reason why SO diverted from the trend as stipulated by other studies. Two factors are well established in many studies; resistances to diffusions in gas exchange in the leaf which mainly reduces loss of water from the plant without significant influencing CO_2 uptake, (Field et al., 1983; Reich et al., 1989), this results in more CO_2 been fixed per the same unit of water lost, and the presence of high N increases Rubisco's surface area for more CO_2 to be fixed during photosynthesis (Field et al., 1983; Reich et al., 1989). In table 3.2 SO is moderately lower in N concentration, suggesting N may not only be the driving force of WUE. In table 3.5, a correlation between WUE Potassium suggests K is important in WUE. Studies which reported exclusively N as a driving factor for WUE were by Field et al (1983) and Reich et al.(1989). Similarly, some studies found no correlation between resorption efficiency and the nutrient status of the foliage (Chapin and

Moilanen, 1991) while others found decline in resorption efficiency as nutrient status increases (Aerts, 1996; Lambers and Poorter, 1992; Kobe et al., 2005). Nutrient use efficiency vary among the cover types, Pines with long living needles fixed more litter biomass per unit of N, P and K while oak especially SO was better in fixing wood biomass compared to all other cover types. Characteristically Pine and SO have common factors of being shade intolerant, faster growth, shorter lifespan and they closely resemble in their WUE (Table 3.1), differently Pine needle lives longer. These could factor NUE differently. Many studies have reported similarly that long living needles and leaves occupy poor site and retain much of their nutrients for long time (Beadle, 1966; Monk , 1966; Chapin, 1980) and WUE is closely linked with NPP (Tian et al., 2010).

Among the oaks, NRE increased with increasing gradient, closely associated with available moisture and soil fertility, which decreased as the gradient increases. Similarly, some studies reported NRE differ by location and by species (Clark, 1977; Turner, 1977) and is more prominent where tissue nutrient concentration is low (Beadle, 1966; Monk, 1966, Haag 1974, Chapin 1980). Other attributed NRE to poor soil quality (Vitousek, 1982; Beadle, 1966; Chapin 1980).

Water use efficiency (WUE), nutrient use efficiency (NUE) and resorption efficiencies (NRE) are strategies to perpetuate the life cycles of the plants despite changes in nutrient status. Indicatively they are reflected in productivity (Tian et al., 2010; Hsiao, 1974; Waring and Running, 2007) such as litter and wood biomass production. Differences in accommodating restrictive factors that make the plants to have efficiency in nutrient use, may result into different responses. Studies have shown that under poor environmental conditions especially in

poor soil plants will produce more biomass because of reuse of nutrient as well having longer

residence time (Grime, 1979; Chapin, 1980; Berendse and Aerts, 1987; Aerts, 1990; May and

Killingbeck, 1992). While other studies attributed gradient as a factor in the differences (Garter

and Taylor, 1992). In this study productivity was closely associated with litter fall mass

production (Table 3.6) probably because plants normally have much of the nutrient

investments in the foliage and by the virtue of slow growth in hardwoods the influences of NRE,

NUE and WUE on productivity would probably be visible in longer terms. Our results in table 3.6

are correlations that encompass all the cover types but when viewed individual, different

relations between use efficiencies and productivity could be apparent. This is justifiable, for

instance in WUE, defines the amount of CO_2 fixed per unit of water lost, which should have

been apparent in productivity variable correlation but was not , probably it was submerged or

masked by the generalized correlations.

We found the cover types with higher foliar nutrient concentration remained high in the litter

concentration, among the oaks except CO, NRE increased as litter nutrient concentration

decreased. In support the association of higher NRE with lower tissue concentration was shown

by Cote et al. (2002), Vitousek (1982) and Aerts (1996) showed resorptions are closely linked

with lower soil fertile and supported by May and KIllingbeck (1992). There was a strong

correlation between WUE and K concentration, K is essential in leaf controls the available water

in the plants. Similarly, a study showed that adequate K supply improves the leaf water content

and decrease water potential to sustain the rate of photosynthesis, transpiration and stomata

conductance (Egilla et al. 2005). The concentrations of the three essential nutrient elements in

balance (N, P and K) are strongly correlated to the KRE; deficiency of one increases the

concentration of the other, which influences the growth negatively. Similar studies have shown that N influences growth of all the leaves, P and K affects growth of lateral branching leaves, reduction of one substantially reduces growth, therefore reduction of one must be balanced by resorbing from the pool, that why all the three elements must be in balance (Jenkins and Mahmood, 2003). This study also found strong correlation between nutrient use efficiencies (NUEL, NUE_{ST} and KUE_{AB}) with nutrient concentration in litter fall and wood. Vitousek (1982) defined forest nutrient use efficiency as gram organic matter lost from the plants or permanently stored; conversely, NUE is an inverse of nutrient concentration. This holds in this study, Pine and SO with lower litter concentration showed a better production of litter and wood respectively.

Studies have shown NRE vary between <0% to 90% and that the correlation between Nutrient status and NRE takes different forms of decrease, increase or no effect with increasing nutrient contents (Schlesinger et al., 1989). Aerts and Berendse (1988) showed that concentration of nutrients both in folia and in litter covary with distribution across fertility gradient; species with lower foliar concentration adapts to low fertility and thus they sort across fertility gradient. In general, apart from *Pinus spp*, resorption efficiency among the oak species follows the gradient along the slope of moisture and fertility gradient uphill. The mean global resorption efficiencies are newly found to be 62.1%, 64.9% and 70% for N, P and K respectively (Vergutz et al., 2012). Our studies found N and P resorption efficacies for WO were 55.9% and 55.6% respectively, which were below the global average while the same elements in other canopy types had higher values than the global rates and we found that with exception of *Pinus spp*. (79%) K resorption efficiency is much lower in all the canopy types than the global estimated resorption

efficiency values, the probable reason is K is not metabolized and form weaker complexes which can easily leach (Fisher, 2007). Folia nutrient concentration in P, N, and K decreased as NUE for P, N and K increases.

3.6   Summary and Conclusions

We found WUE and NUE vary among the cover types, SO had higher WUE, followed by PO and other cover types remained the same. It was not only the water gradient that controls the WUE and NUE of the canopy types but adaption and inherent characteristics may also be involved, because SO being at mid slope in the gradient exhibited higher WUE compared PO and CO found higher up slope. We found NUE varied among the cover types with pine being the highest values in NNUEL, PNUEL and NUEL. We found a strong correlation between NUE and productivity especially with CO and SO. SO alone, had higher WUE correlates with NPP for aboveground and stem biomass (Table 3.1). We found foliar concentration was inversely related NUE for the three elements of N, P and K. The study also found that concentration of the senesced leaves (litter fall) depends upon the amount of the in the green leaves, and we found mixed relationships between the green foliage nutrient contents and the resorption efficiencies, to some the relationship is inverse; higher resorption efficiency was associated with lower nutrient content but in chestnut oak it was a positive relationship where higher resorption efficiency was associated with higher nutrient concentration. Apart from *Pine spp.* an inconsistence correlation exists between NRE and foliage litter NUE in all the three elements (N, P and K).

