# Respiratory Ecophysiology of Woody Stems and Branches in Temperate Forest Trees

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## Chapter 1: Introduction

Woody stems perform a wide variety of critical functions in forest trees. Traditionally, the role of stems is considered to be largely structural. Stems provide the necessary support to prevent the canopy from being shaded by neighboring competitors and serve as physical conduits linking the canopy and the root system by transporting water, nutrients, and fixed carbon products. The magnitude of the support and transport functions of woody stems are truly impressive as stems lift foliage over 100 m in the air in *Sequoia sempervirens* (Koch et al. 2004), persist for more than 4000 years in *Pinus longaeva* (Currey 1965), and conduct more than 800 kg of water daily in *Tsuga heterophylla* (Meinzer et al. 2005). In addition to these primary support and transport roles, woody stems are critical storage organs in trees. Stems and branches are integral to the carbon status of trees as they store large quantities of carbohydrates thereby providing carbon products necessary to support fruiting and masting events, dormant season metabolism, construction of new xylem or foliage in deciduous species, and provide critical reserves for periods of disturbance, insect outbreaks, or drought (Hoch et al. 2003). Furthermore, the inner bark and wood of stems and branches are sites of nitrogen storage (Wetzel et al. 1989; Sauter and van Cleve 1994) and the mobilization of these reserves may provide the nitrogen necessary for construction of new foliage (Millard 1996). The water present in plant stems is also important, particularly to large trees; where 10-25% of daily water requirements are met through stored stem water (Phillips et al. 2003) allowing leaves to operate at favorable water potentials during peak daylight hours. In addition, stems and branches may fix carbon as photosynthetic chlorenchyma tissues are common beneath the periderm of many wood species (Pfanz et al. 2002);

however, the contribution of stem and branch photosynthesis to whole-tree carbon gain is low (Foote and Schaedle 1978; Levy and Jarvis 1998). Most importantly, woody stems and branches are an important sink in whole-tree carbon budgets as 5-25% of fixed carbon is re-released to the atmosphere by respiration in woody stems and branches (Meir and Grace 2002; Damesin et al. 2002) and approximately 20-30% of fixed carbon is allocated to the construction of aboveground woody biomass (Ryan et al. 1996).

Despite the importance of stem processes to trees, and particularly the importance of respiration to whole-tree carbon budgets, the physiology of woody stems and branches remains understudied and fundamental questions regarding woody tissue respiration are unresolved. For instance, rates of woody tissue respiration, typically measured as $CO_2$ efflux from stems or branches, have been found to vary widely both within trees and between stands and finding reliable predictors to consistently account for this variability, such as tissue size or tree age (Sprugel 1990; Lavigne and Ryan 1997), has been elusive. Furthermore, there is no generally accepted basis for expressing rates of woody tissue respiration or scaling these rates to the stand-level. In addition, the commonly utilized scalars, such as stem surface area (Kinerson 1977; Linder and Troeng 1981), sapwood volume (Ryan 1990; Ryan et al. 1994), and tissue nitrogen concentration (Ryan 1991), often produce different stand-level estimates of woody tissue respiration (Stockfors and Linder 1998; Maier 2001; Damesin et al 2002). It is likely that the difficulty in predicting variability in woody tissue respiration "stems" from the failure to integrate the diversity of functions performed by tree stems into ecophysiological studies of respiration in woody stems and branches.

In particular, water flow through the xylem tissues of stems and branches resulting from transpiration has been found to cause significant errors in estimated rates of woody tissue respiration (Nigisi 1982; Teskey and McGuire 2002). Xylem sap contains dissolved gases, including carbon dioxide, and provides a mechanism for the internal movement of $CO_2$ within trees (Negisi 1979; Stringer & Kimmerer 1993). The dissolved $CO_2$ concentration of xylem sap is high, ranging between 2-12% (Eklund 1990 1993; Teskey and McGuire 2002), and may serve as either a source or a sink for the $CO_2$ that diffuses through stems and branches to the atmosphere. In the present study, I aimed to improve the understanding of woody tissue respiration in forest trees by investigating the effects of sap flow and/or the dissolved $CO_2$ concentration of xylem sap on $CO_2$ efflux from woody stems and branches. Ecophysiological measurements for this study were conducted in *Quercus rubra* L. (Northern red oak), a fast-growing, mid-successional hardwood tree that is commonly dominant in deciduous forests in the eastern United States, and *Dacrydium cupressinum* Sol. ex Lamb. (rimu), a long-lived (600-800 years), slow-growing conifer that once dominated old-growth, lowland rainforests in New Zealand (Norton et al. 1988). Due to the global importance of temperate forests as major sinks in the global carbon cycle (Fan et al. 1998; Ciais et al. 2000), this study also sought to develop stand-level estimates of woody tissue respiration for two forests: a lowland podocarp-angiosperm rainforest in South Westland, New Zealand and an aggrading deciduous forest in southwestern New York, United States. These forest-types have regional importance as lowland podocarp rainforests in New Zealand and eastern deciduous forests in the United States account for 20 and 31%,

respectively, of their nation's terrestrial stored carbon (Houghton and Hackler 2000; Hall et at. 2001).

Subsequent to this introductory chapter, this dissertation includes six chapters. Chapter 2 is a thorough review of the scientific literature on woody tissue respiration prior to the present study. This review is necessary to provide general background on woody tissue respiration, highlight deficiencies in the available literature, and provide context for this study's hypotheses. Chapter 3 is a paper published in *New Phytologist* (Bowman et al. 2005); this chapter compares measurements of $CO_2$ efflux from stems and branches of *D. cupressinum* trees with both respiratory activity within these tissues and with physiological and anatomical characteristics of sapwood that may influence the diffusion of respiratory $CO_2$ to the atmosphere. In addition, the relative contribution of xylem transport and internal storage of $CO_2$ to woody tissue respiration is estimated for five *D. cupressinum* trees. By comparing $CO_2$ efflux from trees that varied greatly in size, age, and canopy emergence with estimates of respiratory activity in wood tissues and measurements of sap flow, this chapter intended to find consistent linkages between respiratory production of $CO_2$ within stems, xylem transport of $CO_2$, and the actual $CO_2$ diffusing from tree stems. The primary objective of Chapter 4 is to provide a stand-level estimate of respiration in *D. cupressinum* stems for a mature lowland podocarp rainforest. The contribution of woody stem respiration to the carbon budget in relation to forest gross primary productivity (GPP) is also presented and the effects of within-tree variation in sapwood temperature on the vertical distribution of stem respiration are investigated. Chapter 5 aims to determine if stem $CO_2$ efflux in *Q. rubra* trees is related primarily to local respiratory $CO_2$ production or xylem $CO_2$ concentration and transport by analyzing

measurements of stem $CO_2$ efflux, sap flux density, xylem $CO_2$ concentration, wood respiratory activity, and stem growth from both the growing and dormant seasons in trees that vary considerably in size. Similar to Chapter 3, this chapter intends to ascertain if consistent relationships between stem $CO_2$ efflux and xylem $CO_2$ concentration and transport exist independent of tree size. Chapter 6 investigates the stand-level consequences of the tree-level differences in stem $CO_2$ efflux observed in Chapter 5 by coupling these measurements with data on stand mensuration, tree growth, branch $CO_2$ efflux and physiology, canopy foliage physiology, and climate to derive stand-level estimates of woody tissue respiration, and its proportion of GPP, in three *Q. rubra*-dominated stands that range in age from 40- to 135-yrs. This chapter also investigates variation in $CO_2$ efflux and respiratory physiology between stems and branches in *Q. rubra* trees. Lastly, Chapter 7 is a summary of the major conclusions of the dissertation's chapters and suggests future directions for related research.

# Chapter 2: Review of the Current Literature on Respiration in Woody Stems and Branches in Forest Trees

## 1. Introduction

Respiration in living organisms produces carbon skeleton intermediates, usable energy (in the form of ATP), and reductant (in the form of NADH and NADPH) to support both the construction of new biomass and the maintenance of existing biomass. As a result of respiratory processes, a large fraction of the fixed carbon produced by photosynthesis is converted back to $CO_2$. Plant respiration occurs in all living tissues (foliage, branches and stems, coarse and fine roots) and consumes approximately 50% of carbon produced by photosynthesis (Amthor 1989). Respiration, from both plants and microbial heterotrophs, is also important on the ecosystem-level, typically ranging from 30-70% of gross photosynthesis (Amthor and Baldocchi 2001).

Plant respiration responds to changes in environmental variables differently than photosynthesis. Therefore, global changes in temperature, atmospheric $CO_2$ concentration, precipitation, pollutants, and atmospheric nitrogen deposition may alter the balance between photosynthesis and respiration, thereby potentially affecting the size and direction of net ecosystem carbon fluxes. The magnitude of the global carbon fluxes between the atmosphere and biosphere due to photosynthesis and respiration are large (nearly 120 and 60 billion metric tons, respectively). Compared to these fluxes, the global terrestrial carbon sink and anthropogenic $CO_2$ emissions are relatively small, approximately 2.8 and 8.0 billion metric tons, respectively. Accordingly, the responses of photosynthesis and respiration to changes in the global environment may act as

positive or negative feedbacks thereby potentially impacting the rate and/or magnitude of increase of atmospheric $CO_2$ content and global climate change. As a result, research on the physiological responses of forest trees to environmental change and the impacts of these responses to forest carbon cycles will be essential to accurately predicting global carbon fluxes in the future.

In forested ecosystems, respiration in the aboveground woody tissues of stems and branches is an important flux of $CO_2$ to the atmosphere. Carbon lost through stems and branches may total between 52-1251 g C $m^{-2}$ $yr^{-1}$ (Ryan et al. 1995; Kinerson 1975) and is a significant constraint on forest carbon balances. For example, the $CO_2$ efflux from woody surfaces typically accounts for 5-25% of gross primary productivity (GPP), although higher estimates have been reported for some tropical forests (Ryan et al. 1994; Damesin et al. 2002; Meir and Grace 2002). The magnitude of the carbon flux due to woody tissue respiration varies considerably with forest type. Estimates from boreal forest and temperate forests range between 52-162 g C $m^{-2}$ $yr^{-1}$ and 149-204 g C $m^{-2}$ $yr^{-1}$, respectively. Whereas, higher values are often reported for tropical forests, 220-1251 g C $m^{-2}$ $yr^{-1}$ (Ryan et al. 1995; Malhi et al. 2001). Woody tissue respiration has also been found to be related to leaf area index (LAI) as the ratio of woody tissue respiration to GPP tends to increase with increasing LAI of the forest stand (Meir and Grace 2002). For example, woody tissue respiration accounted for 6% of GPP in a *Pinus ponderosa* forest with an LAI of 1.7 (Law et al. 1999) whereas woody tissue respiration in a tropical rainforest with an LAI of 6.5 consumed 13% of GPP (Ryan et al. 1994). This trend is consistent with the often observed correlation between sapwood area and leaf area in trees (Shinozaki et al. 1964; Grier and Waring 1974). Due to this positive relationship

between LAI and the ratio of woody tissue respiration to GPP, the importance of woody tissue respiration as a component of forest carbon budgets will initially increase with stand age until canopy closure and maximum LAI and then may gradually decline as LAI tends to drops in maturing stands due to mechanical abrasion with neighboring trees (Putz et al. 1984) and/or stand nutrient limitations (Binkley et al. 1995) .

Despite the importance of woody tissue respiration to tree carbon balances and forest ecosystem carbon cycles, our understanding of this physiological process is relatively limited. This limited extent of knowledge is somewhat surprising, considering that the first measurements of woody tissue respiration were conducted long ago on excised stems and branches (Boysenn-Jensen 1933), measurements on wood cores extracted from stems were made approximately sixty years ago (Goodwin and Goddard 1940; Møller and Müller 1938), and *in situ* measurements of $CO_2$ efflux from stems and branches with portable infra-red gas analyzers have been carried out for approximately 25 years (Kinerson 1975; Negisi 1978 and 1979; Linder and Troeng 1981). The limited understanding of woody tissue respiration is primarily due to a number of experimental challenges posed by woody stems and branches. For example, it is difficult to make direct measurements of *in situ* rates of respiration, at the tissue-level, as the living cells within tree stems are interspersed among, more numerous, dead cells. In addition, studies attempting to extract different tissues (phloem, cambium, sapwood) from a living tree for respiration measurements face complications from artificially high rates of respiration due to wounding, altering the environment of the wood tissue, or rapid diffusion of $CO_2$ dissolved in xylem sap (Teskey and McGuire 2004). Second, advances in leaf respiration have been due, in large part, to controlled-environment leaf chambers that allow for

manipulation of temperature and other environmental variables and measurement of physiological responses. The large mass of tree stems and branches prevents this type of manipulative experimentation and the findings of experiments performed on seedlings or sapling must be extended cautiously to mature trees as physiological responses to environmental variables may change with ontogeny (Cavender-Barres and Bazzaz 2000). Lastly, the difficulty of investigating respiration in tree stems and branches is compounded by the lack of a biochemical model of respiration analogous to the Farquhar model of photosynthesis (Farquhar et al. 1980).

This chapter aims to summarize the current understanding of the respiratory ecophysiology of woody stems and branches of forest trees, highlight the significant gaps in this understanding, and propose avenues of research that would contribute to filling these gaps.

## 2. $CO_2$ Efflux from Stems and Branches

### a. The Functional Model of Respiration and its Application to Woody Tissue Respiration

Respiration in stems and branches comprises a wide variety of physiological processes. For example, respiration in the inner bark and cambium is likely to be due to phloem unloading and the division, differentiation, enlargement, lignification, and maturation of new xylem and phloem cells. Respiratory activity located deeper in the stem may be due to translocating carbohydrates and nutrients to and from storage areas in the sapwood or may be associated with the formation of heartwood which involves both production of protective secondary compounds (such as phenolics, gums, and tannins)

and retrieval of carbohydrates and nutrients from senescing sapwood. However, respiration in plant tissues is not typically partitioned based on specific processes, such as those previously listed. Rather, it characterized by dividing total respiration into two components, maintenance and growth respiration, according to the empirical relationships described by deWit et al (1970), McCree (1970) and Thornley (1970). This partitioning is a fairly old concept as even early authors such as Johansson (1933) separated "resting" respiration from "production" respiration. Most of these empirical models of respiration that partition metabolic activity into growth or maintenance respiration are similar to the following equation.

**Equation 1** $$R_t = R_g + R_m = (g_r \times G) + (m_r \times W)$$

Where $R_t$ is total respiration, $R_g$ is growth respiration, $R_m$ is maintenance respiration, $g_r$ is a coefficient describing the amount of $CO_2$ released due to growth per unit of new growth, $G$ is the plant's growth rate, $m_r$ is a coefficient describing the amount of $CO_2$ released for a unit of biomass per unit time, and $W$ is the plant biomass. Maintenance respiration includes respiratory activity associated with the turnover and replacement of proteins and lipids, maintenance of cellular structures and gradients of ions and metabolites, acclimation of cells to changes in the environment, and ontogenic changes in cellular constituents (Penning de Vries 1975). Growth respiration is defined as the respiration required for the conversion of storage materials to new biomass (Amthor 1989). Models of respiration following the deWit-McCree-Thornley paradigm assume that all metabolic processes can be accurately partitioned into maintenance or growth

components, despite the fact that they occur simultaneously and that the biochemical pathways for these components are identical.

Most published studies of woody tissue respiration have estimated total respiration ($R_t$) using removable gas-exchange chambers mounted *in situ* to stems and branches and measured the efflux of $CO_2$ from these tissues with portable infra-red gas analyzers. The rate of $CO_2$ efflux from stem or branch has then been used as an estimate of its respiration. An important assumption of this technique is that the proportion of respired $CO_2$ that diffuses through the bark should be fairly high and constant. Partitioning of the total respiratory $CO_2$ efflux into its maintenance and growth components is typically accomplished by the 'mature-tissue' method. This technique involves developing respiration-temperature response curves for a mature tissue during a time period when the tissue is not actively growing. At these times, the $CO_2$ efflux is expected to be derived solely from maintenance processes. This measurement provides an estimate of the maintenance respiration expected at a given temperature. Subsequent measurements of respiratory activity during periods of growth can then by partitioned into maintenance and growth components by subtracting expected maintenance respiration from the total respiratory activity. In woody stems and branches, maintenance respiration is quantified through measurements during the winter periods and then subtracted from respiration measurements conducted throughout the rest of the year.

Several important assumptions are associated with this technique. For instance, it is assumed that maintenance respiration exhibits no acclimation to seasonal changes in its response to temperature and that maintenance respiration rates are similar during both seasonal periods of growth and non-growth. In support of this first assumption, Carey et

al. (1997) found that maintenance respiration in woody stems did not show acclimation to growth temperature in *Pinus pondersosa* growing in montane and desert environments. In contrast, several studies have shown that respiration rates may acclimate to temperature in branches (Gansert et al. 2004) and leaves (Tjoelker et al. 1999; Atkin et al. 2000). In addition, the second assumption may also not hold in all cases as maintenance respiration processes may differ between quiescent and growing periods (Lavigne et al. 2004) and has been found to be positively correlated with growth rate in both herbaceous (McCree 1982) and woody (Lavigne and Ryan 1997) plants. This indicates that the mature-tissue method should be used with caution and, possibly, that the functional model of respiration may need to be revised.

Despite these deficiencies of the functional model of respiration, it is useful to examine trends in maintenance and growth respiration between dissimilar tree stands. In forest trees, the percentages of total respiration accounted for by maintenance and growth respiration in woody biomass have been found to vary considerably from 20% maintenance respiration and 80% growth respiration in *Pinus contorta* (Ryan and Waring 1992), 50% for both maintenance and growth respiration in *Picea abies* and *Fagus sylvatica* (Stockfors and Linder 1998; Damesin et al. 2002), and 85% maintenance respiration and 15% growth respiration in *Pinus ponderosa* (Carey et al. 1997). The large variability in relative proportions of maintenance and growth respiration is a function of tree age/size with the contribution of maintenance respiration increasing with tree size. However, while the contribution of maintenance respiration to total respiratory activity increases with tree size due to increasing amounts of living biomass and declining growth rates, the rates of maintenance respiration, per unit sapwood volume, often decline with

increasing tree size (Carey et al. 1997; Lavigne and Ryan 1997; Ryan et al 2005), but not always (Law et al. 1999). This may be due to the correlation between maintenance and growth respiration, declining numbers of live cells per unit volume with age, or changes in physiology with ontogeny. This trend may also be due, in part, to a measurement artifact in which increased resistance to $CO_2$ diffusion from the tree surface in larger trees, due to increased bark thickness, is misinterpreted as a decline in maintenance respiration rates; however, to date, no experimental evidence has been published that supports this hypothesis.

### b. Temperature Response of $CO_2$ Efflux from Woody Tissues

Temperature is the most important factor controlling $CO_2$ efflux from stems and branches due to the temperature sensitivity of the enzyme-catalyzed reactions involved in respiration and the increased demand for ATP as metabolic rates increase (Lambers et al. 1998). The response of respiration to temperature is typically characterized by an exponential function similar in form to the following equation (Atkin and Tjoekler 2003).

**Equation 2:** $$Q_{10} = R / R_o^{[10/(T-T_o)]}$$

Where $R$ is the instantaneous respiration rate, $R_o$ is the respiration rate at the base temperature ($T_o$), $T$ is the ambient temperature, and $Q_{10}$ is a parameter defining the shape of the respiration-temperature response curve. In addition, modified Arrhenius functions, as shown in the following equation, may also used to characterize respiration-temperature responses as described in Lloyd and Taylor (1994) and adopted by Turnbull et al (2003).

**Equation 3:** $$R = R_o \times e^{((E_o / R_g) \times (1/T_o - 1/T_a))}$$

Where $R$ is the instantaneous respiration rate, $R_o$ is the respiration rate at the base temperature ($T_o$), $T$ is the ambient temperature (°K), $R_g$ is the gas constant (8.314 J $mol^{-1}$), and $E_o$ is a parameter related to the activation energy of respiratory enzymes. $E_o$ is analogous to $Q_{10}$ in Equation 1, as it also describes the shape of the respiration-temperature response. The advantage to using a modified Arrhenius function is that the $E_o$ parameter is not dependent on the base temperature used, whereas the $Q_{10}$ value may change depending on the temperature range (Ryan et al. 1994; Tjoelker et al. 2001). However, $Q_{10}$ values have been more commonly reported in the literature and, as a result, the following discussion of the response of respiration in woody stems and branches to temperature utilizes published estimates of $Q_{10}$.

A review of $Q_{10}$ values from 22 tree species indicated that the this parameter ranges from 1.0-2.9, although values close to 2.0 are most common (Damesin et al. 2002). Indicating that the rate of respiration tends to double in response to a 10 ºC increase in temperature. Studies which have estimated $Q_{10}$ at different times of the year have produced mixed results with some studies reporting seasonal variations in $Q_{10}$ (Paembonan et al. 1991; Lavigne 1996; Carey et al. 1997; Stockfors and Linder 1998) and others reporting no seasonal changes (Linder and Troeng 1981; Levy and Jarvis 1998; Damesin et al. 2002). In studies reporting seasonal changes in $Q_{10}$, it is expected that $Q_{10}$ would be highest in winter and decrease, due to acclimation, during growing season as temperatures increase. However, not all studies reporting seasonal variations in

$Q_{10}$ exhibit this expected trend as Carey et al. (1997) reported higher values in July compared to September in *P. ponderosa*.

A puzzling feature of reported stem respiration-temperature relationships is that while respiration is nearly always is strongly related to temperature, it is often best correlated with the stem temperatures recorded one to several hours prior to the respiration measurement (Ryan et al. 1990). This can be explained as either a measurement artifact, caused by the measured stem temperature not reflecting the integrated temperature of the entire tree bole, or as a product of the resistance to $CO_2$ diffusion posed by stem tissues. The lag of respiration behind stem temperature may be related to $CO_2$ diffusion from the stem particularly if $CO_2$ efflux is driven more by the stem's interior $CO_2$ concentration from a fairly large volume of wood rather than the respiratory activity of the vascular cambium located proximal to the measurement chamber. The time lag would then be a function of either the time needed to change the internal $CO_2$ concentration of the volume of stem or the permeability of the outer wood to $CO_2$ diffusion. The finding of Stockfors and Linder (1998) that the magnitude of the time lag changes throughout the growing season, with the lag being shortest in the spring and longest in the autumn, indicates that one or both of these mechanisms may be responsible. For example, in the spring, the cambium is more active and may be capable of changing the stem internal $CO_2$ concentration more quickly. In addition, only a fraction of the current year’s growth ring will be present. Alternatively, at the end of the growing season, the cambium is less active and a complete growth ring will have been constructed including a layer of dense latewood, which may be less permeable to $CO_2$ diffusion.

Another peculiar twist on the, normally simple, response of plant respiration to temperature that is often observed in woody stems and branches is a pronounced diel hysteresis (Lavigne et al. 1996; Maier 2001, Damesin et al. 2002). This means that $CO_2$ efflux rates have been found to vary, for a given ambient temperature, depending on the time of day of the measurement. Typically, researchers have found that rates are lower during the day than at night. In fact, Lavigne et al. (1996) found that respiration rates for *Abies balsamea* stems from several stands were, on average, 18% greater than respiration during the day. Diel hysteresis in stem $CO_2$ efflux has typically been hypothesized to be the result of translocation of respiratory $CO_2$ to upper portions of the tree via the transpiration stream. However, only recently have studies provided direct confirmation of this in mature forest trees (McGuire and Teskey, 2004; Bowman et al. 2005).

### c. Seasonal Patters of $CO_2$ Efflux from Woody Tissues

Stem $CO_2$ efflux shows strong seasonal patterns corresponding to largely to variation in cambial activity. The vascular cambium of a woody plant consists largely of actively dividing phloem and xylem mother cells which give rise to xylem and phloem tissues. The annual pattern of wood production by the cambium is typically determined by photoperiod and temperature with cambial activity peaking in the early growing season and then gradually decreasing as exposure to cold temperatures during autumn and early winter induces frost hardening and cambial quiescence during the dormant period. During the growing season, stem respiration rates are strongly influenced by cambial activity (Lavigne et al. 2004) and, accordingly, $CO_2$ efflux has been found to correlate strongly with stem growth increment (Edwards and Hanson 1996; Maier 2001;

Vose and Ryan 2001). Seasonal variation in $CO_2$ efflux may often lag behind changes in increment growth by up to a month, as wood synthesis and maturation occurs after the initial expansion of juvenile xylem cells (Edwards and Hanson 1996). As a result of its dependence on cambial activity, $CO_2$ efflux during the growing season is dependent on the myriad factors that affect biomass production and photosynthetic carbon gain including temperature, soil moisture availability, and nutrient availability.

Some studies have successfully linked changes in $CO_2$ efflux from stems to induced variation in growth increment/stemwood production due to fertilization and irrigation treatments (Maier et al. 1998; Stockfors and Linder 1998; Maier 2001). However, studies that directly link changes in stem $CO_2$ to physiological processes in the canopy or root systems are extremely rare. Lavigne et al. (2004) found that girdling and debudding caused stem $CO_2$ efflux to decrease in *Fraxinus americana* and *Acer rubrum.* In another study, Edwards et al. (2002) that found $CO_2$ efflux from stems to be influenced by short-term variations in substrate supply. These authors reported that $CO_2$ efflux in *Liquidambar styraciflua* stems exposed to elevated $CO_2$ was 23-48% greater than trees in ambient $CO_2$ treatments. Interestingly, when the fumigation gas was turned off in the elevated $CO_2$ treatment both stem $CO_2$ efflux and stem sucrose concentrations decreased. This response was observed less than 24 hrs after cessation of fumigation gas and both efflux and stem sugar concentrations returned to previous levels when $CO_2$ fumigation was resumed. These findings indicate that respiration in woody stems and branches is linked to physiological processes in other organs of the tree, although more research is clearly needed to develop a more integrated understanding (i.e. incorporating canopy, stem, and root systems) of respiration in forest trees.

Respiratory activity in the dormant season has been largely attributed to maintenance respiration in the sapwood due to the large volume of sapwood relative to phloem and cambial tissues. Accordingly, maintenance respiration has been found to be well correlated with sapwood volume in a variety of coniferous (Sprugel 1990; Ryan et al. 1990; Ryan et al. 1996; Will et al. 2001) and some deciduous (Edwards and Hanson 1996) species. Furthermore, other studies have reported correlations between maintenance respiration and sapwood nitrogen content (Ryan 1991; Ryan et al. 1994; Maier 2001; Vose and Ryan 2001). This relationship is expected because approximately 60% of maintenance respiration supports the repair and replacement of proteins, and most of the organic nitrogen in plant tissues is found in proteins (Penning de Vries 1975). However, maintenance respiration is not always found to be correlated with sapwood nitrogen content due to a) a correlation between maintenance respiration and relative growth rate (Lavigne and Ryan 1997) or b) a large proportion of total maintenance respiration being attributable to phloem maintenance respiration (Stockfors and Linder 1998; Bosc et al. 2003).

According to the theoretical assumptions of the 'mature-tissue method', maintenance respiration rates, when normalized to a constant temperature, should exhibit no variation across seasons. However, maintenance respiration may vary seasonally due to changes in the amount, composition, and activity of living tissue. Lavigne and Ryan's findings (1997) that maintenance respiration and growth respiration were correlated within aspen, jack pine, and black spruce stands indicates that seasonal changes in maintenance respiration may indeed occur. In addition, Maier (2001) found that measurements of maintenance respiration collected after the cessation of growth may

differ significantly from those collected prior to the onset of growth perhaps due to temporal differences in respiratory activity that occur as cambial cells transition to dormancy in the autumn and reactivate in the spring (Lavigne et al. 2004). Unfortunately, there are no direct studies reporting seasonal changes in maintenance respiration due to the difficulty of distinguishing maintenance from growth respiration during the growing season.

### d. Differences between $CO_2$ efflux from Branches and Stems

Very few studies on respiration in branches and upper boles have been conducted, but the few that do exist suggest that rates of branch $CO_2$ efflux is substantially greater than those from stems. For example, many recent studies (Sprugel 1990; Ceschia et al. 2002; Damesin et al. 2002) report 10-40x greater rates of $CO_2$ efflux from branches in agreement with early studies (Möller et al. 1954; Yoda et al. 1965). This disparity indicates that care must be taken when developing stand-level estimates of woody tissue respiration, as reliance on $CO_2$ efflux measurements from stems may result in a substantial underestimate of the stand-level flux. In addition, seasonal trends in branch respiration indicate that the early growing season peak in $CO_2$ efflux of branches tends to occur earlier than the corresponding peak in stem $CO_2$ efflux perhaps due to the energy costs of mobilizing storage carbohydrates to be used during the early stages of shoot elongation (Sprugel, 1990; Ceschia et al, 2002), closer proximity apical sources of growth hormones, and/or earlier initiation of diameter growth in branches relative to stems.

Differences in $CO_2$ efflux, when normalized to account for differences in sapwood volume, between stems and branches have been attributed to a variety factors. It is likely that the respiratory activity of cambial and sapwood cells is higher in branches due to greater physiological activity, closer proximity to carbohydrates sources, or greater nitrogen content or live cell volume of branch tissues. However, it is also possible that the thinner bark and less mature wood found in canopy branches is more permeable to $CO_2$ diffusion thereby resulting in greater $CO_2$ efflux. Differences in permeability to $CO_2$ between branches and stems may be particularly important in explaining the greater efflux from branches if the transpiration stream brings significant amounts of $CO_2$, produced by respiration in the lower bole and roots, into these branches.

**e. Conclusions**

It is evident that investigations of woody tissue respiration conducted to date have provided a great deal of valuable information regarding the magnitude of carbon flux from forests to atmosphere derived from stem and branch respiration and the environmental factors that influence this carbon flux. However, it is becoming clear that we have very little understanding of the actual physiological processes within stems that are the ultimate sources of the $CO_2$ that diffuses through stem and branch surfaces into the atmosphere. This is compounded by a lack of understanding of the physical constraints that determine the proportion of respiratory $CO_2$ that diffuses through the bark surface. As stated earlier, use of $CO_2$ efflux from stem or branch surfaces as an estimate of woody tissue respiration assumes that the proportion of respired $CO_2$ that diffuses through the bark is fairly high and constant.

Woody tissue respiration is typically modeled as a function of stem temperature and either stem surface area (Kinerson 1975; Linder and Troeng 1981), sapwood volume (Ryan 1990; Ryan et al. 1994), or tissue nitrogen content (Ryan 1991; Vose and Ryan 2002). In order to develop a more physiologically-accurate model of woody tissue respiration it is necessary to describe the patterns and rates of $CO_2$ production within stems and the anatomical and physiological traits that determine the permeability of a stem or branch to $CO_2$ diffusion. In the following section, a the available literature on these topics will be reviewed and a preliminary framework for developing a mechanistic understanding of woody tissue respiration and $CO_2$ efflux from stems and branches will be outlined.

### 3. Patterns of $CO_2$ Production within Stems and Branches

The first step towards a mechanistic understanding of woody tissue respiration is to characterize the patterns and rates of $CO_2$ production within stems and branches. A primary question is determining if the majority of respiratory $CO_2$ production occurs in the phloem, in the vascular cambium and the immature xylem and phloem cells adjacent to it, in the sapwood, or at the sapwood-heartwood boundary where energetically-expensive tannins and phenolic compounds are produced. Descriptions of radial trends in respiration, from the bark to the pith, in wood cores removed from stems have been conducted in several tree species including *Pinus radiata* (Shain and Mackay 1973), *Picea abies* (Møller and Müller 1938), *Fraxinus nigra* and *Acer rubra* (Goodwin and Goddard 1940). In addition, recent work by Pruyn et al. (2002a, 2002b, 2003) has investigated differences in these radial patterns of respiratory activity caused by vertical

bole position, tree age, and species differences in various tree species in the Pacific Northwest. These studies have indicated that respiratory activity is highest in the inner bark (composed of living phloem and cambial tissues) and declines greatly with depth through the sapwood to the heartwood. It would be interesting to partition respiration from the phloem from cambial respiration; however, this is experimentally difficult as it is hard to visually discern phloem from cambial tissues in extracted cores. Respiratory rates was found to decrease by 83-97% from inner bark to the inner sapwood with the heartwood possessing negligible respiration rates (Pruyn et al. 2002a). However, due to the much larger volume of sapwood within stems compared to the inner bark, inner bark respiratory activity may be only 11-50% of whole stem respiratory activity with the majority of $CO_2$ production, 50-89%, occurring in the sapwood (Pruyn et al. 2003). Volume-based respiratory activity was found to be higher in wood tissues at bole tops, relative to lower portions of the boles (Pruyn et al. 2002a and 2002b). Respiration may be greater in branches due to greater physiological activity associated with growth, fixed carbon metabolism and transport, or a higher proportion of ray parenchyma. This is in agreement with the chamber-based measurements of $CO_2$ efflux that typically report much greater values from branches relative to lower stems.

Respiratory activity in the inner bark is most likely associated with phloem unloading and the division and differentiation of cambial and ray cell initials. The decreasing trend in the sapwood has been attributed to growth and secondary wall formation in the xylem cells closest to the cambium (Goodwin and Goddard, 1940) and a decline in metabolic activity and/or dormancy of sapwood parenchyma cells with increasing depth (Shain and Mckay 1973; Bamber 1976; Dickson 1991; Gartner et al.

2000; Pruyn et al. 2002a). Decreasing metabolic activity with depth in sapwood may also be due to age-related changes (as cells located deep within wood are younger than more surficial cells), increased use of inner parenchyma cells for storage, decreases in ray vigor, or onset of heartwood formation. Increased respiratory activity in outer wood may be related to increased nitrogen (Goodwin and Goddard 1940) and soluble carbohydrate concentrations (Saranpää and Höll 1989; Hoch et al. 2003) in these tissues. Furthermore, Stockfors and Linder (1998) report decreasing proportions of live cell volume with increasing depth from the bark surface.

Several possible experimental artifacts associated with measurements of respiration in excised wood cores exist including the potential for microbial respiration or stored $CO_2$ to confound respiration estimates. A detailed investigation by Pruyn et al (2002b) found the effects of these artifacts on respiration measurements to be negligible or controllable by careful experimental design. For example, to prevent erroneously high estimates of respiration due to wounding or the release of stored $CO_2$, it is advantageous to allow the cores to equilibrate to the measurement conditions for several hours prior to the respiration measurement. Another important limitation of these studies on excised wood cores is that the respiration measurements are made under experimental conditions that are likely to differ from conditions within the tree stem. Respiration activity in excised wood cores was found to be influenced by both experimental $CO_2$ and $O_2$ concentrations with respiration activity decreasing in response to increasing $CO_2$ and decreasing $O_2$ (Pruyn et al. 2002b). Studies have indicated that $CO_2$ concentrations within tree stems are 50-350 times ambient and that oxygen concentrations can reach hypoxic conditions, particularly at the sapwood-heartwood boundary during the onset of

the growing season (Eklund 1990; Pruyn et al. 2002b). This indicates that the experimental conditions, atmospheric $CO_2$ and $O_2$ concentrations, under which respiration measurements of excised cores are typically conducted may cause artificially high respiration rates. In fact, $CO_2$ production in wood cores extracted from *Pseudotsuga menziesii* trees was 3-15 times higher than IRGA measurements of $CO_2$ efflux made with chambers mounted to the tree stems (Pruyn et al. 2002; Cernusak et al. *unpublished data*). As a result, estimates of respiration from excised cores can not be directly compared to respiration estimates derived from chamber-based measurements of $CO_2$ efflux from woody stems and branches. However, respiration estimates from wood cores may provide information pertaining to relative differences in respiratory activity between wood tissue types, between trees, or between stems and branches. It is also possible to conduct measurements of respiration on extracted cores under experimental $CO_2/O_2$ concentration conditions that more closely approximate conditions within a tree stem. This approach is most likely to give respiration rates that are accurate estimates of respiratory $CO_2$ production within actual tree stems.

However, development of accurate estimates of $CO_2$ production within stems and branches would still leave many important questions about the fate of this respiratory $CO_2$. For example, what are the ultimate destinations for this $CO_2$ (possibilities include long-term residence in air spaces located within the stem, diffusion of $CO_2$ to the atmosphere, or translocation to upper parts of the tree via the xylem stream) and what proportion of respired $CO_2$ follow each of these pathways. Relatively little is known about these possible pathways including:

·What is the mean residence time for respiratory $CO_2$ in the stem?

·How long does it take for $CO_2$ to diffuse from its site of production to the atmosphere?

·What proportion of this $CO_2$ is translocated in the xylem stream?

·What is the eventual fate of $CO_2$ that is translocated in the xylem stream (re-fixation in the canopy, loss to the atmosphere through stomata, or diffusion to the atmosphere through branch periderm)?

Unfortunately, very few studies have directly attempted to answer any of these questions. In addition to these physical questions about the $CO_2$ within tree stems, very little is known about how this large reservoir of $CO_2$ is integrated into stem physiology and tree carbon balance. For example, do high $CO_2$ (or low $O_2$) concentrations inhibit respiration rates *in situ* within stems and can this impact wood formation? Or do living cells within stems have adaptations for the high $CO_2$ environment that they are found in? Evidence that this high $CO_2$/ low $O_2$ environment is integrated into stem physiology can be seen in several ways. Wood respiration is not inhibited by $O_2$ concentrations above 5-10% and the observed inhibitory effects below these concentrations are reversible (Spicer and Holbrook, 2005) In addition, the high $CO_2$ concentrations observed deep in sapwood tissues have been shown to be necessary for the synthesis of compounds associated with heartwood formation (Carrodus 1971). Furthermore, trees that exhibit corticular photosynthesis in bark surfaces of stems and branches predominantly utilize $CO_2$ from the interior of stems and branches as a substrate (Pfanz et al. 2002). However, the extent to which the large $CO_2$ reservoir within stem tissues is utilized to improve whole tree carbon gain is largely unstudied, but appears to be small (Foote and Schaedle 1978; Levy and Jarvis 1998)

## 4. Internal $CO_2$ Concentrations Within Trees, the Influence of Sap Flow on $CO_2$ Efflux, and the Permeability of Wood to $CO_2$ Diffusion

### a. Internal $CO_2$ Concentrations: the Ultimate Driver of $CO_2$ Efflux?

Zimmerman (1983) reported that an extensive network of air spaces exists within tree stems consisting of interstitial spaces and MacDougal and Working (1933) referred to this network as a tree's 'pneumatic system'. These interstitial spaces mostly consist of intercellular spaces that form small radial channels, 1-15 $\mu m^2$ in cross-sectional area, within xylem rays (Panshin and de Zeeuw 1980). In addition, longitudinal intercellular channels have been occasionally observed in xylem tissues (Preusser et al. 1961; Isebrands and Parham 1974; Bolton et al. 1975) and may interconnect with radial channels (Bolton et al. 1975). Other isolated air spaces occur in the lumens of embolized fibers, vessels, and tracheids, but these are probably not in direct contact with surrounding intracellular spaces (Zimmerman 1983).

