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Lessons from Montane Forests of the Pacific Northwest

By

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Summary

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For almost two decades, we have been studying the water relations and carbon economy of a wide range of species in the Pacific Northwest of North America. In particular our studies have focused on the montane species, *Abies amabilis*, and have spanned from the foliage to the stand level and from young saplings to old-growth trees. We have examined trees as small as 1.1 m to those over 44 m tall and spanning in age from seedlings to 220 years old. All of our study sites are located within 10 km of each other on the west slope of the Cascade mountain range, at an elevation of 1200 m (± 50 m).This paper focuses on the role that a foundation in production ecology and canopy dynamics has had in our efforts to understand function and to address issues of integration and scaling. For example, what techniques and approaches can be used to scale gas exchange measurements (i.e., transpiration, respiration and photosynthesis) from the shoot level to the tree and stand levels?

Introduction

Beginning with the International Biological Program, researchers at the University of Washington have been studying *Abies amabilis* and forest ecosystems dominated by this species for over 27 years. These studies have yielded valuable information on the production and nutrient ecology, the growth and mortality, carbon and water physiology and rhizosphere biology of this species (BROOKS & al. 1991, 1994, 1996, COLEMAN & al. 1992, EDMONDS 1980, GRIER &

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MILNE 1981, GRIER & al. 1981, HINCKLEY & al. 1984, 1985, LASSOIE & al. 1985, LEVERENZ & HINCKLEY 1990, MEIER & al. 1985, SEGURA & al. 1994, 1995a, b, SPRUGEL 1990, SPRUGEL & al. 1991, 1996, STENBERG & al. 1998, TESKEY & al. 1983, 1984a, b, 1985, TUCKER & al. 1987, TURNER & SINGER 1976, VOGT & al. 1980, 1982, 1983, 1986). These studies have provided a springboard for our current studies on scaling and integration which use this foundation to compare different aged material and measures taken from different scales of biological organization (BUCHMANN & al. 1998, HINCKLEY & al. 1998, MARTIN & al. 1997, 1999).

While covering a wide range of levels and disciplines, all of these studies have the common link of seeking generalities about the functioning of a mid-elevation species. The broad questions that have motivated our research over the last two decades have included: (1) what physiological adaptations have enabled *A. amabilis* to thrive in its subalpine environment, (2) are there measures of form and function that are level-specific, and can indices found at one level be linked to those at other levels, and (3) what readily measured indices provide insight into function? This paper reviews a series of studies carried out in *A. amabilis* trees, forests and ecosystems in the Washington Cascade mountains. Our goals are to illustrate the progression of thoughts and ideas that framed this long-term research program, and to highlight some of the insights gained from these studies.

Study Species

Abies amabilis grows from near 56°N latitude in southeastern Alaska south to 43°N in southern Oregon and from the Pacific coast to just east of the crest in the Cascades. It attains its greatest development on the west side of the Cascade mountains in Oregon and Washington, in the Olympic mountains and on Vancouver Island. It is also the major species of the *Abies amabilis* forest zone (FRANKLIN & DRYNESS 1988). As a species, it shares many morphological and physiological traits with other montane and boreal conifers spread over much of North America (LASSOIE & al. 1985).

Study Stands

The *A. amabilis* stands we have studied are located at ca. 1200 m in the City of Seattle's Cedar River Watershed, western Cascade mountains, Washington. The climate experienced by these stands is characterized by mild, dry summers (mean July air temperature 12°C) and cool, wet winters (mean January air temperature -3.2°C). Annual precipitation in this zone averages 2700 mm, the majority of which falls as snow. Maximum snow accumulations range from 2 to 4 m, and the ground remains snow covered from mid or late November until late May or early June (LASSOIE & al. 1985).

We have studied five *A. amabilis* stands in the Cedar River Watershed (Table 1). Of these five, we have intensively investigated three. The young-low stand (1955) was derived from a 1955 clearcut and the site is relatively nitrogen poor (hence, "low") (MEIER & al. 1985). At least 20% of the trees in this stand, and possibly a much larger fraction, originated from advanced regeneration (KEYES

