AN ABSTRACT OF THE THESIS OF

Allison L. Stringer for the degree of Honors Baccalaureate of Science in Biology and Honors Baccalaureate of Science in Fisheries & Wildlife Science presented on May 17, 2013. Title: Quantifying the synchrony of leaf litter decomposition in a forested landscape.

Abstract approved:

Mark E. Harmon

Plant litter decomposition plays an important role in the global carbon cycle, and contributes large amounts of carbon to soils, which store more carbon than any other terrestrial pool of organic matter. Decomposition plays a fundamental role in nutrient cycling and alters soil properties that shape plant community composition and growth. This study aimed to determine the degree leaf litter decomposition rates vary synchronously from year to year among nearby sites. Litter decomposition rates were determined using a litter bag study conducted at 14 sites in the H. J. Andrews Experimental Forest in Oregon over multiple five year periods. A strong relationship between lignin:N and first year decomposition rate was found, but little to no relationship between climate and first year decomposition rate was observed. Inconsistent synchrony was observed between sites, implying that variation in first year decomposition values at the H. J. Andrews is mostly random in regards to climate. The lack of synchrony in first year decomposition rates at the HJA suggests that localized decomposition rates should not be extrapolated across a complex, mountainous landscape.

Key Words: Decomposition, synchrony, H. J. Andrews, carbon, leaf litter, rolling litter study

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Quantifying the synchrony of leaf litter decomposition in a forested landscape

by

Allison L. Stringer

A THESIS

Submitted to

Oregon State University

University Honors College

In partial fulfillment of
The requirements for the
Degree of

Honors Baccalaureate of Science in Fisheries and Wildlife

Honors Baccalaureate of Science in Biology

Presented May 17, 2013
Commencement June, 2013

Honors Baccalaureate of Science in Biology and Honors Baccalaureate of Science in Fisheries & Wildlife Science project of Allison L. Stringer presented on May 17, 2013.

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

Allison L. Stringer, Author

Acknowledgements

I would like to thank my mentor, Mark Harmon, for his guidance, patience, and interest in my development of critical thinking skills throughout my thesis. I could not have completed the project without his huge commitment of time and energy. I would also like to thank my committee members Stan Gregory and Steven Perakis for their advice and support. Their willingness to help a young scientist is much appreciated.

I would also like to thank Becky Fasth and Jay Sexton and for showing me around the lab and around the H.J. Andrews. Their knowledge and advice was invaluable. I would like to thank Murat Sarginci for helping me process leaf litter samples and for spending long hours in the lab with me.

Finally, I would like to thank the H. J. Andrews LTER grant (DEB-0823380), Kaye and Ward Richardson Endowment, and the Howard Hughes Medical Institute Undergraduate Fellowship for funding my research, and making my undergraduate thesis possible.

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INTRODUCTION

Decomposition, the process of reducing organic matter to its elemental chemical constituents, is a fundamental process in all ecosystems. It plays an essential role in nutrient cycling and alters soil properties (such as soil fertility, texture, water holding capacity, and pH) that shape plant community composition, which in turn affects plant growth rates (Hobbie 1992, Van Breemen and Finzi 1998). Decomposition results in the mineralization of organic carbon to carbon dioxide (CO_2), and on the global scale releases massive quantities of carbon to the atmosphere (Coûteaux et al. 1995, Aerts 1997). Understanding factors that control the release of this carbon source is essential to accurately model the global carbon cycle and the effects that increased anthropogenic emissions of CO_2 will have on that cycle (Smithwick et al. 2002, Currie et al. 2010). The carbon cycle directly contributes to the greenhouse effect, and therefore plays a key role in Earth's changing climate.

Dead leaves and roots—also known as plant litter—supply the largest carbon input to soils, which store more carbon than any other terrestrial pool of organic matter (Post et al. 1982). Decomposition of plant litter consists of three concurrent processes—fragmentation, leaching, and catabolism (Swift et al. 1979). Fragmentation is the process of particle size reduction either by physical processes or ingestion and digestion by detritivores. Often fragmentation results in a change in chemical composition as well as particle size. Leaching of water soluble compounds, an abiotic process, represents a significant portion of early mass loss. Inorganic ions and organic carbon leached from litter may contribute significantly to the total soil input. Catabolism of litter material is carried out primarily by microorganisms, including fungi and bacteria. Aerobic respiration of organic sugars into inorganic molecules such as carbon dioxide and water is the most familiar catabolic process active in decomposition (Aerts 1997). The inorganic molecules resulting from respiration can then be used by plants, transferred downward in the soil, or released to the atmosphere (Swift et al. 1979).

The factors determining decomposition rates are plant litter quality, the microbial decomposer community, and environmental conditions (Swift et al. 1979, Aerts 1997, Coûteaux et al 1995). Lignin concentration, or lignin:nitrogen ratio, has often been considered to exert a strong influence on litter decomposition rates (Berg and Staaf 1980, Melillo et al. 1982, Tian et al. 1992). Parameters other than lignin, however, such as nitrogen (N) concentration, carbon(C):N, phosphorous (P) concentration, or the C:P ratio may also strongly influence decomposition rates (Staaf and Berg 1982, Taylor et al. 1989, Perakis et al. 2012). The microbial decomposer community often receives less attention in litter decomposition studies than litter chemistry and climatic conditions. The dominant soil organisms involved in decomposition include protozoans, fungi, microarthropods, nematodes, earthworms and bacteria (Adl 2001). As noted above, these organisms play important roles in fragmentation and respiration of leaf litter. Climate affects all three processes of decomposition (fragmentation, leaching, and catabolism). Climatic conditions affect decomposition rate directly through temperature and moisture, and indirectly through impact on litter chemistry (Vitousek and Sanford 1986, Lavelle et al. 1993, Swift and Anderson 1989).

Environmental variation in temperature and moisture causes decomposition rates to vary both spatially and temporally. For instance, decomposition at a single site may vary widely between dry and wet years. Historically models have assumed that decomposition rates among geographically adjacent sites are similar and synchronous, meaning that they vary in similar magnitude and direction when influenced by similar conditions. This allows data from one place to be extrapolated across a broader region or landscape. Yet the synchrony of decomposition rates in a complex, mountainous landscape has not been demonstrated experimentally.

My study tests the assumption of decomposition synchrony by measuring spatial and temporal variation in leaf decomposition rates at 14 sites in the H. J. Andrews Experimental Forest in Oregon. The study aims to answer the following question: To what degree do leaf litter decomposition rates vary synchronously from year to year among nearby sites? Two alternative hypotheses were formulated: If there is high spatial synchrony or coherence of temperature and moisture among sites, then litter decomposition rates among sites should have a high correlation because decomposition is sensitive to these variables. If on the other hand, temperature and moisture are not coherent among sites, then litter decomposition rates among sites should not have a high correlation. To understand the causes of decomposition synchrony I address two subquestions: 1) to what degree does substrate quality change from year to year, and 2) to what degree does decomposition vary due to climatic changes year to year?

STUDY AREA

The H. J. Andrews Experimental Forest (HJA) is located on the western slope of the Cascade Range, approximately 80 km east of Eugene, Oregon (44°15’N, 122°10’W). The HJA covers an approximate area of 64 km^2, ranging in elevation from 410 to 1630 meters. Two major vegetation zones span the forests—the *Tsuga heterophylla* (western hemlock) zone from 300-1050 meters and the *Abies amabilis* (Pacific silver fir) zone from 1050-1550 meters. *Pseudotsuga menziesii* (Doulas-fir) and *Thuja plicata* (western red cedar) are common in both zones. *Cornus nuttallii* (Pacific dogwood), *Acer macrophyllum* (bigleaf maple), *Abies procera* (noble fir) and *Arbutus menziesii* (madrone) are scattered throughout the forest as well. Soils are primarily well-drained, deep typic Dystrochrepts (Harmon 1992).

The region has a maritime climate with mild, wet winters and cool, dry summers. At the Primary Meteorological Station (PRIMET) at 430 m elevation, mean monthly temperatures range from 18°C in July to 1°C in January. The mean annual temperature for 1980-2000 was 8°C. 75% of precipitation falls between October and March, and varies with elevation. Mixed rain and snow fall in the winters, with snow more common at elevations above 1000 m. The mean annual precipitation for 1980-2000 was 224 cm (Holub et al. 2005). Roughly two thirds of the forest remains old-growth, over 450 years old, while the remaining area bears young stands varying in composition and density (McKee 1998).

The 14 study sites ranged from a slope of 0° to a slope of 42°, with an average slope of 15° (Table 1). Douglas-fir was the dominant tree at all sites (except site 1 which was open), with western hemlock present at 10 sites, noble fir at 2 sites, western red cedar at 4 sites, Pacific silver fir at 2 sites, and madrone at 1 site. Based on ocular estimates, percent open sky ranged from 4% to 100%, and percent understory coverage ranged from 3% to 90%. Elevation ranged from 442 m to 1295 m, with an average of 835 m. Mean annual temperature ranges from 6.37°C at site 14 to 9.71°C at Site 9, with an average of all sites of 8.07°C (http://climhy.lternet.edu/, http://andrewsforest.oregonstate.edu/data/abstract.cfm?dbcode=MS005&topnav=97). Mean annual precipitation ranged from 165 cm at sites 10 and 16 to 217 cm at site 7, with an average of all sites of 174 cm.

Table 1 Topographic, vegetation, elevation, and climatic descriptions of 14 study sites in the H. J. Andrews Experimental Forest in Oregon.

