

AN ABSTRACT OF THE DISSERTATION OF

Fox S. Peterson for the degree of Doctor of Philosophy in Forest Science presented on November 5, 2012.

Title: Post-Harvest Establishment Influences ANPP, Soil C and DOC Export in Complex Mountainous Terrain

Abstract approved: _____
Kate J. Lajtha

The link between aboveground net primary productivity (ANPP) and resource gradients generated by complex terrain (solar radiation, nutrients, and moisture) has been established in the literature. Belowground ecosystem stocks and functions, such as soil organic carbon (SOC), dissolved organic carbon (DOC), and belowground productivity have also been related to the same topography and resource distributions, and therefore it is expected that they share spatial and temporal patterns with ANPP. However, stand structure on complex terrain is a function of multiple trajectories of forest development that interact with existing resource gradients, creating feedbacks that complicate the relationships between resource availability and ANPP. On a 96 ha forested watershed in the H.J. Andrews Experimental Forest in the Western Cascades range of Oregon, spatiotemporal heterogeneity in the secondary succession of a replanted *Pseudotsugamenziesii* stand following harvest results from the interaction of stand composition and abiotic drivers and may create unique “hot spots” and “hot moments” that complicate

gradient relationships. In this dissertation, I tested the hypotheses that (chapter 3) multiple successional trajectories exist and can be predicted from a general linear model using specific topographic, historical, and biological parameters and that an estimated "maximum ANPP" may better represent stand characteristics than ANPP measured at a particular moment in time. I also test that (chapter 4) the distribution of light fraction carbon (LFC; C with a density of less than 1.85 g/cm^3) is spatially variable, elevated on hardwood-initiated sites (hardwood biomass $> 50\%$ of biomass), and positively correlated with litter fall and ANPP. Chapter 4 also tests that heavy fraction carbon (HFC; C with a density of greater than 1.85 g/cm^3) is a function of both soil mineralogy, stand composition, and ANPP, such that edges observed spatially in site mineralogy (changes in soil type) are reflected in sharp changes in the composition of the forest community and the magnitude of HFC stores. Finally, I hypothesized (chapter 5) that in complex terrain, dissolved organic carbon (DOC) export can be predicted from landform characteristics, relates to ANPP, and may be measured by several methods which are well-correlated with one another. In chapter 6, I discuss how litter fall measurements can be extrapolated to a watershed extent, and use litter fall as an example of the error that can occur in scaling up measurements taken at a small scale, within a heterogeneous stand on complex terrain, to a landscape scale extent.

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Post-Harvest Establishment Influences ANPP, Soil C and DOC Export in Complex
Mountainous Terrain

by

Fox S. Peterson

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APPROVED

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Head of the Department of Forest Ecosystems and Society

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University Libraries. My signature below authorizes the release of my dissertation to any reader upon request.

Fox S. Peterson, Author

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CONTRIBUTION OF AUTHORS

In the first manuscript, Kate Lajtha and Tom Spies provided scientific and editorial advice and assistance, and Jack Peterson aided in programming a biomass calculator. In the second and third manuscripts, Kate Lajtha provided scientific and editorial advice and assistance. In the fourth manuscript, Jay Sexton collected and documented all litter fall measurements, helped with the creation of a scaling factor, and wrote a detailed operations protocol which was essentially paraphrased into this document; Kate Lajtha provided editorial assistance. The fourth manuscript was originally a project for a class of Advanced GIS for the Geosciences, taught by Professor Dawn Wright, and hence Dr. Wright deserves editorial acknowledgement.

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DEDICATION

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CHAPTER 1

A REVIEW OF THE RELEVANT LITERATURE REGARDING INTERACTIONS BETWEEN STAND STRUCTURE, SITE HISTORY, AND ENVIRONMENTAL DRIVERS IN COMPLEX TERRAIN

1.1 Introduction and Literature Review

The primary objectives of this dissertation are to qualify how the complex interactions between aboveground stand structure, site history, and environmental conditions impact belowground resource distributions and availability, and in turn how heterogeneity in these belowground resource distributions affect how we understand ecosystem processes and outputs at the landscape scale. The specific aboveground variables assessed are biomass (Mg/ha), aboveground net primary productivity (ANPP) (Mg/ha/yr), litter fall (Mg/ha/yr) and species composition (hardwood or conifer dominance). The specific belowground variables assessed are soil type, soil moisture capacity, soil depth, percent rock, carbon in the light (<1.85 Mg/ha) and heavy (>1.85 Mg/ha) fractions, dissolved organic carbon (DOC) concentration, and potential nitrogen mineralization (measured through ammonium and ammonium nitrate assays). In this opening chapter of this dissertation, I summarize the relevant literature on the (1) stand structure spatially, temporally, and developmentally, (2) forest soil carbon (both in aggregates and dissolved), and (3) forest soil nitrogen. In the second chapter, I detail the history of the site of “Watershed 1” (WS1) where this study takes place. In the third chapter, I question how stand structure evolved successionally over time on this watershed, looking at variability, peaks in development, and species composition, as well as questioning the

metric of productivity. In the fourth chapter, I ask the question of how belowground carbon relates to productivity, biomass, species composition, potential nitrogen mineralization and litter fall. In the fifth chapter, I ask how concentrations of dissolved organic carbon relate to productivity, biomass, species composition, and litter fall. In the sixth chapter, I use litter fall as an example of a spatially heterogeneous C store and explore uncertainty in extrapolation. In all of the primary chapter topics—ANPP, C stores in the soil, DOC, and litter fall—I find that distributions of resources are heterogeneous spatially and that this spatial heterogeneity manifests itself in stand structure, which in turn complicates our interpretation of drivers and responses in the forest ecosystem. Heterogeneity is not new or unfamiliar in ecology, but has not been well documented at a within-watershed scale, especially on complex terrain. If the ecosystem processes occurring in WS1 are indicative of the behaviors of similar landscapes in the Western Cascades or of complex terrains in general, then process based models, which ultimately function across differential grids of empirical functions, may not be accurate in the estimations they make for large-scale carbon stores and fluxes. Thus, in the final chapter, I summarize the findings and discuss the inherent uncertainty in qualifying these findings at a landscape scale, especially with regards to feedback loops and site history. The goal of this dissertation is not to divulge any “one size fits all” equations about forest ecosystems but rather to ask the small-scale questions that may lead to large error when extrapolated up to large scale models in order to validate (or disprove) assumptions of homogeneity for plant-soil relationships in the complex terrain of the Western Cascades.

1.2 Succession, Nutrient Balance, and Stand Structure

1.2.1. The history of successional theory

The possibility that multiple successional trajectories exist, and the implications of their existence on a deeply incised forested watershed, forms the theoretical foundation of this dissertation. When succession proceeds along multiple trajectories, correlations between stand structure and belowground resource stores differ across the landscape. However, although I employ succession as a mechanism for spatial differences, the initial conceptualization of succession was built on ecological determinism (Christensen and Peet, 1991). When Clements theorized that the temporal development of all plant communities was predictable, he suggested that a forest ecosystem would ultimately converging on a final equilibrium state (Clements in Christensen and Peet, 1991). His argument centered around the view that development of a local plant community is analogous to the development of an organismal life form, with the prime driver of the “life history” of the plant community as regional climate. As a consequence of the five ecological processes he identified as creation, arrival, development, interaction, and modification, a plant community reaches this permanent equilibrium (“stabilization”) with its local conditions that inhibit the re-encroachment of early-seral species (Clements, 1916).

Setting the stage for trajectory-based views of succession, Clementian theory was strongly criticized by Gleason (1917, 1926, 1927, 1939) and Tansley (1935). Gleason renounced the holistic mindset of the plant science community and emphasized that

stochasticity was inherent in the development of individual plant organisms and species. Tansley argued that topography was also a forcing factor driving the successional trajectory to its stable state, theorizing that under the same climatic conditions, topographic position (on a rocky ridge or not, for example) would influence the final plant community living in a place. Unifying theories of succession that incorporated both deterministic and stochastic components were proposed nearly thirty years later by Whittaker (1953), Margalef (1958, 1963, 1968), and Odum (1969). Whittaker advised that a stable state was actually just an image taken from a stable continuum across a landscape; Margalef applied information theory to successional theory to suggest that ecological and trophic complexity that develops over time is the manifestation of accumulating ecological information, and Odum proposed that these trophic levels each represented a set of ecosystem properties following its own trajectory towards a homeostasis of maximum biomass and diversity.

Obtaining experimental support for these more complex successional theories was difficult due to lack of long term experiments, leading scientists to perceive ecological succession in the context of local scale observations and experiments, and potentially inspiring theory towards reductionist and non-equilibrium paradigms that can be observed on the small scale (Pickett, 1976). This acceptance of non-equilibrium allowed for the incorporation of feedbacks (reactive patterns) between plants and the environments, rather than suggesting lop-sided environmental control over plant composition and form (Connell and Slayter, 1977; Drury and Nisbet, 1973; Noble and Slayter, 1980; Peet and Christensen, 1980). Horn (1975, 1976) summarized the holistic

and reductionist approached by suggesting that successional trajectories for a plant community exist and reflect spatiotemporal resource gradients influenced by stochasticity. However, creating a mechanistic model that encompasses all possible trajectories for all possible sites is impossible; the most ameliorative perspective is that each successional trajectory represents one of many possible interplays between population and landscape. This perspective is useful for both scientific and managerial understanding of forest ecosystems because it employs observation of a specific plant community in the context of theoretical relationships between plant and landscape, such that extrapolations can be made to scales and times beyond current spatiotemporal capacity (Glenn-Lewin and van der Maarel, 1992; Miles, 1987).

1.2.2. End goals of the multiple pathways and their implications

It has been suggested that succession in many ecosystems is not entirely deterministic, but also rooted in stochasticity (Botkin, 1992; Glenn-Lewin, 1980; Gleason, 1927; Peet, 1988). Succession nominally implies a forwards-moving, entropic process, so a traditional view of succession is developmental, a series of stages from an initial or pioneer community to a mature or stable community (or communities, in the case of divergence). However, neither convergence to a steady state or divergence to fragmented communities is ecological truism, nor have consistent pathways been observed on the same type of site, or even the same site (Glenn-Lewin, 1980; D'Angela, 1990; Inouye and Tilman, 1988). Multiple pathways in primary succession have been shown in various ecosystems including dunes, glacial landscapes, gravel pits, and salt marshes by

Bradshaw (1982), Borgegard(1990), Londo (1974), and Matthews (1979). Abrams et al. (1985) and Miles (1987) documented multiple pathways in secondary succession in varieties of *Pinus* forests recovering from fire events.

In experimental studies, vascular plant diversity is shown to increase with decreasing soil fertility and productivity. An early argument for this behavior was that as soil fertility declines, diversity is promoted by greater spatial heterogeneity in residual resources.

Tilman (1988, 1990) showed that divergence between pathways with respect to species dominance resulted in landscape modification, reducing the presence of other species by preventing establishment. In this case, the prevention mechanism was related to changes in nutrient stores, rather than in microbial communities, which can be tracked by their signature lipid outputs . However, this finding and its support in Carney, Matson, and Bohannon (2004) differed from experimental works by Cordell (2001), DeDeyn et al. (2004), Scherber et al. (2010). Ecosystem retrogression reduces biomass, NPP, and biodiversity at a small scale, but across a large extent the existence of patches may suggest a diversity increase that can be attributed to microbial or topographic reactions to change in stand composition and structure.

1.2.3. Nutrient Balances

Apart from the discussion of succession, it is known that the structure of vegetation influences light, water, and nutrient balances in a forested ecosystem. For example, water balance is affected by the spatial arrangement of plants, both vertically and horizontally, through the mechanisms interception, transpiration, and evaporation (Calder,

1990). Succession promotes changes in this plant structure and therefore changes in ecosystem stocks. Greenwood (1992) showed that conversion from a non-woody to a forested ecosystem causes change in ecosystem balances by affecting the plants' relationship with the soil. Since succession does not necessarily proceed uniformly across a single landscape, belowground resources may be affected in different ways by different aboveground trajectories. In Northern Europe, it was shown that the planting of *Pinus sylvestris* L. and *Picea abies* coupled with the onset of secondary succession in deciduous broad-leaved forest changed the fundamental hydrology of the ecosystem by promoting two alternate states: acceleration towards late successional communities and return to pioneer species (Griese, 1997; Leushner 1994, 2001).

So far this document has discussed succession through a description of the relationships between biomass, productivity, and diversity, and how these change and diverge over time and space. When dealing with nutrient balances, it is essential to focus on species composition and vegetative structure; studies of primary and secondary plant communities are evaluated based on these variables (biomass, productivity, etc.) responses' to resource availability (Bormann and Sidle, 1990; Christensen and Peet, 1991; Emmer, 1995; Gerlauch et al., 1994; Leuscher et al., 1993; Miles, 1979; Tilman, 1988; Vierick, 1970; Vitousek and Reiners, 1975; Walker et al., 1981). In such a view, competition for water, nutrients and light is the driving factor in succession, although it has been noted that studies specifically focused on net primary production (NPP) generally assess light and nitrogen availability at the loss of assessment of water and belowground resources (Bazzaz and Snipe, 1987; Leuscher and Rode, 1999). For

example, Tilman's (1988) work on resource ratios deals only with the light to nitrogen relationship and its effect on NPP. Likewise, Chapin et al. (1994) attributed primary successional pathways at Glacier Bay to availability of aboveground resources. The blossoming of ecohydrology in the early 2000's incited the idea that vegetation and soil were interactively and dynamically connected by means of water (Bond, 2003; Porporato and Rodriguez-Iturbe, 2000; Zalewski, 2000). Soil water stores, assessed as functions of the plant and topographical features that influence them, may be used as a simple proxy for belowground resource availability, and hypotheses regarding ecosystem balances developed.

The relationships between plants structure and soil water stores can be characterized by two primary types of influence: transpirational (direct) and non-transpirational (indirect). The direct influences are (1) marginal rate, (2) duration, and (3) quality of transpiration, which are determined by stand structure. Marginal rate is related to canopy architecture- a greater surface area increases transpiration rate; duration is related to plant phenology and responses to the growing season; transpiration quantity is related to vertical root extension- more roots can access more water. Non-transpirational (indirect) influences on the soil water include interception loss, net primary productivity, litter fall, and leaf area index (LAI). As examples, interception loss directly influences the amount of water that reaches the soil; plant productivity and litter fall influence the accumulation of forest floor, mitigating rainwater entry into the soil water pool, and LAI controls the radiation reaching the forest floor, moderating the direct evaporation of soil water. Belowground resources, then, through the means of structure and soil water distributions, should be

considered as a function of plant biomass (including biomass in various components such as leaves), productivity (aboveground), and species (for the phenological and phenotypical effects).

1.2.4. Feedbacks- it's complicated

Interactions between soil and plant structure exist and are complicated by species' preferences. Anthropomorphism for specific soil conditions apply across resource gradients such that conditions that are favorable for some voraciously growing species such as yellow-poplar may be deadly for more conservative organisms such as long-leaf pine. For example, in a multi-year study by Dohrenbusch (1992), when acidic soil conditions were ameliorated through liming or fertilization with 120 kg P₂O₅ or bitter spar, losses of trees of 70-90% were seen in a mixed spruce-beech-Douglas-fir stands in all species except for *Sorbus americana* (mountain ash). The rich soil attracted new pests and only mountain ash could resist them. Additionally, in the same study, nitrogen uptake as an indicator of health was not homogeneous between species; fir, spruce, and Douglas-fir thrived in areas that were poorly supplied with nitrogen; beech, alder, and birch thrived in areas of very high nitrogen. Over time, this study also showed no significant change in the nitrogen concentrations of the Douglas-firs, suggesting that nutrient deficiencies in a site persisted even with stand development and may relate to both species and site (Hurlbert, 1984; Ulrich 1970 and 1971; Ulrich, 1975).

In summary, multiple pathways of succession lead to divergence at an ecosystem scale that may increase or decrease biodiversity, often depending on nutrient needs and

availability. Losses of soil nutrients as a result of reduced biodiversity at the small scale are coupled with increases due to species preferences on the large scale. In addition, site history, topography, and resource gradients generate heterogeneous backgrounds on which this multi-scaled nutrient flux occurs. Separating out any direct interactions between structure and nutrient balances is, mechanistically, impossible. However, I attempt to use long-term ecological data to improve how we conceive of biomass, productivity, biodiversity, and nutrient balances at multiple scales, and to show how spatiotemporal patterns exist and developed in one watershed. This work is a case study intended at improving methods for future analyses. With adequate treatment of the included variables, management and scientific regimes can be designed that achieve objectives and increase human understanding of the forest ecosystem.

1.3 Carbon

1.3.1 The Carbon Cycle

It has been estimated that globally forests store 86% of the planet's aboveground carbon and 73% of the carbon belowground (Sedjo, 1993). This carbon is exchanged between a series of "stores" or "pools" (such as leaves, forest floor, bole, and soil aggregates) through various processes (here called "fluxes" or "flows"). I define the system of carbon cycling in this system to the terrestrial stocks and fluxes that remain onsite (thus excluding atmospheric stocks or carbon removed for wood products or fuel). The following flow chart describes, roughly, the important pools in the forest carbon cycle and the flows of carbon through those pools. These flows are named roughly in order to fit the included space and the names should not be taken as the scientific norm.

amount of carbon to photosynthetic tissue; once the stand structure has been established, the bole receives more carbon to build vascular tissue for water conductance (Franklin et al., 2002; Lutz, 2005; Oliver and Larson, 1996). Gower et al. (1992) showed that experimentally changing nutrient and water balances on a site affected biomass allocation, particularly in understory trees, where foliar biomass had not yet reached a plateau. Changes in carbon allocation can be related to both site and species (Valentini et al., 1996). Attribution of structural changes to soil quality in forests has been well studied, but the effects of structural complexity as a function of both stand development and composition on soil carbon in particular is not well known (Franklin et al., 2002; Gower et al., 1992; Lutz, 2005; Kramer et al., 2001; Spies and Franklin, 1999; Tappeiner et al., 1997).

ANPP has been often considered as a metric of vegetative function, biogeochemical cycling, and the availability of ecosystem services (Ito, 2011). I define ANPP as the change in biomass plus mortality plus ingrowth on an annual basis (Acker et al., 1998). Aboveground biomass must be considered as functionally related to, but not equivalent to ANPP. Although increases in aboveground biomass cause by definition increases in ANPP, rapid turnover of plants or their components also may cause increases in productivity by increasing the mortality component. Land-use arguments in favor of short turnover crops, for example, suggest that the increased turnover of grasslands may provide more carbon sequestration (as an ecosystem service) than a fully developed forest (Franklin and Debell, 1988; Fung et al., 2005; White et al., 2011). Global models have shown that ANPP is not spatially homogeneous; at an ecosystem scale heterogeneity also

applies. Given that this heterogeneity is related to structure, and structure to successional state, the question of when to measure ANPP in order to correlate it with vegetative function, biogeochemical cycles, and services need be asked. In this document I approach that question, with particular interest to how ANPP is related to stores of carbon in the soil. I largely focus on the left side of the chart, studying the carbon pools in the tree biomass and soil fractions, to some degree categorizing the microbial pools, and largely ignoring the archived pool (carbon stored in buried wood that may be millennia old). The scope of this analysis is understanding how stand structure affect the inputs to and storage in soil carbon the implications of these patterns across space and time.

1.3.3. Mortality and Litter Fall

Mortality contributes carbon to the soil through the decomposition of coarse woody debris (CWD). Vogt (1991) estimated that 60 percent of a mixed forest's detrital biomass is composed of residues from coarse woody debris. In forest ecosystems, the drivers and patterns of mortality are well-known; in the Pacific Northwest Douglas-fir forest in this study, mortality is associated with density-dependent death resulting from canopy closure. The physical mechanisms causing death are suppression and mechanical failure (Harmon, 1991; Christensen and Peet, 1981; Bormann et al., 1995; Lutz, 2005). Mortality as a part of stand development is driver of successional change, particularly affecting species composition, as new intolerant species may form in the gaps left behind by downed trees. In this case, the quantity and quality of carbon supplied via mortality has both short and long-term effects on the soil. Directly, carbon is supplied to the soil by the downed tree's

biomass and the quality of that carbon depends on the species and the microbial community present. Indirectly, the loss of a tree changes the stand structure, so that new species may form and change the deposition of litter and the community of microbes in a particular area (Harmon, 1991).

Litter deposition (litter fall) is a critical component in this analysis, as it represents a consistent contribution of carbon from the aboveground biomass to the soil carbon store. It has been estimated that at a global level, litter fluxes may be 10 times that of human emissions (Adair et al., 1996). A large litter fall flux, then, represents increased ANPP, but not necessarily increased biomass. Litter fall is species-specific both in terms of rate and the litter stock supplied. Jensen (1984) found that non-leaf inputs (nuts, etc.) account for 20% of litter supply in deciduous forests and up to 40% in coniferous forests; Millar (1974) determined that litter inputs from herbaceous vegetation was negligible in comparison to tree inputs. The differences between hardwood, evergreen, and coniferous tree litter fall rates are relatively straightforward; the quantity and quality of litter supplied more nebulous. Leaf characteristics, particularly surface area and chemistry, affect the ability of the leaf to be decomposed by the fungal and microbial communities. If decomposition is less than fall, litter accumulations on the forest floor may proliferate, and this increase affects how carbon stores in the upper horizon of the soil is quantified (Balldock and Skjemstad, 2000; Hassink, 1996; Six et al., 2002).

1.3.4. Decomposition

Decomposition supplies nutrients to the soil by recycling plant residues. The process of soil formation through decomposition is related to the local decomposer community (fauna and microbes) (Degens, 1997; Lynch and Bragg, 1985; Oades, 1993; Sanderman et al., 2004). Studies have found varying degrees of correlation between decomposer biomass and soil carbon, depending on constitution of soil carbon, decomposer community, and the mineralogy of the soil (Oades, 1993). Chapin (1991) found that the majority of inputs, around 89%, into local decomposition were from the local vegetation (as opposed to atmospherically deposited inputs). The sources of input to decomposition are litter fall, root turnover, and coarse woody debris (CWD). Litter fall and root turnover occur on the decadal time scale, whereas coarse woody debris decomposition occurs over centuries. Just how much of each of these materials contributes to soil C versus being respired is unknown, and is a key question for ecosystem ecologists.

As input material is decomposed, the decomposer community shifts from organisms who can consume labile components to those who are better at breaking down recalcitrant organic matter (Sanderman, 2004). Organic inputs of nitrogen can be decomposed into inorganic forms (mineralization), but organic inputs of carbon cannot be mineralized and instead are respired to the atmospheric pool or stored as or organic aggregates (humification). Most forest floor litter is respired; Schlesinger (1990) estimates that only 0.7% of aboveground input material becomes organic humus. Numerous studies (Broadbent and Nakashima, 1974; Campbell et al., 1991; Rasmussen et al., 1980) have suggested that the importance of litter C is less than expected. Rasse et al. (2005) propose that a greater portion of soil C is derived from the decomposition of roots rather than of

litter. Because roots provide the soil with structure and enhance mycorrhizal networks, root C has greater quality and residence time in the soil than litter does.

The shifts in decomposer community correspond with shifts in decomposition processes; first, fauna cause bioturbation, mixing the old soil with new inputs. Second, microbes and fungi consume roots, leaves, and exudates (including amino acids, sugars, lysates, mucilages, and organic acids). In fact, the presence of complex decomposers, specifically fungi, serve a dual purpose here by both manually aggregating the soil on a large scale with their hyphae, and secreting their own enzymes and polysaccharides for digestion on a smaller scale (Bossuyt et al., 2001; Oades, 1993). Third, soluble organic compounds are leached from the soil (Sanderman, 2004). This includes dissolved organic carbon (DOC) and dissolved organic nitrogen (DON).

Soil mineralogy affects decomposition by providing appropriate materials and conditions for decomposer communities and organic matter stability. Many papers have shown that the N, P, or Ca concentrations in the soil affect decomposition rates (Aerts and De Caluwe, 1997; Berg, 1984, 1987; Meentemeyer, 1978, Melillo and Aber, 1982, Silver and Miya, 2001; Tian et al., 1992; Vitousek et al., 1994). The degree to which mineralogy drives decomposition is also related to structure; Quideau et al. (1998) found that decomposition beneath oaks on the San Dimas National Forest was more driven by concentrations of labile aromatics and alkyls whereas beneath pines recalcitrant aromatic and alkyl decomposition was favored. Soil texture also affects decomposition. Loamy soils decompose 15% faster than clayey soils (McInerney and Bolger, 2000), but some

types of clay are derived from minerals that foster decomposition (Motavalli et al., 1994; Thompson et al., 1999). Deneff and Six (2003) showed that a rich mollisol with 2:1 minerals is more resistant to decomposition than an oxisol, but that over time, the direct effects of mineralogy on decomposition become less important as compared to biotic factors.

1.4 Soil Carbon

1.4.1. Introduction to Soil carbon

Understanding the spatial and temporal dynamics of soil organic carbon (SOC) is essential for the management of forest ecosystems with a goal of long-term nutritive sustainability. Interactions between the soil matrix, the inhabiting biota, and the aquatic flow affect the stocks and fluxes of belowground carbon. Because of these complexities, methods of using “soil aggregates” as surrogate measurements of the soil matrix structure are common (Six et al., 2004). Soil aggregates are clusters of soil organic material held together with a variety of bindings that slow or prevent slaking, decomposition, and the release of carbon through respiration or leaching (Six et al., 2000). Ecosystem functions of soil aggregate include physical protection of organic matter (Tisdale and Oades, 1982), influencing the structure of the soil biota (Hattori, 1988), changing the aerobic state of the soil (Sexstone et al., 1985), regulating the flow of water (Barthes and Roose, 2002; Kostiakov, 1932; Ostiachev, 1936; Philip, 1957; Prove et al., 1990;) and altering nutrient profiles (Linguist et al., 1997; Wang et al., 2001). When deriving information about the soil matrix through the lens of aggregation, it is important to recognize that the functions of aggregates are interactive and furthermore affect and are affected by aboveground flora and fauna, weaving a complex structural-functional web.

1.4.2. History of Aggregate Research

Soil aggregates have been studied since the 1950's when the relationships between organic residue, microbes, soil fertilizers, and exchangeable cations were recognized and implicated as controls for soil fertility (Henin et al., 1958; Kemper and Koch, 1966; Martin et al., 1955). The foundational study for development of a theoretical model of a soil particle was Emerson's 1959 work that claimed that soil was composed of aligned bio-active clays and quartz particles. When slaking occurred, bonds at the quartz level were broken by swelling at the clay level, and it was proposed that this meant the surface area of the clay level is the critical feature for determining the ability of a soil matrix to stabilize soil organic carbon (SOC). Edwards and Brenner (1967) believed that a solid-phase reaction that included three key components (1) clays, (2) organic inputs and (3) polyvalent metal cations (Fe, Al, Ca) was the main process driving the formation of microaggregates (20 to 250 μm), and quartzes were not involved in aggregate formation. Because of this tight binding structure, organic matter in microaggregates was considered inaccessible to microorganisms and completely protected. Tisdale and Oades (1982) proposed that the mechanisms controlling aggregate formation were scale-dependent. Transient and temporary aggregates could form at a large scale through organic interactions (fungi, root hyphae, polysaccharides etc.), while persistent aggregates (bound together by oxides, metal compounds, and alluminosilicates) formed at a smaller one. This theory lead into the work of Oades (1984), who modified it to suggest that microaggregates can form within macroaggregates (250 to 2000 μm).

1.4.3. Changes in Soil Organic Carbon

There are three general ways that SOC content can change: (1) the rate of organic matter input may change, (2) decomposability of organic matter could change if climatic or species change also occurs and (3) the physical protection of SOC may change if inputs of C are purposefully placed at deeper or shallower positions in the soil (Paustian et al., 1997; Six et al., 2000). In a developing forest landscape, these changes may proceed naturally, or be the result of management objectives past or present. For example, Six et al. (1998, 1999, 2004) found that soil organic matter moved from macroaggregates to microaggregates following tillage, and that during this removal a large amount of soil carbon was lost to respiration. The upsetting of the soil during the tillage regime not only changed the aggregate distribution of the SOC, but reduced its gross mass on the site. If surface disturbance reduces SOC stocks, depth placement is adventitious for SOC storage because less disturbance occurs sub-surface. In short, it has been suggested that there is an exponential decline in SOC quantity with intensive management or disturbance (Paustian et al., 1997; Six et al., 2004).

When stand structure is taken into account, studies showed conflicting results with the experimental findings of SOC decline as a result of disturbance due to changes in organic matter quality. Post and Kwon (2000) found that the replacement of low-quality savanna grasses with exotic, high-productivity grasses resulted in significant increases in SOC for three to six years following community conversion. They concluded that under ideal circumstances, it would be possible to increase SOC even when converting from poorly-established forest communities to highly-productive pastures, at least in the short run.

1.4.4. Soil Organic Carbon Saturation?

The question of how much SOC can be held in a particular soil remains unanswered (Stewart et al., 2008, 2009). The saturation of soil C describes the maximum quantity of soil carbon that can be held in a soil, in both the labile fraction and the stable fraction, and whether or not the mechanisms of stabilization and capacity are the same in both. Early analyses suggested that SOC could not saturate, and thus linear models were used to predict soil stores based on inputs from litter. Conflicting data is presented in Burkins et al. (2001) where it is revealed that large stores of C are present in Antarctic Dry Valleys, despite the absence of any current organic matter inputs (past glaciation moved organic matter into the area). Later analyses of the same Antarctic site suggested that saturation exists, at least in the heavy fraction ($> 1.85 \text{ g/cm}^3$), following Michaelis-Menten kinetics where SOC storage is limited by the availability of mineral-associated binding sites (Stewart et al., 2009). However, storage in the light fraction may still be unlimited. This data is better aligned with the Antarctic conclusions, which suggest that SOC in this ecosystem is a complex of both ancient glacial deposits in the heavy fraction and lacustrine and Aeolian deposits in the light (Benninghoff and Benninghoff, 1985; Burkins et al., 2000; Nienow and Friedmann, 1993). Preliminary conclusions drawn across multiple studies suggest that SOC saturation is a function of site and management type, rather than a universal principle (Paustian et al., 1997; Huggins et al., 1998; Reicosky et al., 2002).

The allocation of carbon between the aggregate pools (light or heavy fraction) when approaching saturation is also a point of debate. Stewart et al. (2009) found that as soil approaches a hypothesized C saturation it decreases in stability. This finding is due to the fact that more and more soil is being stored in the light fraction, which is less limited, and is therefore less stable (Balddock and Skjemstad, 2000; Hassink, 1996; Six et al., 2002). However, this finding did not take into effect the acts of management, nor did it compare cross-site climatic, mineralogic, or decompositional effects.

1.5 Particulate Organic Matter and Dissolved Organic Carbon

1.5.1. Particulate Organic Matter

Particulate organic matter (POM) is the substrate from which soil organic carbon is initially formed. Sanderman et al. (2004) distinguish POM from litter, roots, and exudates by suggesting that POM is material that has already entered the decompositional process. Zsolnay (2003) sets the smaller limit on POM as greater in size than 0.45 micrometers and not associated with organic resins or residues from drastic pH changes. The availability of POM has been shown to be a key factor in site productivity and POM quality in terms of nutrient composition and age affects its ability to positively impact the soil (Weil, 1992; Sanderman, 2004) Six et al. (2000) found that the fineness of POM was proportionate to its age in non-treated ecosystems, but doubly proportionate to age in managed (tilled) ones, suggesting that disturbance (in this case human) increases the rate of carbon decomposition and macroaggregate formation. Encrustment of the macroaggregates with microbes and clay particles leads to interior degradation, such that microaggregates are formed within them (Oades, 1984; Elliott and Coleman, 1988; Gale et al., 2000). The formation of these microaggregates promotes carbon sequestration, especially in undisturbed systems, where free surfaces on the microaggregates may sorb plant C readily and without rapid turnover (Six et al., 1998; 2000).

1.5.2. Dissolved Organic Carbon (DOC)

Dissolved organic carbon (DOC) is by mass only a small component of soil C, yet it affects and predicts many terrestrial and aquatic processes and is often used as an

indicator for changes on both local and global scales (Kalbitz and Kaiser, 2003). DOC can be described by a size limit based on the capacity of glass filters to capture it in a given study; in some cases, larger particles containing artifacts of POM or organic resins may be considered (Lajtha, personal communication; Zsolnay, 2003). Available pore space, other inputs (both organic and inorganic) (Leenheer, 1981), and topography (Laane, 1982) have been shown to impact the quality and quantity of leached DOC in terrestrial ecosystems (Zsolnay, 2003). These quality changes are largely due to structural variation created by the addition or removal of charged particles, which affect the polarity, weight, and tertiary structure of DOC or colloids associated with DOC (Gustafsson and Gschwend, 1997). Changes in quantity are a reflection of both the ecosystem itself and how changes in quality are defined by laboratory studies; filters designed for one size of DOC may be inappropriate for some sites (Zsolnay, 2003).

The biodegradability of DOC is its ability to be respired, and this is controlled by DOC quality, as well as soil texture and climactic factors (Marschner and Kalbitz, 2003). When DOC is high in carbohydrates, organic acids, and proteins, its biodegradability is enhanced; when it is found with water high in heavy metals or electrolytes, its biodegradability is reduced. This is expected given the solution potential of these additional chemical structures. Likewise, in certain soils, for example, where the cation exchange capacity is high, where pore size is small, or where water saturation is low, DOC biodegradability is also low, whereas in moist soils, DOC can be biodegraded quickly; however, this is not a truism for all soils (Lajtha, personal communication). The climatic impacts of warmer temperatures, longer wet seasons, and phenology

correspondingly affect soil moisture and therefore DOC concentrations (Marschner and Kalbitz, 2003; Neff et al., 2001; Zsolnay, 1997; Zsolnay et al., 2000). Neff et al. (2001) showed that DOC has a positive feedback on the soil C in a given area, with up to 30% of microbial energy provided by internal DOC fluxes. Additionally, their model revealed that DOC was exactly dependent on the hydrologic flux that resulted from the climactic and topographic conditions specific to a certain microsite. At least in the results of the Neff study, the productivity of a given site is related at least to some degree to the amount of DOC exiting it. This principle is one I will test in my analyses.

1.6 Nitrogen

1.6.1. The Nitrogen Cycle

Many studies have suggested that ANPP is limited by biologically-available nitrogen (Aber et al 1995; Berendse et al, 1983; Schimel et al., 1995; Tilman, 1987). An increase in ecosystem nitrogen stores causes increases in ANPP, plant biomass, and respired C, while often reducing biodiversity through the mechanism of species optimization (Hurlbert, 1984; Ulrich 1970 and 1971; Ulrich, 1975). In recent years, humans have doubled inputs to the terrestrial nitrogen cycle, with measured results of increasing greenhouse gas N₂O, facilitating a loss of soil nutrients including calcium and potassium, acidifying soils and soil water stores, and expediting biodiversity reduction (Galloway, 1995; Vitousek, 1997). For nitrogen to be incorporated into the forest ecosystem, it must be “fixed” from the atmospherically unavailable gas N₂ into biologically available N by microbes, added as fertilizer, or input as “acid rain.” Estimates of annually fixed nitrogen in forests without including the effects of human inputs such as fertilizer generally range from 90 – 150 Tg N/year on the global scale (Soderland and Rosswall, 1982; Paul and Clark, 1989; Schlesinger, 1991, in Vitousek et al., 1997).

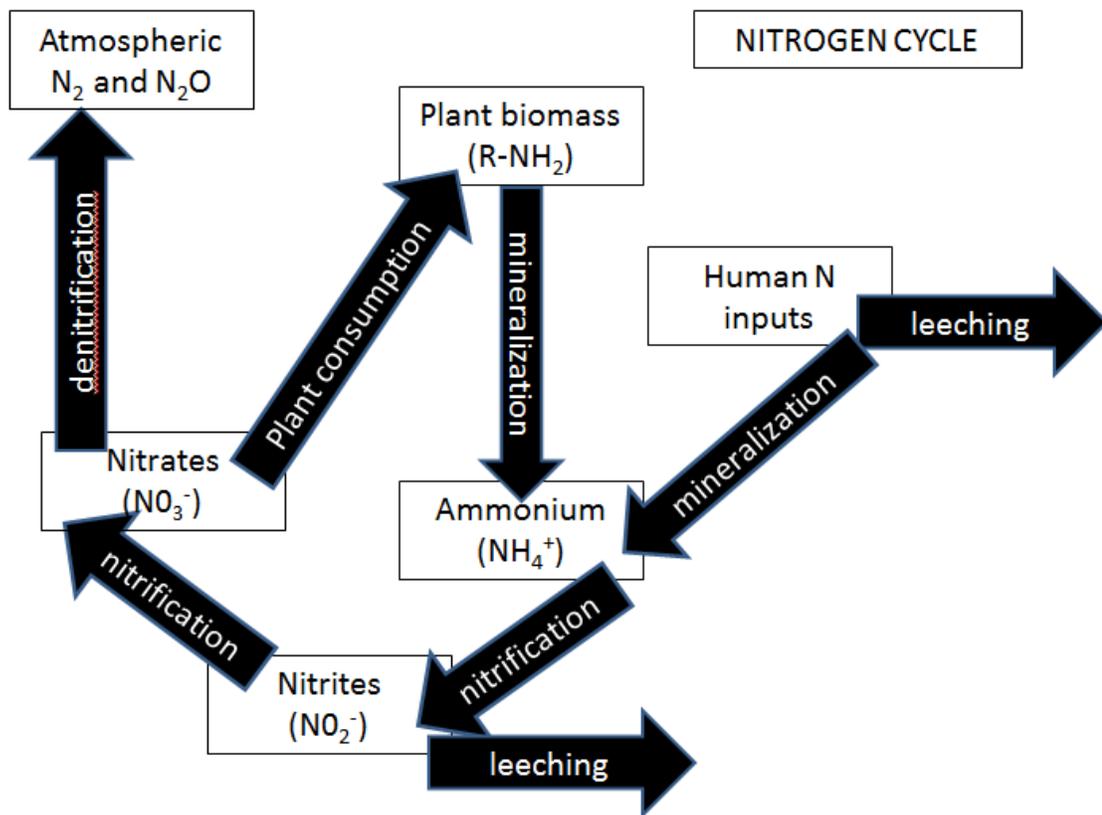


Figure 2. Flow Chart of the nitrogen cycle

The spatial distribution of atmospheric N_2 that has been converted to biologically-available stocks is heterogeneous. Human alterations that directly contribute to biologically available nitrogen include biomass burning, land conversion, and wetland drainage. These activities are important because they foster increased concentrations of NO_x , which is biologically available to plants with the aid of microbial activities and lightning fixation, as opposed to the 78% of the atmosphere that is dinitrogen, and is not available. Thus, a combination of microbial activity and both natural and man-made inputs of N are necessary to change the N dynamics for a particular area or stand.

(Vitousek et al., 1997). On the global level, areas such as northern Europe and northeastern United States have “profoundly” high nitrogen due to substantial direct inputs, while the Pacific Northwest is considered “nitrogen-limited” (Galloway et al., 1982; Berendse et al, 1993; Wright and van Breeman, 1995). Nitrogen availability ultimately dictates not only growth rates based on nitrogen limits, but also is connected to the allocation of carbon within the plant; a plant in nitrogen deprivation may be unable to allocate mass to nitrogen-rich photosynthetic tissue and instead use its carbon as storage structures in roots and stems (Lajtha, personal communication). In soil, nitrogen may be found in the forms of ammonium, nitrite (very rarely), nitrate, or ammonium nitrate, although generally the pools of ammonium and nitrate are considered the most important. In highly unaltered soils in South America, it was found that biologically available nitrogen was held in a ratio of 40% nitrate to 60% ammonium. A substantial portion of nitrogen fixation in forests, between 32 and 53 tg N/ year, is due to N-fixing plants in the legume families who support symbiotic relationships with nitrogen-fixing micro-organisms (Galloway et al., 1995).

Wardle et al. (2012) conducted an “island experiment” to test whether or not fragmentation and time since disturbance caused a decrease in available nitrogen as a result of ecosystem simplification (Wardle et al. 2012). They found that both nitrogen and phosphorus were inversely correlated with ecosystem complexity; that is, a more developed ecosystem should have less N and P than a young, growing forest, but that the total N concentration did not always decline; for example, N in humus increased with increasing ecosystem age, but plant available N, DON, and mineral N in the soil

decreased. Changes in P that were concurrent with those in N were also extant; NaOH-extractable P increased with increasing retrogression, while membrane available P decreased. It is suggested that low available P and N therefore fosters the development of species (such as *Picea abies*) that are N averse. These species often have highly developed defense mechanisms and therefore have highly phenolic leaves, such that their litter fall then causes a positive feedback for their further development at the expense of diversity (Hattenschwiler and Vitousek, 2000; Schimel and Bennett, 2004).

1.6.2. Nitrogen availability and assimilation

The balance of soil nutrients is as important as the amount of any given nutrient (with an emphasis in this case on N) in a forest ecosystem (Schleisinger, 1991). Ingestad's 1979 research showed that the mineral and nutrient requirements of *Pinus silvestris* and *Picea abies var Karst* for optimal growth were proportionally similar to the requirements for *Vaccinium spp.*, although they were not similar to those in all mesic hardwoods. Additionally, Ingestad found that ammonium uptake was greater than nitrate uptake in non-limited laboratory condition; however, in natural environments ammonium uptake is often limited by the immobility of ammonium ions in highly exchangeable soils. Therefore preferential relationships for plant uptake of ammonium are not necessarily present in all natural environments. However, abundant ammonium and nitrate is not always available; environmental conditions as well as microbial processing govern the availability of each. In anaerobic conditions, ammonium is more frequently encountered since oxygen is depleted; however, in forests and deserts, nitrate may be found

prevalently (Nadelhoffer et al., 1984). Nadelhoffer et al. (1984) suggest that since the energetic costs of reducing nitrogen are high, ammonium formation precedes nitrate formation in mineralization, and that nitrate is more easily leached from soil, ammonium will always be the preferred source of N when it is available. An important effect of the physiological preference for either ammonium or nitrate in plants in their natural environment is that the pH of the root zone is preferentially altered; when ammonium uptake is permitted, the root zone becomes acidic, whereas when nitrate is preferred, plants release of organic acids balance the negative charge (Hedley et al., 1982). Ultimately, this affects soil nutrient availability and potential “soil fertility” at a local scale.

Regardless of source, in plants, N is assimilated into amino groups; however, whether this assimilation occurs at the point of uptake (roots) or in the leaf tissue depends on species (Hedley et al., 1982). Physiological location of conversion affects the C:N ratio in leaves and roots, and therefore in time the return inputs of plants into the soil in the forms of litter fall or root die off. Additionally, in some species prior to abscission, nutrients from leaves are reabsorbed into the plant, so that the C:N ratio of live foliage differs from that of the litter input. The form of N in leaves could therefore have an effect on the C:N input from litter fall indirectly due to nutrient concentration in the foliage as well as directly based on quantity of litter fall. This dissertation quantifies the amount of litter fall and discusses litter quality in terms of two basic stand groups: deciduous trees (high “quality” litter rich in N with lower C content and less lignin, facilitating break down) and coniferous trees (lower “quality” litter with more hard-to-decompose C based

compounds).

1.6.3. Nitrogen mineralization and Microbial Communities

N fixation refers to the conversion of atmospheric N₂ into ammonium. This process is conducted by bacteria (and in some cases cyanobacteria) via the enzyme nitrogenase (Schleissinger, 1991). Although some plants such as *Alnus rubra* and *Ceanothus spp.* on WS1 have symbiotic nitrogen fixation, most do not, and they rely on ammonium in the soil already fixed by the heterotrophic microbial community. The rate of N fixation in the soil has been positively with the presence of SOM in studies of litter and coarse woody debris (Granhall, 1981; Granhall, 1987; Roskoski 1980, Silvester et al. 1982) as well as with appropriate nutrient concentrations for fostering microbial growth (Schleissinger et al., 1991). In short, the presence of the microbial community, whether or not it is symbiotic with the plant, and available C substrate for energy appear to be key factors in N fixation in forest soils.

Decomposition links the C and N cycles in forest soils; microbes and fungi consume C for energy while mineralizing, and in some cases converting forms of, N. What factors create variability in N concentrations and N forms in the soil? Six and Paustian (2000) and Theit et al. (2006) suggest that there is a relationship between SOM and decomposer community efficiency, but that this difference does not differ between fungal or microbial communities. In many temperate forests, nitrogen inputs to a nitrogen-limited forest results in increased ANPP, which in turn may increase forest carbon storage and carbon sequestration (Nadelhoffer et al., 1999). The impact of nitrogen on forest carbon storage

is directly related to the stand structure and soil quality of the forest; however, this relationship varies with species and site history (Houghton et al., 1988; Nadelhoffer et al., 1999; Rastetter et al. 1992). Kolling (1993) found that clearcutting of a spruce stand caused an increase in the nitrate concentration of drainage solutions (Meiwes, 1992; Roloff and Linke, 2002). Nykvist (1977) showed that higher N uptake results from greater biomass; however, with regards to the concentrations of N in the soil, noted that it is statistically impossible to distinguish between the changes in soil N content that are due to changes in content from increased nitrogen as a function of litter and changes in the mineral soil. In short, it is difficult if not impossible to detrend N patterns from decompositional, topographical, biometric and historical influences; however, it is very possible to quantify and qualify these patterns in the context of the community, site, stand, and history and analyze empirical relationships that may currently exist. This dissertation works from that premise; understanding correlations in one watershed now is a step towards better understanding of the forest ecosystem in a complex terrain.

CHAPTER 2

A BRIEF HISTORY OF WATERSHED 1

2.1 Introduction

2.1.1. Overview of WS1

Watershed one (WS1) is an exemplary first-order catchment in the western Cascades range in Oregon, a region characterized by steeply-incised topography that houses productive *Pseudotsuga menziesii* and *Tsuga heterophylla* forests (Figure 3).



Figure 3. Lookout Creek

Early documentation of regional history related to forest ecosystems begins in 1840, with record of burning of the Lookout Creek watershed and later parts of the Mack Creek watershed. These events exemplify some of the powerful disturbance events (fire, flood, windthrow, debris flow) which overlay cataclysmic events and slower geomorphic changes (volcanic events, glacial periods, and on a shorter time scale, slow-moving earth

flows) that shape the complex topography of the region. The juxtaposition of productivity and disturbance fosters key questions for scientists. How do such productive forests grow on this dynamic, complex landscape? How do they differ from those on more stable landscapes or those under particular management regimes? What are the implications of managing the western Cascades forests for timber? What are the implications of timber harvesting on these terrains on stream flow or biodiversity?

In the beginning of research in the region, the relationships between forest management and hydrology were questioned. In 1948, research began at the H.J. Andrews Experimental Forest (HJA, formerly Blue River Experimental Forest, designated for research from the Willamette National Forest) that initially focused on hypotheses about watershed responses to harvest activities: what effect would various harvest intensities have on water quality, channel stability, riparian ecosystems, sediment load, and nutrient losses? (Grant and Wolfe, 1967; Rothacher, 1967; Swanson, 2002). Hydrologists also had a set of similar questions: could logging increase annual water yields? Does logging affect flood impacts? Can logging be used as a tool to address stream flow management? As the experimental forest grew, so did the breadth of the fundamental questions; forest scientists moved from addressing direct impacts of forest management to exploring ecosystem processes across a variety of scales and diverse biotic communities. These questions were and are continually facilitated at the HJA by world-class long-term monitoring, supported through interactions with universities and federal agencies, particularly Oregon State University and the USDA's Forest Service. A growing data

legacy provides the necessary structure for understanding the rich environment of the western Cascadian forest. Within the HJA, WS1 might be seen as both a microcosm of both research history and environmental complexity. It has been heavily studied over the past sixty years and significant data has accumulated on topics ranging from microatmospheric dynamics to isotopic measurements to avian inventory. Holistic understanding of WS1's coupled natural and human history would be an invaluable case study for exploring how forests develop and respond to both natural and anthropogenically induced changes. However, despite the available knowledge about WS1, little recent attention has been paid to the consolidation of the growing scientific legacy of the forest with its human history. It is the fundamental objective of this document to provide that clean synopsis of both the natural and human history of WS1, providing the necessary connections between natural history and scientific progress. This document will address nine arbitrarily divided "research periods" in WS1, each of which is described in detail and significant results are presented, particularly those that might be obscured from a casual search for WS1 information. In many cases, there is some overlap between the periods, and there is certainly overlap between research, so the divisions are purely informative. I divide watershed 1 research into nine parts: (1) Pre-harvest, (2) Harvest, (3) Regeneration, (4) Notable early research, (5) Forest Inventory, (6) Floods, (7) Watershed 1 as a "Cyber Forest", (8) Data Management, and (9) LiDAR Reconnaissance. The history of WS1 is inexplicably tied to that of the H.J. Andrews as a whole, and, as will be described, particularly to its "sister watersheds", watersheds 2 and 3 (WS2, WS3). Thus, some research pertaining to these will be mentioned in conjunction with WS1, but

this research will be noted as a support to, rather than a direct outcome from, WS1 science.