We therefore concluded that WUE, NUE, and NRE are important variable, which influences the cover types independently on litter and wood biomass. This would implies that in the case of adaptation for plantations, white oak have the preference for higher moisture, while scarlet oak with its ability of having better WUE and NUE could be grown on much drier area, similarly chestnut oak and pine oak could be grown in drier area. We also conclude that cover types of SO and CO have higher nutrient resorption ability, which is important for input management decision making, to avoid wasting material if application remained the same as for WO, which has low nutrient resorption ability

3.7 Acknowledgements

3.8 Literature Cited

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Table 3.1. Average diameter at breast height (DBH, cm), number of trees per hectare, basal area (m²/ha), aboveground biomass (ton/ha) total and net primary production (NPP) and stem biomass production (ton/ha) and net primary production (NPP), annual litter fall dry mass production and forest site quality index (FSQI) for white oak (WO), scarlet oak (SO), chestnut oak (CO) and PO (Mixture of pine and oak) cover types.

Cover Type		Diameter at Breast Height (cm)	Trees per ha	Basal Area m²/ha	Litter Mass ton/ha/yr	Total Biomass ton/ha	Stem Biomass ton/ha	TOTAL NPP ton/ha	STEM NPP ton/ha	Forest Site Quality Index
SO		36.9a	337	36.1	5.13bc	298.8a	162.8a	6.94ab	3.55bc	11a
WO		30.3ab	350	25.2	6.72a	120.71c	88.5b	2.7de	1.96cd	11a
CO		23.4c	763	32.5	6.06ab	227.9b	179.1a	8.58a	6.72a	9ab
PO	*Total:*	22.2c	863	33.4	4.40cd	147.13c	103. 2b	5.99cd	4.16b	7.5b
	Pine:	22.8c	688	28.1	3.57d	111.89c	77.9b	4.36cd	3.03bc	
	Oak:	19.7c	175	5.3	0.87e	35.24d	25.3c	1.63e	1.13d	

Values with same letters are not significant different while different letter show significant differences among the cover types

Table 3.2. Mean isotope composition δ¹³C of summer foliage and nutrient concentration (N, P and K) for dominant species in each cover type (white oak (WO), chestnut oak (CO), scarlet oak (SO), pine, and chestnut oak in pine).

Cover type		$\delta\ ^{13}C$	%N	%P	%K
WO		-29.9c	2.07a	0.133a	0.84b
CO		-29.6bc	2.09a	0.166b	0.97a
SO		-28.6a	1.75b	0.095c	0.57c
PO	*Total*	-	-	-	-
	Pine	-29.3b	0.82c	0.063d	0.41d
	Oak	-29.8c	2.16a	0.115b	0.99a

Values with same letters are not significant different while different letter show significant differences among the cover types.

Table 3.3. Foliar N concentration in percent and in grams, litter N concentration, [N]sen, resorption of efficiency of nitrogen (NNRE), Nitrogen efficiency in litter production (NNUEL), Nitrogen efficiency in aboveground biomass production NNUE$_{AB}$, Nitrogen use efficiency in stem biomass production (NNUE$_{ST}$).

Cover Type		%N	[N]green g	[N]sen g	N NRE %	N NUEL (kg)	N NUE$_{AB}$ (kg)	N NUE$_{ST}$ (kg)
WO		2.07a	1.28a	0.58a	55.9c	111.2c	77.2c	57.0c
CO		2.09a	1.18a	0.35b	70.9a	165.8b	416b	325.5b
SO		1.75b	0.32b	0.11c	67.3ab	178.4b	1084.5a	550.8a
PO	*Total*	-	-	-	-	-	-	-
	Pine	0.82c	0.36b	0.14c	62.1b	342.5a	504.2b	353.9b
	Oak	2.16a	0.23b	0.06c	72.2a	168.6b	435.6b	306.2b

Values with same letters are not significant different while different letter show significant differences among the cover types.

Table 3.4. Phosphorus concentration in green [P]green and senesced [P]sen leaves, Resorption of efficiency of P (PNRE), Phosphorus use efficiency in litter production (PNUEL), in stem production (PNUE$_{ST}$) and in aboveground production (PNUE$_{AB}$)

Cover Type		Conc. %P	[P]green g	[P]sen g	P NRE %	P NUEL kg	P NUEAB kg	P NUE$_{ST}$ kg
WO		0.133a	0.084a	0.04a	55.6c	1739.1d	1180.1c	871.5c
CO		0.116b	0.066a	0.015b	77.7ab	3968.1c	9731.9b	7616b
SO		0.095c	0.018b	0.005bc	73b	3956.6c	23558.5a	11961.1a
PO	*Total*	-	-	-	-	-	-	-
	Pine	0.063d	0.028b	0.007bc	76.5ab	7053.5a	10667.4b	7491b
	Oak	0.115b	0.017b	0.002c	82.2a	5116.5b	12899.2b	9190.1ab

Values with same letters are not significant different while different letter show significant differences among the cover types

Table 3.5. Potassium concentration in green and senesced leaves, Resorption of efficiency of K (KNUR), K nutrient efficiency in litter production (KNUEL), in stem production KNUE$_{st}$, in aboveground production (KNUE$_{AB}$).

Cover Type		Conc. %K	[K]green g	[K] sen g	KNRE %	K NUEL kg	KNUE$_{AB}$ kg	K NUE$_{ST}$ kg
WO		0.84b	0.53a	0.179a	66.5b	366.0c	248.4c	183.2c
CO		0.97a	0.54a	0.198a	61.8b	295.6c	717.0c	561.0b
SO		0.57c	0.10b	0.04b	63.6b	500.1b	2990.6a	1519.75a
PO	*Total*	-	-	-	-	-	-	-
	Pine	0.41d	0.19b	0.038b	78.8a	1200.9a	1906.4b	1339.2a
	Oak	0.99a	0.096b	0.04b	61.2b	270.4c	716.6c	509.3c

Values with same letters are not significant different while different letter show significant differences among the cover types

Table 3. 6. Correlation between water use efficiencies (WUE), nitrogen use efficiencies for litter (NNUEL), aboveground biomass (NNUE$_{AB}$), stem biomass (NNUE$_{ST}$), phosphorus use efficiencies for aboveground biomass (PNUE$_{AB}$), stem biomass (PNUE$_{ST}$), potassium use efficiencies for above ground biomass (KNUE $_{AB}$) and stem biomass (KNUE$_{ST}$); resorption efficiencies for nitrogen (NRE), phosphorus (PRE) and potassium (KRE) with productivity variables; change in litter, stem above ground biomass production (Total$_{ST}$), net primary productivity of the stem (NPP$_{ST}$), total above ground biomass (Total$_{AB}$) and net primary productivity of the above ground biomass (NPP$_{AB}$). P values in parenthesis.

