

AN ABSTRACT OF THE  
DISSERTATION OF

Clifton E. Cooper for the degree of

Doctor of Philosophy in

Botany and Plant Pathology presented

on June 3, 2005.

Title: Foliar Respiration in an Old-Growth Coniferous Forest.

Abstract approved:

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Foliar respiration forms a large component of the carbon balance of any coniferous forest. We examine seasonal, interannual, spatial and interspecific variation of foliar maintenance respiration in a forest in Washington, USA, with measurements made quarterly for >4 years on ~400-year old trees of *Pseudotsuga menziesii*, *Tsuga heterophylla* and *Thuja plicata*. Most variation is related to temperature, as well as to canopy position and to non-temperature related seasonal effects. Interannual variation is sometimes significant even after taking into account differences in measurement temperatures, suggesting that scaled-up, stand-level canopy respiration may vary significantly between years.

Scaling respiration from the leaf to the stand requires canopy leaf area index (LAI) for each species in each season at each canopy level. Thorough LAI data are available at one time of year (late August). We use a five-year record of monthly leaf litter data to determine changing seasonal LAI for each species at each canopy level. Collected litter leaves are related to monthly changes in live leaf area, then combined with the "standing crop" direct measurements of live LAI from August. Maximum stand LAI (9.05) is 37% greater than the minimum (6.63). Most leaf loss occurs from July-September, earlier than for conifers elsewhere in the world but coinciding with the regional dry season, suggesting that early leaf loss is a drought response.

Values of respiration are scaled to the stand to yield nighttime foliar respiration by conifers, using a respiration-temperature model, with micrometeorological and LAI data. Variation is included using a probability-distribution model for respiration and temperature for the leaf-level measurements, and of air temperatures. Values are found of total foliar maintenance respiration in four consecutive years. The four-year mean is  $3.40 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , with minor interannual differences. Annual carbon investment for new leaf construction is  $1.70 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , meaning that construction and maintenance of leaves may utilize ~1/3 of conifer gross primary productivity. Three recent papers producing divergent estimates regarding the carbon economy of the same forest are brought into closer agreement through substitution of certain results of this study.

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Foliar Respiration in an Old-Growth Coniferous Forest

by

Clifton E. Cooper

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## CONTRIBUTION OF AUTHORS

Dr. Sean Thomas of the Faculty of Forestry, University of Toronto, Ontario, Canada assisted with all aspects of the project which this dissertation describes, including grant proposals, experimental design, field work and data analysis. He provided further assistance with critiquing and improving the writing of sections 2, 3 and 4 of this document.

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## DEDICATION

I hereby dedicate this work to the memory of my father, John Clifton Cooper  
(1934-2005).

# **FOLIAR RESPIRATION IN AN OLD-GROWTH CONIFEROUS FOREST**

## **CHAPTER 1: GENERAL INTRODUCTION.**

### **1.1 OVERVIEW**

#### **1.1.1 Important research goals**

This study involves estimations of large-scale behavior in a tree canopy, based on small-scale measurements. Specifically, for the dominant conifer species in an old-growth forest, we scale-up measured leaf-level foliar respiration to estimate the magnitude of foliar respiration by all conifers in the forest. When carbon is initially fixed as carbohydrate, it has many possible fates, including allocation to growth of new tissues, or for maintenance respiration (Amthor 1989) to support existing tissues (Figure 1.1). Respiration by leaves is one of the largest consumers of carbon by trees, is crucially important to forest carbon balance, and is hence the focus of this study. Here are the specific research goals, and the reasons that they are they important:

- 1) Determine characteristic leaf-level respiration rates for all major conifer species, for all seasons, from multiple canopy levels, in multiple years. Respiration may vary between different species, seasons and canopy levels. Characteristic respiration rates are required for all combinations of these factors, to support efforts to



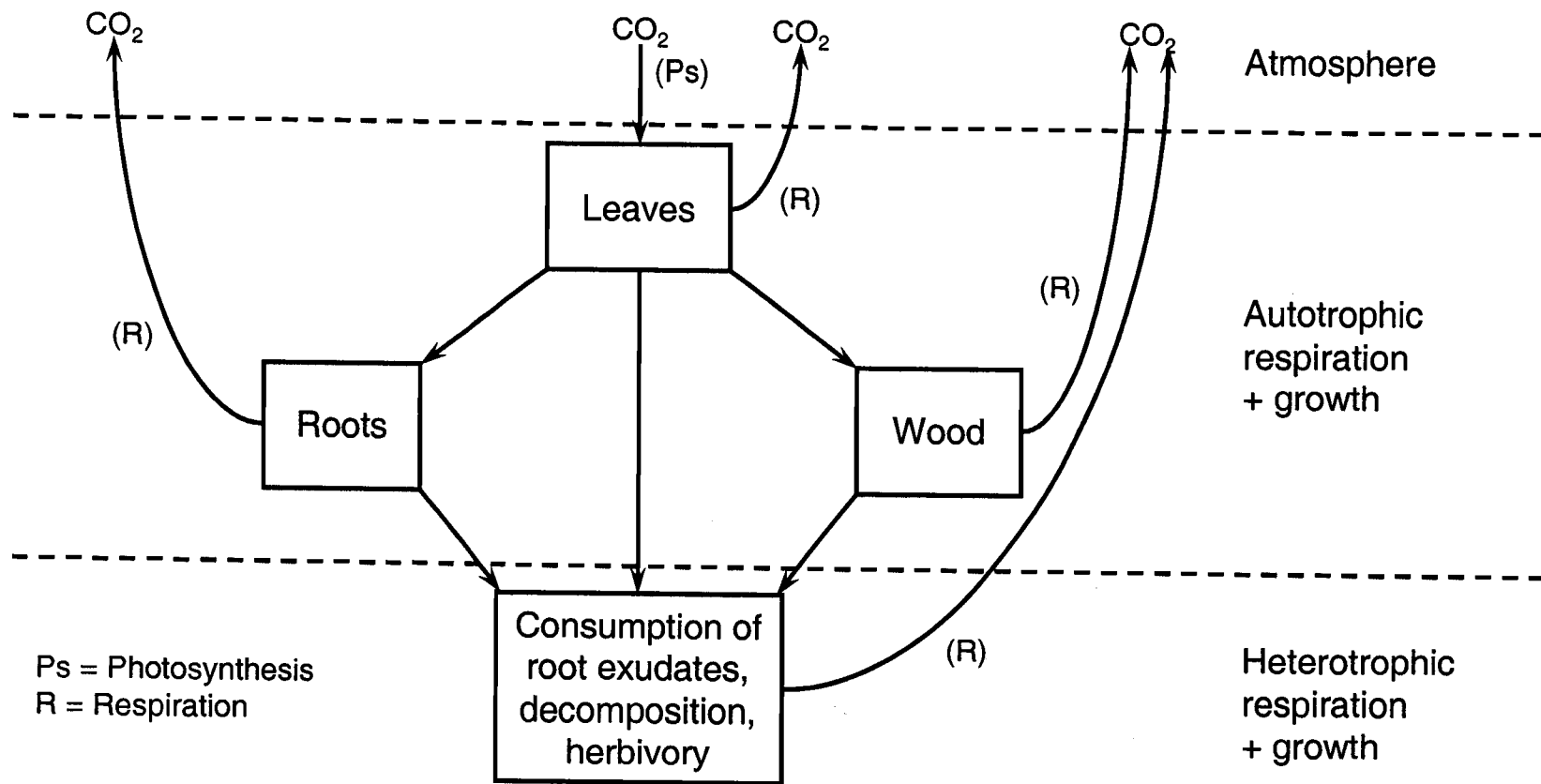


Figure 1.1. Carbon flows and reservoirs in a forest ecosystem. All carbon enters the system by photosynthetic uptake of CO<sub>2</sub> from the atmosphere, nearly all of it through leaves. Carbohydrate is allocated to growth of plant parts including leaves, wood and roots. All living plant parts perform autotrophic respiration, releasing some fixed carbon back to the atmosphere. Roots also exude carbohydrates to soil organisms including mycorrhizal fungi. Herbivores and decomposers consume and degrade plant materials, undergoing growth and performing heterotrophic respiration, releasing more fixed carbon back to the atmosphere. As global processes, total photosynthesis and total respiration are approximately balanced.

scale-up respiration. Measurements must also be performed in multiple years to detect any large, important interannual differences in respiration rates. Also, relationships between respiration and important environmental variables such as leaf temperature are required, so respiration may be extrapolated more generally from sets of particular measurements taken under particular conditions.

2) Determine values of leaf area index (LAI) that match with the timing of the leaf-level respiration measurements. Scaling from conifer leaves to the canopy requires detailed understanding of LAI. A single set of values for the study stand already exists, covering all species, at all canopy levels, at a particular time of year. However, LAI can vary substantially with season, even in an evergreen canopy, meaning that it is highly unrealistic to scale-up using LAI values from a single time of the year.

3) Determine four-year average (1998-2001), stand-level amounts of night-time foliar respiration from conifers at the study site, as well as for individual components such as the amounts of foliar respiration per canopy level, season and species. Such findings reveal the scope of foliar respiration as a part of the total carbon budget, and show which components have the greatest and the least influence. We also study interannual variation in yearly amounts of foliar respiration, to determine whether interannual variability may affect important aspects of carbon balance such as the source/sink behavior of the whole stand.

4) Apply results including those for stand-level foliar respiration, and the revised leaf area index estimates, to recently published studies that, using different methods, have produced divergent estimates of some aspects of the carbon economy

of the same stand (Harmon et al. 2004, Paw U et al. 2004, Winner et al. 2004).

Application of results from this work produces better agreement among the recent studies.

### 1.1.2 About the study site

This project has been conducted in the old-growth forest at the Wind River Canopy Crane Research Facility (WRCCRF) near Carson, Washington. The WRCCRF is in the Washington Cascade Range at 45°49'13.76" N, 121°57'06.88" W, in the southern Gifford Pinchot National Forest (Shaw et al. 2004). The old-growth stand, which is approximately 450 years of age, is dominated by isolated large specimens of *Pseudotsuga menziesii* Mirb. (Franco) var. *menziesii*, as well as numerous *Tsuga heterophylla* (Raf.) Sarg. trees of all ages, and lesser numbers of *Thuja plicata* Donn ex D. Don., also of all ages. The lush understory includes many small conifers including *Taxus brevifolia* Nutt., *Abies amabilis* (Dougl.) Forbes, *T. heterophylla* and *T. plicata*, as well as many other evergreen and deciduous species.

The forest is in the western hemlock zone (Franklin and Dyrness 1973). The site has high mean annual precipitation of 2,759 mm y<sup>-1</sup>, but dry summers with only 5.3% of annual precipitation falling from July through September (data for Wind River, Washington, 1971-2000, on file with the Western Regional Climate Center, <http://www.wrcc.dri.edu>). Elevation at the base of the crane is 371 m.

Because of the unique access that the Canopy Crane provides to a Pacific Northwest old-growth tree canopy, it has been the focus of research by many scientists

studying forest canopy processes. Particular attention has been paid to various aspects of carbon utilization and economy, involving direct measurements of tree growth (Harmon et al. 2004), eddy covariance measurements utilizing instrumentation placed upon and nearby the crane (Paw U et al. 2004), measurements of leaf CO<sub>2</sub> uptake (Thomas and Winner 2002), and modeling using a soil-plant-atmosphere model (Winner et al. 2004).

The Canopy Crane was erected in 1994. At 75 m high it stands above all trees at the site, and reaches over an 85-m radius "crane circle" that encompasses nearly 1,000 live trees with a diameter at breast height  $\geq 5$  cm. The crane lifts researchers to many three-dimensional locations within the crane circle using a personnel gondola (Figure 1.2), thus providing safe and nondestructive canopy access.

## **1.2 SPECIFIC RESEARCH GOALS IN DETAIL**

### **1.2.1 Goal #1: Leaf-level respiration rates**

Foliar respiration plays a crucial role in forest carbon balance. Previous estimates indicate that out of all fates of photosynthetically fixed carbon in forests, foliar respiration is one of the largest. For example, in a 20-year old stand of *Pinus radiata* D. Don, leaf maintenance and production utilizes 21% of the carbon budget (GPP), most of it for leaf maintenance respiration (Ryan et al. 1996). In 180-year old *Abies amabilis*, leaf maintenance and production utilizes 35% of GPP, most for respiration

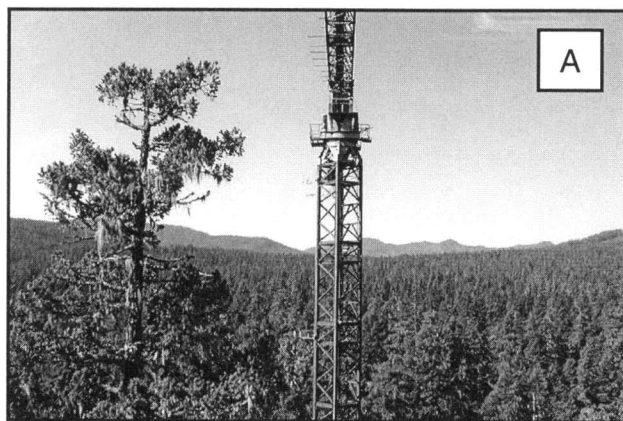


Figure 1.2. The Wind River Canopy Crane, which provides access to all levels of the forest canopy in all seasons, including summer (A) and winter (B). The crane lifts a personnel “gondola” (bottom, C), which may be positioned next to branches allowing research including the foliar gas exchange measurements of the present study (D).

(Ryan 1991b). Another estimate, involving the old-growth stand at the WRCCRF site, has leaf maintenance and production utilizing 38% of GPP, again most for respiration (Harmon et al. 2004). Estimates involving other stands are similar. Clearly, to characterize the carbon budgets at the WRCCRF site, correct estimates of foliar respiration are essential.

Our approach is to measure respiration from representative, small amounts of foliage usually involving 100 or so leaves, and then scale-up to the whole canopy. Respiration rates have been previously reported for many conifer species, but the reported values offer little guidance with regard to what rates are to be expected from foliage in the old-growth stand at the WRCCRF site. For example, most studies have used young trees (e.g. Leverenz 1995), not old ones. Furthermore, most measurements have been performed in the spring and summer only, yet conifer foliage at the WRCCRF site is known to be active year-round (Winner et al. 2004). Previous conifer measurements report leaf-level respiration rates ranging from  $-0.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ leaf s}^{-1}$  in *T. heterophylla* (Leverenz 1995) to  $-2.6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ leaf s}^{-1}$  in *A. amabilis* (Brooks et al. 1991). With previously published values that cover such a wide range, and that generally do not cover old trees or cover all times of the year, much remains unknown, thus making it essential to take systematic, direct measurements in the old-growth canopy in all seasons.

A further issue is that the role of interannual variability in the respiration of old-growth conifer foliage is unknown. No studies of which we are aware have made repeated measurements of foliar respiration in trees in multiple years. However, the

overall, annual amounts of both photosynthesis and respiration could vary between years due to large-scale interannual differences in temperature, light and/or precipitation caused by major weather events such as El Niños. In a forest that may be a very small (Harmon et al. 2004) or at most a moderate (Paw U et al. 2004) carbon sink, sufficiently large interannual fluctuations in any large component of carbon flux, such as foliar respiration, could determine whether the stand as a whole is a sink in one year, and a source in another.

Accordingly, we have conducted a long-term study of all aspects of foliar gas exchange by the three major tree species in the old-growth canopy, including the respiration measurements from 1997-2001 that are reported upon here. We performed repeated leaf-level measurements of photosynthesis, respiration, transpiration and conductance, in March, June, September and December of multiple years, on foliage from specific upper and lower canopy branches of two large representative trees of each species *P. menziesii*, *T. heterophylla* and *T. plicata*. We performed all measurements during the day, which meant that for respiration, foliage was first placed into darkness for several minutes to acclimate to the dark. The ultimate concern was with developing estimates of the amounts of respiration occurring at night, but for logistical reasons, the actual leaf-level measurements needed to be performed on darkened foliage during the day. All measurements were performed on mature, first-year leaves for which all respiration was for maintenance. We used an LI-6400 Portable Photosynthesis System (Li-Cor, Inc., Lincoln, NE) for all measurements, a system that allows measurements of all CO<sub>2</sub> and H<sub>2</sub>O gas exchange properties using intact foliage that

remains attached to its tree for the duration of the measurements. Foliage samples were later harvested and analyzed to determine leaf areas and masses, so respiration could be expressed on both an area and a mass basis (Chapter 2).

### 1.2.2 Goal #2: Seasonally varying leaf area index

Leaves are where trees primarily interact with the sun and atmosphere. Leaves are the primary sites of photosynthesis, and they feed their whole tree with the carbohydrates that they produce. However, photosynthetic capacity comes at a high respiratory cost. In addition to maintenance respiration of existing foliage, new leaves must also grow to replace those that are lost in each year, requiring further carbon investment both for creation of new foliar dry mass and for the associated growth respiration (Amthor 1989).

When expressed on the ground area basis of ecosystem studies, processes such as foliar respiration are affected by LAI, the ratio of leaf one-sided silhouette area : ground area. LAI always exists in forest ecosystem models, whether as a fixed input parameter (SPA model, Williams et al. 1996), or as an internally calculated variable (Forest-BGC model, Waring and Running 1998b). Leaf-level measurements of carbon exchange, expressed as  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ leaf s}^{-1}$ , may be scaled-up to stand-level estimates expressed as  $10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , in part via multiplying by LAI.

LAI fluctuates seasonally in all forests, even evergreen conifer stands. Most new leaves grow out in spring and early summer, while older leaves tend to fall in late summer, fall and/or early winter. Thus, LAI follows a sawtooth pattern, reaching a



peak in early summer as new leaf expansion ceases, and a minimum in spring before new leaf expansion begins. When processes such as leaf respiration are measured in several seasons, and seasonal variation in LAI is large, scaling-up to annual estimates requires distinct seasonal values of LAI.

Fixed values of LAI have been previously determined at the study site (Thomas and Winner 2000a), by a method in which the gondola is moved over many random points within the crane circle, a weighted line is slowly lowered to the ground, all contacts between the line and foliage of each species at each approximate height are recorded, and contact frequencies are converted to LAI for each species at each approximate canopy level. Measurements have been conducted in three consecutive summers on an average late August date, with mean stand LAI of 8.6 including understory plants.

In the present study, we use the previously measured LAI values as reference, fixed values for one time of year. We utilize leaf litter data to determine a full yearly cycle of incremental, monthly changes in LAI, with total annual losses from leaf fall and estimated herbivory being offset by equal growth of new leaf area. Leaf litter collections have been performed since 1998, using 20 litter traps placed randomly in the 4 ha "crane plot." We use a five year record to calculate mean monthly mass accumulation rates in the traps, and use subsamples to determine the proportions of litter contributed by each species at several times of year, and the equivalence between collected leaf litter and changes in live leaf area in the canopy.

In addition, we examine the phenology of leaf fall at the WRCCRF site, comparing seasonal patterns to those from other forests outside the Pacific Northwest, finding distinct differences in timing of leaf fall, and we examine the possible explanatory role of environmental variables such as the seasonal timing of precipitation. We also determine the roles of leaf loss and replacement in the carbon economy of the stand (Chapter 3).

### 1.2.3 Goal #3: Stand-level amounts of foliar respiration

To have larger ecological significance, the leaf level measurements of foliar respiration must be scaled to the stand level, expressed as  $10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  or  $\text{Mg C ha}^{-1} \text{ y}^{-1}$ , the normal units for parameters of ecosystem carbon exchange. The scaled-up measurements represent maintenance respiration only, so growth respiration must be estimated based on the mass of new foliage produced annually. Measurements in each year from 1998 through 2001 cover 24 factorial combinations of four months (March, June, September and December), two canopy levels (upper and lower), and three species (*P. menziesii*, *T. heterophylla* and *T. plicata*). Measurements from each combination are scaled to the nighttime, stand-level respiration contributed by that combination, using a model that incorporates the measured respiration rates, the measurement temperatures, the overnight range of temperatures for that time of year, a relationship between respiration and temperature, and the LAI for the combination. We make certain assumptions to deal with other minor conifer species in the lower canopy, and with all conifers in the understory.

For each factorial combination, we use respiration measurements taken during the day on darkened foliage as surrogates for nighttime rates at equal temperatures. Temperature strongly affects respiration, usually exponentially over a typical biological temperature range with respiration increasing by 2-3x for a 10 °C increase. In our model, the measured rates and their associated temperatures serve as index values, while measured overnight air temperature values are used to calculate overnight respiration at each half-hourly time step, and rates are then averaged through the night. In order to incorporate the observed variability of input values, and to prevent biases in means of results (Ryan 1991a), we apply probability distributions of all measured respiration rates and their associated temperatures, and of the overnight air temperatures. The resulting mean  $\pm$  variation overnight respiration rates, still expressed as  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ leaf s}^{-1}$ , are converted to quarterly stand-level units of  $10^6 \text{ g C ha}^{-1} \text{ season}^{-1}$  in part by applying LAI, and are summed across seasons to yield yearly totals. Total amounts for particular species, seasons and canopy levels are compared to determine which factors are the most important.

Interannual variation in stand-level foliar respiration is crucial to the study. Values are computed separately for each quarter in each year 1998-2001, and summed. Values from each year are compared to each other, and also to previously published values of net ecosystem productivity in the same stand (Harmon et al. 2004, Paw U et al. 2004), to evaluate the effects of interannual variability in annual nighttime conifer foliar respiration upon the source/sink behavior of the stand (Chapter 4).

#### 1.2.4 Goal #4: Previous studies of carbon economy

The old-growth stand at the WRCCRF site has been the subject of intensive study, particularly with regard to its carbon economy. Various studies have used complementary approaches to determining important parameters such as GPP. The site is part of the Ameriflux network and as such, its CO<sub>2</sub> exchanges with the atmosphere have been monitored using eddy covariance techniques (Paw U et al. 2004). Eddy covariance allows real-time measurement of daytime CO<sub>2</sub> uptake by the whole stand (GPP), CO<sub>2</sub> release due to nighttime respiration by the whole stand (total ecosystem respiration, TER), and integration over time to yield the annual totals of GPP, TER, and their difference, net ecosystem productivity NEP.

As another approach, all trees within the 4 ha "crane plot" have been monitored for growth and survival since the Canopy Crane was established in 1994, allowing estimation of the changes in wood volume and biomass over time. Further measurements have been made of all other carbon pools including snags, logs and soil organic C, and estimates have been made of all sources of respiration in the system (Harmon et al. 2004). The result is a set of values for all components of GPP, net primary productivity NPP, TER and NEP. A third approach uses a soil-plant-atmosphere ecosystem model (SPA) to calculate GPP (Winner et al. 2004).

However, the above studies do not agree. Estimates of GPP from eddy covariance (Paw U et al. 2004), forest inventory methods (Harmon et al. 2004) and from the SPA model (Winner et al. 2004) are  $15.5\text{--}15.9 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ ,  $19.06 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  and  $24.6 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , a difference of 59% between the lowest estimate

and the highest. Similarly, estimates of both TER and NEP vary substantially between two studies (Harmon et al. 2004, Paw U et al. 2004). Substitution of certain results of the present study, specifically involving stand-level estimates of annual foliar respiration, annual carbon investment in new leaf production, and mean annual leaf area index, can bring the previous three studies into closer agreement regarding GPP and TER (Chapter 4).