Almost nothing is known about this network of intercellular spaces, including its function, approximate volume, or connectivity with the atmosphere. These channels may serve to supply respiring tissues with oxygen that has diffused radially through the bark or has been delivered by the transpiration stream. It is quite possible, but not rigorously tested, that $CO_2$ efflux from stems and branches is related to the $CO_2$ concentration of nearby portions of this 'pneumatic system' which is likely determined by both the respiration rate of surrounding wood tissues and the dissolved $CO_2$ concentration of xylem sap.

Seasonal variations in the $CO_2$ and $O_2$ concentrations of these intracellular air networks have been measured in several studies. Most of these studies have been

conducted by boring holes into the wood, at various depths, and installing a gas-tight tube and septum into the hole. The air in the tube is considered to be in equilibrium with the intracellular air network, thereby allowing gas samples to be extracted through the tube's septum. The composition of the extracted air is then typically determined by combined gas chromatography-mass spectrometry (Eklund 1990; Pruyn et al. 2002b). In addition, recent use of microelectrodes to directly measure gas concentrations within stems seems to facilitate the collection of measurements such that hourly and diel changes in stem gas concentrations can be observed (McGuire and Teskey 2002).

$CO_2$ concentrations in *Picea abies* were found to be low (< 1%) in early spring, but began to rise in May coinciding with the onset of the growing season, reaching peak concentrations of 10-12% in June (Eklund 1990). These $CO_2$ concentrations are 250-350 times higher than the ambient atmosphere. $CO_2$ concentrations then decreased until October by which levels had returned to those recorded in early spring. A similar seasonal trend was found by Pruyn et al. (2002b). This study also found that $CO_2$ concentrations increased with depth into the stem and the highest $CO_2$ concentrations (4-12%) were found in middle sapwood or sapwood/heartwood boundary. This may provide evidence that the cambium is highly resistant to gas diffusion. Trends in $O_2$ concentrations in intracellular air networks are the inverse of trends in $CO_2$ concentration both radially and seasonally. For example, oxygen concentrations were highest in the winter months and were subsequently drawn down by respiratory activity during the growing season. In addition, oxygen concentrations were highest, and closest to atmospheric levels, in the outer bark (18-24%) while hypoxic conditions (< 5%) were recorded at the sapwood/heartwood boundary (Pruyn et al. 2002b).

Coincident measurements of $CO_2$ efflux were not made in these studies of seasonal variations in the internal $CO_2$ concentration of tree's intracellular air networks. Comparing these two types of measurements would be an excellent test to determine if the $CO_2$ concentration of intracellular air networks is the ultimate driver of $CO_2$ efflux. In general, the seasonal patterns of internal $CO_2$ concentration and $CO_2$ efflux are identical as both peak in the early to mid-spring, decline through the growing season, then remain at a consistent low level from the end of the growing season until the following spring (Eklund 1990; Edwards and Hanson 1996; Damesin et al. 2002; Edwards et al. 2002; Pruyn et al. 2002b). Unfortunately, studies of tree internal $CO_2$ concentrations have typically made measurements on a weekly basis, at most. As a result, it is not known whether mean daily internal $CO_2$ concentrations follow changes in stem temperature over periods of several days, as $CO_2$ efflux from stem and branches typically does. Other studies have determined the dissolved $CO_2$ content of xylem sap by measuring the $CO_2$ concentration of air spaces within the xylem and assumed that $CO_2$ concentration of the air was in equilibrium, and therefore proportional to, the concentration of dissolved $CO_2$ products in the xylem sap (Hari et al. 1991; Levy et al. 1999; Teskey and McGuire 2002). These studies have found that $CO_2$ concentration of the intracellular air spaces of the outer sapwood varies on a diel basis but is not strongly related to sapwood temperature and, instead, tends to be negatively correlated with sap velocity (Teskey and McGuire 2002). However, it is not known what regulates the internal $CO_2$ concentration when sap velocity is negligible at night nor if phloem or inner sapwood tissues exhibit the same diel trend as outer sapwood tissues. As a result, a study that combined measurements of $CO_2$ internal air concentrations, at several depths within

the tree, and $CO_2$ efflux with a sampling schedule that revealed both diel and seasonal patterns would be a significant contribution to the understanding of woody tissue respiration.

If the internal $CO_2$ content of this extensive network of intracellular air spaces is the ultimate driver of $CO_2$ efflux from stems and branches, it would be useful to develop a model describing this relationship. Such a mechanistic treatment of $CO_2$ efflux would greatly facilitate developing and testing of hypotheses about woody tissue respiration, as well as, accurately predicting this carbon flux in models of forest carbon cycles. A simple diffusion model may be a useful starting point for a mechanistic framework of woody tissue respiration. The high $CO_2$ concentration of the internal air spaces within a tree stem results in a steep concentration gradient between the air network and the ambient atmosphere. Thus, $CO_2$ should exit the tree stem through the bark surface according to Fick's law of diffusion. An equation describing stem $CO_2$ efflux in terms of Fick's law is shown in Equation 4. In this equation, the rate of $CO_2$ efflux ($E$) from woody stems should be proportional to both the resistance of wood to $CO_2$ diffusion ($r_w$) and the concentration gradient for $CO_2$ between the stem's internal air spaces ($p_i$) and the atmosphere ($p_a$).

**Equation 4:** $$E = r_w \times (p_i - p_a)$$

This equation could be highly useful in predicting $CO_2$ efflux; however, it will require many field and experimental studies to verify the validity of this relationship. In context of this equation, seasonal patterns and between-tree variation in stem $CO_2$ efflux

are influenced strongly by variation in $p_i$, which is likely to be a function of stem temperature, tree growth rate, and maintenance respiration. In Chapter 5 of this dissertation, this Fick diffusion model of woody tissue $CO_2$ efflux will be investigated by comparing measurements of $p_i$ and $E$ in nearly 20 *Q. rubra* trees. If this study finds that $p_i$ is strongly related to stem $CO_2$ efflux, this would suggest that much of the difficulty in finding consistent relationships between rates of $CO_2$ efflux and tissue types, tree position, tree age, and species may be due to variation in the $r_w$ parameter. A considerable amount of research needs to be completed to validate the relationship between $CO_2$ efflux and the $CO_2$ concentration within tree stems before the role of *rw* in between- and within-tree variation in $CO_2$ efflux can be assessed. However, due to the fact that most studies of woody tissue respiration have ignored the anatomical and physiological characteristics of wood that may influence its permeability to $CO_2$, it is informative to review the sparse literature on these characteristics.

### b. Permeability of Wood to $CO_2$ Diffusion

Unfortunately, there is no quantitative data available on the resistance of living woody tissues to the diffusion of $CO_2$. Theoretically, the outer periderm of woody stems should be highly resistant to diffusion of water vapor, and therefore, to $CO_2$ and $O_2$ as well. This is because both the periderm and the leaf cuticle are adaptations to prevent excessive loss of water to the atmosphere. Interestingly, the permeability of tree periderms to water is fairly similar to that of leaf cuticles. However, woody periderms attain this resistance with a 10 -100x increase in thickness compared with leaf cuticles (Pfanz et al. 2002). Several characteristics of the periderm have been found to influence

its permeability to both water and oxygen including periderm thickness and density, periderm wax content, and the water content of phellum membranes (Groh et al. 2002). In addition, the texture of the periderm may also influence $CO_2$ diffusion, as loss of water vapor through the periderm has been found to be three times greater in tree species with deeply fissured bark (*Quercus*, *Populus*) compared to trees with smooth, dense periderms (*Fagus*, *Betula*) (Pfanz et al. 2002). There is no data relating any of these wood characteristics to $CO_2$ efflux from stems and branches. Accordingly, future research on these wood traits, particularly studies comparing $CO_2$ efflux from different height positions or between trees differing in age or species, would be very informative.

Another factor that may influence the diffusion of $CO_2$ to the atmosphere in tree stems and branches is the density (or specific gravity) of the wood, particularly the sapwood. Recently, Bowman et al. (2005) demonstrated a significant correlation between sapwood density and temperature-normalized rate of $CO_2$ efflux from stems in *Dacrydium cupressinum* trees. Similar to other features of wood anatomy, specific gravity has not been analyzed by most researchers of $CO_2$ efflux from stems despite the relative ease of collecting such data. Specific gravity is typically calculated as the ratio of the ovendry weight of the wood to its fresh volume, as shown in equation 5 (Panshin and de Zeeuw 1980).

**Equation 5:** $$\text{Wood Density} = \frac{\text{Oven Dry Weight of Wood}}{\text{Fresh Volume of Wood}}$$

The relationship between stem $CO_2$ efflux and sapwood density is intriguing due to the potential for density to influence both the permeability of wood to $CO_2$ diffusion

and the rate of sap flow through the xylem. Sap velocity has been demonstrated to affect the internal $CO_2$ concentration within the sapwood (Teskey and McGuire 2002) and Barbour and Whitehead (2003) recently reported that sapwood density explained 94% of variation in average sap velocity in *D. cupressinum* trees with exposed crowns (i.e., trees with two-thirds of crown emerged above neighboring crowns or those growing in significant canopy gaps). Therefore, wood density appears to be an important link between the structural and hydraulic properties of tree stems and the relationship between $CO_2$ efflux and sapwood density in Bowman et al. (2005) suggest that it may also influence the respiratory properties of stems.

Competition and soil fertility within forest stands can impact wood density. For example, sapwood density has been found to increase with suppression in conifers, if variation in stem age and position within the stem is controlled for (Panshin and de Zeeuw, 1980). In addition, wood density is influenced by environmental characteristics such as mean temperature and precipitation and this may be manifested in geographical patterns in wood density. For example, pine species found in the coastal southern United States show increases in specific gravity from northwest to southeast corresponding to increases in precipitation during the growing season (Mitchell, 1963). These general patterns, particularly those related to environmental factors, can serve as testable hypotheses in studies of woody tissue respiration. Furthermore, sapwood density tends to decrease from the base of the bole upward in coniferous trees. This observation may help explain the differences in $CO_2$ efflux observed between stems and branches in forest trees.

A significant benefit to the model proposed in Equation 4 is that it is capable of incorporating variation in the anatomical characteristics of wood, such as sapwood density or bark thickness and wax content, that may influence $CO_2$ efflux from stems through variation in the ($r_w$) parameter. This model may aid in scaling $CO_2$ efflux from chamber measurements to stand-level estimates by improving our ability to predict between- and within-tree variation in CO2 efflux and, at the very least, facilitates the making and testing of hypotheses about woody tissue respiration.

### c. The Influence of Sap Flow on $CO_2$ Efflux from Woody Stems

Researchers investigating $CO_2$ efflux from woody stems and branches have acknowledged for several decades the possibility that some proportion of respiratory $CO_2$ produced within stems or branches does not diffuse through to the atmosphere and, instead, is transported in the xylem stream to the canopy (Johansson 1933; Boysen Jensen 1933; Nigisi 1978 and 1979; Sprugel and Benecke 1991). For many years, there has been credible evidence for interactions between sap flow and $CO_2$ efflux, yet many studies of $CO_2$ efflux from tree stems largely ignore this potential source of error. For example, additions of $^{14}C$ to the transpiration stream of *Pinus elliottii* seedlings resulted in the recovery of ~9% of applied radiolabel in leaf tissues (Zelawski et al. 1970). In addition, authors have documented a decrease in $CO_2$ efflux from stems during times of peak transpiration. For instance, Negisi (1978) found that measured rates of stem $CO_2$ efflux were 50% of predicted rates based on stem temperature and $CO_2$ efflux rates in *Pinus taeda* seedlings were on average 6.7% less during periods of high transpiration (Martin et al. 1994). Recent evidence by McGuire and Teskey (2004) indicates that 15-75% of

respiratory $CO_2$ produced within stems may be retranslocated by the xylem stream during periods of peak transpiration in deciduous trees. However, not all studies attempting to observe interactions between $CO_2$ efflux and sap flow have been successful as limiting transpiration and sap flow by bagging foliage and severing stems had no impact on stem $CO_2$ efflux in *Pinus ponderosa* (Carey et al. 1996). The limited data available suggests the potential for large interactions between sap flow and $CO_2$ efflux from woody stems and indicates that further research on the prevalence of these interactions in trees is greatly needed.

The transport of respiratory $CO_2$ in the xylem stream has been proposed as an explanation for both the diel hysteresis that is often observed in the relationship between stem $CO_2$ efflux and temperature (i.e. different respiration rates at similar temperatures at different times of the day)(Teskey and McGuire 2002) and the high rates of $CO_2$ efflux from branches relative to stems (Sprugel 1990). Other studies have suggested that the xylem stream may serve as a source of $CO_2$, rather than a sink. Levy et al. (1999) documented that stem $CO_2$ efflux was positively correlated with sap flow rates and proposed that $CO_2$ derived from root respiration or the high $pCO_2$ of soil water contributed to stem $CO_2$ efflux. Thus, with various authors claiming that sap flow can have both positive and negative effects on $CO_2$ efflux, it is apparent that there is much to be learned about interactions between sap flux and woody tissue respiration.

Recent studies by Teskey and McGuire (2002 and 2005) have indicated that $CO_2$ efflux from stems is well correlated with total dissolved $CO_2$ of xylem sap and demonstrated significant, and reversible, changes in $CO_2$ efflux by artificially changing dissolved $CO_2$ content of xylem sap in both detached branch segments and *in situ* tree

stems. In addition, it has been demonstrated that during times of peak transpiration ~3x more respiratory $CO_2$ may be transported in the xylem stream than diffuses to the atmosphere (Teskey and McGuire 2004). However, during the night, when no transpiration occurs, nearly all respiratory $CO_2$ escapes to the atmosphere. Furthermore, the residuals from $CO_2$ efflux-stem temperature curves for individual trees were found to be positively correlated with sap flux density (Bowman et al. 2005). This indicates that there was less $CO_2$ diffusing from the tree stem, than would be predicted from stem temperature, during periods of peak transpiration. Another interesting question regarding this internal translocation of respiratory $CO_2$ within the xylem stream is assessing how much of this $CO_2$ makes is transport to sites of photosynthesis in the leaves and does this $CO_2$ contribute to photosynthetic carbon gain. Preliminary estimates indicate that this $CO_2$ can account for up to 15% of photosynthesis and, as a result, this mechanism for internal carbon circulation should be investigated further (Teskey and McGuire 2002). The growing body of evidence suggesting that sap flow can significantly interact with $CO_2$ diffusion through woody tissues indicates that it would be advantageous to incorporate these effects into the proposed diffusion model describing $CO_2$ efflux. However, at our current understanding of woody tissue respiration and stem physiology, it is unclear if xylem sap primarily influences $CO_2$ efflux through its effects on the magnitude of the $CO_2$ concentration gradient ($p_i$) or if it acts as a barrier to $CO_2$ diffusion by retranslocating $CO_2$ towards upper portions of the tree. Research on intra- and inter-specific variation in the effects of internal $CO_2$ concentration and xylem transport of $CO_2$ may help to resolve this question. Integration of such research with our current understanding of woody tissue respiration based on the functional model of respiration

will provide the basis for a new framework for woody tissue respiration that is based upon how $CO_2$ is produced within stems by respiration or how much $CO_2$ is supplied to stems by xylem sap and how much of this $CO_2$ diffuses through the bark of stems and branches to the atmosphere. Integration of internal stem $CO_2$ concentrations and xylem $CO_2$ transport with the functional model of respiration will prompt the development and testing of new hypotheses regarding woody tissue respiration and may make it easier to look for broad taxonomic, ontogenic, ecological, and geographical trends pertaining to woody tissue respiration. These types of trends have been investigated for photosynthesis and leaf respiration (Reich et al. 1997; Reich et al. 1999), but have not been vigorously attempted for woody tissue respiration.

## 5. Conclusions

Although much has been learned about woody tissue respiration in the past few decades, it is becoming increasingly evident that the standard methods of measuring stem respiration, chamber-based measurements of $CO_2$ efflux, are not providing accurate estimates of woody tissue respiration throughout much of the day. This inaccuracy may have little impact on ecophysiological research on forest carbon budgets, as these chamber measurements are valid estimates of the amount of respiratory $CO_2$ exchanged with the atmosphere. On the other hand, selection of an appropriate base for scaling from chamber measurements to stand-level estimates of $CO_2$ flux has proven difficult with woody tissue respiration. Elucidating the role of internal stem $CO_2$ concentration and xylem transport of $CO_2$ may help to explain this difficulty and will therefore aid in the development of accurate assessments of forest carbon budgets.

The most important benefit of incorporating the effects of internal $CO_2$ concentration and xylem transport of $CO_2$ is that it will improve our ability to compare woody tissue respiration measurements between tree species or between age classes. For example, Ryan and Waring (1992), found that an observed increase in maintenance respiration with increasing tree age was not sufficient to explain the decline in net primary productivity observed in these tree stands. The authors implicitly assumed that an equal, and large proportion, of respiratory $CO_2$ diffuses into the atmosphere in each of their tree stands. However, wood resistance to $CO_2$ diffusion is likely to increase with tree age, due to increasing bark thickness, thereby causing artificially low respiration rates in large trees and underestimating the role of increasing maintenance respiration in explaining net primary productivity decline.

This review paper illustrates the importance of acknowledging, and quantifying, the difference between woody tissue respiration and $CO_2$ efflux from stems and branches. It also puts forth several possible anatomical and physiological characteristics of wood that may influence the magnitude of the difference between $CO_2$ production within stems and $CO_2$ release to the atmosphere. The research conducted in the following four chapters endeavors to incorporate these inter-related components of woody tissue respiration. It is hoped that this work will improve both the understanding of woody tissue respiration and our capability to develop accurate estimates of woody tissue respiration in forest carbon budgets.

**Chapter 3: Sap flow rates and sapwood density are critical factors in within- and between-tree variation in $CO_2$ efflux from stems of mature *Dacrydium cupressinum* trees**

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**Abstract**

Measurements of $CO_2$ efflux from stems and branches, sap velocity, and respiratory activity of excised wood cores were conducted in *Dacrydium cupressinum* trees that differed in diameter, age, and canopy emergence. The objective of this study was to determine if consistent linkages exist between respiratory production of $CO_2$ within stems, xylem transport of $CO_2$, and the rate of $CO_2$ diffusing from stem surfaces. Stem $CO_2$ efflux was depressed during periods of sap flow compared to the efflux rate expected for a given stem temperature and was positively correlated with sapwood density. In contrast, no significant relationships were observed between $CO_2$ efflux and the respiratory activity of wood tissues. Between 86 and 91% of woody tissue respiration diffuses to the atmosphere over a 24 h period. However, at certain times of the day, xylem transport and internal storage of $CO_2$ may account for up to 13-38% and 12-18%, respectively, of woody tissue respiration. These results demonstrate that differences in sap flow rates and xylem anatomy are critically important for explaining within- and between-tree variation in $CO_2$ efflux from stems.

**Key Words:**

$CO_2$ efflux, Stem Respiration, Sap Flux Density, Xylem Transport, Sapwood Density, *Dacrydium cupressinum*

**Introduction**

Respiration in stems and branches accounts for 5-42% of total autotrophic respiration in forest ecosystems (Waring and Schlesinger 1985; Lavigne et al. 1997; Damesin et al. 2002) and 5-15% of gross primary productivity (Meir and Grace 2002). Despite its importance to tree carbon balances and forest ecosystem carbon cycles, our ability to predict and scale woody tissue respiration is limited. This is due, in part, to an inadequate understanding of the physiological processes within stems that regulate $CO_2$ production and/or influence the diffusion of $CO_2$ through stems and branches into the atmosphere.

Rates of respiration are determined largely by temperature (Amthor 1989) and exponential temperature response functions are typically used to predict temporal variation in woody tissue respiration. However, there is no generally accepted basis for expressing rates of woody tissue respiration or scaling estimates to the forest stand-level although several methods have been utilized. These methods include stem surface area (Kinerson 1975; Linder and Troeng 1981), sapwood volume (Ryan 1990; Ryan et al. 1994), and tissue nitrogen concentration (Ryan 1991). Also, rates of woody tissue respiration vary widely within trees and between stands, and finding reliable predictors to account for this variability has been elusive. For instance, large variation in respiration has been found within trees as respiration rates in the tree crown may be 19-42 times greater than rates at the base of the stem (Sprugel 1990; Damesin et al. 2002). Additionally, maintenance respiration rates differed by approximately 100-125% between stands of *Abies balsamea* (Lavigne et al. 1996). Lastly, deviations from the expected relationship between respiration and temperature are regularly observed in woody tissues

as measurements of $CO_2$ efflux often exhibit a pronounced diel hysteresis in which different efflux rates are observed at the same temperature at different times of the day (Ryan et al. 1995; Lavigne et al. 1996).

Diffusion of respiratory $CO_2$ from stems and branches to the atmosphere may be strongly influenced by the movement of sap in xylem conduits. Xylem sap contains dissolved gases, including carbon dioxide, and therefore provides a mechanism for the internal movement of $CO_2$ within trees (Negisi 1979; Stringer and Kimmerer 1993). The $CO_2$ concentration of gas in xylem tissues ranges between 2-12% (Eklund 1990, 1993; Teskey and McGuire 2002) and may serve as either a source or a sink for the $CO_2$ that diffuses through stems and branches to the atmosphere. Xylem transport of respiratory $CO_2$ from lower to upper regions of trees may contribute to both the diel hysteresis in the relationship between stem $CO_2$ efflux and temperature and the high apparent rates of respiration from branches. McGuire and Teskey (2004) concluded that $CO_2$ produced by woody tissue respiration either diffuses through the bark to the atmosphere ($CO_2$ efflux), is transported upwards by flowing sap (xylem transport flux), or is temporarily stored in the stem as the result of transient changes in the dissolved $CO_2$ concentration of sap (storage flux). These authors determined that 15-75% of respiratory $CO_2$ produced within woody stems may be retranslocated by the xylem stream during periods of transpiration while, at night, nearly 100% of respiratory $CO_2$ diffuses into the atmosphere (McGuire and Teskey 2004). In this study, measurements of $CO_2$ efflux rates from stems and branches and sap velocity were made in contrasting *Dacrydium cupressinum* (rimu) trees. The objectives were to 1) derive estimates of the respiration rate of woody tissues, the amount of respiratory $CO_2$ transported within the xylem stream, and internal storage

of dissolved $CO_2$ and 2) determine if patterns in stem $CO_2$ efflux, xylem transport, and $CO_2$ storage observed in trees that vary considerably in diameter, age, and canopy emergence.

Additionally, we sought to compare measurements of $CO_2$ efflux from stems and branches with the respiratory activity of underlying tissues and with characteristics of sapwood, such as average sap flux density and sapwood density, that may influence the diffusion of respiratory $CO_2$ to the atmosphere. Descriptions of the radial trend in respiratory activity of wood with depth, i.e. from the bark to the pith, indicate that respiration is highest in the inner bark (composed of living phloem and cambial tissues) and declines with increasing depth into the sapwood (Møller and Müller 1938; Goodwin and Goddard 1940; Shain and Mackay 1973; Pruyn et al. 2002a, 2002b, 2003). Respiration of woody tissues has also been found to increase with tree height in *Pinus ponderosa* (Pruyn et al. 2002a) and *Pseudotsuga menziesii* (Pruyn et al. 2002b) consistent with measurements of high $CO_2$ efflux in upper boles and canopy branches. We hypothesized that variation in $CO_2$ efflux between stems and branches is proportional to differences in the respiratory activity of wood cores excised from these woody tissues. In particular, respiration in the inner bark is likely to influence $CO_2$ efflux due to its high metabolic activity and proximity to the stem surface. To our knowledge, this study serves as the first published attempt to compare $CO_2$ efflux from stem surfaces directly with an estimate of the relative $CO_2$ production.

By comparing $CO_2$ efflux from trees differing greatly in size, age, and canopy emergence with estimates of respiratory activity in wood tissues and measurements of sap flow, we anticipated finding consistent linkages between respiratory production of $CO_2$

within stems, xylem transport of $CO_2$, and the actual $CO_2$ diffusing from tree stems. Reliable patterns would greatly improve our ability to model woody tissue respiration from stems and branches at the stand level and to predict differences both between trees and stands.

## Materials and Methods

### *Site Description*

The study site was situated within a mixed conifer-angiosperm forest located at Okarito Forest, Westland, New Zealand (43.2° S latitude, 170.3° E longitude, 50m above sea level). Mean annual temperature is 11.3 ºC, with a small range between winter and summer of 8.6 ºC, and low air saturation deficit. The forest is located on terrace outwashes from glacial moraines formed ~20,000 years ago. Annual rainfall is high, approximately 3400 mm, and evenly distributed throughout the year. Due to the abundant rainfall, the soils are frequently saturated, highly leached, and extremely acidic (pH 3.8-4.4 to a depth of 500 mm). The soil nitrogen concentration at an adjacent similar site was 633 μmol $g^{-1}$ and the soil-extractable phosphorus concentration was 12 μmol $g^{-1}$ (Richardson et al. 2004). The soils have a high organic matter content (approximately 30%), low permeability, and low porosity.

New Zealand's native lowland forests, such as this field site, are characterized by large, emergent conifer (*Podocarpaceae*) trees with a dense, mixed understory (Ogden and Stewart 1995). The study plot (50 m x 50 m) is dominated by 200-400 year old rimu (*Dacrydium cupressinum* Lamb) trees with a mean canopy height of 20 m. Other common tree species include kamahi (*Weinmannia racemosa*), Westland quintinia

(*Quintinia acutifolia*), miro (*Podocarpus ferruginea*), and southern rata (*Metrosideros umbellata*). The basal area distribution on the study plot was 73% *D. cupressinum*, 12% *W. racemosa*, 10% *Q. acutifolia*, and 5% other species.

*Measurements of $CO_2$ Efflux from Stems and Branches*

Measurements of $CO_2$ efflux rates were made on nine *D. cupressinum* stems, ranging in diameter from 0.18-0.67 m, for up to 160 hours in January of 2002. Measurements were also made on eight canopy branches with diameters between 0.04-0.14 m for 36 hours. Branches were selected from two trees accessible from the 22 m permanent tower located at the study site. Clear polycarbonate gas-exchange chambers were attached to the selected stems at ~1.3m above the ground. The chambers were half-cylindrical in shape, enclosed 0.025 $m^2$ of stem surface, and were equipped with small 24V fans (Model D241L-24VDC, Micronel, Vista, CA USA) to adequately mix the air within the chamber. The chambers used for branch measurements were smaller (~ 0.003 $m^2$ of branch area) and opaque. Also, the small size of the branch chambers eliminated the need for fans to thoroughly mix the air volume in the chambers.

The bark of *D. cupressinum* is smooth and typically did not require scraping of loose bark or fissures to achieve an adequate seal between the chambers and the bark. Closed-cell neoprene foam was fitted to the chamber edges and served as a gasket between the tree and the chambers. In stems, caulking cord (Mortite, Inc., Kankakee, IL USA) was applied around chamber edges to seal small gaps that typically occurred between the foam gasket and the tree. In branches, foam gaskets were not used and the caulking cord was applied directly between the chambers and the bark surface. The

chambers were then secured tightly to stems and branches using ratchet straps or hose clamps. Corticular photosynthesis does not occur in *D. cupressinum* stems as dissection of the inner bark tissue indicated that photosynthetic chlorenchyma tissue is absent.

The difference in $CO_2$ concentration in air entering and leaving chambers attached to trees was measured with an infrared gas analyzer (Model LI-6262, LI-COR Inc., Lincoln, NE USA) in an open flow system. A datalogger and relay driver (Models CR23X and SDM-CD16AC, Campbell Scientific Inc., Logan, UT USA) controlled a series of solenoid valves (Model MEBH-3-0,9-AW-QS-3, Festo AG & Co., Esslingen-Berkheim, Germany) that determined the flow of compressed air (430-470 μmol $mol^{-1}$ [$CO_2$]) through the measurement chambers. Air flow to the chambers was maintained at 0.5 L $min^{-1}$ by a flow controller (Model SR-10, Sierra Instruments, Monterrey, CA USA), but only during measurements. As a result, $CO_2$ accumulated in the chambers between measurements and was then flushed out during the next measurement period. Measurements were only considered valid if the $CO_2$ efflux rate was stable (less than 3% variation) for the last 60 of the measurement period. This criteria prevented artificially high rates of $CO_2$ efflux caused by leaky chambers and/or the slow flushing of accumulated $CO_2$. The sampling duration for each chamber was 12 minutes (5 minutes for branches) with all stems sampled once during each 132 minute measurement cycle (55 minute measurement cycles for branches). A measurement cycle consisted of nine stem (or branch) sampling periods and tests of the zero and span calibrations of the gas analyzer. Sapwood temperatures were measured using constantan-chromega thermocouples placed 15 mm beneath the bark surface and adjacent to the sampling chamber.

The temperature response of $CO_2$ efflux ($E_A$) was determined using a modified Arrhenius function as adopted by Turnbull et al. (2003), where $CO_2$ efflux at a given sapwood temperature is described as:

$$E_A = E_o \cdot e^{\frac{A_o}{R_g}\left(\frac{1}{T_o}-\frac{1}{T_a}\right)} \qquad \text{Equation 1.}$$

where $E_o$ is the $CO_2$ efflux rate (μmoles $CO_2$ $m^2$ $s^{-1}$) at the base temperature $T_o$ (here 288 K or 15 ºC), $T_a$ is the stem sapwood temperature (K), $R_g$ is the gas constant (8.314 J $mol^{-1}$ $K^{-1}$), and $A_o$ is a parameter related to the energy of activation (kJ $mol^{-1}$ $K^{-1}$) which describes the shape of the temperature response. Nonlinear curve fitting for temperature response curves was conducted with SigmaPlot 2001 (SPSS, Inc., Chicago, IL). To facilitate comparisons with other studies, $Q_{10}$ parameters were calculated as the ratio of $CO_2$ efflux at 25 ºC divided by $CO_2$ efflux at 15 ºC.

*Measurements of Sap Flux Density*

Sap flux density ($m^3$ $H_2O$ $m^{-2}$ sapwood $h^{-1}$) was measured concurrently with $CO_2$ efflux utilizing the thermal dissipation technique in five rimu stems (Granier 1985, 1987). Two probes were inserted into the stems to a depth of 20 or 40 mm, with one probe located 40 mm above the other, at a height of 2.5 m above the ground. Sap velocity was related to the temperature difference between the two probes, measured using a thermocouple located midway along each probe every 10 s, and half-hourly averages were recorded on a datalogger (Model CR21X, Campbell Scientific, Inc., Logan, UT USA). A more detailed description of the methods utilized for measuring sap flux density at the Okarito Forest plot can be found in Barbour and Whitehead (2003).

*Estimating Woody Tissue Respiration and Internal Fluxes of $CO_2$*

Measurements of stem $CO_2$ efflux and sap flux density were used to derive estimates of the respiration rate of the underlying woody tissues, the amount of respiratory $CO_2$ transported within the transpiration stream, and the $CO_2$ flux resulting from internal storage of $CO_2$ for five *D. cupressinum* trees ranging in diameter from 0.27-0.61 m. This was accomplished using a modified version of the theoretical framework outlined by McGuire and Teskey (2004),

$$R_S = \beta \cdot E_A + F_T + \Delta S \qquad \text{Equation 2.}$$

in which $\beta$ ($m^2/m^3$) is a tree-specific parameter related to the ratio of stem surface area to sapwood volume, $R_S$ (μmol $CO_2$ $m^{-3}s^{-1}$) is the $CO_2$ produced by woody tissue respiration per unit sapwood volume, $E_A$ (μmol $CO_2$ $m^{-2}s^{-1}$) is $CO_2$ efflux from the bark to the atmosphere per unit stem surface area, $F_T$ (μmol $CO_2$ $m^{-3}s^{-1}$) is xylem transport of $CO_2$ per unit volume, and (μmol $CO_2$ $m^{-3}s^{-1}$) is the storage of $CO_2$ in the stem per unit volume associated with transient changes in the dissolved $CO_2$ concentration of sap. $\Delta S$ is not the quantity of $CO_2$ stored in the stem; but rather it is the rate of change this stored $CO_2$, i.e., the rate at which dissolved $CO_2$ dissolves in or escapes from the xylem sap (McGuire and Teskey 2004).

Direct measurements of $E_A$ and sap flux density were made in five rimu stems for five consecutive days. During the night, $F_T$ and $\Delta S$ were assumed to be negligible, resulting in $E_A$ being equal to $R_S$. This is in accordance with the observations of McGuire and Teskey (2004) in which $\geq 93\%$ of respiratory $CO_2$ diffuses into the atmosphere at night. The night-time temperature response of $CO_2$ efflux, utilizing only data collected

between 0000 and 0600 h, was then used to predict woody tissue respiration ($R_S$) during the day when xylem transport and storage fluxes of $CO_2$ occur.

$$R_S = \beta \cdot E'_o \cdot e^{\frac{A'_o}{R_g} * \left( \frac{1}{T_o} - \frac{1}{T_a} \right)}$$ Equation 3.

where $T_o$ is 15 ºC and $E'_o$ and $A'_o$ are parameters derived from the temperature response of $E_A$ between 0000 and 0600 hours. The domain of this model, which was determined by the range of sapwood temperatures measured between 0000 and 0600 h, accounted for 56.6-74.4% of the daytime temperature range for which values of $R_S$ were estimated. Differences between the predicted rates of $R_S$ and the measured rates of $E_A \cdot \beta$ were then calculated, hereafter referred to as $R_S$ - $E_A$ (μmol $CO_2$ $m^3$ $s^{-1}$), and assumed to be due to xylem transport ($F_T$) and/or storage ($\Delta S$) of $CO_2$. Therefore, positive values of $R_S$ - $E_A$ indicate that the rate of $E_A \cdot \beta$ was less than the rate of $R_S$ predicted from the current sapwood temperature whereas negative values of $R_S$ - $E_A$ suggest that $E_A \cdot \beta$ was greater than the rate of $R_S$.

Values of $R_S$ - $E_A$ were then partitioned into $F_T$ and $\Delta S$ components. The magnitude of $F_T$ was assumed to be dependent solely on the current sap flux density. The proportion of $R_S - E_A$ attributable to $F_T$ was determined by linear regression analyses of the average maximum sap flux density recorded on each measurement day, calculated as the average of sap flux density measurements recorded between 1200-1600 h of that day, and the concurrent average value of $R_S$ - $E_A$. Separate linear regressions were conducted for each of the five sampled trees. Therefore,

$$F_T = \alpha * v$$ Equation 4.

where v is sap flux density and α is a tree-specific parameter representing the slope of the linear relationship between $v$ and $R_S$ - $E_A$. The variability in $R_S$ - $E_A$ that was not

explained by sap flux density was assumed to result from dissolved $CO_2$ moving into or out of storage. Therefore, $\Delta S$ was calculated as the difference between $R_S$ - $E_A$ and the rate of $F_T$ predicted from the sap flux density. Positive values of $\Delta S$ indicate an increase in the dissolved $CO_2$ concentration of xylem sap, whereas negative values represent a decrease in the dissolved $CO_2$ concentration of xylem sap. This method of partitioning $R_S$ - $E_A$ into $F_T$ and $\Delta S$ components requires the assumption that $\Delta S$ is negligible during times of maximum sap flux density. This assumption is supported by the finding that the $CO_2$ concentration of xylem sap is often well correlated with sap velocity (Teskey and McGuire 2002). Therefore, both the rate of change of the $CO_2$ concentration of xylem sap and the resulting changes in storage are assumed to be low during the 3-5 hour peak in sap velocity typically observed in *D. cupressinum*.

*Wood Respiratory Potential: Radial and Vertical Profiles and Temperature Response*

Wood cores were extracted from 11 *D. cupressinum* stems at a height of 1.3 m during January of 2003 with a 5 mm increment borer. Three of these trees were also sampled at four heights along the stem including the lower stem (at 1.3 m height), lower canopy (~1 m above lowest canopy branch), mid canopy (at midpoint between top and bottom of canopy), and upper canopy (~1-2 m from tree top). These three trees differed greatly in diameter (0.18, 0.31, 0.63 m) and height (17.1, 24.1, 28 m), and as a result, sampling points along the stems differed in absolute height. During transportation back to the laboratory, cores were stored in the dark and kept in plastic bags containing a moist paper towel to reduce desiccation of the samples. The excised cores were then cut into sections ~15 mm in length and stored for 24 hours at 4°C. Core segments were cut

corresponding to wood tissue types including inner bark (containing phloem and cambial tissues), outer and inner sapwood, sapwood-heartwood boundary, and outer, middle, and inner heartwood. Discrimination of the sapwood-heartwood boundary was determined visually in the field shortly after the cores were removed from the change in wood coloration. Outer sapwood was defined as the 15 mm section of sapwood located adjacent to the cambium whereas inner sapwood was the 15 mm of sapwood located adjacent to the sapwood-heartwood boundary. The next 15 mm section of wood was identified as the sapwood-heartwood boundary.

Respiratory activity of the core segments was determined by polarographical measurements of oxygen consumption in a Clark-type liquid-phase oxygen electrode (Model D10, Rank Brothers, Cambridge UK). Oxygen consumption was assayed at 20°C in 20 mM MES buffer (Azcon-Bieto et al. 1994) that had been equilibrated in ambient air. Prior to respiration measurements, core segments were incubated at the measurement temperature for 2 hours to allow respiratory activity to stabilize. Excised core segments were placed in the electrode cuvette and the depletion of oxygen was recorded for 20 minutes. Results from these oxygen electrode measurements are presented as the 'respiratory potential' of the extracted wood, following Pruyn et al. (2002a), rather its respiration rate as the electrode cuvette/buffer conditions are significantly different from conditions within the tree stem. As a result, respiratory potential measurements are not directly comparable, in absolute terms, to measurements of $CO_2$ efflux. However, it is hypothesized that the relative differences between trees in both respiratory potential and $CO_2$ efflux will be consistent with each other. Cumulative respiratory potentials for the volume of wood under the $CO_2$ efflux chambers were estimated by multiplying the core-

based measurements by the volume of wood corresponding to that tissue. The total volume of wood under the chamber was assumed to be a sector from the stem's pith to its surface.