Site	Slope (°)	Aspect (°from N)	Dominant Tree[1]	% open sky	% under-story	% bare soil	Elevation (m)	Climate station	Mean annual temperature (°C)	Mean annual precipitation (cm)
1	0	flat	open	100	72	5	442	primet	9.02	170.6
2	5	90	PSME TSHE	25	12	0	444	primet	9.02	170.6
3	10	202	PSME TSHE	10	10	0	1001	central	7.70	174.2
4	12	230	PSME TSHE ABPR	55	80	0	1001	central	7.70	174.2
5	32	180	PSME	35	72	5	513	RS01	9.95	170.6
6	20	270	PSME TSHE THPL	5	80	0	779	Mack creek -central	7.05	174.2
7	17	48	ABAM PSME TSHE	25	90	0	1284	uplo	6.84	216.6
8	16	150	TSHE THPL PSME	15	70	0	786	Mack creek -central	7.05	174.2
9	30	175	PSME ARME	12	35	7	625	RS20	9.71	170.6
10	7	124	PSME TSHE THPL	4	3	0	846	H15MET	8.31	165.0
11	13	140	PSME ABAM ABPR	25	57	0	1295	vanilla	7.21	170.7
13	42	5	TSHE THPL PSME	17	45	1	900	RS02	8.93	170.6
14	6	212	PSME TSHE	12	55	0	790	RS12	6.37	174.2
16	12	180	PSME TSHE	25	40	0	982	RS 26	8.13	165.0

[1] PSME is Douglas-fir, TSHE is western hemlock, ABPR is noble fir, THPL is western red cedar, ABAM is Pacific silver fir, and ARME is madrone.

MATERIALS AND METHODS

Field

Senescent leaves were gathered annually from trees in the HJA in late October. The leaves had all changed color, and were either freshly fallen or loosely attached. All leaves either were handpicked or shaken free onto tarps. The litter was then brought to the laboratory at Oregon State University and air dried at room temperature on mesh trays. The litter was labeled by the year it was collected, hereafter called a vintage. Subsamples of each vintage were oven dried to determine moisture content and provide samples for chemical analysis. The moisture content of these subsamples was measured and used to calculate the oven-dry weight equivalent for each litter bag sample. A portion of each sample was also sent to the Palmer Research Center at the University of Alaska Fairbanks for chemical analysis.

All litter bags were 20 cm X 20 cm with a polyester flag Oxford broadcloth lower panel, and a 1 mm mesh nylon netting upper panel. The litter bags were filled with a predetermined mass of one of three species of leaves—*P. menziesii* (PSME), *C. nuttallii* (CONU), or *A. macrophyllum* (ACMA). Each bag was labeled with a uniquely numbered aluminum tag, and sealed with non-ferrous MONEL staples.

Litter bags were then taken starting in 2003 to 14 sites of varying elevation, aspect, moisture regime, and forest cover in the HJA. At each site, five harvest groups with 2 litter bags each of vintage 2002 bigleaf maple, Pacific dogwood, and Douglas-fir were laid out in parallel lines in random order. Harvest groups were attached with braided nylon seine twine, which was anchored with a pin flag at each end in the field. In 2004, one harvest group was collected, and five vintage 2004 harvest groups were placed at each site (Figure 1). Harvest groups set out in 2004 and later contained two extra litter bags of vintage 2002 Douglas-fir to test the effects of annual climate variation on standardized litter. The same procedure was followed in 2005 (Figure 2), and in each consecutive year until 2009. At this point, harvest groups were still collected but no new litter bags were placed in the field. This design provided annual changes in leaf mass for 5 different time periods for each vintage of litter. It also tracked the decomposition rate of a controlled litter material, vintage 2002 Douglas-fir, throughout multiple years of exposure. This study examines the first year of decomposition for all vintages.

Laboratory

Upon collection each harvest group of litter bags was placed in a large plastic bag for transport to the lab and stored at 2°C until processed. During processing the litter was removed, weighed, and placed in labeled paper bags to be oven dried at 55°C. Bags with tears or large amounts of soil were noted. Moss and rocks were removed from bags if present. The empty paper bags were sorted by weight into 0.05 gram weight groups to minimize error due to variation in bag weight. Final dry weights were recorded for all samples, and moisture content was calculated as a percentage by subtracting the final dry weight from the initial wet weight and dividing by the final dry weight (Equation 1).

$$\text{Moisture Content (\%)} = 100 \times (\text{Wet Weight} - \text{Dry Weight})/\text{Dry Weight}. \qquad (1)$$

Figure 1- Litter bag layout at every site in the HJA in 2004.

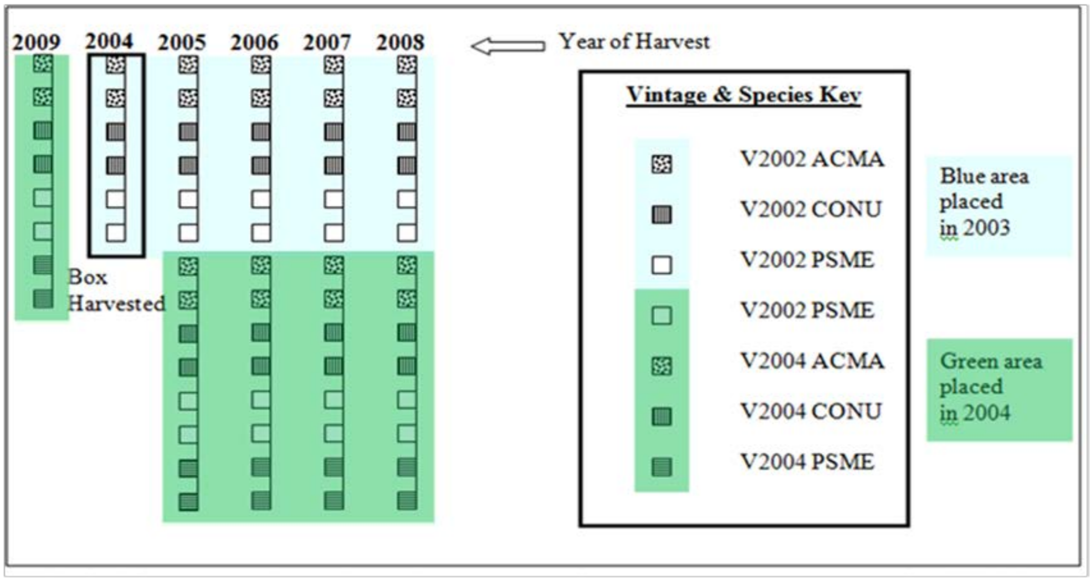
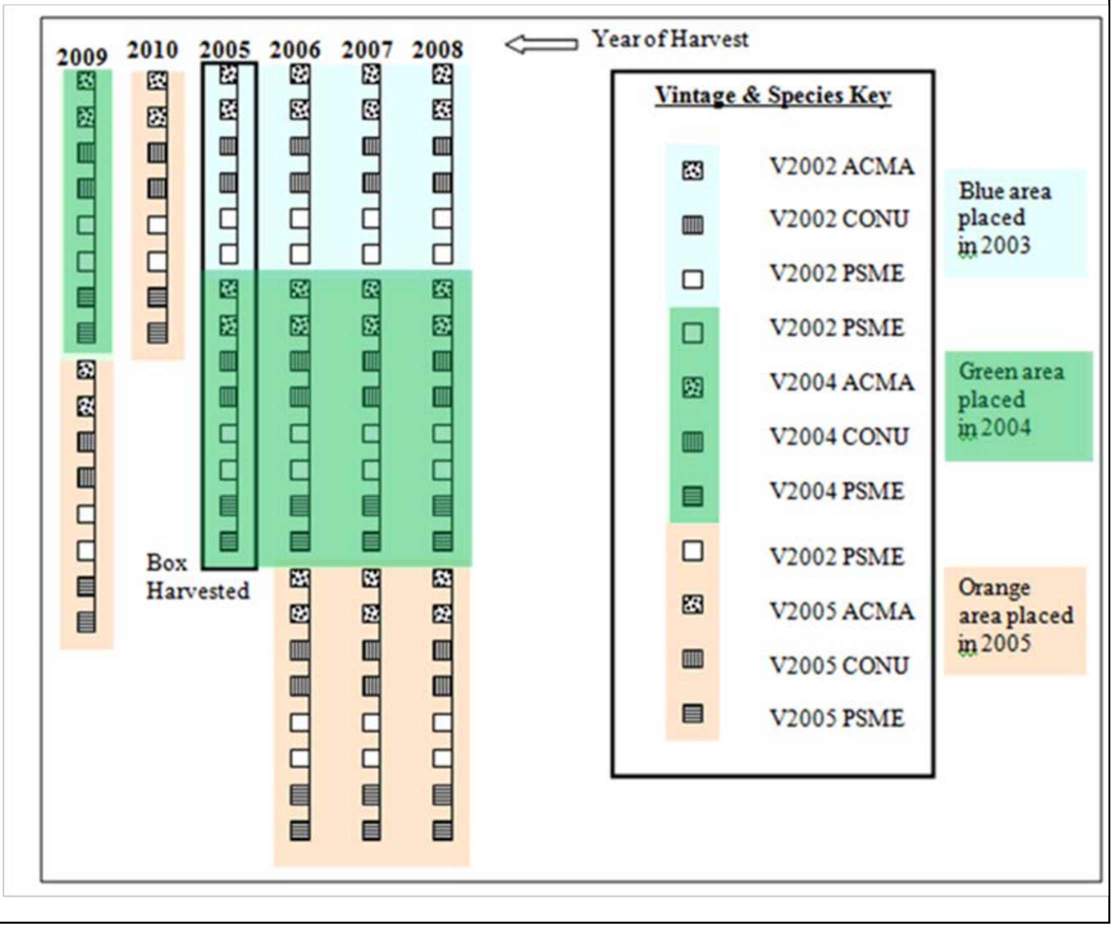


Figure 2- Litter bag layout at every site in the HJA in 2005.