2.1.2 Early Purpose of WS1

WS1 is one of the many small catchments of the HJA's original 6070 ha (15,000 acre) drainage to Lookout Creek. It was originally designated as the clear-cut treatment for paired watershed experiments with its neighboring watersheds, WS2 (old-growth) and WS3 (25% clear-cut). These experiments were proposed in the early 1950's as a response to growing concern about the effects of old-growth harvest on the forested environment, particularly stream dynamics, but with the conscious recognition that harvesting forests to some degree was necessary. The goal of the paired watershed experiments was to "provide the most efficient utilization of old-growth forests without detriment to other forest values that [would] lead to the establishment of young growth with a minimum delay" (Berntsen and Rotchacher, 1967).

Loggers who had previously worked on similar sites near the Columbia River were wary of the lack of comparable regeneration in the western Cascades (Geier, 2008). Research by the U.S. Army Corps of Engineers on stream and snow dynamics in proximal areas had increased federal interest in the science of predicting peak flow responses to natural and human events (Dyrness, 1967). Prior to the paired watershed experiment, local experiments were conducted to test the effects of road cuts and yarder patterns on the forest ecosystem. Nearly thirty miles of forest roads were built, allowing loggers and

researchers to approach the paired watersheds. These watersheds were ideal for comparative analysis because of their accessibility and similarity (tributaries have nearly confluences with Lookout Creek, similar forest communities inhabited them prior to harvest, and the watersheds have similar upslope areas). As interest in forest management and ecosystem response grew, so did hydrological interest in watershed processes, which provided the impetus for the construction of infrastructure for research on stream quality and quantity. Stream measurement stations, including flumes and sieves, were placed at stream outputs in 1952 to monitor peak flows, suspended silt, and stream bedload. Stream discharge records began in 1953, stream chemistry in 1962, and bedload records in 1967 (Geier, 2008).

The historical union between forest science and watershed science has always been strong at H.J. Andrews. Like several other early watershed study/ areas, including the Coweeta, Hubbard Brook, and Fernow Experimental Forests, HJA laid foundational ground for ecosystem studies at the catchment scale. Initially part of the U.S. International Biome Program (IBP) and now affiliated with the National Science Foundation (NSF) Long Term Ecological Research program (LTER), the HJA is enabled by federal aid in its assessment of the relationships between forest harvest and the hydrologic, geologic, and ecological processes to be pursued over a long-time scale with broad goals and meaningful objectives. Findings directly related to the paired-watershed research's initial goals of assessing stream response to forest management are numerous, so only a few early and outstanding results are detailed here. Rothacher found that annual water yield following clear-cut harvest increased by 40-50 cm, with a tendency towards

increased flux in the winter rainy season, attributed to decreased evapotranspiration (a natural consequence of vegetation loss) and consequent increases in soil water stores (Swanson, 2002; Rothacher, 1969). Grant and Wolfe (1991) found that the export of sediment following clear-cuts was nearly 5100 tons per year, double that of patch clear cut, and ten times that of the control. Jones and Grant found that harvesting increased peak stream flow discharge by 50 percent in small basins due to increased drainage efficiency that results from the integration of road and stream networks following management.

2.1.3. Current Environmental Conditions

Watershed 1 epitomizes the steep, V-shaped topography found in the western Cascades ranges, Parent material consists of volcanoclastic tufts and breccias derived from andesite and basalt formed in the late Oligocene to early Miocene period (Swanson and Jones, 2002). The parent materials are derived from the Little Butte Formation, which is characteristically overlain with ash and basaltic-andesite flows of the Miocene Sardine Formation (Swanson and Jones, 2002). Large, "bouldery deposits" of parent material are present on WS1, but their origin is ambiguous; they have been potentially attributed to glacial, volcanic, or mass-movement processes. Geomorphic processes, both rapid (such as sudden debris slides, alluvial and colluvial events) and slow (slumps and earthflows) shape the landscape into a complex surface. Mean slope gradient in WS1 is 63.2 percent; mean channel gradient, 27.8 percent; these gradients are fairly consistent with those of the other two paired watersheds (WS2 at 61.1, 36.4 and WS3 at 52.6, 27.2, respectively). A distinct north-facing and south-facing aspect dynamic exists on WS1, especially in the

deeply incised lower elevations of the watershed, and was recognized as an important ecosystem feature first in 1963 (Dyrness, 1967). Lee calculated that the average intercepting surface of solar radiation on WS1 receives light at a 41.9 degree angle (as compared to a 33.2 for WS2 and a 36.5 for WS3) (1974). Now using ray-tracing algorithms solar insolation can be accurately measured in space and time. Annual precipitation on the site is around 2300 mm per year. Very little of this precipitation falls as snow (Franklin et al., 1971). The average minimum temperature is 5.5 C in January and 23.3 C in August. Extreme wind storms are rare (5-10 years) and concurrent with heavy rain.

2.2 Pre-Harvest

Forest cover prior to harvest consisted of 300 to 500 year old *Pseudotsuga menziesii* and *Tsuga heterophylla*. A strong cohort of *Pseudotsuga menziesii* at age 125 was also present. Understory communities included *Taxus brevifolia*, *Thuja plicata*, *Acer macrophyllum*, *Alnus rubra*, *Castanopsis chrysophylla*, and *Cornus nutallii*. Six classes of herbaceous vegetation were also identified prior to harvest, and were aligned with a moisture gradient ranging from very "dry" communities dominated by *Gaultheria shallon*. to moderately dry communities with *Acer circinatum* and *Rhododendron macrophyllum*, moderate communities with *Coptis lacinata*, and moist communities with *Polystichum munatum*. The *Gaultheria shallon* community was the most abundant and covered approximately thirty percent of the watershed. Estimated DBH of pre-harvested trees was 120 to 136 cm, estimated height pre-harvest was 60 m. This corresponds to the approximate current height of the old-growth *Pseudotsuga menziesii* in the H.J. Andrews as measured with LiDAR to between 60 and 70 meters in 2008.

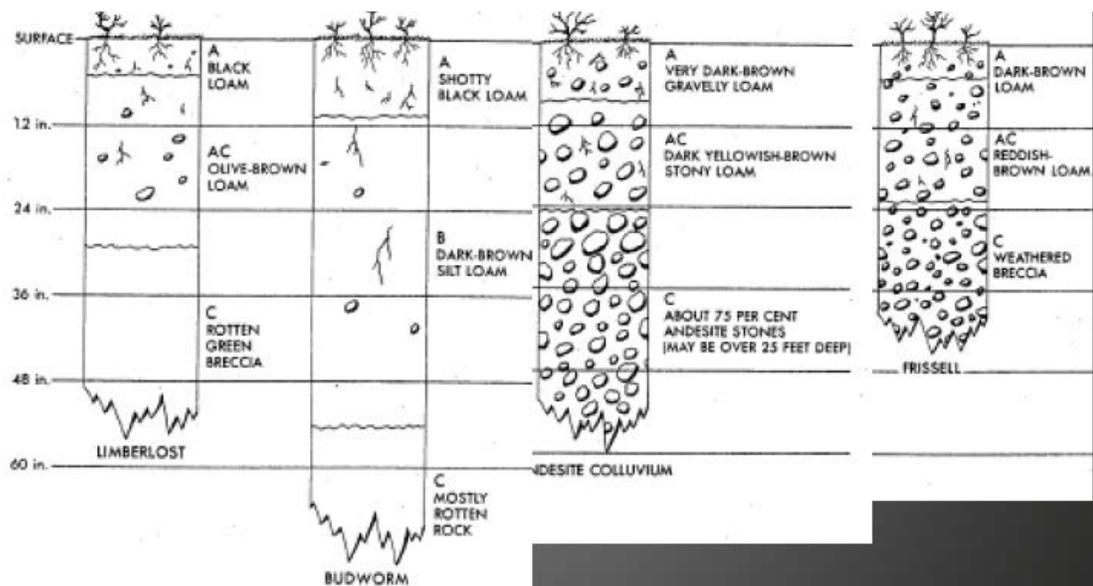


Figure 4. Soil Series Profiles on WS1

Soil classification of WS1 was initially grouped into three groups by parent material or movement. These groups were “soils from green breccia,” “soils from colluvium,” and “soils from red breccia and basalts.” Although most of WS1’s soils are shallow due to steep terrain, they are not prone to overland flow. A clay layer exists on steep slopes and ridges that is formed from andesites and basalts. Deeper soil layers have been noted to have low permeability and high storage capacities, and it has been suggested that the deep layers have more than 50 percent pore space. Stephens (in Rothacher, 1969) named the original soil groups as Limberlost, Budworm, Slipout, and also identified both mixed and andesitic colluvium. Maximum soil depth was measured at 48 inches (120 cm), with the exception of the mixed colluvium, where depths are hypothesized to extend for up to fifty feet. All the soils have been noted to be highly acidic. Following harvest, most

nutrient concentrations decreased to below pre-harvest levels. Soil Surveys on WS1 recently include Padilla's 2005 survey and Keebler's 2007 survey (Appendix 1).

The stability of these soils has been related to their clay mineralogy and rockiness. The clay layer in some areas (high elevations) consists of slick montmorillonite and kaolinite clays, as well as chloritic integrades. The colluvial soils have deposits of rocks and have also been noted for instability. One early (1956) survey intended to summarize the findings on soil plasticity for a single pit named "3-a" provides insight into the pre-harvest soil composition. Clay from this pit is greatest between 5 and 8 feet belowground (Table 1).

Table 1. 1952 soil pit

Source	depth	water %	liquid%	composition	plasticity
3-a	2	52	54	19 clay/27 silt/51 gravel	10
3-a	4	28	40	15 clay/24 silt/53 gravel	4
3-a	5	31	50	22 clay/33 silt/45 gravel	8
3-a	6	56	70	25 clay/38 silt/32 gravel	13
3-a	8	62	61	34 clay/25 silt/45 gravel	9
3-a	10	50	37	17 clay/25 silt/52 gravel	5

Presence of caprocks, talus slopes, and exposed bedrock is also a potential characteristic of WS1, both pre-harvest and following regeneration. Dyrness noted that the prevalence of "several nearly vertical rocky outcrops" with "steep, downward trending ridges and

drainages” that had soils that were shallow and stony. He named these soils into the group “Frissell,” a regosol derived from reddish tufts and breccias. Following harvest these caprocks, taluses, and outcroppings were exposed, especially on the south-facing slope of the watershed. Their presence is apparent even in the bare-earth LiDAR derivatives (Lefsky, 2002).



Figure 5. Large boulder on WS1

Prior to harvest, streamflow was compared between WS1, WS2, and WS3. On WS1, streamflow prior to harvest was documented between 1952 and 1962. The lag between gaging station establishment in 1952 and measurements in 1957 was due to a leak in the

weir. Early hydrographs show streamflow peaks in December and lows in August, with a maximum flow of 60 cm and a minimum flow of 1 cm. Correlation between instantaneous stream flows in WS1 and WS2 were documented at 0.90 prior to harvest verifying measurement precision for the purpose of deriving water yield equations and establishing the suitability of the paired study. However, total annual flow on WS1 prior to clear-cutting was significantly less than on WS2, a difference attributed to insolation by Rothacher (1969).

Watershed 1 is aligned along a distinct north-south gradient and as such receives significant insolation on its south-facing slope throughout much of the year. Pre-harvest hydrographs from WS1 were known to be particularly response to storm conditions. For example, in Decemeber of 1957, a particularly large rainstorm with 37 cm of rainfall fell in 3 days and run off reached its peak of 83 percent of this rain event. Stream chemistry pre-harvest also reflected the seasonality of precipitation in this region. Highest concentrations of suspended bedload were measured in December and January and were on average more than 90 ppm. Lowest concentrations were in August, and measured barely more than 0 ppm. Stream flow was found to be linearly correlated with suspended sediment during the autumnal season, but exponentially related to it mid-winter. Very large storm events were found to generate uniquely large sediment concentrations. No matter the initial sediment concentration, normalization to less than 10 ppm never exceeded 5 days. However, when precipitation was frequent (as in 1961-1962), high suspended sediment was also found.

2.3 Harvest

Watershed 1 was clear-cut between 1962 and 1966 primarily using a skyline yarding system, although a few exceptional areas in the southwest corner of the watershed were harvested via high-lead logging. Skyline yarding was designed to lift the log in its entirety off the ground via a carriage attached to a lead line, with the intent of reducing surface damage. However, it is not necessarily an optimal technique for landscapes such as WS1 where deep, canyon-like ravines and large trees often preclude adequate ground clearance.

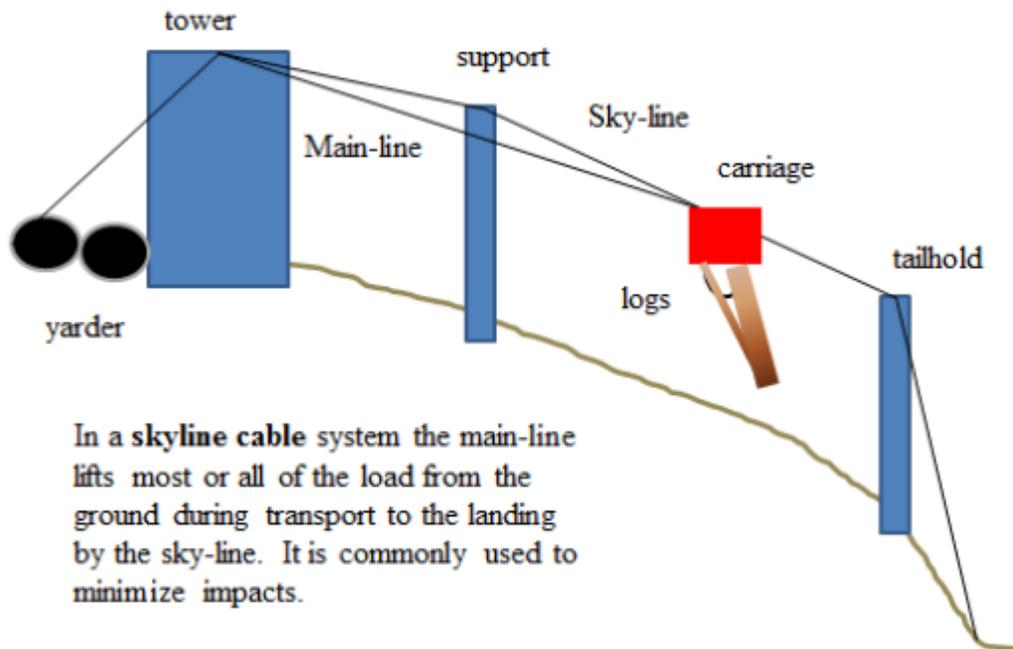


Figure 6. Schematic of skyline logging system

The combination of non-optimal techniques, extremely large trees, and lack of quality spur trees caused delays in the logging of WS1 such that the harvest lasted nearly four

years. Logging work, initially under the direction of Balsinger Logging, was later contracted to the Swiss company Wyssen logging, such that a proper carriage and skyline system could be developed and employed.

On the docket of sale, the purposes of the harvest of WS1 are listed as:

1. [to] study the effects of skyline logging on the quality and quantity of water produced from a small watershed
2. [to] demonstrate the type of equipment that can be used on steep terrains where roads are expensive or destructive.
3. [to] study the economic feasibility of using skyline equipment on steep terrain.

Due to the skyline method, less operational infrastructure (roads, skids, and trails) was built on WS1 than WS3, which had 25% of its area clear cut and lightly burned, resulting in less measured deep-soil disturbances (Dyrness, 1967). This was also an invaluable comparison between skyline and high lead methods. High lead methods allowed the butt of the logs to drag along the ground, potentially disturbing the soil. Dyrness surveyed the disturbance following the harvest of WS1 and WS3 and observed four classes of disturbance which he called “undisturbed” (litter in place with no compaction), “lightly disturbed” (litter removed and mineral soil exposed, or a mixture of litter and mineral, or an inversion of litter and mineral mixed with slash), “deeply disturbed” (soil removed entirely and subsoil exposed) and compacted (existence of skid, spur, or logging road). Attributed to difficulties in logging WS1, bare mineral soil was exposed on 12.1 percent of the watershed, greater than typical damage for a skyline system. Additionally, prior to

burning, he also measured the density of slash as heavy (greater than 25 cm), light (10 percent of plot greater than 25 cm) and absent (less than 10% of slash present). A pre-burn comparison of the slash on WS1 and WS3 produced expected results- on WS1 there was less heavy slash on the ground, so this potentiated damage from erosion. This damage was concentrated on the steep slopes and ridgelines, nearest the skyline structure. Dyrness also noted an abnormal amount of cull logs, particularly near the skyline structure. Mersereau and Dyrness reported that a change to soil bulk density occurred following the harvest in disturbed zones; bulk density increased slightly. In moderately disturbed zones, bulk density of soil only increased where high lead harvesting was used, suggesting that compaction and soil damage occurred exclusively.

HARVEST UNITS ON WS1

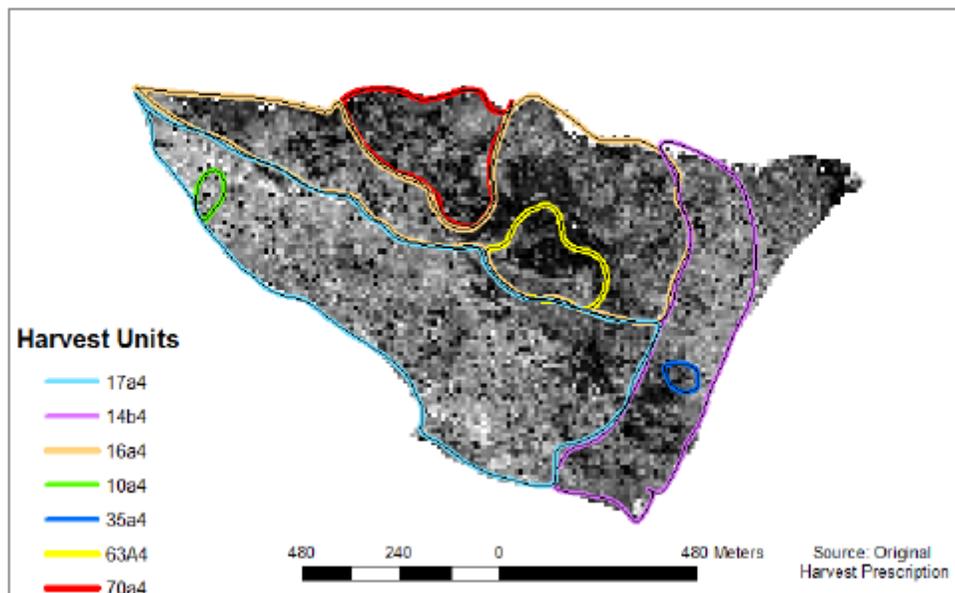


Figure 7. Harvest Units on WS1

However, the skyline method on WS1 did not completely preclude road use. Three roads were constructed adjacent to WS1. Road 16706 runs to the ridgeline at the top of the watershed (now road 2206), and it connects the harvest area to the permanent Mill Creek Road. Road 1553 A runs along the top of WS1 and is now closed. It was originally of the same construction as the 16706. Road 1553 G approaches unit 14B from the opposite side of the watershed.

Midway through the harvest, 2 large storms (100 year events) occurred, which initiated four debris slides. Although no remarks of immediate damage to WS1 were recorded, the events generated landscape instability, which over the course of a few years propagated to introduced several smaller slides between 1968 and 1972. Protection from regenerating tree cover as well as downed wood and woody debris on up-basin sites, coupled with the absence of compaction from roads, mitigated the effects of this event as compared to WS3. However, although downed wood and debris was not released from the watershed, a significant portion of debris was moved into the stream channel. This debris cluster remains today on the watershed near the confluence of the upper tributaries.

Sub unit 17a4, on the north facing slope at a low elevation, was logged first in the fall of 1963 by Ballsinger logging and Wyssen Logging, and 3.3 M board-feet were removed. On this unit, yarding began on the west side of the watershed. Soils were noted as “unstable.” On the boundary of unit 17a4 and 16a4, along the tributary, three smaller instrument sites were located (named 29a4, 30a4, and 31a4). These sites were not

considered harvest units. Sub-unit 18b4 (the southern-most tip of the watershed located nearest the current vegetation plots on the sixth transect) included a sub-unit 33a4 and was logged in the fall of 1964 by Ballsinger Logging. These units were not included in the original harvest diagrams. Unit 18b4 was logged with the high-lead method due to the “gentle slope” that was deemed unsuitable for skyline logging.

Sub unit 63a4 (near the confluence of the tributary and Lookout Creek, on the south-facing slope) was logged in the fall of 1966. This unit was also bated and seeded in 1968 for protection against rodent herbivory, which was noted to prohibit the regeneration of the young *Psuedotsuga menziesii*. Foresters eventually concluded that this area was 80 percent bare rock and was “unplantable.” Sub unit 70a4 (south facing slope at high elevations) was logged in the spring of 1966 along with unit 16a4. It was a smaller unit at a size of only 18 acres. Management on this unit exercised “restriction” due to highly unstable soils.



Figure 8. Watershed 1 mid-harvest

Sub unit 16a4 (south facing slope at low elevations) was logged in the spring of 1966. It was the final area to be yarded. The soils were noted for being “unstable”. Subunit 14b4 is the unit which contains the landing in the harvest diagrams. In some drawings it falls within the boundaries of units 18b4 and 35a4. There was no harvest designated in the site history for the north-western tip of the watershed. It has been noted that the watershed was “burned as a whole” although a current plethora of moderately degraded logs suggests that burning in this area was lighter than others, and the road itself may have been used as a firebreak.

Slash was broadcast burned in a "hot and very satisfactory" burn in 1966. Foresters noted that the burn was not ideal due to "advanced reproduction on many of the north facing slopes," presumably referring to the *Psuedotsuga menziesii* seedlings. The initial burn removed all slash and minor debris from the stream channel to a degree that was noted to be "satisfactory in view of the difficulties imposed by the steep slopes." Debris from the lower one-third of the watershed was then manually removed. Following burning, four re-plantings on the site were attempted. In 1967, aerial seeding was conducted. In 1968, a second, localized seeding was conducted in areas that did not initially take. In 1969, the entire watershed was planted with 2:1 *Psuedotsuga menziesii*, and in 1971, select locations were planted with three year old seedlings. Successive re-plantings were not always successful, particularly in the rocky areas on the south-facing slopes. Nor were the operations to remove channel debris successful. The streams did not stay clean due to after-events from the floods of 1964-1965, which released debris from the upslope to contribute to the channel again. The estimated influx of sediment and debris to the channel was 67 percent one year after the burn (1967) and 28 percent in subsequent years (1968).

In 1986, a thinning treatment was considered by several researchers. At this point the first seeding would have been nearly 20 years of age and prime for the first thinning.

Reviewers dated the standing *Psuedotsuga menziesii* and found that it varied in age between 12 and 18 years, which was to be expected due to multiple regeneration procedures and natural regeneration. They also noticed that the north-facing slope was particularly well stocked; specifically they noticed that older trees that existed top and

bottom (of the slope) with the middle one-half of average height. In short, height growth was favored at high elevations and near the stream, but not on the mid-slope. On the south-facing slope, notes indicate that it was very rocky and stocking was patchy, although trees of greater DBH and height were present. A very high level of brush was noted, with emphasis on the presence of *Acer circinatum*. Another reviewer noticed that many of *Psuedotsuga menziesii* at the time were shorter than the *Ceanothus* plants (some up to seven feet in height) that were located on the watershed. Brush removal was considered by determined uneconomical. Ultimately, thinning was not selected for ecological and experimental reasons (or, as one forester noted snidely, "because it's H.J."), although another noted that "the unit is ready for thinning and may soon be too old."

2.4 Regeneration

Burning and subsequent landscape degradation had significant impacts on regeneration of a new forest community in WS1. In the first years after harvest, erosion and surface flow (450 tons per square kilometer) degraded the soils upper layers. For hardy early-successional plant communities, however, this was the opportunity to thrive in a newly available sunlight. In the first year after burning, 16 percent of the watershed was covered by brush and herbaceous species. Eleven species groups were reported to have established in WS1 within only two years after harvest. These plant communities included *Corylus cornulata*- *Gaultheria shallon*, *Acer circinatum*- *Gaultheria shallon*, *Rhododendron macrophyllum*-*Gaultheria Shallon*, *Acer circinatum*- *Berberis nervosa*, *Coptis lacinata*, and *Polystichum munitium* (Adams et al., 1991).



Figure 9. *Acer circinatum* – *Berberis nervosa* understory, 2011

This re-vegetation was also observed and studied on the clear-cut areas of WS3, where it was determined that immediately after harvest (1 year) soil moisture was 12% higher than on control WS2 due to lack of interception loss, but after 1 year the soil moisture had declined to 2 cm less than WS2, changes which were attributed to site re-vegetation (Adams et al., 1991). These changes in soil moisture following harvest give rise to the establishment of drought-tolerant herbs and shrubs, sometimes at the initial expense of trees. Dyrness (1967) found that following the harvest of WS1, percent cover by overstory species decreased from 21.7 percent to 0.5 percent, and after burning this figure

rose to 2.8 percent; however, initially shrub biomass decreased from 43.7 percent to only 7.1 percent, and then rebounded after fire to 41.9 percent.

On WS1, Halpern (1989) found that early regeneration was related to landscape position, aspect, disturbance severity, and elevation. For example, the *Acer circinatum* community was found predominantly on undisturbed sites or disturbed but unburned sites, which were all located on shallow slopes along the ridgetops at high elevations. Immediately following harvest, residual (from buried seeds not damaged by fire), herbaceous communities of *Rubus ursinus* and *Trientalis latifolia*-*Whipplea modesta*-*Hieracium albiflorum* as well as the invading *Senecio sylvaticus*-*Epilobium paniculatum* – *Conyza canadensis* were found to have major (defined as more than 5 percent) regeneration cover on the remeasurement plots. Over five years, these communities retained their gross abundance, but additionally the shrub/understory layer of *Acer circinatum*-*Polystichum munitum*-*Gaultheria shallon*-*Rhododendron macrophyllum*-*Berberis nervosa*-*Corylus cornulata*-*Tsuga heterophylla* appeared and increased in abundance and cover. Two important conclusions from inventory and abundance analysis of early regeneration communities on WS1 were that (1) 82 percent of the understory species persisted through the logging and slash burning and that (2) the invasion by new species was prolific two to five years following the harvest, and the cessation of which was due to the development of the initial canopy of very young *Tsuga heterophylla* that precluded further herbaceous establishment.

The duration of WS1 harvest may have also provided opportunities for early invaders and regenerating local herbs. Available sites for seeding, particularly for the wind-dispersed and shade-intolerant *Senecio sylvaticus* during the four years of harvest activity, may have allowed for its germination and establishment. The same was noted for the naturally burn-adapted *Epilobium angustifolium*, which was able to sprout from undisturbed rhizomes. Mersereau and Dyrness noted that this plant invaded the watershed one year after harvest, and became 35 percent of the cover over one year. *Ceanothus* also “invaded” the watershed from underground seedbanks soon after harvest. Halpern (1989) determined that the initial regeneration of WS1 followed two main trends: (1) there was persistent proportionality between original cover and initial cover or (2) there was inverse proportionality between long-term regeneration and disturbance intensity. Rothacher noted a distinct relationship between the lack of timber tree growth and the presence of rhododendron, which persists where canopy is sparse.

2.5 Notable Early Research

Understanding the relationship between the magnitude and timing of water yield and clear-cut management was an initial goal of WS1 and early research on stream dynamics quantified the relationship from multiple perspectives. The most straightforward approach was simple time-series regression of the water yield for the post-harvest years. Post-harvest water yield was shown to be moderately autoregressive following the function of

$$Y = 52.2 + 2.05 T$$

where Y is the water yield and T is the years after the logging. And, if precipitation is included,

$Y = 31.41 - 2.08T + 0.091P$, where P is the precipitation, annually. It was also shown that annual increases in water yield from WS1 were seasonal (October to May) due to precipitation patterns and the subsequent higher soil water yields as a result of reduced interception and transpiration. Hydrologic responsiveness of the soils is increased after harvest and removal because less precipitation is required to recharge the soil water.

Additionally, substantial increases in low flows were documented by Rothacher and Harr.

It was concluded that sub-surface flow, not overland flow, delivers water from the streams in recently logged watersheds, although overland flow is increased. Due to variable sourcing, stream concentrations reflect heterogeneous upslope areas, and winter contributing areas are much larger than summer, facilitating increased stream flow and responsiveness. Increases in mass movements after logging, coupled with seasonal

precipitation, drive hydrologic patterns observed in logged watersheds immediately after harvest.

Stream temperatures were also affected by the clear cut. Levno and Rothacher (1969) found that the combination of burning and removing of logs in the lower one third of the channel of WS1 resulted in an increase in stream temperatures to above 65 degrees Fahrenheit for 17 hours, a record for the area. Mesereau and Dyrness (1972) noted that the loss of channel wood also decreases the stream stability, such as the erosion of banks and, due to the displacement of kinetic energy from the debris dams to the bed surface, stream beds.

Following the clear-cut, but not burn in 1967, concentrations of $\text{NO}_3\text{-N}$, Na, Ca, $\text{NC}_3\text{-C}$ and $\text{PO}_4\text{-P}$ increased in stream flow; however, after burn concentrations of K, Ca, Mg, and NCO_3 decreased. In short, the clear cut increased the release of cations, but this release was decreased following the burn.

Geomorphological findings from WS1 united the hydrological changes ensuing after the harvest with the landscape dynamics potentially associated with the same. Following tree removal, reduced interception and transpiration leads to increased soil moisture, which can reactivate creeps and flows. Gray (1973) noted that loss of trees also increases slope instability mechanically by reduced the tensile reinforcement normally surcharged by tree weight. Dyrness (1967) found that land movements were more frequent in areas of pyroclastic rocks versus basalts and andesites; Rothacher (1970) determined that subsurface soil moisture remained unnaturally high following clear cut; in the summer

after harvest, one area remained above field capacity for sub-surface moisture throughout the summer. Additionally, greenish tufts and breccias were more unstable than reddish ones. The rate of post-harvest creep was measured at 0.25 cm per year by Gray.

Mersereau and Dyrness (1972) conducted an intensive survey of the rates of soil movement based on slope, regeneration of herbaceous and shrub plants, and disturbance. Both the aspect and the gradient of slopes correlated with slope movement; in 1967, south-facing slopes lost 6.11 cubic meters of soil per hectare versus a loss of 1.405 cubic meters per hectare on north-facing slopes, a difference attributed to drying and loss of slope cohesion. Rain thereby reduced movement on the south facing slopes, a finding which contrasts the suggestion of increased movement in rainy conditions proposed by Dyrness. It was estimated that 75 percent of slope movement was due to the large-scale movement of Talus slopes, which were noted by both the loggers and early researchers to be “highly unstable” and as Dyrness commented, “reforesting these areas will be a slow process.”

Table 2. Volume of Soil and Rock Debris caught on vegetative slopes (80 and 60% South and North facing slopes) of WS1

Collection Date	80 SF	80NF	60 SF	60Nf
5/3/67	33.5	5.0	0	2.1
9/13/67	54.4	11.7	0	2.1
10/26/67	71.2	11.7	0	2.1
2/15/68	113.7	13.3	0.7	3.2
4/10/68	144.2	14.9	0.7	3.2
5/8/68	148.3	16.2	0.7	3.2
6/19/68	152.4	16.2	0.7	3.2

2.6. Forest Inventory

Forest vegetation is a key component of WS1 that has been seen as an integral of the total ecosystem. To study the vegetation, 131 “permanent” re-measurement plots were established on WS1 immediately following the harvest of the forest. The plots have been in existence since 1962, initially established to examine the effects of harvest on vegetative cover, and they exist in multiple locales in HJA, but are particularly dense in WS1. Classification for forest communities by vegetation plot is generally based on understory composition.

The plots are arranged along six transects spanning the watershed from north to south, with between 10 and 27 plots on each transect. Plot radii are 8.92 m, so that the ground-measured area equivalent to 250 m². Plot centers are 30 m apart. Due to steep slopes, aerial images of the plots are elliptical. In general, the forest inventories of WS1 can be split into the pre-1980 and post 1980 periods. In the pre-1980 period, only shrub and understory vegetation was measured. Plots were intensively subsampled within 4 m² staking and the locations of these plots were determined randomly. Following 1980, the overstory vegetation was measured as well.

2.6.1 Pre-1980 Inventory

Pre-1980 inventory measurements visually estimated projected canopy cover in percent, assessing vascular plants less than 6 m tall. Halpern (1989) studied pre-1980 forest inventory on WS1 using detrended correspondence analysis and found that post-harvest regeneration quickly returned to pre-harvest conditions, but these conditions differed depending on moisture conditions. He noted that on dry sites, flora was diverse but

successionally transient, whereas on moist sites, flora followed unique pathways reflecting a special set of residual plants and invasive colonizers. Thus, when the site was favorable, re-establishment by flora was more permanent than when it was unfavorable. Additionally, he noted that the divergence from residual species was proportional to harvest intensity. DCA revealed that early succession generally corresponded to a gradient in available moisture, but after a few years, compositional change stabilized and the development of overstory vegetation began.

2.6.2 *Post-1980 inventory*

As expected, the dominant tree on most plots on WS1 is *Pseudotsuga menziesii*; however, the most reproductive tree is *Tsuga heterophylla*. Seven inventories were conducted on WS1 between 1980 and 2007 (1980, 1984, 1988, 1991, 1995, 2001, and 2007). During each inventory, DBH was measured for all trees with a DBH greater than 1 cm, and DBA (diameter at basal area) was measured for all trees smaller. Conversion factors for DBA to DBH can be found in Lutz. To assess the biomass of these trees, Halpern's aboveground biomass equations are commonly used (Halpern and Means, 2004). Using a Schumacher based log-form, DBH is related to biomass by allometric scaling. These equations are designed to be accurate for the western Cascades sites and young forests on which they have been validated. The availability of forest inventory data for post-harvest years enables researchers to study the effects of various environmental factors on plant growth with explicitly.

Using forest inventory data, Lutz (2005) concluded that the role of mortality in early successional forests was related more to species than density. Of the 75000 trees tracked by Lutz, there were more than 7000 mortalities, many of which were related to suppression; however, a loss of biomass due to mechanical damage (crushing, windthrow, etc.) was significantly greater than that due to suppression. The rate of mortality in hardwoods was the highest, at 9.7% per year, but where the hardwoods were well established, biomass was capable of increasing as stems remained resilient. In conifers, which had greater biomass initially, more loss occurred due to crushing, especially the nearby 26% loss of *Thuja plicata*. Lutz concluded that spatially condensed loss of trees due to mechanical damage fostered spatial heterogeneity and the establishment of a more diverse forest community. This analysis is directly linked to the gap dynamics studies of Spies et al. (2012), who quantify spatial heterogeneity within and between canopy gaps. In fact, multiple studies from the forest inventory data indicate that mortality, or at least the decline of surviving trees, is more indicative of plant productivity on developing stands than is biomass.

Acker (2002) compared inventory from WS1 with that from WS3 and found that the accumulation of bole biomass was greater in young WS1 than in older WS3, a support for his hypothesis that bole biomass accumulation rates decline with age. Bredensteiner(1998) determined that the role of overstory biomass in the water cycle becomes more significant in the third decade following harvest than prior years. Lindh suggested that the decline in forest biomass accumulation following harvest is a response to local areas failing to regenerate or the increased cover by hardwoods as opposed to conifers. Overall,

forest inventory data from post-1980 showed the importance of forest composition in WS1.

2.7. Floods

Just as forests affect streams, streams also affect forests. WS1's post-harvest sediment yield was considerably higher than its old growth counterpart WS2 (Hall, 1978). This increased yield has been attributed to both increased particulate over time, as well as to seven significant landslide events between 1964 and 1972 that affected the clear-cut watershed more than the old-growth. Hydrological events have also impacted stream sediment and watershed dynamics. In particular, floods of 1964 and 1996 are of interest.

Rothacher and Fredrickson (1967) reported damage from the 1964 and 1965 “Christmas storms.” Preceding the events, a period of very low temperatures was observed. A drop in the snow line coupled with warming temperatures caused extensive rain on snow events, melting excessive water. Stream flow rose quickly and exceeded the 50 maximum-8.25 inches in two days. Snow declined from 18 solid inches to only a patchy distribution in 24 hours. The most intense rainfall ever recorded in the region accompanied the storm – 0.47 inches in an hour. With this event came multiple debris slides, including a three-pulse slide which destroyed the stream gage in WS3. On WS1, no direct debris events occurred, however, an “aftershock” of the event caused a debris slide in 1965 which deposited several tons of material in the stream channel.

In 1996, unusual weather patterns were noted again- low snowlines and a rapid increase in snow. Intense cold weather was noted including many freezing rain events.

Immediately after the freezing rain event, a warm, southwestern jet brought a subtropical storm into the region between February 6 and February 10, and warm temperatures caused the melting of the snow. Streams rose and quickly reached flood stage. Although

the event was of less magnitude than that in the 1960's, it was still important in the development of WS1 (Rothacher and Fredrickson, 1967; Hall, 1978).

2.8 Watershed 1 as a Cyber Forest

With the rest of the world, WS1 entered the new millennium as a center of new technology, and became a “cyber forest.” “Cyber forest” is defined by Henshaw as possessing a “high performance wireless communication enhancing connectivity among remote field research locations, station headquarters, and beyond to the university and outside world.” This data connectivity exists in spite of rugged terrain, thick overstory, and lack of pre-established networks (the only connection into H.J. Andrews is a 56 kB phone line!) One particular asset of WS1 is the telemetry transect, 11 plots on WS1 that are nearest the gaging station and road access. An “almost real-time” sensor array transmits streaming data across high bandwidth to Oregon State University where it is automatically compiled, stored, and checked for quality. Access to this data is nearly immediate for College of Forestry researchers at Oregon State University (Henshaw et al., 2008).

2.8.1 The Telemetry Transect

A primary goal of the telemetry transect, although not the only goal, is to provide the necessary infrastructure for the H.J. Andrews Airshed project. An airshed is a flow of air superimposed onto a watershed which is formed by rapidly cooling near-surface air, denser than the surrounding air, which tumbles down basin on the same paths as water flows. Monitoring the respiration of CO₂ from plants and soil along the transect, as well as at various heights on the tower at the gaging station allow researchers to visualize these paths and test hypotheses about sources of air in the watershed. Preliminary

research indicates that air “pools” like water, and that these pools may be both deep and turbulent (Pypker et al., 2007).

2.8.2 *The FEEL database*

Information about the wind-speed and direction is available online for any user to download and can be accessed as a time series through the program GLITCH (the generalized linear integrator for time series changing). GLITCH allows the aggregated download of wind speeds over the course of minutes or hours, rather than high resolution data. This is useful for long-term datasets at resolutions coarser than those recorded directly by the tower.

Spatially explicit temperature measurements are also taken within the stream of watershed 1 using a 0.66 mile long fiber optic cable that tracks heat gradients. The same technology has also been implemented aerially in WS1 using cross-ways aerial cables set at predefined heights. This information is all recorded in the Forest Ecophysiology and Ecohydrology Telemetry Transect database (FEEL), which is available online for all researchers. A hierarchy of data options allows proprietary content to be protected until quality assured while other content is presented immediately. Open source descriptive data exists. The FEEL data base is unique in that it functions at both the lab-level as well as the dynamic level; as probes and sensors are changed and set up, they are automatically updated in the database. The data model for FEEL is considered advanced due to tab-based navigation and on-the-fly alterability.

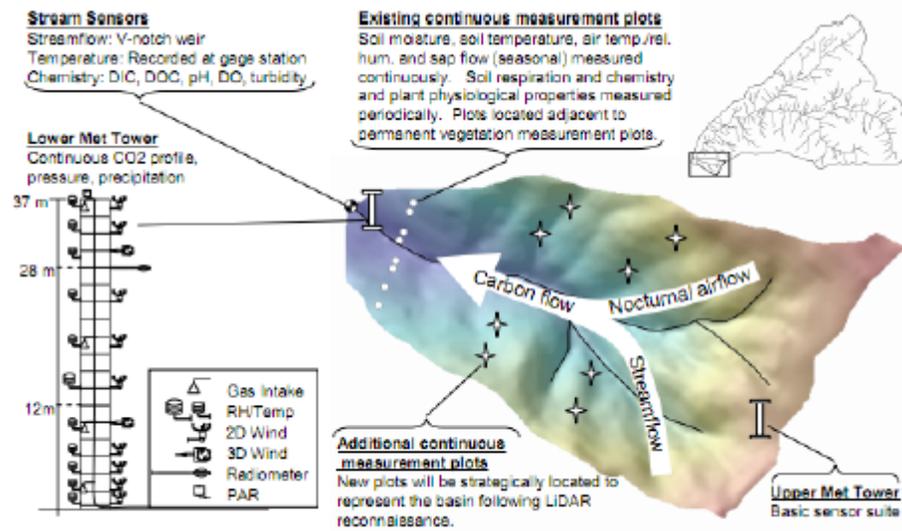


Figure 10. Telemetry Transect and tower deployment

2.9. LiDAR reconnaissance

LiDAR (light detection and ranging) reconnaissance is a method of remote sensing that captures high-resolution, large-extent biophysical measurements in three dimensions (Lefsky et al., 2002). Although LiDAR in itself is not new, its use in ecosystem studies is. LiDAR is fundamentally “laser altimetry”- the difference between return times for light pulses sent to the ground from an airplane mounted sensor is used to detect heights of trees and cover percent. In 2008, LiDAR reconnaissance was flown on WS1 as well as the rest of HJ Andrews. The SLICER method was used, which uses a scanning beam to return a digitized signal that can be analyzed for backscatter, allowing a more detailed identification of canopy components (Andersen et al., 2004). Cover is calculated using a unique formula:

$$\text{Cover} = 1 - \frac{\text{Scaling constant} * \text{Ground Return}}{\text{Canopy Return} + \text{Scaling Constant} * \text{Ground Return}}$$

On the H.J. Andrews, LiDAR has been used to map the bare earth as well as vertical complexity. The bare earth maps reveal the underlying geology of the site and emphasize the forest/floor interactions. They are validated with on the ground inventory. Likewise, trees identified as uniquely tall in the LiDAR reconnaissance can be verified by climbing. For WS1, LiDAR revealed heterogeneity in forest cover, particularly clustering of biomass. LiDAR metrics were used to classify the watershed for sampling. Much of the research here in is based on the fundamental assumptions of cover classes provided by the LiDAR reconnaissance.

Overall, WS1 as a case study for an ecosystem has provided significant information on topics from management to informatics to biology, and may be unprecedented as one of the most studied ecosystems in the world.

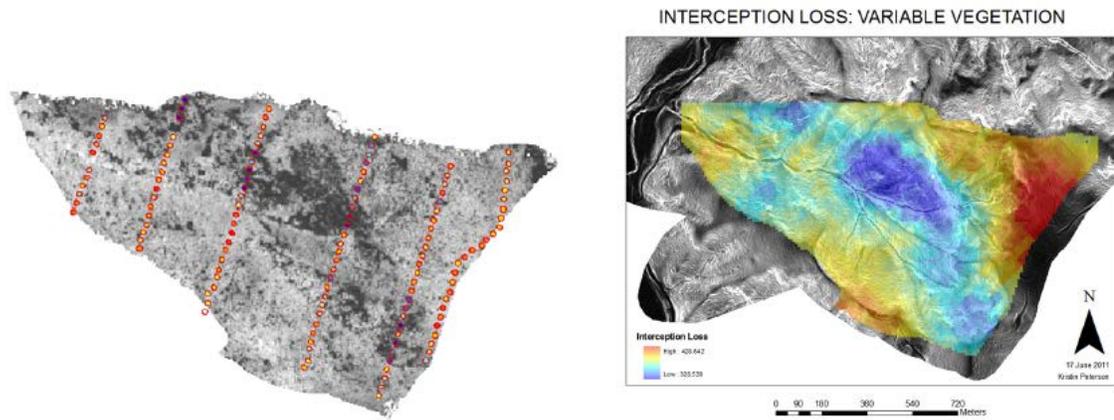


Figure 11. LiDAR Cover Map; Using LiDAR to Predict Interception Loss

CHAPTER 3

**DO PROMINENT DRIVERS OF ANPP CHANGE DEPENDING ON WHEN
ANPP IS MEASURED? A COMPARISON OF METHODS ON A CLEAR-CUT
WATERSHED IN THE WESTERN CASCADES, OREGON**

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3.1 Introduction

Aboveground net primary productivity (ANPP) has been linked to resource gradients such as solar radiation, nutrients, and moisture that are generated by complex terrain (Knapp and Smith, 2001; Pypker, 2007; Raich et al., 1991; Turner, 2005). It has also been suggested that belowground ecosystem stocks and functions, such as soil organic carbon (SOC), dissolved organic carbon (DOC), dissolved organic nitrogen (DON), and belowground productivity are also related to the same topographically-affiliated resource gradients, and therefore share spatial patterns with ANPP (Antos et al., 2003; Burke et al., 1990; Chapin et al., 1994; Burke et al., 1995; Finzi et al., 1998). What is less clear is the degree to which aboveground processes reflect belowground conditions and resources.

For example, the distributions of both soil organic matter (SOM) and leaf litter vary spatially over complex terrain influence ANPP and are also positively correlated with one another (Bazzazz and Sipe, 1987; Leuscher et al., 1993; Miles, 1979; Tilman, 1985; Vierick, 1970; Vitousek and Reiners, 1975). In addition, it is important to take into account the fact that since ANPP varies over time, one time measurements are not necessarily the best metric for studying soil-ANPP relationships. Differences in the rate of stand development due to species composition mean that some parts of a site may appear more productive than others simply because they are at a different developmental stage. Additionally, declines in productivity at the stand level may indicate rapid early growth and a fair site, rather than a poor site. Although young stands grow more rapidly than older stands, this initial growth depends on species. To avoid conflating the different drivers, for example low productivity due to site quality, and low productivity due to rapid early growth and subsequent age-related decline, it is important to recognize ANPP as a complex and possibly emergent process that is affected by multiple, non-linear ecosystem factors. Consequently, ANPP with respect to time as a complex and possibly emergent process that is affected by multiple, non-linear ecosystem factors and that may not be adequately represented by a single observation or imputed productivity from a site index curve. We suggest that the optimal method for exploring structural-functional relationships in forest ecosystems may be better expressed by estimating maximum productivity (mANPP) within the context of site history, stand composition, and stand development. This method of estimating of mANPP is novel to this research; unlike traditional measurements of site quality (such as site index or inferring quality

from remotely sensed color spectra) (Bailey et al., 1998; Drew and Flewelling, 1979; Raich et al., 1999; Tappeiner et al., 1997), the method we propose to use requires long-term stand data and statistical extrapolation to select or predict maximum productivity for a unique stand and location.