In order to compare the effects of temperature on respiratory potential with the temperature response of stem $CO_2$ efflux, additional cores were extracted from three rimu trees at two heights (1.3 m above the ground and the upper canopy). The respiratory potential of each extracted core was then measured sequentially at four different temperatures (10, 15, 20, and 25 ºC). The wood cores were allowed to acclimate to each temperature for two hours prior to measurement in the oxygen electrode. The respiratory response of the cores to temperature was described by fitting data to both modified Arrhenius and $Q_{10}$ functions. Parameters for this Arrhenius function are similar to those used for $CO_2$ efflux except that $P_o$ (nmol $O_2$ $g^{-1}$ $s^{-1}$) is used to describe the rate of respiratory potential at the base temperature of 15 ºC and $T_a$ is the measurement temperature of the oxygen electrode.

Nonparametric Wilcoxon signed rank tests were used to test for differences in respiratory potential and nitrogen content between wood tissues. Differences in the temperature response parameters ($P_o$, $A_o$, and $Q_{10}$) of respiratory potential between wood canopy positions and in comparison to temperature response parameters of $CO_2$ efflux were assessed using paired t-tests. Both analyses were performed using SPSS 13.0 (SPSS, Inc., Chicago, IL) and differences were considered statistically significant if probabilities ($P$) were $< 0.05$.

*Measurements of Wood Density, Water Content, and Nitrogen Concentration*

The oven dry density, or specific gravity (Panshin and DeZeeuw 1980), for each core segment was determined as the ratio of dry mass to fresh volume. Fresh volume was calculated by carefully measuring the length and diameter with electronic calipers at four positions around the circumference of each segment. Dry mass was determined after wood samples were oven dried for 48 h at 75ºC. Volumetric wood water content was determined by dividing the difference between fresh and dried wood mass by fresh wood volume for each sample. The nitrogen concentration of the extracted wood cores was obtained on dried and ground wood material using a CNS autoanalyzer (Carlo Erba NA 1500, Milan, Italy).

**Results**

*$CO_2$ Efflux from Stems and Branches and Interactions with Sap Flow*

Sapwood temperature did not explain all diel variation in $CO_2$ efflux ($E_A$) from woody stems of *D. cupressinum*, (Fig. 1a). At many times during the measurement period, $CO_2$ efflux did not respond to, or declined during, coincident increases in sapwood temperature during the day. However, the response of night-time stem $CO_2$ efflux to variation in sapwood temperature was well described by the modified Arrhenius model (Eqn. 3) in all trees ($r^2$ = 0.65 - 0.87, $P < 0.001$), as shown in Fig. 1b. The standardized residuals from these response curves exhibited uniform variance across the modeled temperature range with a slight tendency for greater variance at sapwood temperatures greater than 18ºC. Stem $CO_2$ efflux at night ($E'_o$) was found to be 0.43-0.95 μmoles $CO_2$ $m^{-2}$ $s^{-1}$ at 15°C and the temperature response parameter ($A'_o$) ranged from 53.65- 91.18 (kJ $mol^{-1}K^{-1}$). Branch $CO_2$ efflux was between 0.96- 5.04 μmoles $CO_2$

$m^{-2}$ $s^{-1}$ at 15°C and was 1.5- 8.0 times greater than efflux rates from the stems of the same trees. Stem $CO_2$ efflux rates were not related to diameter, however, linear regression analysis indicated that branch diameter is a strong predictor of branch $CO_2$ efflux rates ($y = 0.4114x - 0.7156$, $r^2 = 0.82$, $P < 0.01$).

Analysis of the calculated differences between estimated $E_A \cdot \beta$ and predicted $R_S$, ($R_S - E_A$), suggested that there is a diel trend in the proportion of woody tissue respiration that diffuses to the atmosphere. $R_S - E_A$ tended to become more positive, i.e. $CO_2$ efflux was lower than would be expected from the predicted rate of woody tissue respiration, in the late morning (typically between 0930 and 1130 h). This increase in the magnitude of $R_S - E_A$ corresponded to the onset of transpirational sap flux in the *D. cupressinum* stems, as shown in Figure 2. $R_S - E_A$ tended to approach zero, i.e. the measured $CO_2$ efflux was close to the predicted rate of woody tissue respiration, between 0030 and 0300 h at night. These times correspond to the cessation of both sap flux and stem re-filling in the *D. cupressinum* stems. This pattern was observed over several days and in all five of the trees that were sampled for both sap flux density and stem $CO_2$ efflux.

For each of these trees, the maximum sap flux density recorded on each measurement day was found to be positively correlated with the concurrent value of $R_S - E_A$ ($r^2 = 0.54 - 0.82$, $P < 0.001$), as shown in Fig. 3. These relationships only held when examining variation in sap flux density resulting from day-to-day environmental changes and were not consistent for differences in sap flux density between trees on a given day. The respiratory $CO_2$ transported in the xylem stream ($F_T$) was hypothesized to be proportional to $R_S - E_A$ at periods of maximum sap flux density. Therefore, the correlation between $R_S - E_A$ and maximum sap flux density suggests that larger amounts

of $CO_2$ produced by woody tissue respiration ($R_S$) were transported in the xylem stream ($F_T$) on days when high rates of maximum sap flux density were observed.

In all trees, hysteresis was observed in the relationship between sap flux density and $R_S$ - $E_A$, as shown in Fig. 4 a & b. This hysteresis is attributable to variation in the storage flux ($\Delta S$) caused by changes in the dissolved $CO_2$ concentration of xylem sap. Between 0600 and 1200 h, the magnitude of $R_S - E_A$ was typically less then would have been predicted from the linear relationship between daily maximum values of $R_S$ - $E_A$ and sap flux density, indicating that $CO_2$ was being released from storage. In contrast, between 1800 and 0000 h, $CO_2$ tended to enter into storage as the magnitude of $R_S$ - $E_A$ was greater than that predicted from the relationship between daily maximum values of $R_S$ - $E_A$ and sap flux density.

Across all nine sampled trees, the stem characteristic that best predicted between tree differences in stem $CO_2$ efflux was the density of the outer sapwood (Fig. 5). No significant linear relationships ($P > 0.05$) were found between $CO_2$ efflux and tissue nitrogen concentration from inner bark or sapwood tissues, sapwood depth, tree size, cumulative respiratory potential, or respiratory potential from any specific wood tissues (*i.e.*, inner bark, outer and inner sapwood, sapwood-heartwood boundary). In addition, the temperature responses of stem $CO_2$ efflux and respiratory potential of wood tissues from the lower stem were not consistent with each other, as the values of $A_o$ and $Q_{10}$ for stem $CO_2$ efflux were significantly less than those of lower stem respiratory potential (paired t-tests, $P < 0.05$, Table 1).

*Estimates of Woody Tissue Respiration and Internal Fluxes of $CO_2$*

The relative magnitudes of the component fluxes ($E_A$, $F_T$, $\Delta S$) of woody tissue respiration ($R_S$) exhibited substantial diel changes (Table 2). $CO_2$ efflux to the atmosphere ($E_A$) comprised greater than 99% of woody tissue respiration between 0000 and 0800 h when sap flux was negligible. However, between 1600 and 2000 h, $E_A$ accounted for only 70.0% of woody tissue respiration on average and as little as 62.5% in one tree. Xylem transport of $CO_2$ ($F_T$) was negligible during the night and, as expected, increased in relative importance with the onset of sap flux 1-2 h after sunrise, reached a maximum of 12.6- 37.6% of $R_S$ between 1200 and 1600 h, and declined thereafter. The movement of $CO_2$ into and out of storage ($\Delta S$) was also found to be an important component of the diel variations in woody tissue respiration. The movement of dissolved $CO_2$ out of xylem sap to the atmosphere (i.e. $\Delta S$ was negative) was estimated to be greatest between 0800 and 1200 h, accounting for 1.7- 15.8% of $R_S$. In contrast, $CO_2$ tended to move into storage during the late afternoon and evening, reaching a peak of 12.5– 18.4% of $R_S$ between 2000 and 0000 h.

$E_A$, $F_T$, and $\Delta S$ differed greatly in their relative contributions to woody tissue respiration ($R_S$) over a 24 h period (Table 2). The net contribution of $\Delta S$ to woody tissue respiration was found to be small as diffusion of $CO_2$ out of storage was largely offset by movement of $CO_2$ into storage later in the day. Xylem transport of $CO_2$ was more important to the internal cycling of carbon than the storage flux and accounted for 6 - 14% of respired $CO_2$, across the five sampled trees, over the course of an entire day. Although $F_T$ and $\Delta S$ were large components of $R_S$ at various times of the day, $E_A$ was by far the most important $CO_2$ flux and accounted for 86- 91% of $R_S$ over a 24 h period.

Between-tree variation in the 24 h totals for $F_T$ and $\Delta S$ in the five sampled *D. cupressinum* trees was principally related to the tree's 24 h total woody tissue respiration ($R_S$) (Fig. 6a). It is important to note that the $\Delta S$ values shown in Figs. 6a & b represent mean daily totals for the $CO_2$ associated with storage fluxes both into (positive) and out of (negative) the xylem sap. Despite the consistency of ratio of $\Delta S$: $R_S$ suggested by Fig. 6a, variation in the proportion of $R_S$ attributable to $\Delta S$ ranged between 5- 10% and was positively correlated with the volumetric water content of wood, as shown in Fig. 6b.

*Radial and Vertical Trends in Respiratory Potential*

The respiratory potential of extracted inner bark samples (containing phloem and cambial tissues) averaged 0.51 ± 0.03 (SE) nmol $O_2$ $g^{-1}s^{-1}$ and was significantly greater than other wood types ($P < 0.005$, Fig. 7). Respiratory potential declined rapidly with depth into the stem to values of 0.14 ± 0.04, 0.09 ± 0.03, and 0.12 ± 0.03 nmol $O_2$ $g^{-1}s^{-1}$ for outer sapwood, inner sapwood, and the sapwood-heartwood boundary. No significant differences were observed between wood samples from these inner depths. However, a non-significant trend towards slightly increased respiration within the sapwood-heartwood boundary was observed. Volume-based measurements of respiratory potential showed the same trend with inner bark, outer sapwood, inner sapwood, and sapwood-heartwood boundary samples exhibiting rates of 0.25 ± 0.02, 0.06 ± 0.01, 0.04 ± 0.01, and 0.08 ± 0.02 nmol $O_2$ $cm^{-3}$ $s^{-1}$, respectively. Tissue nitrogen concentration was also significantly greater in the inner bark and declined with increasing depth towards the pith ($P < 0.05$, Fig. 7). However, differences in respiratory potential between wood samples within- and between-trees were only somewhat explained by tissue nitrogen

concentration as the overall relationship between respiratory potential and nitrogen content was weak ($y = 0.99x - 0.27$, $r^2 = 0.39$).

Respiratory potential of inner bark samples was found to vary with stem position as respiratory potential tended to be highest in the upper canopy ($P \leq 0.05$, Fig. 8). Due to the large variation in respiratory potential between trees, values are presented relative to the maximum respiration potential observed for each individual tree. Respiratory potential of the extracted wood in the lower stem (for inner bark samples) was lower than that in the upper canopy, but was higher than respiratory potential of wood from the lower or mid canopy. Less intra-tree variation was observed in the respiratory potential of outer sapwood as all stem positions were statistically similar ($P \geq 0.07$, Fig. 8). This trend was partially explained by tissue nitrogen concentration, as this tended to be higher, though not significantly, in the tree canopy. The higher respiratory potential of wood from the upper canopy compared to the lower stem is consistent with the higher rates of $CO_2$ efflux observed in canopy branches relative to that in lower stems.

Respiratory potential in both inner bark and outer sapwood increased in response to increasing measurement temperature. Respiration in upper canopy wood tended to be more responsive to temperature (i.e., $A_o$ and $Q_{10}$ values were higher), but this difference was not statistically significant ($P \geq 0.06$, Table 1). Furthermore, $A_o$ and $Q_{10}$ were similar across tissue types, at both tree heights, as values for inner bark and outer sapwood tissues were not statistically different ($P \geq 0.84$, Table 1).

## Discussion

### *Effects of Sap Flow and Storage on Stem $CO_2$ Efflux*

Studies of woody tissue respiration have long acknowledged the likelihood that the transport of respiratory $CO_2$ produced within stems and branches in the xylem stream may influence $CO_2$ efflux from stems and branches (Negisi 1978; Sprugel and Benecke 1991). This study indicates that the $CO_2$ efflux from *D. cupressinum* stems is influenced by both sap flow and storage of $CO_2$ in xylem water and that these interactions occur in trees that vary greatly in size and canopy dominance. In *D. cupressinum,* we estimate that xylem transport ($F_T$) of $CO_2$ accounts for 10.6 % of woody tissue respiration ($R_T$) over a 24 h period and 13-38% of predicted woody tissue respiration during periods of peak transpiration. This is in general agreement with the findings of McGuire and Teskey (2004) that $F_T$ accounts for 14-15 % of $R_S$, over a 24 h period, in *Fagus grandifolia* and *Liquidambar styraciflua*. Other studies have also reported that transpiration acts to transport respiratory $CO_2$ to higher positions in the plant in both seedlings and mature trees (Negisi 1978; Martin et al. 1994; Teskey and McGuire 2002; McGuire and Teskey 2004). Therefore, it is becoming evident that interactions between sap flow and stem $CO_2$ efflux are commonplace in forest trees.

Our estimates of $\Delta S$ suggest that $CO_2$ efflux from *D. cupressinum* stems is also influenced by transient changes in the concentration of dissolved $CO_2$ in xylem water. Our results predict that dissolved $CO_2$ moved out of storage in the morning and early afternoon, whereas the amount of dissolved $CO_2$ stored in xylem water increased in the late afternoon and evening. This trend is consistent with *in situ* measurements of the dissolved $CO_2$ concentration of xylem water in which rapid decreases in $CO_2$ concentration were observed with the onset of sap flux in the morning and increases in $CO_2$ concentration occurred as sap velocity began to decline in the late afternoon (Teskey

and McGuire 2002). During periods of maximum $CO_2$ transfer into and out of xylem sap, these opposing fluxes averaged 15.8 and –12.1% of $R_S$, respectively. The high percentages of total woody tissue respiration attributable to both xylem transport and storage of respiratory $CO_2$ in xylem sap, at certain times of the day, result in uncertainty in the source of stem $CO_2$ efflux as this $CO_2$ may have been respired locally, in lower positions in the stem or roots, or in the soil.

As may be expected, trees with high respiratory production of $CO_2$ ($R_S$) also tended to have high estimated rates of xylem transport and $CO_2$ storage (Fig. 6a). However, between-tree variation in the proportion of $R_S$ comprised by $\Delta S$ was determined by the volumetric water content of the stemwood (Fig. 6b). This finding is consistent with McGuire and Teskey's (2004) method of measuring $\Delta S$ directly, in which changes in the dissolved $CO_2$ concentration of xylem sap were multiplied by the volumetric water content of the stem segment. In *Acer saccharum*, sapwood water content was found to be higher in trees larger than 0.2 m in diameter than in smaller trees (Pausch et al. 2000) and there was a weak positive linear relationship ($r^2 = 0.18$) between mass-based water content and tree size in *D. cupressinum* trees at this study site (Barbour and Whitehead 2003). Therefore, it is likely that deviations from the expected rate of $R_S$ are likely to be greater in large trees due to their increased water content and greater capacity for dissolved $CO_2$ storage.

Within-tree differences in the amount of the respiratory $CO_2$ transported by sap flow ($F_T$) were well, and positively, correlated with between day differences in maximum sap flux density resulting from variation in air saturation deficit (Fig. 3). Between-trees, the mean daily amount of $F_T$ was driven by the respiratory production of $CO_2$ ($R_S$), Fig.

6a. However, the slopes of the linear relationships in Fig. 3 were not consistent across trees indicating that the amount of respiratory $CO_2$ transported by a unit volume of xylem sap was not constant across trees. The slope of these relationships were not significantly correlated with the sapwood density or sapwood depth of these trees. This finding indicates that the rate of diffusion of respiratory $CO_2$ into xylem sap is likely to be dependent on many variables such as factors that effect the capacity of xylem sap to take up respiratory $CO_2$ (such as the dissolved $CO_2$ concentration, pH, and temperature of xylem sap), anatomical characteristics of tracheids (such as cell wall thickness and diameter as this determines the cell's surface area to volume ratio), and factors that influence the rate of $CO_2$ diffusion to the atmosphere (such as the thickness and permeability of bark to $CO_2$ diffusion). Clearly, further research on the factors limiting both $CO_2$ diffusion into xylem sap and to the atmosphere will be necessary to understand between tree variation in xylem transport of $CO_2$.

*Potential Sources of Error in Modeled Estimates of $R_S$, $F_T$, and $\Delta S$*

The methods used in this paper to estimate woody tissue respiration ($R_S$), xylem transport of $CO_2$ ($F_T$), and storage of $CO_2$ ($\Delta S$) from the measured rates of stem $CO_2$ efflux ($E_A$) at night require several assumptions including 1) $E'_o$ and $A'_o$ do not exhibit diel variation 2) $F_T$ and $\Delta S$ are negligible at night, 3) $F_T$ is solely dependent on sap flux density, and 4) $\Delta S$ is negligible during periods of maximum sap flux density. These assumptions could not be directly tested in this study and therefore serve as potential sources of error in our estimates of $R_S$, $F_T$, and $\Delta S$. While quantification of the relative importance of these assumptions to this study's findings was not feasible, it is possible to

determine the conditions that would violate these assumptions and result in over- or underestimates of this study's estimates of $R_S$, $F_T$, and $\Delta S$.

The first assumption, that $E'_o$ and $A'_o$ do not differ between day and night or over the study period, is required to use the night-time temperature response of $E_A$ to derive day-time estimates of $R_S$. Although previous studies have demonstrated broad seasonal patterns in the temperature-normalized rate of woody tissue respiration (Ryan et al. 1997; Maier 2001) and its temperature response (Lavigne 1996; Stockfors and Linder 1998), little is known about variations in these parameters over shorter periods of time. Acclimation of respiration to temperature, over periods of several days, has been demonstrated in both leaves (Atkin et al. 2000; Bolstad et al. 2003) and roots (Bryla et al. 1997; Covey-Crump 2002) but it is unknown if large woody stems share this capacity to quickly adjust to prevailing temperature conditions. Respiratory acclimation to warmer temperatures during the day would likely result in a decrease in $E'_o$ and/or $A'_o$ therefore would cause potentially large overestimates of daytime values of $R_S$ and $R_S$-$E_A$.

Our study also assumes that $F_T$ and $\Delta S$ are negligible at night such that $E_A$ is equal to $R_S$. McGuire and Teskey (2004) demonstrated that $F_T$ and $\Delta S$ were indeed small (cumulatively less than 10% of $R_S$) at night in *Fagus grandifolia* and *Liquidambar stryraciflua*. However, in *Platanus occidentalis*, $F_T$ and $\Delta S$ comprised a fairly large proportion of $R_S$ at night, 15 and –26%, respectively. This indicates that our assumption of negligible $F_T$ and $\Delta S$ at night may be not be valid in all tree species. The validity of this assumption may also vary seasonally. Stem tissues pose significant barriers to the diffusion of $CO_2$ from the sapwood to the atmosphere (Eklund and Lavigne 1995). As a result, $CO_2$ concentrations within tree stems remain high, relative to the atmosphere,

during both day and night (3-9%, McGuire and Teskey 2002) with concentrations returning to atmospheric levels only after the end of the growing season (Eklund 1990). This suggests that $\Delta S$ may have a broad seasonal trend in which accumulation of $CO_2$ in tree stems ($+\Delta S$ ) occurs in the beginning of the growing season and the release of $CO_2$ ($-\Delta S$ ) to the atmosphere predominates towards the end of the growing season. Therefore, our assumption of negligible $\Delta S$ at night may tend to underestimate $R_S$ in the beginning of the growing season and overestimate $R_S$ at the end of the growing season.

We also assumed that the rate of $F_T$ in the measured *D. cupressinum* trees was solely dependent on sap flux density and that the $CO_2$ storage flux ($\Delta S$) was negligible during the 3-5 hour peak in sap flux density. While $F_T$ is mostly dependent on sap flux density, variation in $F_T$ has been shown to be caused by changes in the dissolved $CO_2$ concentration of the xylem sap even if sap flux density remains constant (McGuire and Teskey; 2004). Large increases or decreases in the xylem sap $CO_2$ concentration could result in either over- or underestimates, respectively, in our estimates of $F_T$. Similarly, large changes in xylem sap $CO_2$ concentration during the midday peak in sap flux density would result in non-negligible rates of $\Delta S$. McGuire and Teskey (2004) found that the contribution of $\Delta S$ to $R_S$ at times of peak sap flux density was typically small (3-13%), but ranged between negligible values (1%) and up to 20% of $R_S$. If the $\Delta S$ during the period of maximum sap flux density in this study's *D. cupressinum* trees were in this upper range it would negatively impact the accuracy of our model's estimates of α and our assessment of $F_T$.

Previous studies have found that stem $CO_2$ efflux exhibits a lagged response to sapwood temperature (Ryan et al. 1995; Stockfors and Linder 1998) and it has been

proposed that heterogeneity of temperature within the stem may explain deviations from the relationship between $CO_2$ efflux and current sapwood temperature, such as diel hysteresis. In *D. cupressinum*, the relationship between stem $CO_2$ efflux and temperature was not improved by using stem temperatures lagged up to six hours. However, it is possible that spatial heterogeneity of both temperature and sap flux density may contribute to variations in $R_S$, $F_T$, and $\Delta S$ with depth into the tree stem. Consideration of the radial variation in sap flux density may be particularly important for our study as our sap flux sensors only measured the outer 2 or 4 cm of sapwood and may have therefore overestimated sap flux density and resulting in underestimates of our assessments of both α and $F_T$. However, this error is likely to be small as both sap flux density (Phillips et al. 1996) and respiratory potential should decline with radial depth into trees.

Future research aimed at improving the understanding of diel and seasonal variation in the dissolved $CO_2$ of xylem sap and the potential for thermal acclimation of woody tissue respiration over short periods of time would greatly reduce potential sources of error in this study's model. Furthermore, future investigations aimed at linking the $CO_2$ diffusing from tree stems to the respiratory production of $CO_2$ within stems, xylem $CO_2$ transport, and internal storage of $CO_2$ should consider incorporating spatial heterogeneity in temperature and sap flux density by measuring both stem temperature and sap flux density at several radial depths.

*Effects of Respiratory Potential on Stem $CO_2$ Efflux*

$CO_2$ efflux from woody stems has been found to be related to tree growth rate (Edwards and Hanson 1996; Lavigne and Ryan 1997, Maier 2001) during the growing

season and tissue nitrogen concentration (Maier 2001; Vose and Ryan 2002) and sapwood volume (Ryan et al. 1995; Maier et al. 1998) during the dormant season. These previous findings led to our initial hypotheses that $CO_2$ efflux from stems should be determined by the local production of $CO_2$ by growth and/or maintenance respiration within stems. In this study, between-tree differences in the local production of $CO_2$ within *D. cupressinum* stems were also estimated by measuring the respiratory potential of excised wood tissues. However, no significant relationships were found between stem $CO_2$ efflux, or estimated rates of $R_S$, and tissue nitrogen concentration, the respiratory potentials from any specific wood tissues (*i.e.*, inner bark, outer and inner sapwood, sapwood-heartwood boundary) or the cumulative respiratory potential for the volume of wood under the $CO_2$ sampling chambers. Furthermore, for respiratory potential in inner bark and outer sapwood tissues from the stems, the temperature response parameters, $A_o$ and $Q_{10}$, were significantly different ($P < 0.05$, Table 1) from these parameter values for stem $CO_2$ efflux. The lack of agreement between respiratory potential and $CO_2$ efflux further suggests that $CO_2$ efflux from stem surfaces is not solely a function of the respiratory activity of the underlying wood. Possible factors that may contribute to this discrepancy between wood respiratory potential and stem $CO_2$ efflux, in addition to xylem transport and storage of $CO_2$, include between tree differences in the dissolved $CO_2$ concentration of xylem sap and differences in the permeability of bark to $CO_2$ diffusion.

*Vertical and Radial Trends in Respiratory Potential*

While wood respiratory potential did not explain between-tree variation in $CO_2$ efflux, the observed trends suggest that respiratory production of $CO_2$ varies predictably within trees. For example, both respiratory potential and wood nitrogen concentration were highest near the bark surface, in inner bark tissues, then declined significantly with depth towards the pith. This trend of declining respiratory potential has been observed in other tree species (Møller and Müller 1938; Goodwin and Goddard 1940; Shain and Mackay 1973; Pruyn et al. 2002a, 2002b, 2003) and is likely to be attributable to higher proportions of live cells in inner bark tissues compared to sapwood (Stockfors and Linder 1998).

Within-tree gradients in respiratory potential were also observed with stem position as respiratory potential for both inner bark and outer sapwood samples was found to be highest in the upper canopy. Similarly, high wood respiratory potentials have been observed in the upper portions of *P. ponderosa* and *P. menzeisii* stems (Pruyn et al. 2002, 2002b). Increased respiratory potentials in the canopy may be due to the close proximity of carbohydrate sources, increased respiration associated with transporting carbohydrates to and from storage locations in the xylem parenchyma (Sprugel 1990), and/or increased live cell volume. This trend towards high wood respiratory potential in the upper canopy is consistent with the high rates of $CO_2$ efflux measured in canopy branches in *D. cupressinum* and in other studies (Sprugel 1990; Damesin et al. 2002). However, significant interactions between sap flux and $CO_2$ efflux found in this study indicate that high rates of $CO_2$ efflux in this study from branches and upper stems are likely due to both the high respiratory potential of underlying wood and the diffusion of respiratory $CO_2$ transported in the transpiration stream to upper parts of the tree.

In contrast to respiratory potential, wood nitrogen concentration did not differ between stem positions. Furthermore, the overall variation in respiratory potential in excised core sections was described weakly by wood nitrogen concentration. The lack of strong agreement between respiratory potential and nitrogen concentration is inconsistent with previous reports of a strong relationship between maintenance respiration and tissue nitrogen concentration (Vose and Ryan 2002) and may be attributable to low nitrogen concentration in *D. cupressinum* wood relative to other tree species (Carey et al. 1997; Maier 2001), differences in stored carbohydrates within the wood cores, growth rate, and/or variation in tree age and size.

*Effects of Sapwood Density on Stem $CO_2$ Efflux*

Sapwood density was found to be strongly correlated to the parameter $E_o$ for $CO_2$ efflux in *D. cupressinum* stems. In light of the effects of xylem transport and $CO_2$ storage on $CO_2$ efflux, it is interesting that sapwood density proved to be the strongest predictor of stem $CO_2$ efflux as this structural trait has been found to regulate trade-offs between various physiological characteristics that determine tree hydraulic characteristics. For instance, decreased wood density is associated with increased hydraulic conductivity (Stratton et al. 2000); however, this also increased the occurrence of xylem cavitation (Hacke et al. 2001) and leaf turgor loss (Stratton et al. 2000).

Wood density may influence both xylem transport and storage $CO_2$ fluxes in woody stems. For example, wood density been found to be negatively correlated with wood saturated water content (Meinzer 2003). Furthermore, Barbour and Whitehead (2003) reported that sapwood density explained 94% of variation in average sap velocity

in *D. cupressinum* trees with exposed crowns. Most of the *D. cupressinum* trees included in our study were in sheltered canopy positions. While this relationship may not be valid in our study's trees, Barbour and Whitehead's (2003) findings highlight the importance of sapwood density to stem hydraulic function and provide a possible linkage between sapwood density and xylem transport of $CO_2$.

In addition, Roderick and Berry (2001) have predicted that, in coniferous trees, wood density will be negatively correlated with tracheid diameter. Variation in tracheid geometry associated with changes in wood density may potentially influence the rate of $CO_2$ diffusion into and out of xylem sap. For example, trees with high wood density may possess smaller diameter tracheids that exhibit greater surface area relative to the volume of xylem water in their lumen. This increased proportion of tracheid surface area available for diffusion may facilitate exchange of $CO_2$ between respiring tissues and xylem sap resulting in increased xylem transport of $CO_2$. In support of this, a weak correlation ($y = 48.7x + 3.8$, $r^2 = 0.15$) was found between the maximum proportion of $R_S$ attributable to $F_T$ and sapwood density. Further research on other tree species and growth environments is clearly necessary to determine the mechanism of this relationship between sapwood density and stem $CO_2$ efflux, as well as, the potential effects of sapwood density on xylem transport and $CO_2$ storage.

Between-tree variation in stem $CO_2$ efflux in *D. cupressinum* trees at Okarito Forest did not scale well with commonly used scalars such as stem surface area, sapwood volume, or nitrogen concentration. Similarly, other studies have reported difficulty in deriving scalars that work consistently across stands (Lavigne et al. 1996). This study demonstrates that xylem transport and storage of $CO_2$ and the hydraulic characteristics of

stems that determine these fluxes are equally important in predicting stem $CO_2$ efflux. Sapwood density may be linked to xylem transport and $CO_2$ storage, as well as, tree growth rates and conditions. For example, variation in sapwood density between conspecific trees may arise from differences in tree age and genotype (Panshin and de Zeeuw 1980), growth rate (Roderick 2000), climate (D'Arrigo et al. 1992; Briffa et al. 2004), atmospheric $CO_2$ concentration (Atwell et al. 2003; Kilpeläinen et al. 2003), and competition between neighboring trees (Larocque and Marshall 1995). Based on the observed linkage between stem $CO_2$ efflux and sapwood density and the potential for sapwood density to influence xylem transport and storage of $CO_2$, we propose that sapwood density may be useful in predicting between-tree differences in $CO_2$ efflux from woody tissues in conifers and that the efficacy of sapwood density as a scalar for $CO_2$ efflux from woody stems and branches should be investigated in other tree species and forest types.

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**Table 1.**

| | **Respiratory Potential** | | | | **Stem $CO_2$ Efflux** |
|---|---|---|---|---|---|
| | Inner Bark | | Outer Sapwood | | |
| | Lower Stem | Upper Canopy | Lower Stem | Upper Canopy | |
| $P_o$ (nmoles $O_2$ $g^{-1}$ $s^{-1}$) | 0.29 (0.02)[a] | 0.40 (0.02)[b] | 0.08 (0.01)[c] | 0.15 (0.02)[d] | |
| $A_o$ (kJ $mol^{-1}K^{-1}$) | 82.3 (15.4)[a] | 43.8 (10.1)[ab] | 79.4 (22.1)[a] | 41.4 (2.1)[ab] | 45.5 (1.8)[b] |
| $Q_{10}$ | 3.31 (0.63)[a] | 1.88 (0.25)[ab] | 3.33 (0.97)[a] | 1.79 (0.05)[ab] | 1.92 (0.05)[b] |

**Table 2.**

| Time (h) | Stem Temperature (ºC) | $CO_2$ Flux Densities | | | | Contribution to $R_S$ (%) | | |
|---|---|---|---|---|---|---|---|---|
| | | $R_S$ | $F_T$ | $\Delta S$ | $E_A$ | $F_T$ | $\Delta S$ | $E_A$ |
| | | *($\mu mol\ CO_2\ m^{-3}s^{-1}$)* | | | *($\mu mol\ CO_2\ m^{-2}s^{-1}$)* | | | |
| 00-04 | 16.7 | 32.2 (17.1, 60.9) | 0.4 (0.0, 1.8) | 0.3 (-0.9, 1.7) | 0.888 (0.57, 1.13) | 0.6 (0.0, 2.9) | 0.7 (-2.8, 5.8) | 99.2 (94.1, 102.8) |
| 04-08 | 16.6 | 31.4 (16.9, 59.5) | -0.5 (-3.0, 0.4) | -1.3 (-3.1, 0.3) | 0.897 (0.60, 1.12) | -0.5 (-5.1, 1.5) | -2.8 (-8.8, 0.0) | 99.4 (98.5, 103.6) |
| 08-12 | 17.7 | 35.2 (18.3, 65.5) | 3.0 (-1.6, 6.7) | -4.7 (-10.1, -1.4) | 0.940 (0.65, 1.24) | 11.1 (-2.4, 20.7) | -12.1 (-15.8, -1.7) | 98.1 (83.5, 102.4) |
| 12-16 | 19.8 | 43.0 (20.8, 81.9) | 9.7 (3.4, 16.7) | -1.7 (-4.8, 0.5) | 0.922 (0.62, 1.26) | 24.3 (12.6, 37.6) | -3.5 (-11.0, 1.4) | 78.4 (73.4, 85.0) |
| 16-20 | 20.8 | 48.1 (22.3, 89.0) | 10.6 (3.2, 13.4) | 5.9 (2.6, 12.0) | 0.913 (0.58, 1.24) | 18.9 (10.6, 31.0) | 11.6 (7.7, 16.2) | 70.0 (62.5, 74.0) |
| 20-00 | 19.2 | 41.3 (20.2, 76.0) | 3.0 (0.5, 11.5) | 6.2 (3.9, 9.4) | 0.915 (0.56, 1.23) | 5.1 (1.2, 15.2) | 15.8 (12.5, 18.4) | 81.3 (77.8, 84.8) |
| 24 h total *($mmol\ m^{-2}$)* | | - | - | - | 79.3 | 10.6 (5.8, 13.7) | 1.4 (-0.9, 3.8) | 88.1 (85.8, 91.2) |
| 24 h total *($mol\ m^{-3}$)* | | 3.33 | 0.38 | .07 | - | | | |

**Table and Figure Captions**

**Table 1.** Parameter values from fitted temperature-response curves for respiratory potential in inner bark and outer sapwood tissues and stem $CO_2$ efflux. Temperature-response curves for respiratory potential were calculated at two stem positions (lower stem and upper canopy), the temperature response of stem $CO_2$ efflux was only measured at the lower stem position. The temperature-response of both respiratory potential and stem $CO_2$ efflux was modeled using both a modified Arrhenius function and a $Q_{10}$ function. Values shown are means (± SE) where n = 3. Within each row, different letters adjacent to listed values indicate statistically significant differences at $P < 0.05$ according to paired t-tests.

**Table 2.** Average flux densities of stem respiration ($R_S$) and its component fluxes ($E_A$, $F_T$, $\Delta S$), the relative contribution of each component fluxes to $R_S$, and 24 h totals for $R_S$ and its component fluxes. Component fluxes of $R_S$ include stem $CO_2$ efflux ($E_A$), xylem transport ($F_T$), and $CO_2$ storage ($\Delta S$) as outlined in Equation 2. Values represent averages derived from measurements on five *D. cupressinum* trees sampled for two days. The minimum and maximum values observed across the five trees for each time interval are shown in parentheses. The average value for the parameter $\beta$ for these five trees was 36.6 ($m^2\ m^{-3}$).

**Fig. 1** The diel variation in stem $CO_2$ efflux and sapwood temperature for two trees (a) and the relationship between stem $CO_2$ efflux at night and sapwood temperature for five rimu trees (b). The fitted curves in (b) result from the modified Arrhenius equation described by Turnbull *et al*. (2003), see Equation 1. Modeled parameter values for $E_o$ (μmoles $CO_2\ m^{-2}s^{-1}$) and $A_o$ (kJ $mol^{-1}K^{-1}$), respectively, were 0.54 and 53.65 for Tree 5, $r^2 = 0.67$; 0.76 and 59.90 for Tree 12, $r^2 = 0.86$; 0.64 and 64.11 for Tree 18, $r^2 = 0.84$; 0.88 and 68.26 for Tree 38, $r^2 = 0.81$; 0.95 and 91.18 for Tree 39, $r^2 = 0.85$. All non-linear regressions were highly significant at $P < 0.0001$.

**Fig. 2** The daily pattern of sap flux density (solid line) and $R_S - E_A$ (closed circles) measured in one *D. cupressinum* tree over five days. $R_S - E_A$ was calculated as the difference between the measured rate of $CO_2$ efflux ($E_A \cdot \beta$) and the predicted rates of woody tissue respiration ($R_S$).

**Fig. 3** Variation in the difference between the predicted rate of $R_S$ and the measured rate of $E_A \cdot \beta$ ($R_S$ - $E_A$) as function of daily maximum sap flux density in five *D. cupressinum* trees over four days. Maximum sap flux density represents the average of measurements between hours of 1200 and 1600 on a single day. The solid lines represent least squares regressions. The $\beta$ parameter values ($m^2\ m^{-3}$) for the sampled trees are: Tree 5 = 28.2, Tree 12 = 69.4, Tree 18 = 33.6, Tree 38 = 28.2, Tree 39 = 23.7.

**Fig. 4** a) A theoretical representation of the xylem transport and $CO_2$ storage components of $R_S$ - $E_A$. Values of $R_S$ - $E_A$ greater than xylem transport, indicated by solid line, are associated with positive values of $\Delta S$ and storage of $CO_2$ in xylem sap. In contrast, values of $R_S$ - $E_A$ less than xylem transport are associated with negative values

of $\Delta S$ and release of $CO_2$ from xylem sap. Solid curved arrows represent the diel pattern of hysteresis observed in the relationship between $R_S$ - $E_A$ and sap flux density. b) Measurements of sap flux density and $R_S$ - $E_A$ for a single tree, Tree 38, over three days. Symbols represent measurements for different times of day. The solid line represents a least squares regression of the relationship between daily maximum sap flux density and $R_S$ - $E_A$, also shown in Fig. 3, for this tree.

**Fig. 5** The relationship between the wood density of outer sapwood and the rate of stem $CO_2$ efflux ($E_o$) normalized to 15 ºC in eight trees. The solid line represents a least squares regression: y = 2.55x + 0.48, $r^2 = 0.66$, $P < 0.05$.