Random samples were also selected for ash analysis using a random number generator to determine the ash content of samples. Representative samples were selected for each species, vintage, and number of years in the field. All of the site 12 samples that were visually judged to have large amounts of soil contamination were also selected. The samples were weighed before and after combustion in a muffle furnace at 500°C for one to two hours to determine percent ash. Samples were stored in desiccators whenever not in the muffle furnace to prevent the uptake of water from the air. Because of high and variable ash contents, sites 12 and 15 were excluded from all analyses.

Samples sent to the Palmer Research Center were analyzed for C, N, lignin, and ash content. Percent neutral detergent fiber (NDF) and acid detergent fiber (ADF) were also determined using the Van Soest method (Van Soest and Wine 1967, Van Soest et al. 1991). Lignin was then determined using the permanganate method (Parkås et al. 2007). Ash content was determined by combustion at 600°C for 12 hours. Carbon and nitrogen content were determined by a TruSpec CHN Macro elemental analyzer using duplicate 50 mg samples.

Mean daily temperature and precipitation values for the four primary meteorological stations and the Mack Creek Gauge Station in the HJA were obtained from the HJA data set at the Climate and Hydrology Database Projects (http://climhy.lternet.edu/) to assess the impact of climate variables on decomposition rates. Mean daily temperature values for the reference stands were obtained from the MS005 data set on the HJA website (http://andrewsforest.oregonstate.edu/data/abstract.cfm?dbcode=MS005&topnav=97).

Calculations and Statistics

The proportion of mass loss was calculated by dividing the final dry weight by the initial dry weight. These proportions were then used to calculate decomposition rates (k) for the three species of leaves. Decomposition of plant organic matter can be described using a simple exponential decomposition model where M_t is the mass remaining at time t, M_0 is the initial mass, and k is the instantaneous fractional rate loss or decomposition rate-constant (Equation 2, Olson 1963). The basic decomposition model was then transformed to a semi-natural logarithm scale and used to calculate first-year k values from M_t and M_o (Equation 3). All k values were based on t=1 year in this study. Average first year k values per species, per year, and per site were calculated from the average percent mass remaining values. It should be noted that averaging all first year k values yielded a slightly different result.

$$M_t=M_0e^{-kt} \tag{2}$$

$$Ln(M_t/M_0)/t=-k \tag{3}$$

To fill in missing data at the climate stations, regression coefficients were calculated among all sites from daily mean temperature and precipitation values, and the correlations with the highest coefficients were used to fill in any missing data points from climate stations. This method was also used for all Reference Stand 01 data points, which was discontinued in 1995, but had a strong correspondence to the climate station at Reference Stand 02. Because the samples were placed in the field in November, the “year” period for 2004 was from November 2003 until October 2004. All climatic data was calculated using this November-October period.

To test the degree that substrate quality changed from year to year, five two-sample, two-tail t-tests were used to compare vintage 2002 Douglas-fir with all other vintages of Douglas-fir. Given that substrate quality, as well as climate, changes from year to year, the effect of vintage was examined for Douglas-fir litter. All statistical tests with a p-value <0.05 were considered significant.

To determine the effect that substrate quality had on first year decomposition rates, various substrate quality indices (such as lignin:N) were plotted against first year *k* values. This data was transformed to a natural logarithm scale to generate a linear regression equation, yielding estimated parameters of the slope (*m*) and the y-intercept (*b*) (Equation 4). The linear equation was then back transformed to yield a regression model, where *x* is the modeled lignin:N ratio and *k* is the first year decomposition rate (Equation 5).

$$lnk=m*lnX+b \tag{4}$$

$$k=x^{m}*e^{b} \tag{5}$$

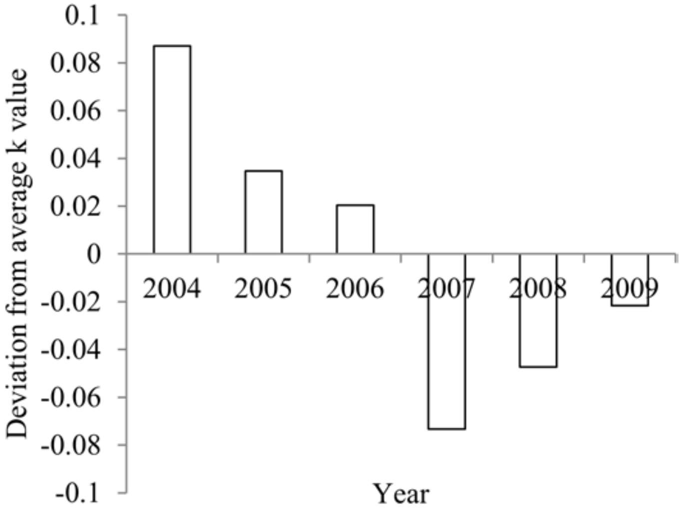
To test the response of decomposition to several key climate variables, regression analyses between mean annual temperature and mean first year *k*, and between total annual precipitation and mean first year *k* were performed. Regressions between mean annual temperature and precipitation at each site and mean first year *k* were also calculated to test how climatic differences among sites might influence decomposition. Two sample, two-tailed t-tests were also used to compare site 1 first year *k* rates to site 2 first year *k* rates to compare a shaded site to a sun-exposed site.

To test the degree of decomposition synchrony among the 14 sites, Pearson’s product moment correlation coefficients (r) between the *k*’s for each site for all the species and vintages were calculated. These were also calculated for each species to avoid possible confounding of species differences and temporal variation in these correlations. Correlations were ranked as high, moderate, or low based on the value of r to gain insight as to which sites were responding similarly. Correlation coefficients greater than 0.811 and having p-values lower than 0.05 were ranked as high, those between 0.811 and 0.729 and having p-values between 0.05 and 0.10 were ranked as moderate, and those less than 0.729 and having p-values greater than 0.10 were ranked as low. Every correlation except for those with Site 4 had 6 data points and four degrees of freedom. Correlations involving site 4 had one fewer data point, and therefore one fewer degree of freedom. The correlation coefficients for Site 4 were ranked as high if greater than 0.878 and having p-values lower than 0.05, moderate if between 0.878 and 0.805 and having p-values between 0.05 and 0.10, and low if less than 0.805 and having p-values greater than 0.10.

RESULTS

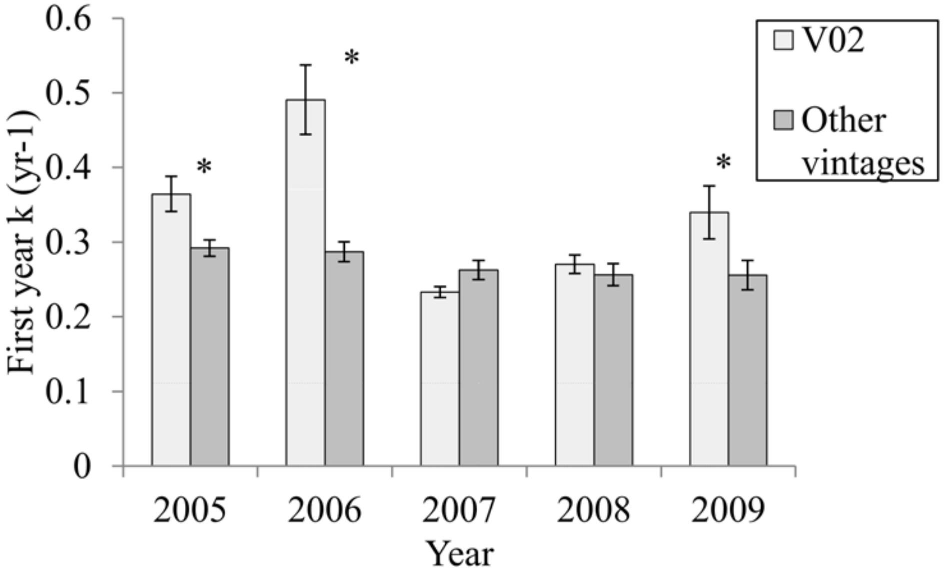
There was up to five-fold variation in *k* depending on the species and year decomposition occurred. The average first year decomposition rate of all species combined for 2004-2009 was 0.459 yr^{-1}. The fastest rate of decomposition for all species combined occurred in 2004, with a *k* value of 0.546 yr^{-1}, and the slowest rate of decomposition occurred in 2007, with a *k* value of 0.386 yr^{-1} (Figure 3). The average first year *k* value for bigleaf maple was 0.319 yr^{-1}, with a range from 0.228 yr^{-1} in 2006 to 0.378 yr^{-1} in 2009. The average first year *k* value for Pacific dogwood was 1.11 yr^{-1}, with a range from 0.904 yr^{-1} in 2007 to 1.46 yr^{-1} in 2006. The average first year *k* value for Douglas-fir was 0.297 yr^{-1}, with a range from 0.247 yr^{-1} in 2009 to 0.378 yr^{-1} in 2004. For vintage 2002 Douglas-fir, the fastest rate of decomposition occurred in 2006, with a *k* value of 0.453 yr^{-1}, and the slowest rate of decomposition occurred in 2007, with a k value of 0.235 yr^{-1} (Figure 4).