Disturbance, whether natural or human, initiates vegetation development that often follows multiple pathways. Within a disturbed area, these developmental pathways are typically not homogeneous (Abrams et al., 1985; Bradshaw, 1982; Borgegard, 1990; Londo, 1974; Matthews, 1979; Miles, 1987). The existence of multiple successional pathways following disturbance has been observed by del Moral et al. (1995), Swanson et al. (1986), Wood and de Moral (1987, 1988), most notably on Mount St. Helens following its 1980 eruption. They found that these pathways were associated with measurable topographic variables. In other locations, the existence of multiple pathways has been related to disturbance intensity (Cattelino et al., 1979; Belsky, 1986; Halpern and Franklin, 1990), seed composition (Abrams et al., 1985; McCune and Allen, 1985), pre-disturbance vegetation (Collins and Adams, 1983; Christensen and Peet, 1984; Halpern and Franklin, 1990), microclimate and climatic responses (Archer, 1995; Likens, 1996). Naturally occurring resource distributions resulting from landform structure (Bormann and Sidle, 1990; Chapin, 1993; Ewing, 2002) may also lead to multiple pathways. Additionally, the designation of successional pathways may also be a function of analytical time range. Divergence between successional pathways was documented by

Fastie (1995) over a short time range while Pickett (1989) documented convergence between pathways over a longer time range over the same forest chronosequences in Glacier Bay, Alaska. The argument that topography drives both nutrient and plant distributions is a “chicken-and-egg” matter, since the allocations of belowground resources cannot be separated from their effects on the aboveground growth, and the time range over which trajectories are designated, as well as the time in stand development at which growth is measured makes it difficult to detrend the effects of a particular site’s history from those of the topography at large. Since multiple pathways of forest development play an important role in both stand structure and belowground resource distributions, it is important to characterize both the stand, its history, and the site in a way that explains observable patterns (Bardgett and Wardle, 2010; Bezemer et al. 2010, Eisenhaur et al., 2010; Porazinska et al, 2003; Wardle al. 1999; Wardle et al, 2004).

Belowground resource distributions are often characterized as being relatively stable in both space and time. For example, soil attributes such as the protection of stable C aggregates (Six et al., 2004; Marin-Spiotta, 2011), N mineralization (Nadelhoffer et al., 1991), soil texture (Burke et al., 1995), or microbial decomposition (Mathes et al., 1985; Flanagan, 1986; Epstein, 2002) are often measured at one point in space. When significant error can be accepted, such as in the case of large-scale modeling, few, infrequent points provide enough data to create predictive equations; however, for understanding processes in complex terrain or mountains, limited sampling not

appropriate because it does not address why observed heterogeneous distributions of belowground resources develop and what effect this heterogeneity may have on landscape-scale estimates of ecosystem stores (McEhinny et al., 2005). Knowledge of fine scale heterogeneity of soil resources and vegetation composition is needed to adequately characterize ecosystem processes at landscape and watershed scales. However, measuring these belowground resources is difficult, and they are often autocorrelated with one another. In many cases, topographic indices may be used as proxies for belowground resources, although it has been noted that ecological processes and patterns that exist at one scale, for example, the plot scale, may not be reflected at another, such as the landscape scale (Allen and Hoekstra, 1990; Berdanier and Klein, 2011; Currie, 2011; Turner, 2005). This lack of integrity across scales further complicates our understanding of the drivers of ANPP in complex terrain; it is critical to quantify to what extent the topography influences belowground resources, and to what extent they are the function of biotic drivers.

It might be expected that a forest plantation established after clear-cutting would be an ideal case for assessing how stand structure is related to biogeochemical function; however, despite management objectives, this management method does not necessarily create an even-aged or uniformly-structured cohort (Christensen and Peet, 1984; Franklin and Forman, 1987). We expected that ANPP patterns would vary across space but remain constant across time because we presumed that a uniformly treated landscape should

produce uniform vegetation. However, heterogeneity in both vegetation and terrain affect ANPP and we surmise that it is also entirely possible and quite likely in mountainous terrain that multiple successional pathways exist even on a uniformly treated site, and the trajectories of ANPP of different successional pathways will be driven by different abiotic and biotic forces. In this study, we aim to quantify existing patterns of ANPP by emphasizing when and where topography and soil may control succession and stand development. We used long-term vegetation plot data, high-resolution spatial data and light detection and ranging (LiDAR) imaging, spatially-intensive soil sampling, and mathematical modeling to address our questions. I had three primary objectives for this research.

First, I characterized the spatio-temporal patterns of aboveground net primary productivity (ANPP) by stand history, topography, and species composition. Under this objective, we tested the hypothesis that "current" ANPP (calculated from the most recent 2001-2007 re-measurement period) is best explained by topographic features rather than by stand composition. To test this hypothesis, I used linear modeling to compare all individual correlations between ANPP and topographic features as well as tested four multiple linear models to evaluate the relationship between ANPP and (1) radiation, (2) soil moisture, (3) stand history and composition and (4) a combination of the above, supplemented by information criteria, and random forests analysis. Our second objective, was to assess productivity potential by modeling "maximum ANPP" (mANPP) using maximum likelihood estimation (MLE); we hypothesized that mANPP would be better explained by biotic factors than current ANPP. The third objective was to

characterize the spatial shifts in high productivity over time based on the hypothesis that forest composition at establishment can generate multiple successional trajectories and that ANPP in the initial re-measurement (1980-1984) may influence current ANPP. To quantify the trajectories, we tested the hypothesis that sites initiated by conifers (> 50% of biomass) and sites initiated by hardwoods follow different successional pathways over time and have significantly different basal area and ANPP values today.

3.2 Materials and Methods

Study area: Watershed 1 (WS1) is a 96 ha catchment on the H.J. Andrews Experimental Forest in the Western Cascades range in Oregon. Originally part of a “paired watershed” experiment to understand the effects of forest harvest on stream flow dynamics, WS1 was clear-cut (1962-1966), burned (1967), and replanted (1968-1971) with *Psuedotsuga menziesii* (Douglas-fir) seed and seedlings (Halpern and Franklin, 1989; Halpern and Franklin, 1990). The harvest of WS1 was conducted using a small area of skidder-based logging (near the landing at the stream outlet) and a large extent of skyline logging. Due to the immense size of the individual trees and the instability of the slopes, the logging progressed slowly over four years and seven spatially distinct harvest units as new technology was implemented, and it has been documented that early regeneration, particularly of shrub-trees *Acer circinatum* (vine maple) and *Rhododendron maximum* (Rhododendron) had established on some of the early harvested units prior to whole-landscape burning in 1967. Burning was “hot and satisfactory” and large stems not removed in logging but downed by burning were removed from the lower one-third of the watershed to clear the stream pathway. Four attempts at regeneration were made; the first attempt was an aerial re-seeding over the whole landscape; the second through fourth were manual replanting on the south-facing slope, with maximum planting attempts devoted to an “unplantable” area in harvest documentation. The plantings in such areas were ultimately not successful in generating as much biomass as other parts of the site.

Mean annual precipitation on site is approximately 2300 mm with a mean temperature of 2 C in January and 18 C in August, with a two to six degree average daily range, as is typical of the region. WS1 is near the confluence of Lookout Creek with the McKenzie River, at a relatively low elevation (410 m – 1080 m). Parent material is largely andesite and breccia, with both green and red breccias present, as well as blackish andesitic scree and large, potentially glacially-deposited boulders (Swanson and Jones, 2002). Four series of andisols exist on the site: Frissell, Budworm, Limberlost, and Andesite Colluvium, as well as a distinct “rock” area (Rothacher, 1967; Dyrness, 1969). Topography controls the microclimate, which differs distinctly by north- and south-facing aspects due to cumulative annual insolation, aspect-oriented day length, and growing season. Diurnal fluctuations in temperature due to adiabatic cooling on steep slopes yield nocturnal cold air drainages on approximately eighty percent of summer nights (Pypker et al., 2007). Nutrient concentrations of WS1 have not been studied in depth, but it has been shown that the site is limited primarily by N, which is typical of the region as a whole (Vitousek and Howarth, 1991).

The current vegetation is dominated by 55 year old, 20 to 30 m height cohort of *Pseudotsuga menziesii* (Douglas-fir), most of which was developed from planted seedlings. However, other species such as *Tsuga heterophylla*, *Alnus rubra*, *Thuja plicata*, *Castanopsis chrysophylla*, *Acer macrophyllum* and *Prunus emarginata* have naturally seeded in from nearby old-growth stands and alder-dominated riparian areas. *Acer*

circinatum and *Rhododendron macrophyllum* exist as tall shrubs. Ground vegetation is primarily *Polystichium munitum*, *Gaultheria shallon* and *Mahonia aquifolium*. These species have been present on site since establishment.

Long Term Data Pre-processing: Long-term data for the site was available in the form of forest inventory flat-files consisting of diameter at breast height (DBH) measurements for each individual tree on 131 circular plot with an 8.92 m radius. The inventories were taken seven times over the past twenty-seven years with an average interval of five years. DBH was measured on all trees greater than one cm DBH; diameter at base (DBA) was used as a proxy for all trees less than 1 cm, and conversion equations were calculated by Lutz (2005). To determine the biomass of individual trees, DBH was used in allometric equations (Pacific Northwest Biomass Component Equation Library, Halpern and Means, 2004) using the methods of Lutz (2005) and Lutz and Halpern (2006). Because the plots were initially laid out using slope distances rather than horizontal distance, we calculated horizontal plot area using an elliptical adjustment based on slope gradient. We calculated ANPP based on the Acker et al. (1998) method, also precedent in Lutz (2005) and Lutz and Halpern (2006). We mapped the aboveground biomass and ANPP for the 131 re-measurement plots and used spherical kriging to extrapolate across the spatial extent (ArcGIS 9.3.1. “Geostatistical Analyst” Toolkit, ESRI 2009). We created a time series of these maps to observe shifts in spatial patterns. We constructed time series of ANPP to quantify the productivity of each plot and visualize trends in curve shapes; we classified the curve shapes by maximum (peak value), maximum slope (fastest growth), normalized

maximum based on initial biomass (in 1980), and normalized slope based on initial biomass (in 1980)

Sampling (soil depth): In the summer of 2011 we visited the 131 long-term re-measurement plots, which are arrayed systematically along six transect lines which bisect WS1 perpendicular to a “y-shaped” tributary and span the one square kilometer site at an angle of approximately 220 degrees SSW to 40 degrees NNE (Acker et al., 1998; Lutz, 2005) (Figure 12).

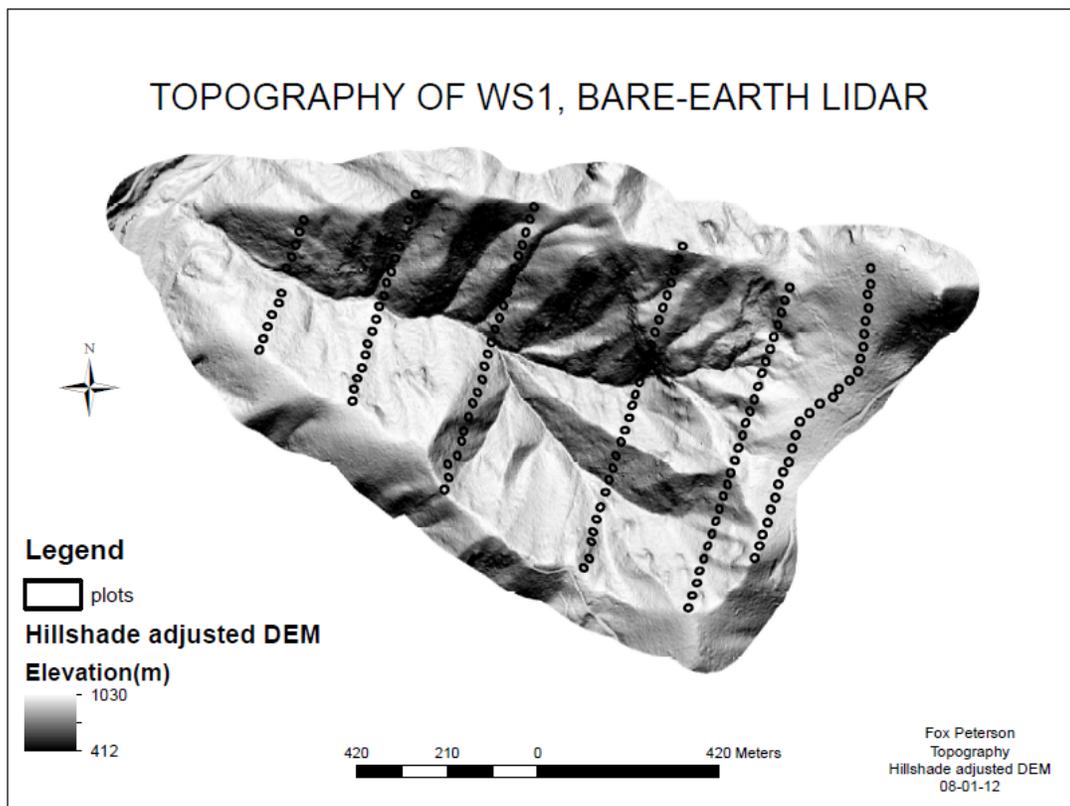


Figure 12. Distribution of vegetation plots and topography in watershed 1.

Initially, we measured soil depth between February to April of 2011 (wet season) using the knocking pole method (see below). This period was selected because of the soil penetrability afforded by moist conditions. To reduce variability due to researcher strength, all measurements were conducted by the same researcher (F.S. Peterson). The knocking pole was penetrated into the soil perpendicular to the surface to a maximum depth of 120 centimeters to account for 90-95 percent of roots (Gasson and Cutler, 1990; Gilman, 1990; Coutts, 1999). The six measurements taken were averaged to a plot-scale mean that was used to estimate soil depth.

Sampling (soil rockiness): Soil rockiness (percent by volume) was measured from excavations of sixteen sets of two soil pits with a 600 cm³ volume on the same subset of plots. Soils were removed from the site manually and returned to the laboratory where they were separated by depth (0-10 cm and 10-20 cm) and sieved by particle size (<2 mm, 2-5 mm, and > 5 mm). Rock bulk density was calculated using the submersion method for each plot individually because volcanic rocks are often lighter than the traditional 2.65 g/cm³ value. Soil rockiness was computed on a volume-of-rock to volume-of-soil basis facilitated by the individual density calculations. We developed a metric of effective soil depth (ESD) similar to that which is used in agriculture to imply the soil volume available for moisture storage (Wolf, 1995; Versegny, 2007). ESD was calculated as

$$\text{ESD (cm)} = \text{TOTAL DEPTH(cm)} - \text{PERCENT ROCKINESS (cm}^3\text{)* TOTAL DEPTH (cm)}$$

ESD was our primary metric for quantifying potential belowground moisture holding capacity.

Bulk Density Eight soil cores of 10 cm depth (approximately 17 cm³ volume) were removed from each plot using the Oakfield Soil Core apparatus, placed in plastic baggies, stored at 4 C, and returned to the laboratory for analysis. The cores were weighed wet, and then a 1 g wet sub- sample was taken from each core and oven-dried at 60 C for 3 days. The oven dried sub-sample was then reweighed and a wet-dry conversion factor was established for each sample. For each sample, bulk density was calculated as:

$$\text{Bulk Density (g/cm}^3\text{)} = \text{oven dry weight (g)} / \text{volume (cm}^3\text{)}$$

The samples were then averaged at the plot scale to determine a representative bulk density for each plot.

Computational analysis (MLE estimation): On this site, current ANPP has been calculated as the change in biomass (Mg/ha) over a time interval (years), plus mortality and ingrowth (Mg/ha) (Acker et al., 1998; Lutz, 2005; Lutz and Halpern, 2006). An empirically-based approach to predicting maximum productivity as a continuation of current time series data was selected in order to retain statistical separation between our dependent variable of interest (ANPP) and the topographic and edaphic metrics against which it was being compared. As a comparison, a regression-based approach to predicting maximum or future productivity as a function of topography and soil structure would have double-counted the predictive power of the independent variables and implied that relationships between landscape and vegetation were fixed over time. We fit

a logistic function to the biomass data ($B(t)$) in a time series based on the general logistic model of biomass development and their variations (e.g. biomass levels off and then declines somewhat) described in Glenn-Lewin et al. (1992). This model has been shown to fit other similar temperate coniferous forest ecosystems. (Whittaker and Marks, 1975; Ketterings et al., 2001). On 21 of the 133 sites, the mANPP predicted for the site occurred in the future and was therefore extrapolated beyond the temporal extent of the data. To reduce error in the extrapolation, we conducted our fits using maximum likelihood estimation, which has been shown in multiple fields of study to be the appropriate error reduction strategy when historical trajectories are well-known (since future trajectories are not known) and the model form has been shown to be appropriate in validation (Jones, 1989; Kreckelburg and Lappe, 1999; Thieme, 2003). mANPP is determined as the slope at the inflection point on the function $B(t)$ (Figure 13; mathematical derivation in Appendix 2). The curves in Figure 13 are reproduced from Christensen and Peet (1982). Only about 15% of plots on the watershed required this method to determine their mANPP; to validate the estimates, the method was used to calculate a predicted trajectory for all stands, even those that had already reached mANPP, and fits of predicted versus actual were assessed using the R^2 criterion. It was found on the validation set that all R^2 values ranged between 0.5 and 0.98.

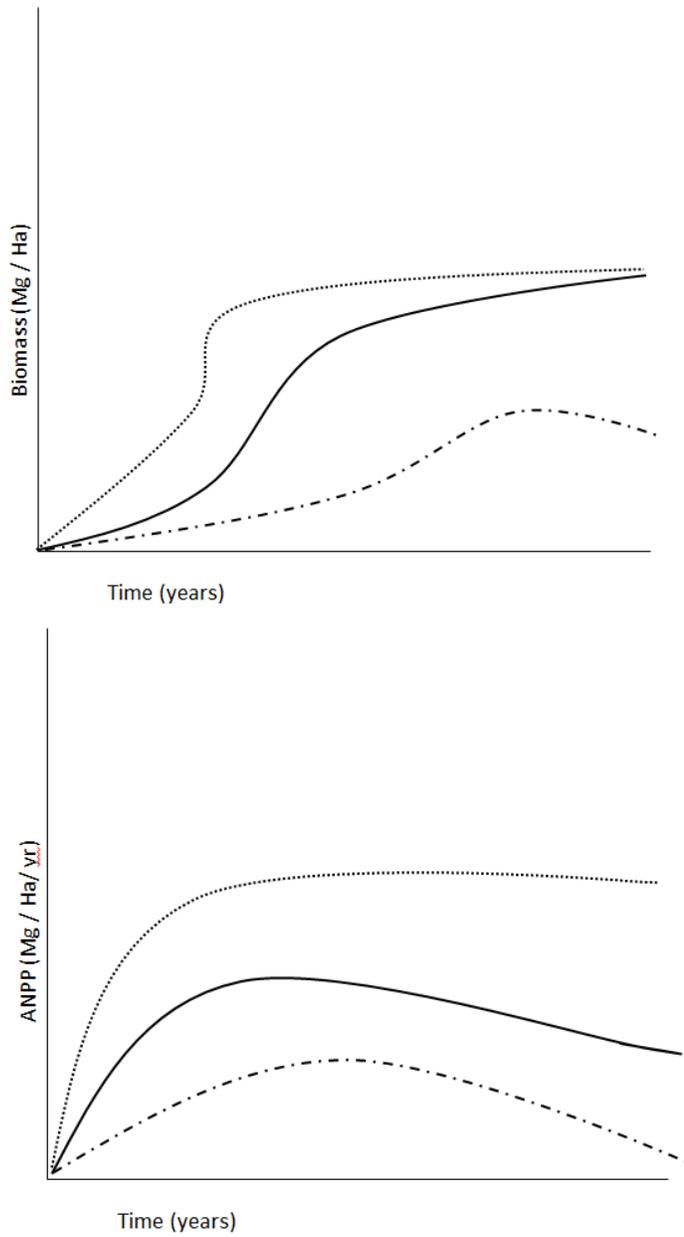


Figure 13. Three potential scenarios for biomass (Mg/ha) and derivative ANPP (Mg/ha/yr). The dotted line is initially a highly productive stand with high

biomass, the solid line a slower growing stand also with high biomass, and the slash-dotted line an initially suppressed stand with less biomass.

Computational analysis (*Fitting the general model*) a script was written in the programming language "R" to test the fit of four general models versus ANPP. Specifically, the metrics we tested within the models were solar radiation, slope, elevation, horizon angle, soil depth, moisture capacity, soil type, number of re-plantings, disturbance history, percent hardwood (at various points in time) and diversity (calculated using the Shannon-Weaver index). These models are highlighted in table 1.

The Akaike's Information Criterion (AIC) was determined for each model and used to rank the models. Additionally, residual analysis was conducted to determine if spatial trends were extant at the scale of interest. We also conducted a non-censored random forests analysis using the R-package "party" which removes weights that might be associated with potential bias or autocorrelation in the data. The purpose of the random forests analysis was to validate the criteria selected by the AIC approach and our GLM's.

Topography We developed a set of 12 topographic metrics within ArcGIS 9.3.1 (ESRI, 2009) using a digital elevation model (DEM, 10 m resolution) and a LiDAR bare-earth map (1 m resolution, reconnaissance flown in 2008). LiDAR was flown with a minimum of nine returns per square meter to approximate vertical protrusions within 13 cm accuracy and horizontal cover within 1 m accuracy. For 1 m topography, the final returns for each of the voxels were averaged to determine bare-earth altitude (Lefsky et al., 1999). To address the influence of topography on stand structure, we derived metrics from the

DEM or LiDAR bare-earth map using ArcGIS's "Spatial Analyst toolkit" or the downloadable "Topography toolkit" (available from ESRI, 2010) topographic metrics such as aspect, slope, elevation, maximum solar insolation, upslope contributing area, angle to the horizon, wind exposure, topographic wetness index (defined as the natural log of the contributing area divided by the slope angle) and Jennings' landform classifications (Dyrness, 1969; Rothacher, 1974; Swanson and Jones, 2002; Sorenson et al., 2006). These topographic metrics we selected serve as remotely-sensed proxies for belowground resource distributions or ecosystem forces that could affect them.

Soil and landscape history We additionally developed a set of 12 soil and landscape history metrics from existing data and field measurements found in (1) intensive site analysis, (2) historical site data available online at the Forest Service Data Bank's H.J. Andrews Website (<http://andrewsforest.oregonstate.edu/lter/>), or (3) developed manually from archived harvest documents. Disturbance history and soil type classification accounted for many of these metrics as binary classifications; five soil groups and four disturbance groups had been previously identified (Dyrness, 1969; Swanson and Jones, 2002). Additionally, the field measurements of effective soil depth and bulk density were used.

Descriptions of soil series can be found online through the H.J. Andrews website; however, a brief description of the four main groups is presented here: Budworm and Limberlost soils are loamy soils derived from greenish breccia; Budworm is found in lower elevations than Limberlost is. Andesite colluvium describes accumulative soils

from earth movements. Frissell soils are derived from reddish breccias and are found at low elevations. Rock is the fifth “soil group” on the site; however, no vegetation is found on rock.

3.3 Results

To quantify relationships between abiotic factors and ANPP, I employed several statistical techniques. First, I tested individual correlations between ANPP and topographic and soil features, as well as multiple linear regressions. When I tested individual correlations between ANPP (over the entire watershed) and the topographic and soil metrics, we found no significant relationships. Next, I created four multilinear models based on drivers (radiation, moisture, species composition, or a combination of these) we associated with ANPP. I ranked the quality of each model based on Akaike's Information Criterion (AIC). I found that the comprehensive model captured the most variability in the predicted data, and that percent hardwood in 1980, Shannon Weaver's diversity index in 1980, horizon angle, and soil type were the most important factors in determining ANPP in 2007 (Table 3).

Table 3. Linear model results for "current" ANPP (calculated from the 2001-2007 re-measurement interval).

model	AIC	parameters included	significant parameters	Fitting Statistics
comprehensive model	577.18	soil type, percent hardwood 1980, Shannon weaver 2007, horizon angle, elevation	percent hardwood 1980, Shannon 1980, horizon angle, soil type (Frissell)	$R^2=0.30$, $F = 6.37$, $\Delta AIC = 0.00$
water model	590.59	bulk density, soil depth, upslope area, slope, topographic wetness index, soil type	soil type (Frissell, Limberlost)	$R^2=0.17$, $F = 3.21$, $\Delta AIC = 13.01$
biotic model	593.18	percent hardwood (1980, 2007), number of trees (1980, 2007), Shannon weaver's diversity index (1980, 2007)	percent hardwood 1980, Shannon weaver 1980	$R^2 = 0.21$, $F = 3.22$, $\Delta AIC = 16.00$
solar model	595.15	solar insolation, aspect, horizon angle, elevation	solar insolation, horizon angle	$R^2=0.14$, $F = 3.56$, $\Delta AIC = 17.97$

The random forests analysis also had similar results, and found that Shannon Weaver's diversity index in 1980, number of re-plantings, topographic wetness index (TWI), percent hardwood in 1980, and horizon angle were the most explanatory classifying variables (Table 4). We only display the top five variables here, as the Party package used for the analysis only shows the top variables which explain the majority of the variance.

Table 4. Results from Random Forests Analysis for current "ANPP" from the 2001-2007 re-measurement interval. Branching criterion indicates at what value of the variable the tree "split". The variance explained is relative to the best predictor, in this case, Shannon Weaver's Diversity Index as measured in 1980.

Variable	Branching Criterion	Variance Explained
Shannon Weaver's Index	< 0.988	0.99
Regeneration Attempts	> 1	0.95
Percent Hardwood 1980	< 4.48	0.82
Topographic Wetness Index	<6	0.73
Horizon Angle	< 22.5	0.44

A chi-squared test was performed within the "party" package to compare predicted ANPP values based on the random forests criteria to calculated values and the prediction was not significantly different than the actual values ($p = 0.24$).

Theoretically, ANPP could be calculated for any re-measurement interval and that value taken as "productivity," which would vary with the time period selected. To avoid this problem, we developed the mANPP metric which compares maximum values of ANPP over a stand's lifespan. mANPP was modeled by fitting a logistic function to biomass data. To evaluate the goodness of fit, we compared predicted and actual values of biomass for each plot (Figure 14).

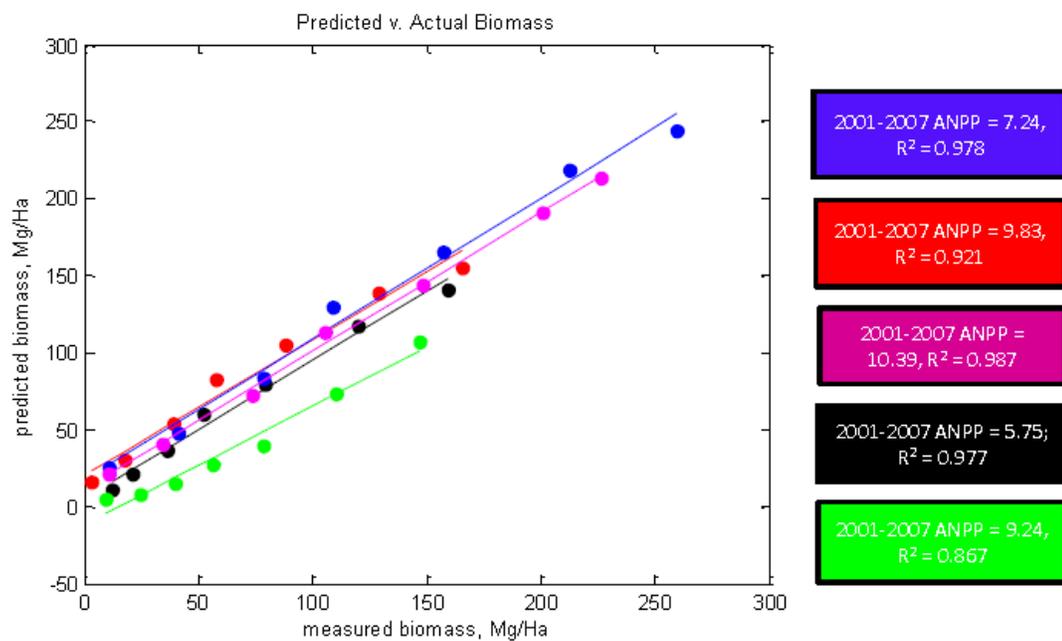


Figure 14. Goodness of Fit tests between biomass (Mg/ha) predicted from logistic function fit using maximum likelihood estimation (MLE) and actual biomass (Mg/ha)

calculated from allometric equations on DBH data for five randomly selected plots. Each point represents one re-measurement interval, 7 re-measurement intervals exist in total. Lines represent the goodness of fit. Color bar displays the R^2 statistic for the goodness of fit for the corresponding line, as well as the current ANPP (2001-2007 re-measurement interval) that corresponds with that plot

Our fits were robust, with correlation coefficients (R^2) ranging from 0.56 to 0.99. The fitting curves shown in Figure 14 represent only a small subset of the validation set for the purpose of visualization. The mean error for all plots' biomass fits was 14.68 Mg/ha, roughly 8% of average biomass as measured in 2007. For the majority of the plots (102 of 124 calculated), mANPP occurred during a measured interval; the mean year for mANPP on all plots WS1 was 1999, or 19 years after the first re-measurement (standard deviation = 10.91 years). As further validation of the appropriateness of the estimations, I summarized the predicted year of mANPP for each plot. For the 22 plots on which mANPP was predicted using a fit to the biomass function, the mean year for mANPP was 51 years after establishment (standard deviation = 7.34 years). The longest time for a modeled plot to achieve mANPP was 62 years following establishment; however, this plot began with extremely low biomass and is located on a poor site (rock soil type).

We tested whether or not current ANPP from the 2001-2007 re-measurement interval and mANPP had the same drivers by comparing the AIC results of the ANPP models with those of the same models regressed onto mANPP (Table 5, 6).

Table 5. Linear model results for mANPP (modeled maximum ANPP).

Model	AIC	parameters included	significant parameters	fitting statistics
biotic model	529.48	percent hardwood (1980, 2007), number of trees (1980, 2007), Shannon weaver's diversity index (1980, 2007)	Shannon weaver's diversity index 1980, percent hardwood 1980, percent hardwood 2007	$R^2 = 0.48$, $F = 10.83$, $\Delta AIC = 0.00$
comprehensive model	582.37	soil type, percent hardwood 1980, Shannon weaver 2007, horizon angle, elevation	percent hardwood 1980, soil type (Frissell, Limberlost)	$R^2 = 0.15$, $F = 2.66$, $\Delta AIC = 52.49$
solar model	589.89	solar insolation, aspect, horizon angle, elevation	aspect (south)	$R^2 = 0.06$, $F = 1.35$, $\Delta AIC = 60.41$
water model	593.13	bulk density, soil depth, upslope area, slope, topographic wetness index, soil type	soil type (Limberlost)	$R^2 = 0.13$, $F = 1.37$, $\Delta AIC = 63.65$

Table 6. Summary of results comparing the current ANPP calculated from the 2001-2007 re-measurement interval linear models to the mANPP as predicted from MLE linear models. R^2 values indicate the fit of the predicted values to the actual; shared parameters are those selected in both models.

Model name	ANPP R²	mANPP R²	shared parameters
solar model	0.14	0.06	
water model	0.17	0.13	soil type
biotic model	0.21	0.48	Shannon Weaver 1980, percent hardwood 1980
comprehensive model	0.30	0.15	percent hardwood 1980, soil type

We found that for mANPP, the biotic model captured the most variability in the predictor data. Between the two models, the parameters of soil type, Shannon Weaver's Index in 1980, and percent hardwood in 1980 were shared. As an example of one of these parameters on WS1, Figure 15 shows the distribution of percent hardwood in 1980.

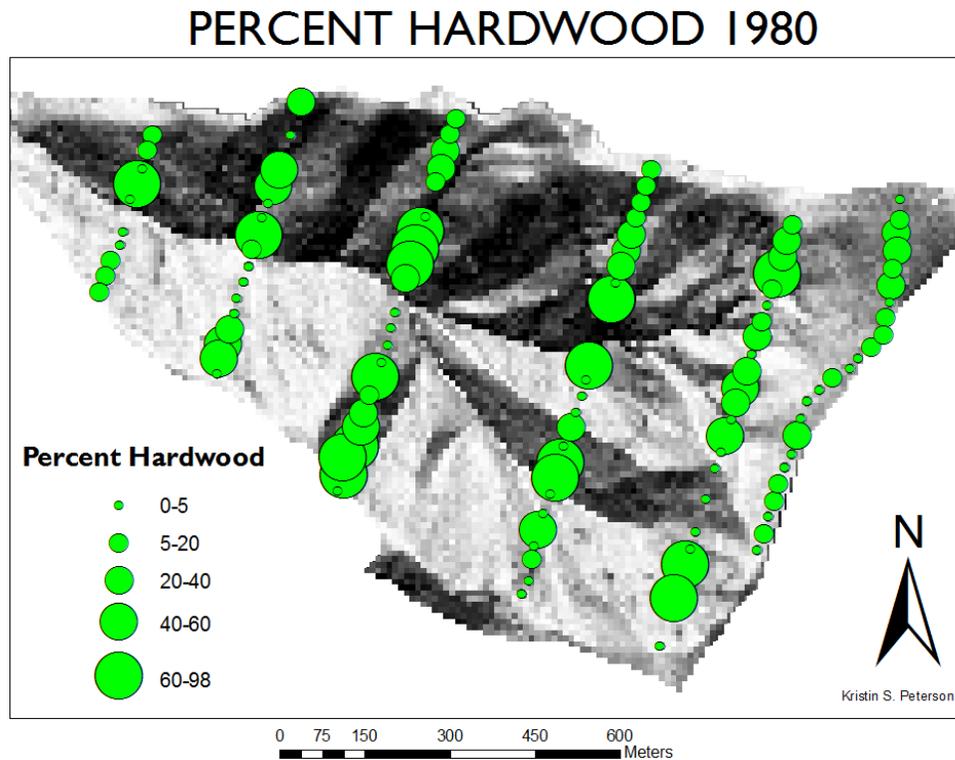


Figure 15. Percent hardwood (in terms of biomass, Mg/ha) by plot in 1980.

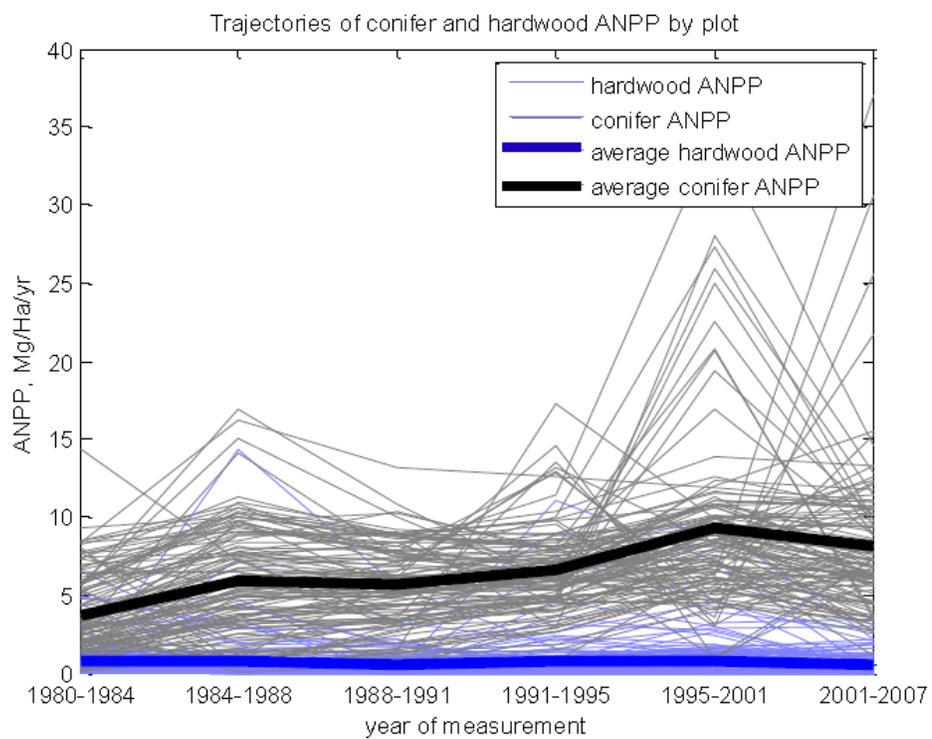
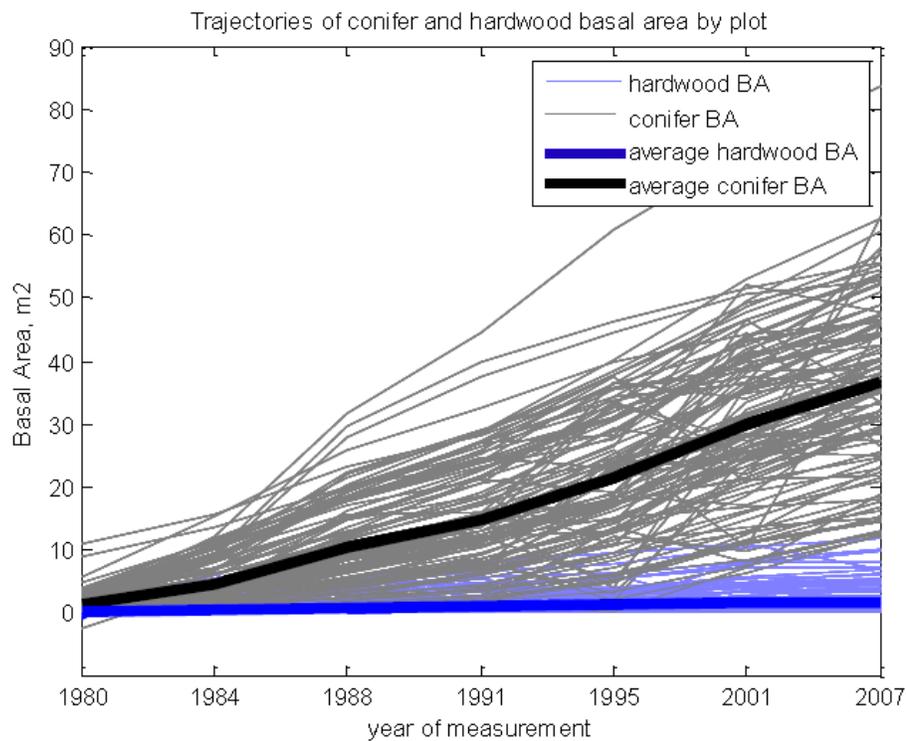
The initial condition of the stand, particularly its composition at establishment, may influence its composition and productivity in the future. To test whether or not the initial composition and ANPP (calculated from the 1980-1984 re-measurement interval) influenced the current (2001-2007) ANPP, we hypothesized that sites established by conifers would follow different successional pathways than those established by hardwoods, and we quantified those pathways in terms of BA/ha and ANPP. Although ANPP for both hardwood and conifer initiated plots was not significantly different during the first re-measurement interval, BA/ha was, but we found that during the current re-measurement interval, both ANPP and BA/ha were significantly different, and that

conifer initiated plots had higher values of both. However, we found that mANPP was not significantly different between conifer and hardwood initiated plots (Table 7).

Table 7. Summary statistics for the test of the influence of initial conditions on current ANPP (2001-2007) classified by hardwood initiated (> 50% of biomass) and conifer initiated (> 50% of biomass) plots.

	Hardwood- Initiated (n=22)	Conifer- Initiated (n= 102)	All Plots	Different
initial ANPP (1980-1984)	5.55 ±2.29	6.09±3.31	5.94±2.44	no, p = 0.4429
initial BA/ha (1980-1984)	0.48 ± 0.36	1.60±1.69	3.88±1.59	yes, p < 0.001
current ANPP (2001-2007)	3.67±3.44	7.58±3.32	7.54±3.46	yes, p < 0.001
current BA/ha (2001-2007)	29.29 ± 11.03	39.72 ±17.15	37.71 ±13.38	yes, p < 0.001
mANPP	9.54±3.44	10.98±2.98	10.01±3.3 2	no, p = 0.1834
mANPP interval	1984-1988	1995-2001	1995-2001	yes

Although BA/ha of both conifers and hardwoods generally increased over time, the BA/ha of hardwoods increased only slightly and actually declined in the most recent re-measurement (Figure 16).



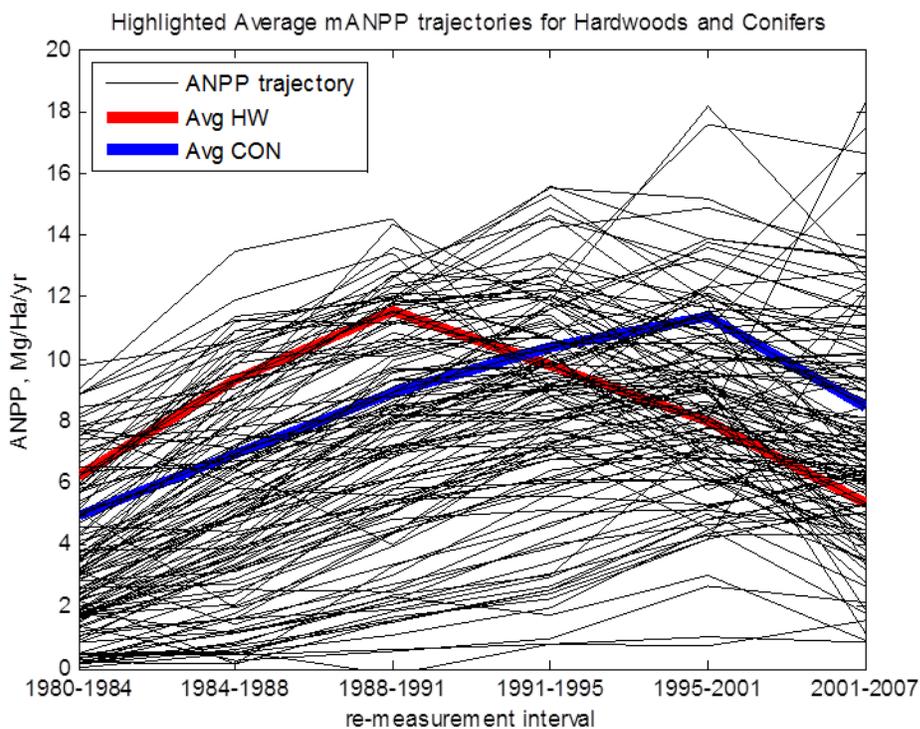


Figure 16. Basal area per hectare (m^2/ha) and ANPP ($Mg/ha/yr$) trajectories for plots that contained $> 50\%$ hardwood (blue) or $> 50\%$ conifer (black) in the 1980-1984 re-measurement interval. Thick lines indicate a mean trajectory for each species group. Each individual line represents one plot. The final graph shows the mANPP trajectory for hardwoods (red) and conifers (blue).

ANPP, on the other hand, was much more variable, particularly for conifers. ANPP of most conifer initiated stands is greater than that of hardwood initiated stands in 2007, but the differences between the average ANPP values is relatively less than the differences between BA/ha.

3.4 Discussion

The current ANPP on WS1 was explained in our analyses best by a combination of physical and biotic parameters. Both a topographic metric (horizon angle) and soil type, which integrates multiple physical and chemical properties of the soil, were important for explaining current ANPP. Biologically, measurements of initial diversity, specifically percent hardwood in 1980 and Shannon-Weaver's diversity index in 1980, were the most important. Unlike current ANPP, mANPP was best explained by biotic parameters alone, specifically Shannon-Weaver's diversity index in 1980, percent hardwood in 1980, and percent hardwood in 2007. From the analyses of ANPP at the current (2001-2007) and maximum value, initial composition unambiguously comes out as a strong driver.

Our results indicate that initial stand structure, as quantified by basal area, species composition, and initial ANPP should influence the current stand structure and ANPP. We divided WS1 into hardwood-initiated and conifer-initiated groups to further investigate this hypothesis. Because WS1 is currently dominated (85% of total trees by mass) by conifers, we expected to find consistency in the curve shape of ANPP trajectories indicating, as we suspected, that initial conditions predict current ANPP (Knapp & Smith, 2001; Laurance et al., 1999; Malhi et al., 2006; Raich et al., 2006; Ryan et al., 2006). Since the vegetation of the watershed was initiated from a clear-cut harvest, we expected and found that initial BA/ha and ANPP amongst conifers and amongst hardwoods were not significantly different. Additionally, we expected and also found that current (2001-2007) ANPP and 2007 BA/Ha were significantly different; this

corresponded with the results of our first analysis, that species composition at establishment influenced current ANPP. However, there was greater variability in ANPP trajectories than we expected, and most importantly, it was not expected that mANPP for hardwood and conifer initiated stands was not significantly different, despite the fact that compositional parameters came out as the most explanatory predictors of mANPP.

It is not clear why initial composition should drive mANPP, yet there is no difference between mANPP on compositionally dissimilar sites. The answer may lie in different pathways of development. The developmental patterns of hardwoods and conifers in the Pacific Northwest differ because hardwoods (such as *Castanopsis chrysophylla*, *Prunus emarginata*, *Rhamnus purshiana* and *Acer circinatum*) are generally smaller and some are more drought-tolerant, although others, such as *Alnus rubra* and *Acer macrophyllum* are better integrated with coniferous trees. Following the harvest of WS1, it was documented that sprouting evergreen hardwood establishment occurred prolifically on disturbed soils despite multiple attempts at replanting *Pseudotsuga menziesii* (Rothacher, 1969). If hardwoods initially established rapidly and were then overtopped by a coniferous overstory that initially had slower growth, then it is possible that hardwood-initiated sites achieved their maximum ANPP during the early succession of the watershed and conifer-initiated sites achieved an equal value of mANPP later in time (Figure 17).

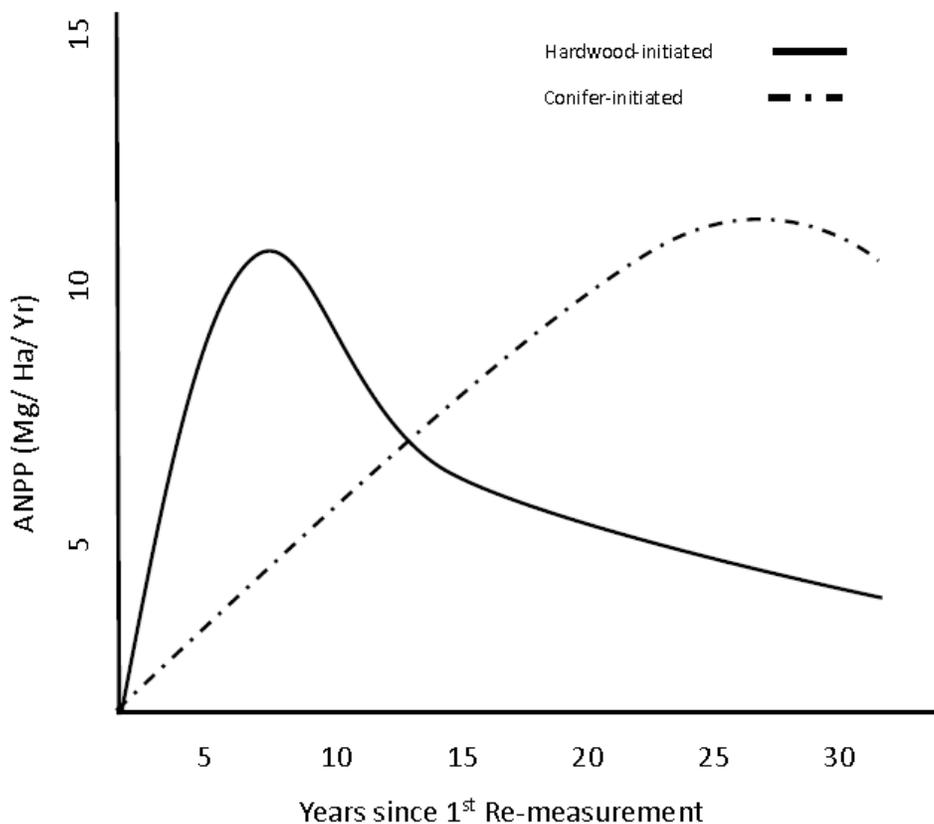


Figure 17. Schematic of hardwood and conifer initiated ANPP trajectories. Although mANPP is statistically not different for both (~ 10 Mg / Ha / Yr), mANPP occurs between years 1984 and 1988 for hardwood initiated plots and between years 1995 and 2001 for conifer initiated plots

Because within the species groups individual species may have very different environmental needs and growth patterns (for example, *Castanopsis chrysophylla* can regenerate from stumps and is more inclined to drier sites, whereas *Alnus rubra* does better under moister, mid-slope conditions), to clarify our expectations about stand

development, we visualized ANPP trajectories by individual species (Appendix 3). In the species' trajectories, we observed three important behaviors: (1) 74 % of plots' populations of *Pseudotsuga menziesii* follow the expected parabolic ANPP trajectory that peaks between 1995 and 2001 (refer to Figure 13), (2) most *Prunus emarginata* have peaks during the 1984-1988 time period, and (3) during the 1995-2001 interval 65 % of plots' populations of *Tsuga heterophylla* reach the inflection point in their ANPP trajectories. Point (1) explains why most plots on WS1 have their maximum ANPP in the 1995-2001 time interval; *Pseudotsuga menziesii* was the desired species for the site and it is both in number and biomass the most prolific. Point (2) is an example of early hardwood proliferation followed by subsequent slowed growth; *Prunus emarginata* can be easily overtopped. As far as behavior (3) is concerned, *Tsuga heterophylla* often establish on nurse logs or in canopy gaps, and if productivity of *Pseudotsuga menziesii* has just maxed, canopy closure may be occurring and *Tsuga heterophylla* experiencing beneficial site conditions, particularly in terms of increased radiation and nutrients.