Variables	Litter	Total $_{STB}$	NPP$_{ST}$	Total $_{AB}$	NPP$_{AB}$
WUE	-0.3187 (0.1709)	0.3977 (0.0825)	0.2624 (0.2637)	0.3770 (0.1013)	0.1668 (0.4821)
NUEL	-0.3861 (0.0927)	-0.119 (0.6207)	0.0642 (0.7880)	-0.1131 (0.6349)	0.1401 (0.5559)
NNUE$_{AB}$	-0.5080 (0.0222)*	0.3991 (0.0813)	0.01463 (0.5383)	0.4122 (0.0709)	0.1885 (0.4261)
NNUE$_{ST}$	-0.5024 (0.0240)*	0.3661 (0.1124)	0.2776 (0.2360)	0.2506 (0.2865)	0.1942 (0.4121)
PNUE$_{AB}$	-0.5403 (0.0139)*	0.3104 (0.1828)	0.1093 (0.6463)	0.2724 (0.2453)	0.1338 (0.5738)
PNUE$_{ST}$	-0.5042 (0.0234)*	0.2296 (0.3320)	0.2016 (0.3940)	0.0715 (0.7645)	0.0972 (0.6835)
KNUE$_{AB}$	-0.4947 (0.0266)*	0.3341 (0.1500)	0.0780 (0.7438)	0.4289 (0.0591)	0.1137 (0.6331)
KNUE$_{ST}$	-0.5076 (0.0223)*	0.2781 (0.2351)	0.1590 (0.5031)	0.2869 (0.2201)	0.1184 (0.6191)
NRE	-0.2996 (0.1994)	0.1028 (0.6662)	0.2404 (0.3074)	-0.1928 (0.4154)	0.0593 (0.8039)
PRE	-0.3776 (0.1007)	-0.0293 (0.9024)	0.1667 (0.4825)	-.03320 (0.1527)	-0.0381 (0.8733)
KRE	-0.0358 (0.8808)	0.0222 (0.9259)	0.0921 (0.6993)	0.1147 (0.6303)	0.1030 (0.6657)

Table 3.7. Correlations between tissue nutrients concentrations (%N, %P and %K) and water use efficiency (WUE), nutrient use efficiencies; nitrogen use efficiency for litter production (NUEL), aboveground biomass (NUE$_{AB}$), stem biomass (NUE$_{ST}$); phosphorus use efficiency for aboveground biomass (PUE$_{AB}$), stem biomass (PUE$_{ST}$); potassium use efficiency for above ground (KUE$_{AB}$) and stem biomass (KUE$_{ST}$) and resorption efficiencies for nitrogen (NRE), phosphorus (PRE) and potassium (KRE).P-Values are in parenthesis.

| Variables	Concentration (% N)	Concentration (% P)	Concentration (% K)
WUE	-0.2555 (0.2768)	-0.3629 (0.1158)	-0.4789 (0.0326)*
NUEL	-0.8956 (0.0001)*	-0.8914 (0.0001)*	-0.6843 (0.0009)*
NNUE$_{AB}$	-0.2141 (0.3648)	-0.4041 (0.0772)	-0.4164 (0.0678)
NNUE$_{ST}$	-0.2853 (0.228)	-0.5153 (0.0201)*	-0.3580 (0.1212)
PNUE$_{AB}$	-0.1168 (0.6239)	-0.3768 (0.1015)	-0.2850 (0.2233)
PUE$_{ST}$	-0.1343 (0.5724)	-0.4226 (0.0634)	-0.1770 (0.4553)
KNUE$_{AB}$	-0.4843 (0.0305)*	-0.5753 (0.0080)*	-0.7216 (0.0003)*
KUE$_{ST}$	-0.6297 (0.0029)*	-0.7300 (0.0003)*	-0.7555 (0.0001)*
NRE	0.3161 (0.1746)	0.0111 (0.9631)	0.3833 (0.0953)
PRE	-0.1361 (0.5671)	-0.4361 (0.0546)	0.0592 (0.8042)
KRE	-0.6721 (0.0012)*	-0.5166 (0.0197)*	-0.5504 (0.0119)*
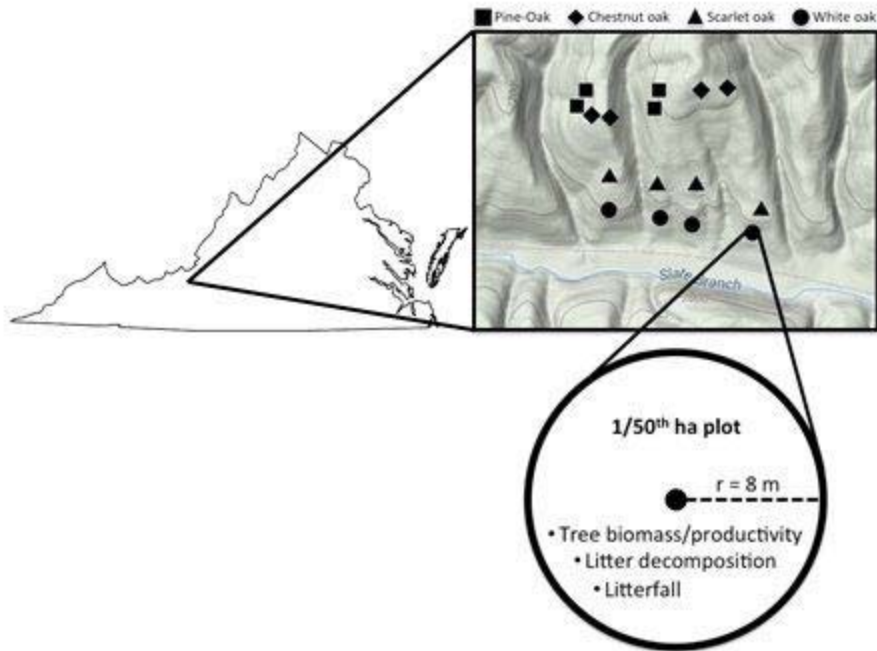
Figure 3.1. Study site location, basic design and variables measured in each plot located in the Valley and Ridge Physiographic Province in Montgomery County, Virginia

Chapter 4. Litter Decomposition across Diverse Canopy Types in a Southern Appalachian Hardwood Forest

Abstract

The Southern Appalachian forest is a diverse mixture of species, which often change over relatively short distances. In this natural forest, growth and regeneration depends in large part on recycling of nutrients through the process of decomposition. We hypothesized that litter decomposition as driven by the environmental, topographic and biotic factors would not differ among the diverse cover types in the short distances. In study goal was to determine mass loss (decomposition) over time, factors associated with the mass loss and its association with productivity. In 1/50th ha plots replicated four times for each of the four cover types (WO *Quercus alba* L, SO *Quercus coccinea* Muech., CO *Quercus montana* Wild., and PO (*Pinus spp* and *Quercus spp*), freshly fallen leaves were collected and oven dried at 65°C to constant dry weight. A known quantity of the dry litter was filled in 20cm x 20cm litter bags made of 1mm mesh. Litterbags (12 containing litter from each cover type and 12 containing CO litter as a common species placed in each cover type) were deployed and collected periodically over the course of one and half years. As expected, mass loss followed an exponential decay rate but there were significant differences among the species. SO litter had the lowest decay rate coefficient (k) of 0.0023. Pine had the highest k of 0.0029 but it was not significantly different from CO and WO with 0.0027 and 0.0026 respectively. The decomposition of CO litter when placed in other stands did not change significantly ranging only from 0.0027 to 0.0030. Soil C:N ratio was strongly correlated to decomposition. We therefore concluded that litter

decomposition rate differed between three oak cover types and a mixed-pine oak cover type, chestnut oak litter decomposition were not different in other cover type and decomposition rate was correlated to site productivity. These differences are important in understanding the litter turnover for better management plans.