Figure 3- Deviation from the average first year decomposition rate (*k*) at all sites



Substrate quality indices varied among the species examined and among the different vintages of Douglas-fir (Table 2). The undecomposed litter samples had C concentrations ranging from 44.6% to 52.6 %, with an average of 48.5 %, and N concentrations ranging from 0.42% to 0.86% with an average of 0.65%. Douglas-fir

Figure 4- First year decomposition rates for vintage 2002 PSME and all other PSME vintages by year in the field[1]



[1] where year in the field is vintage +1 for all vintages except 2002.
* denotes statistical significance at $p<0.05$ level.

had the highest average C concentration of 52.1%, followed by bigleaf maple with 48.3%, and Pacific Dogwood with 44.7%. Bigleaf maple had the highest N concentration of 0.75%, followed by Pacific Dogwood with 0.69%, and Douglas-fir with 0.49%. The NDF concentration ranged from 20.1% to 61.1% with an average of 41.6%, and ADF concentration ranged from 14.0% to 49.4% with an average of 31.6%. Bigleaf maple had the highest concentration of NDF with 55.4%, followed by Douglas-fir with 48.1%, and Pacific dogwood with 21.2%. Bigleaf maple also had the highest concentration of ADF with 42.0%, followed by Douglas-fir with 37.7%, and Pacific dogwood with 15.2%. Lignin concentration ranged from 3.1% to 26.3%, with an average of 15.0%. Bigleaf maple had the highest lignin concentration with a value of 22.0%, followed by Doulas-fir with 19.5%, and Pacific dogwood with 3.4%. The average lignin:N ratio was 29.5 for bigleaf maple, 5.0 for Pacific dogwood, and 40.2 for Douglas-fir. The lowest lignin:N

Table 2-Litter chemistry information for every vintage of bigleaf maple, Pacific dogwood, and Douglas-fir litter collected from the H. J. Andrews Experimental Forest

Species and vintage	% C	% N	%NDF[1]	%ADF[2]	%lignin	Lignin:N
ACMA02	47.68	0.71	53.57	39.33	19.61	27.58
ACMA04	46.50	0.86	55.20	40.46	20.93	24.25
ACMA05	49.81	0.65	53.75	44.47	24.42	37.65
ACMA06	49.02	0.80	52.91	41.06	22.99	28.82
ACMA07	49.21	0.81	61.14	49.40	26.28	32.61
ACMA08	47.52	0.68	55.88	37.13	17.76	25.98
CONUO2	45.11	0.65	20.11	13.97	3.17	4.83
CONUO4	44.79	0.81	21.56	15.72	3.53	4.35
CONUO5	45.37	0.77	20.30	14.02	3.24	4.23
CONUO6	46.20	0.60	20.91	15.14	3.75	6.26
CONU07	45.33	0.68	22.78	16.76	3.56	5.27
CONU08	44.59	0.65	21.47	15.35	3.05	4.75
PSME02	51.64	0.46	43.51	34.34	17.99	39.35
PSME04	52.62	0.42	47.80	40.06	21.06	50.14
PSME05	52.14	0.44	46.10	35.48	18.01	41.34
PSME06	51.27	0.54	43.57	32.20	16.13	29.99
PSME07	52.49	0.53	52.12	41.04	21.49	40.97
PSME08	52.59	0.58	55.26	43.04	22.50	38.91

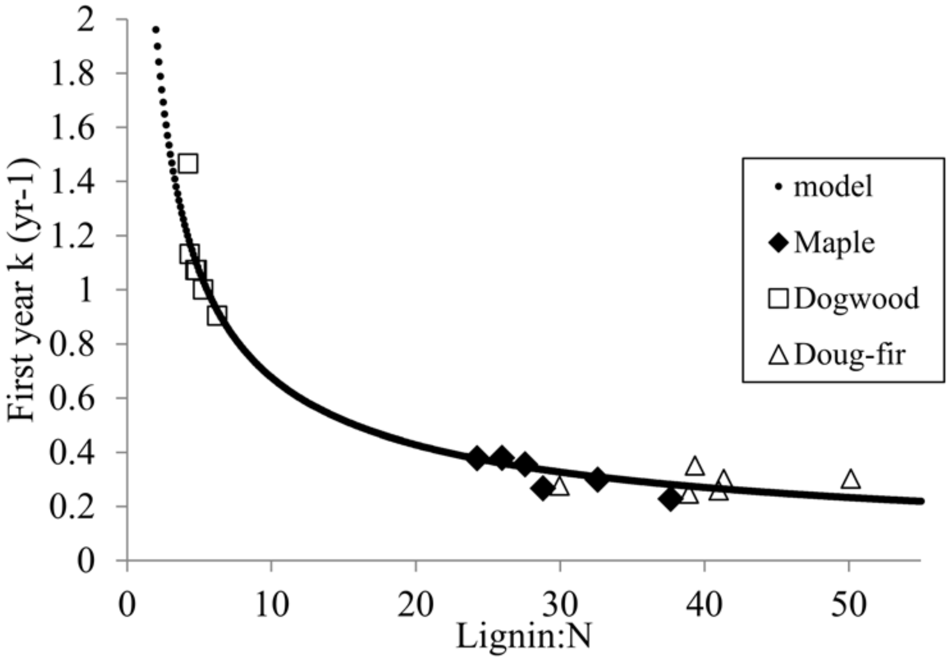
[1] Neutral detergent fiber [2] Acid detergent fiber

ratio for bigleaf maple was 24.2, and the highest was 37.7. The lowest lignin:N ratio for Pacific dogwood was 4.2, the highest was 6.3. The lowest lignin:N ratio for Douglas-fir was 30.0, the highest was 50.1.

The difference in first year *k* among species was explained in part by variations in litter quality. The lignin:N ratio was the litter chemistry factor that best explained first year decomposition variation, displaying an exponential decomposition curve when plotted (Figure 5). The natural logarithm transformed data generated the equation *k*=-0.6612*(Lignin:N)+1.132, yielding an r^2 value of 0.953 (Figure A-1, Appendix A). The back transformed model displayed the observed relationship between lignin:N and first year *k* in the graph closely (Figure 5). When the species were considered separately, Pacific dogwood and Bigleaf maple had significant regressions but Douglas-fir did not.

Other substrate quality indices were also examined. Both lignin and carbon content explained first year *k* variation, but neither as well as the lignin:N ratio (Figures A-2 and A-3, Appendix A). It should be noted that lignin and carbon concentration were related, as lignin has higher carbon content than cellulose or hemicellulose, suggesting that the form of the carbon and not the amount was most important for first year decomposition (Figure A-4, Appendix A). The C:N ratio and N content showed no relationship with first year *k*.

Figure 5- Response of 1st year *k* to Lignin:N averaged over all sites



The two-sample t-test showed significant differences in *k* values between vintage 2002 Douglas-fir and most other vintages (P values: V04= 0.0074, V05=9.4x10^{-5}, V06=0.053, V07=0.48, V08=0.045). Neither the difference between vintage 2006 and vintage 2002 Douglas-fir, nor the difference between vintage 2007 and vintage 2002 Douglas-fir was statistically significant. In general, vintage 2002 Douglas-fir decomposed faster than other vintages of Douglas-fir (Figure 4). Vintage 2002 Douglas-fir's lignin:N ratio was the middle lignin:N ratio of all Douglas-fir vintages, with a ratio of 39.4 (Table 2). The other vintages with lower lignin:N ratio were vintage 2006 (set out in 2007), with a ratio of 30.0, and vintage 2008 (set out in 2009), with a ratio of 38.9. Vintage 2006 was the only vintage to decompose faster than vintage 2002 Douglas-fir with a p-value of 0.053, although not quite to a level of statistical significance (Figure 4). Although vintage 2008 had a slightly lower lignin:N ratio, its *k* was still significantly greater than vintage 2002's *k*.

As expected, average annual temperature and precipitation varied over the period of the experiment. The mean annual temperature for the 2004-2010 period was 7.93°C. The warmest year was 2004, with an average temperature of 8.42°C, and the coldest year was 2008, with an average temperature of 7.09°C (Figure 6). The mean annual precipitation for the 2004-2010 period was 195.4 cm. The driest year was 2005, with a total precipitation of 168.6 cm, and the wettest year was 2007, with a total precipitation of 222.3 cm (Figure 7).

Figure 6- Yearly temperature variation at the H. J. Andrews Experimental Forest

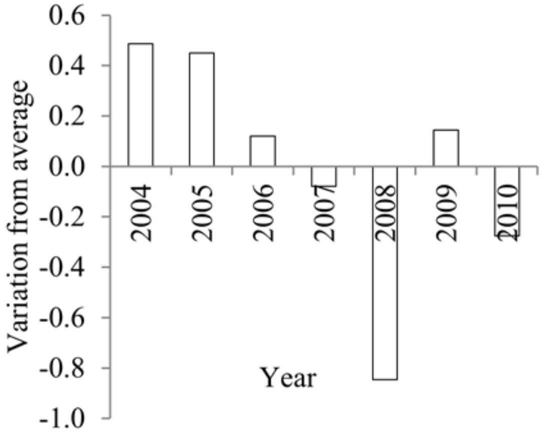
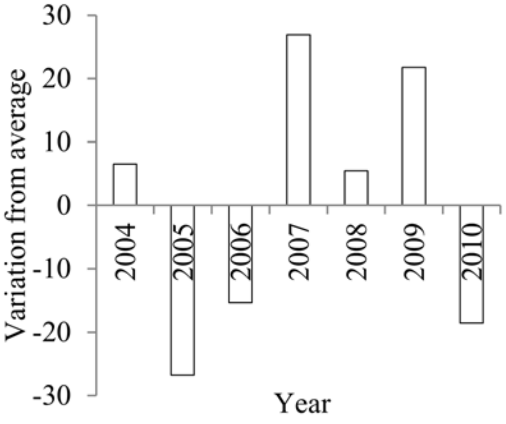
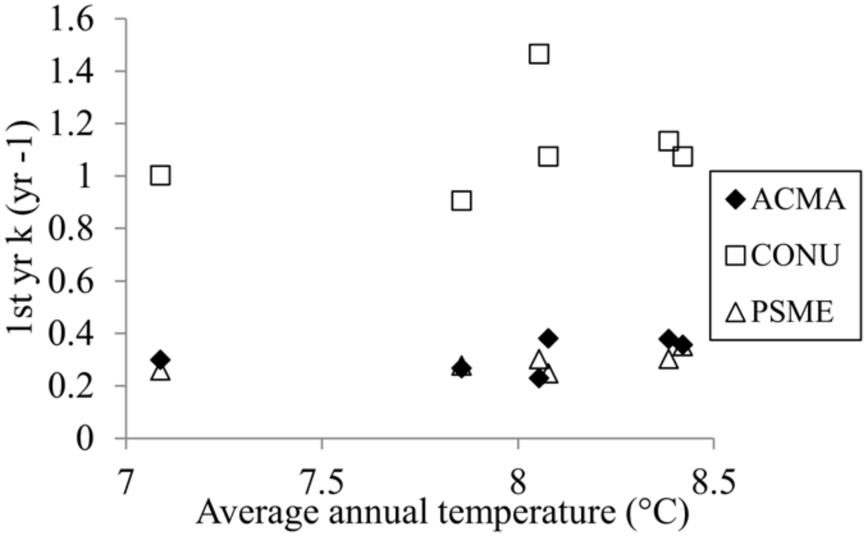