We did find in our analyses that current ANPP (2001-2007) was influenced by site characteristics, particularly the solar parameter of horizon angle and the classification of soil type. In fact, when ANPP trajectories are graphed by soil type similarities in curve shape are evident (Figure 18).

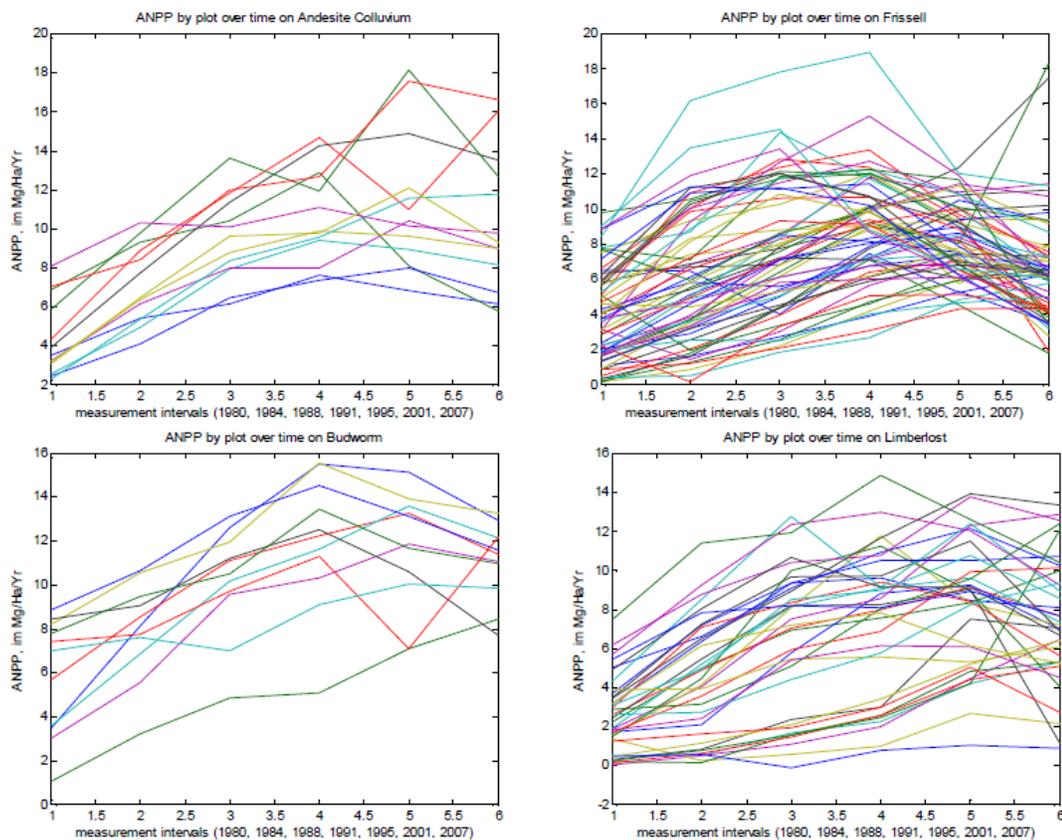


Figure 18. ANPP (Mg/ha/Yr) Trajectories by Soil Type: Andesite Colluvium, Frissell, Budworm, Limberlost. Each thin line represents one plot.

For example, two distinct patterns occur on Budworm soils. On 44 % of these plots, ANPP increases since the first re-measurement, whereas the other 56 % of Budworm plots all have peaks in ANPP in the 1995-2001 time interval. These two patterns are consistent with the trajectories we expected. Additionally, we are aware that some soils on WS1 are extremely poor quality due to rockiness, and have extremely low

productivity and slow growth rates. We noted in LiDAR images canopy cover in 2008 that spatially areas of extremely low ANPP (near or equal to zero) in all time periods corresponded with a cap-rock that represents a shift in lithography from the reddish breccias of the Little Butte Formation to the greenish breccias of the Sardine Formation and volcanic ash flows that overlay it (Swanson and Jones, 2002; Figure 19).

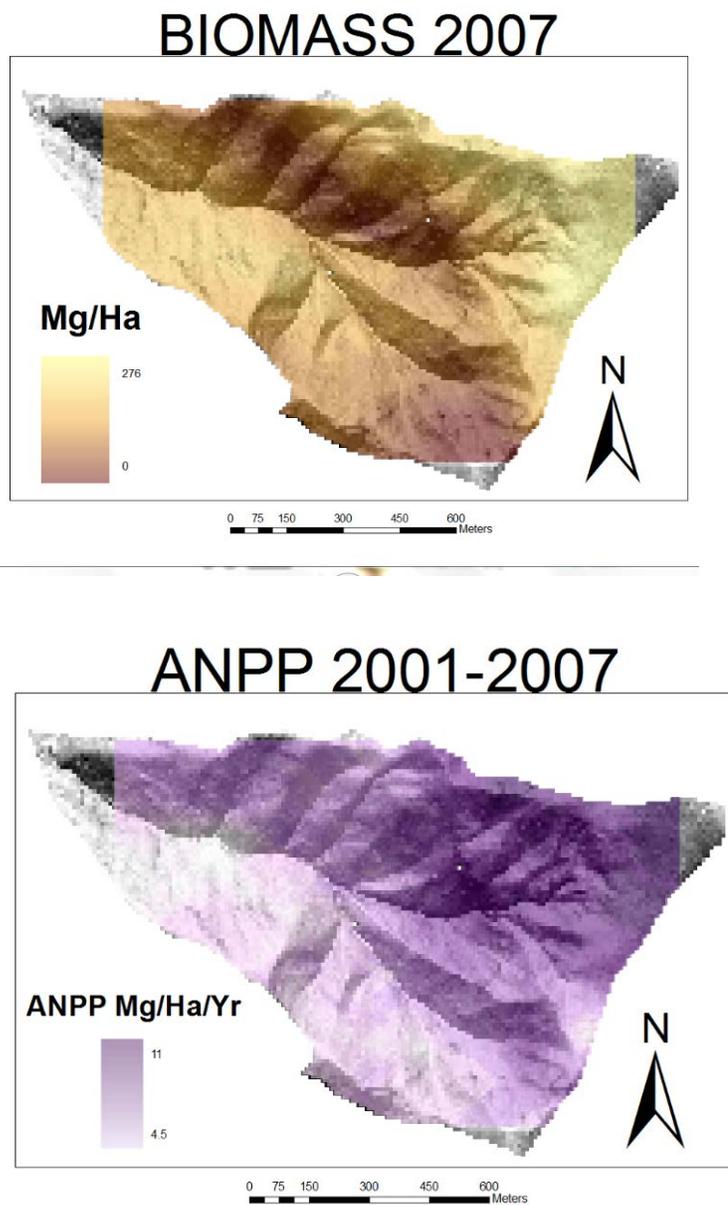


Figure 19. Biomass (Mg/ha) in 2007 and ANPP (Mg/ha/yr) calculated from the 2001-2007 re-measurement interval show different spatial patterns and distinct delineations along topographic features.

To quantify the dearth of biomass on rocky soils, we calculated the probability density function (PDF) for biomass in 2007 and found that on soils classified as "rock" it was less than 41 Mg/ha as compared to a watershed average of 218 Mg/ha; 15 % of watershed surface area contained less than 1 % of biomass, and correspondingly have low ANPP.

We suggest that on WS1, the forest composition and the soil type interact to affect ANPP. Although species composition shows most prominently in our analyses as an explanatory factor, it may be in fact a manifestation of site characteristics, particularly in the case of the mANPP. It is likely that during early stand establishment, high radiation, low soil moisture, and exposed surfaces have a positive effect on ANPP because these factors are beneficial for shade-intolerant hardwoods. During the current re-measurement interval, it is more likely that lower radiation, high soil moisture, and deep protected surfaces have a positive effect on ANPP because these factors contribute to the growth of coniferous stands. Since both site and species influence ANPP in all re-measurement intervals, and their influences are intertwined; mANPP occurs at different times and under different conditions depending on stand composition, the site attributes that are best for one stand type may not be best for others (for example, some species may be shade intolerant or drought tolerant whereas others may prefer shaded or droughty conditions), and thus site may not appear to be influential, despite the fact that it actually is. Our study is novel in that it explores several options for how to characterize ANPP (currently, at its maximum, or in reflection of its initial state) and reveals how this choice may lead to particular, and potentially incorrect, conclusions about ANPP drivers if assessed in isolation. Comparing between the three methods allows us to see the influence of both abiotic and biotic

drivers on ANPP, even when those drivers are not apparent in statistical analyses generated for a selected time.

CHAPTER 4

**HETEROGENEITY IN BELOWGROUND PROCESSING: LITTER FALL
INCREASES WITH ANPP, BUT NEITHER PREDICTS SOIL C**

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San Francisco, CA

4.1 Introduction

Soil is the largest store terrestrial carbon (C) store, holding a global estimate of approximately 2100 Gt C when quantified by geospatial models (Ruesch and Gibbs, 2008; Post and Kwon, 2000; West and Post, 2002). World-wide, the majority of soil C is stored in tropical-subtropical forest, where vegetation inputs are largest, and boreal-tundra grassland soils, where decomposition is slowest (Amundson, 2001; Cambardella and Elliott, 1992; de Deyn et al., 2008; Mahli et al., 1999, 2006; Post and Kwon, 2000). Factors influencing soil storage at the global scale include temperature (Prior et al., 2005; Torbert et al., 2003; West and Post, 2000), forest community (Six et al., 2004), mineralogy (Six and Paustian 2000; Six et al., 2003, 2004;), and available moisture (Prior et al., 2005; Torbert et al., 2003). However, little is known about the extent to which these factors influence spatial patterns in soil C storage at a significantly smaller, “watershed scale” (< 1 km²) and whether or not site history and stand development has a

recognizable impact on current soil C stores. In this study, the relationships among ANPP and stand composition and soil C dynamics were explored, specifically whether or not soil organic carbon (SOC) is related to the ecosystem processes of aboveground net primary productivity (ANPP), litter fall, and N-mineralization (Stewart et al., 2008, 2009). Recent analyses have suggested that processes governing soil C storage may display emergent “hot spot” or “hot moment” patterns; that is, specific locations or times C storage is unexpectedly augmented due to a synergistic intersection of ecosystem patterns and processes. For example, where certain topographic conditions (“hot spots”) exist during certain developmental stages (“hot moments”) of the forest, soil C may be preferentially stored either relatively labile, partially decomposed organic matter (light fraction sensu Sollins et al. 2006) or else in more stable forms, associated and protected by mineral matter (heavy fraction) and relationships with ecosystem processes may emerge, despite being hidden during other developmental stages or at other locations. For example, areas where litter might accumulate may have greater C in the light fraction; where clays might be high and rockiness low, we may find more C in the heavy fraction. Likewise, we expect to see increased C incorporation into the light fraction on cool, moist slopes with high mortality from canopy closure and thus high detrital inputs (Boone, 1994; McClain et al., 2003; Peterson and Lajtha, 2012). We suggest that these hot spots and moments may be related to aboveground net primary productivity (ANPP), which is a function of stand structure and available resources (Acker et al., 2002). Our objective is to better understand the relationships between soil C and ANPP in complex terrain.

ANPP has been correlated with litter fall, which is an important short term contributor to soil C (Gentile et al., 2011; Heal et al., 1997; Hongve et al., 2000; Palm and Sanchez, 1991; Paustian et al., 1997, but see Rasse et al., 2005). In a mixed stand, litter fall is known to vary in both quantity and quality over a spatial extent, but the average rate of C contribution attributed to litter fall as well as the C stored in litter has been estimated in the literature (Adair et al., 1996; Gentile et al., 2011; Hongve et al., 2000). Looking across multiple stand types, Post and Kwon (2000) quantified the contribution of litter fall in terms of an average rate of carbon additions in all forest soil to 33 g C / m² / year. Potter et al. (1993) estimated the mass of C in litter stores for both leaf and coarse woody debris globally to 175 Pt C, with leaf litter contributing to slightly more than half of this mass. Several environmental drivers and ecosystem components have been shown to influence C inputs into soil from litter fall, including temperature, microbial communities, and stand composition (Cambardella and Elliot, 1992). The quality of litter, specifically N content and form of organic C, as well as microbial processing are also important in determining litter decomposition (Gentile et al. 2011; Gleixner et al., 2002; Kiem and Kogel-Knaber, 2003; Kogel-Knabler, 2002). Spatiotemporal variability in decomposition also affects the rate that litter contributes C to the soil (Schlesinger, 1990; Sanderman, 2004).

Stability of soil C depends on soil properties, such as physical protection and mineral association, and in turn affects belowground processes such as microbial respiration and leaching (Six et al, 2000, 2002, 2004). A technique of carbon "fractionation" is used to

partition soil C based on density into "light" and "heavy" fractions. (Buyanovski, 1994; Cambardella and Elliot, 1991; Christensen 1992, 1996; Oades, 1993; Six et al., 2004). The light fraction (LFC), which has a density of less than 1.85 g/cm^3 , is based on the density of litter (1.65 g/cm^3) plus mineral contamination. The heavy fraction (HFC) reflects the organic coating that often forms on primary and secondary minerals, which comes out in solution due to mass. The soil matrix structure, biota, and moisture affect soil C recalcitrance and in turn ecosystem processes such as the leaching of dissolved organic carbon (DOC) (Tisdale and Oades, 1992), aerobic capacity (Sexstone et al., 1985), nutrient capacity (Wang et al., 2001) and water flow (Prove et al., 1990), all of which feedback to the stand's ANPP. This analysis focuses particularly on links between soil C and ANPP. The primary objective of this research is to determine how the different pools of soil C on a mountainous watershed relate to stand structure, ecosystem processes, and topography, and to determine if these relationships emerge conditionally during particular hot moments (critical stages in stand development) or at particular hot spots (areas of hydrologic aggregation, abrupt changes in stand composition, etc.).

Because LFC is ephemeral, it responds quickly to biotic interferences such as productivity and land use change; while HFC is also related to biotic factors, it has been shown to have important relationships to abiotic factors as well (Hongve et al., 2000; Qualls et al., 1991). For example, the presence of C in the heavy fraction has been shown to be limited by available pore space, as Stewart et al. (2008, 2009) suggested, so that heavy fraction C can be modeled as only a function of soil texture and mineralogy. Or, as

Sollins et al. (2006) suggested C protection in LFC pool is a function of both mineralogy and organic composition, particularly protein structure and ligand-exchange carboxylic compounds. In particular, this research addresses the variability of the light and heavy C fractions across the space of a mountainous watershed and whether or not these fractions correlate with a set of (1) topographic factors and (2) measureable ecosystem processes: litter fall, N-mineralization, and ANPP. Spatial fluctuations in litter fall have been observed and correlated with variability in soil C (Boone 1994; Hongve et al., 2000; Post and Kwon, 2000).

However, studies documenting this variability have largely been limited to experimental manipulations of controlled sites using cropping and tillage rather than the natural variability in complex terrain (Beare et al., 1994; Biederback et al., 1994; Bremer et al., 1994). To address the spatial variability in the light fraction C's relationship to ecosystem processes, I tested the hypothesis that (1) the strength of the relationship between aboveground net primary productivity (ANPP) and LFC varies spatially because the LFC is a balance between litter fall and woody inputs versus decomposition outputs, and decomposition rates and processes are both variable and not well known and that (2) on warmer, drier sites, ANPP is inversely related to LFC because highly-productive deciduous hardwoods establish preferably on these sites facilitating leaf litter accumulation due to bad conditions for microbial decomposition and leading to lack of incorporation into the soil. To address the distribution of heavy fraction C, I hypothesized that (3) HFC is a function of soil mineralogy, stand composition, and ANPP, and that edges observed spatially in site mineralogy (changes in soil type) are reflected in sharp

changes in the composition of the forest community and the magnitude of HFC.

4.2 Materials and Methods

Site: Watershed 1 (WS1) is a 96 hectare catchment in the H.J. Andrews Experimental Forest (HJA) in the western Cascades Range of Oregon. The HJA is part of the National Science Foundation's Long Term Ecological Research (LTER) program and provides a wealth of data and resources for spatially and temporally explicit studies of ecosystems (Robertson et al., 2012). WS1 was originally part of an experiment regarding the effect of regeneration cuts on stream flow and sediment fluxes. Between 1962 and 1966, the stand was clear-cut, burned, and replanted with four attempts at seeding (one aerial and three row re-plantings of *Pseudotsuga menziesii*). The forest community on the site is currently dominated (70-80 percent) by *Pseudotsuga menziesii* and *Tsuga heterophylla* of approximately 50 years of age. This site has steep (greater than 100% slopes) and distinct north-south aspects that result in both diurnal and seasonal patterns in radiation. Forest climate is moderate (mean annual temperature of about 9.7 C) and variability in temperature is greater on ridges than in valleys due to temperature inversions and downslope movement of cool air in the evenings. Mean annual precipitation is 2300 mm. Soils on WS1 are derived from basaltic and andesitic parent material; volcanoclastic and glacial rocky features are prominent. Soil moisture gradients have also been identified on this watershed, and as a general rule south-facing slopes are drier with shallower soils than north-facing slopes due to both radiation differences and greater surface damage following harvest fifty years ago.

Long-term re-measurement plots: 133 long-term re-measurement plots are arrayed in six transects spanning the 96 ha watershed perpendicular to the stream. Each re-measurement plot has a radius of 8.92 m² as measured from the ground and areas (from the air) range from 125 to 250 m². Approximately every six years, all trees within the plot are measured using standard forest inventory analysis (FIA) techniques for diameter at breast height (DBH), diameter at base (DBA), condition (live, dead, broken leaders, pests, etc.), and trees within a three meter radius of plot center are tagged for tracking. The Pacific Northwest Biomass Component Equation Library (Halpern and Means, 2011) is considered the standard allometry for calculating the biomass and productivity of these long-term re-measurement plots and is based on empirically designed equations for this specific eco-geo-region. After biomass was calculated, ANPP was determined using the methods described in Acker et al. (2002) as the difference in biomass over the measurement interval, plus the mortality and ingrowth during the measurement interval. To assess structural differences between hardwood, conifer, and evergreen dominated areas specifically, a custom script was written in Python to organize and compile calculated biomasses (Mg/ha) and ANPPs (Mg/ha/Yr) by plot into species groups.

Field Sampling techniques for litter fall: We collected litter from sixteen of the long-term plots on WS1. These plots were selected to represent the distribution of biomass on the watershed based on an imputed measurement of percent cover and tree height determined in LiDAR reconnaissance in 2008. Litter collections were conducted for the years of 2009-2011, from August to August in each year. The litter traps were located just

outside the perimeter of the plots in order to avoid interaction with other vegetative studies on the plots. Each litter trap is square with edges of 43 cm by 43 cm (0.1849 m²). The ground-truthed plot sizes are 250 m²; the aerial plot sizes range to 125 m² due to steep slopes. Five collections of wet litter from the traps were made in the first year and four in the second. Trap status, as well as any anomalies in trap content (bark, debris, etc.) were recorded. For most collection periods, both fine and coarse litter were brought back to the lab and separated with a 12 inch hardware cloth with 12.5 cm openings. To sieve the materials in this manner, a sample was dumped onto the cloth screen, then gently shaken and lightly rubbed to pass the small pieces through the screen. After the separation, twigs which slipped through the screen were returned to the coarse fraction and the needles stuck to the coarse objects were rubbed free and placed in the fine fraction. After the separation wet weight was recorded, the sample was placed in a labeled paper bag and oven-dried. Upon reaching a stable weight in the oven, the dry weight is recorded. A paper bag stapled and labeled like the sample bags is used to tare the bag weight out of the gross weight. Three traps were damaged between collections, so litter mass accumulated for these plots was only recorded prior to damage and a note was taken on the number and extent of damage.

To calculate dry mass of leaves (in Mg) per hectare per period (interval between collections), three conversion factors were created following the form of :

$$\text{Mass per Hectare} = 0.1849 \text{ m}^2 * \text{Number of Traps} * \text{Dried Mass of Leaves} / 100000000$$

The rationale for creating multiple conversion factors was to account for the set of plots on which only three or four samples were valid due to the damage. For the first year, leaf collections were precise to 365 days for almost all plots. Thus, the sum of the collected masses per hectare over the course of that year represented the annual collection. When plots were collected on subsequent days, extending the annual length, one additional day was included in the annual collection period, and the influence of that period on the sum was weighted by a conversion factor of 0.9696. When a trap was damaged, mean values from the other collection periods (early summer and winter) were weighted to the appropriate amount of days and used as a proxy for the missing measurements. When extremely coarse materials such as large chunks of bark and rotted log were found in the sample during one re-measurement, the data was not removed from the set.

Field Sampling Techniques for soil: In the summer of 2011, we visited 128 of the 133 plots (access was prohibited by unstable slopes to the remainder) and took eight soil cores using the Oakfield soil corer. The soil corer was penetrated lightly to a depth of 10 cm with care not to cause compaction of the sample. Soil core locations on each plot were chosen in part based on accessibility and with a goal of maximizing conditional variability to obtain an adequate representation of the plot as a whole. Samples were placed into individual baggies and stored at 4 C, then returned to the laboratory where they were weighed. Following weighing of each sample, the core were bulked and allowed to settle to room temperature.

Soil Bulk Density: We calculated soil bulk density for all 128 visited plots once in the summer of 2011.

Soil porosity: Porosity was calculated under the assumption of total particle density of 2.65 g/cm³ for mineral soil. Porosity is calculated as:

$$\text{Porosity (\%)} = (1 - \text{bulk density} / \text{particle density}) \times 100.$$

Percent moisture of soil: We calculated percent moisture in soil for two subsamples for each of the 128 visited plots in the summer (between May and August) of 2011. Percent moisture was calculated immediately after bringing samples back from the field.

Moisture holding capacity (MHC): MHC chambers were created by placing 10 grams of air-dried soil and 25 grams of water atop glass wool seated in a funnel in the aperture of a pre-weighed cup. The water was allowed to drip through the soil and funnel for 24 hours in a sealed, dark cabinet. After 48 hours, the cup contained water that had dripped through the funnel apparatus. The cup was re-weighed and the amount of water that had passed through determined.

If the total moisture following the analysis was less than 25 mL, percent difference lost to evaporation was also calculated. This percent was taken into account when calculating MHC.

Density Fractionation: From each of the plot samples collected and air-dried, one 25 gram sub-sample was assessed. Organic materials greater than 2000 micrometers were removed. Sub-samples were mixed and shaken with sodium polytungstate (SPT) solution with a density of 1.85 g/cm^3 for 2 hours and centrifuged for 20 minutes (Sollins et al., 2006). Vacuum aspirated light fraction was then washed of residual SPT solution. Washed light fraction was then transferred to pie tins and dried at 60 C for 48 hours. Heavy fraction remaining in the centrifuge tubes was then washed using DDI water. Dried soils were then ground and analyzed for carbon in a Leco True Spec Micro.

Nitrogen Mineralization: Measurements of N-mineralization potentials were conducted following the protocols in the LTER Soil Methods handbook (Robertson et al., 1999) by incubating soil aliquots for 28 days at 60% moisture capacity in a dark chamber. Control and incubated soil was extracted with 1 molar KCl, and $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ content of each extract were assessed using a Lachat Autoanalyzer.

Topographic Indices: Topographic indices were calculated in ArcGIS (ESRI, 2010). Slope and elevation were determined from the input LiDAR returns. TPI (topographic position index) was determined using the Topography toolbox. TPI is an index between 1 and 10 that describes the relative shape of a landform at a particular point, creating a quantifiable metric for characteristics of concavity and slope position. The method used to quantify the effects of radiation and aspect was the Beer's Index. Beer's Index was calculated following the method described in McCune and Keon (2002), which takes into

account the fact that potential direct radiation is not symmetrical about a north-south access, but that in the northern hemisphere slopes in the afternoon sun will have temperatures greater than slopes exposed to a morning sun (Stage and Salas, 2007). This method “rotates” the response surface by 45 degrees such that there is an index peak in the SW. We calculated Beer’s Index using the free GIS software package Whitebox GAT (University of Guelph, 2012). An ASCII grid of the Beer’s Index map was then exported from Whitebox GAT into ArcGIS where it was clipped and averaged to a plot scale.

Spatial analysis: WS1 was divided into spatial zones based on two criteria: soil type and species type. Soil types on WS1 are Frissell (a skeletal Eutocrypt derived from basaltic reddish breccia), Budworm (a well-drained Haplumbrept derived from basalt as greenish tufts and breccias), Limberlost (a monmorillionitic Haplumbrept consisting of basaltic colluvium from greenish tufts and breccias), unclassified Andesitic colluvium, and “rock” (a basic igneous rock). Two of the 133 plots also fall on “rock” and were excluded due to small sample size and lack of vegetation. Species types were separated into hardwoods (*Acer macrophyllum*, *Castanea chrysophylla*, *Alnus rubra*, *Prunus emarginata*, *Rhamnus purshiana*) and conifers (*Tsuga heterophylla*, *Pseudotsuga menziesii*, *Taxus brevifolia*, *Thuja plicata*), as well as a few other species that occurred very infrequently. We also looked at correlations between individual species ANPP and C fractions for some of the most prominent species, namely *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Acer macrophyllum* and *Alnus rubra*.

General Linear Model (GLM) Fitting: A script was written in MatLab to determine all pair-wise correlations between the soil fractions and ANPP, litter fall, topographic indices, and nitrogen mineralization. The same analysis was repeated for the species groups. Non-linear comparisons were also tested using the Matlab “nlmefit” tool. The whole set of data was also divided by soil type and the script run again to compare average values of carbon fractions between different soil types and to test whether or not any of the ecosystem functions (litter fall, ANPP, or N-mineralization) behaved specifically when parsed into a particular soil or species group.

Maximum Likelihood Estimation of Maximum ANPP: Maximum ANPP was computed using a conditional algorithm based on maximum likelihood. If maximum ANPP occurred in a past remeasurement or current remeasurement, then this value was used. Else, if the ANPP time trajectory was monotonically increasing, maximum likelihood was calculated using a maximum likelihood estimate. The derivation of the estimate is described in Peterson et al., 2012.

4.3 Results

I first tested the hypothesis that relationships between ANPP and LFC vary spatially because of interdependencies between ANPP, litter fall, and decomposition rates using regression analyses were first performed at the whole watershed scale. The purpose of this analysis was to evaluate the strength of both linear and non-linear correlations between the dependent variables of ANPP, litter fall, and N-mineralization and second versus the $\text{Kg C} / \text{m}^2$ in the light and heavy fractions, as well as the % C in the heavy fraction. ANPP, as calculated from the 2001-2007 re-measurement interval, was positively correlated with litter fall ($R^2 = 0.65$), but not N-mineralization ($R^2 = 0.12$), and N-mineralization was not correlated with litter fall ($R^2 = 0.05$) (Figure 20).

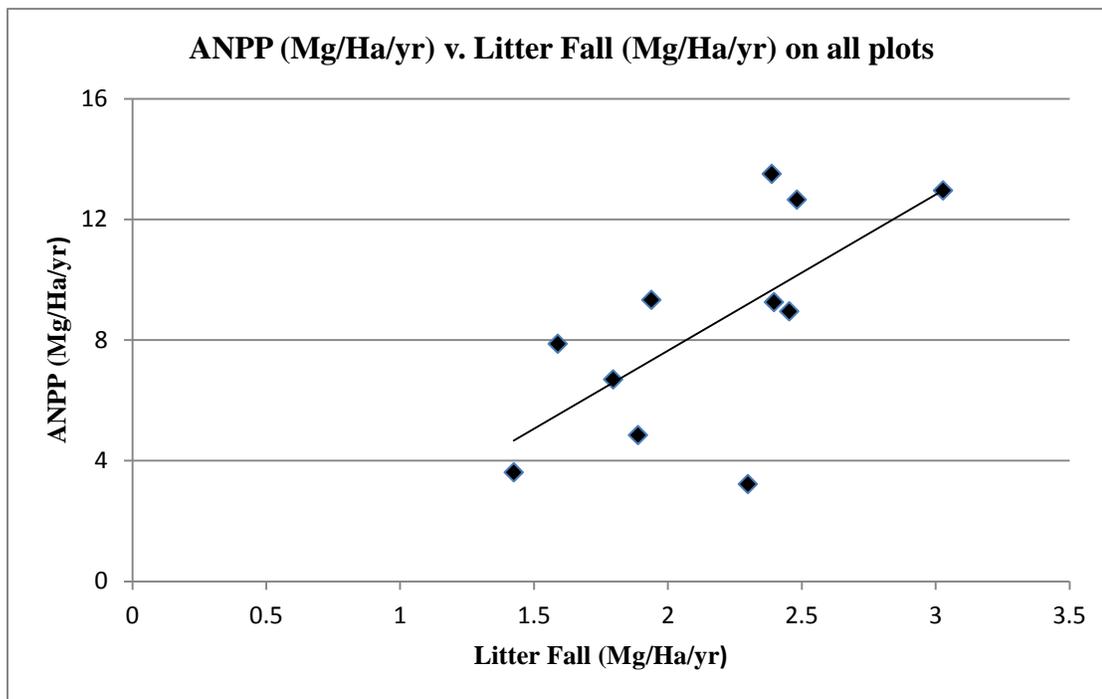


Figure 20. Litter Fall (Mg/ha/Yr) averages by plot for 2010-2012 versus ANPP for the

most recent re-measurement interval of 2001-2007. ($R^2 = 0.65$).

Although ANPP was correlated with litter fall, at the watershed extent neither litter fall nor N-mineralization were independently correlated with light fraction C (Kg C/ m^2) ($R^2 < 0.001$ and $R^2 = 0.02$, respectively). There was also not a correlation between heavy fraction C and ANPP ($R^2 = 0.18$) nor between light fraction C and ANPP ($R^2 = 0.01$) (Figure 21). Two outlier plots with exceptionally high Kg C/ m^2 in the light fraction were plots 105 and 107, both of which are located near the outlet of the watershed.

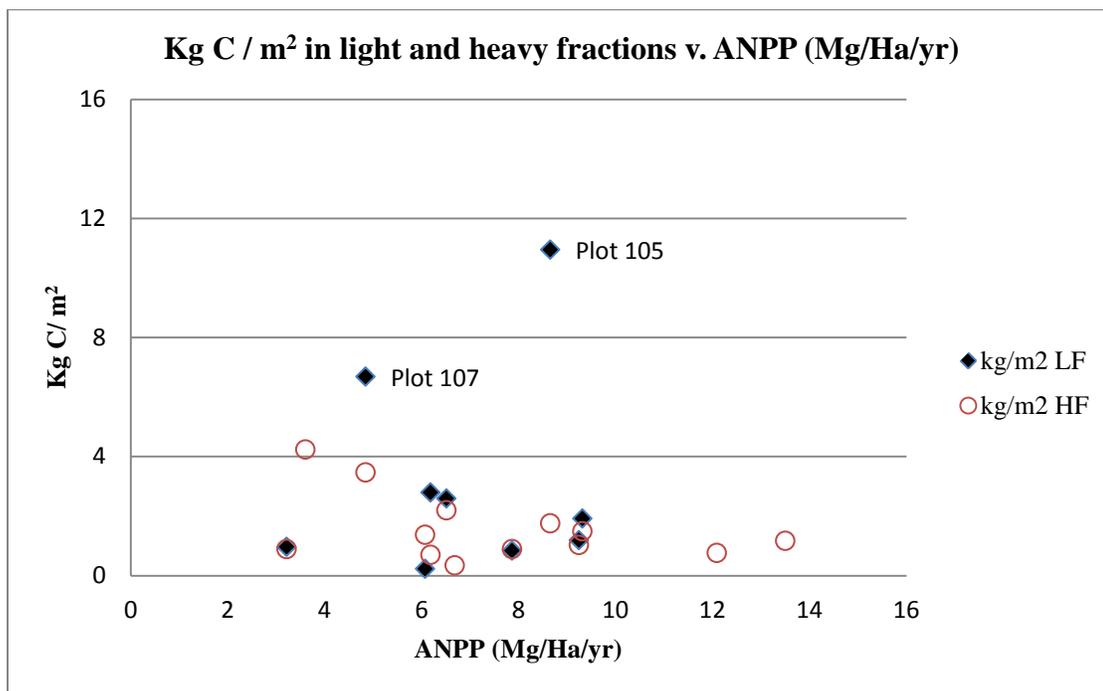


Figure 21. Poor correlation between light fraction C (Kg C/ m^2) and ANPP as calculated from the 2001-2007 re-measurement interval; mild correlation between heavy fraction C (Kg C/ m^2) and ANPP as calculated from the 2001-2007 re-measurement interval ($R^2 = 0.18$).

Nor did I find correlations between % C in the heavy fraction and ANPP ($R^2 = 0.04$), N-mineralization ($R^2 = 0.01$) or litter fall ($R^2=0.17$). Litter fall is shown as an example of the lack of correlation between % C and the ecosystem processes assessed (Figure 22).

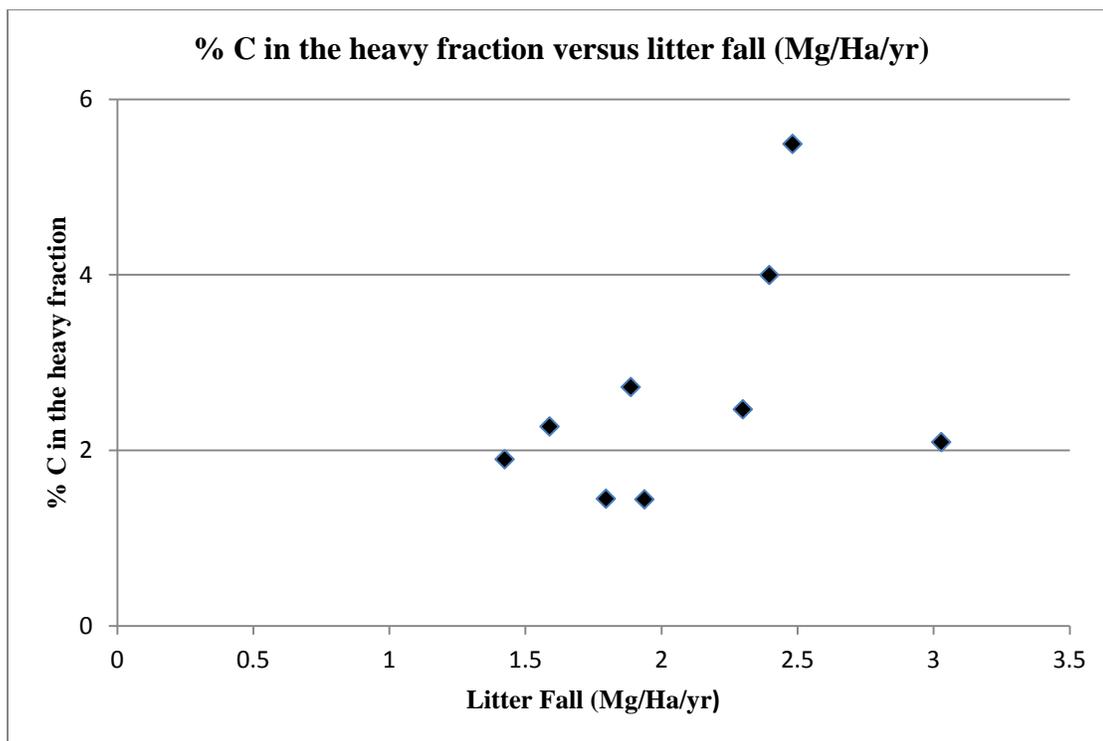


Figure 22. No relationship between % C in the heavy fraction and litter fall (Mg/ Ha/ Yr) from the averages from 2010-2012 collection period ($R^2 = 0.17$).

A general linear model including ANPP from the 2001-2007 re-measurement period, litter fall as calculated from the 2010-2012 collections, and N-mineralization from incubations of 2011 soils was created to look for any possible combination of the expected processes that might function as predictors for either (a) the % C of the heavy fraction or (b) the Kg C / m² in the light or heavy fractions at the watershed scale but no relationships were found that were significantly better than the individual correlations.

To further analyze the first hypothesis on a sub-watershed scale, I classified the plots on WS1 by aspect, soil type, and dominant species group (hardwood, conifer). When

classified by aspect or soil type, I did not find any linear patterns between ANPP, litter fall, and N-mineralization and Kg C/ m^2 in the light fraction that were stronger than those at the whole watershed scale. Because litter outputs and decompositional processes might differ by species composition, and species composition can change throughout stand development, I looked at the percent of conifers in the earliest inventory (taken in 1980) and denoted the conifer group as having greater than 50% conifers by biomass. Conveniently, on the particular set of plots selected for intensive sampling, this coniferous dominance also exists in the most recent re-measurement (2007). All plots not conifer-dominated were called hardwood-dominated. Kg C/ m^2 in the light fraction was compared to the current ANPP (2001-2007), litter fall, and N-mineralization. When classified by dominant species group, I did not find that correlations between ANPP, litter fall and N-mineralization versus light fraction C were improved beyond those at the watershed extent.

Dominant vegetation groups may be a reaction to site characteristics, and these site characteristics may directly influence soil C. The hypothesis was tested that on warmer, drier sites, ANPP is inversely related to LFC. Physical conditions were also expected to influence HFC; it was hypothesized that HFC would be a function of both soil mineralogy, stand composition, and ANPP, such that edges observed spatially in site mineralogy are reflected in sharp changes in the composition of the forest community and the magnitude of HFC stores. Warmer, drier sites are found on this watershed are found at (a) high elevations with (b) steep slopes and (c) an exposed surface (a convex

topographic position), the combination of which may be represented by an elevated value of the (d) Beer's Heat Index (Beer's Aspect), which represents the potential heat to any location on a watershed based on surface shape and radiation angles (Stage and Salas, 1991; Pypker, 2007). Correlations were tested between both mg C / g in the heavy fraction and mg C/ g in the light fraction and elevation, slope, topographic position, and Beer's Heat Index. The best correlation we discovered was that mg C/ g in the light fraction correlated with the Beers Heat Index variable over the whole watershed as well as within soil type divisions (Table 8).

Table 8. Summary of Linear Correlation Coefficients (R^2) between four topographic factors (elevation, slope, Beer's Heat Index (Beer's Index), and topographic position index (Topographic Position) and $\text{mg C} / \text{m}^3$ in the light fraction and heavy fraction by soil type.

ALL SOILS	elevation	slope	Beer's Index	Topographic Position	sample size
mg C / m ³					96
heavy fraction	0.43	0.05	0.4	0.04	
light fraction	0.22	0.09	0.86	0.62	
FRISSELL SOIL					sample size
heavy fraction	0.41	0.38	0.09	0.02	53
light fraction	0.83	0.61	0.12	0.73	
LIMBERLOST SOIL					sample size
heavy fraction	0.39	0.68	0.88	0.17	21
light fraction	0.2	0.15	0.58	0.09	
BUDWORM SOIL					sample size
heavy fraction	0.79	0.03	0.08	0.86	8
light fraction	0.01	0.61	0.05	0.01	
ANDESITE COLLUVIUM SOIL					sample size
heavy fraction	0.34	0.17	0.06	0.46	13
light fraction	0.01	0.23	0.95	0.53	

Although a very strong correlation was found between the Beer's Index on the andesite colluvium soil type and $\text{mg C} / \text{g}$ in the light fraction ($R^2 = 0.95$, $n = 13$), the sample size was small ($n = 13$). However, the correlation for $\text{mg C} / \text{g}$ in the light fraction on all soil types versus Beer's Index showed a very strong positive linear trend ($R^2 = 0.86$) when measured across all samples ($N = 96$). $\text{mg C} / \text{g}$ in the heavy fraction also showed a few substantive linear trends; elevation was the strongest topographic correlate with HFC; as elevation increases, $\text{mg C} / \text{g}$ in the heavy fraction also increases for the watershed as a whole ($R^2 = 0.43$). In particular, there is a strong positive correlation between $\text{mg C} / \text{g}$ in

the heavy fraction on Budworm soils ($R^2 = 0.43$). Slope is negatively correlated with mg C / g in the heavy fraction in the Limberlost ($R^2 = 0.68$), and Frissell ($R^2 = 0.38$) soil types, but is only weakly associated with mg C / g in the heavy fraction in the Andesite colluvium, Budworm, and over the watershed as a whole.

% of C in the heavy fraction as well as kg C / m² in the heavy fraction were compared to ANPP after dividing the watershed by aspects and into the hardwood-dominated and conifer-dominated species groups. % C in the heavy fraction was not correlated with ANPP at the whole watershed extent, nor was it correlated with ANPP when the site was classified into conifers and hardwoods (Figure 23).

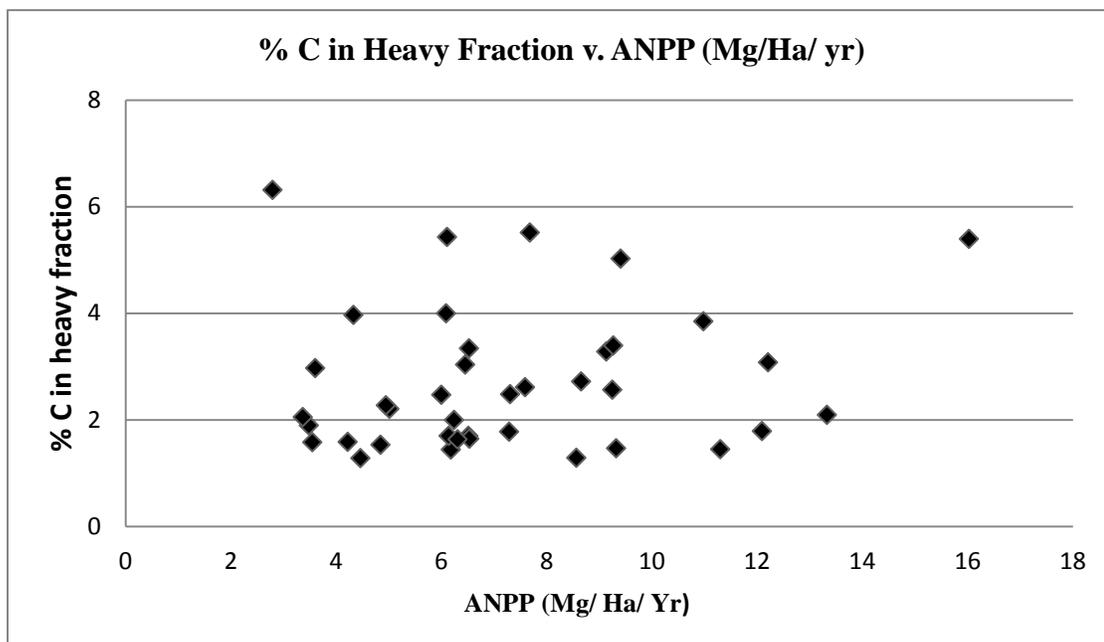


Figure 23. % C in the heavy fraction calculated from samples taken in 2011 v. ANPP for the current re-measurement interval (2001-2007) shows no correlation ($R^2 = 0.04$).

Classifying WS1 by species groups did not improve the correlation.

However, when the watershed was classified by aspect, kg C / m² in the heavy fraction was negatively correlated with ANPP ($R^2 = 0.51$) (Figure 24).

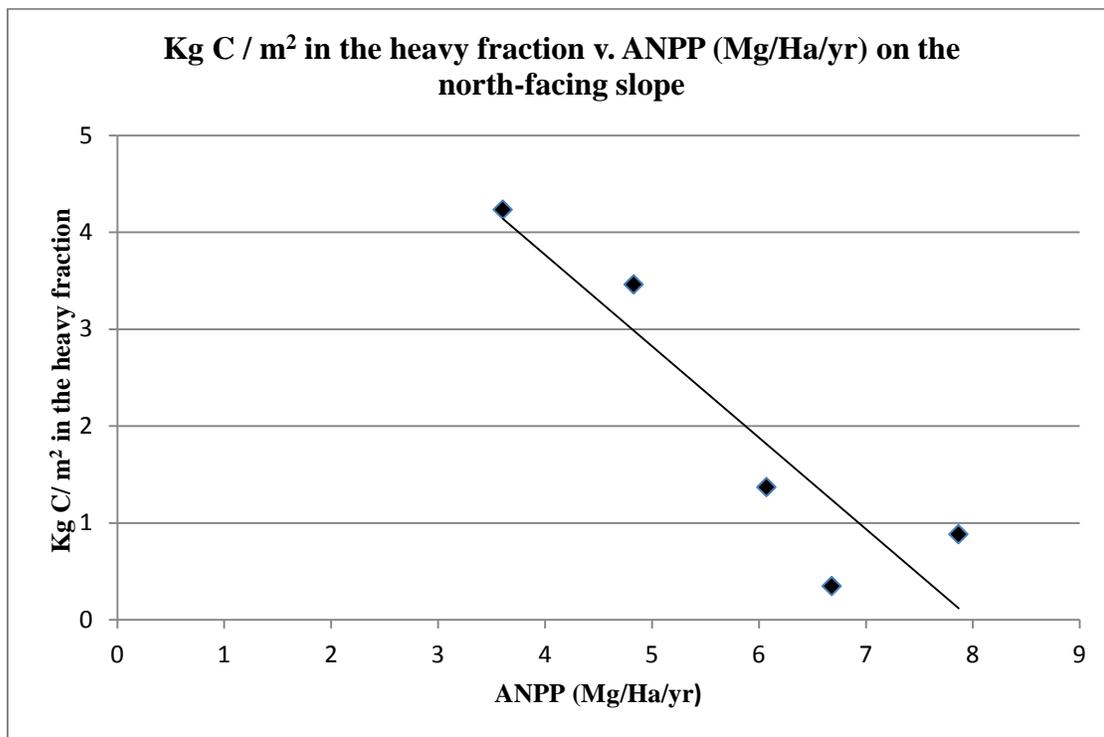


Figure 24. Negative correlation ($R^2 = 0.51$) between Kg C / m² in the heavy fraction and ANPP as measured in the 2001-2007 re-measurement interval on north facing slopes..

Although Kg C / m² in the heavy fraction was not correlated with ANPP at the watershed extent or when divided into species groups, a strong negative correlation existed between ANPP and Kg C / m² in the heavy fraction on north facing slopes.

4.4 Discussion

In complex terrain, relationships between ecosystem processes and their influence on the environment may be highly variable even on a small extent. I expected to find positive relationships between ANPP, litter fall, and N-mineralization, but only found a positive relationship between ANPP and litter fall. This was expected on first principles; more aboveground productivity should lead to more litter fall. Lack of relationship between ANPP and N-mineralization or litter fall and N-mineralization suggests that the drivers of N-mineralization may differ from those of ANPP and litter fall. Generally, this supported our initial assumption that microbial processes, including N-mineralization, were both spatially variable and their drivers not well known.

I expected that, although they might be driven by different forces, both the $\text{Kg C} / \text{m}^2$ in the light and heavy fractions and $\text{Kg C} / \text{m}^2$ in the heavy fraction % of C in the heavy fraction would be positively correlated with ANPP, N-mineralization, and litter fall over the whole watershed extent. The literature supports this expectation; relationships between soil C and ANPP should be positive; increased C inputs should lead to the incorporation of more C in the soil. For example, McGill (1996) and Paustian et al. (1994) found that soil C increases without limit as a response to increasing inputs. Others (i.e. Six et al., 2002) suggest that soil C in a forest ecosystem should increase following a saturation curve, with the saturation level being greater for the light fraction than the heavy. I expected that this young forest ecosystem might manifest a linear pattern of C storage in the soil for both fractions and percent % C in the heavy fraction when

compared to increased inputs (in this case, litter fall (Mg/ha/yr) and by proxy ANPP (Mg/ha/yr) because it was still low in C storage and inputs, so that soil C reflects only the beginning of the C saturation curve (Figure 25).