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**CHAPTER 2: FOLIAR RESPIRATION IN AN OLD-GROWTH  
*PSEUDOTSUGA-TSUGA* FOREST.**

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## 2.1 ABSTRACT

Old-growth forests may be nearly carbon-neutral, balanced between being carbon sinks in one year, and sources in another. Foliar respiration may, by itself, be large and variable enough to substantially affect source/sink behaviors. We examine seasonal, interannual, spatial and interspecific variation of foliar respiration in an old-growth *Pseudotsuga-Tsuga* stand in Washington State, USA, with measurements made at 3-month intervals, for >4 years on ~400-year old trees. Dark-acclimated respiration was measured during the day by gas exchange methods on mature foliage, and is expressed on leaf area and leaf mass bases. Rates generally fall within the range previously reported. There are strong differences in area-based respiration related to canopy height, but not for mass-based respiration. There are strong seasonal differences for all species, with rates in June several times higher than in December. Most seasonal variation is related to differences in temperature, but there are additional time-of-year effects. Significant seasonal variation in leaf mass per area is also detected. For interannual comparisons, rates from each measurement month are normalized to the monthly mean temperature, using a  $Q_{10}$  relationship between respiration and temperature. Interannual variation is sometimes significant, suggesting that scaled-up, stand-level canopy respiration varies significantly between years.



## 2.2 INTRODUCTION

### 2.2.1 Importance of foliar respiration

According to many estimates, foliar respiration forms large portions of the carbon budgets of conifer forests. For example, foliar respiration consumes 17% of the Gross Primary Productivity (GPP) in a 20-year old *Pinus radiata* D. Don stand (Ryan et al. 1996), and consumes 31% and 14%, respectively, of GPP in stands of 180-year old *Abies amabilis* (Dougl.) Forbes and 245-year old *Pinus contorta* Dougl. ex Loud. (Ryan 1991b). In an old-growth *Pseudotsuga menziesii* Mirb. (Franco) var. *menziesii* - *Tsuga heterophylla* (Raf.) Sarg. stand, foliar respiration consumes 30% of GPP (Harmon et al. 2004). In several young coniferous stands, foliar respiration accounts for 1/3 to 2/3 of total autotrophic respiration  $R_A$  (Hagihara and Hozumi 1991), while in some boreal forests, foliar respiration is > 50% of  $R_A$  (Ryan et al. 1997b). In turn,  $R_A$  is usually ~50% of GPP and nearly equals Net Primary Productivity (NPP) (Waring et al. 1998).

Forest productivity NPP, as measured by rates of tree growth, declines with stand age (Ryan et al. 1997a). Likewise, Net Ecosystem Productivity (NEP), the difference between GPP and Total Ecosystem Respiration (TER), declines as stands reach an advanced, old-growth stage (Franklin and DeBell 1988, Harmon et al. 2004, Janisch and Harmon 2002). Old-growth stands are thus nearly carbon-neutral, and relatively small changes in either assimilation or respiration, including foliar respiration, may determine whether a stand is a net carbon source or sink in a particular year.

The carbon balances of various kinds of forests are, in turn, important in understanding changing atmospheric  $[\text{CO}_2]$ , climate change and mitigation by carbon sequestration (Cohen and Harmon 1996, IPCC 2001, Page et al. 2002).

Even if a stand is consistently a sink, interannual fluctuations in total respiration may cause important fluctuations in NEP. As an example, in the Harvard Forest, NEP varied from  $1.4$  to  $2.8 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  through five years during which TER (a negative quantity) ranged from  $-8.1$  to  $-11.4 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  (Goulden et al. 1996). In old-growth conifer stands that are nearly carbon-neutral, especially where foliar respiration is a large proportion of TER (e.g. Harmon et al. 2004), fluctuations in foliar respiration alone may determine whether a stand is a net carbon source to the atmosphere in one year, and a sink in the next. In a study of the NEP of an old-growth conifer stand, it is desirable to measure the magnitude of foliar respiration, and its interannual variability, to determine the overall role that it plays in stand carbon balance.

### 2.2.2 Old growth and respiration

Our study pertains to the foliar carbon balance of an old-growth coniferous forest in western Washington, USA. Old-growth forests once dominated the region. In the early 1800s, 60-70% of forests in the "Douglas-fir region" (the *T. heterophylla* zone of Franklin and Dyrness 1973) may have been in an old-growth state (Spies and Franklin 1988). By another estimate, 55% of forests in western Oregon and Washington were "originally" old-growth (Booth 1991). However, by the mid-1980s, only 17-

18% of the pre-1850 amount remained (Booth 1991, Haynes 1986, Spies and Franklin 1988), and still less remains at present.

Remaining tracts of old-growth are in some respects "museum pieces." Although they no longer dominate, they illustrate how regional ecological processes once functioned. The rates of net carbon storage of individual stands differ greatly, depending on age and history (Harmon et al. 1990, Janisch and Harmon 2002), and overall regional NEP was probably very different in the pre-1850 past dominated by old-growth, late-successional forests, compared to the present when most stands are younger and have been logged. Extensive forested areas in western Oregon and Washington are currently net carbon sources, as a result of past management practices (Cohen and Harmon 1996). Studies of carbon balance, including foliar respiration, in remaining old stands are essential to developing baseline knowledge of the regional ecological behavior that prevailed prior to large-scale human intervention.

Many previous studies have reported foliar respiration rates in conifers. However, most studies have used young trees (e.g. Leverenz 1995, Witowski 1997, Bond et al. 1999). Comparisons of young and old trees reveal age-specific differences in CO<sub>2</sub> exchange behavior (Yoder et al. 1994, Thomas and Winner 2002), that demonstrate the need for direct measurements in old-growth canopies. Most previous measurements have been limited to spring and summer (Groninger et al. 1996, Reich et al. 1998, Roberntz and Stockfors 1998), but conifer foliage in some cases remains active year-round (e.g. Winner et al. 2004). Also, few if any studies have made repeated

measurements in multiple years, so interannual variability is unknown. Comprehensive data regarding respiration in old-growth conifer foliage are lacking.

### 2.2.3 Goals

One way to estimate the magnitude of and variation in canopy foliar respiration is to construct a model incorporating 1) standard leaf-level respiration rates for all major species, for all seasons, in multiple years, from multiple canopy levels; 2) a relationship between the standard rates, and important environmental variables (e.g. temperature); 3) a detailed micrometeorological record; and 4) a detailed leaf area profile of the canopy. Accordingly, we have performed leaf-level measurements of foliar respiration in an old-growth coniferous canopy. We have repeatedly sampled particular branches from all major canopy species, at multiple levels, in four seasons and in several consecutive years. Characterization of interannual changes in respiration is the rationale for conducting our study in multiple years. From these measurements, we have determined characteristic rates for standard conditions, and have examined variability between years, as reported here. Micrometeorological and leaf area data are reported separately.

For our purposes, the 24-hour cycle is divided into day and night components. During the day, the net amount of foliar CO<sub>2</sub> uptake (total photosynthesis – photorespiration – respiration) is usually defined as a single quantity, GPP. Respiration occurring during the day cannot be separately distinguished from the other, simultaneous components of carbon flux using gas exchange techniques, and is usually not

studied as a distinct entity. However, neither photosynthesis nor photorespiration occur at night, so respiration is the sole cause of nighttime carbon exchange. As such, nighttime foliar respiration comprises an important and discrete component of stand carbon balance. Our interest is in defining characteristic, short-term respiration rates that may be scaled-up to estimate the annual, amounts of nighttime foliar respiration in the stand.

## 2.3 METHODS

### 2.3.1 Study site

Our study site is a ~450 year old stand at the Wind River Canopy Crane Research Facility (WRCCRF), in the southern Washington Cascades at 45°49.23' N, 121°57.12' W, elevation 355 m. The "crane circle" encompasses nearly 1000 live trees with a diameter at breast height  $\geq 5$  cm. Climate is temperate and wet except for a summer drought. Local micrometeorological data have been recorded since 1998. Data from 1998-2000 were used for quarterly reference temperatures (Table 2.1). Because foliar gas exchange measurements were taken during the daytime, mean sample leaf temperatures were similar to the mean daytime maximum air temperatures in each of the sampling months (Table 2.2).

The canopy is dominated by three conifer species, *P. menziesii*, *T. heterophylla* and *Thuja plicata* Donn ex D. Don. Others include *A. amabilis* and *Taxus brevifolia*

Table 2.1. Mean air temperatures in each of the sampling months of March, June, September and December, taken at an open field station (1998-2000 data on file with the WRCCRF, 1262 Hemlock Road, Carson, WA 98610).

	Air temperature (°C)		
	Mean	Mean	24-h
	T <sub>max</sub>	T <sub>min</sub>	mean T
March	9.5	-0.2	3.8
June	20.6	7.9	14.5
September	23.4	6.4	14.8
December	3.7	-1.4	0.6

Table 2.2. Mean measurement leaf temperatures for samples in March, June, September and December.

Mean sample leaf temperatures (°C)						
	<i>Pseudotsuga</i> <i>menziesii</i>		<i>Tsuga</i> <i>heterophylla</i>		<i>Thuja</i> <i>plicata</i>	
	Upper	Lower	Upper	Lower	Upper	Lower
March	12.8	10.0	12.2	11.3	10.4	9.8
June	19.0	21.1	20.4	19.7	21.3	21.5
September	18.8	17.6	16.9	18.2	16.0	15.7
December	4.5	5.9	6.1	6.5	5.9	6.4

Nutt. The understory has many small trees, including all conifers except *P. menziesii*. Individual *P. menziesii* trees are the largest (examples, Table 2.3) and contribute ~50% of stand wood, while *T. heterophylla* abounds in all age classes and contributes 46% of canopy leaf area (Thomas and Winner 2000a).

### 2.3.2 Sampling

We began measurements of photosynthesis in 1996 (Thomas and Winner 2002, Winner et al. 2004), and of respiration in June 1997. Repeated measurements were performed in each subsequent March, June, September and December, generally on the same trees and branches. Most measurements were taken between 0800 and 1500 hours. In most sampling periods, respiration was measured on 3 samples from upper and lower canopy branches on 2 trees each of *P. menziesii*, *T. heterophylla* and *T. plicata*, with 36 total samples (3 replicates x 2 levels x 2 trees x 3 species). The data set used for this analysis includes measurements from June 1997–December 2001. Bud break of *P. menziesii* and *T. heterophylla* occur in mid-May (data on file with the WRCCRF, 1262 Hemlock Road, Carson, WA 98610), with leaf expansion complete by mid-July. Leaves are mature by mid-summer (Radoglou and Teskey, 1997). Most (>90%) lifetime respiration in evergreen leaves is for maintenance, as with *P. radiata* (Ryan et al. 1996). Accordingly, we took measurements from the youngest mature leaves, commencing with 4-month old leaves in September and using the same cohort through the following June.



Table 2.3. Old-growth trees used in this study, and the number of total samples taken from each (height and diameter data on file with the WRCCRF, 1262 Hemlock Road, Carson, Washington 98610).

Species	Tree number	Height (m)	Branch height (m)		DBH (cm)	Sample n
			Upper	Lower		
<i>Pseudotsuga menziesii</i>	91	65.8	59.6	29.5	166	105
	242	63.0	49.1	19.8	136	30
	1373	58.3	52.0	31.6	129	90
	1376	57.4	51.7	26.4	110	6
<i>Tsuga heterophylla</i>	410	53.9	44.5	31.1	99	13
	416	53.8	49.5	18.9	100	96
	1184	51.3	46.1	9.8	75	101
<i>Thuja plicata</i>	217	52.5	49.7	19.7	114	90
	1193	43.6	42.1	23.4	104	2
	3096	48.0	45.4	16.7	111	96

### 2.3.3 Field measurements and laboratory techniques

Gas exchange measurements use an LI-6400 Portable Photosynthesis System with a 2 x 3 cm cuvette, and an SI-355 red LED light source (Li-Cor Inc., Lincoln, NE). The LI-6400 controls temperature, humidity, [CO<sub>2</sub>] and light around foliage. It uses infrared gas analyzers to measure [CO<sub>2</sub>] and [H<sub>2</sub>O], and calculates gas exchange properties (equations of von Caemmerer and Farquhar, 1981). Previous studies have used the LI-6400 system to measure respiration in leaves of crop plants (Albrizio and Steduto 2003), *Populus deltoides* Bartr. (Griffin et al. 2002), in several grass, forb, shrub and tree species (Loveys et al. 2003), and photosynthesis in *P. menziesii* and *T. heterophylla* at low light levels (Lewis et al. 2000).

Each sample includes leaves and a stem. Samples are placed in the cuvette while connected to the tree, as 6 mm wide gaskets seal the cuvette window. Cuvette humidity and temperature match the ambient levels, and [CO<sub>2</sub>] was 350 ppm. Foliage is exposed to high light for photosynthesis, then to zero light for respiration. Samples are darkened for ~5 minutes before at least 3 respiration values are logged, at intervals of 20 seconds.

Of necessity, respiration is measured during the day. However, the rates are intended as surrogates for nighttime rates at equal temperatures. Previous studies disagree about the dark period needed to produce fully dark-adapted behavior. Some use  $\leq 10$  minutes (Brooks et al. 1991, Witowski 1997), while others use  $\geq 1$  hour (Reich et al. 1998, Roberntz and Stockfors 1998). In late June 1997, we tested a ~5 minute dark acclimation period. In early afternoon on one day, on 3 large trees each of *P. menzie-*

sii, *T. heterophylla* and *T. plicata*, one upper branchlet was bagged in aluminum foil, and darkened. After 24 hours of darkness, respiration was measured on each, as well as on adjacent control branchlets that were darkened for ~5 minutes. Treatments were compared by t-tests. The first day was overcast, and the second partly sunny.

One reason to perform a lengthy dark acclimation is that lit foliage may temporarily accumulate surplus carbohydrate that stimulates respiration (Amthor 1994). Therefore, rates measured in the day after ~5 minutes darkness may be artificially high, while rates from foliage darkened for  $\geq 1$  hour may be more equivalent to night-time rates at equal temperatures (Sprugel et al. 1995). The branch bag study tests whether dark acclimation continues after 5 minutes.

Samples are clipped, stored on ice, and scanned at 200 dpi. The total silhouette area (Smith et al. 1991),  $A_{TS}$ , is the whole sample area (Figure 2.1). The cuvette silhouette area,  $A_{CS}$ , is that area within the window. Leaves are removed from the stems of *P. menziesii* and *T. heterophylla*, and the *T. plicata* samples are coarsely fragmented. Leaves and fragments are arranged to eliminate overlaps, scanned, then dried and weighed. Images are digitized, and total areas determined using NIH-Image software for Macintosh. Total leaf area is multiplied by  $A_{CS}/A_{TS}$  for the cuvette leaf area, for  $R_{area}$ ,  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ . Total leaf mass is multiplied by  $A_{CS}/A_{TS}$  for the cuvette leaf mass, for  $R_{mass}$ ,  $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ .

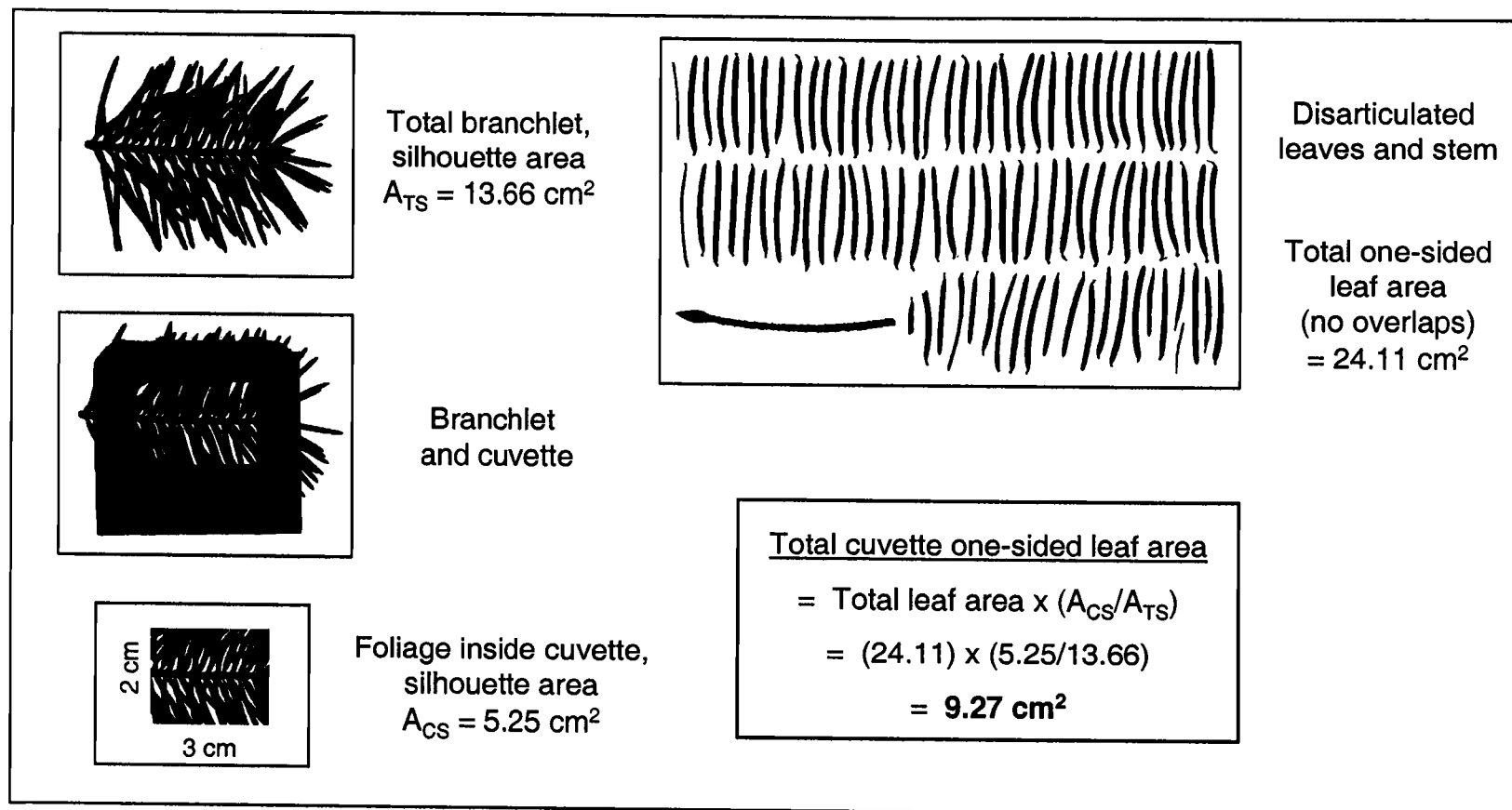


Figure 2.1. Illustrations of leaf area determination for calculations of  $R_{\text{area}}$  (leaf area-based respiration). Example for foliage from a sample of *Pseudotsuga menziesii*. For details of techniques, see text description. Total cuvette one-sided leaf area is greater than the  $6 \text{ cm}^2$  area of the cuvette window because in the live, intact sample, there are many leaf overlaps.

### 2.3.4 Data analysis

Multi-year means are calculated for the directly measured values  $R_{\text{area}}$  and  $R_{\text{mass}}$ , of all 24 factorial combinations of species, levels and months. Means are compared by t-tests, with a 0.05 significance level for this and all tests. Leaf mass per area (LMA,  $\text{g m}^{-2}$ ) is calculated for each factorial combination, using four cohorts of leaves, and analyzed by analysis of variance (ANOVA). Statistics use Data Desk 4.2 (Data Description, Inc, Ithaca, NY) for Macintosh.

Measured values of  $R_{\text{area}}$  are divided into 3 sets by species, and log-transformed into  $\ln(-R_{\text{area}})$ . Each set is tested for linear fits to  $T_{\text{leaf}}$ . Residuals are tested for effects of levels, months, individual trees and years. Nonsignificant terms are removed. ANOVAs use Type III sums of squares. The above analysis examines the necessities of the various classes of factors, including the necessity of measuring respiration in four distinct times of the year.

Interannual variations in  $R_{\text{area}}$  are examined for 1998-2001. Measurement temperatures sometimes vary greatly between years, so to facilitate interannual comparisons, rates from all months are normalized to the monthly mean air temperatures. Air and leaf temperatures are assumed to always be equal. Respiration is modeled as an exponential function of temperature (e.g., Ryan 1991a, Waring and Running 1998):

$$[1] \quad R_2 = R_1 * \exp[b * (T_2 - T_1)]$$

where  $R_1$  and  $R_2$  are the rates at temperatures  $T_1$  and  $T_2$  ( $^{\circ}\text{C}$ ), respectively. A derivation of Eq. [1] allows calculation of normalized rates from measured rates as:

$$[2] \quad R(\text{normalized}) = R(\text{measured}) * \exp[\ln(Q_{10}) * (T_M - T_C) / 10]$$

where  $T_C$  and  $T_M$  are the cuvette and mean monthly air temperatures.  $Q_{10}$ , or  $e^{10b}$  is a function of seasonal temperature, and largest during cold months (Hagihara and Hozumi 1991).

From a global meta-analysis (Tjoelker et al. 2001):

$$[3] \quad Q_{10} = 3.22 - 0.046 * T_M$$

and calculated  $Q_{10}$  values from Eq. (3) for March, June, September and December are 3.05, 2.55, 2.54 and 3.19, respectively, or 2.83 averaged through a year. Normalized respiration values are compared between years. Values from the four years within each factorial combination are then averaged.

## 2.4 RESULTS

### 2.4.1 Dark acclimation

In the validation study using paired foil-wrapped and unwrapped branchlets, there are only small, nonsignificant differences ( $p > 0.05$ ) between mean respiration values for each treatment (Table 2.4), for both  $R_{\text{area}}$  and  $R_{\text{mass}}$ . Thus, it makes no significant difference whether rates are measured after 24 hours or after 5 minutes of darkness. No additional significant dark acclimation occurs after the first 5 minutes of darkness.

Table 2.4. Effects of branch bags vs. controls (no bags) on respiration rates ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , mean  $\pm$  SE) in June 1997, with  $n = 3$  for each species/treatment combination.

	Treatment	$R_{\text{area}}$	% difference	P-value
<i>Pseudotsuga menziesii</i>	Bag	$-1.07 \pm 0.12$	+13.7	0.57
	No bag	$-0.94 \pm 0.45$		
<i>Tsuga heterophylla</i>	Bag	$-1.29 \pm 0.17$	-17.9	0.08
	No bag	$-1.58 \pm 0.33$		
<i>Thuja plicata</i>	Bag	$-1.67 \pm 0.67$	-10.8	0.66
	No bag	$-1.87 \pm 0.46$		
All species combined	Bag	$-1.34 \pm 0.22$	-8.1	0.49
	No bag	$-1.46 \pm 0.25$		

### 2.4.2 Directly measured respiration rates

Directly measured respiration rates tend to be highest in June, and lowest in December (Figure 2.2). For multi-year mean, area-based respiration  $R_{\text{area}}$ , mean rates are always higher in the upper canopy than in the lower canopy, significantly ( $p < 0.05$ ) so in 5 out of 12 comparisons (Figure 2.3). Averaged across all seasons and canopy heights, mean  $R_{\text{mass}}$  values range from  $-2.85 \text{ nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$  in *T. plicata* to  $-4.24 \text{ nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$  in *T. heterophylla*. In June, upper canopy rates of  $R_{\text{area}}$  in *T. heterophylla* and *T. plicata* are nearly twice as high as in *P. menziesii*, while rates for the species in December are more similar.