4.1   Introduction

Litter decomposition is a critical pathway for carbon and nutrient flux in forest ecosystems. It contributes 70% of total annual carbon flux (Aber and Melillo, 1980; Tuomi et al., 2009; Raich and Schlesinger, 1992; Jobbagy and Jackson, 2000; IPCC, 2007; 2009; Shaver et al., 1992, Woodwell, 1994; Couteaux et al., 1995) and is a major nutrient source for plants and microorganism especially in natural forests. Decomposition is driven by many factors. Climate (especially temperature) drives decomposition by influencing enzymes on which bacteria depend on to transform organic material (polymers) into monomers before finally releasing the elementary contents Katterer et al. (1989). The optimal climate (temperature and moisture) for decomposition varies among forest and cover types resulting in different decomposition rates. For instance, in Smoky Mountains and Oak Ridge forest, beech (*Fagus sylvatica* L.) has slower decomposition, mulberry (*Morus alba* L.) is faster and red oak (*Quercus rubra* L.) and sugar maple (*Acer saccharum* Marsh.) are intermediate (Shanks and Olson, 1961). In the first year mulberry (*Morus rubra* L.) mass loss was 64%, white oak *(Quercus alba* L.*)* 39%, maple leaf oak (*Quercus shumardii* Buckl.) 34%, sugar maple 32%, beech 21% (Shanks and Olson, 1961). In different studies, eastern white pine (*Pinus strobus* L.) mass loss was 60%, and dogwood (*Cornus stolonifera* Michx.) was 31% (Melillo et al., 1982; Cook and Papendick, 1970).

Decomposition rates are typically quantified by using a first-order decay rate coefficient (k). Higher temperatures are associated with higher k values and lower temperatures are linked with lower k values. Coefficients of 2.33±0.44 is associated with lower mass remaining while values 0.36±0.17 to 0.35±0.249 yr^{-1} are linked higher mass remaining (Aerts, 1997). Climate controls the microbial community and population directly and litter quality and quantity control decomposition indirectly (Swift and Anderson, 1989). Temperature is mainly associated with mineralization (Lashof, 1989; Post, 1990) which influences net primary production (NPP) (Shaver and Chapin, 1986; Shaver et al., 1992) and may have indirect influence on plant community composition and structure as it influences competition and succession (Shaver and Chapin, 1986; Hobbie, 1996).

At optimal environmental conditions, litter chemistry controls decomposition (Aerts, 1997) which is determined by tissue concentration of nitrogen (N), phosphorus (P), C: N ratio, C:P ratio, lignin and lignin nutrient ratios (Coulson and Butterfield, 1978; Taylor et al., 1989). Litter is substrate for growth and proliferation of heterotrophic microorganism (Hobbie, 1996; Fogel and Cromack, 1977). C: N ratio can easily predict the quality of litter; higher values signify low N concentration (Hobbie, 1996). It has been shown that rapid decomposition reflects higher N-mineralization and nitrification, which is commonly associated with fertile soils (Vitousek and Sanford, 1986). Litter with higher elementary (N, P and K) concentration is associated with higher initial decay rates and higher concentrations of elements in mass remaining (Berg et al., 1993). The majority of the cations are released in the first year of decomposition and the release of the remaining cations continues in the second year but at much slower rates, implying a rapid recycling of cation nutrients available for plant uptake. In contrast, N, S and P

tend to be retained in the initial stages of decomposition (Staaf and Berg, 1982). Although, over 50% of mass loss occurs in the first two years, the net loss of N, S and P remains very small. These three elements act as litter nutrient reserve or sink in the two years of decomposition especially where limitation of nutrients (N, S and P) exists (Staaf and Berg, 1982). This received support by other studies by acknowledging microbial organisms immobilize some elements such as N at the initial stage of decomposition before becoming available (mineralization) for plant uptake (Rustad, 1994; Melillo et al., 1989). The high N concentration in mass remaining can also be attributed to lignin–N complex products and the shift of fungi from complete lignin degradation (white rot fungi) to partial degradation (Keyser et al., 1978). For instance, Melillo et al. (1989) found a 59% N concentration in red pine (*Pinus resinosa Ait.*) needles when only 17% of the mass remained. Suggesting strong accumulation of N as decomposition progressed. Similarly, during the first 51% of mass loss in scots pine (*Pinus syvestris L.*) species there was a rapid release of cations and slow release of N, P and S (Staaf and Berg 1982). Aber and Melillo (1980) found an inverse linear relationships between mass loss and N content in the residual materials in all species and that, the change in mass was due primarily to respiration loss of organic carbon and change in nitrogen content was due to increased microbial protoplasm. Cumulatively mass loss is described by two phases, the initial phase of constant mass loss and a phase of very slow mass loss, which are related to soluble sugars and acid insoluble carbon compounds. Weight loss continues until the exhaustion of readily decomposable substrates leaving recalcitrant secondary products (Aber and Melillo, 1980).

 Howard and Howard (1980) associated litter mass loss to site quality. They found litter from better sites had the highest mass loss. Site quality was closely associated with microorganism activities and population.

In mixed hardwood, decomposition rates in pure and in mixed stands was determined in a period of 2-5 years. The rates in broadleaf forests were faster in the first year compared with rates in conifer forests; thereafter the decomposition of the broadleaf litter became slower than that of the needle litter and by the end, the decomposition rate differences were minor between the two litter types (Prescott et al., 2000). Litter decomposition was faster in broadleaf than in coniferous forest and no differences were found when litter was mixed (Prescott et al., 2000).

Rapid decomposition and mineralization correlates with faster nutrient cycling and productivity (Binkley, 1983). The relationship between litter concentrations and decomposition are confounding as reported by different authors. Perry et al. (1987) found faster decomposition in broadleaf litter because of high litter nutrient concentration, low lignin and polyphenols concentrations than conifer litter. Cornelissen (1996) found the leaves of deciduous species decomposed twice as fast than evergreen leaves under the same conditions. Cole and Rapp (1981) found the turnover in temperate deciduous forests floor was four times faster than temperate coniferous. Some studies attributed decomposition rates to site conditions, Taylor and Parkinson (1988) found that the trembling aspen (*Populus tremuloids Mixhx.*) leaves decomposed more rapidly than pine except under very dry and cold conditions when pine decomposed faster than aspen. The nature of forest floor can also have an influence on

decomposition rate. Mixing of needle litter with broadleaf litter in mixed hardwood forest hastens the decomposition of litter (Fyles and Fyles, 1993; Taylor et al., 1989a; McTieman et al., , 1997), while other studies found no effect of mixed litter on decomposition rate of the species (Klemmedson, 1992; Rustad and Cronan, 1988).