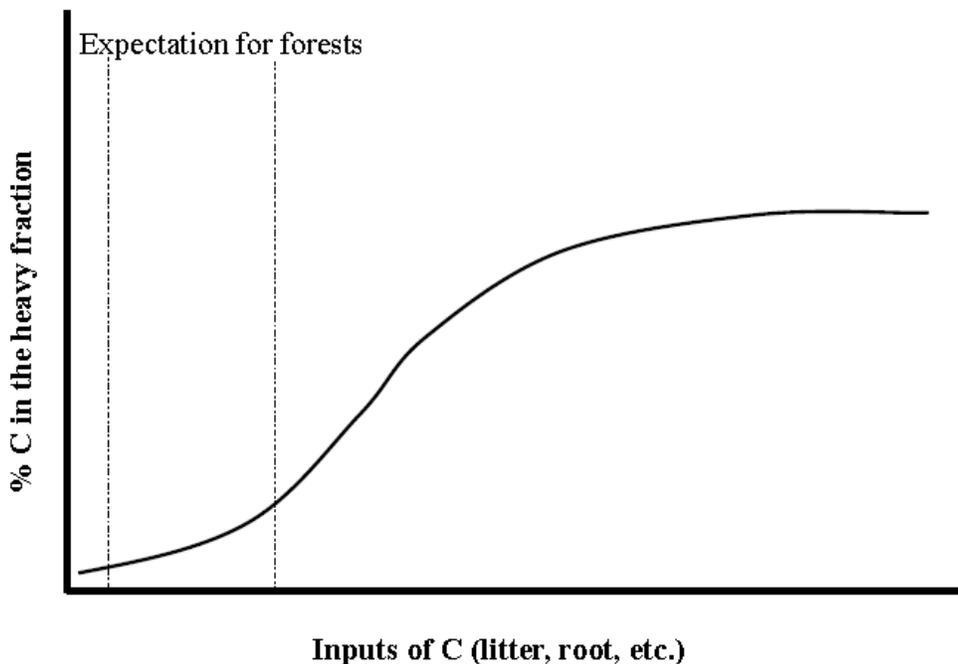


Figure 25. The expectation was that a positive "linear" relationship between C inputs (litter or ANPP) and $\text{Kg C} / \text{m}^2$ in the light and heavy fractions, as well as % C in the heavy fraction (diagrammed) would exist because this forest is not yet near the point of C saturation. However, I found no correlations between any of these. However, there were no correlations between the fractions of C or % C in heavy fraction at a watershed extent. I did find a moderate negative correlation between $\text{Kg C} / \text{m}^2$ and ANPP on the north-facing aspect. No existing models suggest a negative relationship. However, since no relationships were found between soil C and C inputs, this suggests that the other component of soil C incorporation, decomposition, as well as a mechanism

for C losses from the soil, respiration, neither of which were measured in this study, may have stronger and more variable affects than were expected.

Because it was expected that variability would exist at the sub-watershed scale, the watershed was classified into two groups: aspects and species groups. On this landscape, it was expected that these two classifications might be similar because that the north-facing slope and south-facing slope were established by different species group. Harvest documentation notes that after harvest, the north-facing slope took well to the replanting of *Psuedotsuga menziesii*, while the south-facing slope did not (Chapter 2).

Establishment on the south facing slope was dominated by drought-tolerant hardwoods that better tolerate steeper slopes and shallow soils. Species specific ANPP trajectories (Appendix 3) confirm this; for example, that the majority of *Prunus emarginata* and *Castanopsis chrysophylla* are found on the south-facing slope, and have very high productivity at a young age; they experience maximum ANPP in the first re-measurement interval between 1984 and 1988 (Chapter 3). North-facing slopes, on which conifers initially and currently dominate, reached their maximum in the 1995-2001 re-measurement (Table 7). Although the north facing slope is currently undergoing canopy closure, its ANPP is still much greater than that on the south-facing slope (Lutz, 2005, 2006; Peterson et al., 2012).

The hypotheses based on these classifications suggested that multiple mechanisms may drive soil C storage depending on the location and forest community at a within-

watershed scale. I hypothesized that where soil conditions were poor—warm, dry sites—ANPP and light fraction C would be negatively correlated. When the mg of C per gram of soil was compared to these geographic conditions, it was found that warm, dry conditions were negatively correlated with mg C/ g soil. Because I only had a limited number of soil pits, we could not use the kg C / square meter observations robustly at the watershed extent and we did not conduct direct comparisons between mg soil C per unit area and topography; instead the broad aspect classes were used. When the kg C/ square meter in the heavy fraction was classified by aspects, with the expectation that the south facing slope would be negatively related to ANPP; where soils were moist and deep, heavy fraction C was negatively correlated with ANPP. On WS1, sites with poor soil conditions (on the south face slope) also tend to correspond to sites in my “hardwood” classification; they have hardwood species with low biomass but produce the most litter (chapter 6). These sites, however, do not have the most ANPP; high ANPP sites are generally found in the coniferous stands, which simply have far greater biomass than the hardwood stands, despite having less turnover. Ultimately, then the difficulty in relating ANPP to soil C is a problem of within watershed variability, specifically pertaining to unmeasured variables in the belowground C cycle that reflect microbial processing, as well as high variability in the productivity of hardwoods and their resource needs. First (1), the forest community is far more diverse than my classifications captured, and second (2) the processes that I did not measure in this analysis, decomposition and respiration, affect the C balance in the soil, and are highly variable.

(1) Because ANPP looks at the accumulation of all aboveground biomass, not just that which is rapidly turned over, the relationship between litter fall and ANPP may differ by stand type. Although relationships between DBH (as sapwood area) and leaf surface area (LAI) are positive and well-known for many species in both the hardwood and conifer groups (Shinozaki 1964, 1965; Grier and Waring, 1974; Meadows and Hodges, 2002), it is also accepted that the relationship between tree height and leaf biomass is not constant across species or across tree heights, and on WS1 tree heights are highly variable even amongst the *Pseudotsuga menziesii* alone; on the poorly lit north facing slopes taller trees predominate, DBH is smaller, number of trees per plot is greater and biomass is greater than on south facing slopes (Menuccucci and Magnani 2000, McDowell et al., 2002; Pypker et al., 2007). On the north-facing slope, relationships between litter fall and ANPP on WS1 may be due to greater amounts of litter, as well as woody turnover, coming from high biomass coniferous stands versus smaller amounts of litter with quicker turnover coming from deciduous ones. Further evidence of this is that recent suppression and windthrow (Lutz, 2005; Lutz et al., 2006) on the north facing slope and productive coniferous stands of WS1 suggest that at least some of the litter collected on the traps may be dead branches, bark, or twigs.

As an example of differences between the conifer and hardwood classifications of ANPP and how it could be negatively related to soil C in a different ecosystem, Alexander et al. (2012) found that in boreal forests in Alaska transitioning to spruce after fire, ANPP increased while belowground C decreased. They attributed this to the notion that

biomass accumulation was largely in aboveground woody components of the spruce trees, rather than in other components of the early establishing aspens. This situation is paralleled on WS1; current ANPP is highest on conifer dominated plots with significantly greater basal area (Figure 9) than hardwood dominated plots. Thus, increasing ANPP may increase litter fall in both hardwood and coniferous stands, but while hardwoods stands may have more rapid turnover of quickly decomposing leaves; coniferous stands may have greater amounts of slowly recycling needles and woody components. Together, both of these mechanisms would cause increases in ANPP to correlate with increases in litter, but would have vastly different influences on belowground C because different decomposition regimes would be operating.

(2) On WS1, although we did not measure them, we would expect that both decomposition and respiration rates are highly variable, and at the moment this variability is not well known. The literature suggests further that it is difficult to attribute either belowground C directly or decomposition and respiration rates to easily measureable ecosystem parameters, such as those derived from topography, because different microbial communities respond to different environmental stimuli. For example, Song et al. (2012) found that in temperate steppe ecosystems, increased temperature and species composition affected the amount of carbon in the light fraction, but soil moisture did not have an effect. However, Li et al. (2006) found in tropical ecosystems that soil moisture did affect the amount of C in the light fraction. On complex terrain, heterogeneity in decomposition and respiration at a fine scale may preclude relationships between light

fraction C and ANPP to be drawn, even when large classifying groups, such as aspect and species group dominance, are used to reduce variability at a sub-watershed scale.

On watershed 1, species group was defined as majority conifer or hardwoods. Within these groups variability exists, particularly for hardwoods. *Alnus rubra*, for example, is a nitrogen-fixing hardwood that establishes from seed mid-slope, whereas *Castanopsis chrysophylla* is a sprouting hardwood that establishes very well on dry, rocky soils at elevation (Halpern and Means, 2004; Lutz, 2005). Thus the lack of correlation in the hardwoods group between the ecosystem processes and both fractions of C and for the % C may be due to a lack of ecological similarity within species groups, which also may be coupled with differences in decomposer communities related to the species. Future research would benefit from species specific analysis. Topography proved to be a more valuable in determining correlations, although still inadequate, metric for predicting soil C on complex terrain. It is also important to note that topography cannot be fully detrended from species, and in fact, stand composition is a manifestation of both developmental stage of the forest and topographic attributes. For example, in chapter 3 (Peterson et al. (2012)), I attributed the flourishing of hardwoods during early establishment to poor soil conditions (depth, rockiness, etc.) due to disturbances from the harvest and topographic location. Although the sample size was very small, the topographic analysis also revealed that changes in soil type, as well as some topographic features such as elevation, were reflected in the mg C / g soil in the heavy fraction, supporting our hypothesis that mineralogy and topography impact the heavy fraction. Six

et al. (2002) suggested that soil mineralogy affected its C saturation potential, and suggested that the heavy fraction saturates at a lower C content than the light fraction. However, we did not find that the soil type distinctions had significant P-values, suggesting that although relationships between soil mineralogy and C may exist, our soil type classifications may not reflect them. The most notable classification that reduced variability within watershed was the moderate negative relationship between Kg C/ m² in the heavy fraction and ANPP on north-facing slopes. Unlike the hardwoods group, the conifer group is relatively homogeneous in composition, with the majority of the biomass (86%) attributed to *Psuedotsuga menziesii*, and a lesser amount to *Tsuga heterophylla*, *Thuja plicata*, and *Taxus brevifolia*. Although we expected that because heavy fraction C is the "high density organo-mineral fraction... containing more processed SOM" (Tan et al., 2006) and if WS1 is similar to other mixed-coniferous ecosystems such as that studied by Mudrick et al. (2012), than the incorporation of C into the heavy fraction should be high on productive stands on the moist north facing slopes, we found this was not the case, again suggesting that rates of decomposition or respiration may be influencing soil C incorporation. I propose that on WS1, multiple mechanisms for litter accumulation exist, as a result of variability in soil decomposition.

On both the north and south facing slopes of WS1, under both hardwood and coniferous overstories, litter accumulation occurs, but may be driven by different mechanisms. For example, in Figure (9), litter mats that appear in parts of the watershed with large populations of *Acer circinatum* are displayed. These mats correspond with the dry, rocky,

soils of the south facing slope, where decomposition may be limited by heat and lack of moisture. On the north facing slopes of WS1, soils are moist and deep, and decompositional rates should be high. However, the vegetation this slope is coniferous and recently underwent canopy closure, and contains large amounts of decay-resistant coarse woody debris, as well as lignin-rich coniferous needles. Gholz et al. (1985) found that *Pinus elliotii* stands that established successfully experienced reduced decompositional rates with age and attributed this to litter chemistry and use of limited soil nutrients. It is also possible that decomposition on the north-facing slope of WS1 under the coniferous overstory may be limited by nutrient availability, therefore inhibiting microbial ability to break down coniferous litter, or that the presence of very slowly decomposing *Tsuga heterophylla* litter on the north-facing slope is significant. Because we did not measure rates of decomposition, or those of respiration, in this study we cannot verify if any of these hypotheses are true, but in both the case of hardwood-dominated and conifer-dominated sites, it is possible to suggest that variability in decomposition rates and respiration drives variability in litter accumulation, which then complicates the relationship between HFC and ANPP or litter fall.

It is well accepted that the % C in the light fraction should be greater than that in the heavy fraction (Tan et al., 2006; Golchin et al., 1994, 1995). We expected that there might be positive relationships between % C in the heavy fraction and the measured ecosystem processes, but heavy fraction % C was not related to ANPP, litter fall, or N-mineralization on the watershed as a whole, or when we classified it into groups at a sub-watershed

scale. A very weak positive directionality ($R^2 = 0.17$) existed between % C in the heavy fraction and litter fall, but the P-value was not significant and the trend was heteroscedastic at higher values of litter fall. Thus, I conclude that for % C in the heavy fraction on WS1, it is not related to the topographic resources or biotic groups I characterized.

Ultimately, this study highlights two key principles similar to those in Peterson et al. (2012). First, that selection of a time for ANPP—in this case both the re-measurement interval selected and the length of that re-measurement interval—affects how ANPP is interpreted. ANPP values from a stage in stand development where coniferous species are dominant and hardwoods are experiencing declining productivity will reflect largely ANPP dynamics for mid-sized conifers. Defining ANPP over a shorter interval would require more frequent re-measurements, but might be more representative of short-term dynamics. Second, that assessing soil C stores solely by studying ANPP and litter fall (whether directly or by proxy through ANPP) may not be sufficient in complex terrain where the interaction of environmental (temperature and soil moisture) and physiological (litter chemistry and decomposer community nutrition) effects differ at very small scales.

CHAPTER 5

**INTEGRATED TOPOGRAPHIC METRICS ARE MORE RELIABLE THAN
STAND STRUCTURE FOR DESCRIBING THE DISTRIBUTION OF
DISSOLVED ORGANIC CARBON IN COMPLEX TERRAIN**

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5.1 Introduction

In soil, DOC is the critical substrate for microbial respiration, transporting organic C through the soil where it can be used by organisms or immobilized onto minerals. DOC is a product of litter and fine root decomposition; that which is not consumed by microbes moves organic carbon downwards in the soil profile to the mineral layers (Kaiser et al., 2001; Kalbitz et al., 2000; Sanderman et al., 2001) and may play a critical role in SOM stabilization by facilitating vertical carbon transport (Marin-Spiotta et al., 2007, 2009; Ostertag et al., 2008; Sollins et al., 2009). However, despite its importance, little is known about how DOC production and transport is affected by either biotic, such as ANPP, or abiotic, such as slope, factors, especially in complex mountainous terrain where topography and vegetation diversity vary at the scale of a few meters. Species composition and topography have been shown to affect DOC quantity, quality, and distribution within the soil profile but no precedent exists in the literature showing how

these abiotic and biotic factors play out on complex terrain at the landscape scale (for examples, see Bolan et al., 2002; Sanderman et al., 2001; Zsolnay, 2003).

Sanderman et al. (2001) suggested that the primary ecosystem drivers of DOC export are moisture regime, litter quality, and soil chemistry. In complex terrain, soil moisture regime is shaped by topographic patterns across multiple scales; for example, elevation and aspect affect moisture on the regional scale, upslope contributing areas and belowground flow paths affect it on the hill slope scale, and bedrock geometry may determine available moisture on the scale of just a few meters (Hopp and McDonnell, 2009; McDonnell et al., 2007). Because DOC distributions depend on hydrology, it follows that DOC should be related to the same complex topographic variables as those that control site hydrology. However, DOC is also driven by biological processes. While some studies suggest positive feedbacks exist between DOC leachate and other ecosystem processes such as productivity (Romkens et al., 2004; Tibor and Resaka, 2005), others have suggested that although theoretically these processes and DOC should be linked, experimental evidence is lacking due to complexity in forest ecosystems (Aber et al., 1985; Nadelhoffer and Raich, 1992). This study explored how DOC and DOC flux from the ecosystem are related to ANPP, N-mineralization, and litter fall.

In soil water, DOC may be stored in several different "pools" that are each accessible by different DOC capture or extraction techniques (Jones and Willett, 2006; Zsolnay, 2003). Zsolnay (2003) developed a three pool classification for soil DOC: (1) total potentially

available DOC, (2) that which is available but not mobile, and (3) mobile DOC. Three methods of DOC analysis were used to analyze three similar pools: (1) a KCl extraction (all DOC including that bound to minerals by cation bridges), (2) a water extraction (soluble DOC not limited to the saturated flowpath), and (3) tension lysimeters (mobile DOC limited to the saturated flow path and weakly bound DOC freeable by pressure gradients). Typically, biologically available C is separated from soil using a salt-based extraction (KCl extraction), which should capture the most potentially available C because cation bridges binding DOC to soil minerals are displaced by the salt's cations (Jones and Willett, 2006; Zsonay, 1996; Zsonay, 2003). Jones and Willett (2006) found that recovery of dissolved organic nutrients (DOC and DON) was greater when using salt-based extractions than water-extractions and suggest this is due to (1) that tightly bound amino acids can be displaced by KCl, but not by water and (2) trends in water extraction recovery are highly erratic and variable based on the soils being analyzed. Water extractions physically separate soluble DOC from the soil, but do not displace mineral bonds. Tension lysimeters capture leachate in the soil and also draw off some bound DOC (pressure gradients) from soil surfaces, but are contingent on soil saturation and therefore adequate precipitation events (Figure 26).

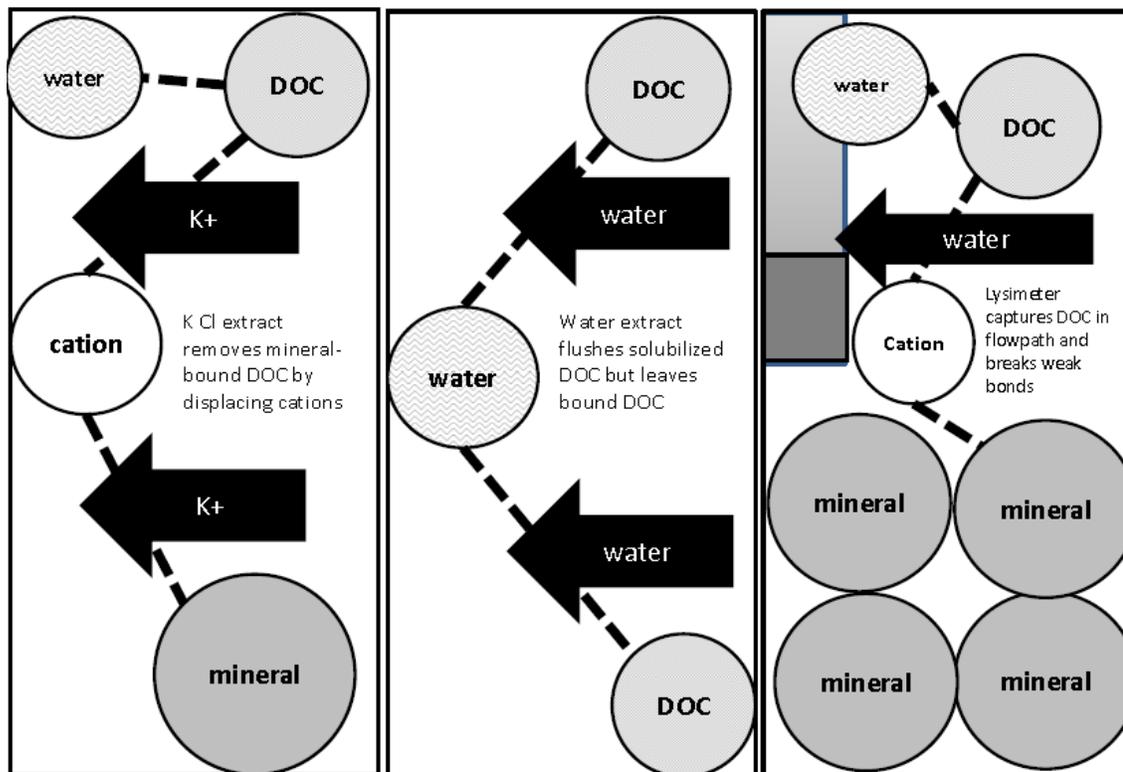


Figure 26. Extraction Methods and Soil Pools. Left, KCl extraction, middle, water extraction, right, tension lysimeters.

This analysis tests how DOC flux and DOC content are related to aboveground ecosystem processes. Available DOC should be related to environmental conditions that influence aboveground productivity (Peterson and Lajtha, 2012) and which undoubtedly produce similar effects on rates of decomposition, litter quality and litter quantity (Cole et al., 1982; Kalbitz and Wennrich, 1998). The primary objective of this analysis was to characterize the topographic and biotic variability associated with DOC and ecosystem drivers of DOC on one small (96 ha) mountainous watershed in the western Cascades range in Oregon and relate DOC to aboveground net primary productivity, litter fall, and

N-mineralization by addressing which environmental factors can be used to predict DOC content and flux, and how methods of measuring DOC compare to one another. To do so, three hypotheses were tested regarding DOC and its relationship to abiotic and biotic drivers on complex montane terrain. First, the expectation was that (a) aboveground net primary productivity (ANPP), litter fall, and N- mineralization are positively correlated with DOC (Peterson et al., 2012; Peterson and Lajtha, 2012). Second, it was tested that (2) in complex terrain DOC export is related to landform characteristics and to stand composition; specifically, it was hypothesized that topographically that soils from microsites with shallow slopes, low elevations, deep soils, and large contributing areas will have greater DOC export than soils from sites at high elevations with steep slopes, shallow soils, and little upslope area. Biologically, it was hypothesized that stands with a dominance of hardwoods would have greater DOC export than those with conifer dominance because hardwoods have more rapid leaf turnover and on WS1 are currently and relatively more productive than conifers. Finally, the expectation was that (3) all three methods (KCl extraction, water extraction, and tension lysimeter) of measuring DOC would be positively correlated with one another.

5.2 Materials and Methods

Study area: Watershed 1 (WS1) is a 96 ha catchment on the H.J. Andrews Experimental Forest in the western Cascades range in Oregon. Originally part of a “paired watershed” experiment to understand the effects of forest harvest on stream flow dynamics, WS1 was clear-cut (1962-1966), burned (1967), and replanted (1968-1971) with *Psuedotsuga menziesii* (Douglas-fir) seed and seedlings (Halpern and Franklin, 1989; Halpern and Franklin, 1990). The harvest of WS1 was conducted using a small area of skidder-based logging (near the landing at the stream outlet) and a large extent of skyline logging. Due to the immense size of the individual trees and the instability of the slopes, the logging progressed slowly over four years and seven spatially distinct harvest units as new technology was implemented, and it has been documented that early regeneration, particularly of shrub-trees *Acer circinatum* (vine maple) and *Rhododendron maximum* (Rhododendron) had established on some of the early harvested units prior to whole-landscape burning in 1967. Burning was “hot and satisfactory” and large stems not removed in logging but downed by burning were removed from the lower one-third of the watershed to clear the stream pathway. Four attempts at regeneration were made; the first attempt was an aerial re-seeding over the whole landscape; the second through fourth were manual replanting on the south-facing slope, with maximum planting attempts devoted to an “unplantable” area in harvest documentation. The plantings in such areas were ultimately not successful in generating as much biomass as other parts of the site.

Mean annual precipitation on site is approximately 2300 mm with a mean temperature of 2 C in January and 18 C in August, with a two to six degree average daily range, as is typical of the region. WS1 is near the confluence of Lookout Creek with the McKenzie River, at a relatively low elevation (410 m – 1080 m). Parent material is largely andesite and breccia, with both green and red breccias present, as well as blackish andesitic scree and large, potentially glacially-deposited boulders (Swanson and Jones, 2002). Four series of andisols exist on the site: Frissell, Budworm, Limberlost, and Andesite Colluvium, as well as a distinct “rock” area (Rothacher, 1967; Dyrness, 1969).

Topography controls the microclimate, which differs distinctly by north- and south-facing aspects due to cumulative annual insolation, aspect-oriented day length, and growing season. Diurnal fluctuations in temperature due to adiabatic cooling on steep slopes yield nocturnal cold air drainages on approximately eighty percent of summer nights (Pypker et al., 2007). Nutrient concentrations of WS1 have not been studied in depth, but it has been shown that the site is limited primarily by N, which is typical of the region as a whole (Vitousek and Howarth, 1991).

The current site vegetation is dominated by 55 year old, 20 to 30 m height cohort of *Pseudotsuga menziesii* (Douglas-fir), most of which was developed from planted seedlings. However, other species such as *Tsuga heterophylla* (western hemlock), *Alnus rubra* (red alder), *Thuja plicata* (western red-cedar), *Castanopsis chrysophylla* (Golden chinquapin), *Acer macrophyllum* (big leaf maple), and *Prunus emarginata* (bitter cherry) have naturally seeded in from nearby old-growth stands and alder-dominated riparian areas. *Acer circinatum* and *Rhododendron macrophyllum* exist as tall shrubs. Ground

vegetation is primarily *Polystichium munitum*, *Gaultheria shallon* and *Mahonia aquifolium*, all of which have been present on the stand since establishment.

Vegetation (biomass and ANPP): Long-term data for the site was available in the form of forest inventory flat-files consisting of diameter at breast height (DBH) measurements for each individual tree on 131 circular plot with an 8.92 m radius (Figure 2). These plots are arrayed systematically along six transect lines which bisect WS1 perpendicular to a “y-shaped” tributary and span the one square kilometer site at an angle of approximately 220 degrees SSW to 40 degrees NNE (Acker et al., 1998; Lutz, 2005). DBH was measured on all trees greater than one cm DBH; diameter at base (DBA) was used as a proxy for all trees less than 1 cm, and conversion equations were calculated by Lutz (2005). From DBH, to determine the biomass of individual trees, allometric equations in the Pacific Northwest Biomass Component Equation Library (Halpern and Means, 2004) were applied to the appropriate species following the precedent set in Lutz (2005) and Lutz and Halpern (2006). Because the plots were initially laid out on the surface rather than aurally, we calculated plot area using an elliptical adjustment based on gradient, and from this determined biomass per unit area (Mg/ha). We calculated ANPP based on the Acker et al. (1998) method, also precedent in Lutz (2005) and Lutz and Halpern (2006). We mapped the aboveground biomass and ANPP for the 131 re-measurement plots and used spherical kriging to extrapolate across the spatial extent (ArcGIS 9.3.1. “Geostatistical Analyst” Toolkit, ESRI 2009).

Soil Sampling: During the summer of 2011, soil cores were taken from all accessible vegetation plots (124 of 133 plots) using an Oakfield soil corer. Eight cores were taken at random locations within the plot, with the intent of capturing microtopographic and microclimatic variability. Soil cores did not include the O-horizon and were 10 centimeters high and 1.7 cm in diameter, unless soil thickness was less than this amount, in which case soil cores reflected the maximum possible penetration up to 10 cm. Sixteen plots selected to represent the variability in biomass across the watershed based on 2007 LiDAR analyses were cored subsequently in March of 2012 for the purpose of obtaining measurements of soil moisture. These 16 plots also house the lysimeters and litter traps used to measure mobile soil water and litter fall, respectively.

Lysimeter collections: Lysimeter leachate was collected during the rainy seasons (October through May) between 2010 and 2012. In summer of 2010, we installed two lysimeters on each of the sixteen intensively measured plots in the soil pit. These lysimeters were placed within PVC housing and surrounded by silica gel to facilitate soil contact. The lysimeters drew water from 70 cm depth. Lysimeters were primed to 15 psi after each collection, and usually collected two days following priming. During the 2010-2011 season, ten lysimeter collections were attempted, with between two and five lysimeters yielding water on any given run. During the 2011-2012 season, four lysimeter collections were made, with five to seven lysimeters yielding water on any given run. Climactic variability occurred between the two years. The rainy season of 2010-2011 began earlier (October) than that of 2011-2012 (November) and did not extend as late into the spring (April versus May). Additionally, during the 2011-2012 season, cooler

temperatures and a lower snowline prevented access to some of the high elevation lysimeters during the early season. We averaged both lysimeters on each plot across time and with one another in order to determine a value for each plot. Because this method has high variability, we use the other methods of measuring soil water (KCl and water extraction) to validate or further explore patterns observed in DOC.

Soil depth: We visited all of the accessible long-term re-measurement plots during spring of 2011. Soil depth was measured using the knocking pole method. This period was selected because of the soil penetrability afforded by moist conditions. The knocking pole was penetrated into the soil perpendicular to the surface to a maximum depth of 120 centimeters to account for 90-95 percent of roots (Gasson and Cutler, 1990; Gilman, 1990; Coutts, 1999). The six measurements taken were averaged to a plot-scale mean that was used to estimate ESD.

Soil Rockiness: Soil rockiness (percent by volume) was measured from excavations of sixteen sets of two soil pits with a 600 cm³ volume on the same subset of plots. In one of these pits, lysimeters were later placed. Soils were removed from the site manually and returned to the laboratory where they were separated by depth (0-10 cm and 10-20 cm) and sieved by particle size (<2 mm, 2-5 mm, and > 5 mm). Rock bulk density was calculated using the submersion method for each plot individually because volcanic rocks are often lighter than the traditional 2.65 g/cm³ value. Soil rockiness was computed on a volume-of-rock to volume-of-soil basis facilitated by the individual density calculations. We developed a metric of effective soil depth (ESD) similar to that which is used in

agriculture to imply the soil volume available for moisture storage (Wolf, 1995; Verseghy, 2007). ESD was calculated as

$$\text{TOTAL DEPTH(cm)} - \text{PERCENT ROCKINESS (cm}^3\text{)* TOTAL DEPTH (cm)} = \text{ESD (cm)}$$

The ESD metric was our primary metric for quantifying potential belowground moisture holding capacity.

Litter fall: We collected litter from sixteen of the long-term plots on WS1. These plots were selected to represent the distribution of biomass on the watershed based on an imputed measurement of percent cover and tree height determined in LiDAR reconnaissance in 2008. Litter collections were conducted for the years of 2009-2011, from August to August in each year. The litter traps were located just outside the perimeter of the plots in order to avoid interaction with other vegetative studies on the plots. Each litter trap is square with edges of 43 cm by 43 cm (1.849 m²). The slope measured plot sizes are 250 m²; the aerial (horizontal) plot sizes range to 125 m² due to steep slopes. Five collections of wet litter from the traps were made in the first year and four in the second. Trap status, as well as any anomalies in trap content (bark, debris, etc.) were recorded. For most collection periods, both fine and coarse litter were brought back to the lab and separated with a 12 inch hardware cloth with 12.5 cm openings. To sieve the materials in this manner, a sample was dumped onto the cloth screen, then gently shaken and lightly rubbed to pass the small pieces through the screen. After the separation, twigs which slipped through the screen were returned to the coarse fraction

and the needles stuck to the coarse objects were rubbed free and placed in the fine fraction. After the separation wet weight was recorded, the sample was placed in a labeled paper bag and oven-dried. Upon reaching a stable weight in the oven, the dry weight is recorded. A paper bag stapled and labeled like the sample bags is used to tare the bag weight out of the gross weight. Three traps were damaged between collections, so litter mass accumulated for these plots was only recorded prior to damage and a note was taken on the number and extent of damage.

To calculate dry mass of leaves (in Mg) per hectare per period (interval between collections), three conversion factors were created following the form of :

$$\text{Mass per Hectare} = 0.1849 \text{ m}^2 * \text{Number of Traps} * \text{Dried Mass of Leaves} / 100000000$$

The rationale for creating multiple conversion factors was to account for the set of plots on which only three or four samples were valid due to the damage. For the first year, leaf collections were precise to 365 days for almost all plots. Thus, the sum of the collected masses per hectare over the course of that year represented the annual collection. When plots were collected on subsequent days, extending the annual length, one additional day was included in the annual collection period, and the influence of that period on the sum was weighted by a conversion factor of 0.9696. When a trap was damaged, mean values from the other collection periods (early summer and winter) were weighted to the appropriate amount of days and used as a proxy for the missing measurements. When extremely coarse materials such as large chunks of bark and rotted log were found in the

sample during one re-measurement, the data was not removed from the set.

Topography: We developed a set of 12 topographic metrics within ArcGIS 9.3.1 (ESRI, 2009) using a digital elevation model (DEM, 10 m resolution) and a LiDAR bare-earth map (1 m resolution, reconnaissance flown in 2008). LiDAR was flown with a minimum of nine returns per square meter to approximate vertical protrusions within 13 cm accuracy and horizontal cover within 1 m accuracy. For 1 m topography, the final returns for each of the voxels were averaged to determine bare-earth altitude (Lefsky et al., 1999). To address the influence of topography on stand structure, we derived metrics from the DEM or LiDAR bare-earth map using ArcGIS's "Spatial Analyst toolkit" or the downloadable "Topography toolkit" (available from ESRI, 2010) topographic metrics such as aspect, slope, elevation, maximum solar insolation, upslope contributing area, angle to the horizon, Beer's Index, wind exposure, topographic wetness index (defined as the natural log of the contributing area divided by the slope angle) and Jenning's landform classifications (Dyrness, 1969; Rothacher, 1973; Swanson and Jones, 2002). These topographic metrics we selected serve as remotely-sensed proxies for belowground resource distributions or ecosystem forces that could affect them.

Nitrogen Mineralization: Measurements of nitrogen mineralization potentials was conducted following the protocols in the LTER Soil Methods handbook (Robertson et al., 1999).

From each plot, one 25 g soil aliquot was incubated for 28 days at 60% moisture capacity in a dark chamber. Every three days, samples were checked for weight maintenance to

ensure evaporation was not occurring, and refilled with water if mass greater than 3% was lost. Following the incubation period, samples were extracted by mixing the soil with 100 mL of 1 molar KCl through shaking on the reciprocal shaker for two hours. After shaking, samples were filtered through a Watman glass number two filter twice. The first extraction was destroyed and the second extraction preserved at 4 C. A second set of samples from each plot was immediately extracted following return from the field. The $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ content of each sample were assessed using a Lachat Autoanalyzer.

DOC Analysis: Concentrations of DOC were calculated using a Leco Micro Spec. 25 g subsamples were used for analysis. A KCl extraction was performed using 1 M KCl and a water extraction using DD1 water. Both were filtered through a Watman Glass Filter #2. The collected leachate from the tension lysimeters was also retained for analysis.

5.3 Results

Both linear and non-linear relationships were tested between DOC, and ANPP, litter fall, and N-mineralization using the linear and non-linear fitting tools in MatLab to conduct this analysis. Some pools of DOC were correlated with ANPP, litter fall, and N-mineralization, and these relationships were improved in certain cases when topographic or biologic constraints were used. In a previous study of the same site, it was found that relationships between litter fall, N-mineralization and ANPP were related to one another and moderated by both topography and stand structure, specifically forest development in the context species composition and both initial and current dominance by hardwoods on some sites (Peterson et al., 2012; Peterson and Lajtha, 2012).

A strong positive relationship existed between DOC leachate (concentrations of DOC collected from lysimeters in 2011-2012) and ANPP as calculated for the most recent evaluation time, the 2001-2007 re-measurement interval ($R^2 = 0.54$) (Figure 27).

Exponential regression slightly increased the correlation (transformed $R^2 = 0.64$), but this is likely due to reduction in variance from the transform, not to an actual physical phenomenon. KCl- extracted DOC ($R^2 = 0.17$) and water-extracted DOC ($R^2 = 0.01$) were not correlated with ANPP.

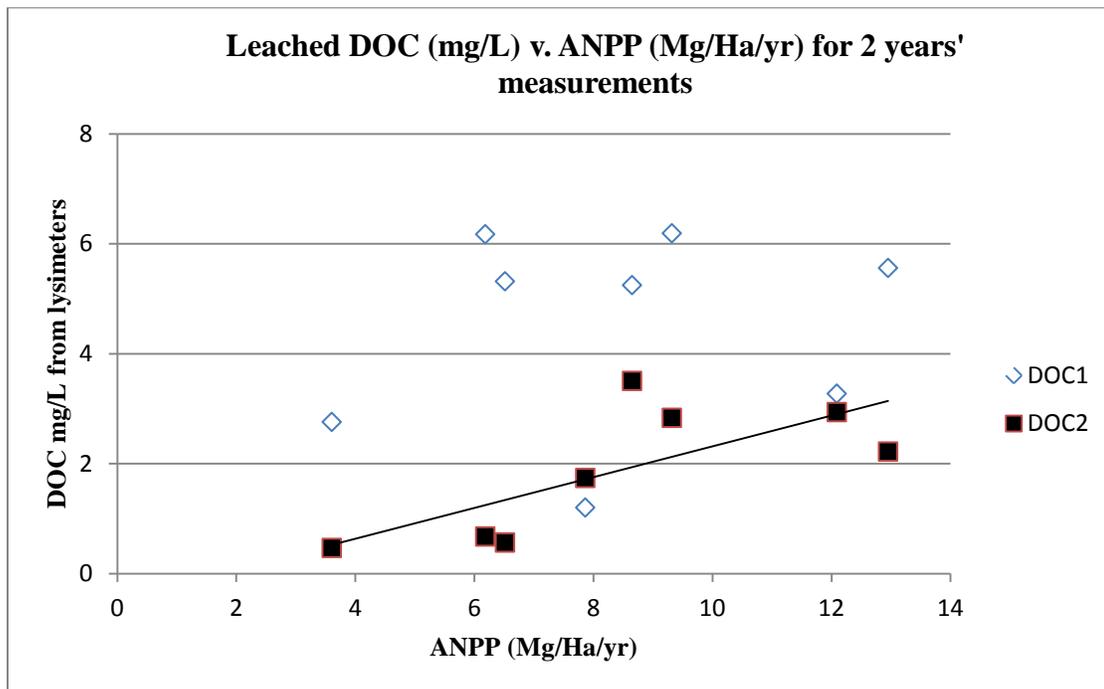


Figure 27. Lysimeter DOC (leached DOC) (mg/L) collected in 2011 and 2012 versus ANPP calculated from the most recent re-measurement interval (2001-2007) ($R^2 = 0.52$). Leached DOC from the previous year was not as well-correlated ($R^2 = 0.30$)

It was also found that at the whole watershed extent, available DOC (from KCl extractions), was not correlated with litter fall ($R^2 = 0.26$) and was correlated with N-mineralization ($R^2 = 0.41$), however this correlation was strongly influenced by outlier plots (Figure 28). The plot with a very low available DOC (0.56 mg/L) is recently experienced very high mortality from suppression and windthrow. The two plots with very high (> 20 mg/L) available DOC are located in a moist area near the stream outlet.

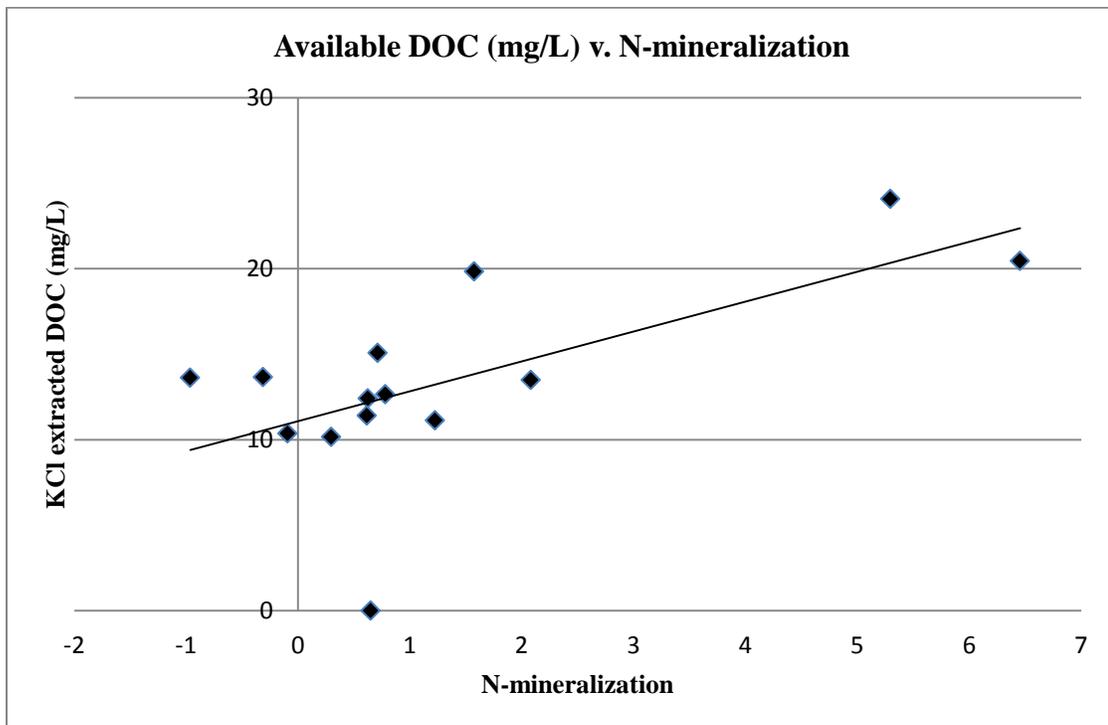
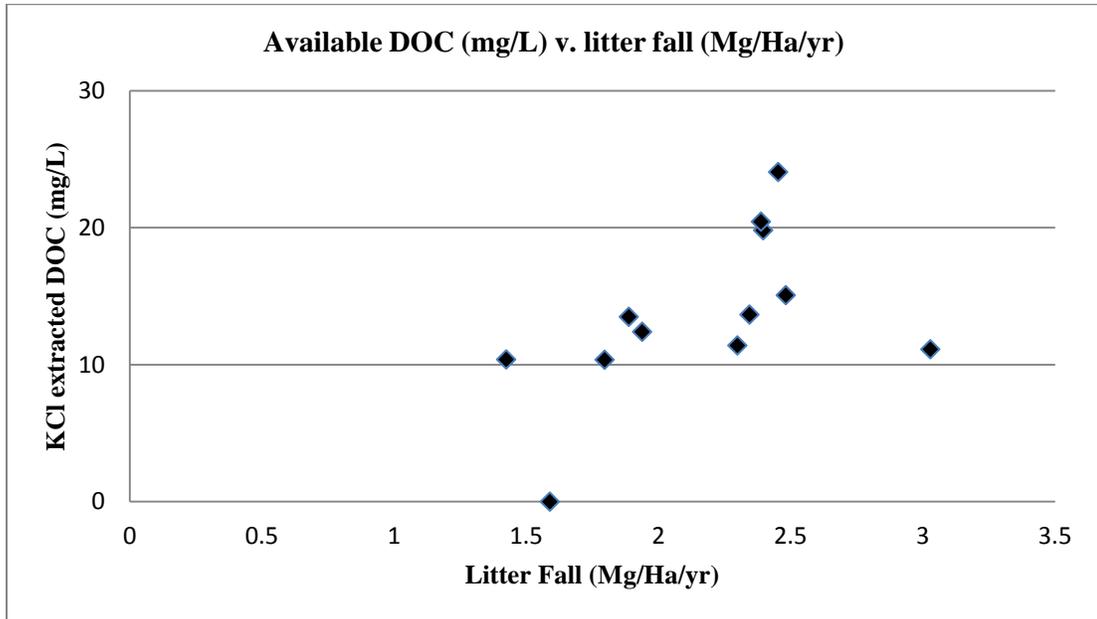
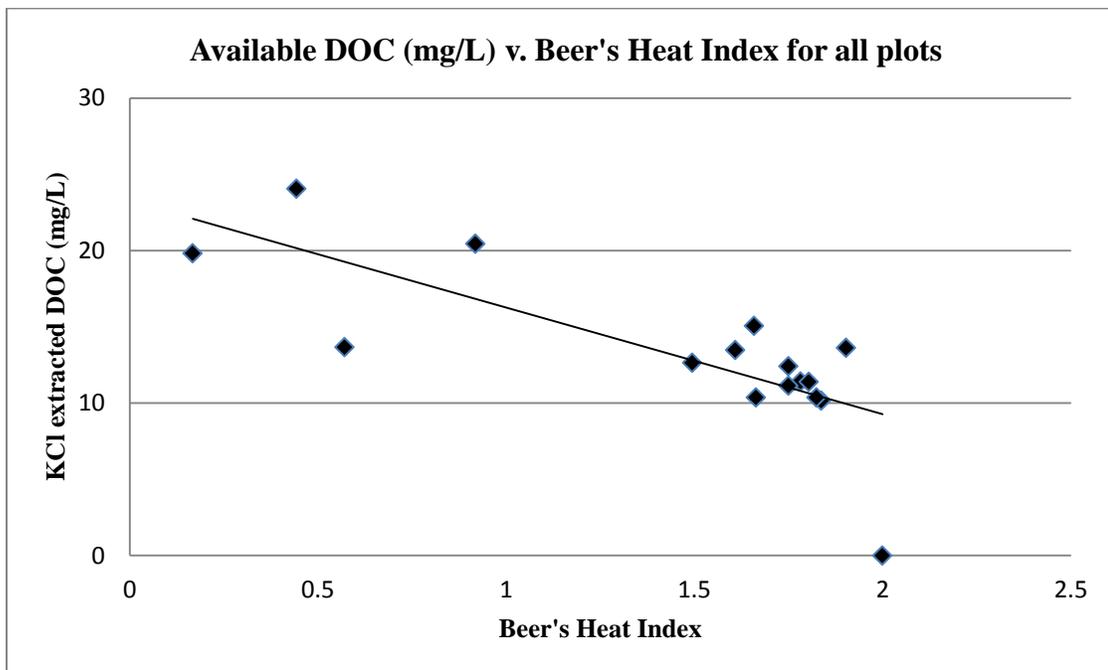
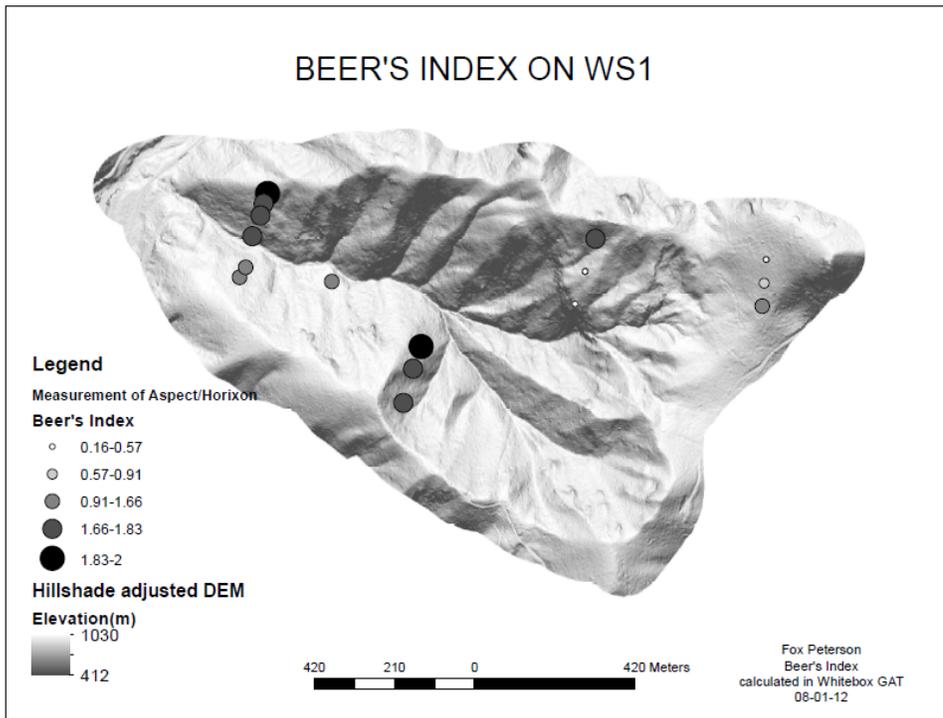


Figure 27. Available DOC (mg/L) from KCl extractions using soils collected in 2011 versus litter fall from 2010-2012 ($R^2 = 0.26$) at the whole watershed extent; available DOC (mg/L) from KCl extractions using soils collected in 2011 versus N-mineralization from a one-month incubation in 2011 ($R^2 = 0.41$).