For the directly measured rates of mass-based respiration,  $R_{\text{mass}}$ , seasonal patterns are similar. However, there is no consistent ranking by which one canopy level has higher respiration rates than the other. Averaged across all seasons and canopy heights, the multi-year mean  $R_{\text{area}}$  values range from  $-0.565 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  for *P. menziesii* to  $-0.746 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  for *T. plicata*.

### 2.4.3 LMA

Mean values of LMA are highest in the order *T. plicata* > *P. menziesii* > *T. heterophylla*, and upper canopy > lower canopy (Table 2.5). These rankings reflect the greater thickness of *T. plicata* fronds vs. needle leaves, and sun vs. shade leaf anatomy (Larcher 1995). Values for *P. menziesii* are similar to those found previously at the site (Ishii et al. 2002). Seasonally, averaged across species and levels, there is a small, 0.3% increase in LMA from September to December ( $p = 0.047$ ). However, the in-



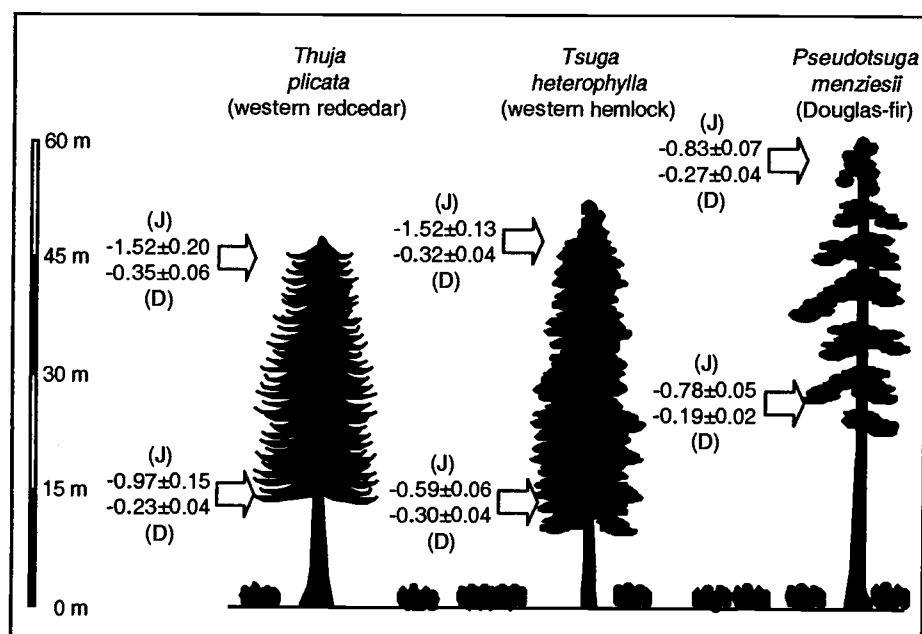


Figure 2.2. Representative measured respiration rates in dominant conifer species. Values are  $R_{\text{area}}$ ,  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , mean  $\pm$  se. Rates are means from 1997-2001, for June (J) and December (D), for upper and lower canopy foliage.

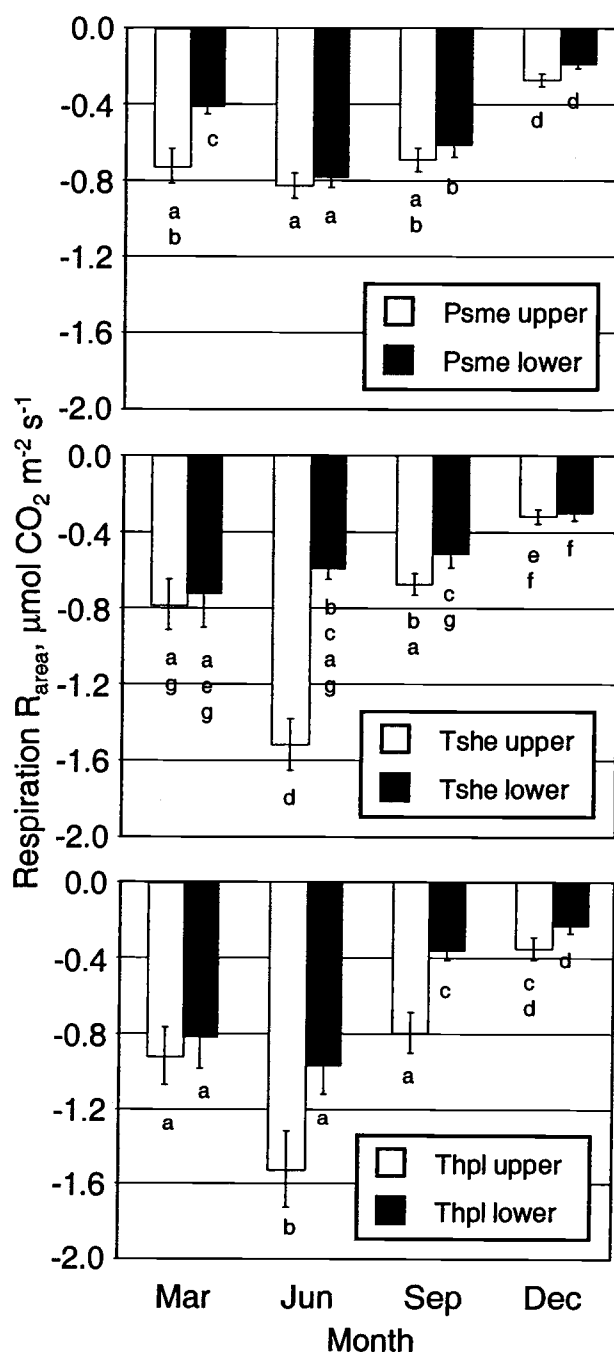


Figure 2.3. Measured  $R_{area}$  and  $R_{mass}$  for *P. menziesii* (Psme), *T. heterophylla* (Tshe) and *T. plicata* (Thpl), for March, June, September and December, upper and lower canopy. Values are mean  $\pm$  se from 1997-2001. Values within a panel, not sharing a letter, are significantly different ( $p \leq 0.05$ , t-test).

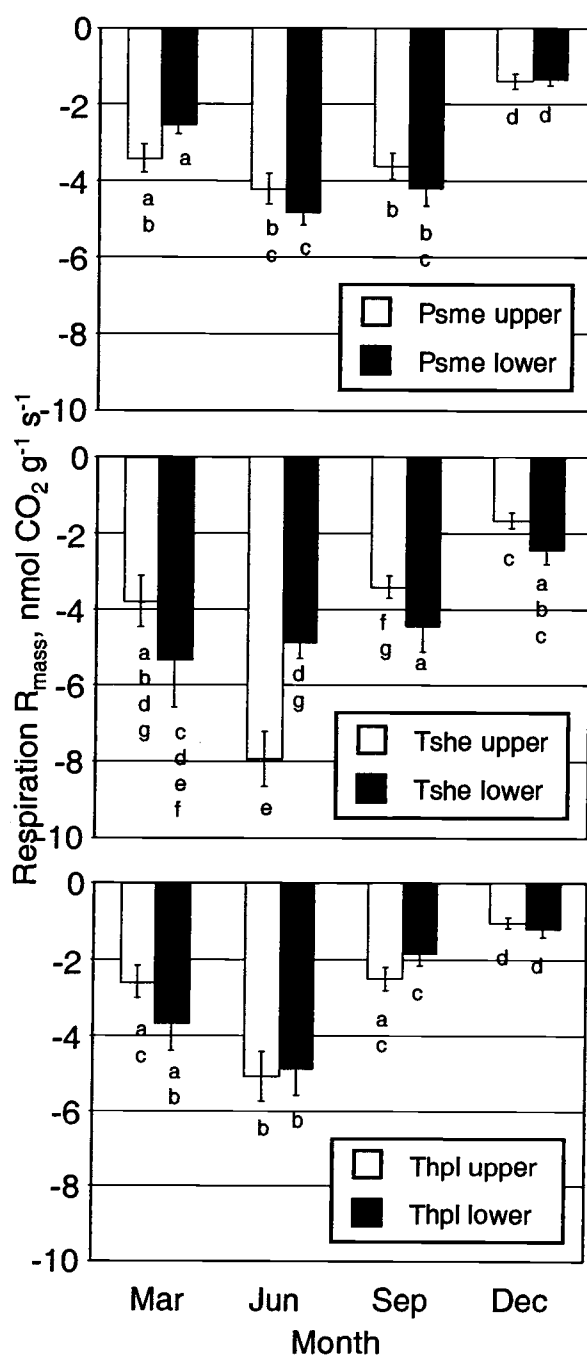


Figure 2.3 (continued). Measured  $R_{\text{area}}$  and  $R_{\text{mass}}$ , for *P. menziesii* (Psme), *T. heterophylla* (Tshe) and *T. plicata* (Thpl), for March, June, September and December, upper and lower canopy. Values are mean  $\pm$  se from 1997-2001. Values within a panel, not sharing a letter, are significantly different ( $p \leq 0.05$ , t-test).

Table 2.5. Leaf mass per area (LMA, mean  $\pm$  se) for the three major canopy species and two canopy heights, pooled from data for four measurement months and four consecutive years.

Species	Canopy Level	LMA, g m <sup>-2</sup>
<i>Pseudotsuga</i>	Upper	201.9 $\pm$ 2.6
<i>menziesii</i>	Lower	155.1 $\pm$ 1.6
<i>Tsuga</i>	Upper	203.2 $\pm$ 3.5
<i>heterophylla</i>	Lower	125.7 $\pm$ 1.9
<i>Thuja</i>	Upper	326.0 $\pm$ 4.6
<i>plicata</i>	Lower	204.4 $\pm$ 3.2

crease of 11.2% from December to March, and the decrease of 9.0% from March to June, are both much larger and highly significant ( $p \leq 0.0001$ ). Values of  $R_{\text{area}}$  and  $R_{\text{mass}}$  are interconvertible using the LMA values.

#### 2.4.4 Respiration and temperature

Linear regressions of  $\ln(-R_{\text{area}})$  vs.  $T_{\text{leaf}}$  show positive relationships (Figure 2.4). All regression slopes are highly significant ( $p < 0.0001$ ), so as expected, rates increase with temperature. The mean slope, averaged across species, indicates that for an increase of 10 °C, measured values of  $R_{\text{area}}$  increase by 2.15 times. Each regression uses data from all seasons, so each is a composite of data from samples acclimated to four different, equally spaced months. Homeostatic seasonal adjustments to rates, involving up-regulation in the winter and down-regulation in the summer, probably produces composite, multi-season respiration-temperature responses that are flatter than those of the short-term  $Q_{10}$  responses.

#### 2.4.5 Analysis of variance

Canopy height is strongly correlated with the residuals of  $\ln(-R_{\text{area}})$  vs.  $T_{\text{leaf}}$  ( $p < 0.0001$ ), consistent with the patterns for  $R_{\text{area}}$ . Variation between years is significant ( $p < 0.05$ ), but there is no significant difference within the groups of trees used for any species ( $p > 0.05$ ). Individual months have temperature-independent effects on respiration rates. Log-transformed rates from some months deviate significantly from a linear function of  $T_{\text{leaf}}$  taken through all data. Log-transformed rates in March are

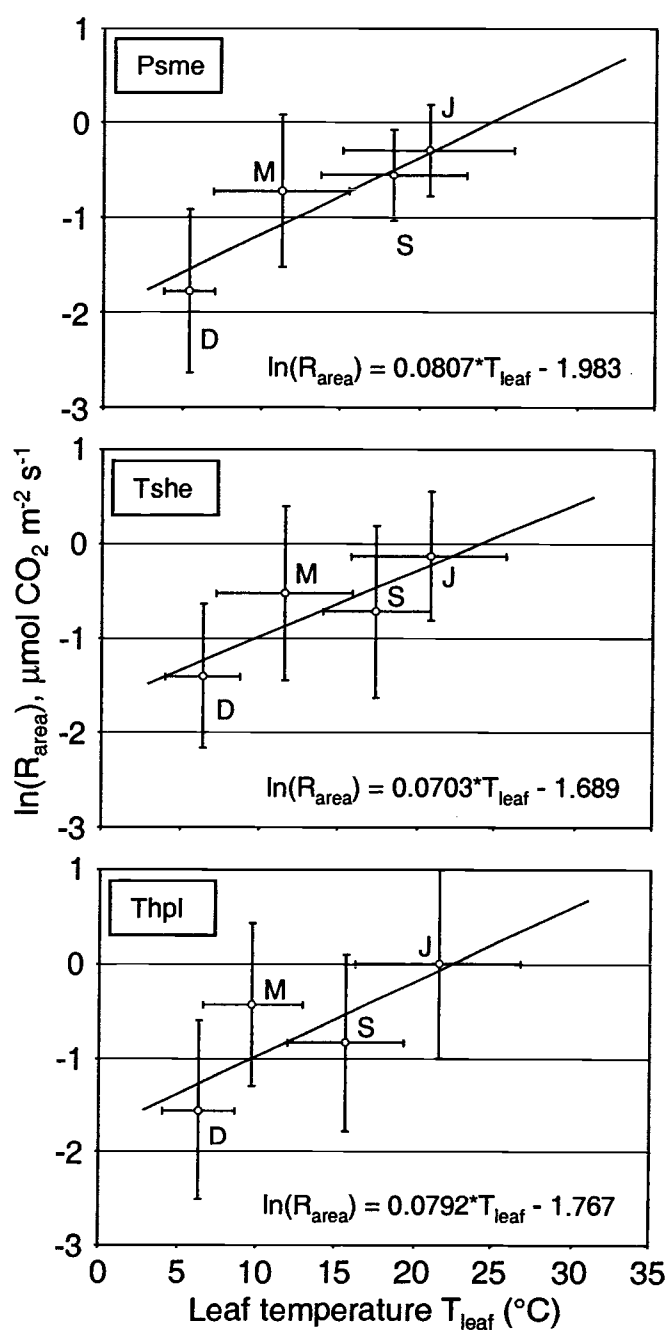


Figure 2.4. Values of  $\ln(R_{\text{area}})$  and their relationships to leaf temperature. Values are for *P. menziesii* (Psme), *T. heterophylla* (Tshe) and *T. plicata* (Thpl), in March (M), June (J), September (S) and December (D). Each panel combines data from at least two trees and from 4-5 consecutive years. Regression equations and lines represent least square fits through all data. Symbols represent mean  $\pm$  se for each month.

more positive than predicted by the regressions, meaning that the measured rates are larger, while log-transformed rates in September are more negative.

In terms of the variation explained by each effect, averaged across species, temperature explains 33.0% of all variation. Month, year and level explain an additional 14.9%. The result, though, is that only 48% of total variation is explained by the measured factors, while 52% is not. Out of the unexplained variation, ~50% exists within sample groups. That is, rates often vary greatly even within groups of samples that are taken at the same time, from the same branches, while exposed to nearly identical conditions.

#### 2.4.6 Interannual variation

Important year-to-year differences exist, even after differences in leaf temperatures are taken into account by normalizing all rates to the monthly mean air temperatures. For normalized rates, in most multi-year comparisons some of the yearly mean values differ significantly ( $p < 0.05$ ) from each other (Figure 2.5). As an example, for *T. plicata*, June, lower canopy, mean  $R_{area}$  values from 1998, 2000 and 2001 do not vary significantly from each other ( $p > 0.05$ ), but the mean  $R_{area}$  from 1999 differs significantly from the others ( $p < 0.05$ ). Overall, *P. menziesii* displays the least interannual variation, while *T. plicata* displays the most. Upper canopy branches also display less variation than do lower branches.

The seasonal patterns of the four-year averages of normalized  $R_{area}$  within each factorial combination (Table 2.6) are similar to those of the measured values. Because

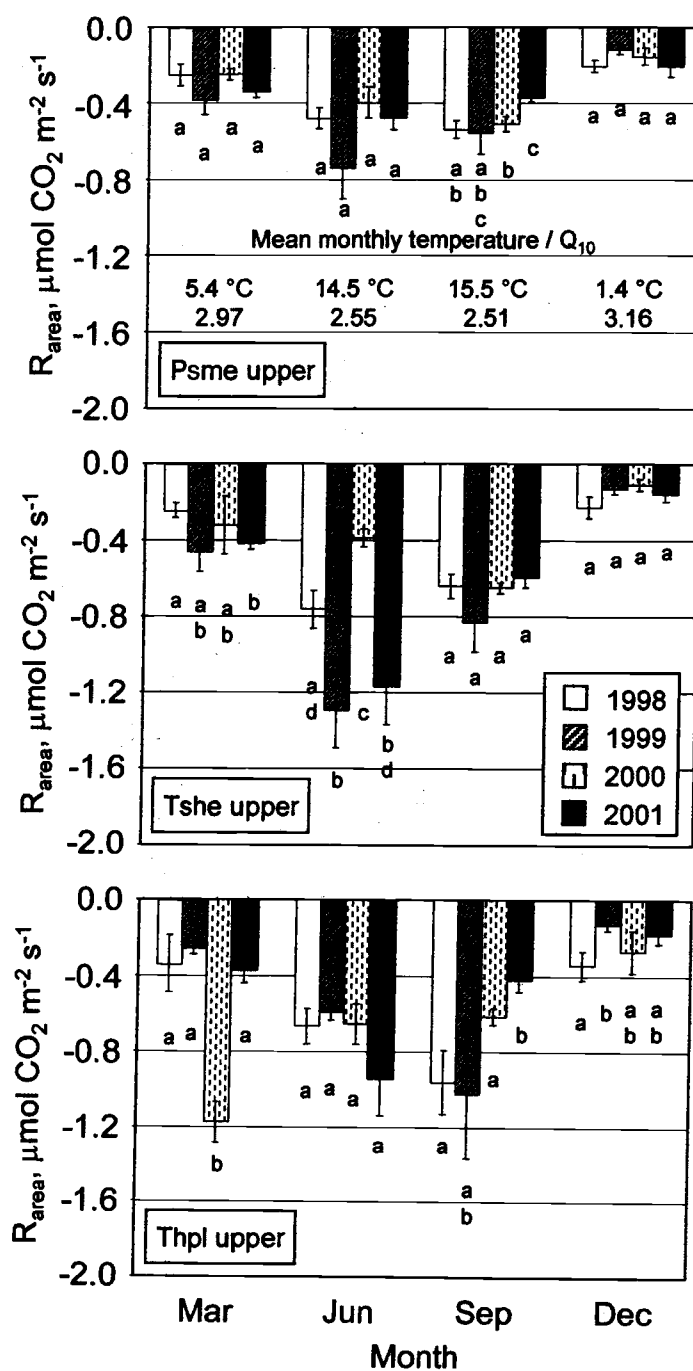


Figure 2.5. Interannual variation of  $R_{area}$ . Values are mean  $\pm$  se. All values are normalized to mean monthly temperatures, for the given  $Q_{10}$  values. Values within each set of four yearly means, not sharing a letter, are significantly different ( $p \leq 0.05$ , t-test). Symbol legend applies to all panels.



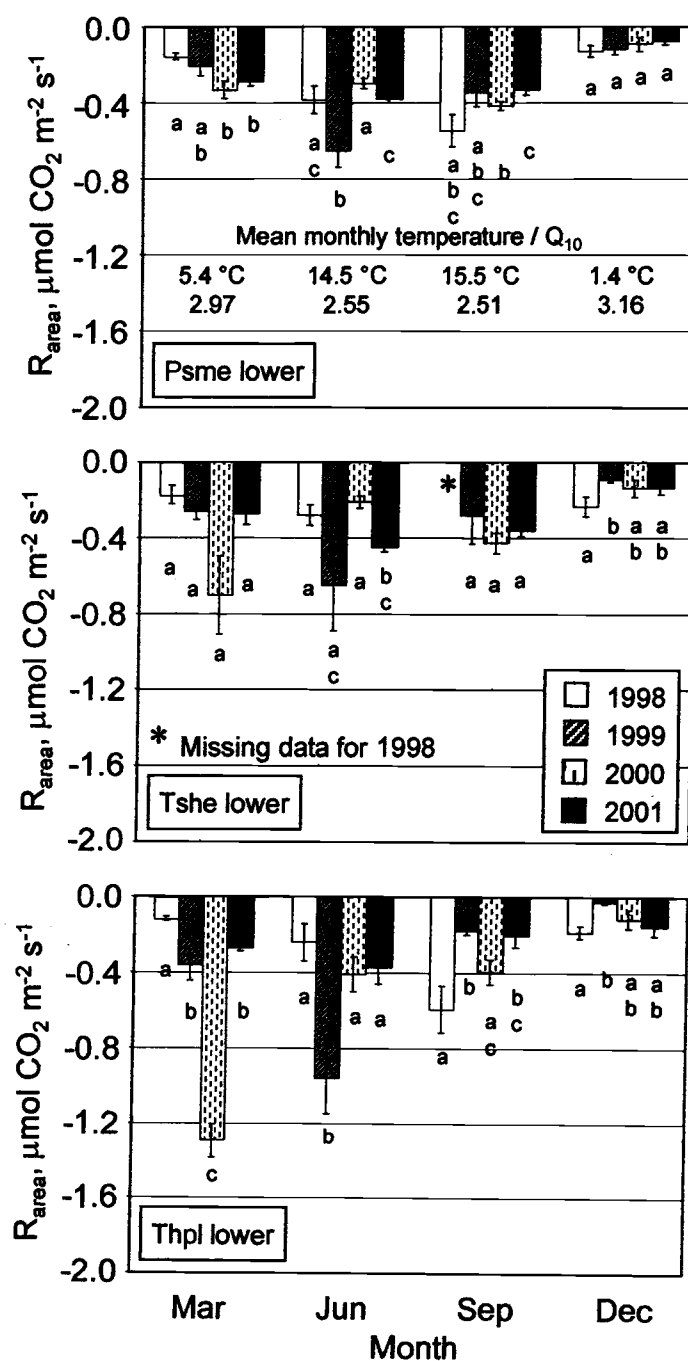


Figure 2.5 (continued). Interannual variation of  $R_{area}$ . Values are mean  $\pm$  se. All values are normalized to mean monthly temperatures, for the given  $Q_{10}$  values. Values within each set of four yearly means, not sharing a letter, are significantly different ( $p \leq 0.05$ , t-test). Symbol legend applies to all panels.

Table 2.6. Multi-year  $R_{\text{area}}$  rates (mean  $\pm$  se, pooled from 1998-2001) from each factorial combination, normalized to the 24-hour mean monthly air temperatures.