1982); the remaining trees developed from seedlings that germinated near the time of clearcutting. Soils are relatively young, are well-drained, have been derived from andesite, and demonstrate podzolization. This stand contains a few *A. procera* and *Tsuga heterophylla*. The maximum average canopy height in 1993 was about 6.4 m. The young-high stand (1945) was released by wind-throw which occurred in the mid-1940s and subsequent salvage logging in 1948. Almost all of the trees presently in the overstory of this stand originated from advanced regeneration trees. We defined stand age from the time of release rather than the age of the oldest members of the stand. The designation of "high" was given to this stand because the soil is deeper and higher in organic matter and nutrient availability than the young-low stand. Both stands have trees that were suppressed and members of the stand prior to the respective disturbances. These advanced regeneration trees were 50 to 100 years old and had attained heights between 0.5 and 2.5 m prior to release. The young-high stand has scattered individuals of *T. heterophylla*. Maximum average canopy heights in 1993 was 20.1 m. The old-growth stand (1774) is in a glacial cirque within the Findley Lake research area. The majority of

Table 1. Selected characteristics of research sites in *Abies amabilis* stands of the Cedar River Watershed of the Washington Cascades. All stands were on slopes between 0 and 24% and all had south or southwest exposures. Elevations ranged from 1140 to 1230 m. The three youngest stands originated from clearcutting, the second oldest stand from windthrow and salvage logging and the oldest was from natural regeneration. Biometric data are for 1979 (KEYES 1982). Above- and belowground biomasses are for trees, shrubs, herbs and epiphytes. The intensive study stands are in bold.

Year of Stand Origin	Age in 1979	Basal Area (m^2 ha^{-1})	Mean Diameter (cm) (range)	Mean Height (m) (range)	Density (# ha^{-1})	Total Ecosystem Live Carbon (Mg ha^{-1}) (% conifer)	Live carbon % of total carbon
1976	3	2.8	0.51 (.2 - 4.1)	0.22 (.1 - 1.2)	38,200	10.55 (16.9)	6.9
1970	9	8.7	0.75 (.2 - 5.2)	0.36 (.1 - 1.8)	53,900	13.49 (30.9)	11.2
1955	**24**	**45.7**	**2.6** **(.5 - 7.0)**	**1.4** **(.3 - 2.6)**	**110,000**	**75.25 (89.4)**	**37.0**
1945	**34**	**82.5**	**18.8** **(1.2-40.6)**	**10.4** **(1.1-15.0)**	**9,300**	**358.00 (99.9)**	**48.6**
1774	**204**	**74.3**	**37.8** **(.2 - 104)**	**22.1** **(.1 - 39)**	**510**	**547.73 (99.6)**	**68.8**

dominant trees in this stand originated around 1774; however, a few of the trees are over 300 years old (KEYES 1982). This stand is also dominated by *A. amabilis*, with 15% of the basal area composed of *T. heterophylla* and *T. mertensiana*. The dominant trees in the stand range in height from 35 to 42 m. Canopies of these stands were accessed using systems of antenna towers and scaffolding.

Historical Research

In 1977, Professors R. EDMONDS, C. GRIER and K. VOGT initiated studies on the production ecology and rhizosphere biology of *Abies amabilis* ecosystems. Their work focused on the 1955 and 1774 stands described previously. Several important insights into the belowground production of *A. amabilis* emerged from these studies. First, both stands allocated considerable quantities of their net annual primary production to belowground production (65 and 73%, respectively) of which fine root growth was the greatest single component. Second, fine root growth began in mid-February when there was still 1.5 to 2.5 m of snow on the ground. In contrast, very little root growth was observed during the summer. During the winter growth period, over 95% of the fine roots were infected by mycorrhizal fungi whereas in the summer, less than 5% were infected. It is important to note that soils do not freeze during the winter (snow packs are deep and persistent) and that summer water deficits are rarely even moderate (see Fig. 6.1 in LASSOIE & al. 1985). Third, nutrient limitations, particularly nitrogen and phosphorus, appeared to influence carbon production and allocation more than any other environmental variable.

As one part of this initial focus on production ecology, KEYES 1982 examined the above- and belowground biomasses and net primary productivities of five different aged stands of *A. amabilis* (Table 1). A number of interesting patterns appear in this chronosequence. The quantity of living carbon (branches, leaves, stems, roots of conifers, shrubs and herbs) increased in both quantity (from 10.5 to almost 550 Mg ha^{-1}) and as a proportion of total site carbon. Keyes noted a close relationship between total conifer foliage biomass and conifer net primary productivity (Fig. 1). In addition, he observed a strong relationship with age—this relationship suggested that foliage biomass and net primary productivity increased as stands aged until some point and then declined. He attributed this decline to the loss of productive potential with tree and stand age whereas VOGT & al. 1986 interpreted this decline as a decrease in nutrient availability as system carbon detritus increased. Our data suggested that the 1945 stand was highly productive because of higher site quality (manifested in terms of deeper soils and higher foliar nitrogen levels). These initial studies provided three important foundations for subsequent ecophysiological studies. First, there was a series of accessible stands for which important information about their structural, carbon and nutrient statuses was known. Second, foliage quantity was directly related to system productivity. Third, the observations regarding the allocation to and timing of fine root production demanded attention.