Litter decay rates of beech (*Fagus spp*), oak (*Quercus spp.*) and chestnut (*Castanea spp.*) species varied depending on the size of the canopy gap. Chestnut had the highest litter decomposition rates, followed by oak and beech. All litter types decomposed faster under closed canopy with smaller gaps, than intermediate and larger gaps. In three years, beech, oak and chestnut mass loss ranged from 31% to 55.4% where north facing slopes had much higher mass loss compared to the mass loss from south facing slopes. Mass loss ranked in the order of gap sizes: closed canopy> small gap>intermediate gap > larger gaps (Sariyildiz, 2008). Larger gaps reduced litter decomposition rates by changing the environmental conditions that reduces nutrient cycling and organic matter turn over (Sariyildiz, 2008).

To understand the influence of soil nutrients on litter quality and decomposition, decomposition was examined in different nutrient fertilization treatments. The lowest k value 0.0027 was from the control, where no fertilization applied. The higher k- values of 0.0069 was from the stand that received mixed fertilization of N and P (Rejmankov and Sirova, 2007). However, Melillo et al. (1982) found k-value (%) range of 0.08 to 0.47 negatively correlated with lignin: nitrogen ratio. In addition, decomposition is described by inverse linear relationships by percent initial mass remaining and nitrogen concentration in the residual materials (Melillo et al., 1982).

Since litter decomposition is a primary source of refurbishing nutrients in natural and unmanaged stands it should be associated with above ground biomass production as influenced by site conditions. Ozalp et al., 2007 determined decomposition and above ground biomass and found relatively drier sites were better in decomposition as compared to the wetter sites, despite their lower NPP.

Southern Appalachian hardwood forests are characterized by changes in cover types in relatively short distance based on topography, moisture gradients and associated changes in site quality (Smith, 1994; Whittaker, 1956). Determining how decomposition is influenced by these changes in site quality and species is important for understanding this diverse landscape. Our objectives are to 1) determine the differences in litter decomposition rate between three oak cover types and a mixed-oak pine cover type, 2) determine how chestnut oak litter decomposition varies in other cover type locations and 3) examine how decomposition rates are related to site productivity of the cover types.

4.2   Material and Methods

4.2.1 Experimental design

We examined four common cover types in a natural mixed hardwood forest distributed along a southern slope in the Ridge and Valley physiographic province in Montgomery County, Virginia. They included white oak (WO, *Quercus alba* L.), scarlet oak (SO, *Quercus coccinea* Muench.), chestnut oak (CO, *Quercus montana* Wild.) and mixed pine-oak (*PO, Pinus spp. & Quercus spp*). Within each of these cover types, 4 circular, 1/50 ha plots were established. The experiment was designed as a randomized complete block with four replications of each cover type (Figure 4.1).

4.2.2 Measurements

In each plot, all trees with >5.1 cm diameter at breast height (DBH, 1.37m above ground), were measured for diameter in March 2015 and March 2016 using a diameter tape. Stem biomass (wood + bark) was estimated by equation $M=aD^b$ where M is mass in kilograms, D is the diameter at breast height in cm, a and b were constants established for each species, WO (a=0.1392, b=2.1844), SO (a=0.1434, b=2.2391), CO (a=0.0741, b=2.5226), and Pine (a=0.0751, b=2.3261). To predict the total above ground biomass, different constants were used, WO (a=0.2022, b= 2.1666), SO (a=0.1241, b=2.4395), CO (a=0.0907, b= 2.5344) and Pine (a=0.1040, b= 2.3373). Further, site quality was estimated using Forest Site Quality Index (FSQI), which was formulated to predict site quality in Ridge and Valley terrain, based on aspect, slope percent and slope position. Using a clinometer, slope percent was established by taking two points in each plot. A compass was used to determine the aspect value. Slope position was determined using a topographic map and knowledge of plot positions. FSQI with values ranging from 1-16 were established for each plot (Meiners et al., 1984; Carmean, 1975).

Litter decomposition was determined using nylon mesh bags, a technique modified from Bocock and Gilbert (1957). The mesh openings were 1mm in size, which was small enough to contain the hardwood litter and permit aerobic microbial activities. Freshly fallen leaves were collected from the forest floor in each plot during the heavy litter fall in late October, 2014 and oven dried at 65°C to constant dry weight. A known weight of the oven dry litter was placed in the nylon mesh bag (20cmx20cm) (Melillo et al., 1982) and 24 bags per plot (12 with cover type

litter and 12 with CO litter) were placed on the forest floor in each plot. CO litter was chosen to be placed in each cover type plot, as it is a common species throughout the entire forest area. At 30-day intervals, two bags (one with CO litter and one with cover type litter) per plot were retrieved and oven dried at 65°C to constant dry weight for determination of mass loss.

At three random sub-sample points, soil temperature and moisture contents were taken. A total of 20 measurements were made between July 2014 and December 2015. In summer, autumn, and winter monthly measurements were carried out. In spring as things changed quickly during bud break, measurements occurred more often. Soil temperature was measured at 10 cm using a digital thermometer (AcuRite 00641, Chaney Instrument Co., and Lake Geneva, WI) and soil moisture was measured at the depth of 0 to 12 cm using a hydrosense soil-water sensor (Campbell Scientific USA, Logan, UT).

Fresh green foliage was also collected from two dominate/co-dominate trees in each plot except in PO where four trees were chosen two each from pine and oak. Foliage was removed by shotgun from the upper one third of the crown. Ten to 20 leaves from oak or needles from Table Mountain pine (*Pinus pungens* Lamb.) were sampled and packed separately in paper bags. In addition, the contents of the two 0.16m^2 litter traps per plot were collected regularly (30 days or more) and sorted according to the cover type species and oven dried to constant weight and the weight was used to determine annual litter production. In addition, part of the collection was used in conjunction with foliar litter to determine nutrient concentration and contents in both green foliage and senesced leaves.

In July 2015 at three sub sample locations per plot, a 30cmx30cm frame was used to sample forest floor litter. The forest floor samples were oven dried to constant weight. From the same sample frame area, top soil and subsoil were excavated and the subsamples mixed on site to obtain one sample of top soil and one sample of sub soil per plot. The soil samples were dried to constant weight, ground to pass through number 20 stainless sieve to eliminate the large particles that would not easily dissolve. The sample were analyzed differently where N was determined by using semi-micro Kjeldahl digestion, P was estimated by bicarbonate extraction and K was by ammonium acetate. Other samples were dried at temperature 65°C to constant dry weights. The samples for foliar and litter concentration as well the mineral soil were further processed for nutrient concentrations.

4.3. Data Analysis

Monthly retrieved litterbag weights were converted to percentages of total mass. Then the percentages were transformed into annual decomposition constants using the modified formula from Olson (1963); $Wt=W_oe^{-kt}$, where W_t and W_0 were plant masses at time t and time 0. The decay rate coefficients (k) were analyzed using ANOVA for mean differences among the cover types. The data from subsamples of R_s, temperature and moisture for each plot were averaged and then subjected to analysis of variance to compare means using student t –test. Foliage and litter nutrient concentrations, as well soil nutrient analysis variables were analyzed for mean differences using a t-test.