One topographic metric, Beer's Heat Index, which is a measurement of azimuth and horizon-corrected aspect which stands as a proxy for potential heat and radiation available was moderately correlated with available DOC ($R^2 = 0.52$) (Peterson and Lajtha, 2012; Stage and Salas, 1991). This correlation was improved when WS1 was classified by aspect. On both the south- and north- facing slopes of the watershed, a strong negative correlation existed between Beer's Index and available DOC, although it was more pronounced ($R^2 = 0.78$ versus $R^2 = 0.62$, respectively) on the south-facing slope (Figure 28). Also, on the north-facing slope, an outlier value of available DOC greatly influences the correlation.



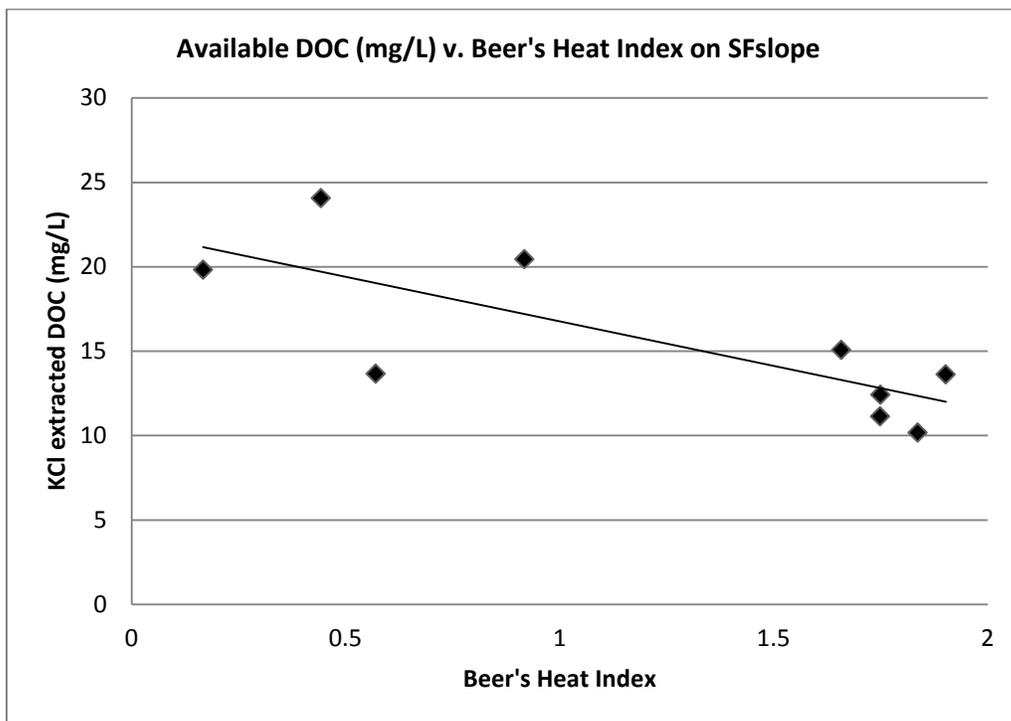
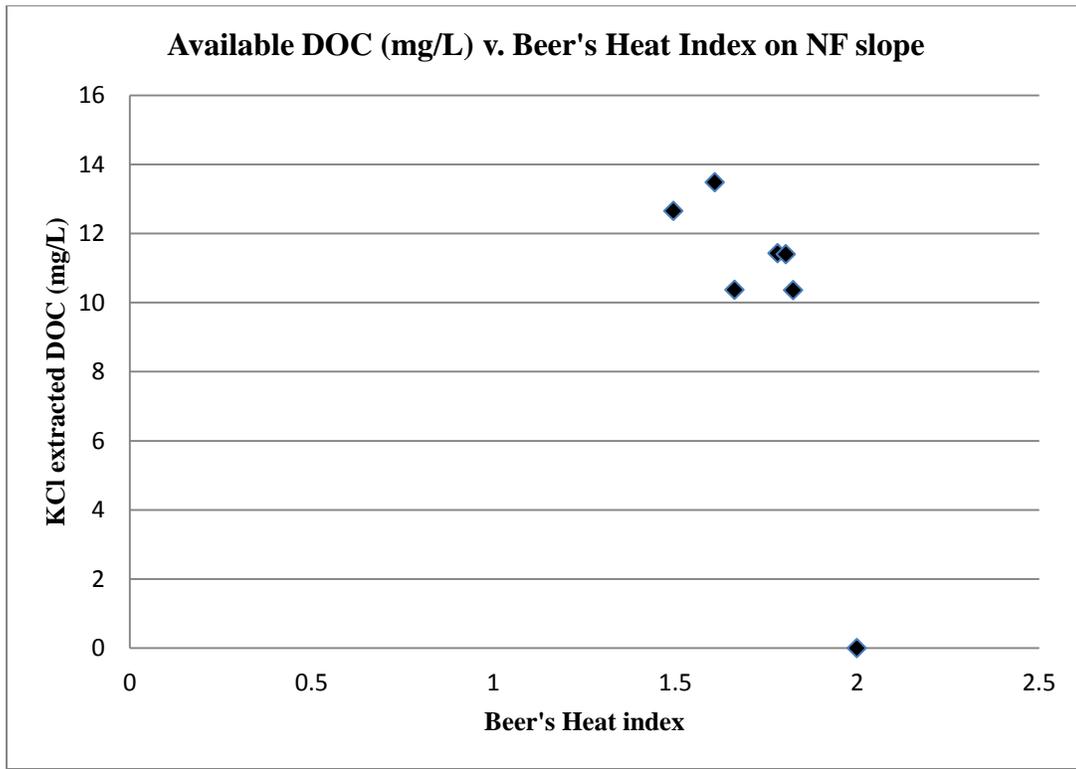


Figure 28. Map of Beer's Heat Index on WS1; Available DOC (from KCl extraction on soils collected in 2011) versus Beer's Heat Index on (a) North facing ($R^2 = 0.62$) and (b) South facing aspects ($R^2 = 0.78$).

Litter fall is not well-correlated with available DOC at the whole watershed extent ($R^2 = 0.26$), and this relationship is not bettered when classifying the watershed by aspect. Likewise, there was also not betterment of the relationship between DOC and N-mineralization (whole watershed, $R^2 = 0.41$) when we divided the watershed by aspect (for whole watershed correlations, refer to figure 26).

Although it appeared in our regressions that andesite colluvium soils were good classifiers for water-extractable DOC, the p-value for the correlation was not significant; the relationship was strung between two small clusters of observations rather than representing a watershed scale trend.

All three methods for determining DOC were significantly different ($p < 0.05$) at a significance level of 0.05. In most plots (except plot 105, located nearest the drainage), the greatest DOC was found in the K Cl-extracted samples (Figure 30).

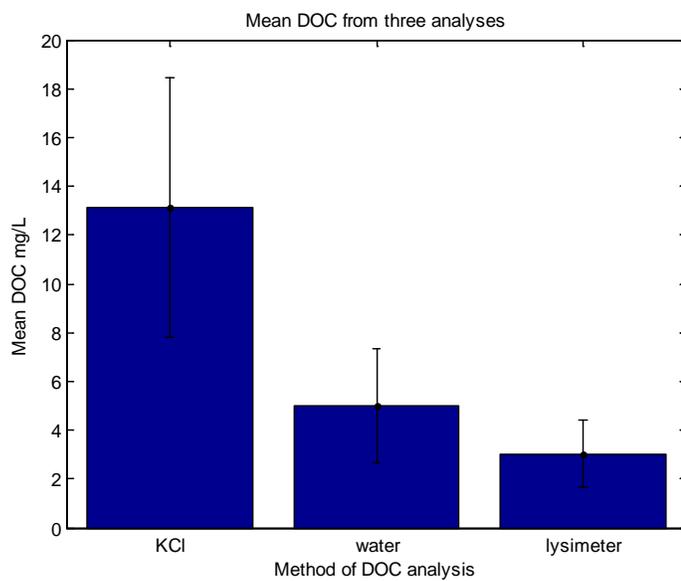
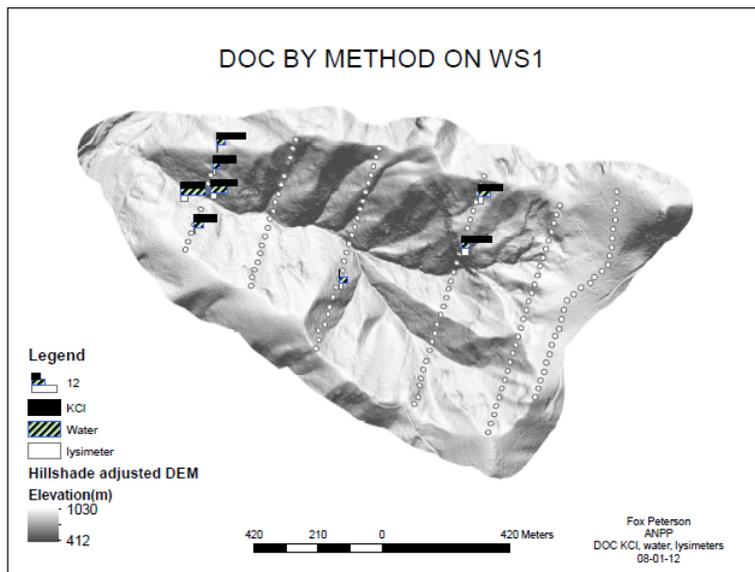


Figure 30. Bar graphs of DOC by method overlaid on the spatial locations of the plots ; black is KCl extraction mg/L, striped is water extraction mg/L, and white is lysimeter leachate mg/L and the mean mg/L collected in each of the DOC methods.

5.4 Discussion

At the whole watershed scale, leached DOC increases with increasing ANPP. This positive relationship was expected, and it suggests the utility of aboveground productivity as a means for predicting C losses in dissolved leachate. It was also found that available DOC was positively correlated to litter fall and N-mineralization, although these relationships were not as strong as between leachate and ANPP. Litter fall provides C to the soil, some of which is used by microbes and some of which is solubilized into DOC. N-mineralization is a microbial activity. If C is available in excess of what is used in microbial processing, it is sensible that at least some of this C would be contributed to the available DOC pool.

On WS1, highly productive stands are currently dominated by coniferous biomass. When WS1 was first replanted following the 1962- 1966 harvest, conifers (specifically *Psuedotsuga menziesii*) thrived on moist, deep-soiled sites and drought-tolerant hardwoods established on dry, shallow-soiled sites where conifer regeneration was unsuccessful; succession on moist sites was expedited in comparison to that of dry sites (Peterson et al., 2012). As of 2007, our last inventory period, the moister sites (found primarily on the north-facing slope) have declining ANPP as a result of canopy closure, which occurred for many trees between 1995 and 2001, or when the stand was around 35 years in age. However, the ANPP of these sites is currently greater than that of hardwood-initiated sites, likely due to the fact that they simply have greater biomass. Areas of high biomass and high ANPP on WS1 are not spatially coherent. On the plots

initiated by hardwoods, although ANPP was initially quite high, current ANPP is low relative to that of the coniferous stands. However, turnover on these sites is still high, and positive feedbacks between soil nutrients, productivity, and litter fall may exist, if the vegetation is not limited and can benefit from increased resources. Although the relative productivity may be less than that of the conifer dominated stands, over the course of stand development, site quality, particularly in terms of soil C and moisture, increases on the south-facing slopes of WS1 in conjunction with increasing productivity, N-mineralization, and litter fall (Glenn-Lewin et al., 1992; Peterson et al., 2012).

The relationship between ANPP and DOC remained strong on both aspects of the watershed, despite very different plant community dominances and soil moisture regimes. However, we found that differences existed across aspects while relating DOC to topographic variables, and that Beer's Heat Index, which emphasizes the solar loading and moisture loss resulting from aspect and exposure, was a strong negative predictor for available DOC on both the moist north-facing slope and the dry south-facing slope. A lack of soil water, whether due to evaporative losses in high heat or drainage due to convex landforms, may reduce microbial activity and soil organic matter break down, thereby reducing DOC. Or, if sites with a high heat load are spatially contiguous and on very sorptive soils, soil C may be held onto mineral surfaces rather than available in solution.

It was expected that classification by species groups (hardwoods and conifers) would improve DOC correlations, especially with respect to ANPP and litter fall. Hardwoods

generate high-quality litter which provides microbial substrate and facilitates the creation of DOC. On hardwood dominated sites I expected to find positive relationships between DOC, ANPP, litter fall, and N-mineralization that were stronger than those on conifer-dominated sites, but did not. This suggests that topographic factors, more than biologic ones, control DOC distribution on WS1. However, the classification of "hardwoods" is very broad, representing species from the very drought-tolerant *Castanopsis chrysophylla* to the mesic nitrogen fixer, *Alnus rubra*. Therefore, biologic controls may still exist for WS1, even pertaining to species composition, but may not have been captured in this analysis.

On WS1, the greatest concentrations of KCl-extractable DOC were found in locations with the greatest upslope area at the basin scale: in general, these are from the lowest elevations and nearest the mouth of the watershed. Not only are these locations saturated for longer periods of time during they year, they also have highly variable and denseforest communities which contribute to variability in microbial processing and soil incorporation. Exploration of the differences between methods for collecting and extracting DOC showed significant variation between all three methods. Although it was expected that the results from each method would be correlated with one another, they were not. One plot, which essentially represents the first order "pour point" of WS1, had particularly high values of water extractable and lysimeter DOC. Differences amongst DOC collections by methods may be attributed to the influence of topography; for example, on the "pour point" plot with higher than expected values of water-extractable and lysimeter DOC, soils are highly saturated, so DOC in the mobile categories may be

increased relative to the available DOC. However, despite that DOC methods were not correlated with one another; we did find that trends over space were corresponding in all points except for one located near the watershed outlet. This stresses the importance of collection and analysis method when researching DOC, as trends in DOC presence, extractable, and leachate cannot be used to predict one another.

CHAPTER 6

**A SPATIALLY EXPLICIT MODEL OF THE ANNUAL LITTER FLUX IN A
YOUNG FOREST IN THE WESTERN CASCADES RANGE, OREGON**

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6.1 Introduction

Litter is an important component of the forest carbon (C) budget (Dyrness, 1967; Grier and Logan, 1977; Harmon, 1991; Adair et al., 2008). The litter stock in the budget represents C transitioning between the foliar biomass pool and the soil carbon pool (Adair et al., 2008; Valentini et al., 2000). On a global scale, the magnitude of the litter fall process has been estimated to be up to ten times greater than the flux of carbon from coal-burning power plants and other industrial sources, so litter may serve as large, albeit short-term, carbon store. Therefore, it is important to quantify where and how much litter fall occurs (Adair et al., 2008; Korner, 2003). However, it is difficult to obtain an estimate of litter fall over complex terrain because heterogeneous vegetation and resource availability complicate relationships between topography and productivity (Korner, 2003; Peterson et al., 2012). Additionally, difficulty arises in sampling from topographic heterogeneity and a large number of samples may be needed to properly represent a variety of plant communities that may exist on a site of interest. Also, bias may develop

towards communities on readily-accessible sites from which traps are preferentially placed and readily collected. Finally, extrapolation of litter mass collected from traps several orders of magnitude smaller than the spatial extent of the catchment being modeled ultimately results in a dampening of spatial variability (Korner, 2003). An existing alternative is to scale foliar biomass calculations from either species-specific DBH-based (diameter at breast height) forest inventory or remotely-sensed NDVI (normalized differential vegetation index) estimates (as a proxy for leaf area index, LAI, the m^2 of leaves per m^2 of ground area), but these methods still require spatial extrapolation (for the inventory) or interpolation (for the satellite data at a sub-grid scale) which are ultimately ground-truthed through sampling with the litter trap-based method (Asner et al., 1998; Hashimoto et al., 2011). Therefore, the strategy in this analysis was to collect samples from litter traps in representative locations based on LiDAR estimates of cover and height distributions taken immediately prior (< 1 year) to collection initiation. This LiDAR distribution was related to plant biomass, from which foliar biomass can be calculated.

Because foliage is recycled rapidly, litter fall represents a pathway between aboveground and belowground biomass (Sayer et al., 2007). Although the biogeochemical processes of litter decomposition are well known, our ability to characterize it over a large spatial extent is limited. Spatially explicit characterizations of litter decomposition need to include heterogeneity in leaf turnover rates and leaf masses, which are in turn based on species, phenotype, stand age and stage in development, and environmental conditions,

such as moisture and temperature, all of which relate to or drive the net primary productivity (NPP) of the forest system (Lusk, 2001). In the case of WS1, an approximately sixty year old stand in the Western Cascades Range in the Pacific Northwest, it was found that current stand composition is a mix of hardwoods (about 20% of forest biomass) and conifers, although within watershed heterogeneity is high. Composition on sample plots ranges from nearly 100 percent conifers (*Pseudeotsuga menziesii* planted on the site intentionally) to 97 percent hardwoods (on dense hardwood sites, *Prunus emarginata* may dominate; seasonally, *Acer circinatum* also provides extensive foliar biomass). By definition, deciduous trees abscise their leaves annually, whereas annual turnover on the conifers is approximately 20 % (Lusk, 2001). As compared to the rate of turnover in the larger biomass components (bole, branches), these rates are relatively rapid (Harmon et al., 2001).

Litter fall has direct, short-term relationships to other ecosystem C processes, notably decomposition and soil respiration (Harmon, 1991). This relationship is generally represented by non-linear saturation functions that depend on microbial biomass and leaf composition. Further, positive feedback exists between litter fall and microbial biomass because litter provides substrate for microbes (Meetenmeyer, 1978). This in turn increases rates of soil respiration, but also increases the rate by which this substrate is consumed (Harmon et al., 2001; Meetenmeyer, 1978; Finzi, 2001; Lindahl et al., 2007). Further, on a macroscopic level, increased litter fall can also alter soil pH, soil water

content, and soil temperature, which may indirectly impact soil respiration and site fertility (Meentemeyer, 1978).

It has been suggested that litter flux may increase in the future if increased atmospheric carbon dioxide (CO₂), temperature, or rainfall occur (Harmon, 1991; Sayer et al., 2007; Nabuurs et al., 2007). Experiments conducted using the Free Air Carbon Enrichment Facilities (FACE) have revealed that under an artificially elevated CO₂ regime, litter fall increased by twenty-five percent (Delucia et al., 1999). Another study at FACE revealed that when temperature was independently increased without a simultaneous increase in carbon, litter fall increased by 0.2 to 0.7 Mg/ha/yr). However, in modeled experiments, it was shown under induced climatic stress (temperature, carbon) that litter C concentration did not change, nor did the relative concentration of C in soil organic matter (Delucia et al., 1999). Because of litter's role in ecosystem function, it is desirable to mitigate the effects of changes in foliar C concentration, which may be detrimental to photosynthetic processes and lead to functional adaptations to increased C. For example, plants adapt to increased C by changing the allocation of other nutrients amongst plant components. (Lindahl et al., 2006). In the soil, decomposition may be limited even in the context of increased C because a decrease in microbial rates occurs as substrate is used up, thus maintaining a stable soil C concentration (Finzi, 2001; Delucia et al., 1999). Additional C may increase site productivity immediately, but ultimately fosters mechanisms that lead to stability and decreased productivity. Furthermore, changes in temperature directly affect litter distribution, and this in turn affects site productivity. Meentemeyer showed

that litter decomposition rates relate exponentially to temperature increases in cool or moist climates, such as those in the Pacific Northwest, no matter the litter composition (Meetenmeyer, 1978). In short, increasing temperatures, increased C concentrations, and changes in stand composition all affect the litter flux, and one another.

It is thereby essential to understand litter fall spatially in order to identify critical areas in which future changes may have the greatest impacts on ecosystem function. Spatial analyses of litter flux are few, although studies of litter dynamics are fairly numerous (Sayer et al., 2007; Meetenmeyer, 1978; Lindahl et al., 2006; Bartha, 2010, e.g.).

Weider's (2009) research on litter fall spatial patterns assessed average litter values with relation to external resource gradients on a large scale using remotely-sensed and simulated information and found that it was positively correlated with rainfall and phosphorus availability; litter decomposition has been shown to relate to light availability and litter density (2009). On an extremely fine scale (< 1m), Bartha et al. (2010) assessed the clustering of litter within a vegetation plot and found effects related to local fauna.

However, on the meso-scale (sub- basin), litter fall spatial patterns may be influenced significantly by factors on multiple scales both in space and time. If this is the case, then stand effects may potentially have an enormous impact on the accounting of a landscape scale carbon budget (Townshend, 2011; Weider et al., 2009). The goal of this analysis was to quantify litter fall and its relationship to other biotic metrics on one mountainous catchment. To do so, I answered the following questions: (1) What is the annual flux of litter on this catchment? (2) To what extent are aboveground net primary productivity

(ANPP) and other stand biometrics as measured in the most recent re-measurement (2001-2007) reflected in litter fall? (3) What is the spatial distribution of litter flux on this catchment and (4) what effects does it have on ecosystem functions in the C cycle?

6.2 Materials and Methods

Study Area: Watershed 1 (WS1) is a 96 hectare catchment in the H.J. Andrews Experimental Forest (HJA) in the western Cascades Range of Oregon. The HJA is part of the National Science Foundation's Long Term Ecological Research (LTER) program and provides a wealth of data and resources for spatially and temporally explicit studies of ecosystems, such as the C-balance study of which this project is a part. WS1 was originally part of an experiment regarding the effect of regeneration cuts on stream flow and sediment fluxes. Between 1962 and 1966, the stand was clear-cut, burned, and replanted with four attempts at seeding (aerial and three row-re-plantings of *Pseudotsuga menziesii*). The forest community on the site is currently dominated (70-80 %) by *Pseudotsuga menziesii* and *Tsuga heterophylla* of approximately 50 years of age. This site has steep (> 100% slopes) and distinct north-south aspects that result in both diurnal and seasonal patterns in radiation. The mean annual temperature is 9.7 C and variability in temperature is greater on ridges than in valleys due to a phenomena of "cold air pooling" caused by temperature inversions causing a downslope movement of cool air in the evenings. Mean annual precipitation is 2300 mm, typical for the region. Soils on WS1 are derived from basaltic and andesitic parent material, exposed cap-rocks and talus slopes are common, although their origin (glacial or volcanoclastic) is not known. Soil moisture gradients have also been identified on this watershed, and as a general rule south-facing slopes are drier with shallower soils than north-facing slopes due to both radiation today and greater surface damage following harvest fifty years ago.

Litter Collection and Analysis: Litter was collected from sixteen plots on WS1. These particular plots have been intensely subsampled for other analyses (Peterson and Lajtha, 2012). The intensely sampled plots were selected to represent the distribution of "cover times height" as measured by LiDAR reconnaissance in 2008. This metric was selected because it was believed to be a good proxy for biomass distribution (Lefsky et al., 2005). Litter collections were conducted for the years of 2009-2011, beginning with collection on 12 August 2009 and ending with collection on 11 August 2011. The litter traps were located just outside the perimeter of the plots in order to avoid interaction with the current vegetative studies on the plots. Each litter trap was square with edges of 43 cm by 43 cm (1.849 m²). The ground-truthed plot sizes are 250 m²; the aerial plot sizes range down to 125 m² due to steep slopes. Five collections of the litter traps were made in the first year. In the second year, four collections were made. Litter was collected wet. Trap status, as well as any anomalies in trap content (bark, logs, etc.) were recorded. For most collection periods, fine and coarse litter were brought back to the lab and separated with a 12 inch hardware cloth with 12.5 cm openings. To sieve the materials in this manner, a sample was dumped onto the screen and gently shaken and lightly rubbed to pass the small pieces through the screen. After the separation, twigs which slipped through the screen were returned to the coarse fraction and the needles stuck to the coarse objects were rubbed free and placed in the fine fraction. After the separation wet weight is recorded, the sample was placed in a labeled paper bag and oven-dried. Upon reaching a stable weight in the oven, the dry weight is recorded. A paper bag stapled and labeled like

the sample bags is used to tare the bag weight out of the gross weight. Some traps were damaged between collections, namely, traps on plots 419, 518, and 522. Litter mass accumulated for these plots was only recorded for non-damaged traps and a note was taken on the number and extent of damage.

To calculate dry mass of leaves (in Mg) per hectare per "period" (interval between collections), three conversion factors were created following the form of :

$$\text{Mass per Hectare} = (1849\text{cm}^2 * \text{Number of Traps} * \text{Mass}) / 100000000$$

Where Mass represents the dried mass of leaves. The rationale for creating three conversion factors was to account for the set of plots on which only three or four trap samples were valid; on these plots the expansion factor must naturally be greater.

For the first year, leaf collections were precise to 365 days for almost all plots. Thus, the sum of the collected masses per hectare over the course of that year represented the annual collection. For a few plots, one additional day was included in the final collection period, and the influence of that period on the sum was weighted by a conversion factor of 0.9696. For one plot (518), 2011 data was damaged for two collection periods, one in the late summer and one in the fall. Mean values from the other two collection periods (early summer and winter) were weighted to the appropriate amount of days and used as a proxy for the missing measurements. This greatly decreases the accuracy of this plot. For another plot (419), large chunks of bark and rotted log were found in the sample

during one re-measurement, because these are still a type of litter, it was not removed from analysis.

Biometric correlates: To compare litter fall and stand biometrics, we calculated the biomass per unit area (in Mg/ha), aboveground net primary productivity (annual change in mass plus mortality (Mg/ha /Yr), percent hardwood (%), stem density, and basal area per hectare (m²/ha) for over-story and mid-story trees. Over-story trees on this site are *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Taxus brevifolia*, *Prunus emarginata*, *Thuja plicata*, *Castanopsis chrysophylla*, *Acer macrophyllum*, *Arbutus menziesii*, *Rhamnus purshiana* and *Lithiocarpus densiflorus*. To calculate these biometrics, we used long-term inventory data of tree diameter at breast height (DBH) collected over seven re-measurement periods (1980, 1984, 1988, 1991, 1995, 2001, and 2007) on 133 established vegetation plots (Halpern and Means, 2004; Halpern and Dyrness, 2010). Plot areas were calculated using aspect and slope-adjusted elliptical plots geo-referenced to scanning LiDAR reconnaissance own in 2008. Site and species-specific allometric equations were specified by the Pacific Northwest Biomass Component Equation Library (PNBCL) were used to calculate biomass from DBH following a power-law scaling form (Halpern and Means, 2004). These allometries were validated against a second set of allometries presented by Lefsky et al. (2005). Annual change in mass plus mortality is aboveground net primary productivity (ANPP) as defined in Acker et al. (2002). When full-extent maps for the current period are used as a background for litter fall discussion, the maps were created based on a regression of LiDAR measured "cover" and height to the on-the-

ground biomass calculations. In comparative analyses, plot data is either used at the plot scale or extrapolated via kriging, with the caveat that neither of these methods is sufficient for characterizing variability in complex terrain where plots are highly variable and the assumptions of kriging may not be met. Metrics were calculated over all time periods due to necessity for other research; however, in this study we only include metrics from stand initiation (1980) and the most current interval (2001-2007, 2007 for inventory metrics) due to the rationale that spatial patterns in litter would likely be the result of either original stand composition or existing stand composition.

Statistical Methods: To calculate the gross flux of litter on the site, we computed the empirical probability distribution of litter fall in Mg/ha on the watershed. We used a Monte Carlo technique to generate 96 random variates from this distribution 1000 times. The Monte Carlo technique was part of the standard library in MatLab 2010. The sum of each set of these variates is an estimate of potential gross flux. We calculated summary statistics for these estimates in order to develop a measurement of confidence around our estimate.

To determine relationships between litter fall and stand biometrics, I conducted simple linear and multivariate regressions. I expected that the relationship between litter fall biomass and vegetative parameters would be linear because in this developed stand leaf biomass represents a proportion of total tree biomass. Regression coefficients were assessed by the R^2 criterion. The set of stand biometrics is named **X** and contains the measurements of ANPP in 2007, ANPP in 1980, aboveground overstory biomass in 2007,

aboveground overstory biomass in 1980, hardwood biomass in 1980, hardwood biomass in 2007, percent hardwood in 1980, percent hardwood in 2007, herbal biomass in 2007 (small shrubs included), and basal area per hectare in 2007. Measurements from 1980 were used as an indicator of stand development exclusive of site characteristics; were litter fall to be correlated with both 1980 and 2007 biometrics, the actual driver of the variability in litter fall might be related to a site feature (topographic) consistently expressed in the metric over time. To test for normality, the Shapiro-Wilk test was used (Shapiro and Wilk, 1965). Covariance in the planar regression was assessed by calculating the covariance matrix (cov \mathbf{X}). High values of covariance would indicate that two metrics were sharing explanatory power. Shared explanatory power would need to be recognized by an interaction term in the model. A model was generated using the MVP regression method, a method of general linear modeling (GLM) specific to models driven by two (largely) independent factors. This model looked at combinations of uncorrelated explanatory biometrics versus litter directly measured on the sixteen plots.

Geo-statistical Methods: To generate a mapping of the spatial pattern of litter fall, we applied the appropriate model calculated with the techniques detailed in 2.4 to the 133 re-measurement plots from forest inventory in 2007. This modeled data was joined to plot data in ArcGIS v. 9.3.1 and then ordinary kriging was conducted using the Geo-statistical Analyst tools in ArcGIS v. 9.3.1. Kriging is a method of geo-statistical interpolation that assumes spatial autocorrelation without isotropy. The Geo-statistical Analyst tool tests for patterns of spatial autocorrelation and isotropy in order to ensure that assumptions

required for adequate predictive maps are met. The model was applied to the plots prior to the interpolation (rather than applied to interpolated spaces of the model parameters) in order to separate the error associated with the model from the error associated with the kriging. We also included the results from a post-kriging model application to show the differences between the techniques. Error in kriging is associated with the neighbor search radius and distribution of observed points. Uncertainty in the kriging technique was quantified using the Root Mean Squared Error (RSME) statistic and its normalized form, the Root Mean Squared Standardized (RMSS) statistic, which is calculated with a native cross validation technique in ArcGIS v. 9.3.1's geo-statistical wizard. The wizard uses a Monte-Carlo simulation to remove one training point from the data set and then conducts kriging on the remaining points, repeating this process for all the training points and calculating the difference between the expected simulated point from the full model and reduced simulated point from the cross-validation for that location. The root mean squared difference of these points is a measurement of the error inherent in the kriging. ArcGIS 9.3.1 was also used to measure the existence and degree of clustering in the modeled litter. Clustering was quantified by the semi-variogram as well as the Getis-Ord G_i^* statistic. This statistic detects local "hot spots" where a given Z-value (here, litter fall) is elevated within a small lag distance, h .

6.3 Results

Results were collected using a custom field notes sheet and tabulated in Microsoft Excel. Comments regarding litter composition are available in the raw data via the open data access at <http://andrewsforest.oregonstate.edu/data> under study code TW006.

I calculated the annual flux of litter on the catchment and found that it was litter flux is 222.24 ± 8.91 Mg (per hectare annual litter flux is 2.32 ± 0.90 Mg/ha/Yr). To further clarify this flux within the year, I plotted the temporal pattern of litter fall (grey) relative to the mean (red) over the two year period using the Sparklines package for Microsoft Excel (Tufté, 2009) (Figure 32). Sparklines are simplified temporal trajectories used to visualize how time series values (here, in gray) relate to a mean (in red). The distribution of litterfall on this watershed is right-skewed normal. The statistical parameters for this distribution without the removal of outliers are mean= 8.91, variance = 0.91, skew= 2.073 and kurt = 11.67 (Figure 33).

Plot ID	Year 1	Year 2	Mean	Sparkline	ANPP
321	2.173	2.426	2.299		3.21
109	1.625	1.163	1.424		3.61
108	2.025	1.750	1.888		4.48
526	1.197	1.235	1.121		5.05
102	1.695	1.429	1.562		6.18
521	3.243	2.006	2.624		6.45
318	1.762	1.830	1.796		6.68
316	1.547	1.631	1.589		7.87
603	2.176	2.731	2.453		8.95
422	2.301	2.491	2.396		9.24
103	2.069	1.806	1.938		9.32
419	3.639	1.163	4.114		12.08
607	2.814	2.150	2.482		12.65
425	3.638	2.418	3.028		12.95
605	2.211	2.565	2.388		13.50
518	5.179	3.489	4.333		17.44

Figure 32. Mean Litter Fall, Sparklines, and ANPP for the Two Years of Litter Collection by Plot. Plots are arranged from least mean litter fall to greatest.

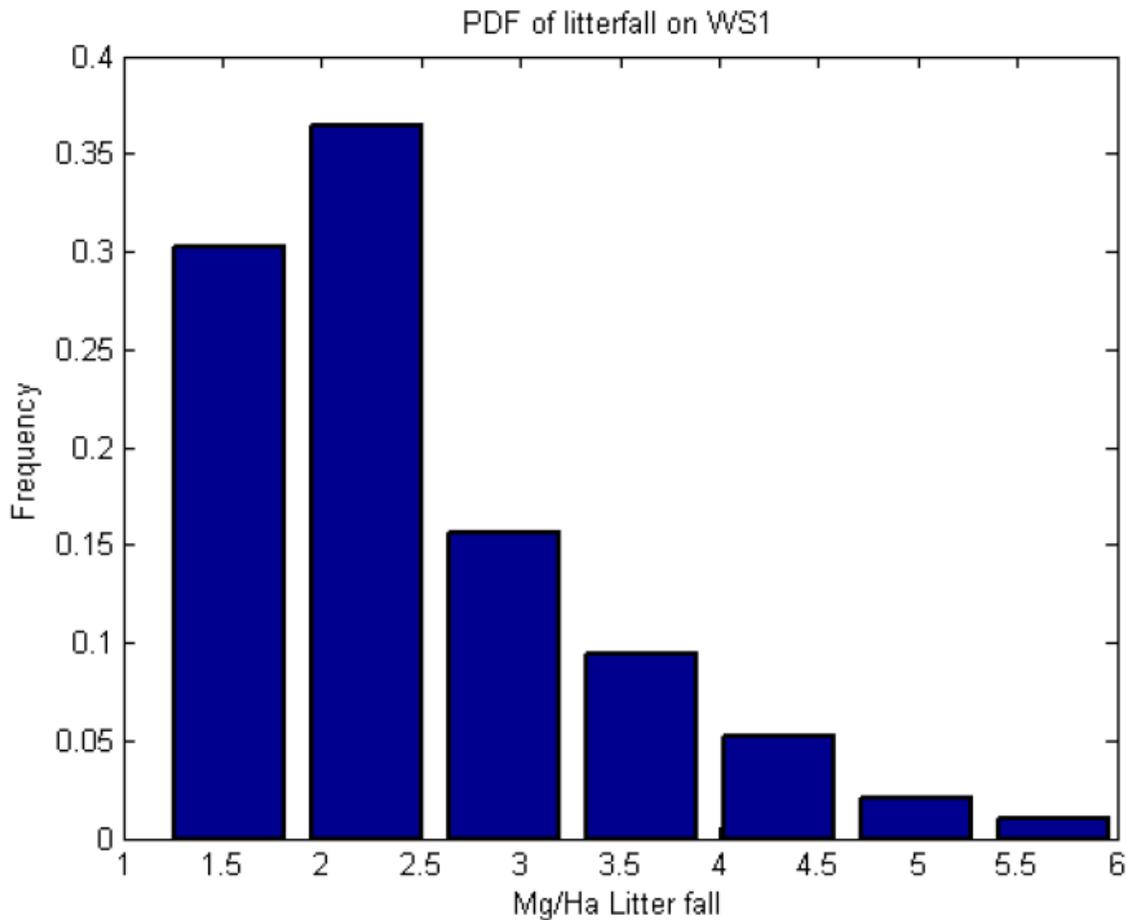


Figure 33. Probability distribution of litter fall (Mg/ha/yr)

To address the spatial distribution of litter on the watershed, ArcGIS 9.3.1 was used to create an overlay image of collected litter (average between year 1 and year 2 of collection) and LiDAR-extrapolated biomass from 2007 re-measurement. The distribution of biomass is bimodal; above 40 Mg/ha, biomass follows a normal distribution, but when biomass is less than 40 Mg/ha, it follows an exponential distribution. The mean biomass for the whole watershed is 118 Mg/ha, but the mean

biomass for the normally distributed area is 218 Mg/ha. Low-biomass was identified spatially using a binary classification based on the LiDAR extrapolated map of biomass (Figure 34).

LITTER AND BIOMASS

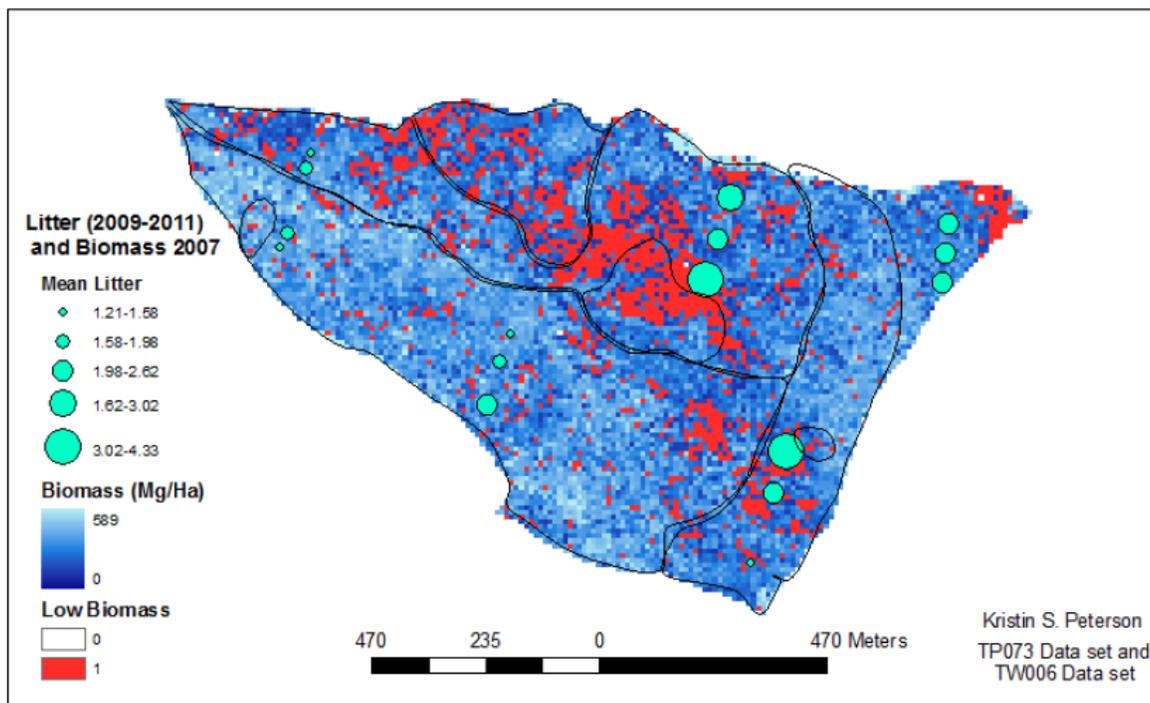


Figure 34. Spatial distributions of litter (Mg/ha/yr) and biomass from 2007 (Mg/ha) on WS1. The thin black lines denote the harvest units. The red areas are the lowest 1% of biomass. The teal circles represent the Mg/ha/yr litter fall from the 2010-2012 collections.

To relate the litter flux to biotic attributes, simple linear models and non-parametric models were fit to several potential associated variables versus litter mass. I tested results

for several variables, including initial (1980) biomass, initial percent hardwood (1980), initial hardwood biomass (1980), hardwood biomass in 2007, percent hardwood in 2007, aboveground net primary productivity (annual between 2001 and 2007), basal area (2007), biomass in 2007, stem density in 2007, and biomass of herbaceous vegetation in 2007. The only significant correlate found was ANPP between 2001 and 2007, with $R^2 = 0.65$ and $p < 0.001$. The purpose of creating this model was to create an interpolation tool that could be used to regulate the spatial distribution of the long term permanent plot data to facilitate kriging. The parameters above were then altered to only include those temporally cohering to the litter fall measurements (i.e. previous measurements of ANPP or biomass were not considered). A stepwise regression procedure was run in MatLab (Mathworks, 2010) to search for valuable parameters, and percent hardwood, basal area per hectare (BAHA) and ANPP were identified.

To quantify the uncertainty in the model, we addressed three issues. First, the error within the model. Second, the uncertainty inherent in the extrapolation (spatial) and third, the uncertainty in the ANPP estimates themselves, all of which are derived metrics from a set of raw data. For the error within the model, error (MSE) = 3.0764. To address the uncertainty in the extrapolation, a cross validation procedure was conducted on the kriging by randomly removing ten percent of points from the kriging and exercising the fit without that point. This procedure was repeated multiple times in order to generate the RMSE. To qualify and quantify the uncertainty within the estimates themselves we note that there are two sources of error for this calculation. First, error in the measurement of

DBH during the inventories or mis-identification of species may be propagated. This error we cannot quantify, but it could be large. Second, error in the allometric equations may also exist. This error was quantified in Lutz (2006) for all species on WS1. Allometric fits were greater than $R^2 = 0.9$. However, many of these fits were linear fits to a log-transformed function, and may not adequately represent trees in the tails of the distribution. We did validate Lutz's equations using those in Lefsky (2005) and found that estimates were significantly different ($p < 0.001$); however, the Lefsky equations included height as calculated by LiDAR, which in this case was our independent variable, and therefore they were not suitable for this analysis. Further, those equations were calibrated for all of Western Oregon, whilst those in the PNBCL are specific to only the western Cascades range, and in some cases, for young stands. Third, error in the temporal structure of this model may be inadequate; the model is fit to an annualized estimate of ANPP between 2001-2007; actual litter collection occurred between 2009 and 2011.

We created two kriged maps of litterfall on the catchment. In one map, we first used the regression model to extrapolate to all 133 plots and then conducted kriging to extrapolate to the entire watershed; in the second, we kriged directly from our data, although they were not well-distributed in space. The goal of the two kriged maps was to visualize the difference between extrapolation methods; because we had few samples that were not well-distributed, comparisons of maps provided a valuable visualization of how using statistical methods only versus a combination of statistical and empirical methods influences conclusions (Figure 35).

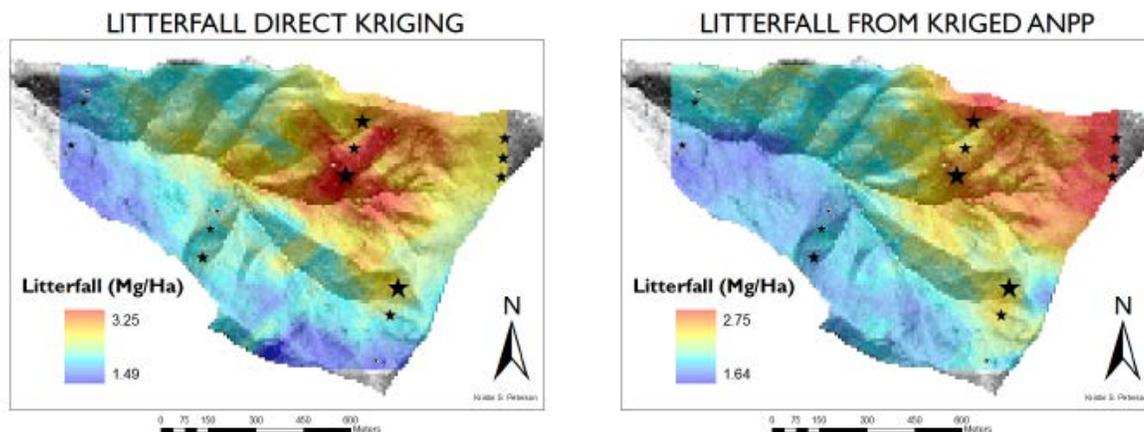


Figure 35. Kriged annual flux of litter on the LiDAR Bare Earth map. On the right, the model is used to increase the point density of the map; on the left, only the field measurements were used. There is increased spatial heterogeneity in the left map.

To quantify the uncertainty in the kriging, we calculated the RMSE, RMSS, and average standardized error (ASE) for the measured and modeled data versus the RSME for kriging the same parameters with only the measured data (RSME = 0.8567, RMSS = 0.9851, ASE= 0.0172 Mg/ha for both; RSME = 0.8123, RMSS = 1.1, and ASE = 0.6718 Mg/ha for measured only). Kriging parameters were nugget = 0.68 Mg/ha, sill = 0.121 Mg/ha, and range was spherically increasing. When the interpolation was not used, vacancies in the distance distribution prevented a robust choice of semi-variogram shape.

6.4 Discussion

The total annual flux of litter on this catchment is 222.24 ± 8.91 Mg, per unit area (Ha) the annual litter flux is 2.32 ± 0.90 Mg/ha/Yr. This was calculated at the hectare resolution using the empirical distribution. Should the mean litter flux be scaled up to the whole catchment, an estimate of 224.61 ± 85.39 Mg/ha is achieved (not significantly different at $\alpha = 0.05$). However, should the values from either year 1 collections or year 2 collections be averaged and scaled up, the results differ significantly from that of the empirically estimated and temporally averaged (year one, $p = 0.0725$; year two, $p = 0.0251$). In this situation, then, scaling up from the mean versus scaling up using an empirical distribution did not make a significant difference and this is even using a mean already dampened by temporal averaging. Over the spatial extent, mean- based extrapolations without the temporal averaging could result in inconsistent estimates.

The maps indicate that the spatial distribution of litter fall is indirectly related to elevation, although this did not come out in regressions against topographic correlates. High litter fall is found on a precipice like area in the northeastern corner of the watershed that is prominent along the ridgeline, even outside the extent of WS1. Although no correlation between litter fall and elevation ($p < 0:001$) existed, based on the conclusions in Peterson et al. 2012, indirect effects of topography may be generated by species-specific responses in productivity, particularly on the hardwood-dominated drier soils found at higher elevations. Initially established by hardwoods, in the current stand this area has increased

ANPP due to the release of the formerly suppressed over-story (Peterson and Lajtha, 2012). Increased productivity, and therefore turnover, at higher elevations is related to the topography of the catchment by the vegetation (and harvest) history. Additional support for this hypothesis is that seed-in is more likely due to proximity to neighboring stands. Many of these "non-plan table rocky areas" precluded crop tree (*Psuedotsuga menziesii*) establishment following harvest and hardwood establishment immediately post-harvest was rapid. Specifically, litter fall is highest in the north-eastern corner of the watershed where crop tree release has recently occurred and vine maples grow rampantly in new sunlight and along "transect four," which contains several plots of almost entirely composed of *Prunus emarginata*, thus facilitating a dense, rapidly changing canopy. For example, plot 423, located between litter plots 422 and 425 (3.1) contains 84% *Prunus emarginata* with an average DBH of 12 cm. Plot 422 contains 60% mixed-hardwood, including *Acer macrophyllum*, *Castanopsis chrysophylla*, *Lithiocarpus dendroctinus*, and *Prunus emarginata* whereas plot 425 is exclusively *Prunus emarginata* (55%) and crop-tree, *Psuedotsuga menziesii* (45%). These plots are both some of the most productive on the watershed and have notably high litter fall. The densest (defined here as most basal area per hectare) stands on WS1 are found in low-elevation, successful *Psuedotsuga menziesii* dominated areas near the watershed's outlet and on a concave slope in the mid-basin region. For example, litter plots 102, 109, 316, and 318 are 87%, 93%, 71% and 93% coniferous, with the plots on the first transect containing only *Psuedotsuga menziesii* and those on the third containing a mixture of *Psuedotsuga menziesii* and *Tsuga heterophylla*. These areas achieved initial success in biomass accumulation following harvest due to

deep, moist soils on the north-facing slope and successful aerial seeding. Currently, canopy closure is leading to self-thinning in these areas, such that productivity is low. A large portion of the included mortality in the ANPP calculation was added in during the 1995-2001 re-measurement period, when self-thinning was at its peak. Now the stand is less dense, but the standing trees are thin and their growth rates are slow. Litter fall on these plots is reduced. From this we conclude that the spatial heterogeneity in productivity to a strong extent drives the spatial heterogeneity in litter fall, although high variance exists due to the temporal relationship between early hardwood presence and later releases of crop and flushes of productivity.