Figure 7- Yearly precipitation variation at the H. J. Andrews Experimental Forest



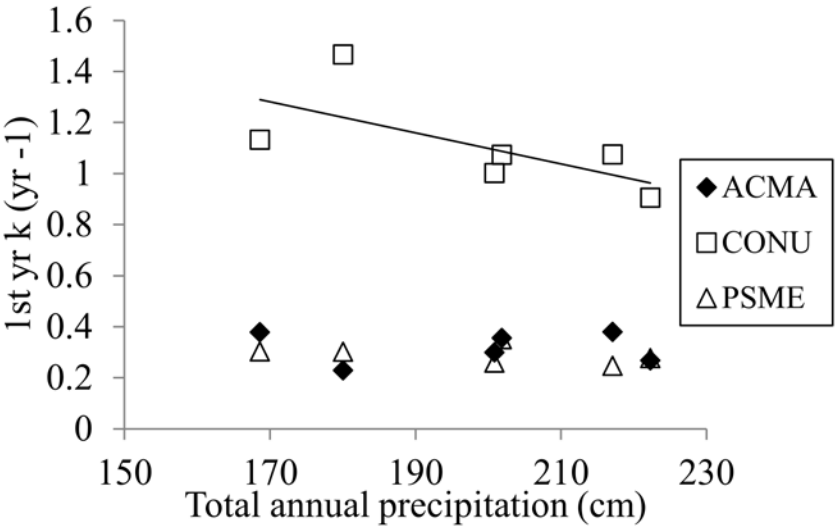
Little or no relationship was found between temperature and first year *k* or precipitation and first year *k* alone (Figure 8 and Figure 9). None of the regressions of either temperature versus first year *k* or precipitation versus first year *k* were significant (Table 3). A slight positive trend between temperature and first year *k* suggests a possible direct relationship between the two variables, and a slight negative trend between precipitation and first year *k* suggests a possible inverse relationship between the two variables; perhaps because wetter years are generally colder than drier years. Therefore increased total annual precipitation may be related to a lower mean annual temperature. No or little relationship was found either when comparing first year *k* to mean annual temperature or total annual precipitation by site and species (Figure 10 and Figure 11). Neither the regression of mean annual temperature and first year *k* nor the regression of total annual precipitation and first year *k* were significant (Table 4).

Figure 8- Response of 1st year *k* to average annual temperature averaged across all sites[1]



[1] No relationships were significant (Table 3).

Figure 9- Response of 1st year *k* to total annual precipitation averaged across all sites[1]



[1]CONU was almost significant while ACMA and PSME were not significant (Table 3).

Table 3-Regression analysis results for first year decomposition versus temperature and precipitation averaged across sites

Temperature-1st year *k*	R^2	Adjusted R^2	F statistic	P-value	Standard error
ACMA	0.1124	-0.1835	0.3799	0.5813	0.0734
CONU	0.1416	-0.1445	0.4949	0.5324	0.2282
PSME	0.4066	0.2583	2.7411	0.1782	0.0323
2002 PSME	0.2701	0.0876	1.4798	0.2907	0.0693
Precipitation-1st year *k*					
ACMA	0.0004	-0.2495	0.0016	0.9702	0.0706
CONU	0.4366	0.2958	3.100	0.1531	0.1607
PSME	0.1620	-0.0475	0.7731	0.4289	0.0383
2002 PSME	0.5899	0.4873	5.7526	0.0745	0.0520

Since the substrate quality of vintages varied, it is possible that the lack of relationship to climate variables was caused by differences in substrate quality. When vintage 2002 Douglas-fir first year decomposition rates were used in regressions against mean annual temperature and total annual precipitation, a stronger relationship resulted (Figure 12 and Figure 13). Neither regression was statistically significant, yet they showed much stronger evidence for a relationship than did the regressions using all of the species and vintages (Table 3). The negative relationship between vintage 2002 Douglas-fir first year *k* and precipitation had a p-value of 0.0745, which was close to significant. The stronger positive trend between temperature and vintage 2002 Douglas-fir first year *k* suggested a direct relationship between the two variables.

Figure 10- Response of 1st year *k* to average annual temperature by site and species

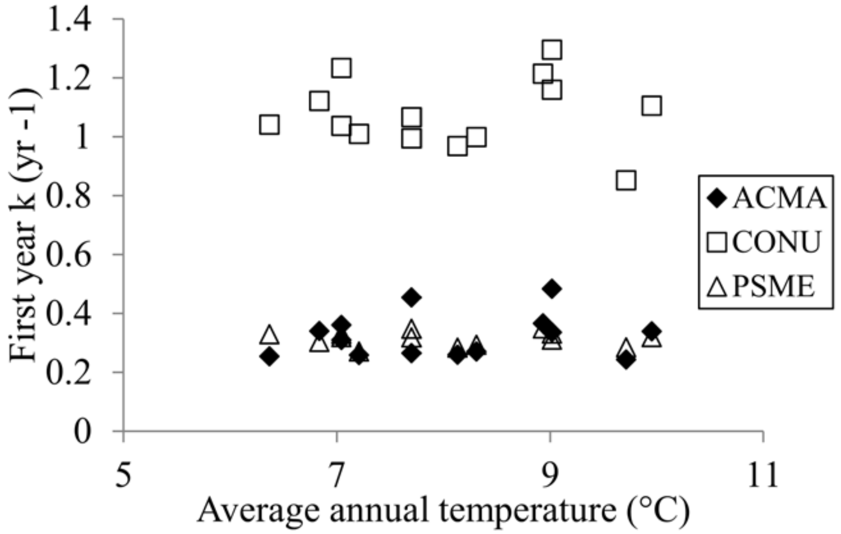


Figure 11-Response of 1st year *k* to total annual precipitation by site and species

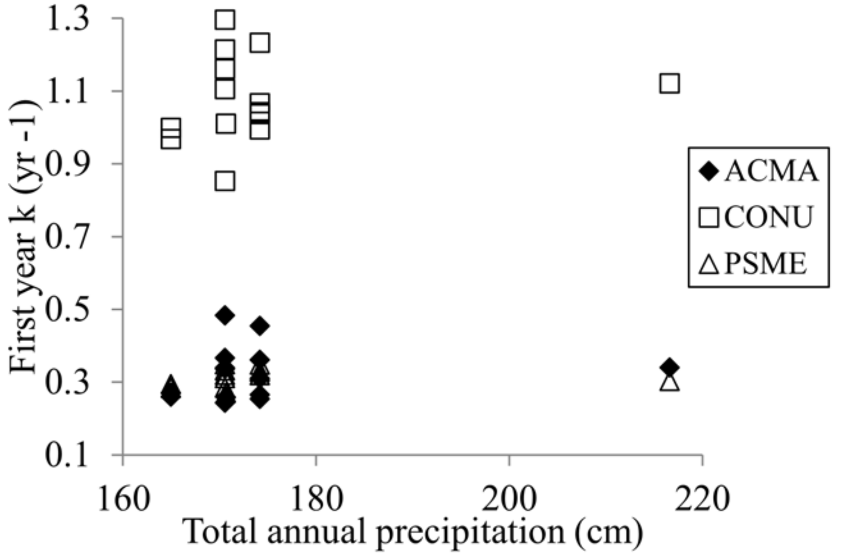


Table 4-Regression analysis results for all species first year decomposition rate versus temperature and precipitation by site

All species and vintages by site	R^2	Adjusted R^2	F statistic	P-value	Standard error
Temperature	0.0096	-0.0730	0.1157	0.7396	0.0591
Precipitation	0.0165	-0.0655	0.2009	0.6620	0.0589

Site 1 and site 2 were compared to test the effect of sun exposure on decomposition. Site 1 had 100% open sky and site 2 had 25% open sky, but they were located less than 500m away from each other (Table 1). The t-test comparison of site 1 first year decomposition rates to site 2 first year decomposition rates was not significant when all species were included (p-value 0.328). When separate t-tests were run by species, Pacific dogwood and Douglas-fir were still not significant (p-values 0.267 and 0.553 respectively). However, bigleaf maple decomposition rates were significantly faster at site one than site two (p-value < 0.01).

When all species were included in decomposition correlations between sites, all the correlation coefficients were significant and positive (Table B-1, Appendix B). However, some of these correlations appeared to depend on the consistent differences among species. However, when broken up by species, the correlation coefficients were much more variable. For bigleaf maple, 13 of the possible correlation coefficients were rated as strong, 6 moderate, and 72 weak (Table B-2, Appendix B). For Pacific dogwood, 20 of the possible correlation coefficients were rated as strong, 8 moderate, and 63 weak (Table B-3, Appendix B). One of the strong coefficients and one of the moderate coefficients were negative, suggesting decomposition rates at these sites were inversely related. For Douglas-fir, 16 of the possible correlation coefficients were rated as strong, 14 moderate, and 61 weak (Table B-4, Appendix B).