4.4   Results

Litter nitrogen concentrations differed among the dominant species (cover types). WO had the highest value of 0.91% N, and pine litter was the lowest (0.30% N, Table 4.1). C: N ratios reflected these litter N concentrations; WO has lower ratios in both soil (26.6) and litter (53.2). Pine has higher soil and litter C: N ratios (40.7 and 171.6, respectively). CO has intermediate values (Table 4.1). SO has C: N ratios, lower in soil C: N (28.9) and intermediate in litter C: N (88.3) (Table 4. 1). The PO cover type has the highest forest floor mass (18.38 ton/ha) while the oak cover types did not differ among themselves and had about 30 % less litter than the PO cover type. Despite having the greatest forest floor mass, the PO stands had the lowest litter fall values of only 4.40 ton/ha. Of the oak cover types, WO had the greatest litterfall mass but it was only significantly higher than the SO cover type (Table 4. 1). Average annual soil moisture was significantly lower in the CO and PO cover types averaging around 10 % compared to nearly 16% in the WO and SO cover types (Table 4.1). Annual soil temperatures did not differ between the cover types.

Litter decay rates were smooth over the course of the study. At the end of the nearly 500 days of incubation roughly 30 % of the mass remained (Figure 4.2). There were significant differences between decomposition of litter types. SO litter had the lowest decay rate coefficient of 0.0023 (Figure 4.2a and Table 4. 2). Decay rate coefficients did not differ between the other cover types. Decay rate coefficients for chestnut oak litter placed in various cover type locations did not differ significantly (Figure 4.2B and Table 4.2).

The soil C:N ratio is strongly correlated (0.7056, p= 0.0005) with the decay rate coefficient

which implying that when C:N is higher k value is high and when the C:N is low k value is low

(Table 4.3). Decay rate coefficient was strongly but negatively related to productivity (Table

4.4), the different correlations between k value and productivity variables includes -0.8242 (p=

0.0001) for above ground biomass (Total$_{AB}$), -0.7783 for FSQI, -0.5584 (p= 0.0105) NPP$_{AB}$ and -

0.7056 for soil moisture. This implies higher k value was associated with lower Total$_{AB,}$ FSQI and

NPP$_{AB}$

4.5   Discussion

Our oak cover type decay rate coefficients (k) fall within the range of values reported by

Witkamp and Olson (1963) and Kuperman, (1999) but slightly lower than the values reported

by Melillo et al. (1982) and Seasredt , (1984). As expected the mass loss slowed with time. This

could be due to the degradation of soluble materials and parts of the cellulose and

hemicellulose components (Fogel and Cromack, 1977), soluble nutrients diminishes as

decomposition progresses, due to increased nutrient concentration, which retards

decomposition rates thereby slowing decomposition (Fogel and Cromack, 1977). Some studies

found higher lignin at any stage of decomposition retards weight loss through reduction or

levelling effects of the of plant nutrients on litter decomposition (Fogel and Cromack, 1977).

Possibly higher lignin concentration or low soluble foliar concentration could explain the slower

decomposition in the SO litter.

We found a strong, positive correlation (0.7056 p=0.0005) between soil C:N ratio and litter

decomposition in our study (Table 4.3) which means higher values of k are directly associated

with higher levels of C:N, in other words soils with poor nitrogen contents foster rapid

decomposition. The k values in PO and CO were high in association with higher soil C: N ratio

(Table 4.2 and Table 4.3) implying microbes from these two cover types majorly depends on the

breakdown of litter. A study by Vitousek et al. (1994) reported decomposition rates

predominately are influenced by site characteristic, along with elevation, and that the senesced

leaves from a drier site decomposed most rapidly and released N and P more rapidly than those

on other site conditions (Vitousek et al. 1994). This is similar to what we found in our study.

CO and PO had the lowest soil moisture contents averaged over the year and the highest

decomposition rates. In addition Vitousek et al. (1994) showed that decomposition strongly

vary with elevation and henceforth with mean annual temperature, slight increase in

temperature along the elevation gradient increase decomposition four or more times.

However, we had no differences in soil temperature on our sites. The higher k values for pine

and CO was also found in soil respiration (Rs) in which both species showed higher values

despite the two cover types being on poor sites higher up the slope as compared to SO with low

soil respiration found in a better site condition (Chapter 2).

Berg et al. (1993) associated higher decay rates to higher litter quality. However, we found

inconsistencies behaviors of cover types, comparatively; WO had high litter N concentration and

low C: N ratio but relatively low decomposition. Pine and SO had low litter N concentrations and

high C: N ratios but pine had relatively high litter decomposition than SO. Studies have shown N

concentration of 32-43% bound to lignin becomes insoluble and restrained within the structure

(Berg and Staaf, 1980). Thus, lignin concentration influences the plant nutrient release, when

lignin concentration is higher than 25%, it reduces decomposition rate (Berg and Staaf, 1980) and

small amounts of N, P and S are lost unless their concentrations of these elements are very high. Thus plant litter nutrient content have no influence on mineralization when lignin concentration is high but mineralization increases with decreasing lignin concentration (Berg and Staaf, 1980). Our study did not evaluate amount of lignin contents, but relied on literature; Alexander and Arthur (2014), showed the initial litter lignin concentrations among the oaks are different, SO had slightly lower percent as compared to chestnut oak and white oak but the presence of soluble easily leached substance might have fastens decomposition in CO than other oaks. This was in support by Pieske et al. (2002) who found higher contents of nonstructural carbohydrates, N, P, Ca and Mg in CO compared to SO. Melillo et al. (1989) showed that the slow decomposition was dominated by lignocellulose, which is acid insoluble carbon compounds. Keyser et al. (1978) attributed a slower dropping in decomposition to N and lignin complex products which are resistant to biological degradations and that the presence of high N shifts fungi towards those with partial lignin degradation.

At a global scale higher k- values as in hotter tropical areas relates higher decomposition rates to lower mass remaining at the end of decomposition while lower k values represent higher mass remaining at the end of decomposition period (Aerts 1997). Our cover types had a range of 66 -79%, which was intermediate between hotter and temperate areas k- values (Aerts 1997) and relatively above the range of other findings 60%-31% (Melillo et al., 1982).

The rates of the CO litter decomposition when placed in the other cover types was not significantly different (Figure 4.2B and Table 4.3) suggesting that the significantly slower decomposition found in SO litter is due to inherent differences in the litter and not site

differences. Similarly, Prescott et al. (2000) did not find a detectable effect on decomposition

when litter was mixed. Zhang et al. (2008) found mixed effects, in one case, they found no

effect but when the species were swapped, the decomposition of one species accelerated while

the other decomposition was retarded.   Similarly, Aponte et al. (2012) found pure or single

litter had higher decomposition than two species decomposed together. We found a negative

correlation between k- value and site quality index (-0.7783, p= 0.0001) reflecting was greater

from poor sites, this was expected because C: N under these cover types were higher an

indication of poor sites. Similarly, Howard and Howard (1980) showed that site quality is

associated with microbial activities and population. Based on this study's finding, lower and

intermediate sites qualities occupied by pine and CO have better decomposition rates

compared to the higher quality sites. However moving the CO litter to SO and WO sites did not

change the decomposition rates.