Despite our expectations, the greatest magnitude of measured litter mass was found in the area of "lowest biomass". No notes in trap collection indicate that this is an anomaly due to collection of large woody material. This finding directly opposes the findings of Grier et al. (1977) who noted that biomass was correlated with litter in old-growth forests, and specifically in watershed 2 (WS2), WS1's paired "neighbor." This could be an artifact of the allometric calculation that lead us to underestimate biomass on plots with small trees and shrubs. Biomass was assessed only for overstory and midstory trees, such as *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Prunus emarginata*, and *Acer macrophyllum*. Two important, but missing, small trees or large shrubs are *Rhododendron macrophyllum* and *Acer circinatum*. Both of these species regenerate early (within 10 years) following harvest and have extensive foliage, and *Acer circinatum* is deciduous. Thus, these species may also contribute significant litter fall to the forest floor, but we would not have

accounted for them in our biomass estimates. Consequently, we expect that these species would be found more on low-biomass, dry sites rather than on high-biomass, moist sites due to previous evidence of their success immediately post-harvest on dry soils located in the up-basin region. Or, the high litter in areas of low-biomass conflict may result from differences in developing stands versus older parts of the stand. Since the stand did not establish homogeneously, younger parts of the stand may have greater productivity despite having less trees because their growth rates are quicker.

These findings may have significant impact on the estimates of decomposition and nutrient availability in a stand; local and momentous fluxes of litter fall may be significantly greater than a watershed mean, resulting in a non-uniform spatial distribution and peaks in ecosystem processes over time. Further, where decomposition is increased, nutrient patterns may differ systematically, resulting in small-scale variability with yet un-quantified impacts in this stand. Although the magnitude of the annual litter flux, around 2.32 Mg/ha, is small compared to stand mean biomass (118 Mg/ha) but significant when compared to low-biomass areas' biomass (< 41 Mg/ha). Significant changes to the site at this scale might lead to different futures than predicted by aggregation-based estimates.

Calculations of the annual litter flux for a small catchment is a key component in a carbon budget and it is small but highly variable. This study showed that annual litter fluxes have significant spatial variability, even within a small catchment. This variability

was attributed to productivity and stand development, which may be integrating and manifesting the historical and topographical heterogeneity that drive ecosystem scale variability. Litter fall variability within a developing stand may be governed by multiple factors. A map of litter fall using the relationships we obtained through regression was compared to a map generated using kriging and I assessed the impacts of extrapolation order for modeling litter flux. Due to the high variability in the litter flux even over a small spatial scale, attention must be paid to sampling and extrapolation in order to achieve an accurate estimate for a C budget.

CHAPTER 7

CONCLUSION

On complex terrain, ecosystem processes and soil carbon stores are linked through both abiotic and biotic factors. Topographic attributes unique to montane environments, such as potential heat loading due to aspect and upslope contributing area, and biotic heterogeneity that emerges from this complex topography, results in SOC distribution and DOC export that is not directly attributable to any easily measurable gradient or biological process. However, stand structure and forest development follow trajectories that can be interpreted in light of belowground resource availability so that we can better understand how, where, and when C was distributed in the complex landscape.

In this dissertation, I drew a primary conclusion and four subsidiary conclusions. The primary conclusion of this dissertation is that stand structure, and particularly the stand structure following disturbance, is a key for exploring ANPP and its effects in complex terrain. Even on a sub 1 square kilometer scale watershed in what was intended to be an even-aged, monocultural stand, ANPP and stand structure are highly variable in both space and time. My subsidiary conclusions are as follows. First, that a common method of measuring productivity at a particular time (which is often used when relating aboveground productivity to belowground resources) is inaccurate in complex terrain because stand development proceeds along multiple trajectories and a new method, such as the maximum likelihood method we propose, may better indicate belowground C than the traditional method. Second, that "aspect" in the general sense of being a north-facing or south-facing slope, is the most important topographic feature in a complex terrain, as it

influences the potential heat, moisture, soil depth, soil type, slope, and possible initiating biota on a site; however, that because aspect is a fairly weak, vaguely defined binary variable, more complex metrics, such as Beer's Index or Horizon Angle, which include many of the attributes resulting from "aspect" are the most useful topographic metrics for classifying ANPP. Third, that the methods and distribution of DOC sampling regimes indicates various DOC attributes (presence, extractable, export) and each attribute is related to different factors in complex terrain, so that the method of sample collection impacts the conclusions we draw about influencers on DOC. Finally, I conclude that soil C dynamics is related to a complex of aboveground and belowground processes and that this study was too limited in scope to fully explore those interrelationships. Future research needs to include information about species, microclimate, and decomposition rates.

The implications of this research for transformational science are that in complex terrain, knowledge of topography alone is not enough to make adequate predictions about soil C storage or export. Nor do biotic trajectories fully describe the relationships that certainly exist between the site and C both above and belowground. However, stand structure is a critical feature of complex terrain, and stand structure is not homogeneous. In order to better our predictions for the anthropocene era, it is critical that the importance of the forest, particularly its development since establishment, be quantified in such a way that our selection of time, interval, or method do not undermine our predictions..

BIBLIOGRAPHY

- Aber, J.D. 1992. Nitrogen cycling and nitrogen saturation in temperate forest ecosystems. *Trends in Ecology and Evolution* 7, 220-223.
- Abrams, M.P., D.G.Sprugel, and D.I. Dickmann. 1985. Multiple successional pathways on recently disturbed jack pine stands in Michigan. *Forest ecology and management* 10,31-49.31-48.
- Acker, S.A., McKee, W.A., Harmon, M.E., and J.F. Franklin. 1998. Long-term research on forest dynamics in the Pacific Northwest: a network of permanent plots. Pp. 93-106 in F. Dallmeier and J.A. Comiskey, eds. *Forest biodiversity in North, Central, and South America, and the Caribbean: Research and monitoring*. UNESCO, Paris.
- Acker, SA., C.B. Halpern, M.E. Harmon, and C.T. Dyrness. 2002. Trends in bole biomass accumulation, net primary production, and tree mortality in *Psuedotsuga menziesii* forest of contrasting age. *Tree Physiology* 22, 213-217.
- Adair, E.D. W.J. Parton, S. Del Grosso, L. S. Whendee, M.E. Harmon, S.A. Hall, I.C. Burkes, and S.C. Hart. Simple three pool model accurately describes patterns of long-term litter decomposition in diverse climates. *Global Change Biology*, 14:2636-2660.
- Adams, P. W. A.L. Flint, and R.L. Fredriksen.1991. Long term patterns in soil moisture and revegetation after clearcut in a douglas-fir forest in oregon. *Forest Ecology and Management*, 41:249-263.
- Aerts R. and De Caluwe H. (1997) Nutritional and plantmediated controls on leaf litter decomposition of Carex species. *Ecology (Washington, DC)* 78(1), 244–260.

Allen, T.F.J. and Hoekstra, T.W. 1990. The confusion between scale-defined levels and conventional levels of organization in ecology. *Journal of Vegetation Science* 1. 5-12.

Alexander, H.M., M.C. Mack, S. Goetz, S. Pieter, A. Beck and E.F. Belshe. 2012. Implications of increased deciduous cover on stand structure and aboveground carbon pools of Alaskan Boreal Forests. *Ecosphere* 3(5), 45-64.

Amundson, R. 2001. The carbon budget in soils. *Annual Review of the Earth and Planetary Sciences* 29, 535-562.

Andersen, H., R.J. McGaughey, W.W. Carson, S.E. Reutebach, B. Mercer, and J. Allan. 2004. A comparison of forest canopy models derived from lidar and insar data in a pacific northwest conifer forest", *International Archives of Photogrammetry and Remote Sensing*, 211-217.

Archer, S. 1995. Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstructing the past and predicting the future. *Ecoscience* 2(1), 83-99.

Austin, M.P. and J.L. Belbin. 1981. An analysis of succession along an environmental gradient using data from a lawn. *Vegetatio* 46, 19-30.

Baas, P., J.E. Mohan, D. Markewitz, J.D. Knoepp. 2012. Nitrogen cycling "hotspots" : An approach for watershed scale assessments. Poster presented at the Long –Term Ecological Research All-Scientists Meeting. Estes Park, Colorado. September 8-13, 2012.

- Bailey, J.D., C. Mayrsohn, P.S. Doescher, E. St. Pierre, and J.C. Tappeiner. 1998. Understory vegetation in young and old Douglas-fir forests of Western Oregon. *Forest Ecology and Management* 112(3), 289-302.
- Bakker, J.P. 1989. *Nature Management by Grazing and Cutting*. Geobotany 14, Kluwer Academic Publishing, Dordrecht.
- Baldock, J.A. and J. O. Skjemstad. 2000. Role of the soil matrix and minerals in protecting natural organic materials against biological attack. *Organic Geochemistry* 31, 697-710.
- Bardgett, R.D. and Wardle, D.A. 2010. *Aboveground-belowground linkages: Biotic interactions: Ecosystem Processes and Global Change*. Oxford University Press, Oxford, UK.
- Bazzaz, F.A. and T.W. Snipe. 1987. Physiological ecology, disturbance, and ecosystem recovery, In Schulze, E.D., Zwolfer H. *Potentials and limitations of Ecosystem Analysis*. Ecological studies 61, Springer, Berlin. Heidelberg, 203-227.
- Beare, M.H., M.L. Cabrera, P.F. Hendrix, D.C. Coleman. 1994. Aggregate-protected and unprotected organic matter pools in conventional and no-tillage soils. *Soil Science of America Journal* 58. 787-795.
- Belsky, A.J. 1986. Revegetation of artificial disturbances in grasslands of the Serengeti national park, Tanzania: Five years of successional change. *Journal of Ecology* 74: 937-951.

Benninghoff, W.S. and A.S. Benninghoff. 1985. Wind transport of electrostatically charged particles and minute organisms in Antarctica. In *Antarctic Nutrient Cycles and Food Webs* (eds. Siegfried W.R. et al.), pp. 592-596. Springer, NY.

Berendse, F., R. Aerts and R. Bobbink. 1993. Atmospheric nitrogen deposition and its impact on terrestrial ecosystems. Pages 104-121 in C.C.Vos and P. Oudam, eds. *Landscape Ecology of a Stressed Environment*. Chapman and Hall, London, England.

Berntsen, C.M. and J. Rothacher. 1959. *A Guide to the H.J. Andrews Experimental Forest*, pp. 1-21.

Berg B. and Wessen B. (1984) Changes in organic-chemical components and ingrowth of fungal mycelium in decomposing birch leaf litter as compared to pine needles. *Pedobiologia* 26, 285–298.

Berg B., Muller M., and Wessen B. (1987) Decomposition of red clover (*Trifolium pratense*) roots. *Soil Biol. Biochem.* 19, 589–594.

Berntsen, C.M. and J. Rothacher. 1959. *A Guide to the H.J. Andrews Experimental Forest*, 1-21.

Bezemer, T.M., M.T. Fountain, M.T.Barea, J.M.Christensen, S. Dekker, S.C. Duyts. 2010. Divergent composition but similar function of soil food webs of individual plants: plant species and community effects. *Ecology* 91, 3027-3036.

Biederbeck, V.O., H.H. Janzen, C.A. Cambell, and R.P. Zentner. 1994. Labile soil organic matter as influenced by cropping practices in an arid environment. *Soil Biology and*

Biochemistry 26. 1647-1656.

Boone, R.D. Light-fraction soil organic matter: origin and contribution to net nitrogen mineralization. *Soil Biology and Biochemistry* 26, 1459-1468.

Bond, B. 2003. Hydrology and ecology meet- and the meeting is good. *Hydrological Processes* 17. 2087-2089.

Borgegard, S.O. 1990. Vegetation development in abandoned gravel pits: Effects of surrounding vegetation, substrate, and regionality. *Journal of Vegetation Science* (1): 675-682.

Bormann, B.T. and R.C. Sidle. 1990. Changes in productivity and distribution of nutrients in a chronosequence at Glacier Bay National Park, Alaska. *Journal of Ecology* 78. 561-578.

Bossuyt, H., Denef, K., Six, J., Frey, S.D., Merckx, R., Paustian, K., 2001. Influence of microbial populations and residue quality on aggregate stability. *Appl. Soil Ecol.* 16, 195-208.

Botkin, D.B. 1992. *The ecology of forests: theory and evidence*, Oxford University Press, New York, New York.

Bradshaw, A.D., R.H. Marrs, R.D.Roberts. 1982. Succession, in *Ecology of Quarries, the importance of natural vegetation* (ed. B.N.K. Davis). Institute of Terrestrial Ecological Symposia. No. 11. P. 47-52.

Braun-Blanquet, J. 1964. *Pflanzensoziologie*, 3rd edition, Springer-Verlag, Wien.

Bremer, E., H.H. Janzen, A.M. Johnston. 1994. Sensitivity of total, light fraction, and mineralizable organic matter on management practices in a Lethbridge soil. *Canadian journal of soil science* 74. 131-138.

Broadbent F E and Nakashima T 1974 Mineralization of carbon and nitrogen in soil amended with carbon-13 and nitrogen-15 labeled plant material. *Soil Sci. Soc. Amer. Proc.* 38, 313–315.

Burke, I. C., D. S. Schimel, C. M. Yonker, W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1990. Regional modeling of grassland biogeochemistry using GIS. *Landscape Ecology* 4: 45-54.

Burke, I. C., Elliott, E. T. and C. V. Cole. 1995. Influence of macroclimate, landscape position and management on soil organic matter in acroecosystems. *Ecological Applications* 5: 124-131.

Burkins, M.B., and C.P. Chamberlain, R.A. Virginia, and D.H. Wall. 2000. The origin of soil organic matter in Taylor Valley, Antarctica. *Ecology* 81(9). 2377-2391.

Burkins, M.B. and R.A. Virginia, D.H. Wall. 2001. Organic carbon cycling the in Taylor Valley, Antarctica: quantifying soil reservoirs and soil respiration. *Global Change Biology* 7. 113-125.

Buyanovsky, G.A., M. Aslam, G.H. Wagner. 1994. Carbon turnover in soil physical fractions. *Soil Science of America Journal* 58, 1167-1173.

Calder, I.R. 1990. *Evaporation in the Uplands*. Wiley, Chichester.

Cambardella, C.A. and E.T. Elliot. 1992. Particulate soil organic matter changes across a grassland cultivation sequence. *Soil Science of America Journal* 56, 777-783.

Cambardella, C.A. And E.T. Elliot. 1993. Carbon and nitrogen distribution in aggregates from cultivated and native grassland soils. *Soil Science of America Journal* 57. 1071-1076.

Campbell C A, Lafond G P, Zentner R P and Biederbeck V. O .1991. Influence of fertilizer and straw baling on soil organic matter in a thin black chernozem in western Canada. *Soil Biol. Biochem.* 23, 443-446.

Carney, K.M., P.A. Matson, and B.J.M. Bohannan (2004). Diversity and composition of tropical soil nitrifiers across a plant diversity gradient and among land use types. *Ecology Letters* (7), 684-694.

Cattelino, P.J., I.R. Noble, R.O. Slatyer, and S.R. Kessel. 1979. Predicting the multiple pathways of plant succession. *Environmental Management* 3: 41-50.

Cavallini, F. 1993. Fitting a logistic curve to data. *College Mathematics Journal* 24 (3): 247-253.

Christensen, N.E. and R.K. Peet. 1991. Secondary forest succession on the North Carolina piedmont. In: West DC, Shugart HH, BOtkin DB (eds). *Forest Succession: Concepts and duplications*. Springer, NY. 230-245.

Christensen, B.T. 1996. Matching measurable soil organic fractions with conceptual pools in simulation models of carbon turnover: revision of model structure. In:

Evaluation of Soil Organic Matter Models (eds. Powlson, D.S. et al.) NATO ASI Series 1, Vol. 38. Springer: Berlin.

Christense, B.T. 1992. Physical fractionation of soil and organic matter in primary particle size and density separates. *Advances in Soil Science* 20, 1-90.

Chapin F. S., III (1991) *Effects of Multiple Environmental Stresses on Nutrient Availability and Use*. Academic Press.

Chapin, F.S., and L.R. Walker, C.L. Fastie, L.C. Sharman. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs* 64. 149-175.

Clements, F.E. 1916. *Plant succession*. Carnegie institute of Washington. Publication 242.

Cole, M. 1982. The influence of soils, geomorphology, and geology on the distribution of plant communities in savanna ecosystems. In: B.J. Huntley and B.H. Walker (eds.) *Ecology of Tropical Savannas*: Springer-Verlag, Berlin. 145-174.

Collins, S.L. And D.E. Adams. 1983. Succession in grasslands: thirty-two years of change in central Oklahoma tallgrass prairie. *Vegetatio* 51: 181-190.

Comeau, P.G. and J.P. Kimmins. 1989. Above and belowground biomass and production of lodgepole pine on sites with different soil moisture regimes. *Canadian journal of forest research* 19(4), 447-454.

Connell, J.H. and Slayter, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*, 111. 119-1144.

Coutts, M.P., Nielsen, C.C.N., and B.C. Nicoll. 1999. The development of symmetry, rigidity, and anchorage in the structural root system of conifers. *Plant and soil* 217: 1-15.

Cramer, W., Kicklighter, D.W., Bondeau, A., Moore, B., C. Churkina, B. Nemry, A. Ruimy, and A.L. Schloss. 1999. Comparing global models of terrestrial net primary productivity (NPP): overview and key results. *Global Change Biology* 5: 1-15.

Currie, W.S. 2011. Units of nature or processes across scales? The concept of ecosystems at age 75. *New Phytologist: Tansley Review*: 1-14.

D'Angela, D.L. and J.C. Waterhouse. 1990. Equilibrium and non-equilibrium concepts in successional models. *Ecological Monographs* 57, 1-21.

De Deyn, G.B., C.E. Raaijmakers, H.R. Zoomer, M.P. Berg, P.C. de Ruiter, H.A. Verhoef. 2003. Soil invertebrate fauna enhances grassland succession and diversity. *Nature* 422. 711-713.

De Deyn, G.B., C.E. Raaijmakers, J. van Ruijven, F. Berendse, W.H. van der Putten. 2004. Plant species identity and diversity on different trophic levels of nematodes in the soil food web. *Oikos* 106, 576-586.

De Deyn G.B., Cornelissen, H. and Bardgett, R.D. (2008) Plant traits and soil carbon sequestration in contrasting biomes. *Ecology Letters* 11: 516-531.

Degens, B.P. 1997. Macro-aggregation of soils by biological bonding and binding mechanisms and the factors affecting these: a review. *Australian Journal of Soil Resources* 35. 431-459.

Del Moral, R., J.H. Titus, and A.M. Cook. 1995. Early primary succession on Mount St. Helens, Washington, USA. *Journal of Vegetation Science* 6: 107-120.

Denef, K., Six, J., 2003. Clay mineralogy modifies macroaggregate stabilization through active root growth, plant residues and associated microbial activity. *Eur. J. Soil Science*.

Dittman, J. A., C. T. Driscoll, P. M. Groffman, and T. J. Fahey. 2007. Dynamics of nitrogen and dissolved organic carbon at the Hubbard Brook Experimental Forest. *Ecology* 88:1153-1166

Dohrenbusch, A., J. Kumke, G. Mackenthum. 1992. Effects of soil amelioration on growth and nutrient supply.

Drew, J.T. And J.W. Flewelling. 1979. Stand density management: an alternative approach and its application to Douglas-fir plantations. *Forest Science* 25: 518-532.

Drury, W.H. and Nisbet, I.C.. 1973. Succession. *Journal of Arnold Arboretum*. 54. 131-168.

Dyrness, C. T. 1969. Hydrologic properties of soils on three small watersheds in the western Cascades of Oregon. Res. Note PNW-111. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 17 pp.

Dyrness, T., J. Franklin, and W. Moir. 1974. A preliminary classification of the communities of the central portion of the western Cascades in Oregon. *Coniferous Forest Biome Bulletin* 4 (132).

Edwards, A.P. and J.M. Bremner. 1967. Microaggregates in soils. *Journal of Soil Science* 18. 64–67.

Eisenhauer, N., H. Bessler, C. Engels, G. Gleixner, M. Habelkost, A. Milcu. 2010. Plant diversity effects on soil microorganisms support the singular hypothesis.

Elliott, E.T. and Coleman, D.C. 1988. Let the soil work for us. *Ecological Bulletins* 3, 23-32.

Emmer, I.M. 1995. Humus form and soil development during the primary succession of monoculture *Pinus silvestris* from forests on poorly developed sandy substrates. Ph.D. thesis. University of Amsterdam.

Emerson, W.W., 1959. Stability of soil crumbs. *Nature* 183, 5.

Epstein, H. E., Burke, I. C., and W. K. Lauenroth. 2002. Regional patterns of decomposition and primary production rates in the U.S. Great Plains. *Ecology* 83:320-327.

Ewing, H.A. 2002. The influence of substrate on vegetation history and ecosystem development. *Ecology* 84: 2766-2781.

Ewing, S.A., J. Sanderman, W.T. Baisden, Y. Wang, and R. Amundson. 2006. Role of

large-scale soil structure in organic carbon turnover: Evidence from California grassland soils. *Journal of Geophysical Research*, 111.

Fastie, C.L. 1995. Causes and ecosystem consequences of multiple pathways of succession at Glacier Bay, Alaska. *Ecology* 76(6): 1899-1916.

Finzi, A.C., Canham, C.D., and Breeman, N.V. 1998. Canopy-Tree-Soil Interactions within Temperate Forests: Species Effects on pH and cations. *Ecological Applications* 8(2): 447-454.

Forcella, F. and T. Weaver. 1977. Biomass and productivity of the subalpine *Pinus albicaulis*- *Vaccinium scoparium* association in Montana, USA. *Vegetatio* 35, 95-105.

Flanagan, P.W. 1986. Substrate quality influences on microbial activity and mineral availability in taiga forest floors. In K. Van Cleve, F.S. Chapin III, P.W. Flanagan, L.A. Vierick, and C.T. Dyrness, editors. *Forest Ecosystems in the Arctic Taiga: Ecological Studies, Analysis, and Synthesis* 57: 138-151.

Franklin, J. and T. Dyrness. 1971. A checklist of vascular plants on the H.J. Andrews Experimental Forest in Western Oregon. *Forest Service Research Notes* 138 (37).

Franklin, J.F. And R.T.T. Forman. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. *Landscape Ecology* 1: 5-18.

Franklin, J. F., and D. S. DeBell. 1988. Thirty-six years of tree population change in an old-growth *Pseudotsuga-Tsuga* forest. *Canadian Journal of Forest Research* 18:633-639.

Franklin, J. F. 1989. Importance and justification of long-term studies in ecology. Pages 3-19 in G. E. Likens, editor. Long-term studies in ecology. Springer-Verlag, New York, New York, USA.

Franklin, J. F., T. A. Spies, R. Van Pelt, A. B. Carey, D. A. Thornburgh, D. R. Berg, D. B. Lindenmayer, M. E. Harmon, W. S. Keeton, D. S. Shaw, K. Bible, and J. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-Fukami, T. and Wardle, D.A. 2005. Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. Proceedings of the Royal Society of London, Series B- Biological Sciences, 272. 2105-2115.

Fröberg, M., D. Berggren, B. Bergkvist, C. Bryant, and H. Knicker. 2003. Contributions of Oi, Oe and Oa horizons to dissolved organic matter in forest floor leachates. *Geoderma* 113:311-322.

Fröberg, M., P. M. Jardine, P. J. Hanson, C. W. Swanston, D. E. Todd, J. R. Tarver, and C. T. Garten. 2007. Low Dissolved Organic Carbon Input from Fresh Litter to Deep Mineral Soils. *Soil Science Society of America Journal* 71:347-354.

Fung, I.Y. and S.C. Doney, K. Lindsay, and J. John. 2005. Evolution of carbon sinks in a changing climate. *Proceedings of the National Academy of Sciences* 102 (32), 11201-11206.

Gale, J., C.A. Cambardell, and T.B. Bailey. 2000. Root-derived Carbon and the formation and stability of aggregates. *Soil Science of America Journal* 64 (2000), 201-207.

Galloway, J.N., G.E. Likens, W.C. Keene, and J.M. Miller. 1982. The composition of precipitation in remote areas of the world. *Journal of Geophysical Research* 87, 8771-8786.

Galloway, J.N., W.C. Keene, and G.E. Likens. 1996. Processes controlling the composition of precipitation at a remote southern hemispheric location: Torres del Paine National Park, Chile. *Journal of Geophysical Research* 101, 6883-6897.

Gasson, P.E. and D.F. Cutler. 1990. Tree root plate morphology. *Arboricultural Journal* 14: 193-264.

Geier, M. 2008. Necessary Work: discovering old forests, new outlooks, and community on the H.J. Andrews Experimental Forest, 1948-2000. General Technical Report, PNW-GTR 687. 357 pp.

Gentile, R., B. Vaanlauwe, and J. Six. 2011. Litter quality impacts short but not long term soil carbon dynamics in soil aggregate fractions. *Ecological Applications* 21(3), 695-703.

Gholz, H.L., S.A. Vogel, W.P. Cropper, K. McKelvey, K.C. Ewel, R.O. Teskey, and P.J. Curran. 1985. Dynamics of canopy structure and light interception in *pinus elliotii* stands, North Florida. *Ecological Monographs* 61(1), 33-51.

Gleixner, G.M., N. Poirier, R. Bol, and J. Balesdent. 2002. Molecular dynamics of organic matter in a cultivated soil. *Organic geochemistry* 33, 357-366.

Gerlauch, A., and E.A. Albers, W. Broedlin. 1994. Development of the Nitrogen Cycle in a Coastal Dune succession. *Archives of the Botanical society*. 189-203.

Gilman, E.F. 1990. Tree root growth and development. 1. Form, spread, depth, and periodicity. *Journal of Environmental Horticulture* 8: 215-220.

Gleason, H.B. 1916. The structure and development of plant association. *Bulletin of the Torrey Botanical Club* 44, 463-481.

Gleason, H.B. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53, 1-20.

Gleason, H.B. 1927. Further views of the succession concept. *Ecology* 8, 299-326.

Gleason, H.B. 1939. The individualistic concept of the plant association. *American Midwest Naturalist* 21, 92-110.

Greenwood, E.A.N. 1992. Deforestation, re-vegetation, water balance, and climate: an optimistic path through plausible, impractical, and controversial. *Advanced Bioclimatology* 1. 89-154.

Glenn-Lewin, D.C. 1980. The individualistic nature of plant community development. *Vegetatio* 43, 141-146.

Glenn-Lewin, D.C., R.K. Peet, and T. Veblen. 1992. *Plant Succession: Theory and Prediction*. Chapman and Hall: London.

Gray, Donald H. 1973. Effects of forest clear-cutting on the stability of natural slopes: results of field studies. Ann Arbor, MI: College of Engineering, Department of Civil Engineering, University of Michigan; Interim report, DRDA project 002790. 119 p.

Griese, F. 1987. Untersuchungen über die natürliche Wiederbewaldung von Heideflächen von niedersächsischen Flachland. PhD thesis, University of Göttingen. Translated.

Gustafsson, O., Gschwend, P.M., 1997. Aquatic colloids: concepts, definitions, and current challenges. *Limnol. Oceanogr.* 42, 519– 528.

Granhall, U. 1981. Biological nitrogen fixation in relation to environmental factors and the structuring of natural ecosystems. 131-144 in F.E. Clark and T. Rosswall (eds). *Terrestrial nitrogen cycles*. Swedish natural resource Council, Stockholm.

Granhall, U. and S.A. Kulassoriya, W.K. Himimburegama, R.S.Y. de Silva and T. Lindberg. 1987. Nitrogen fixation in some soils in Sri Lanka. *World Journal of Microbiology and biotechnology* 3(4), 367-388.

Grant, G.E. and A.L. Wolff. 1991. Long Term Patterns of Sediment Transport after Timber Harvest in the Western Cascades Mountains of Oregon, USA. In the Proceedings of the Vienna IAHS symposium, Vienna, AU, IAHS Publication No. 203, Oxfordshire, UK. International Association of Hydrological Sciences 203, 31-40.

Gower, Stith T., Kristiina A. Vogt, and Charles C. Grier. 1992. Carbon Dynamics of Rocky Mountain Douglas-Fir: Influence of Water and Nutrient Availability. *Ecological Monographs* 62:43–65.

Halpern, C.B. and J.F. Franklin. 1989. Understory development in *Pseudotsuga* forests: multiple paths of succession. Proceedings—land classifications based on vegetation: applications for resource management; 1987 November 17-19, Moscow ID. Gen Tech

Report INT-257. Ogden, UT. US Department of Agriculture Forest Service, Intermountain Research Station. 293-297.

Halpern, C.B. and Franklin, J.F. 1990. Physiognomic development of *Pseudotsuga* forests in relation to initial structure and disturbance intensity. *Journal of Vegetation Science*.

Halpern, C.; Means, J. 2011. Pacific Northwest Plant Biomass Component Equation Library. Long-Term Ecological Research. Forest Science Data Bank, Corvallis, OR.

[Database]. Available:

<http://andrewsforest.oregonstate.edu/data/abstract.cfm?dbcode=TP072> (29 January 2012).

Harmon, M.E. 1991. Coarse woody debris in two old-growth ecosystems. *Bioscience*, 41(9).

Hassink, J. 1996. Preservation of plant residues in soils differing in unsaturated protective capacity. *Soil Science of America Journal* 60. 487-491.

Hattori, T., 1988. Soil aggregates in microhabitats of microorganisms. *Rep. Inst. Agric. Res. Tohoku Univ.* 37, 23-36

Heal, O.W., J.M. Anderson, and M.J. Swift. 1997. Plant Litter Quality and Decomposition: a historical overview. pp. 3-30 in G. Cadish and K.E. Giller, eds. *Driven by Nature: plant litter quality and decomposition*. CAB International Walingford, UK.

Hedley, M.J., J.W.B. Stewart and B.S. Chauhan. 1982. Changes in inorganic and organic soil phosphorus fractions induced by cultivation practices and by laboratory incubations. *Soil Science Society of America Journal* 46. 970-976.

Henin, S., Monnier, G., and A. Combeau. 1958. Methode pour l'étude de la stabilité structurale des sols. *Annals of Agronomy* 1, 73-92.

Hongve, D. and P.A.W. VanHees, and U.S. Lundstrom. 2000. Dissolved components in precipitation water percolated through forest litter. *European Journal of Soil Science*. 667-677.

Horn, H.S. 1975. Markovian properties of forest succession, in ecology and evolution of communities (eds M.L. Cody and J. Diamond), Belknap Press, Cambridge MA, pp.196-211.

Horn, H.S. 1976. Succession in Theoretical Ecology (ed. R.M. May) Blackwell, Oxford, pp.187-204.

Houghton, R. A., Davidson, E. A. & Woodwell, G. M. 1988. Missing sinks, feedbacks, and understanding the role of terrestrial ecosystems in the global carbon balance. *Glob. Biogeochem. Cycles* 12, 25-34 (1998).

Huggins, D.R., and G.A. Buyanovsky, G.H. Wagner, J.R. Brown, R.G. Damody, T.R. Peck, G.W. Lesoing, M.V. Vanotti, and L.G. Bundy. 1998. Soil organic C in the tallgrass prairie-derived region of the corn belt: effects of long term crop management. *Soil and Tillage research* 47. 219-234.

Ingestad, T. 1979. Mineral and Nutrient Requirements of *Pinus Silvestris* and *Picea abies* Seedlings. *Physiologica Plantarum* 45. 4. 373-380.

Inouye, R.S. and D. Tilman. 1988. Convergence and divergence of plant communities along experimental nitrogen gradients. *Ecology* 69, 995-1004.

Ito, Akihiko. 2011. A historical meta-analysis of global terrestrial net primary productivity: are estimates converging? *Global Change Biology* 17(10), 3161-3175.

Jensen V. (1984) Decomposition of angiosperm tree leaf litter. In *Biology of Plant Litter Decomposition* (eds. C. H. Dickinson and G. J. F. Pugh). Academic Press, vol. 1, pp. 69–104.

Jones, R.H. Maximum Likelihood Fitting of ARMA Models to Time Series with Missing Observations. *Technometrics*, Vol. 22, No. 3, 1980, pp. 389-395.

Jones, D.L., V.B. Willett, E.A. Stockdale, A.J. MacDonald, D.V. Murphy. 2012. Molecular weight of Dissolved Organic Carbon, Nitrogen, and Phenolics in Grassland Soils. *Soil Biology and Biogeochemistry* 76(1), 142- 150.

Kalbitz, K. and R. Weinrich. 1998. Mobilization of heavy metals and arsenic in polluted wetland soils and its dependence on dissolved organic matter. *Sci. Total Environment* 209, 27-39.

Kalbitz, K. and K. Kaiser. 2003. Ecological aspects of dissolved organic matter in soils. *Geoderma* 113:177-178.

- Keeling, H.C. and O.L. Phillips. 2007. The global relationship between forest productivity and biomass. *Global Ecology and Biogeography* 16: 618-631.
- Kemper, W.D., Koch, E.J., 1966. Aggregate stability of soils from western United States and Canada. Technical Bulletin #1355. Agricultural Research Services. USDA in cooperation with Colorado Agricultural Experiment Station, pp. 1–52.
- Kiem, R. and I. Kogel-Knabner. 2003. Contribution of lignin and polysaccharides to the refractory carbon pool in C-depleted arable soils. *Soil Biology and Biochemistry* 35: 101-118.
- Kogel-Knabner, I. 2002. The macromolecular organic composition and microbial residues as inputs to soil organic matter. *Soil Biology and Biochemistry* 34: 139-162.
- Knapp, A.K. And M.D. Smith, M.D. Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291: 481– 484.
- Kolling, C. 1993. Die Zusammensetzung der Bodenlösung insturmgeworfenen Fichtenforst (Picea Abies)- Ökosystemen. *Forest Forschungsber Munchen* 122: 1-134. Translated.
- Kostiakov, A.N. 1932. On the dynamics of the coefficient of water percolation in soils and the necessity of studying it from the dynamic point of view for the purposes of amelioration. *Trans. Sixth Committee on International Soil Science*, 17-21.

Kramer, M. G., A. J. Hansen, M. L. Taper, and E. J. Kissinger. 2001. Abiotic controls on long-term windthrow disturbance and temperate rain forest dynamics in southeast Alaska. *Ecology* 82:2749-2768.

Kreckelburg, B. and M. Lappe. 1999. Temporal Recruitment along the trajectory of moving objects and the perception of position. *Vision Research* 39: 2669-2679.

Laane, R.W.P.M., 1982. Influence of pH on the fluorescence of dissolved organic matter. *Mar. Chem.* 11, 395– 401.

Laurance, W.F., Fearnside, P.M., Laurance, S.G., Delamonica, P., Lovejoy, T.E., Rankin de Merona, J.M., Chambers, J.Q. and C. Gascon. 1999. Relationship between soils and Amazon forest biomass: a landscape-scale study. *Forest Ecology and Management* 118: 127–138.

Lee, R. 1963. Evaluations of solar beam radiation as a climatic parameter of mountain watersheds. Colorado State University hydrological papers.

Lee, Y.K. and S.Y. Yoo. Changes in litter, decomposition, N-mineralization and microclimate in *Acacia Mangium* and *Acacia auriculiformis* plantation in Mount Makiling, Philippines. 2012. *International Journal of Physical Sciences* 7(12), 1976-1985.

Leenheer, J.L., 1981. Comprehensive approach to preparative isolation and fractionation of dissolved organic carbon from natural waters and waste waters. *Environ. Sci. Technol.* 15, 578– 587.

- Lefsky, Michael A.; Cohen, Warren B.; Hudak, Andrew; Acker, Steven A.; Ohmann, Janet L. 1999. Integration of lidar, Landsat ETM+ and forest inventory data for regional forest mapping. In: Csathó, Beáta M., ed. International Society for Photogrammetry and Remote Sensing and International Archives of Photogrammetry and Remote Sensing Workshop: mapping surface structure and topography by airborne and spaceborne lasers, Vol. 32: Part 3W14; 1999 November 9-11; La Jolla, CA. Columbus, OH: ISPRS WG III/5 Remote Sensing and Vision Theories for Automatic Scene Interpretation, Byrd Polar Research Center, Ohio State University: 119-125.
- Lefsky, M.A., Cohen, W.B., Acker, S.A., Parker, G.G., Spies, T.A., and Harding, D. 1999. Lidar remote sensing of the canopy structure and biophysical properties of Douglas-fir western hemlock forests. *Remote Sensing of Environment* 70: 339-361.
- Leuschner, C. 1994. Walddynamik auf Sandboden in der Luneburger Heide. NW Deutschland. *Phytocoenologia* 22. 289-324. Translated.
- Leuscher, C. 1998. Water Extraction by Tree Fine Roots in the Forest Floor of a Temperate Fagus-Quercus Forest. *Annual Science Forestry* 55: 141-157.
- Leuscher, C. and M.W. Rode. 2001. The role of plant resources in forest succession: changes in radiation, water, nutrient fluxes, and plants productivity over a 100 year chronosequence in southern Germany. *Perspective on Plant Ecology, evolution, and systems*, pp. 107-147.
- Li, Y., M. Xu, X. Zou. 2006. Heterotrophic soil respiration in relation to environmental factors and microbial biomass in two wet tropical forests. *Plant and Soil* 281, 193-201.

Likens, G.E., Driscoll, C.T., Buso, D.C. 1996. Long term effects of acid rain response and recovery of a forest ecosystem. *Science* 272. 244-245.

Londo, G. 1974. Successive mapping of dune slack vegetation. *Vegetatio* 29, 51-61.

Lutz, J. 2005. The contribution of mortality to early coniferous forest development. M.S. Thesis. University of Washington.

Lutz, J.A. and C.B. Halpern. 2006. Tree mortality during early forest development: a long-term study of rates, causes, and consequences. *Ecological Monographs*. 76(2): 257-275.

Lynch, J.M. and E. Bragg. 1985. Microorganisms of stabilization and earthworm casts and artificial casts. *Biological Fertility of Soils* 9, 163-167.

Mahli, Y., D.D. Baldocchi and P.G. Jarvis. 1999. The carbon balance of temperate, tropical and boreal forests. *Plant, Cell, and Environment* 22, 715-740.

Margalef, R. 1958. *Perspectives in Ecological Theory*, University of Chicago Press, Chicago.

Margalef, R. 1963. On certain unifying principles in ecology. *American Naturalists*, 97.357-374.

Margalef, R. 1968. *Perspectives in Ecological theory*. University of Chicago Press, Chicago.

Marin-Spiotta, E., Chadwick, O.A., Kramer, M., and M.S. Carbone. 2011. Carbon delivery to deep mineral horizons in rain forest soils. *Journal of Geophysical Research* 116:1-14.

Marschner, B. and K Kalbitz. 2003. Controls of bioavailability and biodegradability of dissolved organic matter in soils. *Geoderma* 113: 211-235.

Martin, J.P., Martin, W.P., Page, J.B., Raney, W.A., and J.D. De Ment. 1955. Soil aggregation. *Advanced Agronomy* 7, 1-37.

Mathews, J.A. 1979. A study of the variability of some successional and climate plant assemblages types using a multiple discriminant analysis. *Journal of Ecology* 67. 255-271.

Mathes, K. and T.H. Sriefer. 1985. Soil respiration during secondary succession: Influence of temperature and moisture. *Soil Biology and Biogeochemistry* 17 (2): 205-211.

McClain, M.E., E.W. Boyer, C.L. Den, S.E. Gergel, N.B. Grimm, P.M. Groffman, S.C. Hart, J.W. Harvey, C.A. Johnston, E. Mayorga, W.H. McDowell, and G. Pinay. 2003. Biogeochemical Hot Spots and Hot Moments at the Interface of Terrestrial and Aquatic Ecosystems. *Ecosystems* 6. 301-312.

McCune, B. and T.F.H. Allen. 1985. Forest dynamics in the Bitterroot Canyons, Montana. *Canadian Journal of Botany* 63:377-383.

McDowell, N.G., W. Pockman, C. Allen. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb. *Tansley Review. New Phytologist* 178: 719-739.

McElhinny, C., Gibbons, P., Brack, C., and Bauhaus, J. 2005. Forest and woodland stand structural complexity: Its definition and measurement. *Forest Ecology and Management* 218 (1-3): 1-24.

McGill, W.B. 1996. Review and classification of ten soil organic matter models. In *Evaluation of Soil Organic Matter Models*, Eds D. A. Powlson, P. Smith and J.U. Smith. pp. 111-132. NATO ANSI Series. Springer-Verlag.

McInerney M. and Bolger T. (2000b) Temperature, wetting cycles and soil texture effects on carbon and nitrogen dynamics in stabilized earthworm casts. *Soil Biol. Biochem.*32(3), 335–349.

Meadows, J.S. and J.D. Hodges. 2002. Sapwood area as an estimator of leaf area and foliar weight in cherry bark and green ash. *Forest Science* 48, 69-76.

Mencuccinni, M. and J. Grace. 1995. Climate influences the leaf area/sapwood area ratio in scots pine. *Tree Physiology* 15: 1-10.

Meentemeyer V. (1978) Macroclimate and lignin control of litter decomposition rates. *Ecology* 59(3), 465–472.

Meiwes, K.J. 1992. Amelioration of an acid forest soil.

Melillo J. M. and Aber J. D. (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63(3), 621–626.

Miles, J. 1979. *Vegetation Dynamics*. Chapman and Hall, London.

Miles, J. 1987. Vegetative succession: Past and present perspectives in Colonization, Succession, and stability (eds. A.J.Gray, M.J. Crawby, and P.I. Edwards). Blackwell Oxford, pp. 1-29.

Millar C. S. (1974) Decomposition of coniferous leaf litter. In *Biology of Plant Leaf Litter Decomposition* (eds. C. H. Dickinson and G. J. F. Pugh). Academic Press, vol. 1, pp. 105–128.

Miles, J. 1979. *Vegetation Dynamics*. Chapman and Hall, London.

Monteagudo, L.M.M., A. Neill, D.A., Vargas, P.N., Patino, S., Pitmans, N.C.A., Quesada, C.A., Salomao, R., Silva, J.N.M., Lezama, A.T., Martinez, R.V., Terborgh, J., Vinceti, B. and J. Lloyd. 2004. The above-ground coarse wood productivity of 104 Neotropical forest plots. *Global Change Biology*, 10: 1–29.

Motavalli P. P., Palm C. A., Parton W. J., Elliott E. T., and Frey S. D. (1994) Comparison of laboratory and modeling simulation methods for estimating soil carbon pools in tropical forest soils. *Soil Biol. Biochem.* 26(8), 934–944.

Mudrick, D.A., M. Hoosein, R. Hicks, E.C. Townsend. 2012. Decomposition of leaf litter in an Appalachian Forest: effects of leaf species, aspect, slope, position, and time. *Forest Ecology and Management* 27(94), 48-55.

Nadelhoffer, K.J., J.D. Aber and J.M. Melillo. 1984. Seasonal patterns of ammonium and nitrate uptake in nine temperate forest ecosystems. *Plant and Soil* 80, 321-335.

Nadelhoffer, K.J., Giblin, A.E., Shaver, G.R., and J.A. Laundre. 1991. Effects of temperature and substrate quality on element mineralization in six arctic soils. *Ecology* 72: 242-253.

Nadelhoffer, K.J., B.A. Emmett, P. Gunderson, O.J. Kjonaas, C.J. Koopmans, P. Schleppei, A. Tieternall, and R.F. Wright. 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. *Letters to Nature* 398: 145-149.

Neff, J. C. and G. P. Asner. 2001. Dissolved organic carbon in terrestrial ecosystems: synthesis and a model. *Ecosystems* 4:29-48.

Noble, L.R. and Slayter, R.O. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* 43:5-21.

Oades, J.M. 1984. Soil organic matter and structural stability: mechanisms and implications for management. *Plant and Soil* 76. 319-337.

Oades, J.M. 1993. The role of biology in the formation, stabilization and degradation of soil structure. *Geoderma* 56, 377-400.

Odum, E.P. 1969. The strategy of ecosystem development. *Science* 164. 262-270.

Oliver, C. D., and B. C. Larson. 1996. *Forest stand dynamics*. John Wiley and Sons, New York, New York, USA.

- O'Neill, R.V. 2001. Is it time to bury the ecosystem concept? (with full military honors, of course!) *Ecology* 82 (12): 3275-3284.
- Ostertag, R. 1998. Belowground effects of canopy gaps in a tropical wet forest. *Ecology* 79(4): 1294-1304.
- Ostiahev, N.A. 1936. The law of distribution of moisture in soils and methods for study of the same. *International Congress on Soil Mechanics in Foundational Engineering Research* 20, 203-211.
- Palm, C.A. And A. P. Rowland. 1997. A minimum dataset for characterization of plant quality for decomposition. Pages 37-379 in G. Caidsh and K.E. Giller, eds. *Driven by Nature: plant litter quality and decomposition*. CAB international, Walingford UK.
- Parkin, T.B. 1987. Soil microsites as a source of denitrification variability. *Soil Science of American Journal* 51: 1195-1199.
- Paul, E.A. and E.E. Clark. 1989. *Soil microbiology and biochemistry*. Academic Press, San Diego, California, USA.
- Paustian, K.S. , H.P. Collins, and E.A. Paul. 1997. Management Controls on Soil Carbon. In *Soil Organic Matter in Temperate Agroecosystems: long-term experiments in North America*. Eds. E.A. Paul, K. Paustian, E.T. Elliott, and C.V. Cole. CRC Press. Boca Raton, FL.
- Paustian, K., G. I. Agren, and E. Bosatta. 1997. Modeling litter quality effects on decomposition and soil organic matter dynamics. Pages 313–335 in G. Cadisch and K. E.

Giller, editors. Driven by nature: plant litter quality and decomposition. CAB International, Wallingford, UK.

Paustian, K., H.P. Collins, and E.A. Paul. 1997. Management controls on soil carbon. In Soil Organic Matter in Temperate Ecosystems. Eds E.A. Paul, K. Paustian, E.T. Elliott and C.V. Cole, pp. 15-49, CRC Press, Boca Raton, FL.

Peet, R. K. 1981. Changes in biomass and production during secondary forest succession. Pages 324-338 in D. C. West, H. H. Shugart, and D. B. Botkin, editors. Forest succession. Springer-Verlag, New York, New York, USA. © 2005 James A. Lutz48

Peet, R. K., and N. L. Christensen. 1987. Competition and tree death. *BioScience* 37:586-595.

Peet, R.K. and Christensen, N.L. 1988. Succession: a population process. *Vegetatio* 43. 121-140.

Philip, J.R. 1957. The theory of infiltration: 4. Sorptivity and algebraic infiltration equations. *Soil Science* 83, 345-347.

Pickett, S.T.A. 1976. Succession: an evolutionary interpretation. *American Naturalist*.110. 107-119.

Porazinska, D., Bardgett, R.D., Blaauw, M.B., H. Hunt, A. Parsons, T.R. Seastedt, and D.H. Wall. 2003. Relationships at the above-ground belowground interface: plants, soil biota, and soil processes. *Ecological Monographs* 73, 377-395.

Porporato, A. and I. Rodriguez-Iturbe. 2000. Ecohydrology: a hydrologic perspective of climate-soil-vegetation dynamics. *Water Resources Research* 23. 349-357.

Post, W. M. and K. C. Kwon. 2000. Soil Carbon Sequestration: Land use change and potential. *Global Change Biology* 6(3). 317-321.

Prior, S.A., G.B. Runin, H.H. Rogers, H.A. Torbert, D.W. Reeves. 2005. Elevated atmospheric CO₂ effects on biomass production and soil carbon in conventional and conservation cropping systems. *Global Change Biology* 11 (4), 657-665.

Prove, B.G., Loch, R.J., Foley, J.L., Anderson, V.J., and DR. Younger. 1990.

Improvements in aggregation and infiltration characteristics of a krasnozem under maize with direct drill and stubble retention. *Australian Journal Soil Research* 28, 577-590.

Pypker, T.GH. R. Barnard, M. Hauck, E. W. Sulzman, M. H. Unsworth,, A. C. Mix, A. M. Kennedy, and B. J. Bond. Can Carbon Isotopes be used to predict watershed-scale transpiration? 2007. *Agricultural and Forest Meteorology* 145: 149-166.

Qualls, R.G., B.L. Haines. and W.T. Swank. 1991. Fluxes of dissolved organic nutrients and humic substances in deciduous forests. *Ecology* 72, 254-266.