Species	Canopy level	Respiration Rate ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )			
		March	June	September	December
<i>Pseudotsuga</i>	Upper	$-0.31 \pm 0.05$	$-0.53 \pm 0.11$	$-0.50 \pm 0.06$	$-0.17 \pm 0.05$
<i>menziesii</i>	Lower	$-0.25 \pm 0.04$	$-0.43 \pm 0.06$	$-0.41 \pm 0.06$	$-0.10 \pm 0.02$
<i>Tsuga</i>	Upper	$-0.36 \pm 0.09$	$-0.90 \pm 0.14$	$-0.68 \pm 0.09$	$-0.16 \pm 0.04$
<i>heterophylla</i>	Lower	$-0.35 \pm 0.06$	$-0.40 \pm 0.10$	$-0.36 \pm 0.09$	$-0.15 \pm 0.05$
<i>Thuja</i>	Upper	$-0.54 \pm 0.07$	$-0.72 \pm 0.11$	$-0.76 \pm 0.15$	$-0.23 \pm 0.07$
<i>plicata</i>	Lower	$-0.51 \pm 0.06$	$-0.50 \pm 0.13$	$-0.34 \pm 0.09$	$-0.12 \pm 0.04$

the average difference between the mean measurement temperatures and standard temperatures is relatively small, 5.2 °C, the normalized rates are relatively insensitive to the  $Q_{10}$  values. If the year-round average  $Q_{10}$  of 2.83 is, in fact, overestimated by 10%, then the normalized rates are underestimated by 5%.

## **2.5 DISCUSSION**

### **2.5.1 Insensitivity to dark acclimation**

Respiration rates are insensitive to the length of the dark acclimation period. It makes no significant difference whether foliage is darkened for 5 minutes or for 24 hours. Therefore, we argue that our measured rates may in fact be used as surrogates for nighttime rates at equal temperatures. Actual overnight rates may therefore be estimated from the daytime rates using Eq. [1], as long as the overnight temperatures are known.

Why is respiration apparently unaffected by recent photosynthesis? Conceptually, respiration may be regulated by substrates, respiratory enzymes and/or products. Substrate (carbohydrate) concentration is affected by sunlight and photosynthesis. Growth respiration may be mainly "pushed" by substrates; while maintenance respiration, dominant in mature leaves, may be mainly "pulled" by demand for respiratory products (Amthor 1994). If so, respiration in mature leaves should be insensitive to the amount of recent photosynthesis.

### 2.5.2 Measured rates

Some previously reported rates in conifers range from  $-0.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in *T. heterophylla* (Leverenz 1995) to  $-2.6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in *A. amabilis* (Brooks et al. 1991). Most studies have involved summer measurements on young trees, and conversely, few previously measured winter rates are available for comparison. Our measured and normalized rates generally fall within the above range, except in December.

As expected (Bolstad et al. 1999, Sprugel et al. 1995), leaf temperature strongly affects rates. Therefore, temperature is commonly used to model respiration using an exponential relationship (e.g. FOREST-BGC, Waring and Running 1998; SPA, Law et al. 2000). However, we find that because of seasonal acclimational adjustments to rates, a simple respiration-temperature relationship is not adequate to predict respiration across seasons.

One seasonal adjustment involves larger (more negative) rates in March than predicted. A possible cause is that before bud break, mature leaves produce materials that they later export to new leaves (Sprugel et al. 1995, Vose and Ryan 2002); a process consistent with the observed seasonal variation in LMA, with higher leaf masses in March than in December and June. Mature leaves may have higher than expected rates and masses in March as they create surplus materials, with both quantities diminished by June, after the materials have been exported.

Differences in rates between species are sometimes important. The greatest interspecific difference is for the upper canopy in June, when the mean normalized

rate for *T. heterophylla* is 72% larger than for *P. menziesii*. Rates are more similar at other times, and in general, interspecific differences are similar to those seen previously within mixed coniferous (Reich et al. 1998) and mixed broadleaf (Bolstad et al. 1999) forests.

The height-dependent differences in  $R_{\text{area}}$  are predicted from the characteristic differences between sun-adapted and shade-adapted leaves (Larcher 1995). Similar effects are seen in *Pinus taeda* L. and *Pinus strobus* L. (Groninger et al. 1996). However, there are no significant height-dependent differences for  $R_{\text{mass}}$ . Thus, for each species, a single, standard value of  $R_{\text{mass}}$  applies through the thickness of the canopy. Conversely, for each species,  $R_{\text{area}}$  varies with LMA.

### 2.5.3 Interannual variation and normalized rates

As seen, *P. menziesii* displays the least variable interannual rates, while *T. plicata* displays the most variable. Some possible causes of interannual variability may include heat and cold damage from extreme weather events that require large amounts of metabolic activity to repair damaged cells. Some differences in rates between years may also be caused by interannual climatic differences, as with annual precipitation. Possibly, *P. menziesii* and *T. heterophylla* are both more resistant to damage from extreme weather, or are less affected by climatic variability, than *T. plicata*. Also, measurement dates for given seasons were not identical between years. Possibly, differences in sampling dates, or in conditions other than temperature (e.g. time of day, humidity), account for some of the observed interannual variation in measured rates.

#### 2.5.4 Modeling overnight stand-level respiration

Stand-level foliar respiration may be modeled by combining standard rates for each factorial combination, appropriate LAI values, and detailed overnight temperature data. Here, we report the standard respiration rates. LAI values have been (Thomas and Winner 2000a), and are being produced. Suitable temperature data are also available (data on file with the WRCCRF, 1262 Hemlock Road, Carson, WA 98610). Using the multi-year record of measured rates and temperatures, we may produce stand-level estimates of respiration for several distinct years, as well as a multi-year average. Such estimates may help to resolve disputes that currently exist, regarding the carbon economy of the same stand (e.g. Harmon et al. 2004, Paw U et al. 2004).

#### 2.5.5 Wider inference

The major conifer species at the Wind River site dominate most natural forests in western Oregon and Washington. The respiratory behaviors of foliage from the same species, elsewhere in the region, are probably similar, although they may be affected by local differences in climate and/or soils. One difference may be that at higher elevations, severe winter conditions may cause foliage to become temporarily dormant, not the case at the Wind River site (Winner et al. 2004).

The relative dominance of each species in a mixed stand differs with stand age. The 450-year old Wind River stand is currently co-dominated by *P. menziesii* and *T. heterophylla*. However, the successional trajectory for this type of forest is for it to first be dominated by *P. menziesii*, but for shade-tolerant *T. heterophylla* to later

come to dominate (Franklin and Dyrness 1973). Canopy composition thus varies over time, with consequent changes in the total amounts of foliar respiration contributed by each canopy species that are related both to interspecific differences in leaf-level respiration, and to the total amounts of leaf area contributed by each species in the canopy. Therefore, estimates of past or future stand respiration require that the changing composition of the forest be taken into account.

## **2.6 ACKNOWLEDGEMENTS**

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### CHAPTER 3: LITTERFALL AND ITS RELATIONSHIP WITH LEAF AREA INDEX IN AN OLD-GROWTH *PSEUDOTSUGA-TSUGA* FOREST.

#### 3.1 ABSTRACT

Leaf area index (LAI) varies seasonally in all forests, potentially affecting rates of stand-level processes including photosynthesis, respiration, and transpiration. Even in evergreen coniferous forests, LAI varies because leaf lifespans are finite, periods of new leaf growth and peak leaf loss do not coincide, and some understory plants are winter-deciduous. In an old-growth *Pseudotsuga-Tsuga* stand in Washington, USA, we use leaf litter to determine seasonal LAI variation. Litter was collected monthly except in winter, sorted, and identified by species. Litter leaves are related to monthly changes in live leaf area that are combined with previously obtained baseline, "standing crop" LAI values from midsummer. Including the understory, maximum stand LAI (9.05, July 15) is 37% greater than the minimum (6.63, April 1). Most conifer leaf loss occurs from July through September, earlier in the year than for coniferous forests elsewhere in the world but coinciding with a distinctive, regional summer dry season, suggesting that early leaf loss is a drought response. Comparing three conifer species, leaf lifespans are positively associated with specific leaf masses, i.e. thicknesses. The monthly values of LAI obtained here will aid in modeling stand ecophysiological processes.

## 3.2 INTRODUCTION

### 3.2.1 Seasonal variation of LAI and its importance

Leaf area index (LAI) fluctuates seasonally in all forests, including evergreen conifer stands. LAI strongly affects the stand-level rates of many canopy ecosystem processes, including photosynthesis, foliar respiration and transpiration. Accordingly, LAI is an explicit or implicit component of forest ecophysiology models (e.g. Forest-BGC, Waring and Running 1998b). Seasonal variations in LAI necessarily influence the seasonal rates all such modeled canopy processes.

Conifer leaves have finite lifespans, usually several years, requiring their periodic replacement. The seasonal periods of new leaf growth and peak leaf loss do not coincide, as new leaves grow during spring and early summer, while most older leaves are shed in late summer, fall and/or winter (e.g., peak leaf litterfall rates in November–December for *Pinus taeda* L. in Mississippi, Hinesley et al. 1991). Evergreen coniferous LAI thus attains its maximum in early summer after new leaf growth is complete, and minimum in early spring before new leaf growth commences. Nonconiferous understory plants may have separate, seasonal patterns of LAI, such as winter deciduous habits, increasing the amplitude of LAI for the whole stand.

Seasonally, the LAIs of twelve evergreen conifer stands in Oregon and Washington are reported to vary by 25%–150% (mean  $\pm$  SD = 80%  $\pm$  36%) including nonconiferous understory plants, with variation computed as:

$$[1] \quad \text{Variation (\%)} = [( \text{Maximum LAI} / \text{Minimum LAI} ) - 1] \times 100$$

when understory variation is included (Spanner et al. 1990). Thus, in some evergreen coniferous forests in the region, maximum stand LAI is 1.5x - 2x the minimum, with consequent strong effects on the seasonal, stand-level rates of many canopy processes.

### **3.2.2 The Pacific Northwest and other areas**

The Pacific Northwest (PNW) region of North America supports the largest evergreen conifers in the world, due in part to moderate temperatures, high mean annual precipitation (MAP) and dry summers (Waring and Franklin 1979). However, coniferous forests exist in many other areas, often with distinctly different climates. The typical situation in the PNW is for only ~5% of annual precipitation to fall during the warm and bright period of July-September. Outside the PNW, precipitation tends to be much more even through the year, although MAP is often lower (Walter et al. 1975).

Although high MAP supports maintenance of a large leaf area, extreme seasonality of precipitation may cause high evergreen LAI to become a periodic liability due to excessive transpiration, especially in a situation, such as that in the PNW, when the driest months are also the warmest. Under such a case, there may be pressure for trees to shed most leaves during the dry, warm summer, rather than later in the year which is the general pattern outside the PNW. In that region of the world where the largest conifers grow, the PNW, there may therefore be distinctive differences in leaf phenology that are related to the unusual climate of the region.

### 3.2.3 Leaf turnover and carbon economy

A corollary of seasonal variation in LAI is it relates to leaf longevity and hence leaf turnover time. Sites in Oregon dominated by *Tsuga heterophylla* (Raf.) Sarg. and *Pseudotsuga menziesii* Mirb. (Franco) var. *menziesii* experience 25% (Gholz 1982) and 30% (Runyon et al. 1994) annual leaf turnover, with mean leaf lifespans of ~4 years. Mismatch between the times of new leaf expansion and major leaf loss allows seasonal conifer LAI to vary by 20% or more.

Mean leaf lifespans may be positively related to leaf construction costs (Wright et al. 2002). Tree species that produce heavier, thicker leaves may retain them for a longer period of time, to make efficient use of the carbon invested in leaf construction. An old-growth forest, with declining Net Primary Productivity (NPP) (Ryan et al. 1997), may come under special pressure to maintain an efficient carbon economy, and thereby maximize the trade-off between carbon investment and lifetime productivity of leaves.

### 3.2.4 Goals of this study

Here, we study seasonally varying LAI in an old-growth coniferous stand in the PNW. Midsummer values of LAI were previously obtained using a line-drop method (Thomas and Winner 2000a). Leaf litterfall has been monitored since 1997, allowing extension of the existing, summer "snapshot" view of canopy LAI into a dynamic representation of the seasonal variation in LAI by all major species. Major goals are to:



(1). Extend the static view of LAI obtained by the line-drop method, to give a month-by-month view of total and species-specific LAI. Such a detailed accounting of LAI supports efforts to scale-up stand-level canopy processes from leaf-level measurements conducted at multiple times per year.

(2). Examine the timing of major phenological events such as leaf fall, and compare to those known from other coniferous sites. If there are phenological differences between the conifers at Wind River and those from other sites, examine whether there are environmental differences between the sites (e.g., precipitation patterns) that offer an ecophysiological explanation.

(3). Examine leaf mass data for the major conifer species, and relate them to the typical leaf lifespans for each species, and to considerations of carbon economy including leaf construction costs and leaf growth respiration.

Results of this study will be useful for ongoing studies of stand-level foliar processes at the research site, and may provide more general insights about the relationships between environment and conifer phenology in the Pacific Northwest.

### **3.3 METHODS**

#### **3.3.1 Study site**

Our study site is a ~450 year old forest at the Wind River Canopy Crane Research Facility (WRCCRF) in the southern Washington Cascades at 45°49.23' N,

121°57.12' W, at 355 m elevation. The climate is moist and temperate except for dry summers, with winter snowpack from December 1-March 31. The site is in the western hemlock zone (Franklin and Dyrness 1973). The canopy is dominated by large specimens of *P. menziesii*, *T. heterophylla* and *Thuja plicata* D. Don. The understory includes many shrubs, herbs and small trees.

### 3.3.2 Previous summer LAI measurements

Previously, LAI was determined for the stand based on line-drop intercept measurements performed in 1997, 1998 and 1999, on a mean date of August 28 (Thomas and Winner 2000a). Frequencies of contacts by a weighted line with foliage of each species in the upper canopy, middle canopy, lower canopy and understory were converted to estimated LAI of each species at each level, using species-specific foliage angle-distribution functions (Thomas and Winner 2000b) (Table 3.1). The resulting mean, summer LAI, including all species and averaged across three years, was 8.6. There was no significant difference ( $p > 0.05$ ) between the overall LAI values from the three years.

### 3.3.3 Leaf litter and variable seasonal LAI

Autumn leaf litter collection has been used as a nondestructive method to determine summer LAI of winter-deciduous canopies in Tennessee (Chason et al. 1991), North Carolina (Vose et al. 1995), and Mexico (Maass et al. 1995), where the collected dead leaves are related to live leaf area. Although litter collection has also

Table 3.1. Measured leaf area index (LAI) values, by species and canopy level (after Thomas and Winner 2000a).

Species	Level	LAI
Canopy foliage		
<i>Pseudotsuga menziesii</i>	Upper	1.10
	Middle	1.11
	Lower	0.19
<i>Tsuga heterophylla</i>	Upper	0.57
	Middle	1.25
	Lower	1.35
<i>Thuja plicata</i>	Upper	0.24
	Middle	0.50
	Lower	0.47
Other conifers	Lower	0.12
Total canopy		<b>6.90</b>
Understory foliage		
<i>Tsuga heterophylla</i>	Ground	0.26
<i>Thuja plicata</i>	Ground	0.04
Other conifers	Ground	0.15
All other plants	Ground	1.24
Total understory		<b>1.69</b>
Grand total		<b>8.59</b>

been used to study conifer LAI (Gholz et al. 1991, Law et al. 2001), leaf litter alone cannot determine the "standing crop" of live leaf area in an evergreen canopy. However, systematic, monthly litter measurements are able to reveal the incremental, monthly litter-losses of LAI. Coupled with an understanding of leaf ingrowth, litter analysis provides a dynamic view of the monthly gains and losses of leaf area by each species. If combined with reference measurements of standing, live LAI at a single time of year, systematic litter sampling then creates a complete, dynamic view of changing seasonal LAI. Such an opportunity exists at the Wind River Canopy Crane site, because of the potential to pair the monthly leaf litter analysis of changes in live leaf area with the summer measurements of standing, live LAI by all species (Thomas and Winner 2000a).

#### **3.3.4 Fine litter collection and litterfall rates**

Fine litter was collected in a 4-ha area, with five 40 cm x 40 cm litter traps randomly placed in each hectare. Litter was collected on the first day of each month, except when traps were under snow, with an average of 9.2 annual collections from 1998-2002 (data on file with the WRCCRF, 1262 Hemlock Road, Carson, WA 98610). Conifer leaves were sorted into "brown" (shed after senescence) and "green" (lost while functional) categories, then dried and weighed. Litter traps do not account for the toppling of whole trees, or of large live branches. However, leaf litter from such discrete events is considered negligible compared to the much larger, continuous inputs from fine litter rain.

Mean monthly leaf-litterfall rates are calculated for 1998-2002. Values for months without collections are interpolated. Collections from April, June, August and October of 2000 and 2001 are examined for the proportions of litter mass by species, then interpolated between months. Peak leaf litterfall is expected in summer and/or early fall, as with other sites in the PNW (e.g. July-October for *T. heterophylla* in the Hoh Rainforest, Washington, Edmonds and Murray 2002).

### 3.3.5 Relating litterfall to LAI

For each species, we expect a relationship between leaf litter mass and live LAI, leaf area in the canopy before leaves are shed. However, there are three questions. (1) What are the decay and/or leaching rates for leaves in the traps? (2) Is leaf area affected by senescence? (3) How much do leaves shrink when dried?

Except in winter, leaves spend 0.5 months on average within the traps. Leaf litter mass decay rates of 3.5%, 5.9% and 2.8% month<sup>-1</sup>, respectively, have been seen for *P. menziesii*, *T. heterophylla* and *T. plicata* in the Hoh Rainforest of Washington (Harmon et al. 1990). Leaves may therefore lose 1.5–3.0% of mass in 0.5 months, from decay. However, the traps partially exclude decomposers, reducing decay rates. We thus assume negligible decay. Leaves collected in early spring, after spending as long as several months under snowpack, may also lose an undetermined amount of mass due to leaching. However, litter input rates in winter are low compared to other seasons, so leaching mass losses are also discounted as negligible.

Senescence causes losses of dry leaf mass of up to 30% in *T. heterophylla* and 49% in *T. plicata* (Keenan et al. 1995). However, leaf area is a stable character after growth was complete (Fahey and Birk 1991), except for shrinkage from drying. We examine shrinkage using samples from one tree each of *P. menziesii*, *T. heterophylla* and *T. plicata*. Leaves were arrayed, nonoverlapping, scanned at 200 dpi, and analyzed with NIH-Image software on a Macintosh G3 to find areas. Leaves were dried, then scanned again. Typical area losses from drying (mean  $\pm$  SE) are  $10.2 \pm 1.1\%$  (*P. menziesii*),  $6.1 \pm 1.4\%$  (*T. heterophylla*) and  $6.9 \pm 0.6\%$  (*T. plicata*).

### 3.3.6 Calculation of live area

LMAs of dry, brown leaves are determined using litter from April, June, August and October of 2000 and 2001. Leaves of *P. menziesii*, *T. heterophylla* and *T. plicata* were selected randomly, then scanned, analyzed as above and weighed to determine LMA. Values are interpolated between months. We also determine LMAs of first-year fresh, green leaves collected from each major species in March, June, September and December of 2001. The fresh LAI equivalents of all brown and green litter are calculated, using litter masses of each species from each month, the interpolated LMAs, and shrinkage ratios.

### 3.3.7 Leaf ingrowth, lifespan and carbon economy

The annual gains and losses of leaf area are expected to offset each other. Growing leaves reach full expansion in their first year, so the youngest cohort of

leaves produces all new leaf area. For *P. menziesii* and *T. heterophylla*, bud break and stem elongation occur from mid-May to late June (data on file with the WRCCRF, 1262 Hemlock Road, Carson, WA 98610). Because new leaves of *P. menziesii* grow for 6-8 weeks (Montano and Proebsting 1988), we assume that new leaves grow in at constant rates from mid-May through mid-July.

The fate of 10% of conifer leaves is to be eaten from the trees (Harmon et al. 2004). If herbivory and litterfall together cause all leaf loss, then annual new leaf expansion creates 111% of the LAI represented by litter. Herbivores are assumed to annually consume LAI equivalent to 11% of the annual total leaf litter, at a constant rate from May 1–October 31.

Mean leaf lifespans are the ratio of maximum LAI : annual LAI loss for each species. The inverse ratios represent annual turnover rates. Leaf carbon construction costs, including growth respiration, are 125% of the annual carbon lost from litterfall and herbivory (Ryan 1991b), with leaf carbon masses equal to 50% of dry weight (Waring and Running 1998a). Materials withdrawn during senescence are assumed to be re-used within the trees.

### 3.3.8 The nonconiferous understory

Out of all conifers with DBH > 5 cm, 59% are understory trees 1-15 m tall. Conifer foliage remains active year-round (Winner et al. 2004), so in all seasons, conifer foliage at all levels actively contribute to forest ecophysiological processes. However, nonconiferous understory species are either deciduous or else buried by winter

snowpack. Buried leaves are expected to be dormant, so the nonconiferous understory has zero functional LAI in winter. At other times, nonconiferous evergreen plants are active, but deciduous species only carry full foliage from June through September. Accordingly, we model the LAI of the nonconiferous understory as 1.24 from June 1–September 30 (Thomas and Winner 2000a), zero from December 1–March 31, and transitional from April 1–May 31 and October 1–November 30.

### 3.4 RESULTS

#### 3.4.1 Monthly variation in LAI

Leaf masses per area are found for brown leaves of the major species (Table 3.2), facilitating conversion of leaf litter masses of each species into equivalent live LAI. The LMAs of *T. plicata* are the highest, while those for *T. heterophylla* are the lowest, a consequence of the relatively thick *T. plicata* fronds vs. the thinner *T. heterophylla* needles. Although LMA values are expected to be higher in the upper canopy than in the lower, as a consequence of the typical differences between sun and shade adapted leaves (Larcher 1995), separate upper and lower canopy values of brown LMA cannot be determined because there is no way to determine the original growth positions of individual leaves that fall into traps.

Because the green leaf analysis uses samples collected from upper and lower canopy levels, green LMA values are height-specific (Table 3.3), with larger values in



Table 3.2. Leaf mass per area (LMA, mean  $\pm$  SE) of brown leaves collected from litter traps in 2000 and 2001, with yearly mean weighted according to monthly litter masses.

Species	LMA (g m <sup>-2</sup> leaf)				Yearly mean
	April	June	August	October	
<i>Pseudotsuga menziesii</i>	145.5 $\pm$ 0.3	182.4 $\pm$ 2.1	184.1 $\pm$ 7.6	181.2 $\pm$ 0.9	172.9 $\pm$ 6.3
<i>Tsuga heterophylla</i>	152.2 $\pm$ 10.1	151.0 $\pm$ 2.9	148.4 $\pm$ 10.2	146.6 $\pm$ 4.2	148.8 $\pm$ 3.0
<i>Thuja plicata</i>	172.2 $\pm$ 7.6	NA	NA	227.8 $\pm$ 14.1	215.0 $\pm$ 17.3

Table 3.3. Green leaf LMA (mean  $\pm$  SE ) for major conifer species, based on samples collected in the canopy in March, June, September and December of 2001, and weighted according to the vertical stratification of LAI of each species in a simplified two-layer canopy model.