We found productivity variables of total aboveground and stem biomass and the net primary

production of the above ground biomass were strongly correlated to decomposition rates

(Table 4.4). Decomposition is a process of refurbishing the soil nutrients for plant uptake and

microbial uses and thus contributes to plant productivity. Similarly, another study found

decomposition rate is associated with k- values whereby higher values reflects higher

decomposition with most of the nutrients released to the soil, while lower k- value was

associated with partial decomposition and less enrichment of the soil (Aerts, 1997).

Decomposition in relation to productivity through being a source of mineralization for plant and

microbial uses (Lashof, 1989; Post, 1990), a source of nutrients for use in net primary

production (Shaver and Chapin, 1986) and a source of for plant composition and structure

(Hobbie, 1992; Shaver and Chapin 1986). We in this study found site quality negatively correlates decomposition rate. Soil respiration (Rs) rates in the process of decomposition increased from high site quality to low site quality. Studies showed that mass loss inversely relates to elevation (Shank and Olson, 1961) but Howard and Howard (1980) found mass loss was better in high quality class.

4.6   Summary and Conclusions

Mass loss declined steadily with time, depicting loss of easily decomposable nonstructural and some structural carbohydrates and complex structured carbohydrates. The decomposition rates closely related to slope gradient. Higher rates were observed in pine and CO at the poor and moderate site qualities. The inherent chemistry of the litter was more important than the site changes as reflected by no change in CO decomposition in other cover types. CO decomposition strongly associated with productivity, by having higher litter production, net primary production of the stem and total above biomass production. The decomposition of CO in other cover types did not show significant differences. Only soil C: N ratio showed stronger correlation to decomposition rate constant, pine and CO had higher ratio while WO and SO had lower C: N ratio implying pine and CO were in low nitrogen (N) concentration. Though we did not find correlation between nutrient concentration and decomposition, however, a trend considering the nutrient concentration of the cover types and decomposition could be drawn.

From the summary, it could be concluded that the cover types from poor sites quality, low moisture and nutrients have higher litter turnover and this was coupled with high rates of R_s as

was for CO and PO. This implied that much of the sources of nutrient in the drier ridge come

mainly from decomposition of litter.

4.7 Acknowledgements

4.8 Literature cited

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Table 4.1. Litter N concentration and content, soil and litter C:N ratio, forest floor mass (metric tons per hectare), litter mass (metric tons per hectare), soil temperature and moisture and Forest site quality index.

Cover Type		Litter N Conc.	Litter N Content	C/N Ratio Soil	C/N Ratio Litter	Forest Floor Mass	Litterfall Mass	Soil Temp.	Soil Moisture	Forest Site Quality Index
		% N	kg/ha			Ton/ha	Ton/ha/yr	°C	%	
WO[1]		0.91a	36.1a	26.6c	53.2c	13.00b	6.72a	13.4a	15.7a	11.0a
CO		0.61b	21.9b	35.2b	81.8b	12.15b	6.06ab	13.8a	9.8b	9.0ab
SO		0.56b	12.8bc	28.9c	88.3b	11.48b	5.13bc	13.4a	15.8a	11.0a
PO	*Total*	-	-	40.7a	-	18.38a	4.40cd	13.6a	10.0b	7.5b
	Pine	0.30c	8.6c	-	171.6a	-	3.57d			
	Oak	0.60b	3.8c	-	83.3b	-	0.87e			

[1]WO = white oak, CO = chestnut oak, SO = scarlet oak, PO = pine-oak

Values with same letters are not significant different while different letter show significant differences among the cover types

Table 4.2. Decay rate coefficient (k value) for the cover type litter, white oak (WO), scarlet oak (SO), chestnut oak (CO) and Pine (Pine) and of chestnut oak litter placed in other cover type locations.

	Cover Types				CO in Cover Types			
	WO	**SO**	**CO**	**P**	**WO**	**SO**	**CO**	**P**
k- value	0.0026ab	0.0023b	0.0027a	0.0029a	0.0028a	0.0030a	0.0027a	0.0030a

Values with same letters are not significant different while different letter show significant differences among the cover types

Table 4.3. Correlation coefficients between litter decay rate coefficient (k) and various litter and soil parameters

% N Litter	% P Litter	% K Litter	C:N Litter	C:N Soil
-0.0829	-0.0823	0.2321	0.2911	0.7056
(0.7283)	(0.7302)	(0.3049)	(0.2130)	(0.0005)*

Table 4. 4. Correlation coefficients between litter decay rate coefficient and site productivity variables; forest site quality index (FSQI), above ground net primary productivity biomass (NPP$_{AB}$), Total above ground biomass (Total$_{AB}$), stem above ground biomass (Total $_{ST}$) and stem net primary production biomass (NPP$_{ST}$)

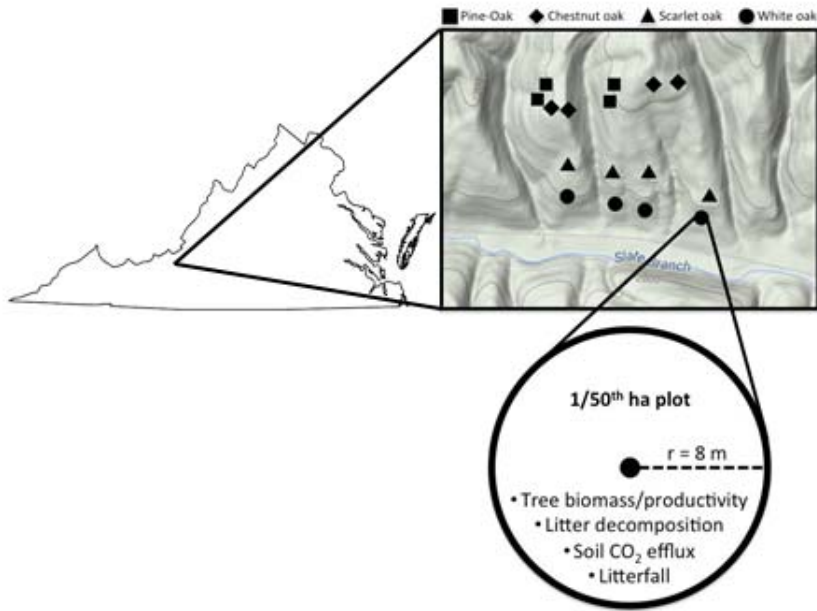| FSQI	NPP$_{AB}$	Total$_{AB}$	Total $_{ST}$	NPP$_{ST}$	Soil moisture
-0.7783	-0.5584	-0.8242	-0.6355	-0.2377	-0.7056
(0.0001)*	(0.0105)*	(<0.0001)*	(0.0026)*	(0.313)	(0.0005)*