Quideau S. A., Graham R. C., Chadwick O. A., and Wood H. B. (1998) Organic carbon sequestration under chaparral and pine after four decades of soil development. *Geoderma* 83(3-4), 227-242.

Raich, J.W., Russell, A.E., Kitayama, K., Parton, W.J. and P.M. Vitousek. 2006.

Temperature influences carbon accumulation in moist tropical forests. *Ecology* 87: 76-87.

Raich, J.W., E.B. Rastetter, J.M. Melillo, D.W. Kicklighter, P.A. Steudler, B.J. Peterson, A.L. Grace, B. Moore, and C.J. Vorosmarty. 1991. Potential Net Primary Productivity in South America: Application of a Global Model. *Ecological Applications* 1, 399-429.

Rasmussen P E, Allmaras R R, Rhode C R and Roager N C Jr. 1980. Crop residue influences on soil carbon and nitrogen in a wheat fallow system. *Soil Sci. Soc. Am. J.* 44, 596–600.

Rasse, D.P., C. Rumpel, M.F. Dignac. 2005. Is Soil Carbon Mostly Root Carbon? *Plant and Soil*. 269. 341-356.

Rastetter, E. B., McKane, R. B., Shaver, G. R. & Melillo, J. M. 1992. Changes in C storage by terrestrialecosystems: how C±N interactions restrict responses to CO₂ and temperature. *Wat. Air Soil Pollut.* 64, 327-344 (1992).

Reicosky, D.C., and S.D. Evans, C.A. Cambardella, R.R. Amaras, A.R. Wilts, and D.R. Huggins. 2002. Continuous corn with moldboard tillage: residue and fertility effects on soil carbon. *Journal of Soil and Water Conservation* 57, 277-284.

Robertson, G.P., D.C. Coleman, C.S. Bledsoe, P. Sollins, eds. 1999. *Standard Soil Methods for Long-Term Ecological Research*. LTER Publication. New York: Oxford.

Robertson, G.P., S.L. Collins, D.R. Foster, N. Broksaw, H.W. Ducklow, T.L. Gragson, C. Gries, S.K. Hamilton, A.D. McGuire, J.C. Moore, E.H. Stanley, R.B. Waide, and M.W. Williams. 2012. *Long-Term Ecological Research in a Human-Dominated World*. *Bioscience* 62 (4).

- Roloff and Linke, 2002. Agricultural herbs as auxiliary plants in stand establishment.
- Roskowski, P. 1980. Nitrogen fixation in the hardwood forests of the northeastern united states. *Plant and Soil science* 54, 33-44.
- Rothacher, J., C. Dyrness, and R.L. Fredricksen. 1967. Hydrologic and Related Characteristics of Three Small Watersheds in the Oregon Cascades. 1-54.
- Ruesch, A. and H.K. Gibbs. 2008. New IPCC Tier-1 Global Biomass Carbon Map for the year 2000. Available online from the Carbon Dioxide Information Analysis Center. Oak Ridge National Laboratory. Oak Ridge, TN.
- Ryan, M.G., Phillips, N., and B.J. Bond. 2006. The hydraulic limitation hypothesis revisited. *Plant Cell and Environment* 29: 367–381.
- Sanderman, J. and R. Amundson. 2004. Biogeochemistry of decomposition and detrital processing. Pages 249-316 in H. D. Holland and K. K. Turekian, editors. *Treatise on Geochemistry*. Elsevier Press, Amsterdam.
- Scherber, C., N. Eisenhaur, W.W. Weisser, B. Schmid, W. Voigt, M.Fisher. 2010. Bottom up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468, 553-556.
- Schimel, D.S., I.G. Enting, M. Heimann, T.M.L. Wigley, D. Raynard, D. Alves, and U. Siegenthaler. 1995. CO₂ and the Carbon Cycle. Pages 39-71 in J.T. Houghton, L.G. M. Filho, J. Bruce, H. Lee, B.A. Callander, E. Haites, N. Harris, and K. Maskell, eds.

Climate Change 1994: radiative forcing of climate change. Cambridge University Press, Cambridge, England.

Schlesinger W. H. and Hasey M. M. 1981. Decomposition of chaparral shrub foliage: losses of organic and inorganic constituents from deciduous and evergreen leaves. *Ecology* 62(3), 762–774.

Schlesinger W. H. 1990. Evidence from Chronosequence Studies for a low carbon-storage potential of soils. *Nature(London)* 348(6298), 232–234.

Schlesinger, W.H. 1991. *Biogeochemistry: An analysis of Global change*. Academic Press, San Diego, California, USA.

Scott, N.A. and D. Binkley. 1997. Foliage litter quality and annual net N mineralization: comparison across north american forest sites. *Oecologia* 111, 151-159.

Sedjo, R. 1993. The carbon cycle and global forest ecosystems: water, air, and soil pollution 70. 295-307.

Sexstone, A.J., Revsbech, N.P., Parkin, T.B., and J.M. Tiedje. 1985. Direct measurement of oxygen profiles and denitrification rates in soil aggregates. *Soil Sci. Soc. Am. J.* 49, 645–651.

Shinozaki, K., K. Yoda, K. Hozumi, T. Kira. 1964. A quantitative analysis of plant form: the pipe modeling theory. *Basic Analysis. Japanese Journal of Ecology* 14: 97-105.

Shinozaki, K., K. Yoda, K. Hozumi, T. Kira. 1964. A quantitative analysis of plant form: the pipe model theory: Further evidence of the theory and its application in plant ecology. *Japanese Journal of Ecology* 14: 133-139.

Silver W. L. and Miya R. K. 2001. Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia* 129(N3), 407–419.

Silvester, W.B. , P. Sollins, T. Verhoeven, and s.p. Cline. 1982. Nitrogen fixation and acetylene reduction in decaying conifer boles. Effects of incubation timing and moisture content. *Canadian Journal of forest research* 12, 646-652.

Silvester, W.B. 1989. Nitrogen cycling between sediment and the shallow-water transition zone of the Potomac River and estuary. 1. Nitrate and ammonium fluxes. *Estuarine, Coastal, and Shelf Science* 25, 483-497.

Six, J., Elliott, E.T., Paustian, K., Doran, J.W. 1998. Aggregation and soil organic matter accumulation in cultivated and native grassland soils. *Soil Sci. Soc. Am. J.* 62, 1367–1377.

Six, J., Elliott, E.T., Paustian, K., 1999. Aggregate and soil organic matter dynamics under conventional and no-tillage systems. *Soil Sci. Soc. Am. J.* 63, 1350–1358

Six, J. E.T. Elliott, and K. Paustian. 2000. Soil macroaggregate turnover and microaggregate formation: a mechanism for C sequestration under no-tillage agriculture. *Soil Biology and Biogeochemistry* 32. 2099-2103.

Six, J. and R.T. Conant, E.A. Paul, K. Paustian. 2002. Stabilization Mechanisms of soil organic matter: implications for C-saturation of soil. *Plant and Soil*, 241. 155-176.

Six, J., P. Callewaert, S. Lenders, S. De Gryze, S. J. Morris, E. G. Gregoriche, E. A. Paul and K. Paustian. 2003. Measuring and Understanding soils by physical fractionation. *Soil Science of America Journal* 66(6).

Six, J., H. Bossuyt, S. Degryze, and K. Denef. 2004. A history of research on the link between (micro)aggregates, soil biota, and soil organic matter dynamics. *Soil and Tillage Research* 79, 7-31.

Sollins, P., C. Swanston, M. Kleber, T. Filley, M. Kramer, S. Crow, B. Caldwell, K. Lajtha, and R. Bowden. 2006. Organic C and N stabilization in a forest soil: evidence from sequential density fractionation *Soil Biology and Biochemistry* 38:3313-3324.

Sollins, P., M. Kramer, M. Kleber, K. Lajtha, C. Swanson, T. Filley, A. Aufdenkampe, R. Bowden. 2009. Organic C and N stabilization acrosssoils of contrasting mineralogy: further evidence from sequential density fractionation. In press.

Song, B., S. Niu, Z. Zhang, H. Yang, L. Li. 2012. Light and Heavy Fractions of Soil Organic Matter in Response to Climate Warming and Increased Precipitation on a Temperate Steppe. *PLoS ONE* 7(3).

Sorenson, R., U. Zinko, and J. Seibert. 2006. On the Calculation of the topographic wetness index: evaluation of different methods based on field observations. *Hydrology and Earth System Sciences* 10: 101-112.

Spies, T. A., and J. F. Franklin. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. Pages 90-109 in L. F. Ruggeri, K.B. Aubry, A.B. Carey, and M.H. Huff, technical coordinators, Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service General Technical Report PNW-GTR-285.

Soderland, R. and Rosswall, T.H. 1982. The nitrogen cycles. Pages 62-81 in O. Hutzinger, editor. Handbook of environmental chemistry. Springer-Verlag, Berlin, Germany.

Spies, T. A., and J. F. Franklin. 1996. The diversity and maintenance of old-growth forests. Pages 296-314 in R. C. Szaro, and D. W. Johnson, editors. Biodiversity in managed landscapes: theory and practice. Oxford University Press, New York, New York, USA.

Sprugel, D.G. 1985. Natural disturbance and ecosystem energetics, in *The Ecology of Natural Disturbance and Patch Dynamics* (eds. S.T.A. Pickett and P.S. White). Academic Press, NY, 335-352.

Stage, A.R. and C. Salas. 2007. Interactions of Elevation, Aspect, and Slope in Models of Forest Species Composition and Productivity. *Forest Science* 53(4). 486-492.

Stewart, C.E., K. Paustian, R.T. Conant, Alain F. Plante and J. Six. 2007. Soil carbon saturation: concept, evidence, and evaluation. *Biogeochemistry* 86(1), 19-31.

Stewart, C.E., A.F. Plante, K. Paustian, R.T. Conant, and J. Six. 2008. Soil carbon saturation: linking concept and measurable carbon pools. *Soil Science Society of America Journal* 72, 379-392.

Stewart, C.E., K. Paustian, R.T. Conant, A.F. Plante, and J. Six. 2009. Soil carbon saturation: implications for measurable carbon pool dynamics in long-term incubations. *Soil Biology and Biogeochemistry* 41(2), 357-366.

Swanson, F.S. 1980. Geologic field trips in western Oregon and Southwestern Washington. Geological Society of America Cordilleran meeting Proceedings. 1-32.

Swanson, F.J. 1987. Ecological effects of the eruption of Mount St. Helens: an overview. In Bilderback, David E., ed. Mt. St. Helens 1980: botanical consequences of explosive eruptions. Los Angeles, CA: University of California Press: 1-2.

Swanson, F.J. and J.A. Jones. 2002. Geomorphology and hydrology of the H.J. Andrews Experimental Forest, Blue River, OR. In Moore, G.W. ed. Field Guide to Geologic processes in Cascadia: field trips to accompany the 98th annual meeting of the Cordilleran section of the Geological Society of America; Corvallis, OR. Special Paper 36. Portland, OR. Oregon Department of Geology and Mineral Industries. 288-314.

Tan, Z., R. Lai, L. Owens, and R.C. Izaurralde. 2006. Distribution of light and heavy fractions of soil organic carbon as related to land use and tillage practice. *Soil & Tillage Research* 92(1-2):53-59.

Tansley, A.G. 1935. The use and abuse of vegetation concepts and terms. *Ecology* 16, 284-307.

Tappeiner II, J. C., D. Huffman, D. Marshall, T. A. Spies, and J. D. Bailey. 1997. Density, ages, and growth rates in old-growth and young-growth forests in coastal Oregon. *Canadian Journal of Forest Research* 27:638-648.

Ter Braak, C.J.F. 1986. Canonical Correspondence Analysis: A new eigenvector technique for multivariable gradient analysis. *Ecology* 67 (5): 1167-1179.

Thieme, H.R. 2003. *Mathematics in population biology*. Princeton University Press. Princeton, NJ.

Thiet, R. S. D. Frey, and J. Six. 2006. Do growth yield efficiencies differ between soil microbial communities differing in fungal: bacterial ratios? Reality check and methodological issues. *Soil Biology and biogeochemistry* 38 (4), 837-844.

Tillman, D. 1988. *Plant strategies and The Dynamics and Structure of Plant Communities*. Monographs of Population Biology. Princeton University Press Princeton NJ.

Thomsen I. K., Schjonning P., Jensen B., Kristensen K., and Christensen B. T. (1999) Turnover of organic matter in differently textured soils: II. Microbial activity as influenced by soil water regimes. *Geoderma* 89(3-4), 199-218.

Tian G., Kang B. T., and Brussaard L. (1992) Biological effects of plant residues with contrasting chemical—compositions under humid tropical conditions—decomposition and nutrient release. *Soil Biol. Biochem.* 24(10), 1051-1060.

- Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological monographs* 57, 189-214.
- Tilman, D. 1988. *Plant strategies and The Dynamics and Structure of Plant Communities. Monographs of Population Biology.* Princeton University Press Princeton NJ.
- Tilman, D. 1990. Mechanisms of plant competition for nutrients: the elements of a predictive theory of competition, in *Perspectives on Plant Competition* (eds. J.B. Grace and D. Tilman). Academic Press, New York. 117-141.
- Tisdale, J.M. and J.M. Oades. 1982. Organic Matter and Water Soluble aggregates in soils. *Journal of Soil Science* 62, 141-163.
- Torbert, H.A., S.A. Prior, and H.H. Rogers. 2003. Effect of Elevated CO₂ and Temperature on Soil C and N Cycling. *Field Crops Research*.
- Turner, M.J. 2005. Landscape Ecology: What is the state of the science? *Annual Review of Ecology, Evolution, and Systematics*: 319-344.
- Ulrich, B. 1970. Die reaction von calcium carbonat bei der einarbeitung von kalkmergel in stark versauerten Waldboden mit Auflagehumus. *Allg Forest Jagdztg* 141, 5-9. Translated.
- Valentini R, DeAngelis P, Matteucci G, Monaco R, Dore S, Scarascia Mugnozza GE (1996) Seasonal net carbon dioxide exchange of a beech forest with the atmosphere. *Global Change Biology* 2:199-20

Verseghy, D.L. 2007. Class—A Canadian land surface scheme for GCMS. 1. Soil Model. *Journal of Climatology* 11: 111-133.

Vierick, 1970. Forest Succession and soil development adjacent to the Chena River in interior Alaska. *Arctic Alpine Resources* 2. 1-26.

Vitousek, P. and Reiners. 1975. Ecosystem succession and nutrient retention, a hypothesis. *Bioscience* 25. 376-381.

Vitousek, P.M. and R.W. Howarth. 1991. Nitrogen limitation on land and sea: how and when can it occur. *Biogeochemistry* 13(2): 87-115.

Vitousek P. M., Turner D. R., Parton W. J., and Sanford R. L. 1994. Litter decomposition on the Mauna Loa environmental matrix, Hawaii: patterns, mechanisms, and models. *Ecology (Tempe)* 75(2), 418–429.

Vitousek, P. M., J.D. Aber, R.W. Howarth, G.E. Likens, P.A. Matson, D.W. Schindler, W.H. Schlesinger, and D.G. Tilman. 1997. Human alteration of the Global Nitrogen Cycle: Sources and Consequences. *Ecological Applications* 7(3), 737-761

Vogt K. (1991) Carbon budgets of temperate forest ecosystems. *Tree Physiol.* 9(1–2), 69–86.

Walker, J., and C.H. Thompson, J.F. Fergus, B.R. Tunstall. 1981. Plant succession and soil development in the coastal sand dunes of subtropical eastern Australia. West DC, Shugart Hill, Botkin DB. *Forest Succession: Concepts and Applications*. Springer, NY. 107-131.

Wang, X., Yost, R.S., and B.A. Linquist. 2001. Soil aggregate size affects phosphorus desorption from highly weathered soils and plant growth. *Soil Science Society of America Journal* 665, 139–146.

Wardle, D.A., K.I. Bonner, G.M. Barker, G.W. Yeates, K.S. Bardgett, R.N. Watson, and A. Ghani. 1999. Plant removals in perennial grassland: vegetation dynamics, decomposers, soil biodiversity and ecosystem properties. *Ecological Monographs* 69.535-568.

Wardle, D.A., R.D. Bardgett, J.N. Klironomos, H. Setälä, W.H. Van der Putten, and D.H. Wall 2004. Ecological linkages between aboveground and belowground biota. *Science* 304. 1629-1633

Wardle, D.A., M. Johnsson, S. Bansal, R.D. Bardgett, M.J. Gundale, and D.B. Metcalfe. 2012. Linking vegetation change, carbon sequestration, and biodiversity: insights from island ecosystems in a long-term natural experiment. *Journal of ecology*. 100.16-30.

Waring, R.H., W.G. Thies, D. Muscato. 1990. Stem Growth Per Unit of Leaf Area: a measure of tree vigor. *Forest Science* (26), 112-117.

Weil R. R. (1992) Inside the heart of sustainable farming. *The New Farm* January, 43–48.

West, T.O. and W.M. Post. 2002. Soil Carbon Sequestration by Tillage and Crop Rotation: A Global Data Analysis. *Soil Science Society of America Journal*.

White, S.R., C.N. Carlyle, L.H. Fraser, and J.F. Cahill. 2011. Climate change experiments in temperate grasslands: synthesis and future directions. *Biology letters*, doi:

10.1098/rsbl.2011.0956.

Whittaker, J. 1953. A consideration of climax theory: the climax of population and pattern. *Ecological Monographs* 23: 41-78.

Wilson, K.G. 1971. The renormalization group (RG) and critical phenomena 1. *Physical Review B* (4): 3174.

Wolf, J. and C.A. Van Diepen. 1995. Effects of climate change on grain maize yield potential in the European community. *Climatic Change* 29: 299-331.

Wood, D.M. and del Moral, R. 1987. Mechanisms of early primary succession in subalpine habitats on Mount St. Helens. *Ecology* 68: 780-790.

Wood, D.M. and del Moral, R. 1988. Colonizing plants on the pumice plains, Mount St. Helens, Washington. *American Journal of Botany* 77: 1411-1418.

Woodwell, G.M. 1967. Radiation and the patterns of nature. *Science* 156, 461-470.

Woodwell, G.M. and Whittaker, R.H. 1968. Effects of chronic gamma irradiation on plant communities. *Quarterly Review of Biology* 43, 42-55.

Wright, R.F. and van Breeman, N. 1995. The NITREX project: an introduction. *Forest Ecology and Management* 71, 1-6.

Zalewski, M. 2000. Ecohydrology- the scientific background to use ecosystem properties as management tools toward sustainability of water resources. *Ecological Engineering* 16: 1-8.

Zenner, E.K. 2005. Investigating scale-dependent stand heterogeneity with structure-area curves. *Forest Ecology and Management* 102: 87-100.

Zsolnay, A., Steinweg, B., 2000. The in situ availability of dissolved organic matter to combine with hydrophobic compounds. In: Croue, J.-P., Frimmel, F. (Eds.), *IHSS 10*, Toulouse, France, pp. 313– 316.

Zsolnay, A. 2003. Dissolved organic mater: artefacts, definitions, and functions. *Geoderma* 113:187-209.

APPENDICES

Appendix 1. Historical Soil Surveys

Table 1. Soil Bulk Density following logging on WS1 *skyline* and WS3 *high-lead*

Timing	Skyline	High Lead
Before Logging	0.677+-0.023	0.712+-0.016
Undisturbed	0.730 +-0.032	0.753+-0.019
Slightly Disturbed	0.668+-0.030	0.785+-0.032
Heavily Disturbed	0.858 +-0.025	0.990+-0.026

Table 2. Padilla's 2005 Soil Survey

Aspect	LAI	Avg C:N	Slope (%)	Texture
South	7.89	17+-6.05	65	Loam / clay loam
South	7.91	19.4+-2.13	65	Sandy clay loam
North	5.75	19.6+-1.93	80	Sandy loam
North	5.78	24.2+-1.83	73	Sandy loam

Table 3. Part1/6 of Keebler's 2007 Soil Survey (south-facing slope of WS1)

Material	depth	horixon	>2mm (%)	texture	munsell
Organic	2	clear-smooth	-	-	-
Mineral	-9	gradual-wavy	0	loam	7.5YR4/4
Mineral	-30	diffuse-wavy	25	silty-loam	10YR4/4
Mineral	-42	diffuse-wavy	0	silt	10YR5/6
Mineral	-60	diffuse-wavy	5	silt	10YR6/8
Mineral	>60	-	50	silt	10YR6/8

Table 4. Part 2/6 of Keebler's 2007 Soil Survey (south-facing slope of WS1)

Material	mottling	concretion	redox	pH	OM (%)
Organic	-	-	-	4.5	-
Mineral	0	0	aerated	5	0.15
Mineral	0	0	aerated	5	0.9
Mineral	0-2	black Mg	reducing	5	0.6
Mineral	15-40	black Mg	reducing	5	0.3
Mineral	>40	black Mg	reducing	5	0

Table 5. Part 3/6 of Keebler's 2007 Soil Survey (south-facing slope of WS1)

Material	structure	texture	bulk den	root count	root fraction
Organic	-	-	-	-	-
Mineral	subangular blocky	fine	1.1	20-50	fine
Mineral	subangular blocky	fine	1.2	50-200	fine
Mineral	subangular blocky	fine	0.9	20-50	coarse
Mineral	subangular blocky	fine	1.2	1-20	fine
Mineral	subangular blocky	fine	1.0	1-20	fine

Table 6. Part 4/6 of Keebler's 2007 Soil Survey (south-facing slope of WS1)

Horizon	Thickness	OM kg/m²	pore	field capacity
O	-	-	-	-
A	0.9 dm	1.49	53	20 L/m ²
IIAB	2.1 dm	1.70	39	32 L/ m ²
B	1.2 dm	0.65	49	34 L/m ²
CB	1.8 dm	0.62	47	-
BC	-	-	25	1-20 L/ m ²

Table 7. Part 5/6 of Keebler's 2007 Soil Survey (north-facing slope of WS1)

Material	depth	horizon	>2mm	texture	munsell
Organic	4	clear-smooth	-	-	-
Mineral	-14	diffuse	30	silty loam	7.5YR4/3
Mineral	-28	diffuse	35	silty loam	7.5YR4/4
Mineral	-64	diffuse	45	loamy sand	7.5YR4/3
Mineral	>60	diffuse	25	silty loam	7.5YR4/4

Table 8. Part 6/6 of Keebler's 2007 Soil Survey (north-facing slope of WS1)

Material	mottling	concretion	redox	pH	OM(%)
Organic	-	-	-	4.5	-
Mineral	-	-	aerated	5	0.15
Mineral	-	-	aerated	5	0.9
Mineral	0-2	black Mg	reducing	5	0.6
Mineral	>15	black Mg	reducing	5	0

Appendix 3. Calculation of the Maximum Likelihood Estimator for mANPP

We assume that $B(t)$ follows the logistic function, which is classically employed in growth models for population biomass.

$$B(t) = \frac{K}{1 + Ce^{-rt}}$$

where B is biomass in Mg/ha, K is the carrying capacity (population limit), t is time in years, r is a modeled growth rate parameter, and C is an arbitrary coefficient. To calculate $ANPP$ from B , then, we assumed that $ANPP$ was simply the derivative of B in the form:

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

This is requisite for solving for mANPP, which occurs where the second derivative of $B(t)$ or the first derivative of $B'(t)$ is equal to zero. On the graph of $B(t)$ this is the point of inflection.

$$B''(t) = \frac{CKr^2e^{rt}(C - e^{rt})}{(C + e^{rt})^3} = 0$$

This is true when the numerator equals zero, which occurs when $C=e^{rt}$. Substituting back into $B(t)$ with the parameter t_0 for the point in time when inflection occurs, we solve $B(t)$ without the C constant as

$$B(t) = \frac{K}{1 + e^{-r(t-t_0)}}$$

The goal for fitting the logistic function to our data points is to simultaneously minimize least squares error on the parameters K (“biomass capacity of the site”), r (rate of growth), and t_0 (inflection time). The least squares error is represented as:

$$e = \sum_{i=1}^n (B(t_i) - B_i)^2$$

We use the method of logistic curve fitting developed by Cavallini (Cavallini, 1993).

Essentially, a pseudo-parameter h is substituted into the logistic function such that

$$h(t) = \frac{1}{1 + e^{-r(t-t_0)}}$$

from which the error function can be written as

$$e = K^2 \langle \mathbf{H}, \mathbf{H} \rangle - 2K \langle \mathbf{H}, \mathbf{B} \rangle + \langle \mathbf{B}, \mathbf{B} \rangle$$

This is justifiable through a rather lengthy proof in Cavallini (1993). Minimization of total squared error involves setting the partial derivatives for each parameter equal to zero.

By solving simultaneously

$$\frac{\partial e}{\partial K} = 0$$

$$2K\langle\mathbf{HH}\rangle - 2\langle\mathbf{HB}\rangle = 0$$

a function of e with respect to \mathbf{H} and \mathbf{M} is defined. This allows minimization of error on the logistic function with respect to only the parameters r and t_0 . This method is particularly valuable in the calculation of biomass for slow-growing sites because it is difficult to estimate K when $B(t)$ has not yet reached its inflection.

We developed a function in MatLab (MathWorks, 2010) to minimize error on the parameter space of r and t_0 . Initial guesses for ranges of applicable r were calculated by solving the ANPP equation for r such that

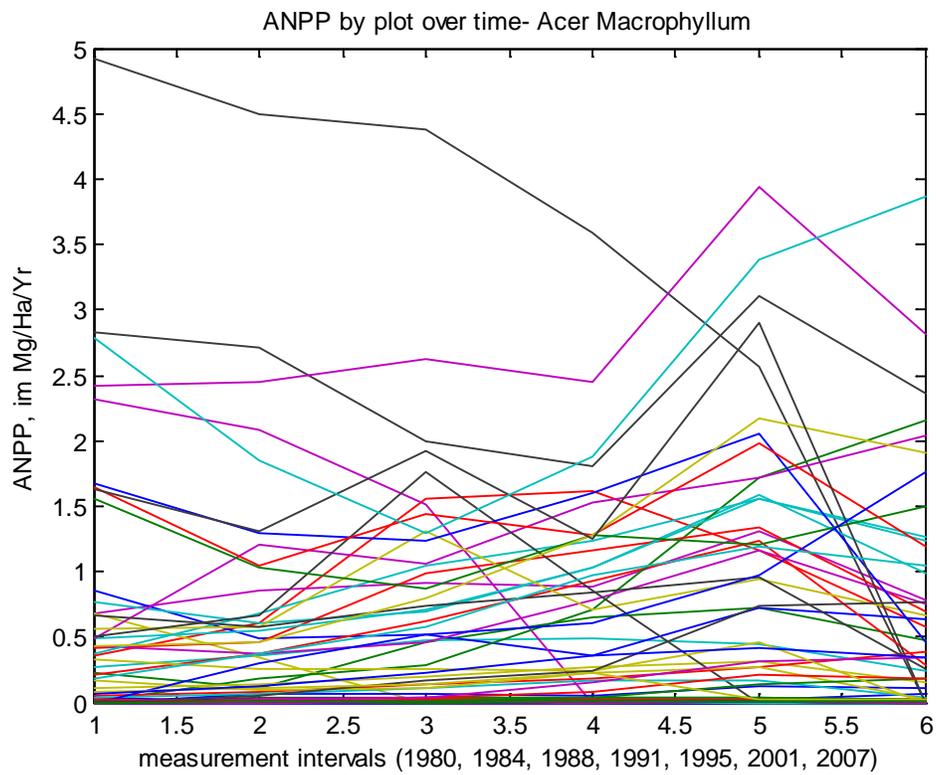
$$r = \frac{4B'(t_0)}{K}$$

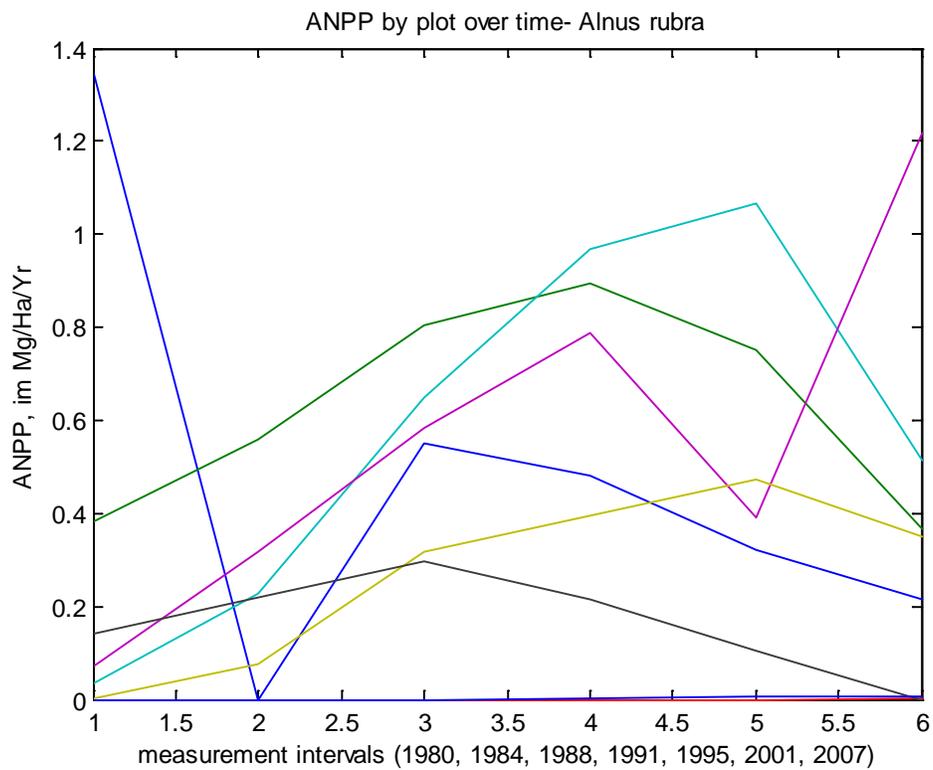
$B'(t_0)$ was calculated by the point-slope form except when the largest $B'(t_0)$ occurred during the most recent re-measurement

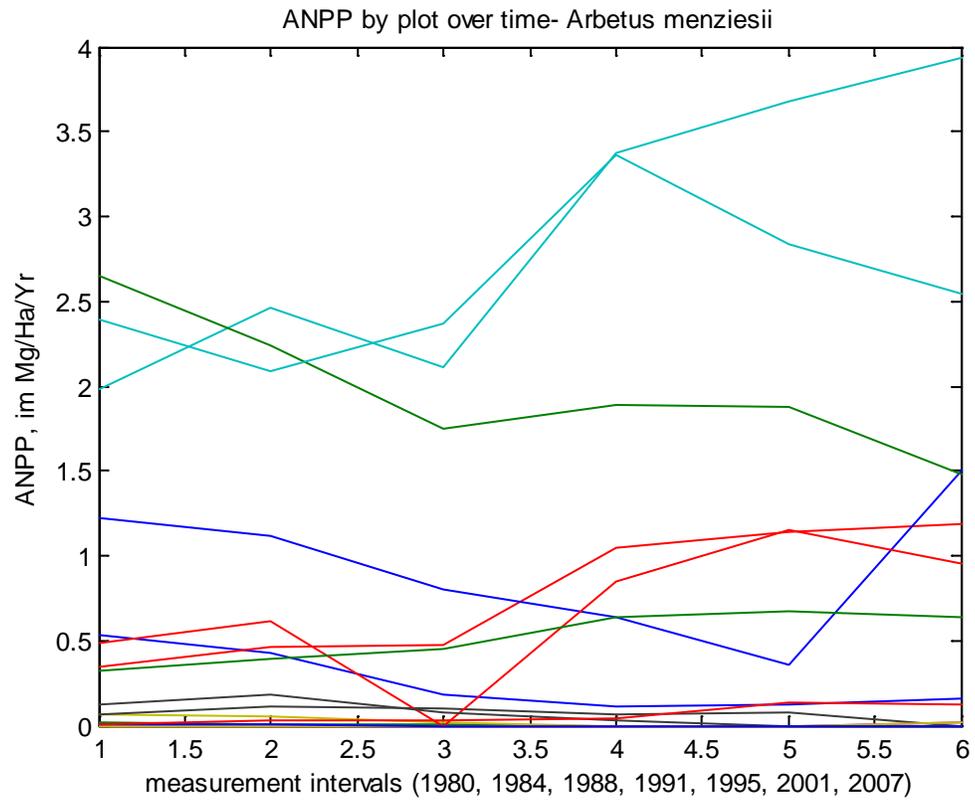
$$B'(t_0) = \frac{B_{i+1} - B_{i-1}}{t_{i+1} - t_{i-1}}$$

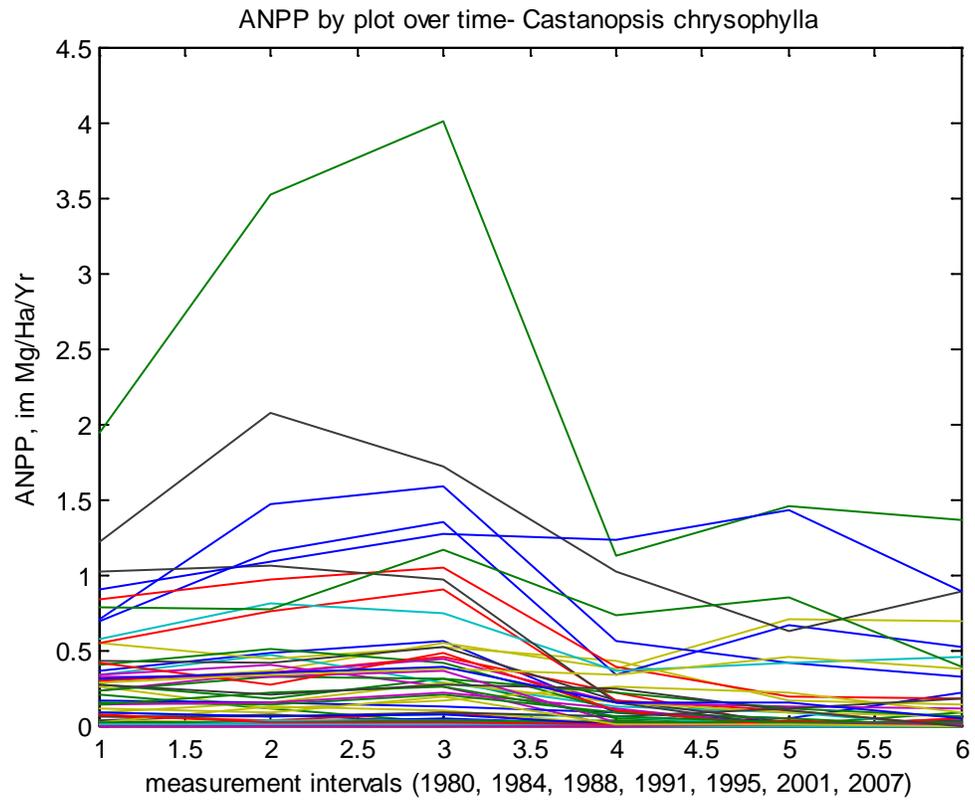
$$B'(t_0) = \frac{B_i - B_{i-1}}{t_i - t_{i-1}}$$

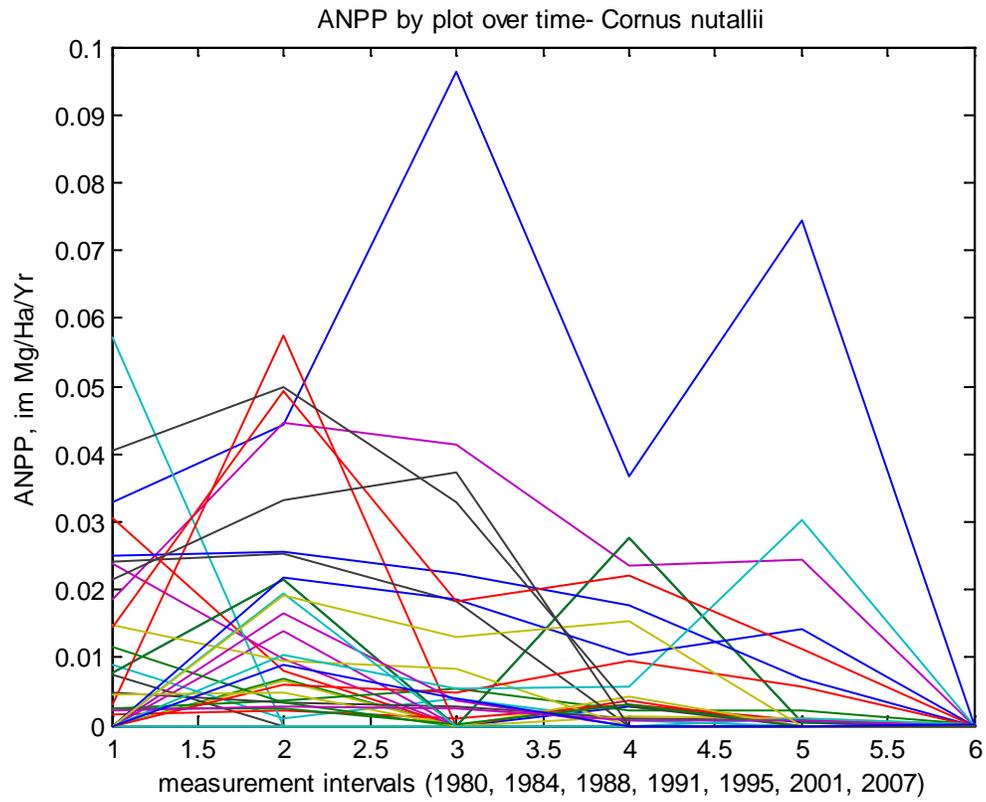
The range of r was inclusive of all potential values of r from substituting $B'(t_0)$ into the equation for r . The range for t_0 has to be tested iteratively using a sensitivity analysis. Because slow-growing plots may have not reached their point of inflection during the 28 year duration of our data (1980-2007), it was necessary to test values for t_0 that exceeded the 28 year range. We conducted the error minimization on the error space of $t_0 = [0,28]$, $t_0 = [0, 50]$, and $t_0=[0,100]$. The same local minima were found in most error spaces, such that the estimated K is equivalent, no matter the initial guess within these ranges. Equivalent estimates of K mean that r and t_0 , when substituted into the ANPP equation for error minimization will predict the same results for t_0 . In some cases, however, dual minima were found when the t_0 range or the r range was too small. In these cases, several initial guesses were tested until a local minimum could be reached. $B(t_0)$ was calculated and returned to the ANPP equation along with the estimated K , r , and t_0 . ANPP at t_0 is the maximum ANPP for the site.

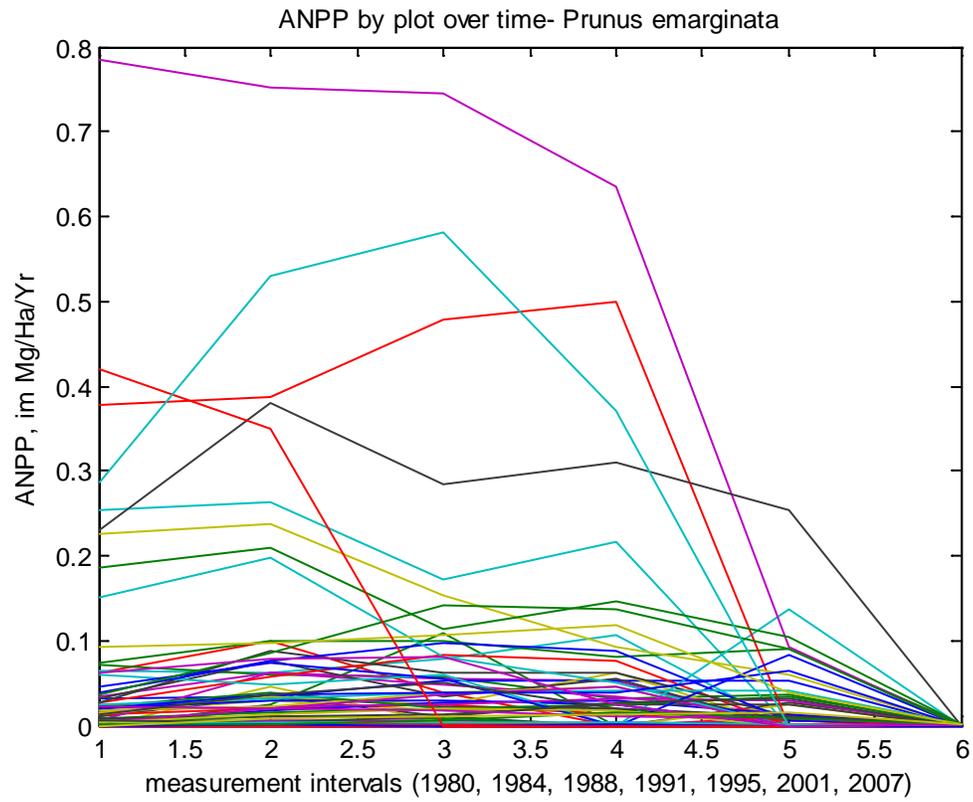
Appendix 3. ANPP trajectories by species

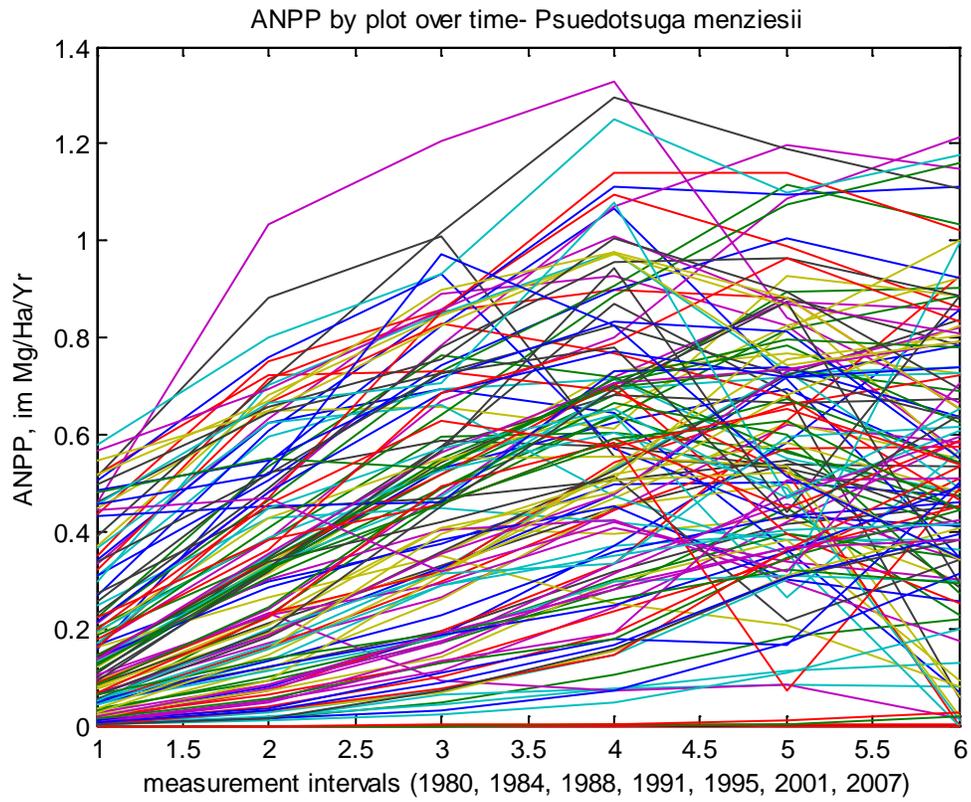


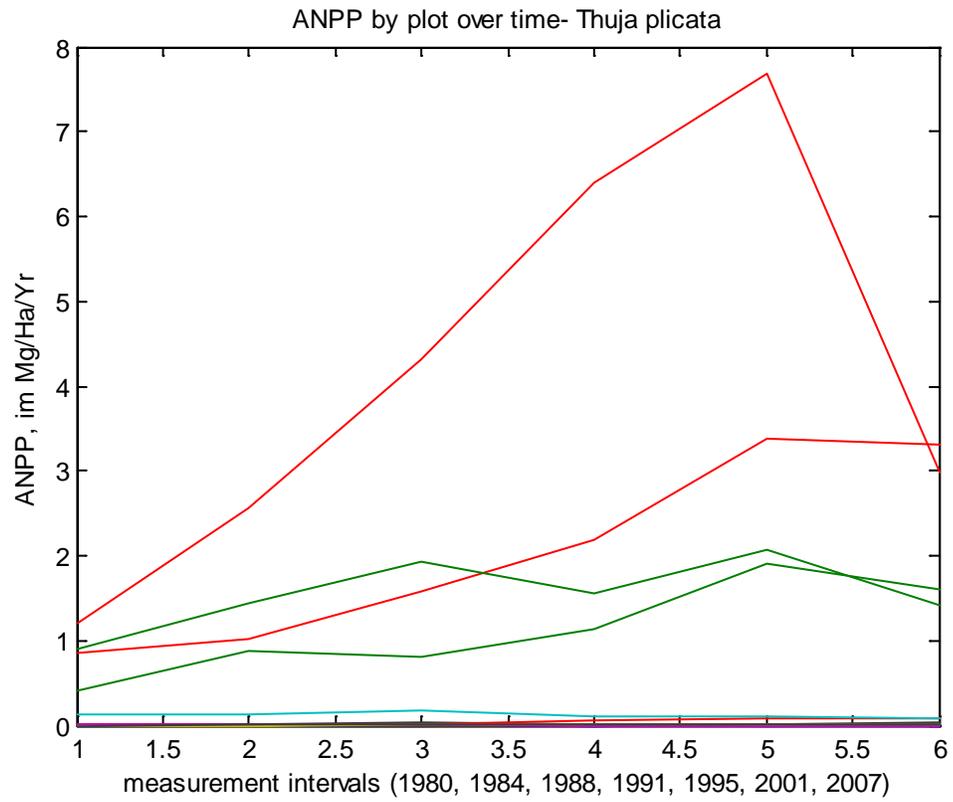












Appendix 4. Soil Properties on WS1

Table 2.--Particle-size distribution, textural class, and stone content of eight soil series occurring in three small watersheds

Soil series	Surface soil						Subsoil						Textural class		
	Percent sand		Percent silt		Percent clay		Percent sand		Percent silt		Percent clay				
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range			
	Percent stones (by volume--by dry weight for surface 48 inches of soil)														
From reddish tuffs and breccias:															
McKenzie River (10) ^{1/2}	34.4	23.4-56.3	38.2	26.0-44.2	27.4	17.7-34.4	Clay loam	22.4	4.6-50.5	16.7	8.1-34.1	41.7	37.3-45.4	41.6	28.6-51.8
Frissell (7)	35.0	18.5-61.7	60.4	19.2-50.6	24.6	16.1-32.2	Loam	43.4	17.0-81.8	31.1	16.6-53.7	43.4	26.3-50.7	23.2	18.6-32.8
From greenish tuffs and breccias:															
Slipout (2)	40.8	30.6-50.9	37.2	26.3-48.1	22.0	21.3-22.8	Loam	15.2	9.9-20.5	26.2	20.4-31.9	37.5	31.6-43.4	36.3	36.2-36.5
Budora (7)	37.6	31.4-43.6	39.6	34.3-54.3	22.8	14.3-27.3	Loam	24.6	8.9-59.7	25.3	18.6-30.8	47.0	42.4-53.2	27.7	21.5-34.0
Limbriest (13)	38.0	25.8-64.7	39.2	19.4-50.5	22.6	16.0-26.6	Loam	46.6	15.7-72.3	35.9	27.3-59.6	40.5	25.7-50.9	23.6	14.7-31.6
From basalt:															
Funky (2)	48.6	33.4-63.7	36.7	27.7-45.8	14.7	8.6-20.8	Loam	76.2	75.9-76.6	49.4	45.0-53.9	31.6	29.8-33.3	19.0	16.3-21.7
From andesite colluvium:															
A soil (15)	47.0	34.9-59.4	32.1	22.5-41.0	26.9	11.0-27.9	Loam	48.0	6.2-72.7	38.9	18.2-60.6	36.4	25.7-73.8	21.7	8.0-34.3
From mixed colluvium:															
M soil (1)	36.4	--	36.4	--	27.2	--	Clay loam	15.7	--	15.5	--	47.7	--	36.8	--

^{1/2} Numerals in parentheses indicate number of soil profiles in sample.