**Fig. 6** a) The relationship between mean daily woody tissue respiration ($R_S$) and 1) mean daily xylem transport of $CO_2$ ($F_T$; closed circles) and 2) mean daily amount of $CO_2$ associated with both positive and negative storage ($\Delta S$; open circles) fluxes in five trees over five days. b) The relationship between wood volumetric water content and the cumulative amount of $CO_2$ associated with both positive and negative storage fluxes as a proportion of total woody tissue respiration ($\Delta S/R_S$) over the same time. The solid lines represent a least squares regressions. a) $F_T$, y = 0.139x - 0.070, $r^2 = 0.96$, $P < 0.01$; $\Delta S$, y = .122x - .088, $r^2 = 0.93$, $P < 0.01$ b) y = 16.14x + 0.49, $r^2 = 0.73$, $P = 0.05$. For both a) and b) error bars represent ± SE.

**Fig. 7** The observed trends in respiratory potential (nmol $O_2$ $g^{-1}$ $s^{-1}$) and wood nitrogen concentration (g $kg^{-1}$) with increasing radial depth from bark surface (mm). Open circles are mean respiratory potential and closed circles represent mean nitrogen content (± SE) where n=12. The four data points, moving from bark surface towards pith, for both respiratory potential and nitrogen content correspond to inner bark (IB), outer sapwood (OS), inner sapwood (IS), and sapwood-heartwood boundary (SH). Respiratory potential and nitrogen content values for inner bark are statistically different from remaining wood tissue types at $P < 0.05$ according to nonparametric Wilcoxon signed rank tests, as indicated by asterisk adjacent to inner bark data points.

**Fig. 8** Within-tree variation in respiratory potential for inner bark and outer sapwood sampled at four vertical stem positions. Respiratory potential (nmol $O_2$ $g^{-1}$ $s^{-1}$) is represented as a percentage of the maximum respiratory potential observed within a given tree. Values shown are means (± SE) where n = 3. Different letters adjacent to bars indicate statistically different values at $P < 0.05$ according to paired t-tests.

Figure 1.

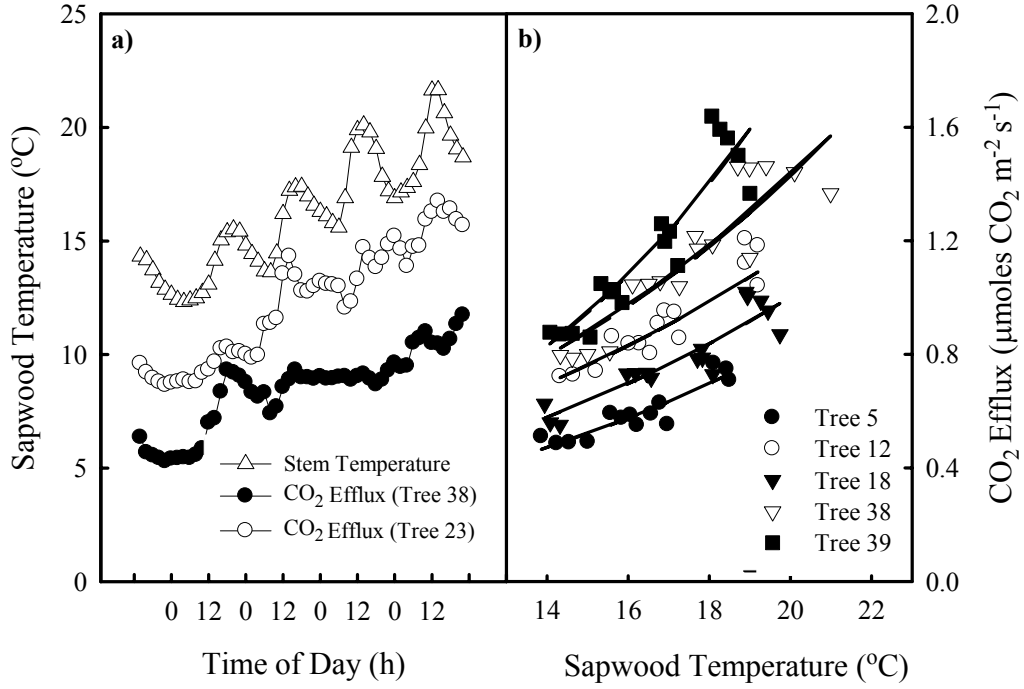

a)
b)
Sapwood Temperature (°C)
$CO_2$ Efflux (μmoles $CO_2$ $m^{-2}$ $s^{-1}$)
Stem Temperature
$CO_2$ Efflux (Tree 38)
$CO_2$ Efflux (Tree 23)
Tree 5
Tree 12
Tree 18
Tree 38
Tree 39
0 12 0 12 0 12 0 12
Time of Day (h)
14 16 18 20 22
Sapwood Temperature (°C)

Figure 2.

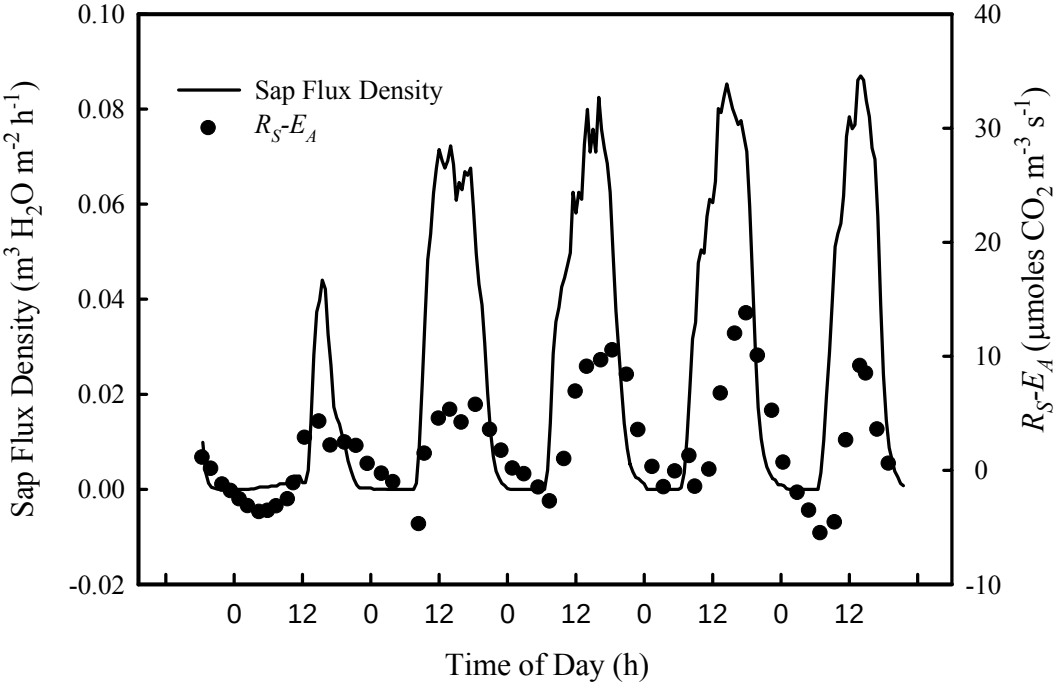

Sap Flux Density
$R_S$-$E_A$
Sap Flux Density ($m^3$ $H_2O$ $m^{-2}$ $h^{-1}$)
$R_S$-$E_A$ (μmoles $CO_2$ $m^{-3}$ $s^{-1}$)
0.10
0.08
0.06
0.04
0.02
0.00
-0.02
40
30
20
10
0
-10
0
12
0
12
0
12
0
12
0
12
Time of Day (h)

Figure 3.

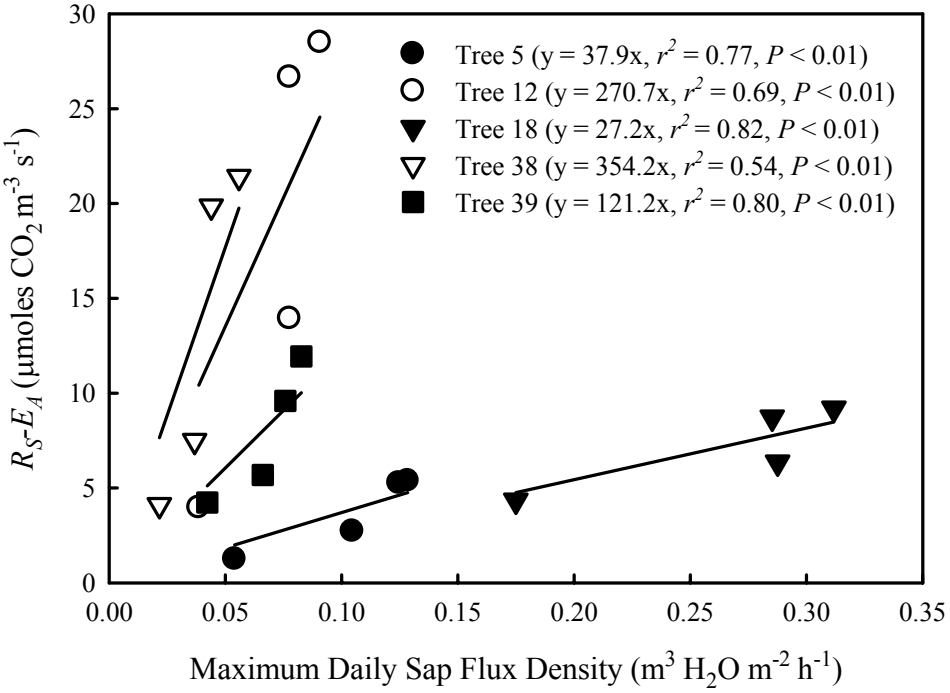

Tree 5 (y = 37.9x, $r^2$ = 0.77, $P$ < 0.01)
Tree 12 (y = 270.7x, $r^2$ = 0.69, $P$ < 0.01)
Tree 18 (y = 27.2x, $r^2$ = 0.82, $P$ < 0.01)
Tree 38 (y = 354.2x, $r^2$ = 0.54, $P$ < 0.01)
Tree 39 (y = 121.2x, $r^2$ = 0.80, $P$ < 0.01)
$R_S$-$E_A$ (µmoles $CO_2$ $m^{-3}$ $s^{-1}$)
Maximum Daily Sap Flux Density ($m^3$ $H_2O$ $m^{-2}$ $h^{-1}$)
0
5
10
15
20
25
30
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35

Figure 4.

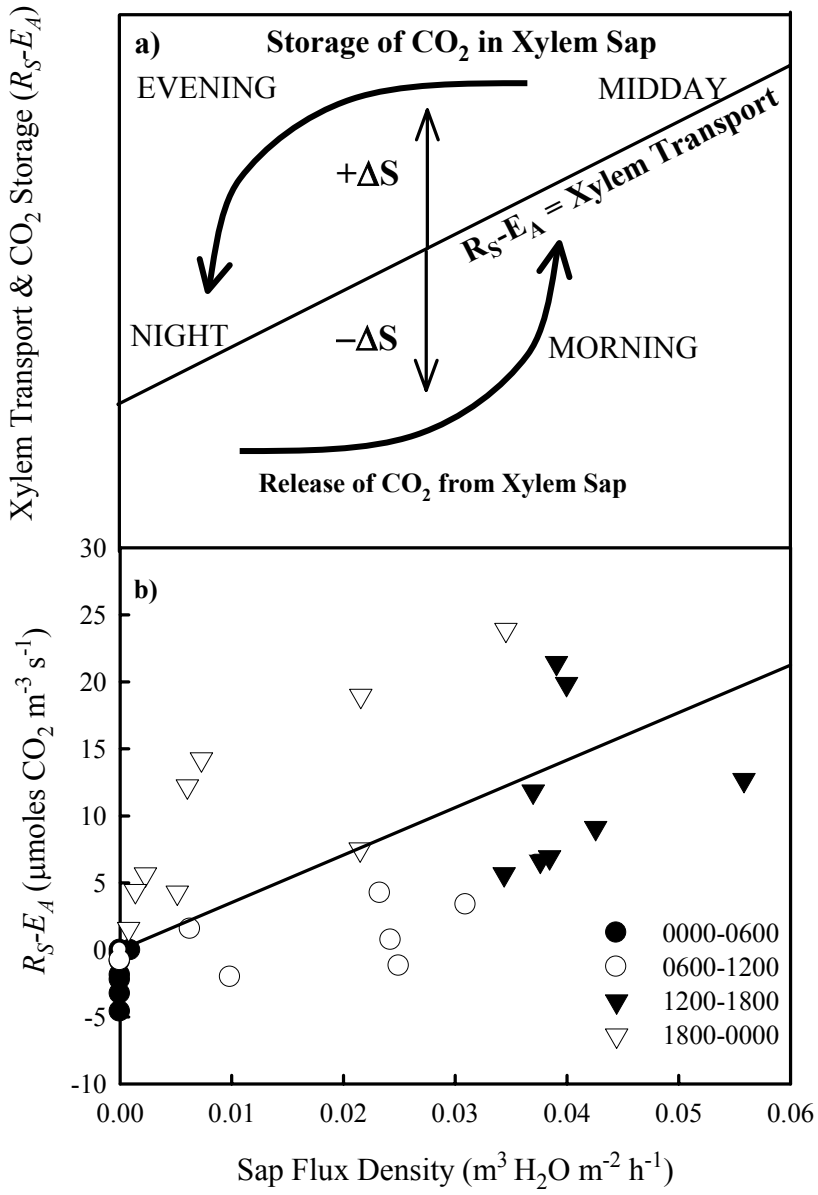

a)
Storage of CO2 in Xylem Sap
EVENING
MIDDAY
+ΔS
RS-EA = Xylem Transport
NIGHT
−ΔS
MORNING
Release of CO2 from Xylem Sap
Xylem Transport & CO2 Storage (RS-EA)
b)
RS-EA (μmoles CO2 m-3 s-1)
30
25
20
15
10
5
0
-5
-10
0.00
0.01
0.02
0.03
0.04
0.05
0.06
Sap Flux Density (m3 H2O m-2 h-1)
0000-0600
0600-1200
1200-1800
1800-0000

Figure 5.

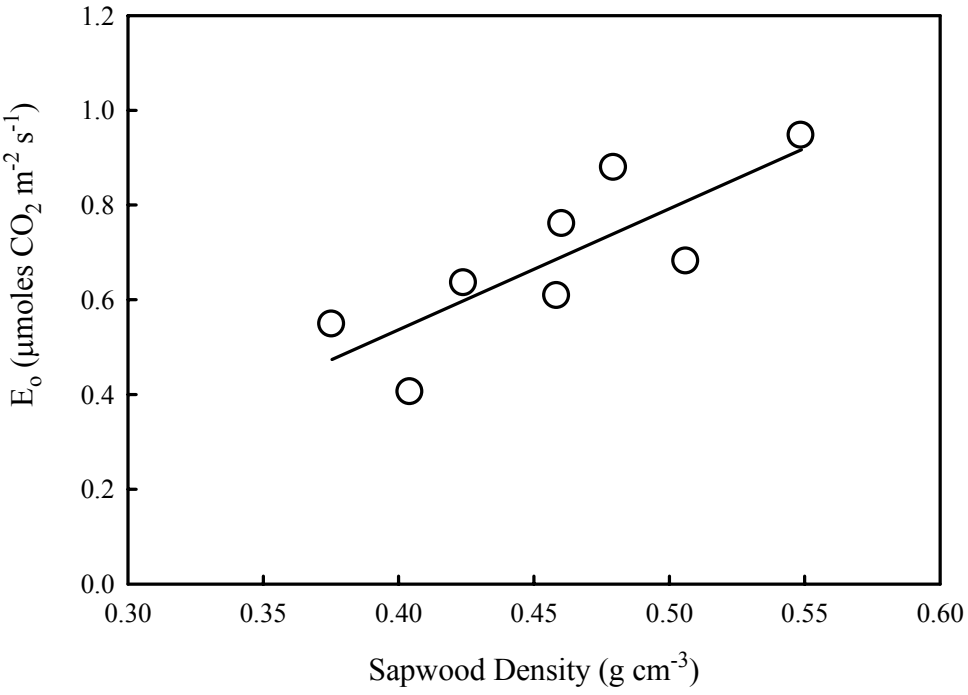



Figure 6.

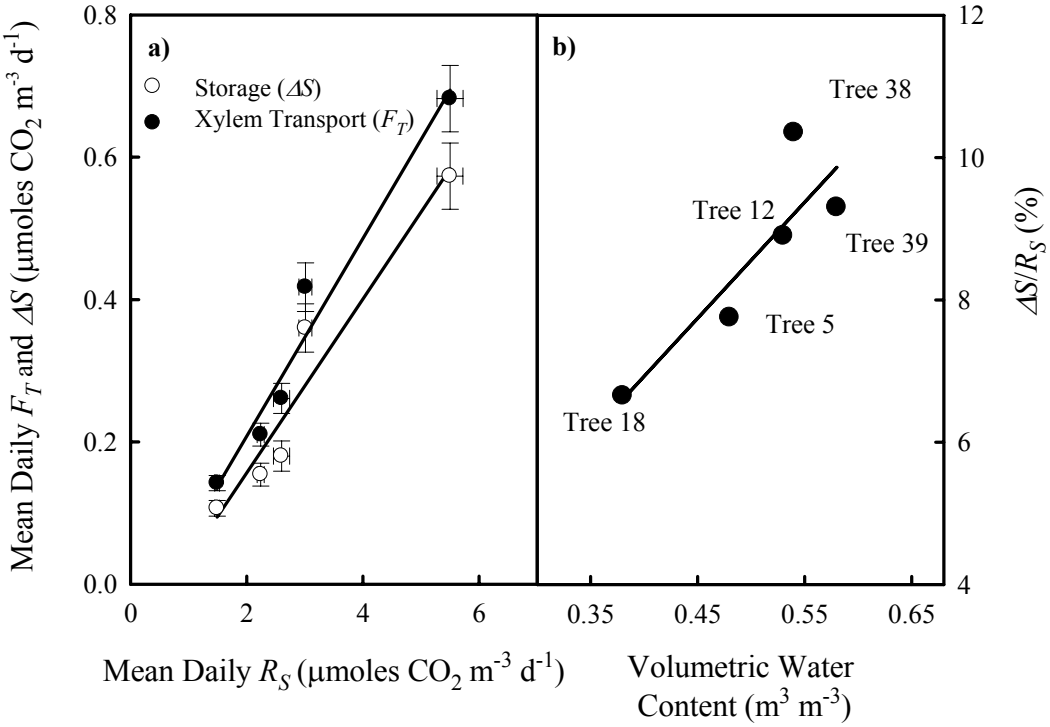

a)
b)
Storage ($\Delta S$)
Xylem Transport ($F_T$)
Tree 38
Tree 12
Tree 39
Tree 5
Tree 18
Mean Daily $F_T$ and $\Delta S$ (µmoles $CO_2$ $m^{-3}$ $d^{-1}$)
Mean Daily $R_S$ (µmoles $CO_2$ $m^{-3}$ $d^{-1}$)
Volumetric Water Content ($m^3$ $m^{-3}$)
$\Delta S/R_S$ (%)
0.0
0.2
0.4
0.6
0.8
0
2
4
6
0.35
0.45
0.55
0.65
4
6
8
10
12

Figure 7.

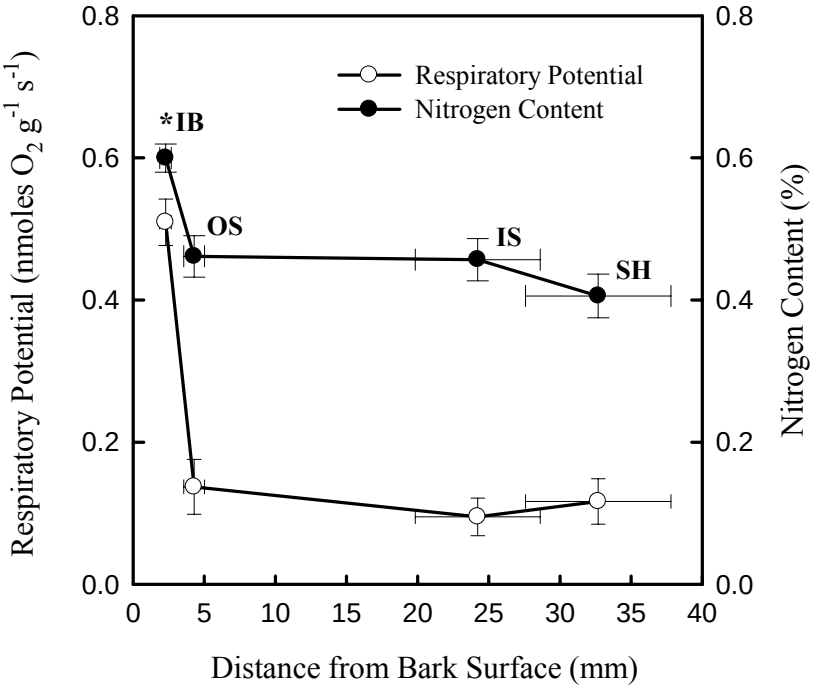
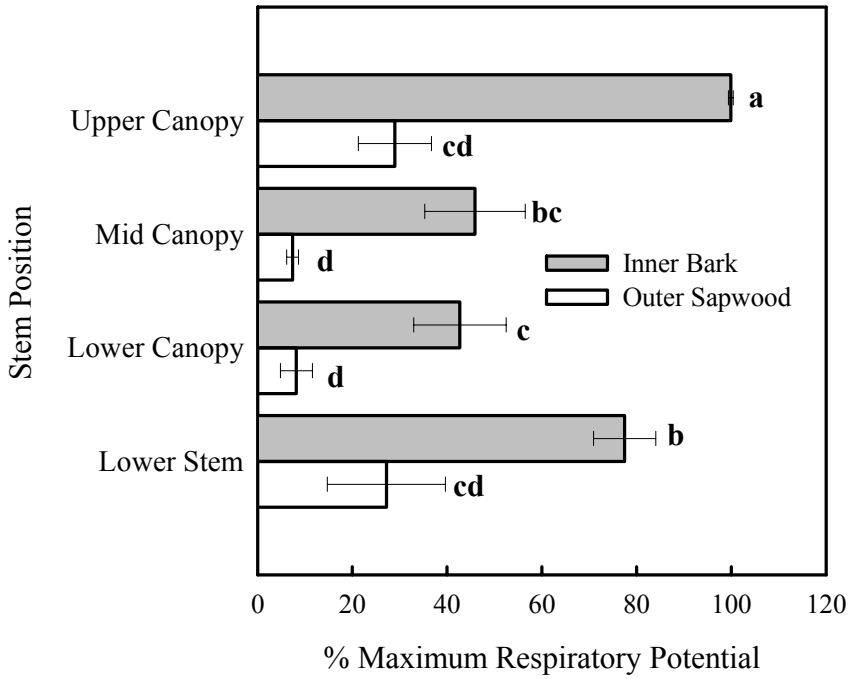



Figure 8.


Upper Canopy
Mid Canopy
Lower Canopy
Lower Stem
Stem Position
a
cd
bc
d
c
d
b
cd
Inner Bark
Outer Sapwood
0
20
40
60
80
100
120
% Maximum Respiratory Potential

# Chapter 4: The Contribution of Stem Respiration to the Carbon Balance of a Mature Lowland Podocarp-Broadleaf Rainforest in South Westland, New Zealand

WILLIAM P. BOWMAN, MATTHEW H. TURNBULL, DAVID T. TISSUE, DAVID WHITEHEAD, and KEVIN L. GRIFFIN

**Abstract**

Quantification of respiration in the woody stems of forest trees is important to understanding the productivity of forest ecosystems and contributes to our ability to predict carbon sequestration in forests. We measured stem $CO_2$ efflux and within-tree temperature gradients in mature *Dacrydium cupressinum* trees located in a lowland podocarp-angiosperm rainforest in South Westland, New Zealand. Stem respiration was found to account for an annual carbon flux to the atmosphere of 1.22-1.29 Mg C $ha^{-1}$ and consumed ~6-7% of this forest's gross primary productivity. Rates of respiration in the stems of *D. cupressinum* trees varied between 13.7–75.2 μmol $CO_2$ $m^{-3}$ (sapwood volume) $s^{-1}$ and 0.44-0.97 μmol $CO_2$ $m^{-2}$ (stem surface area) $s^{-1}$ at 15°C. Scaling measurements made at the tissue level to the entire stand was complicated by the lack of a constant relationship between stem respiration and stem surface area, sapwood volume, and/or tissue nitrogen concentration amongst trees. Although large within-stem gradients in sapwood temperature (up to 6 ºC) were observed in these *D. cupressinum* trees, they did not significantly influence the vertical distribution of stem respiration over periods longer than a few days and were not critical for deriving a stand-level estimate of stem respiration.

**Key Words:**

Stem Respiration, Sapwood Temperature, *Dacrydium cupressinum*, $CO_2$ Efflux**Abstract**

## Introduction

New Zealand's native forests contain 900-1000 Mt of carbon (Tate et al. 1997; Hall et al. 2001) in the biomass of living trees. Lowland podocarp-angiosperm forests comprise ~20% of both stored carbon and New Zealand's total forest area (Hall et al. 2001). These forests are characterized by large, emergent conifers (*Podocarpaceae*), predominantly rimu (*Dacrydium cupressinum*), with a dense, mixed understory (Ogden & Stewart 1995). Previous management of these lowland forests was primarily related to timber production (Franklin 1973; Six Dijkstra et al. 1985; James and Norton 2002), but recent interest in these forests has shifted towards conservation, biodiversity, and carbon sequestration. Monitoring of carbon storage in indigenous forests is currently required in the New Zealand Carbon Accounting System developed for maintaining compliance with the United Nations Framework Convention on Climate Change (UNFCCC) and the Kyoto Protocol (New Zealand Ministry of the Environment 2004).

The sequestration of carbon in the biomass of forest trees results from the small difference between photosynthetic carbon uptake, or gross primary production (GPP), and carbon loss through plant respiration. The remaining carbon, or net primary production (NPP), is then available for incorporation into existing biomass or construction of new foliage, stems, or roots. Consequently, the response of forest NPP or carbon storage to long-term changes in climate and atmospheric $CO_2$ concentration depends on the effects of these environmental perturbations on the rates of both GPP and plant respiration. For example, ecosystem respiration is critical to the regulation of forest productivity (Falge et al. 2002; Valentini et al. 1996) as plant respiration consumes ~50% of GPP (Farrar 1985; Amthor 1989; Ryan 1991). Furthermore, respiration in the woody

stems and branches is an important component of respiration in forest trees as it accounts for 7-42% of total plant respiration (Ryan et al. 1994; Ryan and Waring 1992; Waring and Schlesinger 1985) and typically consumes 5-15% of GPP (Meir and Grace 2002). Accordingly, forest stand-level estimates of woody tissue respiration are necessary to complete carbon budgets and estimate NPP in forest ecosystems.

Despite its importance to the carbon balance of forests, developing stand-level estimates of stem $CO_2$ efflux has been confounded by several issues. For example, there is little consensus on the best scalar for developing annual, stand-level estimates from short-term measurements of $CO_2$ efflux from woody stems and branches. Various bases have been used for scaling measurements of $CO_2$ efflux from stems to the stand level including stem surface area (Kinerson 1975; Linder and Troeng 1981; Lavigne 1988), sapwood volume (Ryan 1990; Sprugel 1990; Ryan et al. 1994; Ryan et al. 1995; Edwards and Hanson 1996; Will et al. 2001), and sapwood nitrogen content (Ryan 1991; Ryan et al. 1994; Maier 2001; Vose and Ryan 2001). To date, no scalar has been found to be consistently superior.

Another potential difficulty in developing stand-level estimates of stem $CO_2$ efflux is accounting for the effects of within-tree variation in temperature on the vertical distribution of respiration in forests. Respiration rates are strongly related to temperature (Amthor, 1989) and exponential temperature response functions are typically used to predict temporal variation in stem respiration. Due to differences in stem size and exposure to direct sunlight, stem temperatures vary considerably within trees. For example, Stockfors (2000) found that the mean temperature variation in a *Picea abies* tree was 3.7 °C during a 40 day measurement period and was >10 °C for over 8% of the

time. Therefore, within-tree temperature gradients may influence the vertical distribution of respiration within a tree stem and failure to account for this temperature variation may result in errors in stand-level estimates of stem $CO_2$ efflux. Lastly, respiratory $CO_2$ may dissolve in xylem sap and be transported vertically during transpiration leading to underestimates of stem respiration (McGuire and Teskey, 2004). For instance, previous research at this study site estimated that xylem transport of $CO_2$ significantly influenced stem $CO_2$ efflux during times of peak transpiration (13-38% of stem respiration), but over a 24 h period, 86- 90% of stem respiration was estimated to diffuse to the atmosphere (Bowman et al. 2005).

In this study, our primary objective was to develop a stand-level estimate of woody stem respiration in a mature lowland podocarp rainforest dominated by the conifer *Dacrydium cupressinum* in South Westland, New Zealand. We quantified the contribution of woody stem respiration efflux to the carbon budget in relation to GPP for the forest. Previous work on the carbon uptake in this forest found that net canopy carbon uptake was low at 11 kg C $m^{-2}$ $y^{-1}$ (Whitehead et al. 2002). Our stand-level estimate of stem respiration was based upon night-time measurements of stem $CO_2$ efflux to minimize the potential for errors caused by the transport of respiratory $CO_2$ in the transpiration stream (McGuire and Teskey 2004; Bowman et al. 2005). Our specific objectives were to 1) determine the most appropriate scalar (stem surface area, sapwood volume, or sapwood nitrogen concentration) for stem respiration in mature *D. cupressinum* trees, 2) measure the within-tree variation in sapwood temperature and estimate the effects of this variation on the distribution of stem respiration, and 3) use these findings to develop a stand-level estimate of stem respiration for this forest. We

hypothesize that tissue nitrogen concentration will be well correlated with $CO_2$ efflux from woody stems due to the low nitrogen availability of the study site (Whitehead et al. 2002), the observed correlation between leaf respiration and area-based nitrogen concentration in *D. cupressinum* at this site (Turnbull et al. 2003), and the strong influence of nitrogen availability on stem respiration (Maier et al. 1998; Stockfors and Linder 1998). We also hypothesize that the effects of within-tree variation in temperature on the distribution of stem $CO_2$ efflux will be large in Okarito Forest due to the relatively open nature of the forest canopy, with relatively low branch biomass causing large sections of upper stems to be exposed to direct sunlight during mid-day hours. Therefore, due to increased stem temperature in the sunlit canopy and the exponential response of respiration to temperature, we further hypothesized that stem $CO_2$ efflux in the upper canopy will contribute substantially to stand-level stem $CO_2$ efflux. The findings of this study will further our understanding of the physiological processes and environmental factors limiting carbon balance and productivity in lowland conifer-broadleaf forests so that accurate predictions can be made about the long-term effects of climate change on carbon storage in these extensive indigenous forests.

## Materials and Methods

### *Site Description*

The study site was situated within a native lowland forest located in Okarito Forest, Westland, New Zealand (43.2° S latitude, 170.3° E longitude, 50m above sea level) and featured a 25 m tall tower to access the forest canopy. The site is dominated by 200-400 year old rimu (*Dacrydium cupressinum* Lamb) trees with a mean canopy

height of 20m occupying 78% of the basal area (Walcroft et al. 2005). Other common tree species include kamahi (12% of basal area; *Weinmannia racemosa*), Westland quintinia (10% of basal area; *Quintinia acutifolia*), miro (*Podocarpus ferruginea*), and southern rata (*Metrosideros umbellate*).

Mean annual temperature is 11.3 ºC, with a small range between winter and summer of 8.6 ºC, and low air saturation deficit. Annual rainfall is high, approximately 3400 mm, and evenly distributed throughout the year. As a result, soils are frequently saturated, highly leached, and extremely acidic (pH 3.8-4.4 to a depth of 500 mm). The soil nitrogen concentration at an adjacent similar site was 633 μmol $g^{-1}$, soil-extractable phosphorus concentration was 12 μmol $g^{-1}$ (Richardson et al. 2004), and soils have a high organic matter content (approximately 30%), low permeability, and low porosity.

*Measurements of $CO_2$ Efflux in D. cupressinum Stems*

$CO_2$ efflux from stems was measured every 2.2 hours for seven days in January of 2002 in nine rimu stems (ranging in diameter from 0.18-0.67 m), as described in Bowman et al (2005). Only night-time measurements (from 0000-0600 NZST) were used in this study to eliminate the potential for measurement errors caused by the transport of respiratory $CO_2$ in the xylem stream during daylight hours (McGuire and Teskey, 2004; Bowman *et al.*, 2005). $CO_2$ efflux rates were determined with an infrared gas analyzer (Model LI-6262, LI-COR Inc., Lincoln, NE USA) installed in an open flow, manifold system with polycarbonate gas-exchange chambers attached to each stem at a height of ~1.3m above the ground. The flow of compressed air (43-47 Pa [$CO_2$ concentration]) to the chambers was maintained at 0.5 L $min^{-1}$ by a flow controller

(Model SR-10, Sierra Instruments, Monterrey, CA USA). The gas-exchange chambers were half-cylindrical, enclosed 250 $cm^2$ of stem surface, and were equipped with small 24V fans to ensure adequate mixing of air within the chamber. A gasket of closed-cell neoprene foam was fitted to the edges of the chambers to facilitate attachment to tree stems and caulking cord (Mortite, Inc., Kankakee, IL USA) was applied over fissures between the chambers and tree stems to create air-tight seals. The chambers were then secured tightly to the stems with ratchet straps. The sampling duration for each chamber was 12 minutes with all stems sampled once during each 132 minute measurement cycle which consisted of nine stem sampling periods and tests of the zero and span calibrations of the gas analyzer. Sapwood temperatures were measured using constantan-chromega thermocouples placed 15 mm beneath the bark surface and in close proximity to the sampling chamber.

The temperature response of stem $CO_2$ efflux ($E_A$) was determined using a modified Arrhenius function as adopted by Turnbull *et al.* (2003), where $CO_2$ efflux at a given sapwood temperature is described as:

Eqn. 1: $$E_A = E_{15} \cdot e^{\frac{A_o}{R_g}\left(\frac{1}{T_{15}} - \frac{1}{T_a}\right)}$$

where $E_o$ is the $CO_2$ efflux rate at the base temperature $T_o$ (here 15 ºC), $T_a$ is the stem sapwood temperature (K), $R_g$ is the gas constant (8.314 J $mol^{-1}$ $K^{-1}$), and $A_o$ is a parameter related to the energy of activation which describes the magnitude of the temperature response. Nonlinear curve fitting for temperature response curves was conducted with SigmaPlot 2001 (SPSS, Inc., Chicago, IL).

*Within-Tree Temperature Gradients and Effects on Woody Tissue Respiration*

Sapwood temperature was measured at four heights in three *D. cupressinum* trees in summer during the period January 17 to March 6, 2003. Measurement positions included the lower stem (at 1.3 m height), lower canopy (~1 m above the lowest canopy branch), mid canopy (~halfway between the lowest canopy branch and the tree apex), and upper canopy (~ 1-2 m from the tree apex). These three trees differed in diameter (0.18, 0.31, 0.63 m) and height (17.1, 24.1, 28 m), and thus, measurement positions along the stems differed in absolute height. Constantan-chromega thermocouples were inserted ~15 mm below the bark surface, at each measurement position, in small holes drilled in the stem and held in place with a small amount of caulking cord. Temperatures were measured every 30 min and recorded with a Campbell CR10 data logger and AM25T thermocouple multiplexer (Campbell Scientific, Logan, UT). Differences in daily maximum, daily minimum, and mean sapwood temperature between stem positions were assessed using a two-way mixed model analysis of variance (DataDesk 6.0) and considered statistically significant if probabilities ($P$) were < 0.05. The potential for within-tree gradients in temperature to determine the spatial distribution of stem $CO_2$ efflux was assessed by calculating rates of stem $CO_2$ efflux (μmol $CO_2$ $m^{-3}$ $s^{-1}$) and daily $CO_2$ fluxes per unit sapwood volume (μmol $CO_2$ $m^{-3}$ $d^{-1}$) for each stem section (lower stem, lower canopy, mid canopy, and upper canopy) in response to temperature with the assumption that $E_o$ and $A_o$ do not vary with stem height.

*Measuring Sapwood Volume and Nitrogen Concentration*

Sapwood thickness was measured to calculate the sapwood volume under each gas exchange chamber. Increment cores (5 mm in diameter) were extracted from each

tree at ~1.3 m and in proximity to the chamber. Sapwood and bark thickness were then identified visually by differences in wood color. The nitrogen concentration of the outermost 15 mm of sapwood was determined from dried and ground wood material using a CNS autoanalyzer (Carlo Erba NA 1500, Milan, Italy). Comparisons between temperature-normalized $CO_2$ efflux rates ($E_{15}$), sapwood volume, and sapwood nitrogen content were accomplished using general linear model procedures in Sigma Plot 2001 (SPSS, Inc., Chicago, IL).

*Variation in Stem Respiration With Stem Height and Season*

To account for variation in stem respiration with height, we used $E_{15}$ values specific to each stem section. Consistent with previous measurements of wood respiratory activity in these trees (Bowman et al. 2005), $E_{15}$ values for upper, mid, and lower canopy stem sections were assumed to be 129.1, 44.9, 40.8%, respectively, of the $E_{15}$ measured for lower stems. The parameter $A_o$ for stem respiration was assumed to be uniform with stem height and equal to the $A_o$ measured for lower stems, as $A_o$ of wood respiratory activity does not vary with stem height (Bowman et al. 2005). Using these assumptions of $E_{15}$ and $A_o$, daily stand-level $CO_2$ fluxes were calculated for each stem section incorporating the within-stem temperature variation measured in summer between January 17 to March 6, 2003.

Minimum rates of stem respiration at 15 °C ($E_{15}$) were assumed to occur during the coldest month of the austral winter (July) and were assumed to be 40% of those measured during January ($E_{15,MAX}$) consistent with the findings of Ryan et al. (1997), Law et al. (1999), and Maier (2001) where non-growing season rates were found to be 31.6-

55.5% of growing season rates. Monthly values of $E_{15}$ were then derived by assuming that seasonal changes in $E_{15}$ approximate the form of a sine curve, described in the following equation, in which the apex occurs in January ($E_{15,MAX}$) and the nadir occurs in July ($E_{15,MIN}$):

Eqn. 2: $$E_{15} = \left(E_{15,MIN} + a\right) + \left(a \times \sin\left(\frac{2\Pi x}{b} + c\right)\right)$$

in which $a$ is the amplitude of the curve and is equal to $\left(0.5 \times \left(E_{15,MAX} - E_{15,MIN}\right)\right)$, $b$ is the period of the curve and is equal to 365 days, $c$ is a parameter related to the phase shift of the curve and is equal to 1.3, and $x$ is the Julian day. This model was employed to account for the commonly observed acclimation of respiration to seasonal changes in ambient temperature (Atkin and Tjoelker, 2003). Seasonal variations in $A_o$ were assumed to be negligible (as has been found in Lavigne 1996, Carey et al. 1997, Stockfors and Linder 1998; but not in Maier 2001, Damesin et al. 2002) and equal to the value of $A_o$ derived from the response of stem $CO_2$ efflux to sapwood temperature in January.