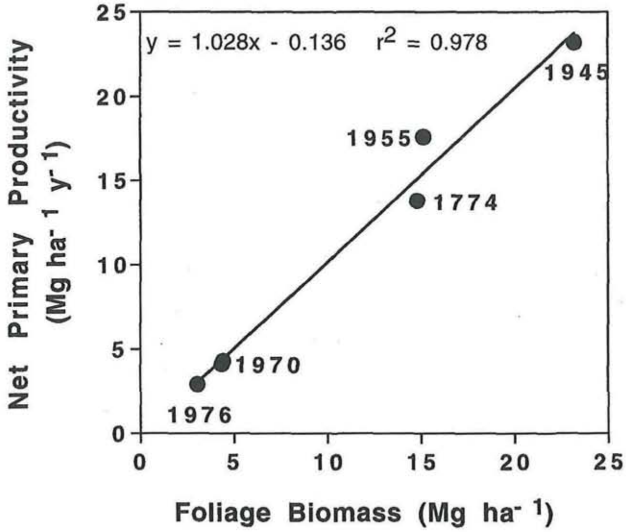

Fig. 1. Relationship between foliar biomass and net primary productivity in five different *Abies amabilis* stands (KEYES 1982) (Table 1). Data are for only the conifer component in each stand. Stands were measured in 1979. Approximately 16 years later the foliage biomasses were remeasured for the 1774, 1945 and 1955 stands and were 15.4, 26.5 and 23.0 Mg ha^{-1}, respectively.

In 1980, Professor R. TESKEY initiated physiological studies documenting the diurnal and seaonal patterns of stomatal conductance, water relations and net photosynthesis in *A. amabilis*. From these studies (TESKEY & al. 1983, 1984a, b, 1985), he observed that roots of this species can take up water at very low temperatures (< 1°C), that stomata remain tightly closed in the winter when soil temperatures are low (< 5°C), and that summer-time water limitations are rare (in fact, he found that up to 35% of the root system could be removed without having a short-term, negative impact on water potential or stomatal conductance). Simultaneous with Teskey's observations, emerged the observations of Professor C. MEIER (MEIER & al. 1985) who documented the extent of nutrient limitations in these ecosystems. These results, when linked to those of EDMONDS, GRIER and VOGT, offered an explanation regarding the timing of root growth in this species. Because major pulses of water through the snowpack and decomposing litter can occur in mid-winter and these pulses have both nitrogen and phosphorus in them, root growth is stimulated in this nutrient-limited ecosystem. The deep snow pack and the relatively mild winter temperatures insulate the soil -- soil temperatures less than 0.5°C were never measured (KEYES 1982). Root growth and mycorrhizal infection are restricted in the summer when aboveground growth is occurring and water is likely not limiting.

In the mid-1980's, a series of studies to understand carbon allocation and the loss of carbon via respiration were initiated (BROOKS & al. 1991, HINCKLEY & al. 1998, SPRUGEL 1990, SPRUGEL & al. 1995). Emerging from these studies was an appreciation of the utility of branches as an appropriate biological level of study and of the role of canopy position on function. These ideas were formally synthesized and critiqued in a review on branch autonomy (SPRUGEL & al. 1991). Specific conclusions reached were as follows:

- The physiological activity of a leaf, shoot, or branch is primarily determined by its own position in the canopy, not the canopy status (dominant, co-dominant, suppressed) of the tree it is attached to.

- During the majority of the growing season branches within a single tree are largely autonomous with respect to carbon: carbon fixed in one branch is rarely if ever exported from that branch and imported into a different branch on the same tree.

- Before and immediately after budbreak branch autonomy is relaxed; carbon fixed throughout the tree before budbreak is stored in the stem, and then when bud break occurs, carbon from the stem is exported to growing tips wherever they occur.

Since canopy position exerted such a strong control on function, the next series of studies addressed the role of position as it affected the light environment and how light impacted foliage morphology (SPRUGEL & al. 1996, STENBERG & al. 1998) and how then foliage both adapted to and acclimated (with changing light and age) to light (BROOKS & al. 1994, 1996). These studies demonstrated that certain morphological features were fixed during foliage elongation and maturation whereas other physiological features were far more responsive to the current light environment. Also emerging from these studies were a series of useful morphological indices which provide sound clues about the environment in which the foliage developed and the current physiological potential of the foliage. The relative effects of aging versus shading were elucidated in this species.