Figure 4.1. Study site location and basic design in the Valley and Ridge Physiographic Province in Montgomery County, Virginia.
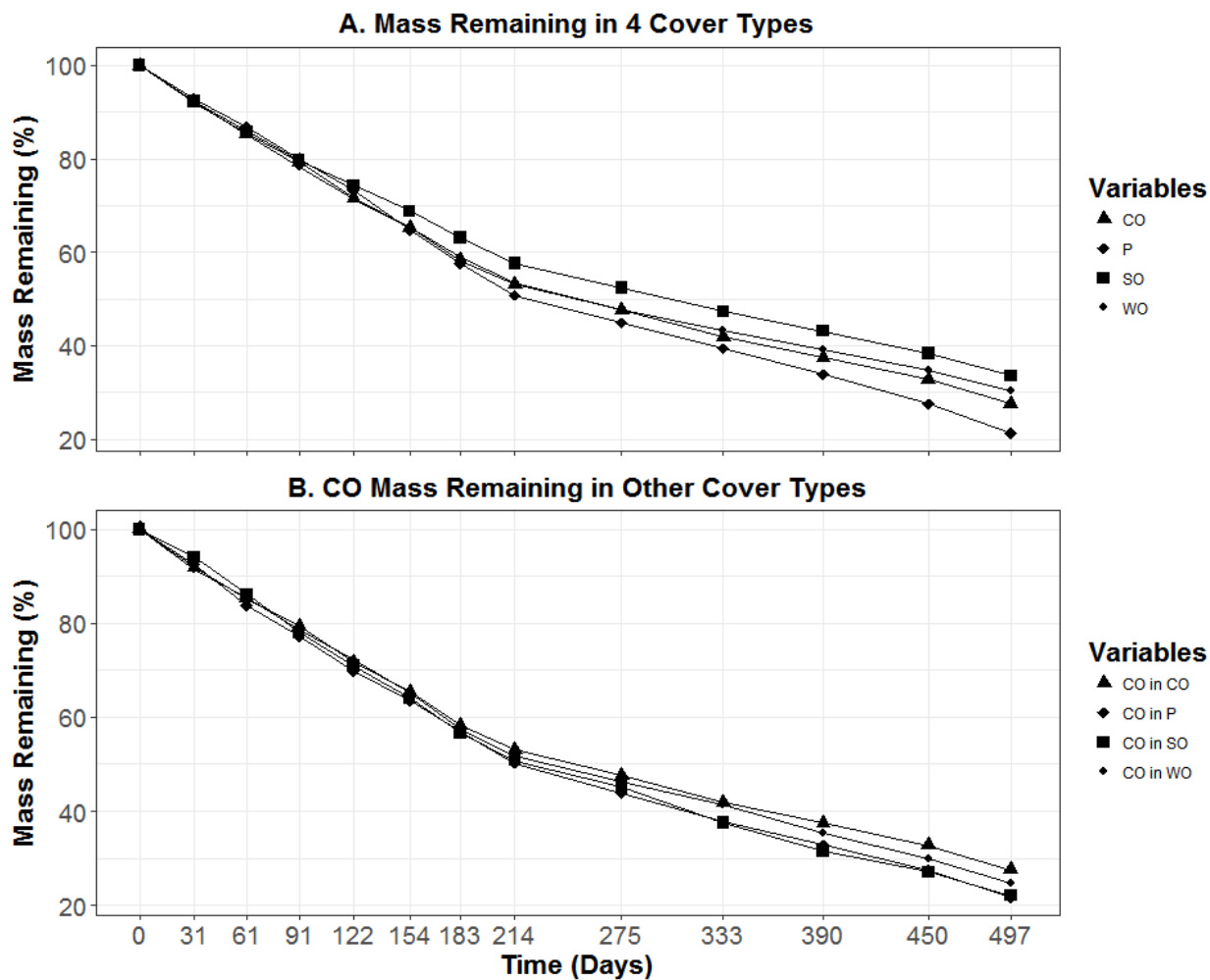
Figure 4. 2. (A) Mass Remaining over time for the four cover types of white oak (WO), scarlet oak (SO), chestnut oak (CO) and Pine (P), and (B) CO mass remaining in other cover types.

Chapter 5.   Synthesis

We investigated the dynamics of soil respiration R$_s$, water use efficiency (WUE), nutrient use efficiency (NUE) and nutrient cycling (litter decomposition) in natural Appalachian hardwood forest composed mainly of WO, SO, CO and pine oak (mixed pine and oak). Our general goals were to 1) improve our understanding of environmental drivers of soil respiration (R$_s$) and to ascertain the influence of changing oak and pine cover types on R$_s$ (Chapter 2), 2) determine NUE and WUE in various oak and pine cover types and examine how they relate to forest productivity in these natural forests (chapter 3), and 3) develop an understanding of the litter decomposition rates in these Appalachian cover types and determine if changes are related to productivity (chapter 4).

The responses of R$_s$, WUE, NUE and decomposition rate coefficients (k) in the cover types differed and were related to changes in productivity. Among oak species, SO behaved differently with regard to many of the measured variables. SO had low R$_s$ rates (low temperature response), slowest litter decomposition, lowest foliar nutrient concentration, highest WUE and some of the highest nutrient use efficiencies. Likely the high nutrient use efficiencies in SO allowed the productivity rates we observed but resulted in low litter decomposition rates and consequently lower R$_s$. In the pine oak cover type, R$_s$ had the greatest response to temperature and the pine and CO litter (in PO cover type) had the greatest decomposition. Pine litter also had the highest litter nitrogen use efficiency, which likely contributed to its competitiveness on these drier nutrient poor sites.

Cover types exhibiting similar response variable (e.g. R_s, WUE or NUE) often differed in their productivity. For example, CO and pine both exhibited higher values in R_s and decomposition rates (k-value) but differed in litter and wood biomass production with CO higher than pine. Among the oaks, the variables related to productivity also differed. The higher R_s and decomposition rates in CO were related to its biomass production. In SO, water use efficiency (WUE) and NUE were related to and likely contributed to its productivity. The relationship between R_s and k value in CO is likely related to increased enzymatic activity related to this cover type's greater R_s and k response to temperature (Chapter 2 and chapter 4). The relationship of WUE and NUE to productivity in SO is likely related to stomatal responses and nutrients that refurbish Rubisco enzymes (photosynthetic capacity) although this was not measured in this study. Future studies may wish to focus more attention on scarlet oak leaf physiology and finer scale nutrient use efficiency such as photosynthetic nitrogen use efficiency and measures of leaf stress such as water potential or xylem embolism. On average, the productivity in CO and SO where equal because of the tradeoff between interactive forces of R_s and k in CO, and WUE and NUE in SO (chapters 2, chapter 3 and chapter 4). The WO cover type on the lower slopes had good foliar and litter nutrient concentrations but remained very low in all the measured variables (R_s, WUE, NUE and k), resulting in low lower productivity.   Perhaps at the finer scale used in this study, the cover types had different adaptations and acclimations that gave each a different responses to the variables that were related to their productivity.