Species	Level	LMA (g m <sup>-2</sup> ) by level	LAI Proportions	Weighted LMA (g m <sup>-2</sup> )
<i>Pseudotsuga</i>	Upper	218.4 $\pm$ 1.7	0.690	201.9 $\pm$ 1.2
<i>menziesii</i>	Lower	165.4 $\pm$ 1.1	0.310	
<i>Tsuga</i>	Upper	239.1 $\pm$ 5.6	0.348	168.7 $\pm$ 2.2
<i>heterophylla</i>	Lower	131.1 $\pm$ 1.5	0.625	
<i>Thuja</i>	Upper	330.5 $\pm$ 5.7	0.392	259.9 $\pm$ 2.6
<i>plicata</i>	Lower	214.3 $\pm$ 2.3	0.608	

the upper canopy as expected. Weighted LMA values are calculated, based on the vertical stratification of standing leaf area in a simplified two-layer canopy model, dividing the original mid-canopy layer (Thomas and Winner 2000a) between the upper and lower layers. All weighted green LMA values are larger than the yearly mean values for brown leaf LMA, indicating that brown leaves lose at least 12-17% of their mass via senescence, decay and leaching. Actual mass losses from brown leaves may be greater, because brown leaves are older than the first-year green leaves used to determine green leaf LMA, and evergreen leaves continue to add mass during each year of life (Ishii et al. 2002). With regard to scaling from litter to equivalent live LAI, brown leaves are the most important, because ~95% of leaf litter consists of brown leaves.

Baseline values of LAI were measured on an average date of August 28 (Thomas and Winner 2000a), and are assumed here to apply to September 1. Litter collected on October 1 represents the live LAI lost as litter during September, and thus represents an incremental decrease from the measured LAI values, and so forth. Through a year, the monthly litter-losses of LAI are calculated for each major species. Each loss is calculated using the appropriate litter mass, interpolated LMA and drying correction for each species and month. The total, annual LAI equivalents of the leaf litter from each species are 0.47 (*P. menziesii*), 0.97 (*T. heterophylla*) and 0.15 (*T. plicata*), a total annual LAI loss of 1.60, 53% occurring from July-September (Figure 3.1). Of the total amount of leaf-litter LAI loss, 95% involves shedding of brown leaves.

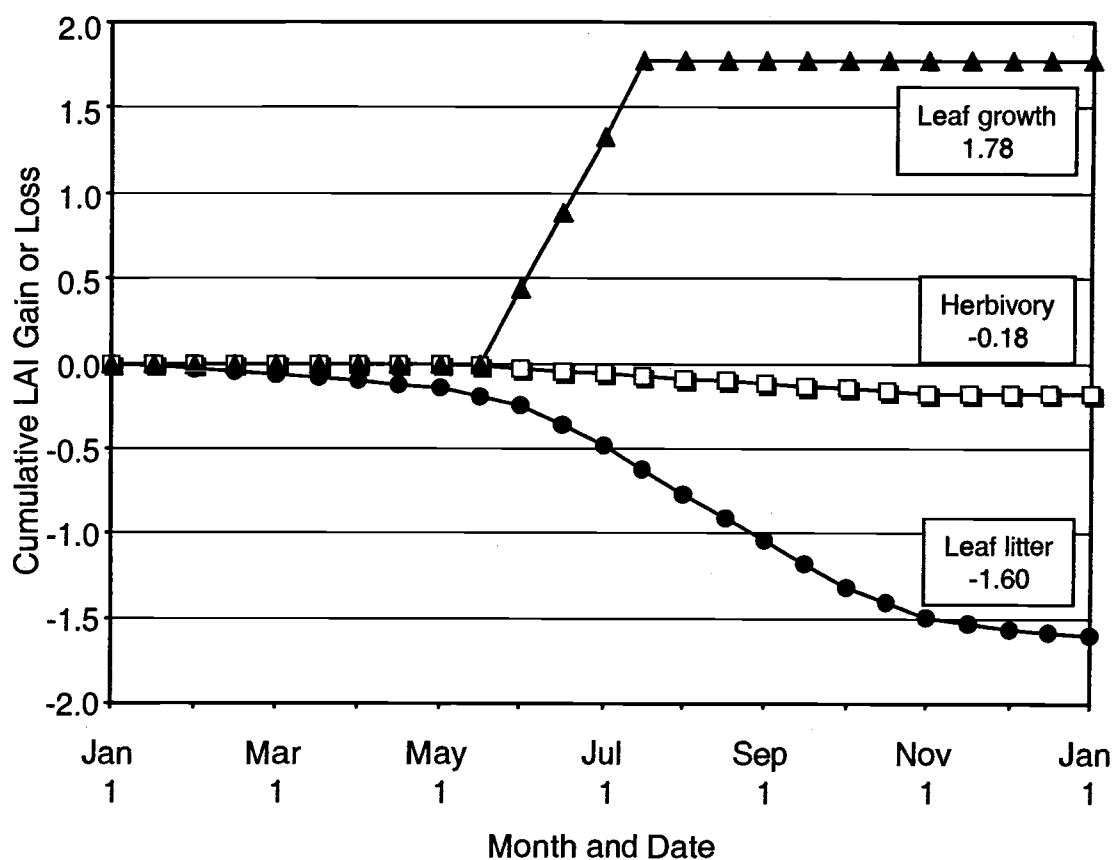


Figure 3.1. Cumulative, annual changes in conifer LAI, due to new leaf growth (additions), herbivory (losses) and leaf litterfall (losses). Boxed values indicate yearly totals from each process. Annual gains and losses of LAI are assumed to be equal.

To offset both herbivory and litterfall, the annual LAI of new leaf production is  $(1.60) \times (111\%) = 1.78$  (overall), and for individual species, 0.53 (*P. menziesii*), 1.08 (*T. heterophylla*) and 0.16 (*T. plicata*). As for herbivory, LAI losses by all conifer species is 0.18, and for particular species, 0.05 (*P. menziesii*), 0.11 (*T. heterophylla*) and 0.02 (*T. plicata*). Annual gains and losses of LAI are assumed to be in balance.

All LAI estimates are interpolated to the midpoints of each month, to allow inclusion of the process of new conifer leaf expansion from mid-May through mid-July. The maximum conifer LAI, 7.81, occurs at mid-July, as leaf expansion ceases (Figure 3.2). The minimum of 6.52 occurs at mid-May, at the start of new leaf expansion. Individual species differ with regard to their seasonal stability of LAI. The most changeable species is *T. heterophylla*, while the most stable species is *T. plicata*.

### 3.4.2 Timing of conifer leaf fall

Conifer leaf litterfall rates vary greatly. Rates are low in the winter and early spring, but then rise sharply to a nearly constant peak of  $0.428 \times 10^6 \text{ g ha}^{-1} \text{ month}^{-1}$  averaged from July through September (Figure 3.3). Total, annual leaf litterfall is  $2.372 \times 10^6 \text{ g ha}^{-1} \text{ y}^{-1}$  by dry mass, 54% of which falls from July-September. Brown leaves account for 94.5% of total mass, while green needles account for only 5.5%; similar to results from a *T. heterophylla*-dominated stand in the Hoh Rainforest, Washington (Edmonds and Murray 2002).

Seasonal litterfall patterns differ by species, with *P. menziesii* and *T. heterophylla* losing leaves in all months, while *T. plicata* loses leaves during a more

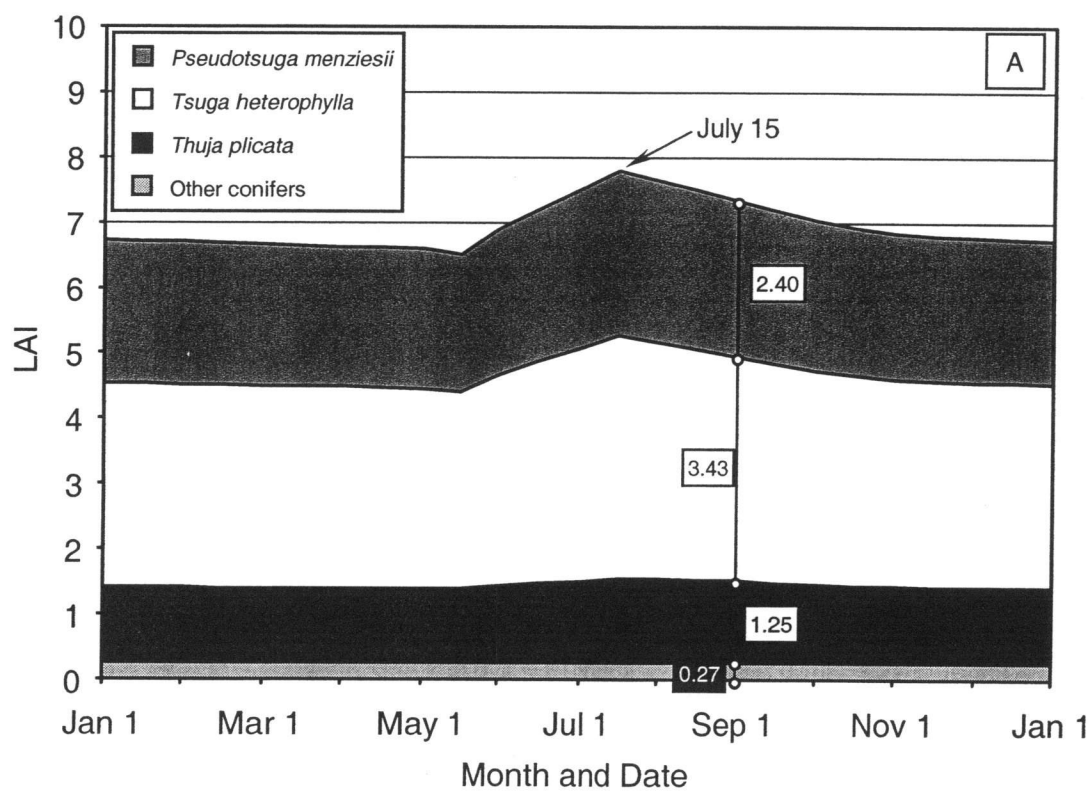


Figure 3.2. Calculated stand LAI, without (A) and with (B) the nonconiferous understory. Values for conifers include leaves from all levels including the understory. Vertical lines in the panels, and the associated values, indicate the directly measured LAI values (Thomas and Winner 2000a).

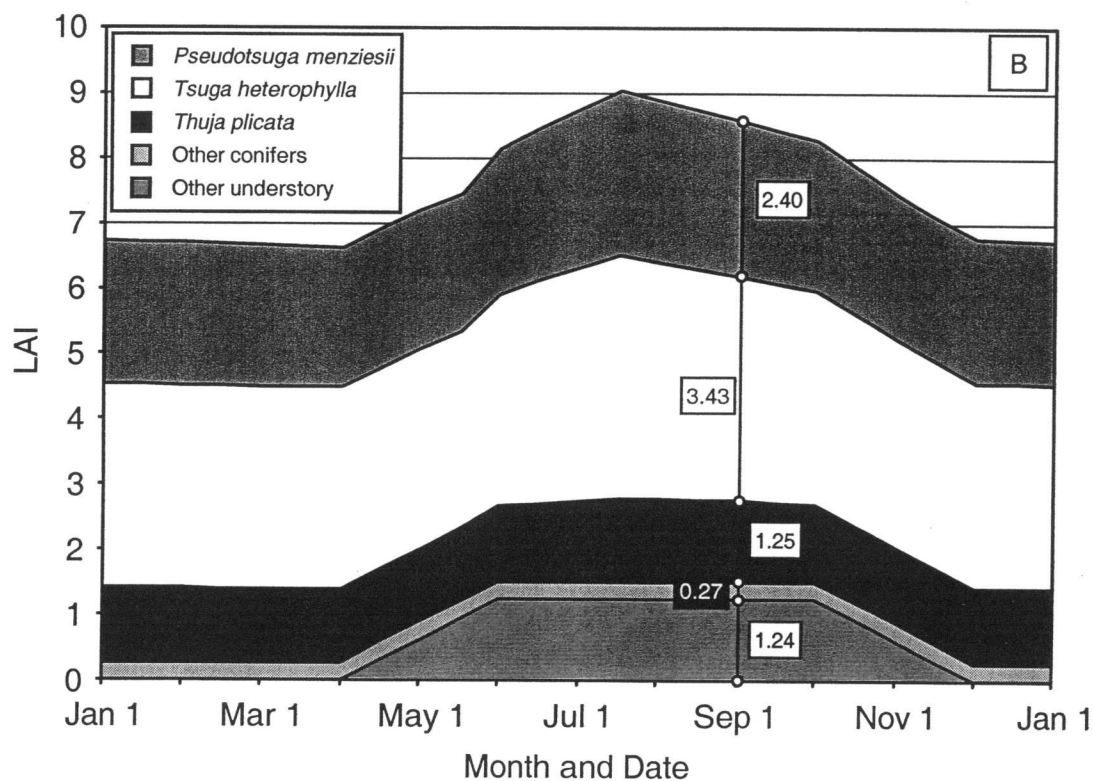


Figure 3.2 (continued). Calculated stand LAI, without (A) and with (B) the nonconiferous understory. Values for conifers include leaves from all levels including the understory. Vertical lines in the panels, and the associated values, indicate the directly measured LAI values (Thomas and Winner 2000a).

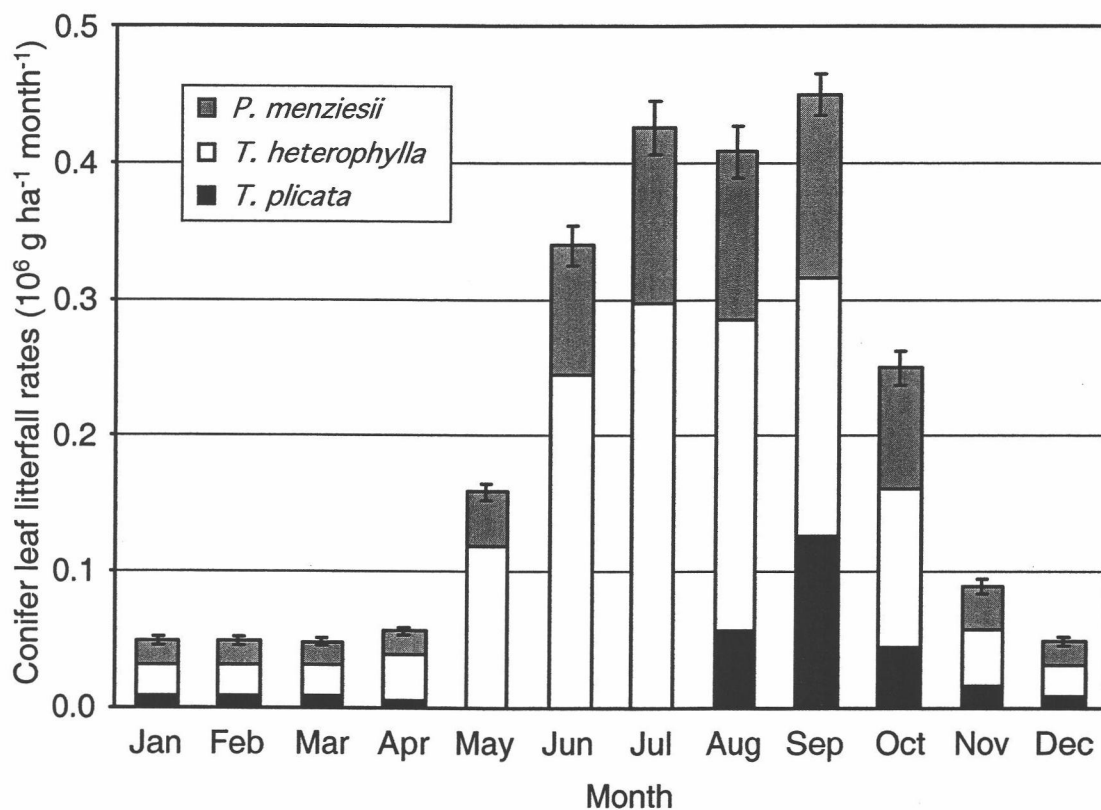


Figure 3.3. Monthly litterfall rates, using pooled 1998-2002 data. Total values are the measured total masses of “brown” and “green” conifer leaves of all species. Error bars represent  $\pm 1$  SE of total leaf litter. The amounts of litter contributed by each species are interpolated from collections in April, June, August and October of 2000 and 2001. Total litter amounts in the December-March period are interpolated.



restricted period. *Tsuga heterophylla* produces the greatest proportion of leaf litter, and *P. menziesii* the second greatest, in all months (Table 3.4). We interpolate to estimate the litter masses produced by each major species in each month. No leaves are identified from other conifer species.

### 3.4.3 Conifer leaf lifespans and carbon economy

Leaf lifespans and turnover rates differ between species. As a consequence of the highly variable LAI of *T. heterophylla*, its leaves have the shortest mean lifespan and the highest turnover rate (Table 3.5). Conversely, *T. plicata* leaves have the longest lifespan and the lowest turnover rate, with less seasonal variation in LAI. Values for *P. menziesii* are intermediate. Because *T. heterophylla* has the greatest standing LAI of any species, and relatively short-lived leaves, it dominates the litter rain with 61% of total litter LAI.

The leaf lifespan for each species is strongly related to LMA, both for green and brown leaves (Figure 3.4). Species with higher LMA, or heavier leaves, retain them for a longer period. For both brown and green leaves, the correlations between mean leaf lifespan and mean LMA are very high ( $r^2 = 0.996$ ). However, the slopes of the linear regressions are significant but not highly so ( $p = 0.0402$ ), because each represents only three species and has one degree of freedom.

Annual conifer leaf mass losses from litterfall are  $2.372 \times 10^6 \text{ g ha}^{-1} \text{ y}^{-1}$ . In addition, using the herbivory-LAI losses for the major conifer species, annual leaf mass losses from herbivory are  $0.339 \times 10^6 \text{ g ha}^{-1} \text{ y}^{-1}$ . If leaves are 50% carbon by dry

Table 3.4. Species percentages (mean  $\pm$  SE) of total conifer leaf litter collected at four times, in 2000 and 2001.

Collection date	Percentage of litter mass per species		
	<i>Pseudotsuga menziesii</i>	<i>Tsuga heterophylla</i>	<i>Thuja plicata</i>
April 1	35.6 $\pm$ 0.7	46.7 $\pm$ 1.2	17.7 $\pm$ 0.5
June 1	25.4 $\pm$ 19.8	74.6 $\pm$ 19.8	0.0 $\pm$ 0.0
August 1	30.2 $\pm$ 3.7	69.9 $\pm$ 3.7	0.0 $\pm$ 0.0
October 1	29.8 $\pm$ 0.8	42.2 $\pm$ 1.3	28.0 $\pm$ 2.1

Table 3.5. Mean conifer leaf lifespans for the major species, and the proportions of leaves replaced in each year, with values of annual LAI loss including leaves lost by both litterfall and herbivory.

	Maximum LAI	Minimum LAI	Annual LAI Loss	Annual Turnover (%)	Mean Leaf Lifespan (years)
<i>Pseudotsuga menziesii</i>	2.53	2.13	0.53	20.9	4.79
<i>Tsuga heterophylla</i>	3.73	3.01	1.08	29.0	3.45
<i>Thuja. plicata</i>	1.28	1.12	0.16	12.5	7.81

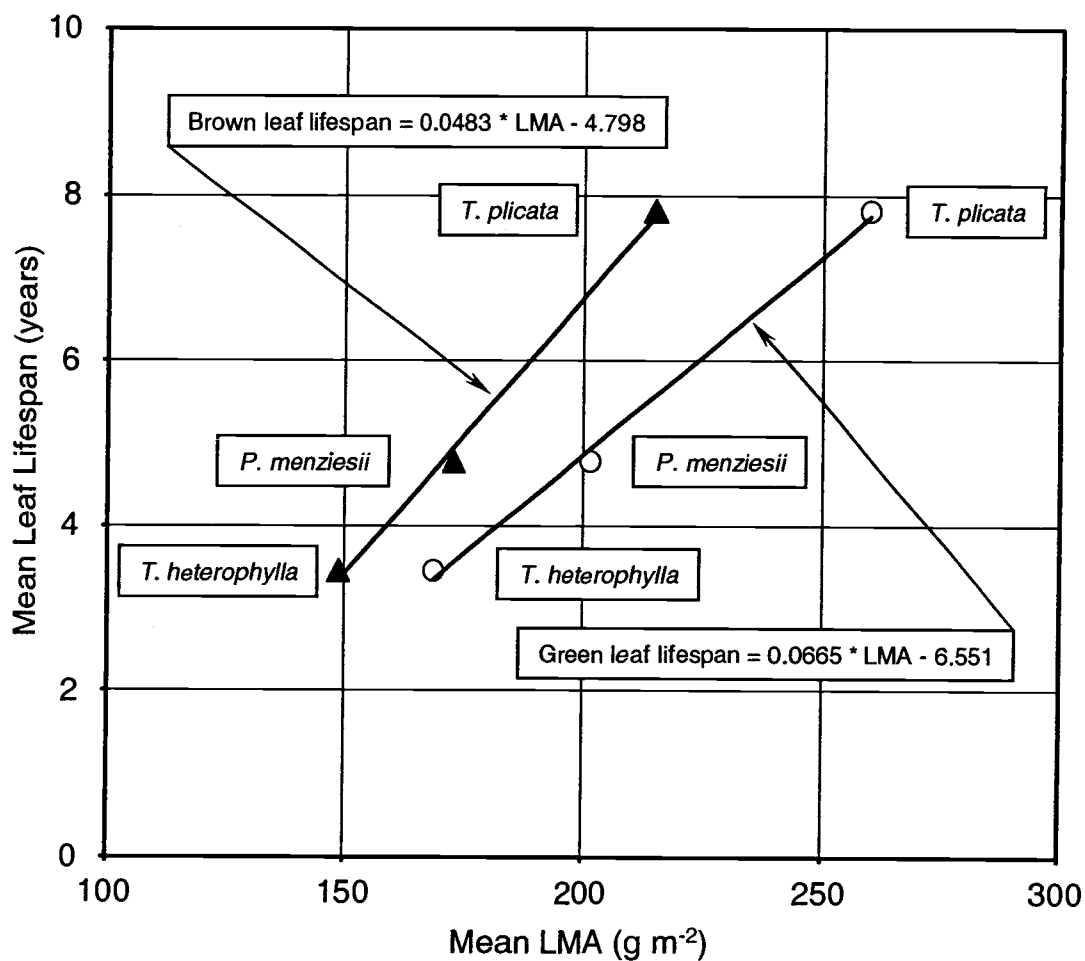


Figure 3.4. Relationship between mean leaf lifespan of major conifer species and mean LMA, for both brown and green leaves. Open circles: green leaves. Closed triangles: brown leaves. Correlations for regressions:  $R^2 = 0.996$ ; significances of slopes:  $p = 0.0402$ .

weight, and construction cost including growth respiration is 125% of carbon weight, then annual conifer leaf construction costs are  $1.694 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ . Costs are not calculated for nonconiferous understory plants.