Figure 12- Response of vintage 2002 PSME first year *k* to mean annual temperature

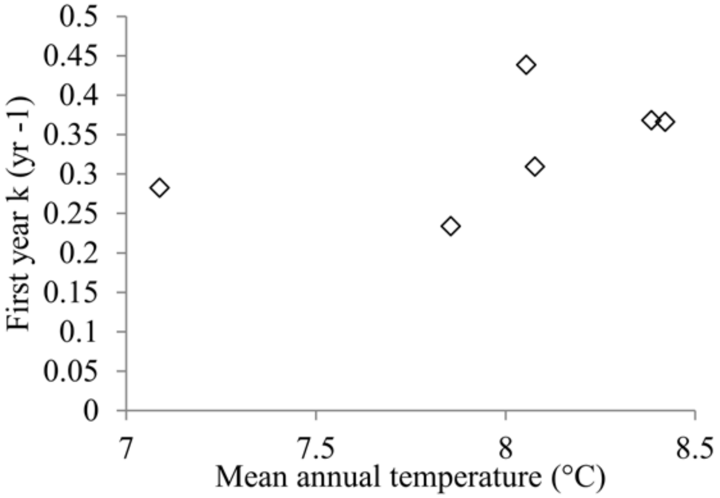
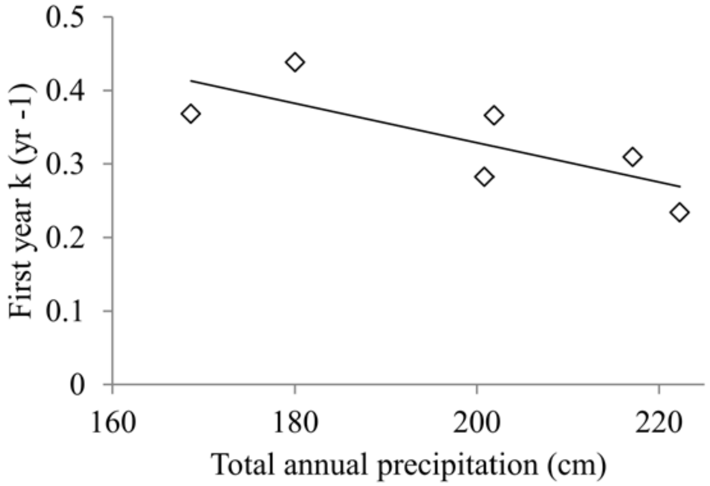
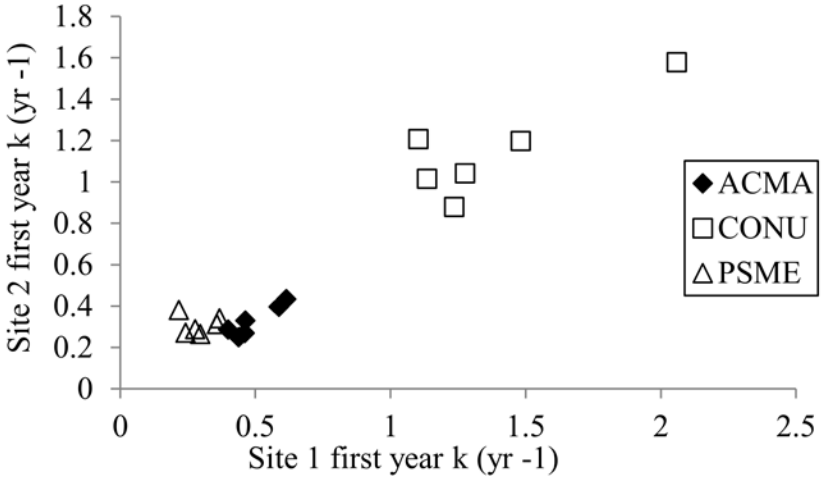


Figure 13- Response of vintage 2002 PSME first year *k* to total annual precipitation



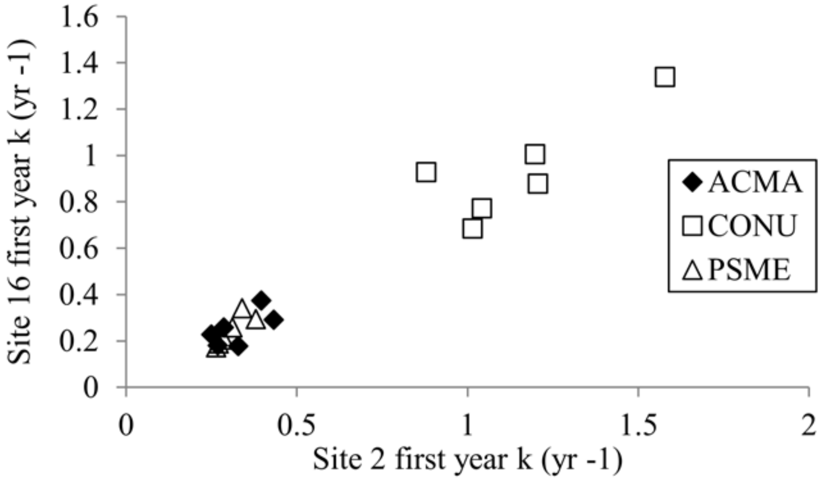
No consistent pattern of synchrony among sites and species was observed. For example, the correlations of site 1 and site 2 for bigleaf maple and Pacific dogwood were both statistically significant, but for Douglas-fir was not (Figure 14). The correlations of site 2 and site 16 for Pacific dogwood and Douglas-fir were both statistically significant, but for bigleaf maple was not (Figure 15). The correlations for site 11 and site 14 for bigleaf maple and Douglas-fir were both statistically significant, but for Pacific dogwood was not (Figure 16). Two correlations were statistically significant for bigleaf maple and Pacific dogwood, four for Pacific dogwood and Douglas-fir, and one for bigleaf maple and Douglas-fir. No correlation was significant for all three species.

Figure 14- Correlation of site 1 first year *k* and site 2 first year *k*



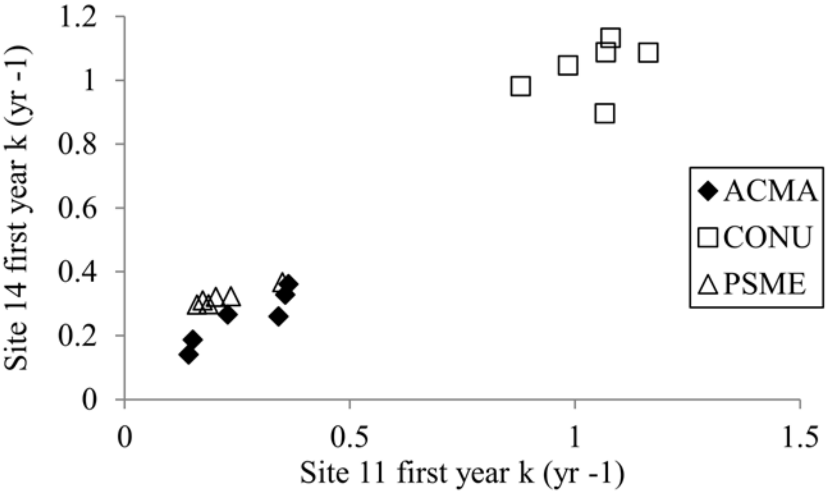
The ACMA and CONU regressions were both significant.

Figure 15- Correlation of site 2 first year *k* and site 16 first year *k*



The CONU and PSME regressions were both significant.

Figure 16- Correlation of site 11 first year *k* and site 14 first year *k*



The ACMA and PSME regressions were both significant.

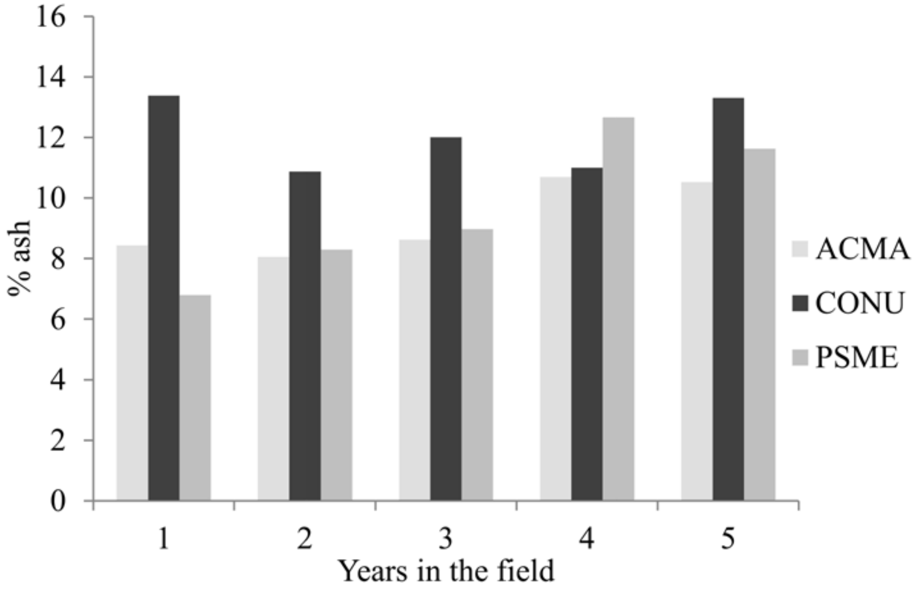
DISCUSSION

First year litter decomposition rates in the HJA across species were responsive to substrate quality, but not to climate. Differences in decomposition rates were best explained by lignin:N ratios, which were consistently different among species and vintages (Table 2). The effects of climate on first year *k* were clearest when vintage 2002 Douglas-fir was considered alone, but none of the relationships were significant among years or sites. Some first year decomposition synchrony was observed, but this was inconsistent and generally weak. Several factors could account for the lack of climate effect, and therefore lack of synchrony among sites.