*Estimating Stem Volume and Stem Surface Area at the Stand-Level*

In order to estimate the stem volume and surface area of the study site's *D. cupressinum* trees, a stem taper function was derived to estimate stem diameter at any tree height. A third-degree polynomial was used to describe stem taper:

Eqn. 3: $$d = b_0 + b_1h^1 + b_2h^2 + b_3h^3$$

Where $d$ is the relative diameter (the ratio of the diameter at a given point to the diameter at 1.3m), $h$ is the relative height (the ratio of the height at a given point to the tree's maximum height), and $b_0$ through $b_3$ are polynomial parameters. In this study, stem diameter was measured in three trees at the four positions used for assessing within-stem

temperature gradients. Derivation of polynomial parameters and fit statistics from diameter and height measurements was conducted using nonlinear-curve fitting procedures in Sigma Plot 2001. Using this third-degree polynomial and an inventory of the diameter and height of each tree in the study plot (W.S.F. Schuster, unpublished data), estimates of stem diameter were made for all *D. cupressinum* trees at 0.5 m intervals from the ground to the stem apex. Each 0.5 m stem section was assumed to approximate the shape of the frustrum of a circular cone. The volume and surface area of each stem section were calculated and then summed to produce estimates of stem volume and surface area for each tree and for the entire stand.

*Estimating Sapwood Volume at the Stand-Level*

Sapwood ($S_T$) and bark ($B_T$) thickness were measured in twelve *D. cupressinum* trees ranging in diameter from 0.11-0.67 m at 1.3 m above ground level ($D_B$). Both $S_T$ and $B_T$ were assumed to remain constant with height along stems and equal to $S_T$ or $B_T$ at $D_B$. The relationship between sapwood and bark thickness to stem diameter was assessed with the following model where $y$ is $S_T$ or $B_T$, and then used to predict $S_T$ and $B_T$ for all *D. cupressinum* trees at this study site (Sigma Plot 2001).

Eqn. 4: $$y = \beta_0 + (\beta_1 \cdot \ln D_B\ )$$

Wood thickness ($W_T$) and heartwood thickness ($H_T$) were derived for both ends of each 0.5 m stem section by subtracting $2(B_T)$ or $2(B_T + S_T)$, respectively, from the stem diameter estimated from the taper equation. Volumes of both wood ($W_V$), heartwood ($H_V$), and sapwood ($S_V$) were then calculated geometrically. Sapwood volumes ($S_V$) of

each stem section were summed to produce estimates of sapwood volume for each tree and for the entire stand.

*Estimating Stem Respiration at the Stand-Level*

Annual stem respiration was estimated using the monthly estimates of $E_{15}$, stand-level estimates of sapwood volume ($S_V$) and stem area ($S_A$) for four stem segments (lower stem, lower canopy, mid canopy, and upper canopy), and hourly stem temperature for each segment. Estimates were made on both sapwood volume and surface area bases for each stem segment and for the entire stand. The annual stand-level $CO_2$ flux attributable to woody stem respiration was estimated as proportions of the annual net canopy carbon uptake and GPP for the site.

**Results and Discussion**

*Sapwood and Bark Thickness, Stem Taper, and Stem Volume*

The relationships between sapwood ($S_T$) and bark ($B_T$) thickness and stem diameter ($D_B$) were well described by Eqn. 4 as it yielded both significant parameters ($P < 0.01$) and overall model fits ($P < 0.05$). The $R^2$ values for the relationships between stem diameter and sapwood thickness and bark thickness were 0.33 and 0.74, respectively (Fig. 1). Some large outliers from the relationship between sapwood thickness and stem diameter were observed as some large trees were found to have very narrow bands of sapwood around the outside of the stem. Both relationships were curvilinear as sapwood and bark thickness increased rapidly with stem diameter but the rate of increase declined at high stem diameters. The relationship between sapwood

thickness and stem diameter has also been found to be curvilinear in several species of northwest conifers (Pruyn et al, 2003), but was linear in *Liriodendron tulipifera* (Wullschleger & King, 2000); while no relationship was found in *Pinus banksania*, *Larix laricina*, and *Pinus contorta* (Yang *et al*., 1985; Yang & Murchison, 1992).

The stem taper of the three sampled *D. cupressinum* trees was well described ($R^2$ = 0.97, $P < 0.0001$) by the following fifth degree polynomial model shown in Eqn. 5 and Fig. 2:

Eqn. 5: $$d = -2.05h^3 + 2.61h^2 - 1.69h + 1.16$$

where $d$ is the relative diameter calculated as the ratio of the diameter at a given height to the diameter at 1.3m and $h$ is the relative height calculated as the ratio of the height at a given point to the tree's maximum height. All model parameters were highly significant ($P \leq 0.005$). Although this model is simplistic, it accurately reflects the common assumption that the form of tree stems approximates that of three linked geometric solids with the lower bole assumed to be a neiloid frustrum, the middle bole a parabolic frustrum, and the upper bole a cone (Avery and Burkhart 2002).

This stem taper equation and relationships between sapwood and bark thickness and stem diameter were utilized, together with the diameter and height inventory of all *D. cupressinum* trees in the study plot (W.S.F. Schuster, unpublished data), to estimate the area and volume of the stems at the stand level. Stand-level stem volume (outside bark), sapwood volume, and stem surface area were determined to be 616.8 $m^3 ha^{-1}$, 194.4 $m^3 ha^{-1}$, and 7245.4 $m^2 ha^{-1}$, respectively. The stand-level stem volume predicted by this study was in close agreement with an estimate of the stem volume at this site of 543.4 $m^3 ha^{-1}$ derived using an allometric equation for rimu trees in Westland, New Zealand (Ellis,

1979). A strong vertical distribution of sapwood volume exists as 56.5 ± 3.7 % of tree-level totals are found below the lower canopy in the three sampled rimu trees while only 18.6 ± 1.6 % of sapwood is found in the mid canopy or above (Table 1). Similar vertical distributions of stand-level stem volume and stem surface area were observed (*data not shown*).

*Stem Respiration Rates and Selection of Scalar*

Despite the low rates of annual wood production and canopy carbon uptake observed in this *D. cupressinum* forest (Whitehead et al. 2002), the rates of stem respiration ($E_o$) from *D. cupressinum* stems (0.44- 0.97 μmol $CO_2$ $m^{-2}$ $s^{-1}$ or 13.7 – 75.2 μmol $CO_2$ $m^{-3}$ $s^{-1}$ at 15°C) were broadly similar to those reported for other conifer species and ecosystems. For example, stem respiration (at 15°C) was 0.2-1.0 μmol $CO_2$ $m^{-2}$ $s^{-1}$ across eight boreal forests stands (Ryan et al. 1997) and 13-55 μmol $CO_2$ $m^{-3}$ $s^{-1}$ in a temperate *Pinus strobus* stand (Vose and Ryan 2002). The wide variation in $CO_2$ efflux observed between *D. cupressinum* trees was not related to stem surface area (surface area-based $E_{15}$ varied by more than 200% despite uniform stem area enclosed within chambers), sapwood nitrogen content (Fig. 3a), and sapwood volume (Fig. 3b).

The lack of a strong, scalable relationship between $E_{15}$ and stem surface area and sapwood volume is likely to be caused by between tree differences in the distribution of living parenchyma cells within the large volumes of dead cells in stem tissues. For example, live cell volume is ~25-70% in phloem tissues (Stockfors and Linder 1998; Damesin et al. 2002) and 2-30% in sapwood tissues (Panshin and de Zeeuw 1980; Stockfors and Linder 1998; Ryan 1990). Furthermore, respiratory activity is highest in

the inner bark (composed of phloem and cambial tissues) and declines with increasing depth into the stem (Pruyn et al. 2002). Due to low proportions of live cells in these woody tissues and the differences in live cell volumes and respiratory activity between phloem and sapwood tissues, it is difficult to find a single measure of the living biomass in wood that is correlated to respiration at the tissue-, tree-, and stand-level.

The lack of a relationship between sapwood nitrogen content and stem respiration is in contrast with many previous studies (Maier 2001; Ryan et al. 1994; Vose and Ryan 2001) and with the observation that foliar respiration is related to foliar nitrogen concentration in these *D. cupressinum* trees (Turnbull et al. 2003). However, the relationship between respiration and nitrogen does occasionally fail in both leaves and stems (Cropper and Gholz 1991; Byrd et al. 1992; Lavigne and Ryan 1997; Stockfors and Linder 1998). In this study, the lack of a relationship between respiration and nitrogen may be due to the limited number of trees and small range of nitrogen concentration in the sampled wood (0.34 – 0.55%). For example, Maier (2001) and Vose and Ryan (2002) reported a relationship between stem respiration and sapwood nitrogen across a 5-7 fold difference in nitrogen concentration between trees and a weak relationship was found in *D. cupressinum* between the respiratory activity of extracted wood cores and nitrogen concentration when the nitrogen concentration varied from 0.26-0.84 % (Bowman et al. 2005).

Due to the lack of a robust linear relationship between $E_{15}$ and stem surface area, sapwood volume, or tissue nitrogen content, average values for $E_{15}$, on both an area and volume basis to scale-up to the stand level. Average values for $E_{15}$ (± SE) for the eight sampled *D. cupressinum* trees are (0.72 ± 0.02 μmol $CO_2$ $m^{-2}$ $s^{-1}$ and 29.3 ± 2.4 μmol

$CO_2$ $m^{-3}$ $s^{-1}$) on a stem surface area and sapwood volume basis, respectively. These values were assumed to represent maximum annual rates of stem respiration ($E_{15, MAX}$) and were used to calculate $E_{15,MIN}$ and other monthly values (shown in Table 2) from the sine model in Eqn. 2. These estimated values were selected to be consistent with other studies that measured seasonal variation in stem respiration in forest trees. For example, Maier (2001) found that rates of stem respiration in *Pinus taeda* during the non-growing season (November-February) were 32.2% of peak rates during the growing season (observed in April). In *Picea mariana* (Ryan et al, 1997) and *Pinus ponderosa* (Law et al., 1999) stem respiration during the non-growing season were found to be approximately 32 and 56%, respectively, of peak growing season rates.

*Within-Tree Variation in Sapwood Temperature and Stem Respiration*

Large within-tree gradients in sapwood temperature were observed in the sampled *D. cupressinum* trees (Fig. 4). During the day, upper regions of the trees exhibited significantly greater maximum sapwood temperatures, between 11.6 ± 0.06 and 43.7 ± 0.51% (1.6 – 6.0 ºC), than the lower stems due to greater absorption of solar radiation (Two-Way ANOVA, $P < 0.05$, Table 3). At night, the temperature gradient was reversed with upper canopy temperatures between 10.7 ± 0.16 and 21.5 ± 0.29% less (0.9 - 1.7 ºC) than lower stem positions due to greater radiative cooling in the canopy and absorption of long-wave radiation from soil by the lower stems. Therefore, the higher sapwood temperatures observed in the canopy during the day were offset by lower temperatures at night, such that there was either no or small (less than 1°C) gradients in average daily sapwood temperature between the lower stems and canopy positions (Table 3). This is

consistent with the findings of Yanez-Espinosa et al. (2003) that high daytime temperatures in the canopy are balanced by lower temperatures at night resulting in only a small (~1 ºC) enhancement of canopy temperature over several days.

Due solely to within-tree variation in temperature, upper canopy positions are predicted to exhibit 20-40% (31.23 ± 0.004% on average) increases in respiration rate relative to lower stem positions during the day and 5-20% (10.12 ± 0.001% on average) decreases in respiration during the night (Figure 5a). Yet over the seven week period in which within-tree temperature gradients were measured, average daily $CO_2$ flux per unit sapwood was estimated to be only 5.87 ± 0.14, 5.65 ± 0.12, and 2.33 ± 0.06 % greater in the upper, mid, and lower canopy, respectively, relative to the lower stem (Fig. 5b). Additionally, the daily $CO_2$ flux at the stand level attributable to respiration in the lower stem segments of *D. cupressinum* trees greatly exceeds that from the upper, mid, and lower canopy segments (Fig. 5c) due to the vertical distribution of stem biomass (Table 1). Therefore, although large within-tree temperature gradients are likely to be common in forest stands, these gradients are not likely to be important for deriving stand-level estimates of stem respiration due to 1) the opposing effects of day-time warming and night-time cooling on respiration in the forest canopy and 2) the small fraction of the respiring woody biomass located in the canopy.

Stockfors (2000) concluded that within-tree variations in sapwood temperature may significantly affect the accuracy of scaled-up estimates of stem respiration for trees and whole stands. Our findings indicate that inclusion of within-stem temperature variation will likely result in only small improvements in the accuracy of tree- or stand-level estimates of stem respiration, particularly for time periods longer than a few days.

Interestingly, within-canopy variation in temperature is also not of great importance when scaling certain leaf physiological processes to the canopy level. Despite the importance of leaf temperature in regulating enzymatic rates of carboxylation, electron transport and respiration, studies have reported good results in modeling canopy carbon exchange using "big-leaf" models that ignore vertical gradients in leaf physiological parameters and microclimatic characteristics within canopies (Amthor, 1994; Lloyd *et al.*, 1995). Furthermore, incorporation of canopy gradients in temperature and other micrometerological characteristics had little (<3%) influence on modeled net canopy carbon uptake in a temperate deciduous forest (Baldocchi & Wilson, 2001).

The lowland podocarp-angiosperm forest investigated in this study has a relatively low leaf area index (LAI) of 3.5 $m^2/m^2$ (Walcroft et al. 2005) and, consequently, high exposure of stems, at all heights, to direct sunlight. Within-tree differences in temperature may be greater in forest stands with more closed canopies and higher LAI values where upper stems and branches may be exposed to the sun but lower stems receive little direct sunlight. As result, the conclusions of this study should be extended cautiously to forest stands that differ greatly in LAI or canopy structure.

*Annual Stand-level Estimate of Stem Respiration*

Having derived the sapwood volume ($S_V$) and stem area ($S_A$) for the four stem segments (lower stem, lower canopy, mid canopy, and upper canopy) and the hourly stem temperature for each segment, the monthly estimates of $E_o$ (Table 2) were used to assess the amount of carbon released by stem respiration at the stand-level (Fig. 6). We estimate that respiration from *D. cupressinum* stems accounts for 1.22-1.29 Mg C $ha^{-1}$ $yr^{-}$

$^{1}$ in this lowland podocarp-angiosperm forest. Surface area-based estimates of stem respiration were slightly higher (~6 %) than sapwood-volume based estimates. The magnitude of this estimate of stand-level stem respiration for this forest is broadly consistent with stand-level estimates from a wide range of other tree species and forest types. Our estimates are higher than those for a *Pinus ponderosa* stand (0.54 Mg C $ha^{-1}$ $yr^{-1}$, Law et al. 1999) and eight boreal forest stands (0.22-1.23 Mg C $ha^{-1}$ $yr^{-1}$; Ryan et al. 1997). Annual stand-level stem respiration in this podocarp-angiosperm forest is comparable to that from an *Acer-Quercus* forest (1.49-2.04 Mg C $ha^{-1}$ $yr^{-1}$, Edwards and Hanson 1996) but lower than those for European beech forests (3.25-3.83 Mg C $ha^{-1}$ $yr^{-1}$, Damesin et al. 2002; 5.44 Mg C $ha^{-1}$ $yr^{-1}$, Valentini et al. 1996) and many tropical forests (2.20-3.50 Mg C $ha^{-1}$ $yr^{-1}$, Ryan et al. 1994b; 4.00 Mg C $ha^{-1}$ $yr^{-1}$, Malhi et al. 1999).

These stand-level estimates show that annual stem respiration fluxes range widely depending on species, climate, and stand age. However, Meir and Grace (2002) have reported that stand-level woody tissue respiration is curvilinearly related to stand LAI. According to a model derived in Meir and Grace (2002), the Okarito lowland podocarp-broadleaf forest (LAI = 3.5 $m^2/m^2$) is predicted to have a stand-level woody tissue respiration flux of 1.44 Mg C $ha^{-1}$ $yr^{-1}$ (close to the estimate derived in this study). Meir and Grace (2002) have also determined that the proportion of GPP consumed by aboveground woody tissue respiration is linearly related to stand LAI such that in the Okarito Forest, woody tissue respiration is expected to account for 9.1% of GPP. A process-based model of canopy carbon uptake has been employed at this field site and it has been determined that canopy GPP, during the same May 2001-April 2002 measurement period, was 18 kg C $m^{-2}$ $y^{-1}$ (Whitehead et al. 2002). Stem respiration in

this podocarp-angiosperm forest therefore accounts for 6.7-7.2% of forest GPP at this site and is close to the proportion of GPP predicted by the formula of Meir and Grace (2002).

In conclusion, our study has confirmed that stem respiration is an important component of the carbon balance of temperature forests. In addition, our results indicate that, while we still have much to learn about scaling $CO_2$ efflux measurements to the tree- and stand-level, accounting for within-tree gradients in sapwood temperature is not necessary for developing accurate estimates of stem respiration at the forest stand-level.

**Acknowledgements**

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**Table 1:** Sapwood volumes of four stem segments at the stand level and the proportion of the total stand level sapwood volume comprised by each stem segment.

| Stem Position | Sapwood Volume ($m^3$ $ha^{-1}$) | Proportion of Stand Total (%) |
|---|---|---|
| *Base to Lower Canopy* | 109.8 | 56.5 |
| *Lower to Mid Canopy* | 49.1 | 25.3 |
| *Mid to Upper Canopy* | 27.8 | 14.3 |
| *Upper Canopy to Apex* | 7.5 | 3.9 |
| **Total** | 194.2 | |

**Table 2:** Estimated monthly values of $E_o$ on stem surface area and sapwood volume bases derived from January values ($E_{o,Max}$) of 0.72 μmol $CO_2$ $m^{-2}$ $s^{-1}$ and 29.3 μmol $CO_2$ $m^{-3}$ $s^{-1}$, respectively. Air temperatures represent monthly averages from May 2001 through April 2002.

| | **% of $E_{o,Max}$** | **$E_o$** $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ | **$E_o$** $\mu mol\ CO_2\ m^{-3} s^{-1}$ | **Air Temperature** °C |
|---|---|---|---|---|
| **May** | 0.54 | 0.40 | 16.1 | 10.94 |
| **June** | 0.44 | 0.32 | 12.9 | 8.68 |
| **July** | 0.40 | 0.29 | 11.7 | 6.96 |
| **August** | 0.44 | 0.32 | 12.9 | 8.99 |
| **September** | 0.54 | 0.39 | 15.8 | 11.06 |
| **October** | 0.70 | 0.50 | 20.5 | 13.24 |
| **November** | 0.85 | 0.61 | 24.9 | 13.38 |
| **December** | 0.96 | 0.69 | 28.1 | 15.96 |
| **January** | 1.00 | 0.72 | 29.3 | 17.77 |
| **February** | 0.96 | 0.69 | 28.1 | 16.73 |
| **March** | 0.85 | 0.61 | 24.9 | 13.98 |
| **April** | 0.70 | 0.50 | 20.5 | 12.80 |

**Table 3:** Daily average, maximum, and minimum sapwood temperatures (± SE) for three *D. cupressinum* trees at four stem positions from January 17 through March 5, 2003. Within each stem position and column, means sharing a common letter do not differ significantly at $P < 0.05$ according to a two-way, mixed model analysis of variance.

| | Daily Average Sapwood Temperature (ºC) | Daily Maximum Sapwood Temperature (ºC) | Daily Minimum Sapwood Temperature (ºC) |
|---|---|---|---|
| **Tree 5** | | | |
| *Upper Canopy* | 14.6 (± 0.31)$^{a}$ | 21.0 (± 0.09)$^{a}$ | 10.9 (± 0.06)$^{a}$ |
| *Mid Canopy* | 14.9 (± 0.30)$^{b}$ | 20.3 (± 0.09)$^{b}$ | 11.9 (± 0.05)$^{b}$ |
| *Lower Canopy* | 14.1 (± 0.24)$^{c}$ | 16.3 (± 0.05)$^{c}$ | 11.8 (± 0.05)$^{b}$ |
| *Lower Stem* | 13.5 (± 0.16)$^{d}$ | 15.0 (± 0.04)$^{d}$ | 11.8 (± 0.05)$^{b}$ |
| **Tree 18** | | | |
| *Upper Canopy* | 13.6 (± 0.25)$^{a}$ | 17.0 (± 0.06)$^{a}$ | 10.3 (± 0.31)$^{a}$ |
| *Mid Canopy* | 13.7 (± 0.25)$^{bc}$ | 16.4 (± 0.06)$^{b}$ | 11.3 (± 0.31)$^{b}$ |
| *Lower Canopy* | 13.8 (± 0.24)$^{b}$ | 15.8 (± 0.05)$^{c}$ | 11.9 (± 0.31)$^{c}$ |
| *Lower Stem* | 13.6 (± 0.21)$^{ac}$ | 15.4 (± 0.04)$^{d}$ | 11.7 (± 0.31)$^{d}$ |
| **Tree 30** | | | |
| *Upper Canopy* | 13.9 (± 0.30)$^{a}$ | 19.9 (± 0.06)$^{a}$ | 9.4 (± 0.31)$^{a}$ |
| *Mid Canopy* | 13.8 (± 0.27)$^{b}$ | 17.8 (± 0.06)$^{b}$ | 9.9 (± 0.31)$^{b}$ |
| *Lower Canopy* | 13.7 (± 0.25)$^{b}$ | 16.9 (± 0.06)$^{c}$ | 10.5 (± 0.31)$^{c}$ |
| *Lower Stem* | 13.8 (± 0.32)$^{ab}$ | 16.5 (± 0.05)$^{d}$ | 11.1 (± 0.31)$^{d}$ |

**Figure Captions**

**Fig. 1** The relationship of sapwood thickness ($S_T$, mm) and bark thickness ($B_T$, mm) to stem diameter ($D_B$, m) for *D. cupressinum* trees. The fitted curves result from the logarithmic model described in Equation 3. Modeled parameter values for $\beta_0$ and $\beta_1$ were 45.39 and 14.82, respectively, for sapwood thickness ($r^2 = 0.33$, $P = 0.01$) and 9.19 and 3.52 for bark thickness ($r^2 = 0.74$, $P = 0.0007$).

**Fig 2.** Measured stem taper curve derived from diameter and height measurements from three *D. cupressinum* trees. The solid line represents a third degree polynomial shown in Eqn. 6 ($r^2 = 0.97$, $P = 0.0001$).

**Fig. 3** a) The relationship between nitrogen concentration of outer sapwood and rate of stem respiration ($E_o$) normalized to 15º C in eight *D. cupressinum* trees. The solid line represents a least squares regression: $y = 1.40x + 0.08$ , $r^2 = 0.28$, $P = 0.17$. b) The relationship between the sapwood volume under the measurement chamber and rate of stem respiration ($E_o$) normalized to 15º C in eight *D. cupressinum* trees. The solid line represents a least squares regression: $y = 0.14x + .72$, $r^2 = 0.0004$, $P = 0.96$.

**Fig. 4** Diel variation in sapwood temperature at four stem heights (lower stem, lower canopy, mid canopy, and upper canopy) in a single *D. cupressinum* tree from February 14-16, 2003.

**Fig. 5** a) Diel variation in the ratio of the difference between the estimated rates of stem respiration from upper canopy, mid canopy, lower canopy positions (Δ Respiration) and the lower stem positions relative to the estimated rates of respiration from the lower stem positions from January 30 – February 9, 2003. Data points represent mean rates for three *D. cupressinum* trees. b) The ratio of the difference between the daily $CO_2$ flux (per unit sapwood) in upper canopy, mid canopy, lower canopy positions and the lower stem positions (Δ Daily $CO_2$ Flux) relative to the daily $CO_2$ flux in the lower stem positions. Data points represent mean fluxes for three *D. cupressinum* trees. c) The daily $CO_2$ flux, at the stand level, attributable to respiration in each of the four stem segments (lower stem, lower canopy, mid canopy, and upper canopy).

**Fig. 6** Seasonal variation in monthly sapwood temperature and estimated stand-level stem respiration in *D. cupressinum* trees in a lowland podocarp-broadleaf forest in Westland, New Zealand.

**Figure 1.**

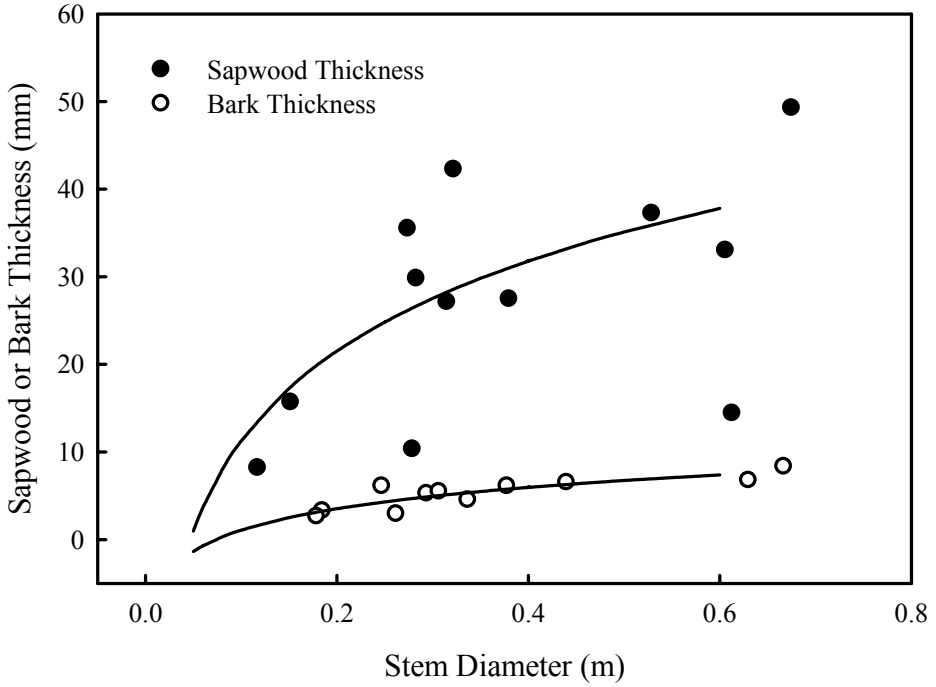

Sapwood Thickness
Bark Thickness
Sapwood or Bark Thickness (mm)
Stem Diameter (m)
0
10
20
30
40
50
60
0.0
0.2
0.4
0.6
0.8

**Figure 2.**

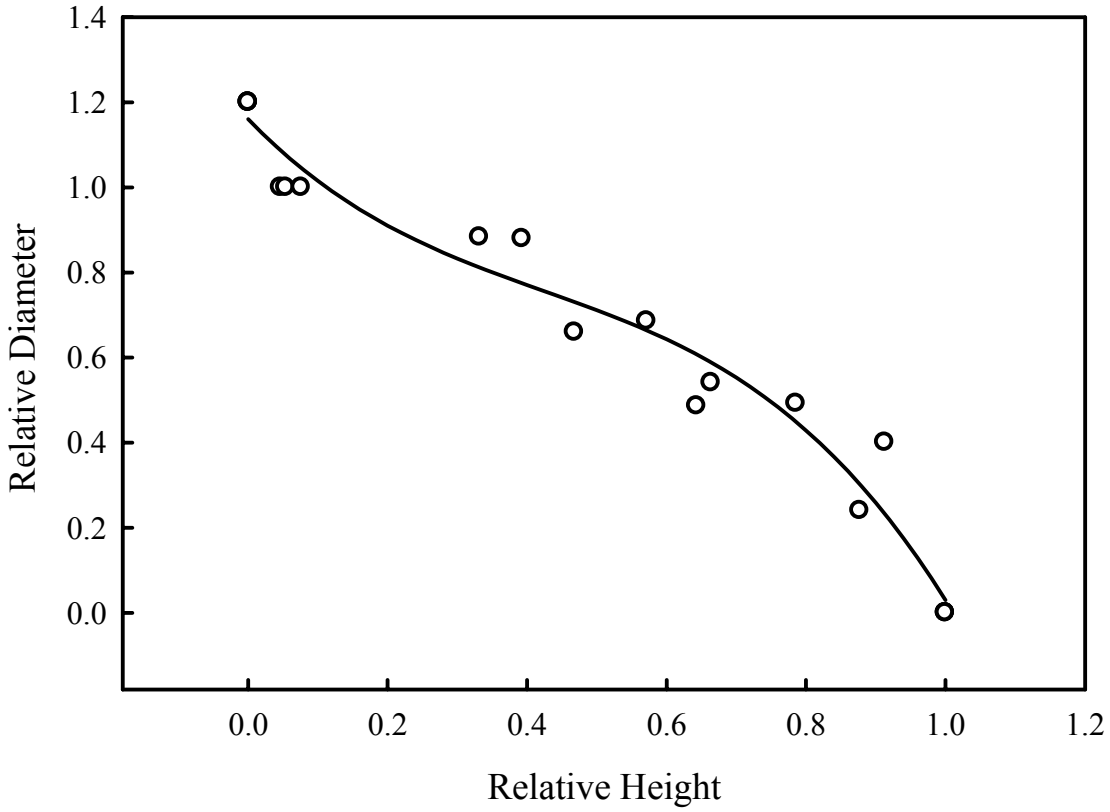

Relative Diameter
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
Relative Height

**Figure 3.**

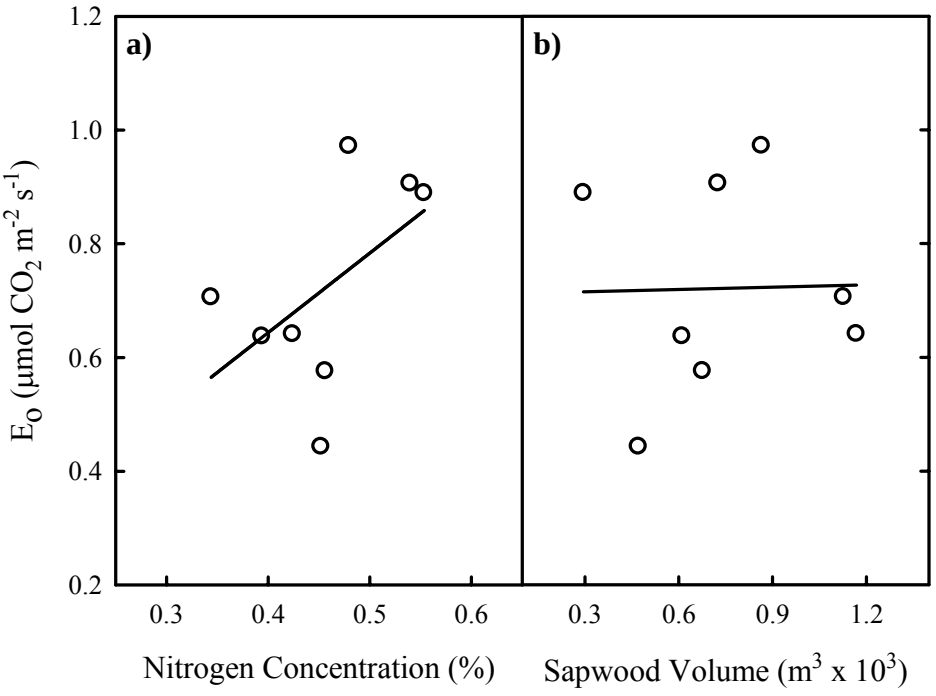

a)
b)
1.2
1.0
0.8
0.6
0.4
0.2
$E_o$ (µmol $CO_2$ $m^{-2}$ $s^{-1}$)
0.3
0.4
0.5
0.6
0.3
0.6
0.9
1.2
Nitrogen Concentration (%)
Sapwood Volume ($m^3$ x $10^3$)

**Figure 4.**

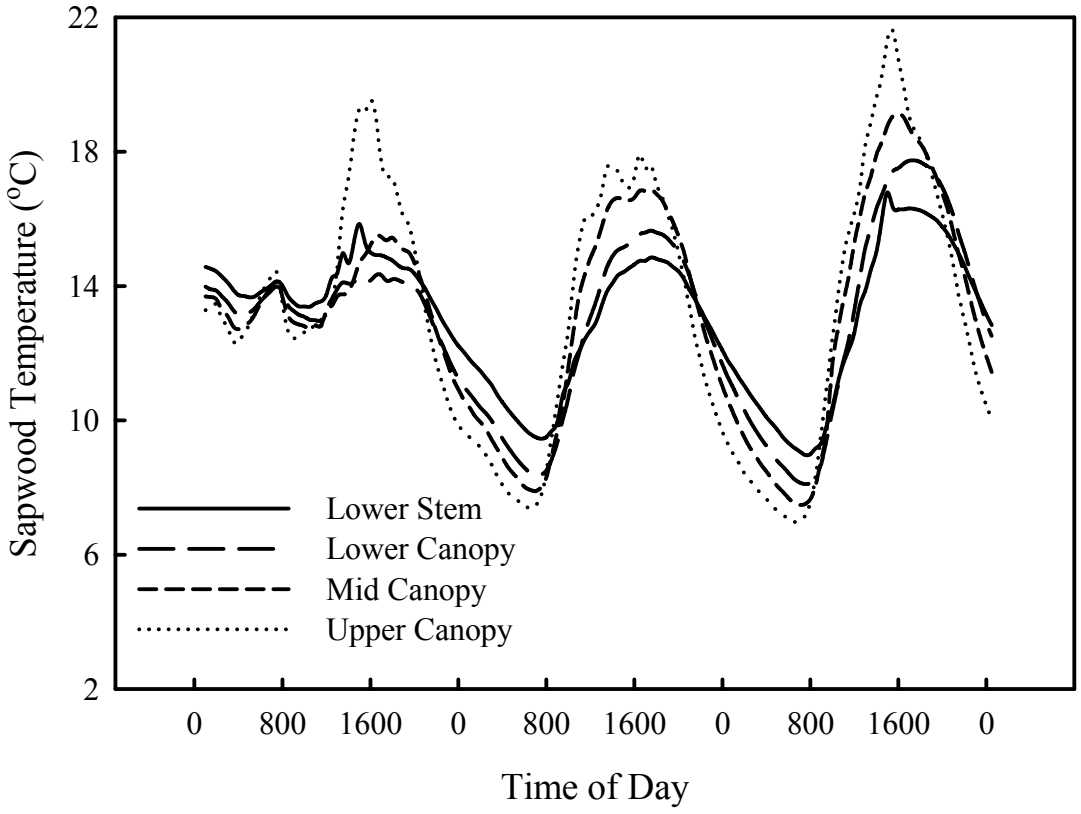

22
18
14
10
6
2
Sapwood Temperature (°C)
Lower Stem
Lower Canopy
Mid Canopy
Upper Canopy
0
800
1600
0
800
1600
0
800
1600
0
Time of Day