#### 3.4.4 Understory and the whole stand

The nonconiferous understory is modeled with its maximum LAI of 1.24 (Thomas and Winner 2000a) from June 1–September 30, and smaller values at other times representing periods when understory plants are leafless and/or buried by snow-pack. When combined with the patterns for conifers, the nonconiferous understory increases the seasonal amplitude of LAI for the whole stand. Maximum stand LAI, 9.05, occurs in mid-July, while the minimum, 6.63, occurs at the beginning of April.

### 3.5 DISCUSSION

#### 3.5.1 Seasonal range of LAI

Conifer LAI, including conifers in the understory, varies from 6.52 to 7.81. Thus, overall seasonal variation in conifer LAI is 20%, by Eq. [1]. Of the conifers, the most and least changeable are *T. heterophylla* and *T. plicata*, with maximum LAI values 24% and 14% larger than their minima, respectively. Values for *P. menziesii* are intermediate. For the whole stand, including the entire understory, LAI varies from 6.63 to 9.05. Thus, maximum stand LAI is 37% greater than the minimum. Variation

is less than that previously reported, using different methodology including remote sensing, for 10 out of 12 Oregon and Washington evergreen conifer stands (Spanner et al. 1990). Nevertheless, LAI variation is great enough at the WRCCRF site that modeling of stand-based, leaf-related processes including foliar respiration must take into account seasonal changes in LAI.

### 3.5.2 Phenological timing and climate

At the WRCCRF site, the peak rate of leaf loss occurs from July through September. Overall timing of leaf fall is similar to that elsewhere in the PNW, with peak rates from July-October for *T. heterophylla* in the Hoh Rainforest, Washington (Edmonds and Murray 2002), and from August-September for *T. heterophylla*-*A. amabilis* stands on Vancouver Island (Keenan et al. 1995). Other stands on Vancouver Island, dominated by *T. plicata* with lesser amounts of *T. heterophylla*, have peak rates in October, later than that of the overall leaf litterfall rates at the WRCCRF site, but similar to the timing there for *T. plicata*, specifically.

Outside the PNW, peak conifer leaf litter rates usually occur later in the year than at the WRCCRF site, such as in October for *Pinus banksiana* Lamb. in Alberta (Fyles et al. 1996); November-December for *P. taeda* in Mississippi (Hinesley et al. 1991); October for *Pinus ponderosa* Laws. in Arizona (Klemmedson 1990); "late summer and autumn" for *Pinus sylvestris* L. in Finland (Kouki and Hokkanen 1992); and May-June (equivalent to the Northern Hemisphere November-December) for *Pinus elliottii* Engelm. in Queensland, Australia (Maggs 1985).

The climate at the WRCCRF site is distinctly different than that of the Alberta, Mississippi, Arizona, Finland, and Queensland sites, and may explain the differences in phenology. The Wind River climate, like that of the PNW in general, is summer-dry. Overall, the WRCCRF site is very wet, with MAP of  $2,759 \text{ mm y}^{-1}$ , but only 5.3% of annual precipitation falls from July through September (data for Wind River, Washington, 1971-2000, on file with the Western Regional Climate Center, <http://www.wrcc.dri.edu>). Globally, mesic regions with a winter-wet, summer-dry climate are uncommon (Walter 1975). Climatic differences therefore distinguish the PNW from most other regions of the world. The sites in Alberta, Mississippi, Arizona, Finland, and Queensland are all relatively summer-wet, although none experience as much total annual precipitation (Figure 3.5).

The early leaf fall at the WRCCRF site may be a regional adaptation to the summer dry season. Midday leaf water potentials in 60-m specimens of *P. menziesii* change little during summer, from  $-2.7 \text{ MPa}$  in June to  $-2.9 \text{ MPa}$  in September (Phillips et al. 2002). However, midday crown stomatal conductance decreases by 60%, from  $\sim 50 \text{ mmol m}^{-2} \text{ s}^{-1}$  in June to  $\sim 20 \text{ mmol m}^{-2} \text{ s}^{-1}$  in September. Thus, one drought response of the trees is to reduce conductance, thereby reducing transpiration and minimizing damage from excessively low water potentials. High overall annual precipitation provides an abundant water supply to support a large LAI, but such a large transpiring surface may become a liability during the summer. Thus, a second drought response may be for trees to selectively shed their older leaves primarily in summer

Figure 3.5. Monthly precipitation (2759 mm mean annual precipitation, MAP) and noon vapor pressure deficit at WRCCRF site. Precipitation data from the Western Regional Climate Center, <http://www.wrcc.dri.edu>. VPD data from 60 m level, means from 1999-2001, data on file with the WRCCRF, 1262 Hemlock Road, Carson, WA 98610. Comparison with precipitation for five coniferous stands. Sources: data for Jackson, Mississippi, 1408 mm MAP; Brisbane, Australia, 1187 mm; Flagstaff, Arizona, 581 mm; and Kuopio, Finland, 608 mm from the World Weather Information Service of the World Meteorological Organization, <http://www.worldweather.org>. Data for Slave Lake A, Alberta, 503 mm, from Environment Canada, [http://weatheroffice.ec.gc.ca/canada\\_e.html](http://weatheroffice.ec.gc.ca/canada_e.html). Note the seasonal reversal for Brisbane.



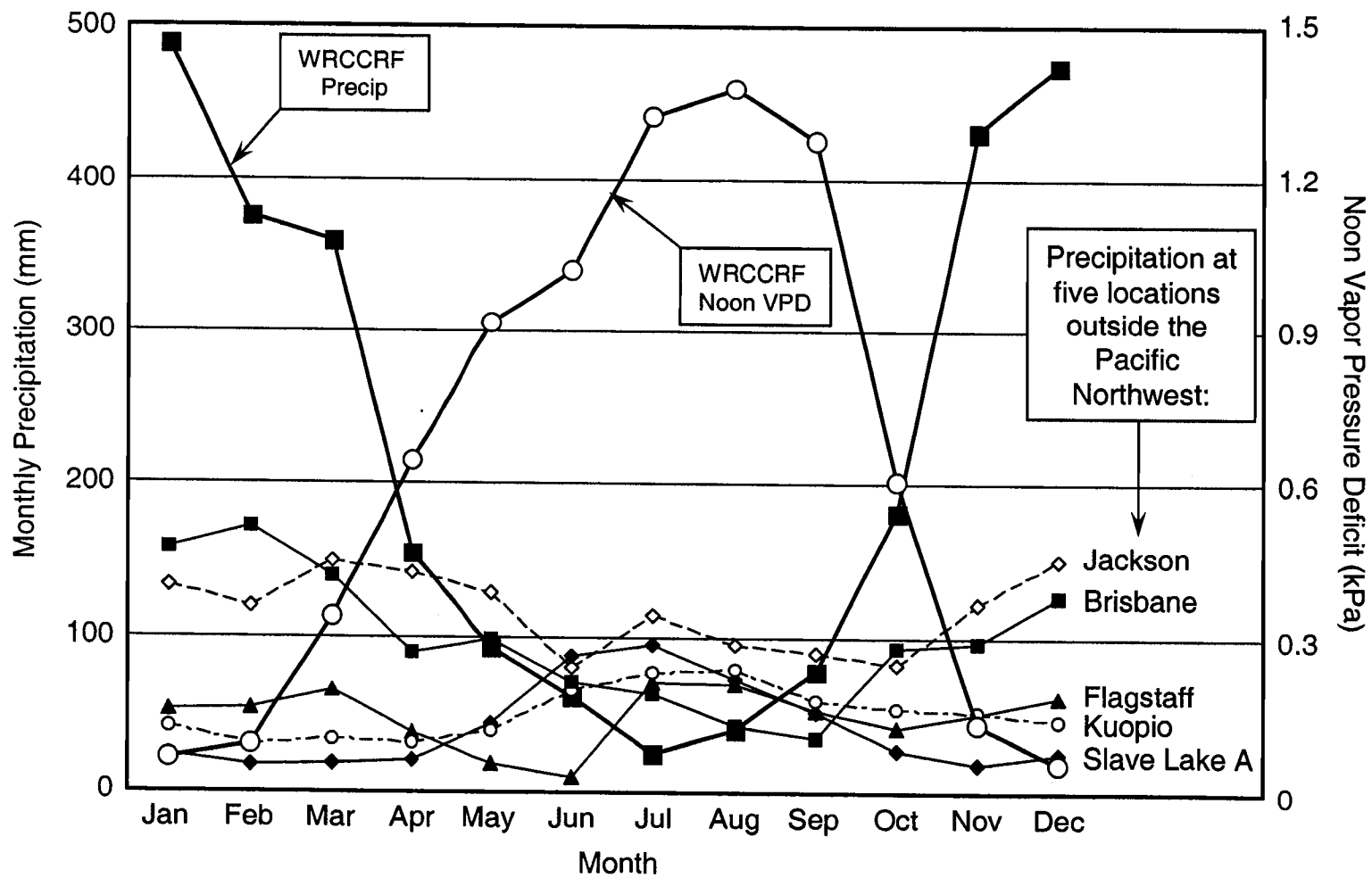


Figure 3.6

rather than in fall, to reduce transpiring area and thereby also prevent excessively low values of water potential.

Conifers at the WRCCRF site appear to exhibit a limited version of the drought-deciduous strategy. The seasonal leaf fall dynamics at Wind River may occur at sites across the PNW, because the summer dry season is a defining regional characteristic. However, early leaf fall is not necessary in other regions with more equable precipitation, allowing trees there to retain their older leaves through the summer, and maximizing their opportunities for carbon gain.

Unlike leaf fall, bud break occurs at a more typical time. Bud break happens in March for *P. taeda* in Alabama (Boyer and South 1989), early May for *Pinus nigra* ssp. *laricio* var. *Corsicana* in France (Guehl et al. 1993), late May for *Picea glauca* (Moench) Voss in Ontario (Groot and Carlson 1996), and mid-June for *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco in New Mexico (Billow et al. 1994). The timing of bud break at the WRCCRF site, in mid-May, is not anomalous.

### 3.5.3 Leaf lifespans and carbon economy

One estimated value of conifer Gross Primary Productivity at the WRCCRF site is  $17.03 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  (Harmon et al. 2004). Therefore, the conifer leaf construction cost of  $1.694 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , including growth respiration, represents 10% of the carbon made available to the trees by photosynthesis. Such a large investment of resources must be used efficiently, especially in an old-growth stand with declining productivity (Ryan et al. 1997).

Comparing conifer species, there is an association between mean leaf mass (LMA) and leaf longevity, which is one strategy for trees to optimize their return on investment. Other strategies are possible, but do not apply here. For example, a hypothetical species in a mixed stand might produce thick leaves that preferentially grow in the brightest environments and/or have the highest photosynthetic capacity  $A_{\max}$ , thereby making a rapid return on investment due to high productivity, despite high leaf mass. However, at the WRCCRF, leaves of *P. menziesii* dominate the bright upper canopy and have the highest  $A_{\max}$  (Winner et al. 2004), yet have intermediate values of LMA and lifespan. Both *T. heterophylla* and *T. plicata*, with lower values of  $A_{\max}$ , dominate the darker lower canopy, yet have divergent values of both LMA and lifespan. The only clear strategy here by which the various tree species optimize their return on investment is that by which the heavier leaves have longer lifespans.

#### 3.5.4 In summary

At a local level, this study has produced a detailed picture of changing LAI in an old-growth stand. The resulting LAI values are useful for ongoing studies at the site involving stand-level processes, including work to scale-up leaf-level measurements to produce stand-level estimates of photosynthesis and foliar respiration. In addition, this study demonstrates that the litterfall dynamics in the PNW are distinct from those of most other coniferous forests in the world, probably because of climatic differences.

### 3.6 ACKNOWLEDGEMENTS

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## CHAPTER 4: STAND-LEVEL FOLIAR RESPIRATION IN AN OLD-GROWTH CONIFEROUS FOREST.

### 4.1 ABSTRACT

Foliar respiration is a large component of the carbon balance in an evergreen coniferous forest. In a Pacific Northwest old-growth forest, values of respiration measured at the leaf level on several major tree species are scaled to the stand level to yield nighttime foliar respiration by conifers, using a respiration-temperature model, with micrometeorological and LAI data. Variation is included using a probability-distribution model for respiration and temperature for the leaf-level measurements, and of air temperatures. Values are found of total maintenance respiration in four consecutive years. The four-year mean is  $3.40 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , with minor inter-annual differences, potentially utilizing 22% of gross photosynthetic carbon gain in the stand. Annual carbon investment for construction of new leaves is  $1.70 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  including growth respiration, potentially utilizing another 11% of carbon gain. Thus, annual construction and maintenance of leaves may utilize  $\sim 1/3$  of Gross Primary Productivity (GPP). The most important species is *Tsuga heterophylla*, which has the greatest leaf area and produces 46% of conifer foliar respiration. Three recent papers regarding the same forest, that have produced divergent estimates of GPP and other carbon budget parameters, are brought into closer agreement through substitution of results of this study.



## 4.2 INTRODUCTION

### 4.2.1 Foliar respiration and forest carbon balance

Foliar respiration strongly affects carbon balance in evergreen coniferous forests. Although leaves are the sites of photosynthesis and are therefore strong net carbon absorbers, they also carry high respiratory and construction costs, and consequently consume photosynthate in quantities similar to the amounts required for the production and maintenance of wood and roots. In a 20-year old stand of *Pinus radiata* D. Don, foliar respiration accounts for 14% of Gross Primary Productivity (GPP) (Ryan et al. 1996). In 180-year old stands of *Abies amabilis* (Dougl.) Forbes and 245-year old stands of *Pinus contorta* Dougl. ex Loud., foliar respiration accounts for 31% and 14% of GPP, respectively (Ryan 1991b). Similarly, in young coniferous stands, foliar respiration accounts for 1/3 to 2/3 of autotrophic respiration  $R_a$  (Hagihara and Hozumi 1991), which in turn is usually ~50% of GPP (Waring et al. 1998).

An important consideration regarding older forests is that Net Ecosystem Productivity (NEP), the difference between GPP and Total Ecosystem Respiration (TER), declines over time (Franklin and DeBell 1988, Harmon et al. 2004, Janisch and Harmon 2002). An old-growth stand may become nearly carbon-neutral (with NEP approximately zero), in which case any single large, variable component of carbon balance, possibly including foliar respiration, may determine whether the forest is a net carbon source or sink. A stand that is essentially carbon-neutral may be a source in one year and a sink in another, if a particular component, i.e., foliar respiration, varies

sufficiently between years. The source/sink behaviors of forests are crucial to understanding changing atmospheric  $[\text{CO}_2]$  and its implications for climate change (Cohen and Harmon 1996, IPCC 2001).

#### 4.2.2 Studies of carbon balance in a particular old-growth stand

The old-growth forest at the Wind River Canopy Crane Research Facility (WRCCRF) (Shaw et al. 2004) is an example of an older evergreen coniferous stand. The WRCCRF site is the focus of studies of carbon flux and utilization in the old-growth stand. Several complementary studies (Harmon et al. 2004, Paw U et al. 2004, Winner et al. 2004) have estimated GPP, TER and/or NEP. However, they disagree substantially on certain findings, such as the magnitude of GPP. The estimates of stand-level foliar respiration produced in this study should aid in reaching a consensus about carbon utilization at the WRCCRF site.

Estimates of GPP at the WRCCRF site differ considerably. One study, in part using direct measurements of biomass accumulation rates to determine NPP, combined with estimated  $R_a$ , calculates GPP to be  $19.06 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  (Harmon et al. 2004). However, another estimate, using eddy covariance measurements, is lower,  $15.5 - 15.9 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  (Paw U et al. 2004). Meanwhile, a third estimate of GPP, based upon a soil-plant-atmosphere (SPA) model, is larger, at  $24.6 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  (Winner et al. 2004).

Likewise, estimates of TER differ between two studies. The first, using eddy covariance measurements, estimates TER as  $-14.0 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  (Paw U et al.

2004), using the sign convention that respiration is negative. However, in a second study, TER is calculated as  $-18.86 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  (Harmon et al. 2004), or 35% greater than in the first study. In the second case, nighttime respiration from tree foliage is estimated as  $-5.77 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , accounting for 30% of TER, and consuming 30% of GPP. Daytime foliar respiration is not considered.

The value of NEP is also in dispute. One study (Paw U et al. 2004) provides an estimate of  $1.5$  to  $1.9 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , indicating that the stand is a moderate sink, but another (Harmon et al. 2004) provides an estimate of  $0.2 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , suggesting that the stand is essentially carbon-neutral. For GPP and TER, the estimates of stand-level foliar respiration from the present study, as well as the improved, seasonal estimates of leaf area index (LAI) (Chapter 3) can be applied to derive a closer agreement between the results of the complementary approaches.

#### 4.2.3 Goals for this study

Specific goals are to:

- (1). Determine the four-year average (1998-2001), stand-level amounts of foliar respiration from the old-growth conifers at the WRCCRF, and individual components such as the amounts per season and species. These averages will illustrate the baseline importance of conifer foliar respiration, and will demonstrate the relative importance of all components, temporal, spatial and species-specific.

- (2). Examine the total annual respiration from four individual, consecutive years, and compare interannual differences for magnitude and significance. In par-

ticular, determine effects that interannual variability in foliar respiration may have on the source/sink behavior of the whole stand.

(3). Apply the results for stand-level foliar respiration, and those regarding LAI (Chapter 3), to the earlier, divergent estimates of carbon balance (Harmon et al. 2004, Paw U et al. 2004, Winner et al. 2004). In doing so, produce better agreement between the earlier studies regarding the values of stand-level GPP and TER.

## 4.3 METHODS

### 4.3.1 Study site

Our study site is a 450-year old forest surrounding the canopy crane at the Wind River Canopy Crane Research Facility (WRCCRF). The crane is located in the southern Cascade Range of Washington State at 45°49.23' N, 121°57.12' W, at 355 m altitude (Shaw et al. 2004). The climate is moist and mild except for dry summers, and the site is in the western hemlock zone (Franklin and Dyrness 1973). The tree canopy is dominated by large, mature *Pseudotsuga menziesii* Mirb. (Franco) var. *menziesii*, *Tsuga heterophylla* (Raf.) Sarg., and *Thuja plicata* D. Don., and also includes *Abies amabilis* (Douglas) J. Forbes, and *Taxus brevifolia* Nutt. The understory includes many shrubs, herbs and trees, including all canopy conifers except *P. menziesii*.

### 4.3.2 Scaling from leaf to stand

At the WRCCRF site, all leaf-level respiration rates (Chapter 2) have been measured at discrete times, using small samples with ~100 conifer leaves. For the measured rates to have larger ecological significance, they must be scaled over ground area, and inferred over time. The measurements are stratified according to all combinations of two canopy heights, three major tree species and four seasons. Total respiration from all factorial combinations are integrated here to yield annual canopy foliar respiration.

Conversion from respiration expressed on a leaf area to a ground area basis requires information about LAI, which is well quantified (Chapter 3). Separate LAI values are known for each species, at each approximate canopy level, in each season. Overnight respiration values are calculated from the short-term measurements (Chapter 2), performed during the day using darkened foliage. The daytime measurements are used as surrogates for nighttime rates at equal temperatures.

There is normally an exponential relationship between short-term respiration rates and temperature (e.g., Bolstad et al. 1999, Sprugel et al. 1995). Accordingly, computer modeling of respiration incorporates such a relationship, as with FOREST-BGC (Waring and Running 1998b), BIOME-BGC (Running and Hunt 1993), and SPA (Law et al. 2000). Models may also include other variables such as leaf nitrogen content (Law et al. 2000, Ryan et al. 1991b, Ryan et al. 1996). However, apart from temperature, models do not include other conditions from the physical environment (e.g. atmospheric  $[CO_2]$ , windspeed or humidity), when calculating respiration.

Accordingly, our model of overnight respiration uses daytime measurements of respiration on darkened foliage representing all factorial combinations of three species, two canopy levels and four seasons as index values of respiration, which are used to estimate nighttime respiration rates using many measurements of overnight temperatures and a respiration-temperature relationship. Respiration values from each factorial combination are then scaled over ground area using the appropriate LAI for each combination.

#### **4.3.3 Leaf-level measurements of foliar respiration**

Leaf-level foliar respiration has been measured through multiple years in large, old-growth trees, using mature first-year leaves (Chapter 2). Measured CO<sub>2</sub> efflux represents maintenance respiration (two-compartment model, Amthor 1989). The study species are *P. menziesii*, *T. heterophylla* and *T. plicata*, which support ~98% of canopy LAI (Thomas and Winner 2000a). Most measurements use upper and lower canopy branches of two trees of each species, in the survey months of March, June, September and December. Measurements are thus stratified according to all factorial combinations of species, canopy heights and times of year. Measured values of foliar respiration and the associated leaf temperatures serve as the basis for making more general diurnal estimates of respiration.

Respiration has been measured during the day on intact samples, using an LI-6400 Portable Photosynthesis System (Li-Cor, Inc., Lincoln, NE). Cuvette conditions include ambient humidity and temperature, and [CO<sub>2</sub>] of 350 ppm. We measure pho-

tosynthesis at ambient and high light levels, and respiration after ~5 minutes of darkness. Rates measured in this manner are used as surrogates for estimating the nighttime rates (Table 4.1).

#### 4.3.4 Temperature and foliar respiration

Typically, foliar maintenance respiration varies with temperature as:

$$[1] \quad R_2 = R_1 * \exp[\ln(Q_{10}) * (T_2 - T_1) / 10]$$

where  $R_1$  and  $R_2$  are the rates at temperatures  $T_1$  and  $T_2$  (°C), respectively, and  $Q_{10} = R_2/R_1$  when  $T_2 - T_1 = 10$  °C. Models often set leaf  $Q_{10}$  equal to 2.0 (Law et al. 2000, Running and Hunt 1993, Ryan 1991b, Waring and Running 1998b). However,  $Q_{10}$  may vary linearly with seasonal mean temperature  $T_{sm}$  (Hagihara and Hozumi 1991, McGuire et al. 1992). From a global meta-analysis (Tjoelker et al. 2001):

$$[2] \quad Q_{10} = 3.22 - 0.046 * T_{sm}$$

From Eq. [2],  $Q_{10}$  values for the  $T_{sm}$  values in March, June, September and December of 3.8 °C, 14.5 °C, 14.8 °C and 0.6 °C, respectively (Chapter 2), are 3.05, 2.55, 2.54 and 3.19, respectively. Because respiration is insensitive to the length of the dark acclimation period, overnight rates may be calculated from rates measured in the day in each survey month, using the appropriate  $Q_{10}$  values and temperature data. The literature-derived relationship between temperature and  $Q_{10}$  is used to derive seasonal values of  $Q_{10}$ , rather than curve fits through the respiration data from four seasons,

Table 4.1. Leaf-level respiration measurements  $R_m$  ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ leaf s}^{-1}$ ) for the upper and lower canopy from 1998-2001, and corresponding measured leaf temperatures  $T_m$  ( $^{\circ}\text{C}$ ), data pooled across years with all values mean  $\pm$  SD.