Current Studies

BROOKS' 1987 used leaf-level measures of foliage respiration integrated up in space and time to estimate carbon flux at the canopy level (HINCKLEY & al. 1998), highlighting the value of studies which use integration as a tool to 1) understand drivers of variation at sub-canopy levels and 2) draw conclusions about function at higher levels of organization, such as the canopy. One drawback to the Brooks study, however, was that there was no independent measure of canopy-level respiration against which to compare the integrated estimate. This led us to perform a series of intensive studies in the mid-1990s in which water relations and morphological data were collected at the shoot, branch and whole-tree levels in *A. amabilis* trees (MARTIN & al. 1997, HINCKLEY & al. 1998). The existence of this multi-level information allowed us to perform integrations from level to level, and then check the results of those integrations against independent measurements at the level of interest. Again, the branch provided a useful intermediate level by which process information could be integrated or scaled to higher levels. Emerging from these studies have been four broad generalities:

First, understanding the nature and pattern of variation is critical in efforts to scale and integrate. For example, BROOKS 1987 and BROOKS & al. 1991 found that foliage respiration varies sharply with temperature, foliage age and exposure to light. She noted that trees of different crown classes have very different rates of respiration. Suppressed trees not only have less foliage than dominant trees; their foliage also has a lower specific respiration rate because it is more shaded. Also, foliage on dominant trees is more exposed to and tends to be warmer on sunny days than foliage on suppressed trees, which further increases its respiration rate. Understanding and quantifying this variation in foliage respiration is critical to accurately estimating foliage respiration for an entire stand.

Second, morphological studies provide one with a powerful tool by which variation within a crown, a branch and a shoot might be better documented and understood. Knowing the nature of variation then enables one to design the process level studies. For example, the measurement of whole tree sap flow typically involves the placement of sensors in one or more positions around a stem. Sap flow varies around a stem based upon the crown of a tree and its position in a stand, the presence of live or dead branches, the presence of roots, etc. Without knowing the radial and circumferential flow pattern, it then becomes difficult to place sensors. It is fairly simple to introduce a dye into a small tree (< 40 cm); however, larger trees are not so easy.

Third, branches offer promise as a practical spatial scale for the study of mechanistic physiology (SPRUGEL & al. 1991). Although we have found that there are caveats for the use of branch studies, this level of biological organization offers a tractable means of understanding water and carbon exchange in large trees.

Fourth and finally, as many others have noted, it is critical to know the quantity of foliage on a shoot, branch, tree and stand (Fig. 2). Achieving a robust estimate of leaf area and leaf quantity, particular for the tree and the stand, is not easy. For example, almost 2000 person hours were devoted to generating the data in Fig. 2. Although the distribution of total foliage is provided in Fig. 2, the methods used to estimate this distribution also provided information about solar equivalent leaf area, leaf area or biomass distribution by age class, and area and biomass distribution both vertically and radially from a tree. Our initial studies began on a foundation of production ecology. We have been able to use this information about foliage quantity and distribution to understand the behavior of stable isotopes (BUCHMANN & al. 1998) and light in these forests (ROBERTS & al. 1998). Our current and future research continue to reside and depend upon this foundation.