**Figure 5.**

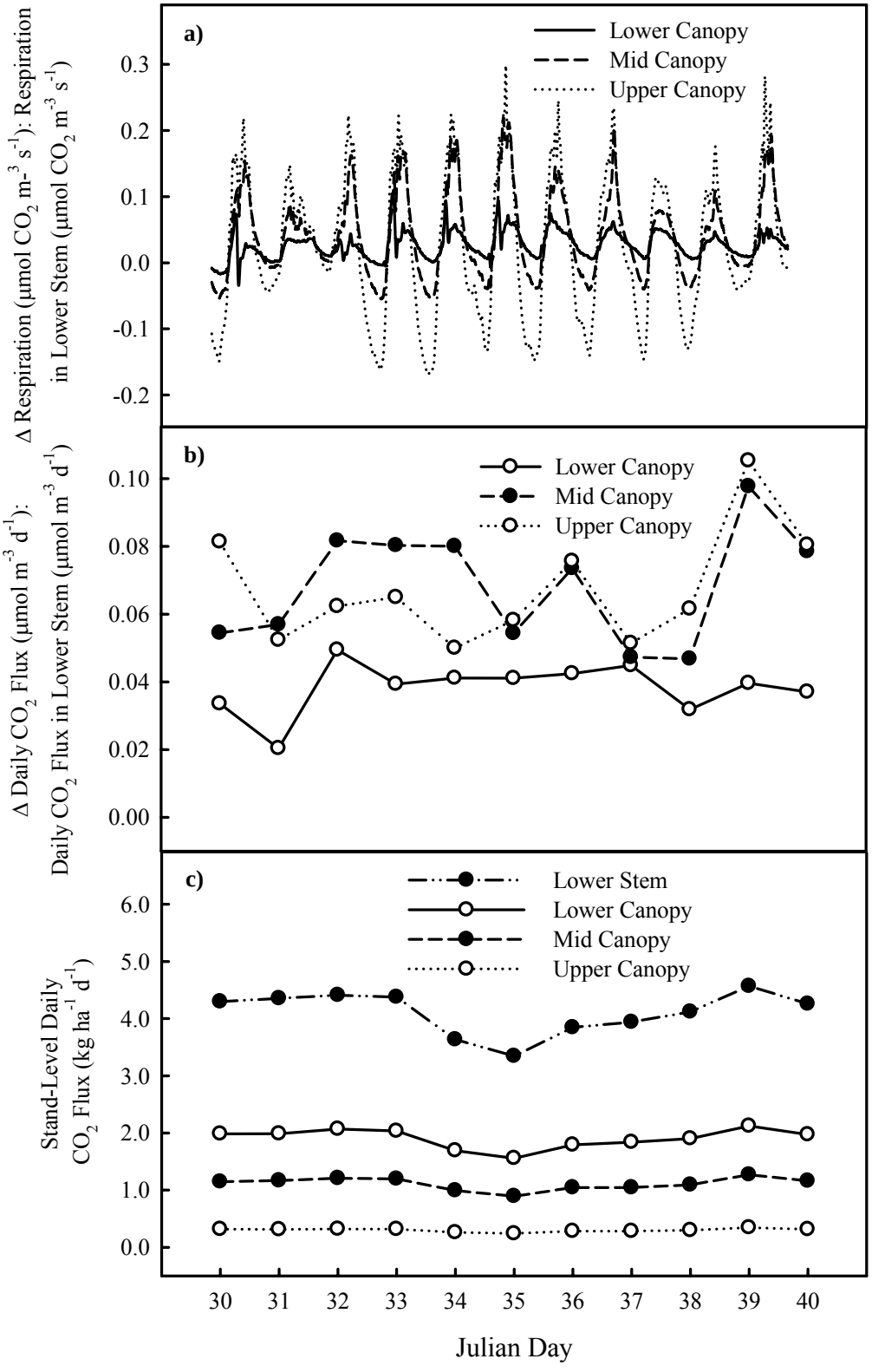
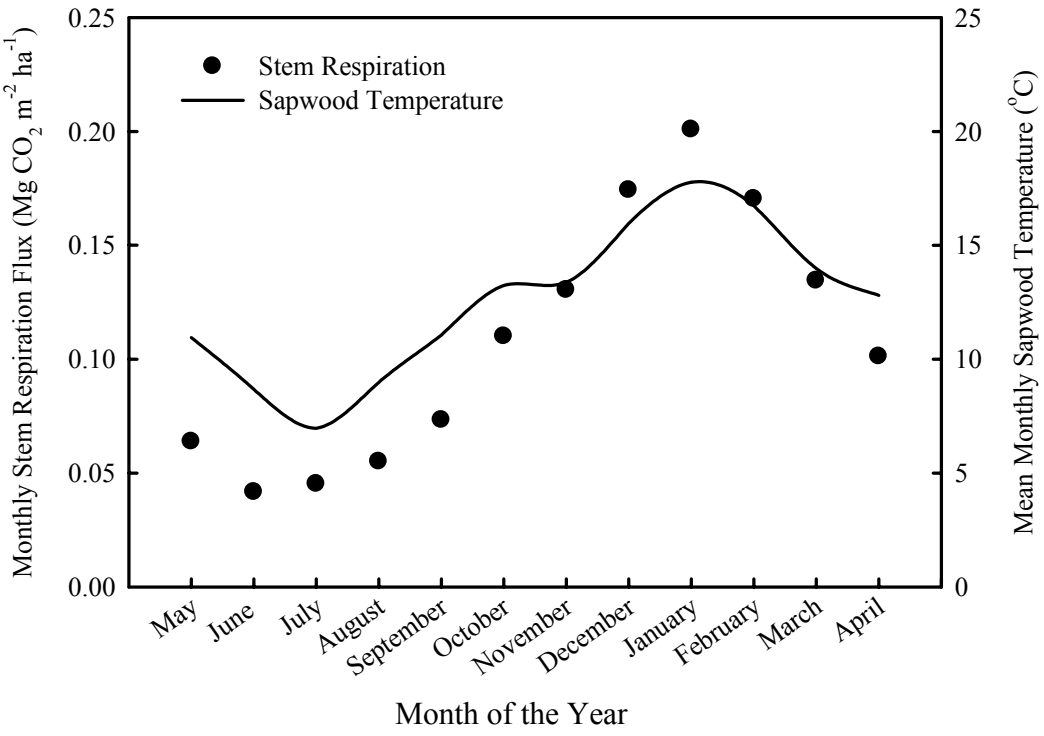

a)
Lower Canopy
Mid Canopy
Upper Canopy
Δ Respiration (μmol CO2 m-3 s-1): Respiration in Lower Stem (μmol CO2 m-3 s-1)
0.3
0.2
0.1
0.0
-0.1
-0.2
b)
Lower Canopy
Mid Canopy
Upper Canopy
Δ Daily CO2 Flux (μmol m-3 d-1): Daily CO2 Flux in Lower Stem (μmol m-3 d-1)
0.10
0.08
0.06
0.04
0.02
0.00
c)
Lower Stem
Lower Canopy
Mid Canopy
Upper Canopy
Stand-Level Daily CO2 Flux (kg ha-1 d-1)
6.0
5.0
4.0
3.0
2.0
1.0
0.0
30
31
32
33
34
35
36
37
38
39
40
Julian Day

**Figure 6.**


Stem Respiration
Sapwood Temperature
Monthly Stem Respiration Flux (Mg CO2 m-2 ha-1)
Mean Monthly Sapwood Temperature (°C)
0.25
0.20
0.15
0.10
0.05
0.00
25
20
15
10
5
0
May
June
July
August
September
October
November
December
January
February
March
April
Month of the Year

# Chapter 5: Between Tree Variation in Stem $CO_2$ Efflux is Related to Diameter Growth or Wood Respiratory Activity, Not Xylem [$CO_2$] and Sap Flux Density, in *Quercus rubra*

WILLIAM P. BOWMAN, WILLIAM S.F. SCHUSTER, and KEVIN L. GRIFFIN

**Abstract**

$CO_2$ efflux from woody stems is often associated with either the quantity of biomass under the bark surface (e.g. sapwood volume or live cell volume) or the respiratory activity of this biomass (e.g. growth rate or nitrogen concentration). However, recent findings have clearly indicated that measurements of stem $CO_2$ efflux are very likely to be confounded by variation in xylem $CO_2$ concentration and transport. In this study, measurements of stem $CO_2$ efflux, sap flux density, xylem $CO_2$ concentration ($[CO_2]$), wood respiratory activity, and stem growth were made in *Quercus rubra* trees ranging in size from 0.13-0.64 m DBH, during both the growing and dormant seasons. These trees were located in one of three stands comprised of 40, 95, or 135 yr old trees within a *Quercus* dominated forest in southwestern New York. During the growing season, stem $CO_2$ efflux was best predicted by tree diameter growth across all age classes and within the 40 and 95 yr old trees. During the dormant season, stem $CO_2$ efflux was positively correlated with the respiratory potential of excised inner bark tissues. Xylem $[CO_2]$ during the growing season ranged from 1.44-18.54%, but was not significantly related to environmental conditions or physiological or growth characteristics of the trees. Relationships between stem $CO_2$ and xylem $[CO_2]$ or sap flux density were observed, but were not consistent across age classes. Stem $CO_2$ efflux was positively correlated with xylem $[CO_2]$ in 40 yr old trees, but not in the older trees; whereas, $CO_2$ efflux was negatively correlated with sap flux density in the 95 and 135 yr old trees, but not in the youngest trees. These findings indicate that stem $CO_2$ efflux in *Quercus rubra* trees is largely determined by local respiratory production of $CO_2$ in both

the growing and dormant season and that interactions between stem $CO_2$ efflux and sap transport may increase with tree age.

**Keywords:** Woody Stems, $CO_2$ Efflux, *Quercus rubra*, Sap Flux Density, Xylem $CO_2$ Concentration, Stem Respiration

**Introduction**

Autotrophic respiration consumes ~50% of the carbon fixed by photosynthesis (Farrar 1985; Amthor 1989; Ryan 1991), and respiration in stems and branches accounts for 5-42% of this total (Waring and Schlesinger 1985; Lavigne et al. 1997; Damesin et al. 2002). Estimates of respiration in woody tissues are typically derived from measurements of the $CO_2$ efflux from stem and branch surfaces and have been conducted for several decades (Johannson 1933; Woodwell and Botkin 1970; Kinerson 1975; Edwards and McLaughlin 1978; Linder and Troeng 1981). These studies have made the implict assumptions that 1) respiration in the phloem, cambium, and sapwood tissues underlying stem and branch surfaces is the only source for the $CO_2$ that diffuses to the atmosphere and 2) a large and constant proportion of the $CO_2$ produced by respiration in stems and braches diffuses through the bark to the atmosphere. Evidence plainly suggests that these assumptions are not always valid in the woody tissues of forest trees as xylem sap can act as both a source and sink for $CO_2$ (Nigisi 1978; Martin et al. 1994; McGuire and Teskey 2004; Bowman et al. 2005).

The $CO_2$ concentration ($[CO_2]$) of xylem sap is typically much greater than the ambient atmosphere (2-20%: Eklund 1990; Hari et al. 1991; Eklund 1993) and may serve as a significant source of the $CO_2$ diffusing from stem and branch surfaces. For example, stem $CO_2$ efflux in a mature *Quercus alba* tree more than doubled in response to the experimental infusion of high $[CO_2]$ water into the transpiration stream (Teskey and McGuire 2002) and stem $CO_2$ efflux from *Liquidambar styraciflua* and *Platanus occidentalis* saplings was directly proportional to experimentally manipulated xylem $[CO_2]$ (Teskey and McGuire 2005). Conversely, xylem sap can act as a sink for

respiratory $CO_2$ as a portion of this $CO_2$ may dissolve in the xylem sap and then be transported to higher regions of the tree during transpiration. For example, midday estimates of woody tissue respiration were reduced by 15-76% in three temperate angiosperm tree species (Teskey and McGuire 2004) and 13-38% in the conifer, *Dacrydium cupressinum*, (Bowman et al. 2005) by xylem transport of $CO_2$. Xylem transport of respiratory $CO_2$ also provides a mechanism for observed declines in efflux rates during periods of peak transpiration (Nigisi 1975; Martin et al. 1994), diel hysteresis in stem $CO_2$ efflux rates (Lavigne et al. 1996), and elevated rates of $CO_2$ efflux from branches (Sprugel 1990; Damesin et al. 2002).

These findings have clearly indicated that estimates of woody tissue respiration derived from measurements of stem $CO_2$ efflux are very likely to be confounded by variation in xylem $CO_2$ concentration and transport. However, numerous studies have established that $CO_2$ efflux from woody stems is reliably associated with either the quantity of respiring biomass under the bark surface or the respiratory activity of this biomass. For example, during the dormant season, stem $CO_2$ efflux is often correlated with sapwood volume (Sprugel 1990; Ryan 1990; Edwards and Hanson 1996; Ryan et al. 1995; Will et al. 2001), live cell content (Ryan 1990; Stockfors and Linder 1998), or sapwood nitrogen content (Ryan 1991; Ryan et al. 1994; Maier 2001; Vose and Ryan 2001). While during the growing season, stem $CO_2$ efflux typically exhibits a strong seasonal pattern that corresponds to periods of cambial activity and wood synthesis and is often strongly correlated with stem growth (Maier 2001; Vose and Ryan 2001; Damesin et al 2002) and photosynthetic supply of substrate (carbohydrates) (Edwards and McLaughlin 1978; Edwards et al. 2002). Furthermore, stem $CO_2$ efflux rates have been

found to increase in response to changes in tree productivity in experimental manipulations of resource availability such as nitrogen fertilization (Ryan et al. 1996; Stockfors and Linder 1998) and $CO_2$ enrichment (Wullschleger et al. 1995; Edwards et al. 2002). These studies indicate that stem $CO_2$ efflux is largely the result of local production of $CO_2$ through respiratory processes involved in the wood biosynthesis and the maintenance of existing living tissues.

In this study, we measured stem $CO_2$ efflux, xylem $CO_2$ concentration ($[CO_2]$), sap flux density, and several proxies for local respiratory $CO_2$ production (stem diameter growth, wood respiratory activity, and wood nitrogen content) in twenty one *Quercus rubra* trees, ranging in size from 0.13-0.64 m DBH, during both the growing and dormant seasons. Our primary objective was to determine if stem $CO_2$ efflux in *Q. rubra* is more related to local $CO_2$ production or xylem $[CO_2]$ and sap transport. We hypothesized that, during the growing season, between tree variation in stem $CO_2$ efflux would be directly proportional to xylem $[CO_2]$ and both would be negatively correlated with sap flow rate. During the dormant season, stem $CO_2$ efflux was expected to be associated with the respiratory activity of the underlying wood tissues, particularly the inner bark (composed of phloem and cambial tissues), and wood nitrogen content. Additionally, we sought to determine if the physiological drivers of $CO_2$ efflux are consistent across trees that vary in size and reveal relationships between xylem $[CO_2]$ and tree size, growth rate, and sap transport.

By comparing both stem $CO_2$ efflux and xylem $CO_2$ concentration to likely proxies for $CO_2$ production (such as stem diameter growth, wood respiratory activity, nitrogen content, and sapwood volume) and potential sinks for respired $CO_2$ (sap flux

density), we aim to integrate previous research that has linked $CO_2$ efflux to local $CO_2$ production with the recent data stressing the importance of the effects of xylem $CO_2$ concentration and transport on stem $CO_2$ efflux. An improved understanding of any variation in the physiological drivers of $CO_2$ efflux across age classes would improve our ability to explain between-tree and -stand variation in stem $CO_2$ efflux and more accurately model woody tissue respiration at both the tree- and stand-level.

## Materials and Methods

### *Site description*

The Black Rock Forest is a 1530 ha scientific and educational preserve located in the Hudson Highlands physiographic province in Cornwall, NY, USA (lat 41º 24′ N, lon 74º 01′ W). Mean annual precipitation is 1190 mm and air temperature is strongly seasonal with monthly means ranging from –2.7º C in January to 23.4º C in July (Ross 1958; Turnbull et al. 2001). The forest soils are medium-textured loams and typically shallow in depth (0.25-1.0 m) with granite gneiss bedrock or glacial till parent material (Olsson 1981). The soils are acidic (pH 3.65-4.55), nutrient availability is low, and the site index ranges from poor to average (Lorimer 1981) Due to repeated logging and fires, forest regeneration has typically occurred through sprouting from hardwood stumps (Tryon 1939). Red oak (*Quercus rubra*) and chestnut oak (*Quercus prinus*) are the dominant tree species accounting for 66% of the forest's basal area (Friday and Friday 1985).

*Study Trees*

Twenty one *Q. rubra* trees, ranging in size from 0.13-0.64 m DBH, were selected from three tree stands of known age (40 yrs, 95 yrs, and 135 yrs) identified from records of timber harvesting in Black Rock Forest. The stands are located on a gently sloping (5-12 %) hill face with a northeast aspect and an elevation of 380-400 m. The maximum distance between the study trees is 340 m. The mean size of *Q. rubra* trees increases from 0.15 m in the youngest stand to 0.56 m in the oldest stand. *Q. rubra* is the dominant canopy species at each site comprising 46-80 % of the basal area in all stands with *Q. prinus*, red maple (*Acer rubrum*), and yellow birch (*Betula alleghaniensis*) also common as co-dominant or suppressed trees. The understory shrub layer consists mostly of witch-hazel (*Hamamelis virginiana*), mountain laurel (*Kalmia latifolia*), and/or lowbush blueberry (*Vaccinium angustifolium* and *V. vacillans*). Important characteristics of these stands are summarized in Table 1.

*Measurements of $CO_2$ Efflux*

$CO_2$ efflux rates from woody stems were measured in twenty one trees, ranging in diameter from 0.13- 0.64 m, for 150-250 hours each in June-July 2004 and for 120-170 hours in November-December 2004. Measurements in the autumn were conducted after leaffall to remove the effects of growth, cell expansion, and sap flow on stem $CO_2$ efflux. $CO_2$ efflux and other physiological measurements were conducted on nine trees in the 40 yr old stand, eight trees in the 95 yr old stand, and four trees in the 135 yr old stand. The methods utilized for measuring $CO_2$ efflux were similar to those described in Bowman et al. (2005). Polycarbonate gas-exchange chambers (~250 $cm^2$) were attached to the north-

side of the selected stems at a height of ~1.4 m. The edges of the chambers were fitted with closed-cell neoprene foam to serve as a gasket between the chamber and the stem. Caulking cord (Mortite Inc., Kankakee, IL,USA) was used to seal small gaps that occurred between the foam gasket and the tree. The chambers were then secured tightly to the tree using ratchet straps and then vigorously leak tested.

$CO_2$ efflux was measured with an infrared gas analyzer (LI-6262; Li-Cor Inc., Lincoln, NE, USA) in an open flow system connected to an automated manifold controlled by a datalogger and relay driver (CR23X and SDM-CD16AC; Campbell Scientific Inc., Logan, UT, USA). The flow of compressed air with near ambient [$CO_2$] was supplied to the chambers at a rate of 0.5 l $min^{-1}$ using a mass flow controller (SR-10; Sierra Instruments, Monterrey, CA, USA). The sampling duration for each chamber was 12 min with stems sampled once during each 132 min measurement cycle. A measurement cycle consisted of nine stem sampling periods and tests of the zero and span calibrations of the gas analyzer. Sapwood temperature proximal to the $CO_2$ efflux sampling chamber was measured using constantan-chromega thermocouples inserted 15 mm into the sapwood.

The $CO_2$ efflux rates were corrected for variation due to temperature using a modified Arrhenius function as adopted by Turnbull et al. (2003), where $CO_2$ efflux at a given sapwood temperature is described as:

Eqn. 1: $$E_A = E_o \cdot e^{\frac{A_o}{R_g}\cdot\left(\frac{1}{T_o}-\frac{1}{T_a}\right)}$$

where $E_o$ is the $CO_2$ efflux rate at the base temperature $T_o$, $T_a$ is the sapwood temperature, $R_g$ is the ideal gas constant (8.314 J $mol^{-1}$ $K^{-1}$), and $A_o$ is a parameter related to the overall activation energy which describes the magnitude of the temperature response. Nonlinear

curve fitting for temperature response curves was conducted with SigmaPlot 2001 (SPSS, Inc., Chicago, IL).

*Measuring Xylem [$CO_2$]*

The [$CO_2$] within the xylem of the selected *Q. rubra* stems was measured with $CO_2$ microelectrodes (Model MI-720; Microelectrodes, Bedford, NH) following the protocol described in McGuire and Teskey (2002). The microelectrodes were installed in the tree stems ~0.1 m from the $CO_2$ efflux sampling chambers. A 5 mm diameter hole was drilled ~20 mm into the xylem and a 25 mm brass tube (Model TTRB-5; Small Parts, Inc., Miami Lakes, FL, USA) was inserted into the hole to a depth of 15 mm. A microelectrode was inserted into the tube and caulking cord was used to seal the juction between the microelectrode and the brass tube, as well as, to seal the tube to the tree stem. The [$CO_2$] of the air in the small headspace within the brass tube and exposed to the sapwood was assumed to be in equilibrium with the xylem sap (Hari et al., 1991; Levy et al., 1999; McGuire and Teskey, 2002). The xylem [$CO_2$] was measured every 10 s and 5 min averages were recorded with a datalogger (Model CR21X; Campbell Scientific, Inc., Logan, UT, USA). For each tree, xylem [$CO_2$] was measured for at least 48 h during the period in which stem $CO_2$ efflux and sap flux density were measured. Prior to installation into the tree stem, the microelectrodes were calibrated according to McGuire and Teskey (2002) and the calibration for each microelectrode was checked after measurement periods. Due to diel changes in xylem [$CO_2$], comparisons between trees were accomplished by examining the average [$CO_2$] between 0100-0500 h.

*Measuring Sap Flux Density*

Granier-type heat dissipation probes (Granier 1985, 1987; Phillips et al. 1996) were utilized to measure sap flux density in each *Q. rubra* stem concurrently with $CO_2$ efflux during the growing season. A reference probe and heated probe were inserted into each stem, with one sensor located 40 mm above the other, at ~1.3 m above the ground. The downstream probe was heated by dissipating a constant voltage across an insulated fine-gauge constantan heating wire coiled around the probe. The temperature difference between the two probes was measured with constantan-chromega thermocouples located within each probe every 10 s with averages recorded every 5 min with a datalogger and multiplexer (Models CR21X and AM25T; Campbell Scientific, Inc, Logan, UT, USA). Sap flux density ($v$) was calculated using the equation (Granier 1985):

Eqn. 2: $$v = 119 \times 10^{-6} ((\Delta T_m - \Delta T) / \Delta T)^{1.231}$$

where, $\Delta T_m$ is the temperature difference between the two probes during conditions of no sap flow (0100-0500 h) and $\Delta T$ is the temperature difference during active sap flow. The $\Delta T$ values were corrected following Clearwater et al. (1999) to account for between-tree differences in the proportion of the heated sensor in contact with sapwood.

*Measuring Wood Respiratory Potential*

Wood respiratory potential was measured for each *Q. rubra* tree during both the growing season (July) and the dormant season (November) using the procedure outlined in Bowman et al. (2005). Three wood cores ( ~40 mm in length) were extracted from each *Q. rubra* stems at a height of 1.3 m with a 5-mm increment borer. During transportation back to the laboratory, wood cores were stored in the dark and kept in

plastic bigs containing a moist paper towel to reduce dessication of the samples. Inner bark (consisting of phloem and cambial tissues) and sapwood samples were excised from each core and stored at 4ºC for 24 h.

The respiratory activity of the inner bark and sapwood samples was measured polarographically as the oxygen consumption in a Clark-type liquid-phase oxygen electrode (Model D10; Rank Brothers, Cambridge, UK). Prior to the measurements, wood samples were incubated at the measurement temperature for 2h to allow the respiratory activity to stabilize. Respiratory activity was then assayed at 20ºC in 20 mM MES buffer (Azcón-Bieto et al. 1994) and the depletion of oxygen in the electode cuvette recorded for 20 min. Oxygen consumption of the excised wood samples are presented as the 'respiratory potential' of the wood tissues, following Pruyn et al. (2002), as the electode chamber/assay buffer conditions are significantly different from environmental conditions within the tree.

*Measurements of tree growth and wood nitrogen concentration*

Stem diameter growth was monitored with manual band dendrometers (Model D1-L; UMS GmbH, Munich, Germany). These dendrometers were installed in May 2003 and measured weekly during the 2004 growing season. Dendrometers were consistently measured between 1100-1300 h to minimize errors associated with diel fluctuations in stem diamter due to transpiration and the use of water stored within stems. Stem diameter increment was calculated for the entire growing season and for the three week period surrounding the measurements of stem $CO_2$ efflux, xylem [$CO_2$], and sap flux density. The inner bark and sapwood samples used for respiratory potential

measurements were dried, ground, and then analyzed for nitrogen concentration using a CHNS/O auto-analyzer (Model 2400 Series II, Perkin Elmer, Inc., Wellesley, MA).

*Statistical Analyses*

Effects of tree age and season on stem $CO_2$ efflux parameters and wood respiratory potential were analyzed using a nested 2 x 3 two-way analysis of variance (ANOVA) (DataDesk 6.0; Data Description, Inc., Ithaca, NY). An ANOVA was used to compare sample means and avoid the increased liklihood of Type I errors associated with emplying multiple t-tests. A nested model (with individual trees nested within age class) was used to account for between-tree variation in efflux parameters and respiratory potential (Underwood 1981) when determining the effects of season on stem $CO_2$ efflux parameters and wood respiratory potential. Differences between age classes were compared using least significant difference (LSD) post-hoc analysis and considred to be statistically significant if $P \leq 0.05$ (Sokal and Rohlf 1981). The effects of tissue type or age class on wood nitrogen concentration were determined seperately with paired *t*-tests (DataDesk 6.0). Regression analyses were performed to examine relationships between $CO_2$ efflux parameters and xylem [$CO_2$], sap flux density, respiratory potential, and stem growth both within and across age classes using the general linear model function in SigmaPlot 2001 (SPSS, Inc., Chicago, IL).

**Results**

Diel variation in $CO_2$ efflux from the woody stems of *Q. rubra* trees corresponded closely to sapwood temperature, increasing during the day and declining at night (Fig. 1). The modified Arrhenius model (Eqn. 1) significantly described the response of stem $CO_2$

efflux to diel temperature variation significantly in all trees from each age class and during both the growing (Fig. 2, $r^2$ = 0.13-0.89; $P < 0.01$) and dormant (Fig. 3, $r^2$ = 0.36-0.94; $P < 0.01$) seasons. The $CO_2$ concentration within the xylem tissues of *Q. rubra* stems exhibited diel variation that corresponded strongly to changes in sap flux density as xylem [$CO_2$] typically decreased during the day in response to the onset of transpiration and increased in the evening as rate of sap flow slowed (Fig. 1). Mean nighttime xylem [$CO_2$] (between 0100-0500 h) varied substantially between trees, ranging from 1.44 to 18.54 % (Table 2). This variation was not significantly related to measurement temperature and linear realtionships between xylem [$CO_2$] and characteristics of the trees such as size, growth rate, or mean maximum sap flux density were not significant across all age classes. During the dormant season, reliable diel patterns in [$CO_2$] were not observed, due perhaps to the low temperatures and [$CO_2$], as measured [$CO_2$] was less than 2% in all trees. Mean maximum daily sap flux density (between 1200-1600 h) ranged from 0.36-1.60 kg $H_2O$ $dm^{-2}$ $h^{-1}$ (Table 2) and, similar to [$CO_2$], showed no consistent liner trends, across all age classes, with tree size, growth rate, or sapwood thickness.

During the growing season, stem $CO_2$ efflux rates ($E_{20}$) at 20 ºC were significantly higher in the 40 and 95 yr old trees (3.13 ± 0.24 and 3.36 ± 0.35 μmol $CO_2$ $m^{-2}$ $s^{-1}$, respectively) than the 130 yr old trees (1.09 ± 0.31 μmol $CO_2$ $m^{-2}$ $s^{-1}$) (Table 3; $P < 0.05$). During the dormant season, the 90 yr old trees had greater $CO_2$ efflux rates ($E_5$) at 5 ºC than the 40 and 135 yr old trees (Table 3; $P < 0.05$). Normalization of both growing and dormant season $CO_2$ efflux rates to 15 ºC demonstrate significant seasonal differences in stem $CO_2$ efflux rates in the 40 and 95 yr old trees (Table 3; $P < 0.01$), but

not in the 135 yr trees ($P$ = 0.16), with greater efflux rates observed during the growing season. $CO_2$ efflux rates in the dormant season were, on average (±SE), 29.7 (±4.6), 32.6 (±2.9), and 52.0 (±10.7)% of the efflux rates in the growing season in the 40, 95, and 135 yr old trees, respectively.

Inner bark respiratory potential (0.80-2.51 nmol $CO_2$ $g^{-1}$ $s^{-1}$) was significantly greater than that of sapwood samples (0.23-1.01 nmol $CO_2$ $g^{-1}$ $s^{-1}$) in all age classes and seasons (Table 4; $P \leq 0.01$). Mean (± SE) nitrogen concentrations of inner bark samples were significantly greater than sapwood tissues (0.41 ± 0.02 % and 0.23 ± 0.02%, respectively; paired t-test, $P < 0.01$) with no significant differences between age classes. Respiratory potential declined significantly with tree age during the growing season, but not during the dormant season, and no age related trends in respiratory potential were observed for sapwood tissues (Table 4; $P < 0.05$). Measured rates of respiratory potential of both inner bark and sapwood tissues were greater in the growing season than the dormant season (Table 4; $P < .03$); however, this seasonal variation was not as pronounced as that found in the $CO_2$ efflux from the *Q. rubra* stems. Significant differences in wood respiratory potential between the growing and dormant season were only observed for inner bark samples from the 40 yr old trees and for sapwood samples in the 40 and 95 yr old trees. Rates of respiratory potential from inner bark samples in the dormant season were, on average, 67.5 ±10.4, 95.4 ±8.1, and 109.8 ±26.1% of the rates in the growing season in the 40-, 95-, and 135-year old trees, respectively (Table 4). Similarly, sapwood respiratory potential rates in the dormant season were, on average, 54.9 (± 6.7), 70.0 (±20.1), and 103.3 (±19.3)% of the efflux rates in the growing season in the 40-, 95-, and 135-year old trees, respectively.

During the growing season, stem $CO_2$ efflux at 20 ºC ($E_{20}$) exhibited substantial between tree variation within each of the three age classes. Across age classes, variation in stem $CO_2$ efflux was best predicted by the growth rate of the *Q. rubra* stems during the measurement period, as shown in Figure 4a ($y = 54.48x + 1.05$, $r^2 = 0.78$, $P < 0.01$), and over the entire growing season ($y = 99.03x + 0.47$, $r^2 = 0.60$, $P < 0.01$). Within the age classes, positive correlations between stem $CO_2$ efflux and stem diameter increment were observed in the 40- and 95- yr old trees ($y = 38.58x + 1.66$, $r^2 = 0.96$, $P < 0.01$; $y = 54.00x + 1.29$, $r^2 = 0.68$, $P < 0.02$), but not in the 135-yr old trees where a negative correlation between diameter increment and stem $CO_2$ efflux was observed ($y = -126.07x + 2.14$, $r^2 = 0.96$, $P < 0.13$) (Fig. 4b). No significant linear relationships between stem $CO_2$ efflux and xylem [$CO_2$] or sap flux density were observed across all age classes. However, in the 40-yr old trees, variation in $E_{20}$ was also found to be proportional to the mean [$CO_2$] within xylem tissues ($y = 0.12x + 2.06$, $r^2 = 0.52$, $P < 0.05$) as shown in Fig. 5. Xylem [$CO_2$] was not a strong predictor of between tree variation in stem $CO_2$ efflux in either of the older age classes. Likewise, relationships between $CO_2$ efflux and sap flux density were not consistent across age classes. In the older age classes, $E_{20}$ was found to be negatively correlated sap flux density (Fig. 6; 95 yr old trees: $y = -1.89x + 5.45$, $r^2 = 0.69$, $P < 0.05$; 135 yr old trees: $y = -1.26x + 2.26$, $r^2 = 0.90$, $P = 0.20$) while no relationship between sap flux density and stem $CO_2$ efflux was found in the 40 yr old trees. Diameter growth was weakly correlated with xylem [$CO_2$] in the trees from the 40 yr old stand ($y = 186.8x + 2.57$, $r^2 = 0.44$, $P = 0.10$) and negatively correlated with sap flux density in the trees from the 95 yr old stand ($y = -19.8x + 1.87$, $r^2 = 0.48$, $P = 0.08$).

During the dormant season, $CO_2$ efflux from *Q. rubra* stems was also strongly influenced by the respiratory $CO_2$ production in the underlying wood tissues. For example, $E_5$ was found to be positively correlated with the respiratory potential of excised inner bark tissues within each of the age classes, as shown in Fig. 7. However, this relationship between $E_5$ and respiratory potential was not consistent across age classes. Across age classes, the respiratory potential of inner bark tissues was weakly related to tissue nitrogen content ($y = 2.60x + 0.16$, $r^2 = 0.23$, $P = 0.03$). Furthermore, there was no relationship between dormant season stem $CO_2$ efflux and sapwood volume ($y = 0.01x + 0.46$, $r^2 = 0.04$, $P = 0.43$) while a weak relationship between $CO_2$ efflux and sapwood nitrogen content was found ($y = 1.08x + 0.23$, $r^2 = 0.18$, $P = 0.08$).

**Discussion**

Due to the absence of transpirational sap flow and high xylem [$CO_2$], dormant season rates of $CO_2$ efflux from woody stems of *Quercus rubra* trees are well correlated to local respiratory production of $CO_2$, as was expected. However, in contrast with our original hypotheses, variation in growing season rates of stem $CO_2$ efflux across age classes were not related to xylem [$CO_2$] and, instead, were also largely correlated to local respiratory production of $CO_2$. The relationships between growing season stem $CO_2$ efflux rates and 1) $CO_2$ production within the stems (as indicated by stem diameter growth), 2) the magnitude of the concentration gradient between sapwood and the atmosphere ([$CO_2$]), and 3) the capacity for xylem transport of $CO_2$ were not consistent across age classes and suggest that the influence of local $CO_2$ production on stem $CO_2$

efflux decreased with tree age while the effects of xylem $CO_2$ transport on stem $CO_2$ efflux increased.

*Growing Season*

During the growing season, variation in stem $CO_2$ efflux was associated with tree-level differences in wood biosynthesis, measured as stem diameter increment, either across all age classes or within the trees from either the 40 or the 95 yr old trees stands. These findings are in agreement with those from previous studies reporting that total stem respiration (Vose and Ryan 2002) or growth respiration (total respiration minus maintenance respiration; Maier 2001; Damesin et al. 2002) were well correlated with stem growth rate. Recent studies describing significant interactions between stem $CO_2$ efflux and xylem $CO_2$ transport and storage (Teskey and McGuire 2002 and 2005) have called into question the validity of scaling measurements of $CO_2$ efflux to the tree- or stand-level. This study indicates that in *Q. rubra* measurements of stem $CO_2$ efflux are indeed related to the respiratory activity of underlying wood and that techniques for deriving stand-level estimates of woody tissue respiration in the growing season based on measurements of biomass production (such as in Edwards and Hanson 1996; Carey et al. 1997; Lavigne and Ryan 1997) are appropriate for *Q. rubra* stands.

Interestingly, in the trees from the 40 yr old stand, the between-tree variation in stem $CO_2$ efflux was also found to be significantly related to differences in xylem [$CO_2$]. Recent studies suggest that between-tree variation in xylem [$CO_2$] can influence stem $CO_2$ efflux as experimental manipulation of xylem [$CO_2$] in the severed stems of *L. styraciflua* and *P. occidentalis* saplings (Teskey and McGuire 2005) and in a large, field-

grown *Q. alba* tree (Teskey and McGuire 2002) have induced substantial changes in stem $CO_2$ efflux. Our study provides field-based evidence that natural, between-tree variation in xylem [$CO_2$] may indeed contribute to differences in stem $CO_2$ efflux, particularly in young trees. However, this phenomena does not explain variation in stem $CO_2$ efflux across age classes in *Q. rubra*. It is more likely that local $CO_2$ production from wood synthesis is 1) affecting both stem $CO_2$ efflux and xylem [$CO_2$] as a weak correlation was found between stem growth and xylem [$CO_2$] ( $r^2$= 0.44, $P$ = 0.10) and/or 2) xylem [$CO_2$] is primarily affected by respiratory processes in the roots or soils that covary with stem growth in these 40 yr old trees. In this second case, both local and remote $CO_2$ production would both be affecting stem $CO_2$ efflux as fast-growing trees would have greater $CO_2$ efflux rates than slowing-growing trees due to both higher local construction respiration and higher xylem [$CO_2$] resulting from greater respiratory $CO_2$ production in the roots or soils. At this time, our understanding of the variables that influence between-tree variation in xylem [$CO_2$] is extremely limited and further research on this will greatly facilitate separating the relative effects of local $CO_2$ production and xylem [$CO_2$] on stem $CO_2$ efflux and identifying conditions in which high [$CO_2$] is likely to confound measurements of stem $CO_2$ efflux.

Likewise, in the trees from the 95 yr old stand, local production of $CO_2$ and carbon transport and storage in xylem water appeared to interact as stem $CO_2$ efflux was positively correlated with stem growth and negatively correlated with maximum sap flux density. Furthermore, a weak negative correlation between stem growth and sap flux density observed across the 95 yr old trees ($r^2$ = 0.48, $P$ = 0.08). Thus, fast-growing

trees both produced more respiratory $CO_2$ and had less capacity for xylem transport of $CO_2$, due to lower sap flux densities, resulting in more $CO_2$ efflux to the atmosphere.

In contrast with trees from the 40 and 95 yr old stands, stem $CO_2$ efflux was not related to local $CO_2$ production due to stem growth in the trees from the 135 yr old stand. In these oldest trees, xylem sap acted as the primary sink for respiratory $CO_2$ as indicated by the negative correlation with maximum sap flux density and possibly by the shallow temperature response of stem $CO_2$ efflux. For example, in these 135 yr old trees, $CO_2$ produced by respiration during warm daylight periods may be transported in the transpiration stream rather than diffusing to the atmosphere, thereby, resulting in a shallow temperature response of stem $CO_2$ efflux. We hypothesize that the strong influence of xylem $CO_2$ transport on $CO_2$ efflux rates in these older trees results from the low rates of $CO_2$ production due to reduced rates of diameter increment, increased whole tree water use, and/or higher resistance to $CO_2$ diffusion to the atmosphere due to thicker bark tissues.

Previous findings indicate that there is substantial inter-specific variation in the effects of xylem transport on stem $CO_2$ efflux as xylem $CO_2$ transport ranged between 25-71% of total woody tissue respiration in *Fagus grandifolia*, *L. styraciflua*, and *P. occidentalis* (Teskey and McGuire 2004). Although local respiratory production of $CO_2$ largely determines stem $CO_2$ efflux in *Q. rubra*, this study also indicates that the relationships between stem $CO_2$ production, xylem [$CO_2$], and xylem transport may exhibit intra-specific variation. In *Q. rubra*, the influence of local $CO_2$ production on stem $CO_2$ efflux decreases with tree age and the effects of xylem $CO_2$ transport on stem $CO_2$ efflux increases with tree age. Various studies been unable to find consistent

predictors for intra-specific variability in stem $CO_2$ efflux across stands that differ in stand density (Lavigne 1987), geographic site (Lavigne and Ryan 1997), and stand age (Lavigne et al 1996). The intra- and inter-specific variability in the relationships among stem $CO_2$ production, xylem [$CO_2$], and xylem transport is clearly a sign of the complexity of internal circulation of $CO_2$ within forest trees and may be responsible for the difficulty in finding reliable predictors of woody tissue respiration across stands and species.

*Dormant Season*

During the dormant season, in the absence of transpirational sap flow, stem $CO_2$ efflux was found to be positively correlated with inner bark respiratory potential within each age class. To our knowledge, this is the first study to link variation in *in situ* $CO_2$ efflux from stem surfaces with a direct estimate of the respiratory activity of the underlying wood. In addition, no significant relationships were found between $CO_2$ efflux and sapwood volume or sapwood nitrogen content in contrast with previous studies on *Quercus* (Edwards and Hanson 1996) and conifers (Ryan et al. 1995; Sprugel 1990; Ryan et al. 1994; Vose and Ryan 2001). The observed correlation between $CO_2$ efflux and inner bark respiratory potential and the lack of a relationship between $CO_2$ efflux and sapwood volume or respiratory potential may be due to the small amount of sapwood typical of *Quercus* and other ring-porous species and a resulting increase in the proportion of maintenance respiration attributable to phloem and cambial tissues relative to sapwood tissues.

Measurements of stem $CO_2$ efflux in the dormant season have typically been related to characteristics of the sapwood, such as sapwood volume and nitrogen concentration, due to the larger mass of sapwood tissues and the ease in scaling sapwood volume based measurements to the whole tree- or stand-level. In contrast, the potential contribution of maintenance respiration in phloem tissues to $CO_2$ efflux in the dormant season is typically neglected in most studies despite the fact that live cell volume (Stockfors and Linder 1998) and respiratory potential (Pruyn et al. 2002) are higher in the phloem or inner bark than the sapwood. For example, Stockfors and Linder (1998) used statistical techniques to partition maintenance respiration into phloem and xylem components and estimated that phloem maintenance respiration was 2.0-3.9 times greater than that of xylem tissues in *Picea abies*. Thus, maintenance respiration in the inner bark and phloem tissues may be an important component of stem $CO_2$ efflux in the dormant season and has the potential to explain instances, such as this study, in which the relationship between dormant season $CO_2$ efflux and sapwood volume or nitrogen concentration fails.