First year *k* values in this study were similar to values obtained in other leaf litter decomposition studies in the HJA for bigleaf maple, Pacific dogwood, and Douglas-fir. Fogel and Cromack found an average decomposition rate of 0.26 yr^{-1} for Douglas-fir (1976), and Valachovic et al. found an average first year decomposition rate of 0.27 yr^{-1} for Douglas-fir (2004). These values varied 14.2% and 10.0% from the average Douglas-fir first year decomposition rate obtained in this study, respectively. Valachovic et al. also found a first year decomposition rate of 0.34 for bigleaf maple and 1.02 for Pacific dogwood (2004). These varied only 6.18% and 8.82% from the average first year decomposition rates in this study, respectively.

When ash content analysis was run on the decomposed litter samples, a wide range of ash contents was recorded. This could have caused an underestimation of the mass lost while in the field, as percent mass remaining values were not ash corrected. Sites 12 and 15, which had greater than average ash contents, were not used in analyses to avoid this problem. To have a directed effect on *k* values, ash error would need to be nonrandom and consistently biased. Generally, ash content seemed to increase with the number of years of decomposition for bigleaf maple and Douglas-fir, although not for Pacific dogwood (Figure 17). The average first year ash content for bigleaf maple was 8.45%, for Pacific dogwood was 13.38%, and for Douglas-fir was 6.80%. Even a doubling in ash content at this level would only result in an ≈18% change in *k* on average, which is far below the observed variation in *k* (as stated in the results, up to fivefold variation). Average ash contents do not appear to be large enough to affect *k* greatly.

Figure 17-Average ash content for each species by the number of years decomposing in the field.



This study analyzed first year decomposition of leaf litter, but full decomposition of litter may take many years (Harmon et al. 2009). Subsequent years of decomposition may respond differently to climate and substrate quality. The longer the decomposition period, the less substrate quality and climate can explain *k* (Currie et al. 2010). The decomposition rate does not always remain constant over time. Leaf and root litter often undergo two phases of decomposition—an initial fast phase followed by a slow phase. (Harmon et al. 2009). This model can be described by a dual exponential model, where M_t is the mass remaining at time t, M_f is the mass of material that decomposes is the fast phase, k_f is the decomposition rate during the fast phase, M_s is the 1-M_f (the mass that decomposes in the slow phase), and k_s is the decomposition rate during the slow phase (Equation 5).

$$M_t=M_f*e^{-kf*t} + M_s*e^{-ks*t} \tag{5}$$

Initial analyses show similar M_s values among sites, but variable k_s values. This suggests that first year k is less responsive to climate, and more responsive to substrate quality than longer term k.

Differences in climate among sites and years would be expected to cause decomposition rates to vary in space and time. However, this was not reflected in the first year decomposition values in this study. Variation from year to year in k was observed, but was not explained by climate. This may have been because the climatic differences between 2004 and 2009 were not variable enough to show a response in decomposition rates. Additionally, climate was approximated at sites based on the availability of climate station data. This did not account for microclimate differences, which may drive decomposition rates within a landscape more than macroclimate differences (which do not vary to the same degree). Yet, when two adjacent sites were compared with very different microclimates, they were neither consistently nor significantly different (site 1 versus site 2). Although site 1 had 100% open sky and site 2 had only 25% open sky (Table 1), decomposition rates were not significantly different between the sites for Pacific dogwood, Douglas-fir or when all species were included. Bigleaf maple decomposition rates were the exception- *k* values were significantly faster at site one, the open site, than site two.

Another potential explanation for the lack of climate response was that precipitation was used as an index for moisture. Decomposition responds to moisture, not precipitation, which is determined by more than simply rainfall. The approximation of moisture represented by precipitation may not have been totally accurate. Also, the total annual precipitation value lacks a seasonal component, which may be important. Heavy rainfall during the winter will not be enough to make up for an extraordinarily dry summer, which could affect decomposition rates.

While this study did not find a significant response of first year decomposition to climate, that does not mean that decomposition is truly insensitive to climate. Studies have found that at the global scale, climate expressed as actual evapotranspiration exerts the strongest influence on litter decomposition, and at the local scales, litter chemistry exerts the strongest influence (Meentemeyer, 1978, Berg et al. 1993, Aerts 1997). In contrast, Prescott (2010) found that climate and substrate quality thresholds exist at which one factor becomes rate-controlling. Below a mean annual temperature of 10°C, and above a lignin:N ratio of 40, decomposition is uniformly low. At temperature above 10°C and lignin:N ratios below 40 decomposition may be slow or fast depending on other factors.

First year litter decomposition in the HJA showed a major response to lignin:N. Differences among lignin:N in species, and even vintages of the same species, exerted a strong influence on first year *k* (Figure 5). Because the experimental design did not control for litter quality, this could have masked the climate signal. The first year *k* for vintage 2002 Douglas-fir, the only vintage to be set out every year, showed a much stronger response to climate for years and for sites. Additionally, evergreen litter is formed in an earlier year than it falls, so there could be a disconnection between the effect of climate on litter quality and the effect of climate on decomposition in a different year. Litter was only collected from one place, though results indicate that litter at different sites may vary greatly in substrate quality (Table 2).

However, even if vintage was controlled, the decomposition response among sites could be inconsistent. This would indicate that local factors, such as the decomposer community, were interacting with the litter. The decomposer communities were not examined or quantified at any site. Differences in these communities could have accounted for some of the differences, or lack thereof, between *k* values among sites. The composition of local soil fauna has been found to substantially modify *k* values among sites (Coûteaux et al. 1995, Coûteaux et al. 1998). If substantial differences in decomposers existed between sites, this could account for the lack of response to climate.

Although no significant response to climate was found, a strong relationship between litter quality and first year *k* was found. In this study, substrate chemistry (lignin:N) was the best explanatory variable for first year decomposition. The significant difference between vintage 2002 Douglas-fir first year *k* values and other vintages' first year *k* values demonstrates the importance of fluctuations in litter quality. Based on my results, first year decomposition in the HJA does not appear to be synchronous. This implies that variation in first year *k* values year to year is mostly random in regards to climate, although the correct index for climate may not have been used. Random variation among local sites may dampen the landscape level variation in decomposition rates. This means that although first year decomposition may vary widely by site, it may remain fairly static on the landscape level. The lack of synchrony in first year decomposition rates at the HJA suggests that localized decomposition rates should not be extrapolated across a complex, mountainous landscape.

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APPENDICES

Appendix A

Figure A-1- Ln lignin:N ratio versus 1st year decomposition rate

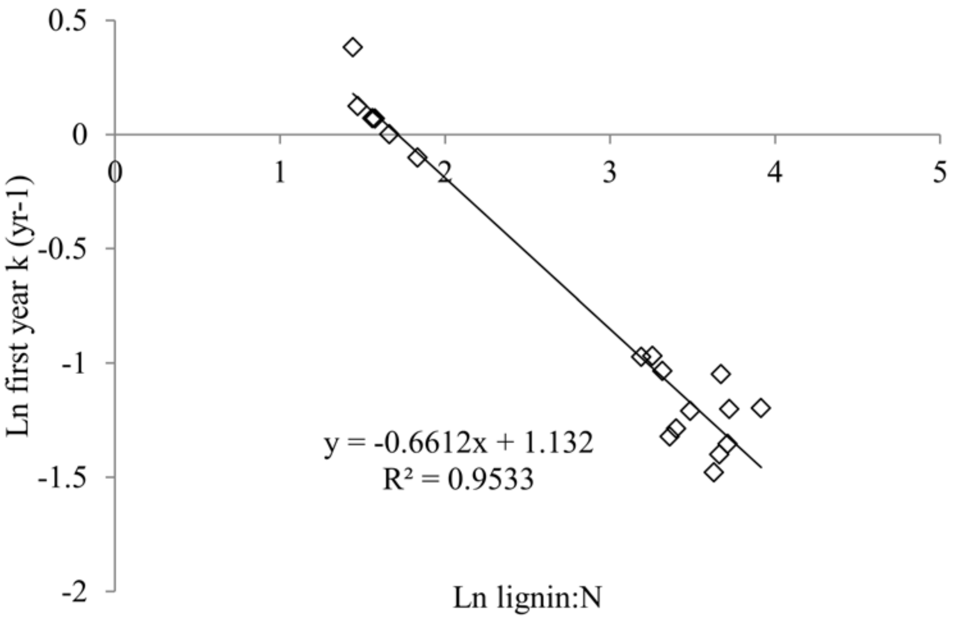


Figure A-2- Response of 1st year decomposition rate to lignin concentration.

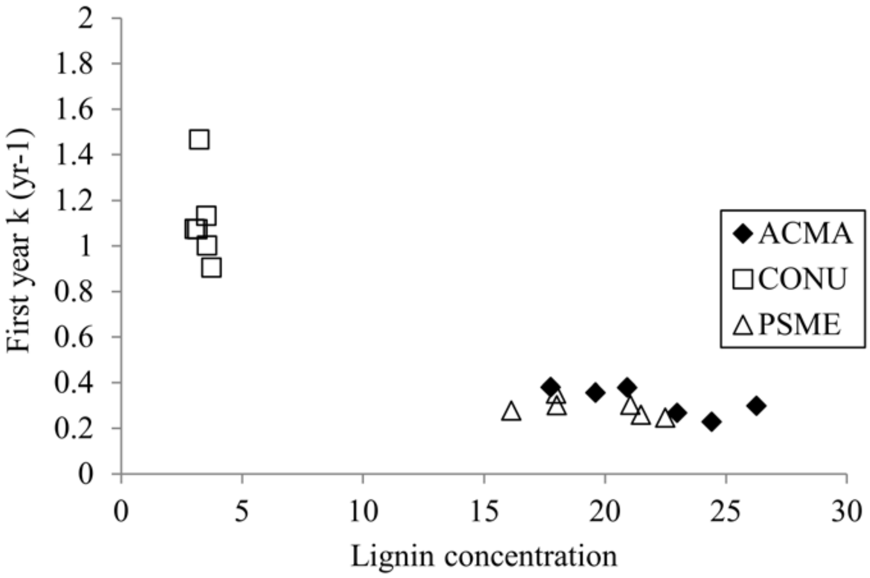


Figure A-3- Response of 1st year decomposition rate to C concentration.