Canopy level	Measurement type	Month	<i>Pseudotsuga menziesii</i>	<i>Tsuga heterophylla</i>	<i>Thuja plicata</i>
Upper	$R_m$	March	$-0.70 \pm 0.33$	$-0.72 \pm 0.66$	$-0.92 \pm 0.33$
		June	$-0.79 \pm 0.31$	$-1.51 \pm 0.79$	$-1.45 \pm 0.75$
		September	$-0.70 \pm 0.20$	$-0.76 \pm 0.19$	$-0.80 \pm 0.38$
		December	$-0.22 \pm 0.20$	$-0.29 \pm 0.18$	$-0.36 \pm 0.26$
	$T_m$	March	$12.41 \pm 0.46$	$12.56 \pm 0.91$	$10.37 \pm 0.30$
		June	$18.81 \pm 2.69$	$20.52 \pm 3.36$	$21.59 \pm 2.66$
		September	$18.57 \pm 1.81$	$17.79 \pm 0.35$	$16.00 \pm 0.30$
		December	$4.93 \pm 1.12$	$6.38 \pm 0.28$	$6.15 \pm 0.77$
Lower	$R_m$	March	$-0.41 \pm 0.12$	$-0.72 \pm 0.22$	$-0.82 \pm 0.26$
		June	$-0.78 \pm 0.22$	$-0.56 \pm 0.36$	$-0.97 \pm 0.57$
		September	$-0.54 \pm 0.20$	$-0.36 \pm 0.20$	$-0.36 \pm 0.19$
		December	$-0.18 \pm 0.10$	$-0.26 \pm 0.20$	$-0.20 \pm 0.17$
	$T_m$	March	$9.99 \pm 0.17$	$14.82 \pm 0.06$	$9.77 \pm 0.53$
		June	$21.12 \pm 1.13$	$19.74 \pm 3.80$	$21.55 \pm 1.69$
		September	$18.00 \pm 0.65$	$15.68 \pm 0.35$	$15.71 \pm 0.07$
		December	$6.04 \pm 0.29$	$6.92 \pm 0.39$	$6.77 \pm 0.34$



because the daytime-only respiration measurements do not span the full diurnal ranges of temperature in the seasons and therefore do not always have the necessary explanatory power to determine seasonal  $Q_{10}$  values.

#### **4.3.5 Temperatures and night lengths**

Air temperatures,  $T_a$ , were measured at heights of 60, 20 and 2 m, and are applied in modeling to the upper canopy, lower canopy and understory levels, respectively. All micrometeorological stations log data at half-hourly intervals, beginning in February 1998 (data on file with the WRCCRF, 1262 Hemlock Road, Carson, WA 98610). We use nighttime  $T_a$  from March, June, September and December of 1998-2001, plus December 1997. Values from 1998-2000 are averaged to illustrate daily profiles (Figure 4.1), with each point based on ~90 measurements. Leaf and air temperatures are assumed equal, because of the small leaf sizes.

Typical night lengths are determined using light intensity ( $I$ ) data for 1998-2000, measured at the 60-meter high level on the canopy crane. Night is defined as the period when  $I < 1 \mu\text{mol PAR m}^{-2} \text{s}^{-1}$ . Nights are modeled as occurring during the hours (PST) of 1845-545, 2045-415, 1915-515 and 1715-745 in March, June, September and December, respectively.

#### **4.3.6 Modeling nighttime maintenance respiration**

The average rate of nighttime maintenance respiration is calculated for each of the 24 factorial combinations of species, canopy level and month. The model of night-

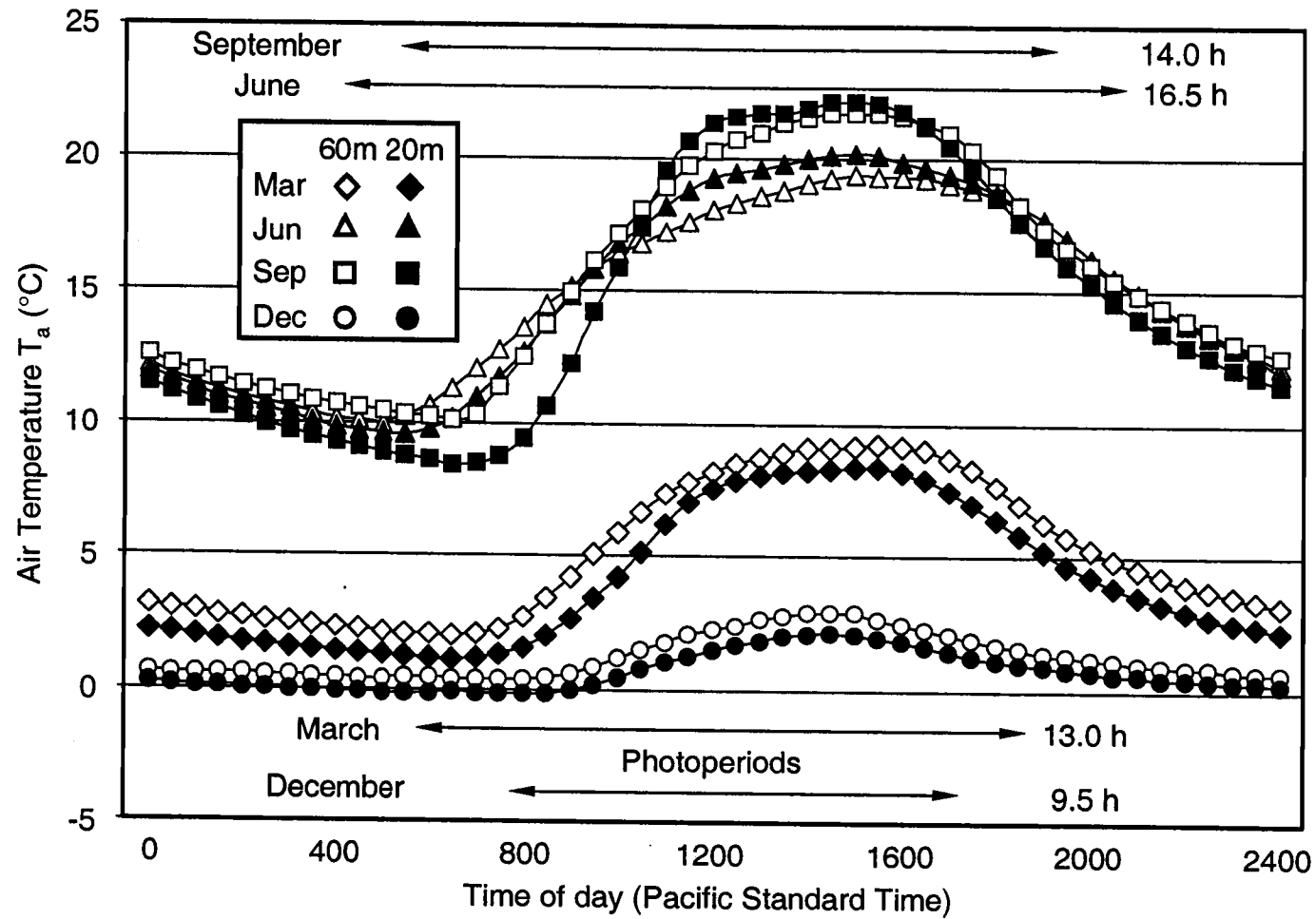


Figure 4.1. Air temperatures ( $T_a$ ) at canopy heights of 60 and 20 meters. Temperatures are means of March, June, September and December data for those months in 1998, 1999 and 2000. Approximate photoperiods are also shown for the same months.

time maintenance respiration ( $R_n$ ) combines an exponential function of temperature with measured respiration rates. It uses air temperature to calculate respiration values at half-hourly steps for which air temperatures  $T_a$  are known, that are then averaged through the whole night. The model is:

$$[3] \quad R_n = R_m * \exp[\ln(Q_{10}) * (T_a - T_m) / 10]$$

where  $R_m$  and  $T_m$  are the measured respiration rates and leaf temperatures for a factorial combination,  $T_a$  is air temperature at a time step, and  $Q_{10}$  is from Eq. [2].

The simplest way to calculate mean respiration for a factorial combination at a time step is to apply to Eq. [3] the single values of the mean measured  $R_m$  and  $T_m$  for the combination, and mean  $T_a$  for the time step. However, two problems with such a simplified approach are that: 1) The resulting mean is biased, toward a smaller than correct value (Ryan 1991a), and 2) The approach using mean input values alone cannot yield measures of variation of the results such as standard deviation.

Bias occurs because of the nonlinear, exponential relationship between respiration and temperature (Ryan 1991a). For any given time step, such as 2000 hours in June 2000, there are 30 measured values in each year (Figure 4.2), which generally follow a normal distribution. To simply apply the mean of 30 normally distributed values directly to Eq. [3], rather than applying randomly chosen values from different days and then taking the mean through multiple calculations of respiration, produces a systematic underestimate of the mean respiration rate for any particular time step.

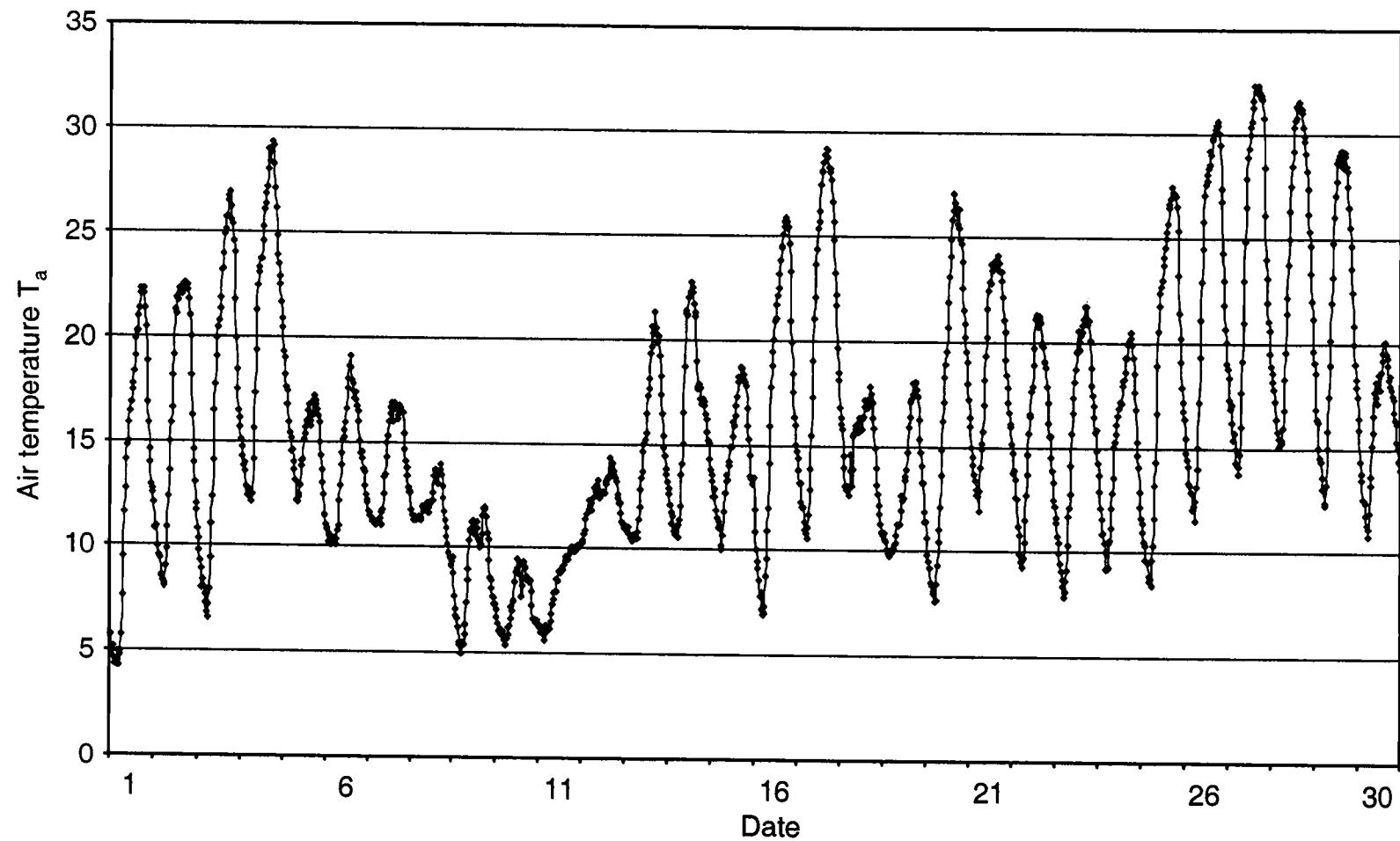


Figure 4.2. Example of measured air temperature ( $T_a$ ) data, for June 2000, at the 60-m level on the Canopy Crane, corresponding to the upper canopy. Temperatures are measured at half-hour intervals, 48 times per day.

As an initial estimate of mean respiration rates, we do calculate mean respiration at each time step using single values of  $R_m$  and  $T_m$  for each factorial combination, and of  $T_a$  at each time step. However, because of the noted deficiencies of such an approach, we also go further with a more complex analysis that incorporates the observed variability for  $R_m$  and  $T_m$  in each factorial combination, and of  $T_a$  at each time step.

In the more complex analysis, we use each measured mean  $\pm$  SD of  $R_m$  and  $T_m$  to independently generate normal distributions of 500 simulated values of each for each factorial combination of species, canopy level and month in each year 1998-2001 (DataDesk 4.2 for Macintosh, Data Description, Inc.). As for  $T_a$  at each time step, 25 values are randomly chosen from the total pool of  $\sim 30$  available in each survey month in each year. Simulated values of  $R_m$  and  $T_m$ , and the values of  $T_a$ , are independently, randomly combined in Eq. [3] to generate 500 simulated values of  $R_n$ , at each step, in each factorial combination, in each year. Thus, each time step is assigned a mean  $\pm$  SD of respiration. Distributions of  $R_n$  are so calculated for all nightly time steps in each combination, then summed and averaged, leading to an overall mean  $\pm$  SD for night-time respiration in each combination in each year (Example, Table 4.2).

For understory and other lower canopy conifers, the same steps are performed. However, no actual measured values of  $R_m$  and  $T_m$  are available for understory conifers or for the minor conifer species *A. amabilis* and *T. brevifolia* in the lower canopy. Therefore, understory *T. heterophylla* and *T. plicata* are assumed to behave as their lower canopy counterparts, and all *A. amabilis* and *T. brevifolia* are assumed to behave

Table 4.2. Example of randomized cases, for *P. menziesii*, lower canopy, in March 1998, with all respiration values as  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , all temperatures as  $^{\circ}\text{C}$ , mean  $\pm$  SD values of  $R_m$  and  $T_m$  of  $-0.483 \pm 0.090$  and  $15.80 \pm 0.38$ , respectively, used to generate cases,  $T_a$  values chosen randomly from 20 m high on the Canopy Crane, and  $Q_{10} = 3.05$ .

Case	R <sub>m</sub>	T <sub>m</sub>	Random T <sub>a</sub>				Calculated R <sub>n</sub>				Mean R <sub>n</sub>
			at times (PST)				at times (PST)				Whole night
			1900	1930	.	0530	1900	1930	.	0530	
1	-0.677	15.84	3.08	2.37	.	-2.67	-0.143	-0.133	.	-0.076	-0.156
2	-0.672	15.70	5.35	7.83	.	-0.23	-0.186	-0.245	.	-0.100	-0.154
3	-0.378	16.24	5.99	1.72	.	4.66	-0.106	-0.066	.	-0.091	-0.084
4	-0.607	15.49	9.88	7.93	.	6.64	-0.286	-0.229	.	-0.199	-0.158
5	-0.573	15.82	3.61	2.82	.	-0.94	-0.129	-0.119	.	-0.077	-0.138
.	.	.	.	.	.	.	.	.	.	.	.
500	-0.439	16.28	1.73	7.04	.	4.49	-0.109	-0.197	.	-0.149	-0.098
Mean	-0.480	15.80	6.21	5.61	.	2.13	-0.155	-0.145	.	-0.098	<b>-0.113</b>
SD	0.087	0.37	3.11	3.34	.	3.38	0.063	0.061	.	0.042	<b>0.023</b>

as the average of lower canopy *P. menziesii* and *T. heterophylla*. Nonconiferous plants in the understory are not examined.

#### 4.3.7 Scaling-up

Leaf-level measurements and stand-level estimates of respiration, expressed as  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  and  $10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , respectively, are linked by LAI. Values of conifer LAI appropriate for the survey months (Chapter 3) are applied to the “quarters” of February–April, May–July, August–October and November–January, respectively (Table 4.3). For quarterly estimates, the mean  $\pm$  SD  $R_n$  values for each factorial combination are scaled-up using the night length, number of days and LAI. In each year results are summed across all combinations, including those for understory and other lower canopy conifers, to yield a probability distribution of 500 simulated values of annual, stand-level respiration, with a mean  $\pm$  SD. Similar calculations are made of individual components, including the amounts of respiration occurring in individual quarters, and contributed by individual canopy levels and species. Calculations of long-term, four-year means  $\pm$  SDs use the methods of pooled standard deviations and linear combinations of means (Ramsey and Schafer 1997).

Standard errors of all means are calculated as:

$$[4] \quad \text{SE} = \text{SD} * n^{-0.5}$$

where  $n$  is the number of samples per factorial combination (6), and hence the number of measurements of  $R_m$  and  $T_m$ . Although the model (Eq. [3]) also includes  $T_a$ , stan-

Table 4.3. Estimated LAIs of conifer species in the survey months (Chapter 3), following on the analysis of Thomas and Winner (2000a), with the original middle canopy layer distributed equally between the upper and lower canopy.

Species	Canopy level	Estimated LAI (at mid-month)			
		March	June	September	December
<i>Pseudotsuga menziesii</i>	Upper	1.49	1.62	1.63	1.52
	Lower	0.67	0.72	0.73	0.68
<i>Tsuga heterophylla</i>	Upper	1.08	1.19	1.17	1.10
	Lower	1.77	1.95	1.93	1.80
<i>Thuja plicata</i>	Upper	0.44	0.47	0.48	0.45
	Lower	0.65	0.69	0.70	0.66
<i>Abies amabilis</i>	Lower	0.02	0.02	0.02	0.02
<i>Taxus brevifolia</i>	Lower	0.10	0.10	0.10	0.10
Total canopy		6.22	6.76	6.76	6.33
<i>Tsuga heterophylla</i>	Understory	0.23	0.26	0.25	0.24
<i>Thuja plicata</i>	Understory	0.04	0.04	0.04	0.04
<i>Abies amabilis</i>	Understory	0.07	0.07	0.07	0.07
<i>Taxus brevifolia</i>	Understory	0.08	0.08	0.08	0.08
Total understory		0.42	0.45	0.44	0.43
Total all levels		6.64	7.21	7.20	6.76



dard error calculations do not include the number of  $T_a$  measurements, because calculations of stand-level respiration utilize  $\sim 100 \times$  more measurements of  $T_a$  than of  $R_m$  or  $T_m$ . Uncertainty is primarily a function of the small number of foliage samples.

#### **4.3.8 Growth respiration for new leaves**

Development of new conifer leaves requires investment of carbohydrates, to provide new carbon skeletons and to support associated growth respiration (Amthor 1989). The carbon cost of growth respiration is 25% of the carbon in the new leaves (Ryan 1991b), and conifer leaves are approximately 50% carbon by dry weight (Waring and Running 1998b). Therefore, if annual rates of leaf loss and production are equal, annual growth respiration for new leaf production (in  $10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ ) equals 1/8 the dry mass of all leaves lost annually by leaf fall and herbivory (Chapter 3).

### **4.4 RESULTS**

#### **4.4.1 Four-year trends in foliar maintenance respiration**

The mean annual amount of nighttime, stand-level conifer foliar maintenance respiration through 1998-2001 is  $-3.40 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  (Table 4.4). The annual total represents 22% of the gross annual carbon gain for the stand calculated by eddy covariance (Paw U et al. 2004). Annually, the proportions of respiration by each major species match their proportions of LAI, e.g., *T. heterophylla* accounts for 46.2% of annual

Table 4.4. Annual estimates (mean  $\pm$  SE) of nighttime, stand-level maintenance respiration from conifer foliage of all species at all levels (upper and lower canopy, and understory), pooled results from 1998-2001.

Species	Level	Respiration ( $10^6$ g C ha $^{-1}$ y $^{-1}$ )
<i>P. menziesii</i>	Upper	-0.80 $\pm$ 0.04
	Lower	-0.26 $\pm$ 0.01
<i>T. heterophylla</i>	Upper	-0.74 $\pm$ 0.04
	Lower	-0.74 $\pm$ 0.04
	Understory	-0.10 $\pm$ 0.01
<i>T. plicata</i>	Upper	-0.33 $\pm$ 0.02
	Lower	-0.30 $\pm$ 0.02
	Understory	-0.02 $\pm$ 0.00
Others	Lower	-0.05 $\pm$ 0.00
	Understory	-0.06 $\pm$ 0.00
<i>P. menziesii</i>		-1.07 $\pm$ 0.04
<i>T. heterophylla</i>	All	-1.57 $\pm$ 0.06
<i>T. plicata</i>	combined	-0.65 $\pm$ 0.02
Others		-0.11 $\pm$ 0.00
All combined	Upper	-1.87 $\pm$ 0.05
	Lower	-1.35 $\pm$ 0.05
	Understory	-0.17 $\pm$ 0.01
All combined	All combined	-3.40 $\pm$ 0.08

foliar respiration, and contributes 46.7% of conifer leaf area (Thomas and Winner 2000a). Measured, interspecific differences in respiration rates, although sometimes significant in particular seasons, are not consistent over four years. Upper canopy conifer foliage accounts for 55.0% of annual respiration, although it only contributes 45.6% of measured conifer leaf area. Respiration rates in the brighter upper canopy are usually higher than in the lower canopy, an expected feature of sun-adapted foliage (Larcher 1995).

As for seasonal differences in respiration, the August-October period produces the greatest total amount, 30.0% of the annual total, while November-January produces the least, 18.8% of the annual total (Table 4.5). Total respiration in May-July is only 1.45 times greater than the total for November-January, even though mean overnight rates are 3.1 times greater in June than in December (Figure 4.3). The total amounts of respiration per quarter vary much less than the instantaneous overnight respiration rates because nights are much longer during the colder months, partially compensating for lower rates. Always, the trend is for respiration rates to be highest at the beginning of night, and to diminish as night progresses and temperature declines. However, seasonal differences in behavior are important, with overnight rates in December being nearly stable because of the small diurnal temperature amplitude then, while overnight rates in June and September are highly changeable.

Table 4.5. "Seasonal" estimates (mean  $\pm$  SE) of nighttime, stand-level maintenance respiration from conifer foliage of all species at all levels (upper and lower canopy, and understory), pooled results from 1998-2001.