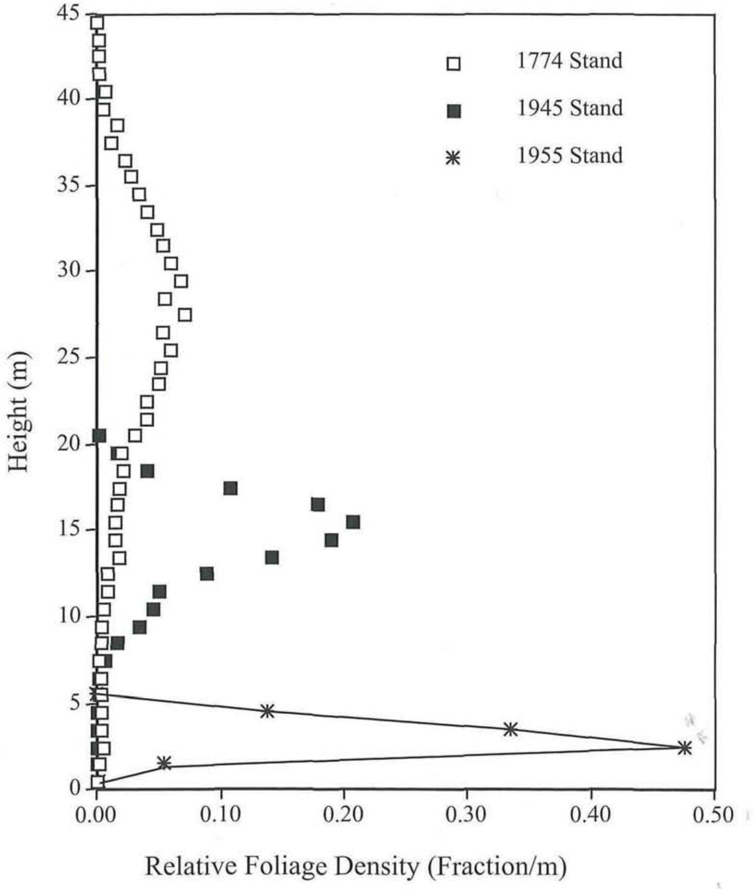

Fig. 2. The vertical distribution of foliage density for the three intensively studied *A. amabilis* stands is illustrated.

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Appendix I. Organic matter distribution for five different-aged *Abies amabilis* stands of the Washington Cascade mountains (after KEYES 1982). All biomass values are expressed in terms of kg ha^{-1}. Numbers above columns refer to the approximate date of stand origin or release. Stands were measured in 1979.

	1976	1970	1955	1945	1774
ABOVEGROUND BIOMASS	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}
Trees					
Stemwood	521	1440	25000	189000	294000
Stembark	79	213	2650	30500	62200
Live branch	158	517	7750	39300	67800
Foliage	308	930	13600	23200	14800
TOTAL	1066	3100	49000	282000	438800
Epiphytes	T[a]	T	T	120	1700
Shrubs					
Stem	3400	2300	2240	T	10
Foliage[b]	596	428	250	T	T
Herb Layer	2150	3740	1310	T	12
TOTAL	6146	6468	3800	T	22
Total Living	7212	9568	52800	282120	440544
Dead Branches (attached)	85	290	200	4900	7900
Standing Dead Trees (or stumps)	52260	38500	60500	12700	15700
Total Dead	52345	38790	60700	17600	23600
Aboveground Total	59557	48350	113500	299720	464144
BELOWGROUND					
Trees					
Fine root	296	406	4670	5180	8010
Coarse root	415	658	13600	70700	98700
TOTAL	711	1064	18270	75880	106710
Shurb and Herb					
Fine root	2040	2510	3610	T	229
Coarse root	585	345	571	T	10
TOTAL	2625	2855	4181	T	239
Total Living	3336	3919	22451	75880	107188
Necromass					
Fallen logs	38100	31600	19900	255000	75000
Forest floor[c]	52900	36100	47800	105600	150000
Total Dead	91000	67700	67700	360600	225000
Belowground Total	94336	71619	90151	436480	332188
Ecosystem Total (excluding soil)	153893	119969	203651	736200	796332

[a] Amounts less than 10 kg ha^{-1} or less than 0.1% are indicated by T.

[b] All Shrub and herb foliage are peak growing season biomass

[c] Ash Free dry weight at 70°C.

Appendix II. Net primary production for five different-aged *Abies amabilis* stands of the Washington Cascade mountains (after KEYES 1982). All values are expressed in terms of a biomass increment where the units are kg ha^{-1} y^{-1}. Numbers above columns refer to the approximate date of stand origin or release. Stands were measured in 1979.

	1976	1970	1955	1945	1774
ABOVEGROUND					
Tree					
Foliage	44	153	220	10	T
stemwood	153	260	2850	11900	1580
stembark	18	83	290	1190	360
branch	51	113	900	1200	380
TOTAL	266	609	4260	14300	2320
Shrub					
Stem	588	755	60	T	T
Above Biomass Increment	854	1364	4320	14300	2320
Detritus Production					
Tree					
needlefall (current)	T	T	80	121	196
needlefall (senescent)	21	24	960	1750	834
dead branch	61	33	50	985	177
mortality	36	870	380	130	39
TOTAL	118	927	1470	2986	1246
Shrub and Herb					
leaf-fall	616	440	250	T	T
mortality (turnover)	398	660	320	T	50
TOTAL	1014	1100	570	T	50
Aboveground Detritus Production	1132	2027	2040	2986	1296
Aboveground Net Primary Production	1986	3391	6360	17286	3616
BELOWGROUND					
Biomass Increment					
Tree coarse root or TOTAL	95	201	1780	2600	700
Detritus Production					
Tree fine root	50	75	5920	3300	9180
Shrub and Herb fine root	782	447	3400	T	390
TOTAL	832	522	9320	3300	9570
Belowground Net Primary Production	927	723	11100	5900	10270
Ecosystem Primary Production	2913	4114	17460	23186	13886

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