*Seasonal Variation in Stem $CO_2$ Efflux and Respiratory Potential*

Across the three age classes, differences in the magnitude of the observed decline in stem $CO_2$ efflux and respiratory potential between the growing and dormant seasons were consistent with the partitioning of woody tissue respiration into maintenance and growth respiration components (McCree, 1974). For example, measurements of wood respiratory potential declined by 33% and 45% in inner bark and sapwood of the trees from the 40 yr old stand, respectively, but were statistically unchanged in the older trees.

This is consistent with younger trees possessing greater ratios of growth: maintenance respiration than the older trees as has been previously observed in *Pinus contorta* (Ryan and Waring 1992), *P. ponderosa* (Carey et al. 1997), and *P. banksiana* (Lavigne and Ryan 1997). Stem $CO_2$ efflux was significantly influenced by season in all age classes (Table 3) as efflux rates at 15 ºC decreased by 72 and 41% in the 40 and 135 yr old trees, respectively, between the growing and dormant seasons. The larger decline in $CO_2$ efflux between the growing and dormant season, compared with that of wood respiratory potential, may be the result of 1) the large decrease in [$CO_2$] from 3-18% to less than 2% between the growing and dormant season or 2) the measurement of wood respiratory potential at high temperatures (20 ºC) and not be representative of true respiratory activity under ambient conditions.

*Linkages to Water Relations*

Further research aimed at identifying the conditions in which $CO_2$ transport with xylem sap and xylem [$CO_2$] are expected to confound estimates of respiration in woody stems and branches is necessary to integrate the effects of xylem [$CO_2$] and transport into tree- and stand-level carbon balances. We hypothesize that $CO_2$ efflux from woody stems is most likely to directly reflect the respiratory activity in the underlying wood in cases where either 1) sap flow, and therefore the capacity to transport respiratory $CO_2$, is low and/or 2) internal xylem [$CO_2$] is low. In the first case, the capacity to transport $CO_2$ may be low when xylem [$CO_2$] is high if uptake of respiratory $CO_2$ is limited by small amounts of xylem water or $CO_2$ saturation of xylem water. Furthermore, we suggest that in *Q. rubra*, xylem characteristics and water relations, but not internal xylem [$CO_2$],

contribute to the strong association between stem $CO_2$ efflux and local production of $CO_2$ from wood synthesis. The xylem [$CO_2$]'s observed in *Q. rubra* were not lower than those in McGuire and Teskey (2004) and Teskey and McGuire (2005) in which stem $CO_2$ efflux was significantly influenced by xylem [$CO_2$] or transport; and the diel pattern of xylem [$CO_2$], declining during the day and increasing at night, in *Q. rubra* was similar to other studies (Teskey and McGuire 2002). Given that the magnitude and pattern of xylem [$CO_2$] in *Q. rubra* was not dissimilar to those in other studies, we suggest that reliable correlation between stem $CO_2$ efflux and local respiratory $CO_2$ was not due to the absence of a high concentration source of $CO_2$ in the sapwood, but rather was related to tree water relations.

Xylem [$CO_2$], during the growing season, in this and other studies are two to three orders of magnitude greater than the atmosphere. Interestingly, xylem [$CO_2$] also seems to be greater than soil [$CO_2$] which typically ranges between only 0.4 and 1.1% (Piñol et al. 1995; Tang et al. 2003; Jassal et al. 2005). This large discrepancy between soil [$CO_2$] and xylem [$CO_2$] suggests that root respiration may substantially contribute to the high [$CO_2$] observed in xylem tissues. Furthermore, both soil [$CO_2$] and root respiration exhibit diel patterns in response to temperature; therefore, the diel pattern in xylem [$CO_2$], in which xylem [$CO_2$] decreases during the day, is likely caused by an influx of relatively low [$CO_2$] water, from the soil, into the stem.

Sap flux densities observed in this study (0.36 –1.60 kg $H_2O$ $dm^{-2}$ $h^{-1}$, Table 2) were broadly consistent with those reported for *Q. rubra* and *Q. alba* by (Phillips et al. 1996; Wullschleger et al 2001; Engel et al 2002; Spicer and Holbrook 2005). Estimates of sap flux density and whole tree water use by *Quercus* are often lower than other

temperate-broadleaf species (Oren and Pataki 2001; Wullschleger et al. 2001; Bovard et al. 2005; Spicer and Holbrook 2005) consistent with the high water use efficiency (Turnbull et al. 2002) and tolerance of xeric sites (Abrams 1990) typical of *Quercus* species. We hypothesize that the narrow radial width of sapwood and the low volumetric water flow typical of *Quercus* species results in lower capacity for xylem transport of $CO_2$ and, therefore, contributes to a strong relationship between stem $CO_2$ efflux and local respiratory activity during the growing season. Consequently, we also expect xylem transport of $CO_2$ to have greater influence on stem $CO_2$ efflux in diffuse-porous and tracheid anatomy trees than in trees with ring-porous anatomy; old trees than young trees; and trees from hydric or mesic habitats versus trees from xeric habitats.

In conclusion, stem $CO_2$ efflux in *Quercus rubra* trees is more closely related to local respiratory production of $CO_2$ than xylem $CO_2$ concentration or sap transport. As a result, stand-level estimates of woody tissue respiration in the growing season may be reliably based on measurements of biomass production in *Q. rubra* stands. Evidence for the effects of xylem $CO_2$ concentration or sap transport on stem $CO_2$ efflux was observed and suggest that interactions between xylem transport of $CO_2$ and stem $CO_2$ efflux increase with tree age. These age-related changes in the potential physiological drivers of stem $CO_2$ efflux suggest that we have much to learn about respiration in the stems of forest trees and that an integration of tree water relations may greatly facilitate the understanding intra- and inter-specific variation in stem $CO_2$ efflux.

**Acknowledgments**

The authors appreciatively acknowledge logistical support at Black Rock Forest from J. Brady and M. Munson. We also thank H. Fung for the processing of wood samples for nitrogen concentration. This work was funded by (who paid for the stem system construction?) and a Black Rock Forest Grant to KLG. WPB also gratefully acknowledges graduate support from Columbia University's Center for Environmental Research and Conservations and a National Science Foundation GK12 grant to the Columbia University Department of Chemistry.

**Table and Figure Captions:**

**Table 1.** Characteristics of Vegetation in Study Plots. Tree age, diameter, and height values represent means (standard error) for *Quercus rubra* trees on the study plots.

**Table 2.** Mean (standard error), minimum, and maximum values for nightime xylem [$CO_2$] and maximum daily sap flux density of 40, 95, and 135 yr old *Quercus rubra* trees measured from June 14 to July 19 2004 at Black Rock Forest. For 40 yr old trees, $n = 9$; 95 yr old trees, $n = 8$; 135 yr old trees, $n = 3$.

**Table 3.** Modeled $CO_2$ efflux parameters derived from fitted temperature response curves (Eq. 1) as a function of tree age and time of year in *Quercus rubra* trees from Black Rock Forest, NY. $E_{15}$ is the stem $CO_2$ efflux rate at 15 ºC calculated from the fitted $CO_2$ efflux-temperature response curves during the growing season (June-July 2004) and dormant season (November-December 2004). $A_o$ is a modeled parameter related to the energy of activation. $E_{20}$ is the stem $CO_2$ efflux rate at the base temperature (20 ºC) used to fit Eqn. 1 to the $CO_2$ efflux-temperature data measured during June-July 2004. $E_5$ is the stem $CO_2$ efflux rate at the base temperature (5 ºC) used to fit Eqn. 1 to the $CO_2$ efflux-temperature data measured during November-December 2004. Values shown are means (standard error); for 40 yr trees, n = 9; for 95 yr trees, n = 8; for 135 yr trees, n = 4. Significance of factor effects for tree age (Age), time of year (Season), and the interaction between age and time of year (A x S) are indicated by the *P*-value or a nonsignificant (NS). Different letters within rows adjacent to listd values indicate statistically significant differences at $P < 0.05$ based on least significant difference of means.

**Table 4.** Mean respiratory potential (nmol $O_2$ $g^{-1}s^{-1}$) for inner bark and sapwood tissues extracted from 40-, 95-, and 135-yr old *Quercus rubra* trees during the growing season (July) and dormant season (December) of 2004. Values shown are means (standard error); for 40 yr trees, n = 9; for 95 yr trees, n = 8; for 135 yr trees, n = 4. Significance of factor effects for tree age (Age), time of year (Season), and the interaction between age and time of year (A x S) are indicated by the *P*-value or a nonsignificant (NS). Different letters within rows adjacent to listed values indicate statistically significant differences at $P < 0.05$ based on least significant difference of means.

**Figure 1.** Diel patterns of sap velocity, xylem [CO2], stem CO2 efflux, and sapwood temperature measured in a 43 cm diameter *Q. rubra* tree between July 2 and July 5 2004 at Black Rock Forest.

**Figure 2.** The relationship between stem $CO_2$ efflux and sapwood temperature for five *Quercus rubra* trees during the growing season (June 14 to July 19 2004). Circles represent 40-yr old trees, triangles represent 95 yr old trees, and squares represent 135 yr old trees. The fitted curves result from the modified Arrhenius model (Eqn 1). All non-linear regressions were significant at $P < 0.01$. Mean parameter values for $E_o$ and $A_o$ for each age class are reported in Table 2.

**Figure 3.** The relationship between stem $CO_2$ efflux and sapwood temperature for five *Quercus rubra* trees during the dormant season (November 16 to December 8 2004). Circles represent 40-yr old trees, triangles represent 95 yr old trees, and squares represent 135 yr old trees. The fitted curves result from the modified Arrhenius model (Eqn 1). All non-linear regressions were significant at $P < 0.01$. Mean parameter values for $E_o$ and $A_o$ for each age class are reported in Table 2.

**Figure 4.** The relationship between stem diameter increment and the rate of stem $CO_2$ efflux ($E_{20}$) normalized to 20 ºC for 40 yr old (circles), 95 yr old (triangles), and 135 yr old (squares) *Quercus rubra* trees during the growing season. Lines represent least squares regressions. In a), the solid line represent the relationship between diameter increment and $E_{20}$ for all trees ($y = 74.48x + 1.05$, $r^2 = 0.78$, $P < 0.0001$). In b), age-specific regression lines are shown: 40 yr, solid line, $y = 38.58x + 1.66$, $r^2 = 0.96$, $P < 0.01$; 95 yr, dashed line, $y = 54.00x + 1.29$, $r^2 = 0.68$, $P < 0.02$; 135 yr, dotted line, $y = -126.07x + 2.14$, $r^2 = 0.96$, $P < 0.13$.

**Figure 5.** The relationship between the average measured [$CO_2$] within the xylem tissues and the rate of stem $CO_2$ efflux ($E_{20}$) normalized to 20 ºC for 40 yr old *Q. rubra* trees during the growing season. The solid line represents a least squares regression: $y = 0.12x + 2.06$, $r^2 = 0.52$, $P < 0.05$

**Figure 6.** The relationship between average sap flux density (measured between 1200 and 1600 hours) and the rate of stem $CO_2$ efflux ($E_{20}$) normalized to 20 ºC for 95 yr old (triangles) and 135 yr old (squares) trees *Quercus rubra* trees during the growing season. Error bars represent ± standard error and the solid lines represent lest squares regressions: 90 yr, $y = -1.89 + 5.45x$, $r^2 = 0.69$, $P < 0.05$; 130 yr, $y = -1.26 + 2.26x$, $r^2 = 0.90$, $P = 0.20$.

**Figure 7.** The relationship between the respiratory potential of inner bark and the rate of stem $CO_2$ efflux ($E_{15}$) normalized to 15 ºC during the dormant season in for 40, 95, and 135 yr old *Quercus rubra* trees. Respiratory potential measurements represent means from three inner bark samples per tree and error bars ± SE. The solid lines represents least squares regressions: 40 yr trees, $y = 0.41x + 0.09$, $r^2 = 0.79$, $P < 0.05$; 95 yr trees, $y = 0.67x - 0.22$, $r^2 = 0.44$, $P < 0.05$; 135 yr trees, $y = 0.88x – 0.28$, $r^2 = 0.41$, $P < 0.05$.

**Table 1.**

| Site # | Tree Age (yr) | Diameter (m) | Height (m) | Stand density (trees $ha^{-1}$) | Basal Area ($m^2$ $ha^{-1}$) | *Q. rubra* Basal Area (%) | LAI ($m^2/m^2$) |
|---|---|---|---|---|---|---|---|
| 1 | 38.8 (0.6) | 0.15 (0.01) | 14.0 (0.7) | 780 | 10.5 | 46.1 | 2.15 |
| 2 | 93.0 (1.1) | 0.38 (0.02) | 19.9 (0.7) | 520 | 16.0 | 62.6 | 2.67 |
| 3 | 134.8 (3.3) | 0.56 (0.02) | 23.9 (1.0) | 368 | 19.7 | 79.7 | 2.80 |

**Table 2.**

| Tree Age | Xylem [$CO_2$] (%) | | | Maximum Sap Flux Density (kg $H_2O$ $dm^{-2}$ $h^{-1}$) | | |
|---|---|---|---|---|---|---|
| | Mean | Min | Max | Mean | Min | Max |
| 40 | 10.2 (1.9) | 5.7 | 18.5 | 0.44 (0.10) | 0.36 | 0.99 |
| 95 | 5.8 (1.5) | 3.1 | 13.9 | 0.98 (0.18) | 0.55 | 1.60 |
| 135 | 11.4 (1.7) | 8.2 | 13.8 | 0.82 (0.18) | 0.50 | 1.15 |

**Table 3.**

| | Growing Season | | | Dormant Season | | | |
|---|---|---|---|---|---|---|---|
| | 40 yr | 95 yr | 135 yr | 40 yr | 95 yr | 135 yr | **ANOVA Statistics** |
| $E_{15}$ (μmol $CO_2$ $m^{-2}s^{-1}$) | 2.24 (0.19)[a] | 2.72 (0.33)[a] | 0.91 (0.26)[b] | 0.61 (0.09)[b] | 0.90 (0.14)[b] | 0.54 (0.12)[b] | Age < 0.01<br>Season < 0.01<br>A x S 0.02 |
| $A_o$ (kJ mol $K^{-1}$) | 47.3 (2.0)[a] | 31.8 (7.1)[b] | 25.1 (9.3)[b] | 37.8 (5.1)[ab] | 36.4 (4.8)[ab] | 47.4 (4.1)[a] | Age NS<br>Season NS<br>A x S 0.03 |
| $E_{20}$ (μmol $CO_2$ $m^{-2}s^{-1}$) | 3.13 (0.24)[a] | 3.36 (0.35)[a] | 1.09 (0.31)[b] | - | - | - | Age < 0.01 |
| $E_5$ (μmol $CO_2$ $m^{-2}s^{-1}$) | - | - | - | 0.34 (0.04)[b] | 0.50 (0.06)[a] | 0.27 (0.07)[b] | Age 0.02 |

**Table 4.**

| | Growing Season | | | Dormant Season | | | |
|---|---|---|---|---|---|---|---|
| | 40 yr | 95 yr | 135 yr | 40 yr | 95 yr | 135 yr | **ANOVA Statistics** |
| **Inner Bark** | 1.85 (0.12)[a] | 1.46 (0.13)[b] | 0.97 (0.21)[c] | 1.17 (0.14)[bc] | 1.23 (0.06)[bc] | 0.98 (0.06)[c] | Age < 0.01<br>Season 0.03<br>A x S NS |
| **Sapwood** | 0.56 (0.06)[a] | 0.65 (0.06)[a] | 0.53 (0.15)[a] | 0.28 (0.02)[b] | 0.32 (0.02)[b] | 0.47 (0.06)[ab] | Age NS<br>Season < 0.01<br>A x S NS |

**Figure 1.**

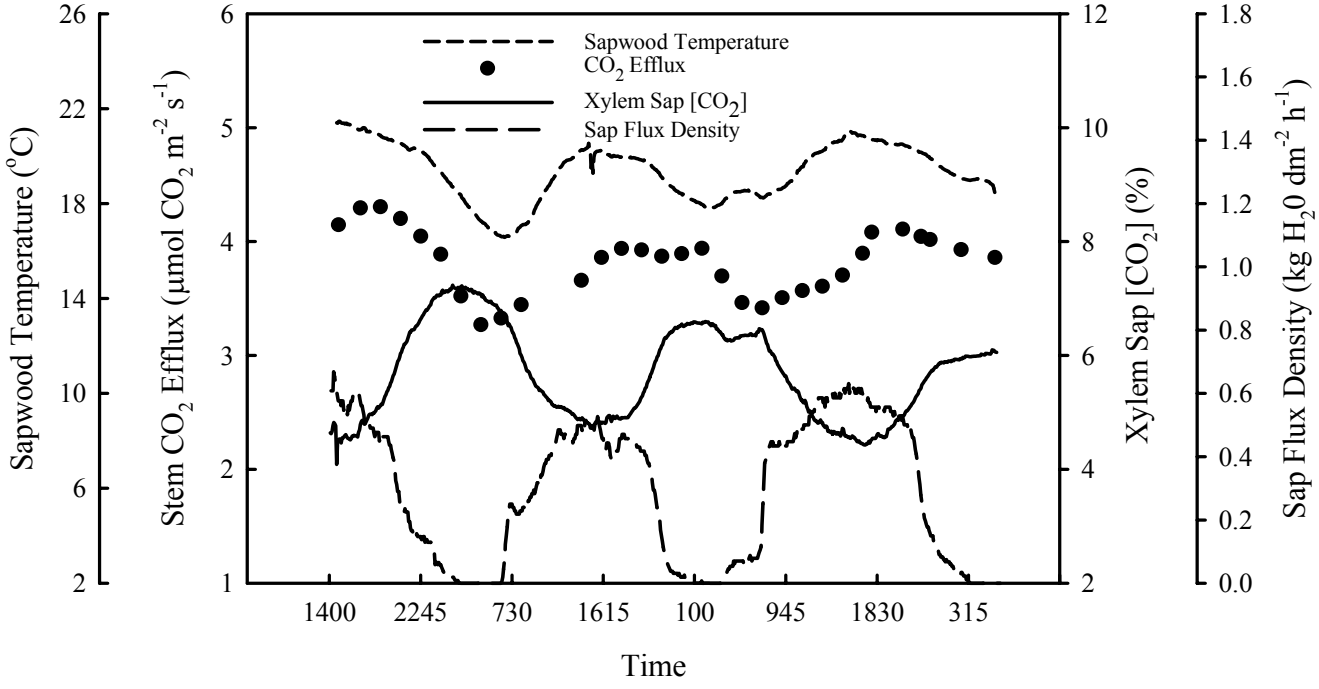

Sapwood Temperature
CO2 Efflux
Xylem Sap [CO2]
Sap Flux Density
Sapwood Temperature (°C)
Stem CO2 Efflux (µmol CO2 m-2 s-1)
Xylem Sap [CO2] (%)
Sap Flux Density (kg H20 dm-2 h-1)
26
22
18
14
10
6
2
6
5
4
3
2
1
12
10
8
6
4
2
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1400
2245
730
1615
100
945
1830
315
Time

**Figure 2.**

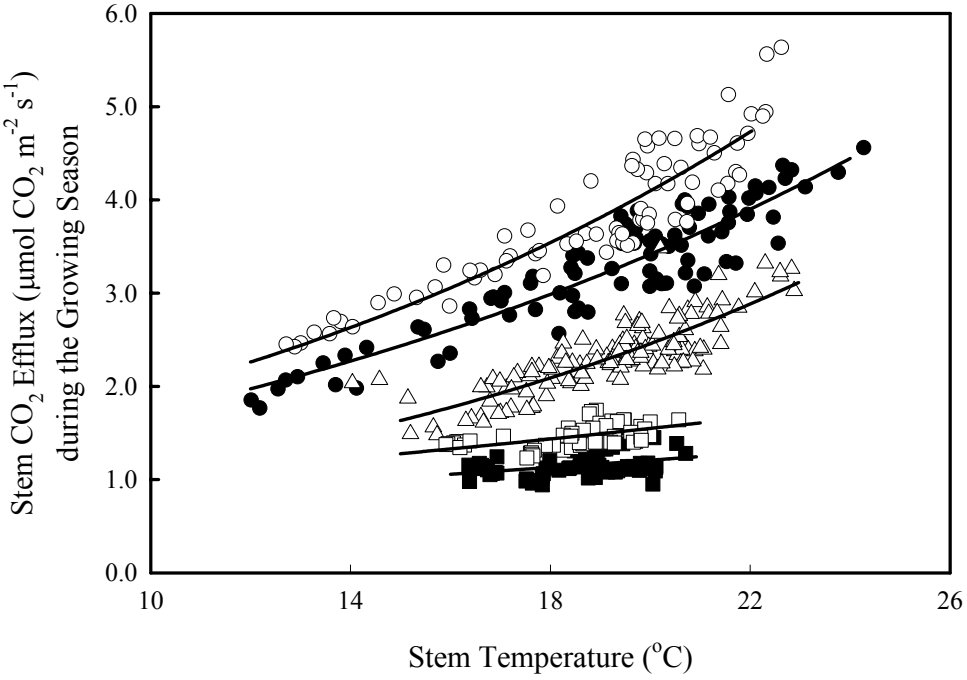

Stem $CO_2$ Efflux (μmol $CO_2$ $m^{-2}$ $s^{-1}$) during the Growing Season
6.0
5.0
4.0
3.0
2.0
1.0
0.0
10
14
18
22
26
Stem Temperature ($^oC$)

**Figure 3.**

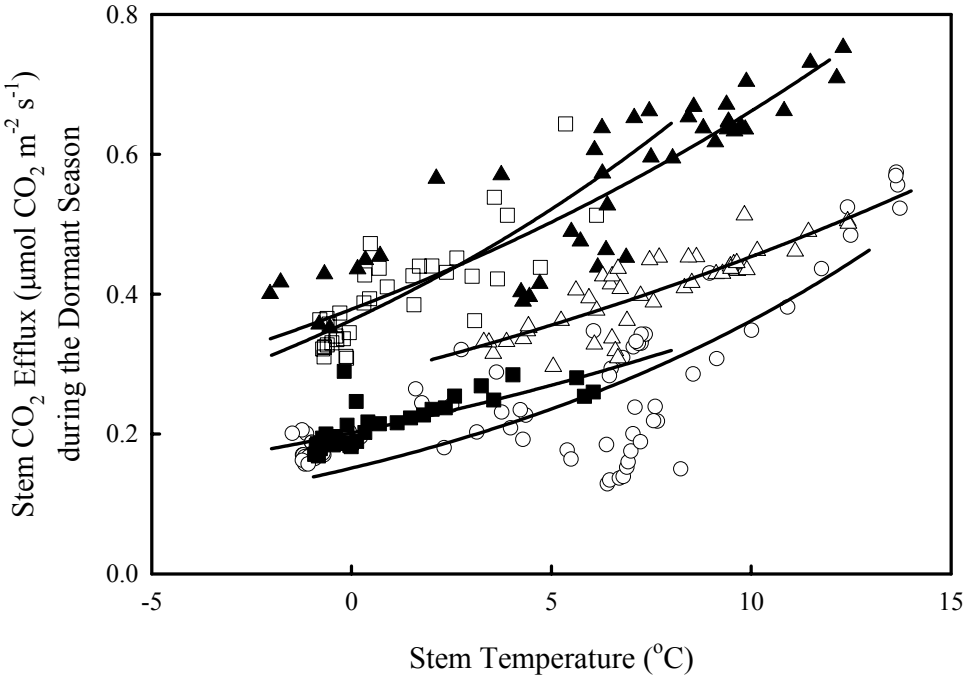

0.8
0.6
0.4
0.2
0.0
-5
0
5
10
15
Stem CO2 Efflux (μmol CO2 m-2 s-1)
during the Dormant Season
Stem Temperature (°C)

**Figure 4.**

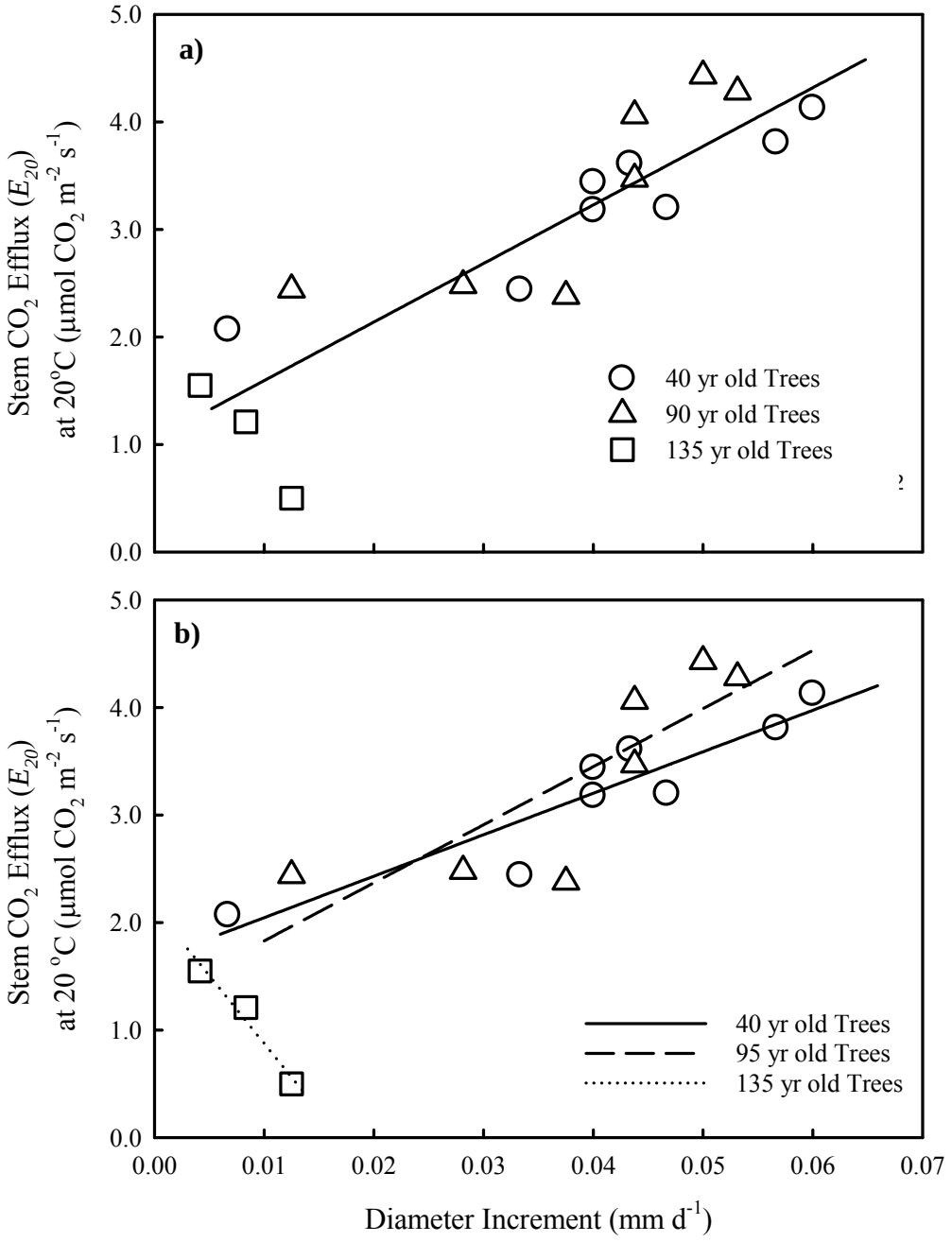

a)
b)
Stem $CO_2$ Efflux ($E_{20}$) at 20°C (µmol $CO_2$ $m^{-2}$ $s^{-1}$)
40 yr old Trees
90 yr old Trees
135 yr old Trees
95 yr old Trees
Diameter Increment (mm $d^{-1}$)
0.0
1.0
2.0
3.0
4.0
5.0
0.00
0.01
0.02
0.03
0.04
0.05
0.06
0.07

**Figure 5.**

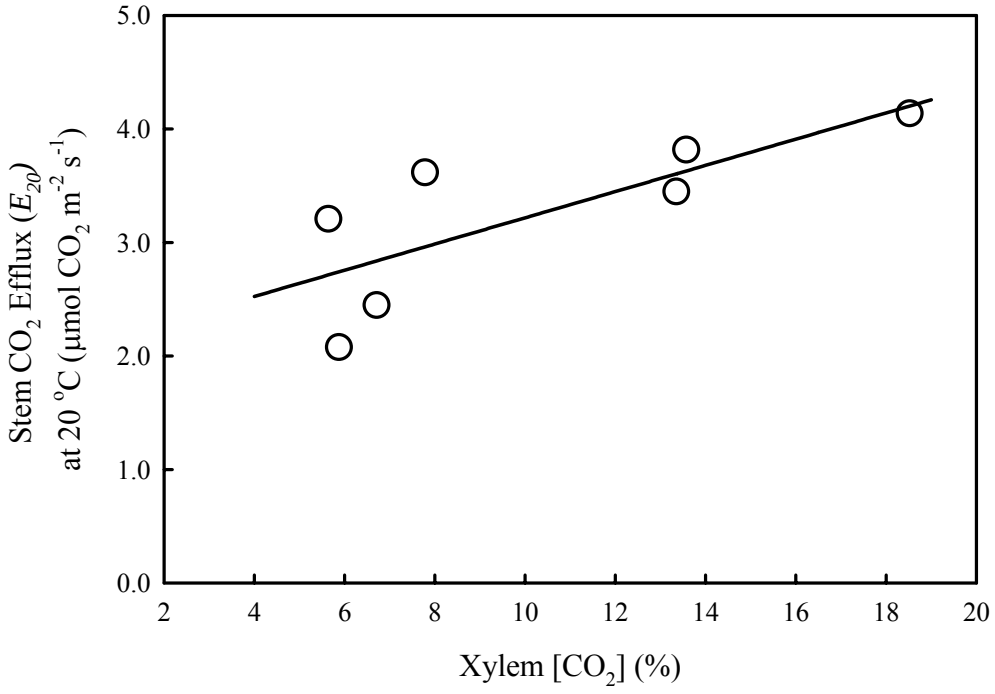

5.0
4.0
3.0
2.0
1.0
0.0
2
4
6
8
10
12
14
16
18
20
Stem $CO_2$ Efflux ($E_{20}$) at 20 °C (µmol $CO_2$ $m^{-2}$ $s^{-1}$)
Xylem [$CO_2$] (%)

**Figure 6.**

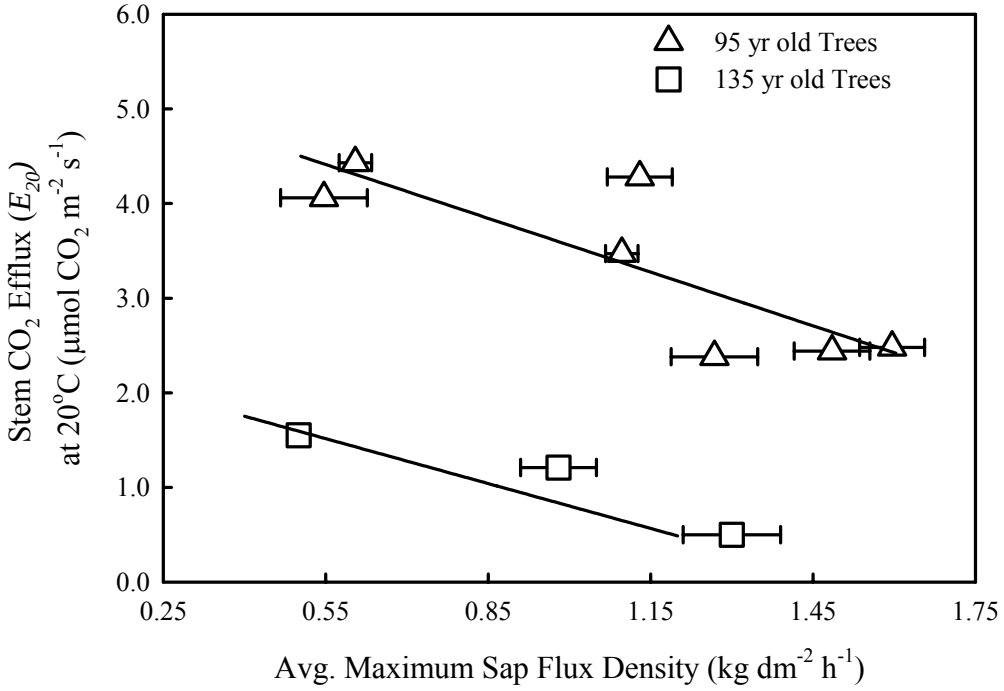
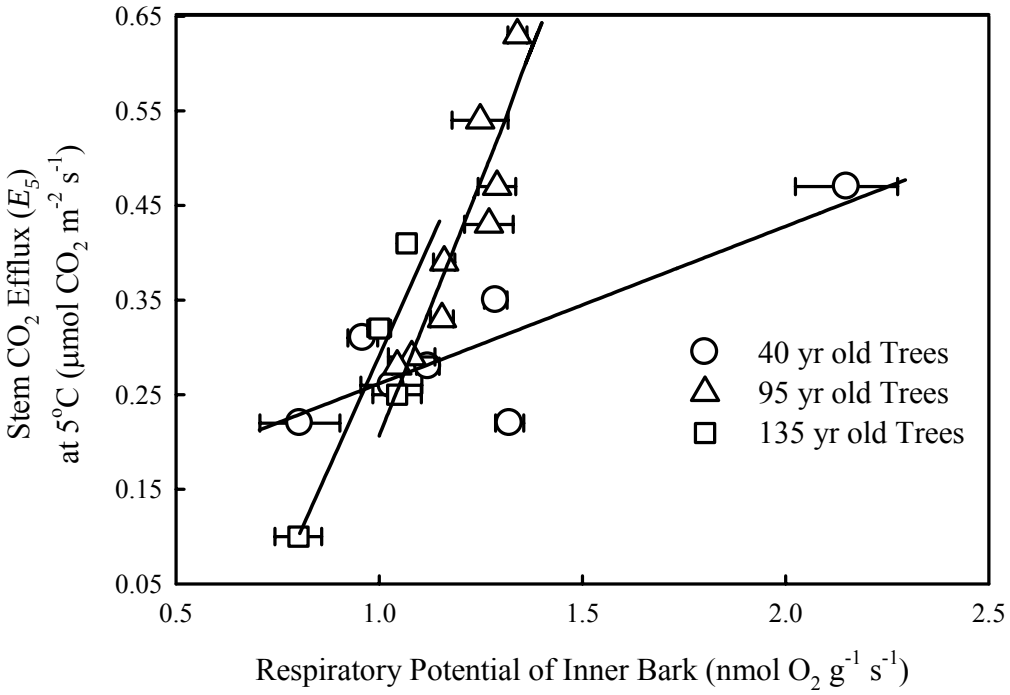

95 yr old Trees
135 yr old Trees
Stem $CO_2$ Efflux ($E_{20}$) at 20°C (µmol $CO_2$ $m^{-2}$ $s^{-1}$)
Avg. Maximum Sap Flux Density (kg $dm^{-2}$ $h^{-1}$)
6.0
5.0
4.0
3.0
2.0
1.0
0.0
0.25
0.55
0.85
1.15
1.45
1.75

**Figure 7.**


0.65
0.55
0.45
0.35
0.25
0.15
0.05
0.5
1.0
1.5
2.0
2.5
Stem $CO_2$ Efflux ($E_5$) at 5°C (µmol $CO_2$ $m^{-2}$ $s^{-1}$)
Respiratory Potential of Inner Bark (nmol $O_2$ $g^{-1}$ $s^{-1}$)
40 yr old Trees
95 yr old Trees
135 yr old Trees

## Chapter 6: The Contribution of Woody Tissue Respiration to the Carbon Balance of Red Oak Stands in Southwestern New York

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**Abstract**

Aggrading temperate deciduous forests in the eastern United States are an important sink in the global carbon cycle. We measured stem $CO_2$ efflux from respiration in woody stems was measured in three *Quercus rubra* stands ranging in age from 40- to 135-yrs to determine annual stand-level flux in an aggrading forest in southwestern New York. Annual estimates of $CO_2$ efflux from respiration in woody stems and branches ($E_T$) were derived from seasonal measurements of stem $CO_2$ efflux, hourly temperature measurements, and allometric equations. Annual wood production and canopy carbon uptake were also estimated for each stand. $E_T$ was found to be an important component of the carbon balance of temperate deciduous forests accounting for a flux to the atmosphere of 114-172 g C $m^{-2}$ $yr^{-1}$ and 10.3-16.9% of GPP which ranged between 998-1112 g C $m^{-2}$ $yr^{-1}$. $E_T$ did not increase consistently with stand age as rates of stem $CO_2$ efflux in the trees from the oldest stand (135 yrs) were significantly lower than those from the younger stands (40 and 95-yrs) during both the growing and dormant seasons. This reduction in $CO_2$ efflux rate offset the larger biomass in the oldest stand thereby supporting the conclusion that increases in woody tissue respiration with biomass accumulation in aging forests do not cause age-related declines in wood production.

**Keywords**

Stem Respiration, Temperate Deciduous Forest, *Quercus rubra*, $CO_2$ Efflux

## Introduction

Temperate forests in both North America and Eurasia are of global importance as they serve as major sinks in the global carbon cycle and are estimated to uptake 1.8-2.1 Pg C of atmospheric $CO_2$ annually (Fan et al. 1998; Ciais et al. 2000). In the eastern United States, forest land area has been steadily increasing since 1880-1920 (Houghton and Hackler 2000; Hall et al. 2002), due to the abandonment of farmland in the northeastern and southeastern states, and now consist largely of aggrading mid-successional deciduous forests (50 to 100 yrs old). These forests contain approximately 9.3 Pg C and account for 11% of land area and 31% of terrestrial stored carbon in the coterminous United States (Houghton and Hackler, 2000). Carbon uptake in these re-growing forests is likely to have been enhanced by a variety of direct and indirect anthropogenic factors including fire suppression (Mouillot and Field 2005), longer growing seasons (Myeni et al. 1997), elevated atmospheric $CO_2$ (DeLucia et al. 2005), increased diffuse radiation due to atmospheric pollutants (Farquhar and Roderick 2003; Rocha et al. 2005) and deposition of nitrogen (Townsend et al. 1996). Many studies have suggested that carbon uptake in US forests may decline or saturate in the future as these forests age (Birdsey et al. 1993; Turner and Koerper 1995; Field and Fung 1999; Hurtt et al. 2002); while others point out that successional changes in species composition and continuous recruitment of young trees to the canopy may lead to continued carbon uptake in maturing forests (Ryan et al. 1997; Carey et al. 2001). Further research on the carbon budgets of aggrading forests are necessary to determine if carbon uptake and sequestration will change as stands age in North American temperate deciduous forests.