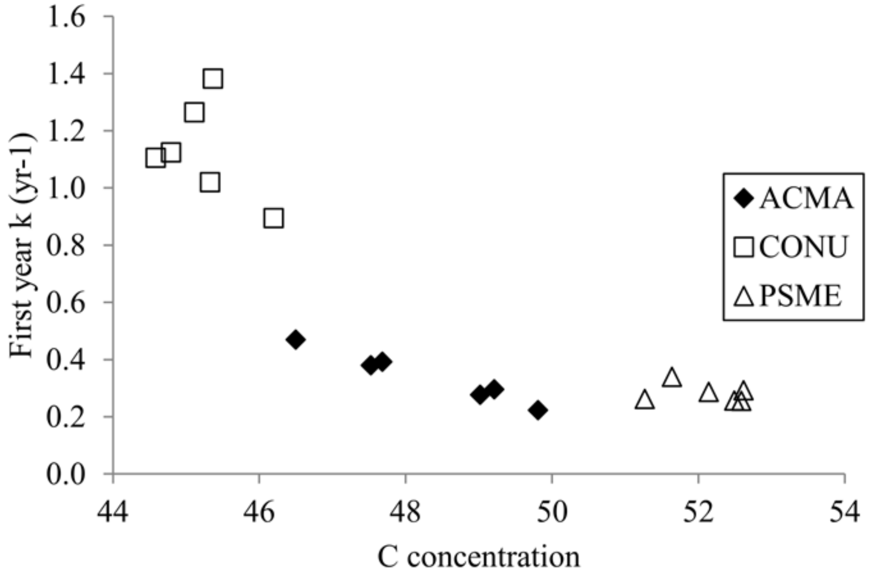
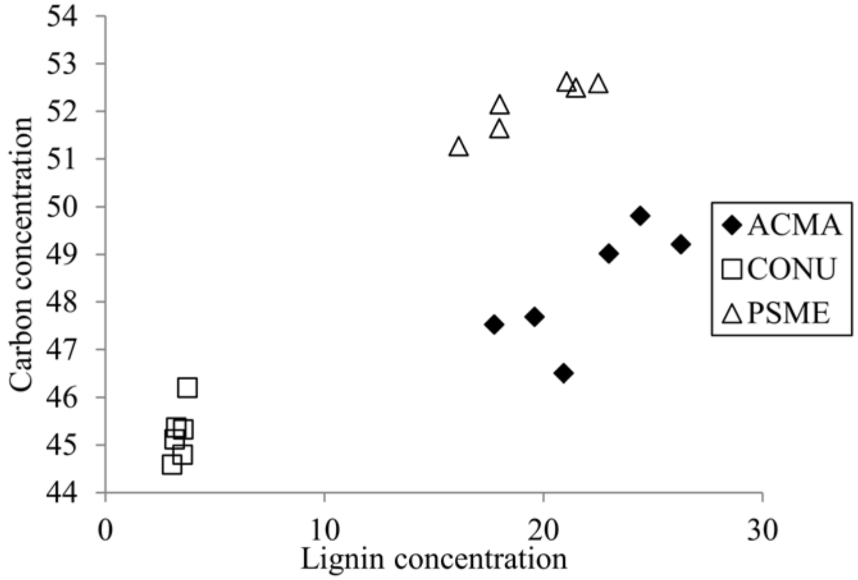


Figure A-4- Carbon concentration versus lignin concentration.



Appendix B

Table B-1- Correlation coefficients for first year *k* at all sites, for all species.

site	1	2	3	4	5	6	7	8	9	10	11	13	14
1	1												
2	0.965*	1											
3	0.8448*	0.906*	1										
4	0.953*	0.945*	0.833*	1									
5	0.966*	0.969*	0.915*	0.963*	1								
6	0.957*	0.972*	0.93*	0.939*	0.981*	1							
7	0.916*	0.969*	0.92*	0.937*	0.957*	0.969*	1						
8	0.878*	0.946*	0.964*	0.840*	0.918*	0.940*	0.944*	1					
9	0.904*	0.964*	0.902*	0.885*	0.930*	0.935*	0.959*	0.931*	1				
10	0.872*	0.933*	0.977*	0.833*	0.919*	0.937*	0.931*	0.981*	0.943*	1			
11	0.913*	0.960*	0.971*	0.880*	0.946*	0.955*	0.949*	0.987*	0.940*	0.988*	1		
13	0.975*	0.984*	0.892*	0.972*	0.985*	0.980*	0.965*	0.907*	0.953*	0.905*	0.933*	1	
14	0.852*	0.918*	0.977*	0.810*	0.908*	0.916*	0.906*	0.976*	0.934*	0.989*	0.979*	0.889*	1
16	0.97*	0.975*	0.86*	0.913*	0.957*	0.963*	0.929*	0.911*	0.935*	0.896*	0.923*	0.973*	0.883*

* denotes high correlation, statistically significant.

Table B-2- Correlation coefficients for bigleaf maple first year *k* at all sites.

site	1	2	3	4	5	6	7	8	9	10	11	13	14
1	1												
2	0.921**	1											
3	-0.070	0.018	1										
4	0.015	0.173	0.911**	1									
5	0.347	0.423	0.678	0.822*	1								
6	0.139	0.115	0.916**	0.718	0.604	1							
7	0.312	0.320	0.721	0.859*	0.802*	0.605	1						
8	0.540	0.809*	0.332	0.548	0.538	0.210	0.467	1					
9	0.617	0.463	-0.513	-0.296	-0.075	-0.455	0.187	0.118	1				
10	0.744*	0.887**	0.165	0.243	0.229	0.217	0.286	0.854**	0.280	1			
11	0.715	0.904**	0.318	0.430	0.470	0.331	0.399	0.941**	0.141	0.955**	1		
13	0.188	0.103	0.725	0.755	0.612	0.661	0.939**	0.202	0.159	0.136	0.186	1	
14	0.727	0.911**	0.138	0.401	0.507	0.065	0.488	0.945**	0.427	0.861**	0.909**	0.229	1
16	0.671	0.669	-0.197	0.028	0.040	-0.218	0.380	0.533	0.845	0.675	0.540	0.305	0.732*

** denotes high correlation, statistically significant, * denotes moderate correlation.

Table B-3- Correlation coefficients for Pacific dogwood first year *k* at all sites.

site	1	2	3	4	5	6	7	8	9	10	11	13	14
1	1												
2	0.841**	1											
3	-0.504	-0.230	1										
4	0.883**	0.886**	-0.236	1									
5	0.900**	0.769*	-0.301	0.941**	1								
6	0.775*	0.784*	-0.129	0.792	0.880**	1							
7	0.487	0.819**	0.094	0.716	0.624	0.790	1						
8	-0.083	0.324	0.569	-0.023	-0.104	0.311	0.528	1					
9	0.361	0.695	-0.200	0.620	0.451	0.468	0.837**	0.173	1				
10	-0.516	-0.127	0.92**	-0.176	-0.248	0.003	0.344	0.649	0.108	1			
11	0.241	0.538	0.660	0.398	0.285	0.477	0.593	0.787*	0.178	0.607	1		
13	0.917**	0.918**	-0.390	0.973**	0.937**	0.840**	0.747*	-0.002	0.674	-0.277	0.302	1	
14	-0.78*	-0.516	0.923**	-0.566	-0.640	-0.469	-0.181	0.458	-0.330	0.845**	0.385	-0.693	1
16	0.922**	0.821**	-0.607	0.727	0.774*	0.797*	0.533	0.082	0.406	-0.529	0.163	0.843**	-0.825**

** denotes high correlation, statistically significant, * denotes moderate correlation.

Table B-4- Correlation coefficients for Douglas-fir first year *k* at all sites.

site	1	2	3	4	5	6	7	8	9	10	11	13	14
1	1												
2	-0.059	1											
3	0.031	0.863**	1										
4	-0.391	-0.181	0.090	1									
5	0.124	0.847**	0.699	0.034	1.000								
6	0.405	0.596	0.754*	-0.227	0.640	1							
7	-0.429	0.798*	0.768*	0.433	0.781*	0.413	1						
8	-0.075	0.750*	0.663	0.381	0.923**	0.430	0.886**	1					
9	-0.057	0.829**	0.927**	0.332	0.763*	0.556	0.876**	0.843**	1				
10	0.131	0.800*	0.985**	0.027	0.599	0.755*	0.651	0.549	0.880**	1			
11	-0.496	0.691	0.794*	0.546	0.594	0.381	0.953**	0.750*	0.876**	0.707	1		
13	0.403	0.717	0.561	-0.130	0.949**	0.662	0.55	0.808*	0.603	0.489	0.331	1	
14	-0.543	0.593	0.709	0.638	0.565	0.420	0.925**	0.706	0.771*	0.606	0.968**	0.307	1
16	0.375	0.867**	0.688	-0.566	0.773*	0.672	0.427	0.529	0.572	0.673	0.266	0.798**	0.166

** denotes high correlation, statistically significant, and * denotes moderate correlation.