Species	Level	Respiration ( $10^6$ g C ha <sup>-1</sup> season <sup>-1</sup> )			
		Feb-Apr	May-Jul	Aug-Oct	Nov-Jan
<i>P. menziesii</i>	Upper	-0.17 $\pm$ 0.01	-0.21 $\pm$ 0.02	-0.27 $\pm$ 0.02	-0.16 $\pm$ 0.02
	Lower	-0.05 $\pm$ 0.00	-0.07 $\pm$ 0.00	-0.09 $\pm$ 0.01	-0.05 $\pm$ 0.00
<i>T. heterophylla</i>	Upper	-0.13 $\pm$ 0.02	-0.26 $\pm$ 0.03	-0.23 $\pm$ 0.01	-0.13 $\pm$ 0.01
	Lower	-0.20 $\pm$ 0.01	-0.17 $\pm$ 0.02	-0.20 $\pm$ 0.02	-0.17 $\pm$ 0.02
	Under	-0.03 $\pm$ 0.00	-0.02 $\pm$ 0.00	-0.03 $\pm$ 0.00	-0.02 $\pm$ 0.00
<i>T. plicata</i>	Upper	-0.09 $\pm$ 0.01	-0.08 $\pm$ 0.01	-0.11 $\pm$ 0.01	-0.05 $\pm$ 0.01
	Lower	-0.10 $\pm$ 0.00	-0.08 $\pm$ 0.01	-0.07 $\pm$ 0.01	-0.04 $\pm$ 0.01
	Under	-0.01 $\pm$ 0.00	-0.00 $\pm$ 0.00	-0.00 $\pm$ 0.00	-0.00 $\pm$ 0.00
Others	Lower	-0.01 $\pm$ 0.00	-0.01 $\pm$ 0.00	-0.01 $\pm$ 0.00	-0.01 $\pm$ 0.00
	Under	-0.01 $\pm$ 0.00	-0.01 $\pm$ 0.00	-0.02 $\pm$ 0.00	-0.01 $\pm$ 0.00
<i>P. menziesii</i>		-0.22 $\pm$ 0.01	-0.28 $\pm$ 0.02	-0.36 $\pm$ 0.02	-0.21 $\pm$ 0.02
<i>T. heterophylla</i>	All levels	-0.35 $\pm$ 0.02	-0.45 $\pm$ 0.04	-0.45 $\pm$ 0.03	-0.32 $\pm$ 0.02
<i>T. plicata</i>	combined	-0.19 $\pm$ 0.01	-0.17 $\pm$ 0.01	-0.19 $\pm$ 0.01	-0.10 $\pm$ 0.01
Others		-0.03 $\pm$ 0.00	-0.03 $\pm$ 0.00	-0.03 $\pm$ 0.00	-0.02 $\pm$ 0.00
All species combined	Upper	-0.38 $\pm$ 0.03	-0.55 $\pm$ 0.04	-0.60 $\pm$ 0.03	-0.34 $\pm$ 0.02
	Lower	-0.37 $\pm$ 0.02	-0.34 $\pm$ 0.03	-0.38 $\pm$ 0.03	-0.27 $\pm$ 0.02
	Under	-0.05 $\pm$ 0.00	-0.04 $\pm$ 0.00	-0.05 $\pm$ 0.00	-0.04 $\pm$ 0.00
All species combined	All levels combined	-0.79 $\pm$ 0.03	-0.93 $\pm$ 0.05	-1.03 $\pm$ 0.04	-0.64 $\pm$ 0.03

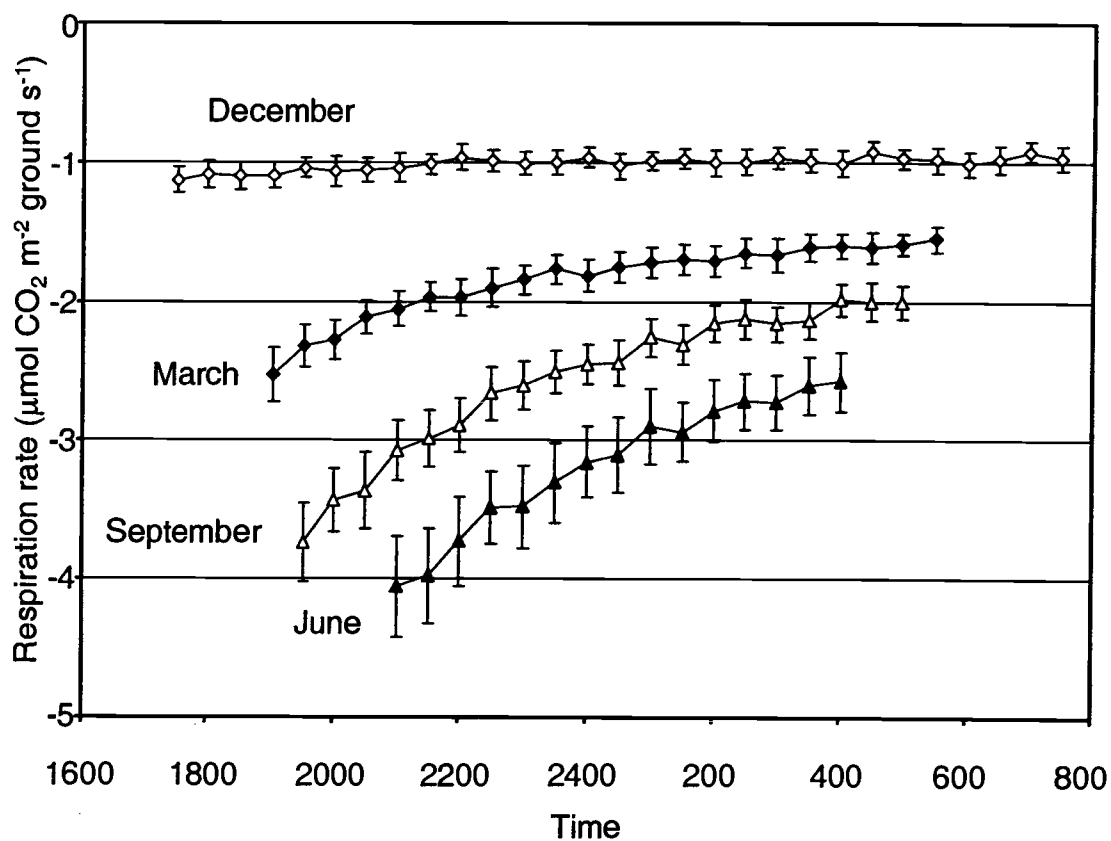


Figure 4.3. Instantaneous, nighttime foliar respiration rates (mean  $\pm$  SE) in March, June, September and December, for all combined conifers, converted to ground area basis. Combined, pooled data from 1998-2001.

#### 4.4.2 Interannual differences

Total amounts of respiration for individual years differ from the multi-year mean by 8% or less. The individual, yearly totals do not differ significantly ( $p \geq 0.05$ ) from each other through either the 1998-2000 or 1999-2001 periods, although the values for 1998 and 2001 do differ significantly ( $p < 0.05$ ) (Table 4.6). Comparisons assume that there are no interannual differences in LAI, and that changes of LAI within years follow a repeatable, consistent cycle. Unusual events, such as major leaf and tree loss from severe windstorms, could potentially cause large deviations from the assumption of cyclical LAI. However, no major destructive events have occurred during the study, and stand LAI did not differ significantly between the three years, 1997-1999, in which it was measured (Thomas and Winner 2000a).

#### 4.4.3 Leaves as part of the carbon budget

The annual dry mass loss of conifer leaves from all causes is  $2.71 \times 10^6 \text{ g ha}^{-1} \text{ y}^{-1}$  (Chapter 3). If equal mass is invested annually in new leaves, and 50% of dry mass is carbon (Waring and Running 1998a), then the NPP of leaf production is  $1.36 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , similar to a previous estimate of  $1.50 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  (Harmon et al. 2004). If growth respiration equals 25% of carbon invested (Ryan 1991b), then annual growth respiration for conifer leaves is  $-0.34 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ . Thus, total annual conifer investment in new leaves, including new leaf dry mass and growth respiration, is  $1.70 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , potentially 11% of total GPP (Paw U et al. 2004), while maintenance respiration may represent another 22%. If the estimate of GPP from eddy

Table 4.6. Total nighttime, annual conifer foliar maintenance respiration (mean  $\pm$  SE) from 1998, 1999, 2000 and 2001, with years not sharing a letter (a or b) having significantly different means (2-tailed t-test,  $p \leq 0.05$ ).

Year	Annual conifer foliar respiration
	$10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$
1998 (a)	$-3.65 \pm 0.15$
1999 (ab)	$-3.35 \pm 0.22$
2000 (ab)	$-3.40 \pm 0.14$
2001 (b)	$-3.18 \pm 0.13$
1998-2001 average	$-3.40 \pm 0.08$

covariance (Paw U et al. 2004) is underestimated, or the calculations of maintenance respiration here are overestimated, then the proportions of leaf investment and/or maintenance vs. total GPP are less. Maintenance respiration, which is  $-3.40 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , is 10x greater than growth respiration.

#### 4.4.4 Model quality checks

There are two checks: 1) A test of the sensitivity of annual results to changes in  $Q_{10}$ , and 2) Comparisons of findings for the model based solely on mean values of  $R_m$ ,  $T_m$  and  $T_a$ . For the first check, the annual model of respiration uses four seasonally-adjusted  $Q_{10}$  values. We examine  $Q_{10}$  sensitivity by increasing all  $Q_{10}$  values by 10% for 1998. The result is that annual respiration for 1998 decreases, from  $-3.65 \pm 0.15$  to  $-3.49 \pm 0.15 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , a reduction of 4.4%. The diurnal temperature range is small enough that annual results are not strongly affected by the precise values of  $Q_{10}$ . For the second, we calculate four-year average values (Table 4.7), as well as values for individual years. The four-year mean,  $-3.19 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , is 6% lower than the mean of  $-3.40 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  produced using probability distributions of the input variables. Also, the mean total amounts of respiration estimated for individual years are consistently lower by 5-7%. These results verify that using solely mean input values in Eq. [3] causes underestimation of respiration (Ryan 1991a).



Table 4.7. Annual estimates of nighttime, stand-level respired carbon from all conifer foliage in the upper and lower canopy, and understory; pooled results from 1998-2001, based on mean values of  $R_m$  and  $T_m$ , and mean  $T_a$  values.

Species	Level	Respiration
		( $10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ )
<i>P. menziesii</i>	Upper	-0.75
	Lower	-0.25
<i>T. heterophylla</i>	Upper	-0.69
	Lower	-0.70
	Understory	-0.09
<i>T. plicata</i>	Upper	-0.31
	Lower	-0.28
	Understory	-0.02
Others	Lower	-0.04
	Understory	-0.06
<i>P. menziesii</i>		-1.00
<i>T. heterophylla</i>	All	-1.48
<i>T. plicata</i>	combined	-0.61
Others		-0.10
All combined	Upper	-1.75
	Lower	-1.28
	Understory	-0.16
All combined	All combined	-3.19

## 4.5 DISCUSSION

### 4.5.1 Leaf age effects

As noted, all measurements used mature, first-year leaves. However, the canopy contains leaves of all ages. Is it then justified to scale to the whole canopy using leaves of a single age cohort? First-year leaves are, by definition, the most abundant. Leaves of all ages are subject to being shed, not simply those in the oldest cohort (Keenan et al. 1995). Therefore, first-year leaves are the most typical. It is possible that older cohorts of leaves have lower respiration rates, as seen for *A. amabilis* (Brooks et al. 1991), a process that may occur as older foliage becomes shaded and nutrients are transferred from the older leaves to the younger ones. If such a process occurs with some or all of the conifer species at the WRCCRF site, then the calculations of stand-level foliar respiration in this study may be overestimates.

### 4.5.2 Effects on Gross Primary Productivity at the WRCCRF

Estimates of GPP include  $15.5$  and  $15.9 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  (Paw U et al. 2004),  $19.06 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  (Harmon et al. 2004), and  $24.6 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  (Winner et al. 2004). The second study uses the relationship (with modified sign conventions):

$$[5] \quad \text{GPP} = \text{NPP} - R_a$$

with NPP (Net Primary Productivity) measured from biomass accumulation rates and determined to be  $5.97 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  for the whole stand including understory

plants, the values for  $R_a$  calculated, the annual foliar  $R_a$  (including nighttime maintenance and growth components) estimated as  $-5.77 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , and the NPP of leaf growth estimated as  $1.50 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ . However, the new estimates here for foliar  $R_a$  (including growth and maintenance respiration) and the NPP of leaf growth are  $-3.74 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  and  $1.36 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , respectively. Substitution into Harmon et al. (2004) reduces GPP from  $19.06 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  to  $16.89 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , more similar to the results from eddy covariance (Paw U et al. 2004). Substitutions cause both NPP and  $R_a$  to shrink, from 5.97 and  $-13.09 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  (Harmon et al. 2004) to 5.83 and  $-11.06 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , respectively.

Separately, the GPP of  $24.6 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  from the SPA model (Winner et al. 2004) is too high because it uses a constant LAI of 9.6, higher than the year-round average LAI of 7.5 (Chapter 3). Application of the correct LAI value should cause a reduction in modeled GPP, although because a coniferous canopy is expected to absorb most (>90%) incident light whether LAI is 7.5 or 9.6, the reduction of GPP with lower LAI may not be large. Regardless, a revised SPA analysis should produce a lower GPP value, yielding closer agreement with the other estimates of GPP.

#### 4.5.3 Effects on Total Ecosystem Respiration

Published estimates of TER are  $-14.0 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  (Paw U et al. 2004) and  $-18.86 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  (Harmon et al. 2004). The second estimate uses  $-13.09 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  for autotrophic respiration  $R_a$ . Substitution of the corrected  $R_a$  of  $-11.06 \times$

$10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  leads to a revised TER of  $-16.83 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , closer to the results from eddy covariance (Paw U et al. 2004).

#### 4.5.4 Effects on Net Ecosystem Productivity

Published estimates of NEP are  $1.5$  and  $1.9 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  (Paw U et al. 2004), and  $0.2 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  (Harmon et al. 2004). The latter value uses the relationship (with modified sign conventions):

$$[6] \quad \text{NEP} = \text{NPP} + R_h$$

with NPP as described above, and the values for  $R_h$  (heterotrophic respiration) calculated. Substitution of the revised conifer leaf NPP of  $1.36 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , in place of the original value of  $1.50 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  (Harmon et al. 2004), causes a small reduction of NEP from  $0.20$  to  $0.06 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ .

Values from the present study do not eliminate the difference of  $1.3$  to  $1.7 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  between the two previous estimates of NEP, and the question of whether the stand is essentially carbon-neutral (Harmon et al. 2004) or is a moderate sink (Paw U et al. 2004) remains unresolved. If the stand is essentially carbon-neutral, then the interannual differences in stand-level conifer foliar respiration are great enough to cause the stand to be a small sink in some years, and a small source in others. However, if the stand is a moderate sink (Paw U et al. 2004), the interannual differences in foliar respiration have little effect on the behavior of stand NEP.

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## CHAPTER 5: GENERAL CONCLUSIONS.

### 5.1 MAJOR FINDINGS REGARDING RESEARCH GOALS

#### 5.1.1 Goal #1: Leaf-level respiration rates

Leaf-level respiration rates were measured on > 600 foliage samples, approximately 200 from each major conifer species. Measurements were performed on multiple trees of each species, on upper and lower branches, at four times of the year and in several consecutive years. The most obvious observational pattern is that for each species, there is a strong relationship between measurement temperatures and respiration rates. Indeed, temperature variation explains 33% of the observed variation in log-transformed respiration rates, more than any other factor. Thus there is a clear difference in respiration rates between warm and cool seasons, with rates in summer months being much higher than in the winter.

Other important influences on the respiration rates include differences in canopy levels and measurement months for all species, and between years for *T. heterophylla* and *T. plicata*. That is, even after differences in measurement temperature are taken into account, upper canopy foliage has significantly ( $p \leq 0.05$ ) higher rates than lower canopy foliage for all species (with respiration on a leaf area basis), and there are residual, significant differences in the observed rates between months and between some years. Significant interannual differences for particular species, even after tem-



perature differences have been taken into account, indicate the possibility that scaled-up, stand-level foliar respiration may also vary significantly between years. However, there are no significant differences ( $P > 0.05$ ) within the groups of trees used for each species. Therefore, data within each group of trees are pooled.

The result is that for scaling-up to the canopy, 24 factorial combinations of two canopy levels (upper and lower), three species (*P. menziesii*, *T. heterophylla* and *T. plicata*), and four measurement months (March, June, September and December) must be used for each year, because there are significant residual differences between rates from different measurement months and canopy levels even after temperature differences have been taken into account. Thus we establish characteristic respiration rates for each factorial combination in each year from 1998-2001. Because of the expected and demonstrated strong relationship between respiration and temperature, each set of respiration values is paired with an associated set of measurement temperatures. The respiration-temperature relationship is to later be utilized to extrapolate from the measured rates taken from darkened foliage in the daytime, to the estimated rates that occur at night.

### 5.1.2 Goal #2: Seasonally varying leaf area index

Leaf litter collections from most months in 1998-2002 are analyzed to determine monthly changes in live conifer leaf area index. Total collected conifer leaf masses are partitioned into estimated masses per species, based on species identification using subsamples. The annual total dry mass collected is  $2.372 \times 10^6 \text{ g ha}^{-1} \text{ y}^{-1}$  by dry

mass, of which 95% is contributed by "brown," or senescent, leaves. Dry masses are converted into estimated live leaf area by each major conifer species.

The annual LAI equivalents of leaf litter, by species, are 0.47 for *P. menziesii*, 0.97 for *T. heterophylla*, and 0.15 for *T. plicata*, for a total litter-LAI loss of 1.60. Additionally, herbivory-LAI loss is an additional 0.18 for all species combined. Thus, for canopy and understory conifers to maintain a long-term steady state of live leaf area, they must collectively replace LAI of 1.78 annually. Although *T. heterophylla* supports 47% of standing LAI, the species accounts for 61% of annual conifer LAI turnover because of relatively short-lived leaves. Maximum conifer LAI of 7.81 occurs as leaf expansion ceases in mid-July, while minimum conifer LAI of 6.52 occurs as new leaf expansion begins in mid-May. These estimates compare with total conifer LAI, measured using a line-drop method, of 7.35 in late August (Thomas and Winner 2000a). The estimated monthly values of conifer LAI may be utilized in scaling-up efforts involving foliar respiration. Additional growth and loss of nonconiferous understory plants creates a greater seasonal amplitude for LAI of the whole stand.

The overall peak rate of conifer leaf litterfall occurs from July through September, when 54% of leaf litter mass falls. Timing is similar to that from other Pacific Northwest sites, but is months earlier than that seen at sites elsewhere. In many areas outside the PNW, typical maximum leaf fall rates occur in late summer, fall and/or early winter (e.g., peak leaf litterfall rates in November-December for *Pinus taeda* L. in Mississippi, Hinesley et al. 1991). The different phenological behavior in the PNW may be a regional adaptation to the characteristic summer dry season, which is typical

for the northwest but is distinct from most climates elsewhere (Walter et al. 1975).

Other sites tend to have precipitation with lower annual totals but more even seasonal distribution. The situation at the WRCCRF site, with its high annual total precipitation but warm and very dry summer (Shaw et al. 2004), provides abundant water through most of the year to support a large leaf area but may have too little to support the full LAI during the warmest months. Therefore, to minimize damaging drought stress, the trees may selectively shed leaves through summer that in a more equable climate would otherwise be retained for longer.

There is a strong correlation between mean leaf lifespan, for a particular species, and the leaf mass per area for the species. The relationship holds for both fresh, green leaves and for senescent, brown leaves, and suggests that there is a trade-off regarding carbon economy between leaf turnover time and construction cost. Leaf construction costs, including growth respiration, may utilize 10% (after Harmon et al. 2004) or more (after Paw U et al. 2004) of available fixed carbon (GPP) for conifers.

### **5.1.3 Goal #3: Stand-level amounts of respiration**

Leaves utilize fixed carbon in three general manners, as 1) the carbon contained in new leaf tissues, 2) the carbon released as  $\text{CO}_2$  due to respiration associated with growth of new tissue, and 3) the carbon released as  $\text{CO}_2$  due to respiration associated with maintenance of existing tissue. Of the three sinks, for evergreen conifers the largest is maintenance respiration, because of long leaf life spans. We measure maintenance respiration at the leaf level, using mature foliage. Our scaled-up results

using the 24 factorial combinations of leaf respiration and measurement temperature are for maintenance respiration only, and the other two sinks are calculated separately.

The mean annual amount of conifer foliar maintenance respiration is  $-3.40 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , potentially representing 22% of total GPP for the stand (Paw U et al. 2004). The annual total amounts of respiration by each species are proportionate to the LAI of each species, with *T. heterophylla* contributing almost half. Overnight, instantaneous rates (expressed as  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ leaf s}^{-1}$ ) vary strongly with measurement month primarily because of temperature, but the total amounts of respiration per quarter vary much less because the months with lower rates have longer nights. The upper canopy contributes disproportionately higher amounts of total respiration, as a result of higher leaf-level rates associated with sun foliage (Larcher 1995). Interannual variability in total annual amounts of maintenance respiration for all conifer foliage are small, with yearly totals that deviate by 8% or less from the long-term average of 1998-2001. Scaled-up results are insensitive to the exact values used for the respiration-temperature exponential parameters  $Q_{10}$ , because seasonal day/night temperature differences are not large.

#### **5.1.4 Goal #4: Previous studies of carbon economy**

In addition to the 1998-2001 annual average for conifer foliar maintenance respiration, the annual carbon investment in new leaf tissue is  $1.36 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , and the annual growth respiration associated with new conifer leaves is  $-0.34 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ . Total annual conifer investment in leaf growth and maintenance is then 5.10

$\times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , 33% of one estimate of stand GPP (Paw U et al. 2004), although less than a previous estimate of  $7.27 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  for total carbon investment in conifer leaves of the same stand (Harmon et al. 2004).

Previous divergent estimates of stand GPP are harmonized by substitution of certain values from the present study, including 1) conifer annual maintenance + growth foliar respiration of -3.74, in place of  $-5.77 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  (Harmon et al. 2004), 2) Conifer leaf NPP of 1.36, in place of  $1.50 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  (Harmon et al. 2004), and 3) stand LAI of 7.5 (year-round average for all species) in place of 9.6, with a consequent reduction in the predicted GPP value from the SPA model (Winner et al. 2004). For GPP, published estimates of 15.5 to 15.9, and  $19.06 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$  (Paw U et al. 2004, Harmon et al. 2004, respectively) are changed to 15.5 to 15.9, and  $16.89 \times 10^6 \text{ g C ha}^{-1} \text{ y}^{-1}$ , respectively.

Other substitutions lead to a similar, closer alignment between two divergent estimates of TER, while estimates of NEP remain virtually unchanged (Paw U et al. 2004, Harmon et al. 2004). Thus, the question whether the stand is a moderate sink (Paw U et al. 2004) or is virtually carbon-neutral (Harmon et al. 2004) is unresolved. If the latter case is true, then the observed interannual variability in conifer foliar respiration is sufficient to cause the stand to be a small sink in some years, and a small source in others. However, if the stand is a moderate sink overall, then the interannual variability in conifer foliar respiration has little effect.

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