Stems and branches are important components of the carbon budget of forest ecosystems as these woody tissues store carbon for long periods compared to leaves and fine roots. Respiration in stems and branches accounts for an annual flux of 50-500 Mg C $ha^{-1}$ to the atmosphere (Ryan et al. 1995; Valentini et al. 1996) and typically consumes 5-15% of forest gross primary productivity (GPP) (Meir and Grace 2002). However, most stand-level estimates of woody tissue respiration have been conducted in single-aged stands and few studies present data from more than one forest stand. As a result, there are relatively few predictions about the response of woody tissue respiration to environmental change or forest maturation. The limited available demonstrate that rates of woody tissue respiration and stand-level estimates differ greatly between stands (Lavigne et al. 1996; Lavigne and Ryan 1997; Ryan et al. 1997) and may respond to environmental perturbations as shown by experimental additions of nitrogen (Ryan et al. 1996; Maier et al. 1998; Stockfors and Linder 1998) and atmospheric $CO_2$ (Edwards et al. 2001; Zha et al. 2005). Trends in woody tissue respiration with forest age have been the subject of conjecture as early theoretical work proposed that woody tissue respiration increased with the accumulation of biomass accompanying stand age thereby consuming an increasing fraction of assimilated carbon and causing declines in forest productivity with stand age (Odum 1956; Yoda et al. 1965; Kira and Shideii 1967; Whittaker and Woodwell 1967). In contrast, recent studies suggest that woody tissue respiration rates and stand-level estimates of woody tissue respiration tend to decline with stand age (Ryan and Waring, 1992; Lavigne and Ryan 1997; Ryan et al. 2005) and that increased woody tissue respiration is not responsible for age-related declines in forest productivity.

However, the majority of these studies have been conducted on conifers and less in known about woody tissue respiration in angiosperms. In addition to the importance of temperate deciduous forests to the global carbon cycle, research on woody tissue respiration in these forests needs to be expanded to account for functional differences between conifer and angiosperm stems, such as higher sapwood cross-sectional area and increased role of sapwood for mechanical support in conifer stems (McCulloh et al. 2004). In addition, deciduous forest tree species have the potential for an increased contribution of woody tissue respiration to annual carbon budgets caused by the long leaf-less periods when respiration in woody stems and branches persists, albeit at a low rate, in the absence of photosynthesis.

In a previous study, measurements of stem $CO_2$ efflux from *Quercus rubra* (Northern red oak) trees in a temperate deciduous forest in southwestern New York state were found to be dependent on the respiratory activity of the underlying wood tissues, tree age, and time of year (Chapter 5). Specifically, rates of stem $CO_2$ efflux, on a stem surface area basis, were significantly lower in 135-year old *Q. rubra* trees than 95-yr old trees during the growing and dormant seasons. Carey et al. (2001) suggested that failure to account for age-related changes in $CO_2$ efflux rate when scaling to the stand-level may result in overestimates of woody tissue respiration in older forest stands by 200-500%. In this study, we investigate the stand-level consequences of observed tree-level differences in stem $CO_2$ efflux by coupling these measurements with data on stand mensuration, tree growth, branch $CO_2$ efflux and physiology, canopy foliage physiology, and climate to 1) derive stand-level estimates of $CO_2$ efflux ($E_T$) from respiration in woody stems and branches in three *Q. rubra*-dominated stands that range in age from 40- to 135-yrs, 2)

establish what proportion of stand-level $CO_2$ efflux is attributable to maintenance and growth processes in these three stands (Amthor 1986), 3) determine if patterns in stand-level $CO_2$ efflux across these stands reflect patterns in wood production or biomass accumulation, and 4) estimate what proportion of stand GPP is released back to the atmosphere as $CO_2$ efflux from woody tissues in these stands. We also analyze within-tree patterns in $CO_2$ efflux and respiratory physiology in *Q. rubra* trees to determine the importance of considering differences in $CO_2$ efflux between stems and branches in our stand-level estimates. Lastly, we discuss the observed trends in stand-level $CO_2$ efflux and its proportion of GPP in context of the debate over age-related declines in forest productivity.

## Materials and Methods

### *Site description*

Measurements of stem $CO_2$ efflux were made on *Quercus rubra* trees from three forest stands in Black Rock Forest in Cornwall, NY, USA (lat 41º 24′ N, lon 74º 01′ W). Meterological and soil characteristics for Black Rock Forest are presented in Chapter 5. Stand regeneration has typically occurred through sprouting from hardwood stumps after epeated timber harvest and fires (Tryon 1939). The youngest stand (39-yr old in 2004, referred to as 40-yr old stand) was thinned in 1935 then a small area (~0.32 ha) was clearcut in 1965. The trees in this stand were ~45-55 years old when the clearcut was conducted. The 95-yr old stand was heavily thinned in 1966 and mean tree age of study trees in this stand is currently 93.0 ± 1.1 yrs old. During this thinning, the superior red oak trees, and some white oak, were left standing while all other merchantible trees were

removed. The oldest stand was also thinned in 1934-1935; however, many trees were left standing at this site and the mean tree age of the study trees in this stand is currently 134.8 ± 3.3 years. During this thinning treatment, all chestnut oak, birch, and other dead or poorly-formed trees were removed. The three selected sites were located within 120-350 m of each other to minimize between site differences. *Quercus rubra* is the dominant tree species at each site accounting for 60.8 - 87.0 % of the aboveground woody biomass. *Quercus prinus* (chestnut oak) is abundant in the 40-yr old stand and accounts for 26.0 % of the woody biomass. *Acer rubrum* (red maple), *Quercus alba* (white oak), and black birch (*Betula lenta*) are also present as co-dominant or understory trees at all three sites.

A rectangular plot 400-900 $m^2$ in size was established within each stand with each plot containing 11-37 trees. Stem diameter was measured at 1.3 m height, on each tree greater than 0.05 m in diameter within each plot. Aboveground woody biomass (stem wood, stem bark, and branches) and sapwood volume were estimated from these diameter measurements using allometric equations for *Q. rubra* trees provided in Martin et al (1998). Aboveground woody biomass in five felled *Q. rubra* trees from Black Rock Forest (Schuster and Griffin, unpublished data) showed good agreement with this allometric equation as the actual dry weight of sampled trees was between 2.3 to –8.9% of predicted woody biomass for four sampled trees, while one tree differed substantially (-39.1%) from the predicted value (Fig. 1). Stand characteristics for the three plots are shown in Table 1. Stand leaf area index (LAI; $m^2$ leaf area $m^{-2}$ ground area) was measured by collection of foliage biomass with leaf litter traps in 2002 and 2004. Ten litter traps (~0.2 $m^2$ in area) were randomly placed within each plot. Leaf litter was

collected bi-weekly from mid-September to mid-November. Leaf area was determined for a sub-sample of 10-20 leaves per tree species for each collection period and then dried for at least 48 hrs at 70 ºC to determine the ratio of leaf area: leaf dry mass. The remaining leaf litter was separated by species then dried and weighed to derive stand-level LAI for each plot.

Air temperature data from a nearby micrometeorological station were used to estimate sapwood temperature at the plots. The station is located on an open exposed ridge top (elevation of ~350 m) with hourly temperatures recorded at a height of 2 m above the ground. To accurately predict hourly sapwood temperature at the study plots from weather station air temperature data, linear regressions were derived from time periods with concurrent measurements of air temperature and sapwood temperature (collected during stem $CO_2$ efflux measurements). These regressions serve to correct for disparities between sapwood and station air temperature caused by differences in elevation, site exposure, and canopy shading. During the leafless period (November-April), the relationships between plot sapwood and station air temperature was well described by stand-specific linear regressions (40-yr stand, Spwd Temp = 0.91* Air Temp – 0.23, $r^2$ = 0.92; 95-yr stand, Spwd Temp = 0.66* Air Temp + 1.61, $r^2$ = 0.75; 135-yr stand, Spwd Temp = 0.45* Air Temp + 0.61, $r^2$ = 0.78). During the growing season, separate day and night equations were necessary to account for the moderating effect of canopy shading and stem size on daytime sapwood temperatures in the 95- and 135-yr old stands, as shown in Fig. 2a. Correction equations for the growing season were: 40-yr stand, Spwd Temp = 0.69* Air Temp + 5.28, $r^2$ = 0.88; 95-yr stand, Day: Spwd Temp = 0.42* Air Temp + 9.68, $r^2$ = 0.73, Night: Spwd Temp = 0.62* Air Temp +

7.01, $r^2$ = 0.65; 135-yr stand, Day: Spwd Temp = 0.43* Air Temp + 10.12, $r^2$ = 0.62, Night: Spwd Temp = 0.58* Air Temp + 7.80, $r^2$ = 0.72. Application of these equations to station air temperature data accounted for 70.2 - 91.8% of the observed diel and seasonal variability in sapwood temperature, depending on the stand or season, as shown in Fig 2b.

*Measurements of $CO_2$ Efflux*

Measurements of $CO_2$ efflux rates from woody stems of *Q. rubra* trees in the plots were made during eight sampling periods in 2002 and 2004. During each sampling period, 95-150 hours of $CO_2$ efflux data were collected for each tree. Measurements in the 40-yr old stand were made in June 2002 and 2004, September 2002, and November 2004; measurements in the 95-yr old stand were made in June 2004 and November 2004; measurements in the 130-yr old stand were made in July 2002 and 2004; September 2002; and December 2004. November-December sampling periods were conducted after leaffall to remove the effects of growth, cell expansion, and sap flow on stem $CO_2$ efflux. $CO_2$ efflux measurements were made on nine trees in the 40 yr old stand (0.12- 0.22 m DBH), eight trees in the 95 yr old stand (0.32-0.48 m DBH), and four trees in the 135 yr old stand (0.51-0.64 m DBH). The methods utilized for measuring $CO_2$ efflux were similar to those described in Bowman et al. (2005). Polycarbonate gas-exchange chambers (~250 $cm^2$) were attached to the north-side of the selected stems at a height of ~1.4 m. The edges of the chambers were fitted with closed-cell neoprene foam to serve as a gasket between the chamber and the stem. During the 2002 sampling periods, smaller chambers (~50 $cm^2$) made from 2 cm (inside diameter) plastic pipe cut in half

lenghtwise were utilized. Caulking cord (Mortite Inc., Kankakee, IL,USA) was used to seal small gaps that occurred between the chamber and the tree. The chambers were then secured tightly to the tree using ratchet straps and then vigorously leak tested.

$CO_2$ efflux was measured with an infrared gas analyzer (LI-6262 in 2004 measurements, LI-6251 in 2002 measurements; Li-Cor Inc., Lincoln, NE, USA) in an open flow system connected to an automated manifold controlled by a datalogger and relay driver (CR23X and SDM-CD16AC; Campbell Scientific Inc., Logan, UT, USA). Each chamber was sampled for 12 min with each chamber sampled once during each 132 min measurement cycle. A measurement cycle consisted of nine stem sampling periods and tests of the zero and span calibrations of the gas analyzer. Measurements were only considered valid if the $CO_2$ efflux rate was stable (less than 3% variation) for the last 60 s of the measurement period. Sapwood temperature proximal to the $CO_2$ efflux sampling chamber was measured using constantan-chromega thermocouples inserted 15 mm into the sapwood. In this study, all $CO_2$ efflux rates are presented on a sapwood-volume basis. Sapwood thickness was measured with a 5 mm increment core taken adjacent to the $CO_2$ efflux chamber. Sapwood thickness was determined visually by the difference in color between sapwood and heartwod tissues and measured with a digital caliper. Sapwood volume under the chamber was calcualted by multiplying sapwood thickness by the surface area enclosed within the stem chamber. The $CO_2$ efflux rates were corrected for variation due to temperature using a modified Arrhenius function as adopted by Turnbull et al. (2003), where $CO_2$ efflux at a given sapwood temperature is described as:

Eqn. 1: $$E_A = E_o \cdot e^{\frac{A_o}{R_g}\cdot\left(\frac{1}{T_o}-\frac{1}{T_a}\right)}$$

where $E_o$ is the $CO_2$ efflux rate at the base temperature $T_o$, $T_a$ is the sapwood temperature, $R_g$ is the ideal gas constant (8.314 J $mol^{-1}$ $K^{-1}$), and $A_o$ is a parameter related to the overall activation energy which describes the magnitude of the temperature response. Nonlinear curve fitting for temperature response curves was conducted with SigmaPlot 2001 (SPSS, Inc., Chicago, IL).

*Measurements of Within-Tree Variation in $CO_2$ efflux and Respiratory Potential*

Efflux of $CO_2$ from mid-stems and branches was measured in three *Q. rubra* trees (DBH 0.21, 0.25, and 0.37 m) on a neighboring site where a 7m scaffolding tower allowed canopy access. Measurements were made for 2-3 weeks in late September to early October in 2004 at heights of 1.3 (lower stem, n = 3), 4.5 (mid stem, n = 2), and 6.5 (branch, n =3) m corresponding to mid stem and branch diameters ranging from 0.7 – 0.13 m. $CO_2$ efflux chambers were covered with opaque plastic sheeting to prevent measurements errors due to corticular photosynthesis. Wood respiratory potential and nitrogen concentration of inner bark and outer sapwood tissues were measured at each $CO_2$ efflux sampling position following the procedures described in Chapter 5.

*Estimates of Biomass Production and Canopy Carbon Uptake*

Weekly and annual aboveground woody biomass increment for each forest stand were derived from measurements of stem diameter growth using manual band dendrometers (Model D1-L; UMS GmbH, Munich, Germany). These dendrometers were installed in May 2003 and measured weekly during the 2004 growing season on 8-12 trees within each plot. Dendrometers were measured between 1100-1300 h to minimize

errors associated with diel fluctuations in stem diamter due to transpiration and the use of water stored within stems. Relative woody biomass increment (g of new biomass $kg^{-1}$ of exising biomass) and growth efficiency (g of new biomass $m^{-3}$ of canopy volume) were calculated using allometric equations (Martin et al. 1998) and canopy volume data (Carson 2005). The mean relative woody biomass increment calcualted for the trees fitted with dendrometer bands was applied to all trees in each study plot to estimate stand-level annual aboveground woody biomass production.

A forest canopy model was used to estimate daily values for canopy photosynthesis and determine both annual canopy carbon uptake or gross primary productivity (GPP) and the ratio of stand-level woody tissue $CO_2$ efflux to GPP for each stand. This one-dimensional, multi-layer model has been previously described and utilized to estimate canopy carbon uptake in a *Quercus* canopy located in a more mesic portion of Black Rock Forest by Whitehead et al (2002) and (2004). The forest canopy is partitioned into twenty homogeneous layers based on the vertical distribution of canopy leaf area of a mixed *Quercus* forest described in Hutchinson et al. (1986). The model scales of leaf physiological processes to the canopy level by estimating radiative transfer, energy balance, evaporation, and photosynthesis (Leuning et al. 1995) for each canopy layer. Soil water balance is also predicted to incorporate the effects of soil water deficit on canopy carbon uptake (Whitehead et al. 2002). Micrometeorological inputs required by the model are daily maximum and minimum temperature, shortwave radiation (400-700 nm), and rainfall from which hourly values of temperature, irradiance, and air saturation deficit are calculated according to Goudriaan and van Laar (1994). Leaf energy balance and a coupled photosynthesis-stomatal conductance sub-model (Leuning,

1995) are used to calculate photosynthesis for sunlit and shaded foliage in each layer (Leuning et al. 1995). The rate of photosynthesis of a leaf is determined by the minimum of the rates of Rubisco- (ribulose-1,5 bisphosphate) catalyzed carboxylation ($V_{cmax}$) and regeneration ($J_{max}$) of RuBP (ribulose- 1,5 bisphosphate) (Farquhar et al. 1980). Values for $V_{cmax}$ and $J_{max}$ parameters were derived from measurements made on canopy leaves from twelve *Q. rubra* trees in each of the three forest stands in June and September of 2004 (Table 2, *Griffin et al. unpublished data*). The temperature dependence of photosynthesis was represented according to Bernacchi et al. (2001) using parameter values derived from Walcroft et al (1997). Total photosynthesis is estimated across canopy layers and daily values are obtained using Gaussian integration following Goudriaan and van Laar (1994). In addition to $V_{cmax}$ and $J_{max}$, seven other parameters ($Rd$, $\alpha_{leaf}$, $\beta$, $a$, $g_{s0}$, $g_{smax}$, and $D$) are required to describe the physiological responses of leaves (see Table 2 for definitions and parameter values). The parameters *Wmin* and *Wmax*, describing root-zone water storage, were used to derive daily calculations of soil water balance (Whitehead et al. 2002) and determine a coefficient to limit photosynthesis and respiration when daily root-zone water storage fell below 50% of its maximum value.

*Annual Stand-Level Estimates of Woody Tissue $CO_2$ Efflux and Its Maintenance and Growth Components*

Total $CO_2$ efflux from woody stems and branches ($E_T$) for each *Q. rubra* stand was estimated throughout the year using mean values of $E_{15}$ and $A_o$ for each stand, hourly sapwood temperature data, the temperature response function described in Eqn. 1, and allometric estimates of stand sapwood volume. We assumed that the $CO_2$ efflux rate for

branch sapwood was the same as that measured for stem sapwood. During the growing season, measurements of $E_{15}$ and $A_o$ collected in June-July 2004 and September 2002 were used to estimate $E_T$ for the months of April-July and August-October, respectively. Due to the absence of measurements in September 2002 for the 95-yr old stand, $E_{15}$ for August-October was assumed to be 55% of the measured value in June-July consistent with the seasonal changes in $E_{15}$ observed in the 40- and 135-yr old stands. $E_{15}$ and $A_o$ measured in November-December 2004 were used to estimate $E_T$ for the dormant season months of January-March and November-December.

The proportion of $E_T$ attributable to maintenance respiration ($R_M$), *i.e.* respiration associated with protein synthesis and turnover, membrane repair, and maintenance of ion gradients (Penning de Vries, 1975), was similarly estimated by extrapolating $E_{15}$ and $A_o$ measurements obtained in November-December 2004 throughout the year using sapwood temperature and stand sapwood volume. The proportion of $E_T$ attributable to growth respiration ($R_G$), *i.e.* respiration associated with construction of new biomass, was calculated using two methods. In the first method ($R_{G1}$), growth respiration was estimated as the difference between $E_T$ and $R_M$. This technique is referred to as the mature tissue method (Sprugel and Benecke 1991) and assumes that $E_{15}$ and $A_o$ of maintenance respiration are conservative throughout the year. For stand-level estimates of $E_T$, $R_M$, and $R_{G1}$, values for $A_o$ are presented in Table 3 of Chapter 5. In the second method, growth respiration was calculated at bi-weekly intervals based on diameter increment measured on 8-12 trees and using a growth coefficient ($r_g$; 0.23 g C produced by respiration per g of new biomass constructed) derived from the construction cost of *Quercus* sapwood (Wullschleger et al. 1995). In order to covert diameter increment to

woody tissue mass, sapwood density was determined for each tree in which $CO_2$ efflux was measured from wood cores extracted from each stem at a height of 1.3 m with a 5 mm increment borer. Sapwood density, or specific gravity, was measured as the ratio of fresh wood volume and dry mass (Panshin and de Zeeuw, 1980). Fresh volume was calculated by carefully measuring the length and diameter with electronic calipers at four positions around the circumference of each sapwood segment. Dry mass was determined after wood samples were oven dried for 48 h at 70ºC.

*Statistical analysis*

The effects of tree age and season on stem $CO_2$ efflux at 15º C ($E_{15}$) were analyzed with a two-way analysis of variance (ANOVA) (DataDesk 6.0; Data Description, Inc., Ithaca, NY). Differences between age classes were compared using least significant difference (LSD) post-hoc analysis and considred to be statistically significant if $P \leq 0.05$ (Sokal and Rohlf 1981). The effect of stand age on stem diameter increment, growth efficiency, and stem $CO_2$ efflux at 5 and 20º C ($E_5$ and $E_{20}$, respectively) and the effect of tree position on wood respiratory potential and nitrogen concentration were determined with one-way ANOVAs (DataDesk 6.0). Paired *t*-tests were used to determine the effects of tree position on $E_{15}$ and $A_o$ of $CO_2$ efflux (DataDesk 6.0). Regression analyses were performed using the general linear model function in SigmaPlot 2001 (SPSS, Inc., Chicago, IL).

## Results

*Between-Tree, Within-Tree and Seasonal Variation in Stem $CO_2$ Efflux*

Sapwood-volume based rates of stem $CO_2$ efflux at a common temperature of 15 ºC ($E_{15}$) exhibited significant seasonal variation in the 40- and 95-yr old *Q. rubra* trees as $E_{15}$ values were greatest in the early to mid growing season (June and July) and then declined significantly through the year (Fig. 3, Table 3, two-way ANOVA, $P < 0.01$). In contrast, the more gradual decline observed in $E_{15}$ in the 140-yr old stand was not statistically significant (Fig. 3, Table 3, $P > 0.05$). No significant differences in $E_{15}$ values were observed between the September and November-December measurement periods. Within seasons, comparisons of $CO_2$ efflux rates across age classes were made at seasonally appropriate temperatures, 20 ºC and 5 ºC, for the June-July and November-December measurement periods, respectively. The 40- and 95-yr old trees exhibited significantly greater $E_{20}$ values, 105.2 ± 19.6 to 125.3 ± 12.1 and 119.3 ± 9.9 μmol $m^{-3}$ $s^{-1}$, respectively, and the 135-yr old trees, 40.6 ± 11.2 to 57.7 ± 5.9 μmol $m^{-3}$ $s^{-1}$ (Table 4, one-way ANOVA, $P < 0.01$). Similarly, during the dormant season, the 135-yr old trees had significantly lower $CO_2$ efflux rates at 5ºC, 11.3 ± 2.4 μmol $m^{-3}$ $s^{-1}$, than the 40- and 95-year old trees, 18.9 ± 2.2 and 21.0 ± 1.8 μmol $m^{-3}$ $s^{-1}$, respectively (Table 4, one-way ANOVA, $P < 0.05$).

$CO_2$ efflux at 15 $^{o}$C ($E_{15}$) rates and the temperature response of $CO_2$ efflux ($A_o$) exhibited no significant differences between the lower stems and branches in *Q. rubra* (Table 5, Paired t-test, $P > 0.05$). In addition, the respiratory potential of inner bark and sapwood tissues did not vary with tree height (Table 5, one-way ANOVA, p = 0.49 and 0.70) nor did inner bark nitrogen concentration show significant differences between tree positions ($P = 0.443$). In contrast, sapwood nitrogen concentration did vary with tree height ($P = 0.02$) with branches exhibiting significantly greater nitrogen concentrations

(0.29 ± 0.02 g $g^{-1}$) relative to mid- and lower stems (0.21 ± 0.01 g $g^{-1}$). Both mean respiratory potential (1.04 ± 0.08 nmol $CO_2$ $g^{-1}$ $s^{-1}$) and nitrogen concentration (0.40 ± 0.01 g $g^{-1}$) were significantly greater in inner bark tissue than that of sapwood tissues (0.28 ± 0.03 nmol $CO_2$ $g^{-1}$ $s^{-1}$ and 0.23 ± 0.01 g $g^{-1}$, respectively) (paired t-tests, $P <$ 0.01). There was a significant positive relationship between the $CO_2$ efflux from a given branch and that branch's sapwood thickness (Figure 4, y = 39.21x +0.2, $r^2 = 0.59$, $P <$ 0.01), but this relationship was not found for $CO_2$ efflux from the lower stems. No significant relationships between branch $CO_2$ efflux and other potential predictors of respiratory $CO_2$ production such as branch size, nitrogen content, or respiratory potential were observed.

*Annual Estimates of Carbon Accumulation, $CO_2$ Efflux, and Canopy Carbon Uptake*

Prior to the 2004 growing season, the aboveground woody biomass was 63, 145, and 226 Mg $ha^{-1}$ for the 40-, 95-, and 135-yr old stands, respectively. Stem diameter growth, shown as woody biomass increment, was found to commence at the end of April and increase rapidly, attaining maximum values in mid July (Figure 5 a-c). Biomass increment then declined sharply and ceased by mid September. The periods of high stem growth corresponded to high values of $E_{15}$ observed in June and July in all stands. As expected, mean biomass increment per tree increased substantially with tree size from 5.5 ± 0.8 kg $tree^{-1}$ in the 40 yr old trees to 28.3 ± 3.3 kg $tree^{-1}$ in the 135 yr old trees while annual stem diameter increment showed a slight, yet significant, decline with increasing tree age from 4.2 (± 0.4) mm in the 40 yr old trees to 2.7 (± 0.3) mm in the 135 yr old trees ($P < 0.01$, one-way ANOVA, Table 6). Similarly, the annual aboveground

production of woody biomass in the young stand (4.44 Mg $ha^{-1}$) greatly exceeded that of the older stands which accumulated approximately 3 Mg $ha^{-1}$. However, mean stem growth efficiency, measured as the ratio of biomass increment (kg $tree^{-1}$) to tree leaf area ($m^2$ $tree^{-1}$) (tree leaf area data from *R. Carson, unpubl. data*), did not decrease significantly with tree age ($P > 0.05$, one-way ANOVA, Table 6). Sapwood in these *Q. rubra* trees was found to have a mean carbon concentration of 46.6 %, therefore, the aboveground biomass increment in these stands equates to carbon accumulation of 2.1 Mg C $ha^{-1}$ $yr^{-1}$ in the youngest stand and 1.4 Mg C $ha^{-1}$ $yr^{-1}$ in the older stands in 2004.

Estimated annual stand-level $CO_2$ losses from the woody stems and branches ($E_T$) are presented in Table 7 and seasonal variation is shown in Figure 5 d-f. Stand-level $E_T$ were predicted to be similar in the 40- and 135-yr old stands, 116.2 and 114.1 g C $m^{-2}$ ground area $yr^{-1}$, respectively, but ~50% higher in the 95-yr old stand at 172.7 g C $m^{-2}$ $yr^{-1}$. The stand-level contribution of $R_M$ to $E_T$ ranged from 53.2 to 101.6 g C $m^{-2}$ $yr^{-1}$ and increased with stand age. Estimates of stand-level $CO_2$ efflux ($E_T$) greatly exceeded the sum of maintenance respiration ($R_M$) and growth respiration ($R_{G2}$) in the 40- and 95-yr old stands, but not in the 135-yr old stand. As a result, estimates of $R_{G1}$ and $R_{G2}$ differed substantially for the 40- and 95-yr old stands. The growth coefficient ($r_g$) for these *Q. rubra* trees, calculated as the slope of the relationship between amount of carbon in newly constructed wood biomass and the amount of $CO_2$ efflux from stems attributable to growth processes within the stems, was estimated to be 0.34 g C respired $g^{-1}$ C in new tissue (Figure 6). This estimate of $r_g$ is higher than the value from Wullschleger et al. (1997) for *Quercus* sapwood (0.23 g C $g^{-1}$ C) that was used to calculate $R_{G2}$.

Model estimates of the canopy carbon uptake (GPP) were similar across these three stands with predicted estimates ranging from 985 to 1115 g C $m^{-2}$ ground area $yr^{-1}$ (Table 7). Canopy carbon uptake was greatest in mid-June (~8-10 g C $m^{-2}$ $d^{-1}$) coinciding with the seasonal maximum in day length and canopy interception of radiation (Figure 5 a-c). Canopy carbon uptake then declined in all stands throughout the summer, with predicted canopy carbon uptake rates of ~2-3 g C $m^{-2}$ $d^{-1}$ in late September, until leaf fall in mid- to late October. The decline in predicted assimilation corresponded to 1) seasonal changes in leaf photosynthetic and respiratory parameters 2) decreased soil water availability and 3) decreased canopy light interception due to decreasing day length. The variability in canopy carbon uptake throughout the growing season was caused by declines in photosynthesis on overcast days. The fraction of gross assimilated carbon re-released as $CO_2$ efflux from the stems and branches ($E_T$) ranged between 10.2 – 17.0 % and was not related to stand age.

## DISCUSSION

### *Between-Tree, Within-Tree, and Seasonal Variation in $CO_2$ efflux*

In *Quercus rubra*, sapwood volume-based stem $CO_2$ efflux rates exhibited seasonal variation and tended to be higher than those from other temperate hardwood trees. Mean values of $CO_2$ efflux at 15 ºC ($E_{15}$) ranged from 40.6 ± 11.2 to 125.3 ± 12.1 μmol $CO_2$ $m^{-3}$ $s^{-1}$ in the early to mid growing season and 22.3 ± 4.0 to 38.4 ± 5.5 μmol $CO_2$ $m^{-3}$ $s^{-1}$ during the dormant season. $E_{15}$ decreased significantly between the growing and dormant seasons in the 40- and 95-yr old trees, whereas the 135-yr old trees showed

no significant seasonal variation. This lack of a seasonal trend in the 135-yr old trees is attributable to the relative importance of maintenance respiration in these older trees. These values are slightly lower than previous estimates of stem $CO_2$ efflux in *Q. rubra* and other congeneric species (*Q. prinus* and *Q. alba*) (Edwards and Hanson 1996; Curtis et al. 2005). Data from this and other studies suggest that stem $CO_2$ efflux rates from *Quercus* species and other ring-porous trees (such as *Fraxinus pennsylvanica*, 130.9 μmol $CO_2$ $m^{-3}$ $s^{-1}$, Bolstad et al. 2005) are generally greater than those from other temperate deciduous trees (18.9-64.6 μmol $CO_2$ $m^{-3}$ $s^{-1}$, Bolstad et al. 2005) perhaps due to the small sapwood volume typical of ring-porous species. Therefore, due to large differences between diffuse-porous and ring-porous trees, generic rates of sapwood volume-based $CO_2$ efflux for hardwood trees should not be used for scaling $CO_2$ efflux from woody tissues to the stand level.

Stem $CO_2$ efflux rates declined with tree age in *Q. rubra* as has been observed in several other studies. For example, stem $CO_2$ efflux declined in *Pinus banksania* trees between the ages of 16-26 and 60-70 years (Lavigne and Ryan 1997) and in 1-6 yr old *Eucalyptus saligna* trees (Ryan et al. 2005). In *Pinus ponderosa*, Carey et al. (1997) reported a negative correlation between $CO_2$ efflux and stem size, while no difference was found between 50 and 250 yr old trees (Law et al. 1999). The age-related decreases in sapwood volume-based $CO_2$ efflux rates found in this study were similar to those observed for surface area-based $CO_2$ efflux rates (Chapter 5) During the growing season, age-related decreases in $CO_2$ efflux at 20 ºC ($E_{20}$) were attributable to decreases in diameter increment (Table 6) as $E_{20}$ rates on both sapwood volume (this study) and surface area (Chapter 5) bases were significantly greater in the 40- and 95-yr old trees

than in the 135-yr old trees in June and July. During the dormant seasons, sapwood volume-based $E_5$ was also significantly lower in the 135-yr old trees than the 40- and 95-yr old trees. However, it is likely that this is due to a decrease in inner bark, not sapwood, respiratory activity as *Q. rubra* $CO_2$ efflux during the dormant season was correlated with the respiratory potential of inner bark tissues (Chapter 5). Surface area-based $E_5$ also confirm that respiratory activity was lower in the 135-yr old trees than the 95-yr old trees, but not the 40-yr old trees, as there was no significant difference between surface area-based $E_5$ in the 135- and 40-y r old trees (Chapter 5).

Stem and branches were found to be physiologically similar in *Q. rubra* as rates of $CO_2$ efflux from branches were not significantly different than those from lower stems. Furthermore, there were also few significant differences in various proxies for the amount of metabolic activity within woody tissues between branches and lower stems, including wood respiratory potential, inner bark nitrogen concentration, and sapwood thickness. These findings are in contrast with many previous studies that have observed branch $CO_2$ efflux rates that were 20-40 times greater than stem $CO_2$ efflux rates (Sprugel 1990; Ryan et al. 1996; Maier et al. 1998; Ceschia et al. 2002; Damesin et al. 2002). Elevated $CO_2$ efflux in branches has typically been attributed to increased metabolic activity in branches due to growth, transport, and proximity to substrate supply from leaves (Sprugel 1990) and/or the transport of dissolved $CO_2$ in the xylem sap from lower portions of the tree (Teskey and McGuire 2002).

$CO_2$ efflux from branches and mid stems was found to be strongly related to sapwood thickness. This is similar to studies that have reported correlations between branch $CO_2$ flux and branch volume in tree species where branches were assumed to be

entirely sapwood (Ryan at al. 1996). However, the relationship between efflux and sapwood thickness was not valid for lower stems and there were no significant differences in either sapwood thickness or $CO_2$ efflux between stems and branches. The failure of this relationship to include both lower stems and branches may be due to greater bark thickness, and therefore more resistance to $CO_2$ diffusion, in lower stems.

The absence of differences in $CO_2$ efflux, respiratory potential, and sapwood thickness between stems and branches indicates strongly that stem and branches are physiologically more similar in *Quercus rubra* than would expected from previous studies of branch $CO_2$ efflux. Previous studies have concluded that failure to account for differences in $CO_2$ efflux between stems and branches can result in large errors (30-40%) when scaling up to the stand-level (Damesin et al. 2002). The similarity of $CO_2$ efflux rates between stems and branches observed in this study suggests that this is not the case for *Q. rubra* and that estimating stand-level woody tissue respiration solely from stem $CO_2$ efflux measurements is suitable in forest stands dominated by this species. A potential source of error in this analysis is that the measurements of $CO_2$ efflux from these stems and branches were made at the end of the growing season in mid- to late September. Many studies have attributed increased branch respiration rates to transport of $CO_2$ in the transpiration stream. It is not likely that xylem transport of $CO_2$ to branches had stopped prior to our measurements as 1) efflux measurements were made four to five weeks prior to leaf fall and during active sap flow and 2) studies have shown that elevated xylem $CO_2$ concentrations, *i.e*. greater than 4%, are observed throughout September and into October (Eklund 1990; McGuire and Teskey 2004). Therefore, we propose the lack of elevated $CO_2$ efflux rates in branches during periods of transpiration

is further evidence that xylem transport of $CO_2$ is not significant in *Q. rubra*, and perhaps in all *Quercus* species, as put forth in Chapter 4. Similarly, $CO_2$ efflux rates did not vary with stem/branch position in *Quercus mongolica* during both the growing and dormant seasons (Utsugi et al. 2005). While elevated rates of $CO_2$ efflux in branches are widely accepted, published reports are limited to coniferous tree species and *Fagus sylvatica*. Our findings suggest that elevated rates of $CO_2$ efflux from branches, relative to stems, may not be ubiquitous in forest trees.

*Annual Woody Tissue Respiration, Aboveground Biomass Increment, and Canopy Carbon Uptake*

Our stand-level estimates of the $CO_2$ flux to the atmosphere from respiration in woody stems and branches ($E_T$) ranged from 114-172 g C $m^{-2}$ $yr^{-1}$ in the three *Quercus* stands and are consistent with a *Quercus-Acer* forest in Tennessee (149-204 g C $m^{-2}$ $yr^{-1}$; Edwards and Hanson 1996). These estimates from *Quercus*-dominated forests tend to be lower than those from other temperate-broadleaf forests such as 325-544 g C $m^{-2}$ $yr^{-1}$ from European beech forests (Valentini et al. 1996; Damesin et al. 2002) and 225-242 g C $m^{-2}$ $yr^{-1}$ in *Acer saccarhum* stands (Bolstad et al. 2004), but higher or similar to estimates from various *Populus* stands (77-124 g C $m^{-2}$ $yr^{-1}$, Ryan et al. 1997; 19-20 and 148-159 g C $m^{-2}$ $yr^{-1}$, Bolstad et al. 2004; 166 g C $m^{-2}$ $yr^{-1}$, Curtis et al. 2005).

The annual aboveground biomass and carbon increment ranged between 3.0-4.4 Mg biomass $ha^{-1}$ $yr^{-1}$ and 1.4-2.1 Mg C $ha^{-1}$ $yr^{-1}$, respectively, for these three *Q. rubra* stands. As expected, annual wood production per unit area was substantially lower in the 95- and 135- yr old (3.0 Mg C $ha^{-1}$ $yr^{-1}$) stands than the 40-yr old stand (4.4 Mg C $ha^{-1}$ $yr^{-}$

$^{1}$) consistent with the decline in aboveground net primary productivity typically observed with age in even-aged forest stands (Kira and Shidei 1967; Gower et al. 1996, Landsberg and Gower 1997). Similar results have been found in *Q. alba* where maximum stand growth occurred at 30 years and then declined by 50% over the next 30 years (Gingrich, 1971). The rates of biomass and carbon increment observed in this study are greater than the long-term average aboveground biomass accumulation of 2.17 Mg biomass $ha^{-1}$ $yr^{-1}$ from 1930-2000 and the average forest-wide rate of aboveground carbon accumulation in Black Rock Forest between 1994-2000 of 1.2 Mg C $ha^{-1}$ $yr^{-1}$ (Schuster et al. *In review*). These measures of stand productivity in Black Rock Forest are broadly consistent with the aboveground carbon increment in Harvard Forest (1.4 Mg C $ha^{-1}$ $yr^{-1}$, Barford et al. 2001) and aboveground woody biomass production for Orange County, NY (4.1-6.0 Mg biomass $ha^{-1}$ $yr^{-1}$, Brown and Schroeder 1999).

Canopy carbon uptake or gross primary productivity (GPP) exhibited little variation (~10%) between the three *Q. rubra* stands ranging between 985-1115 g C $m^{-2}$ $yr^{-1}$. The slight increase in canopy carbon uptake was due largely to increases in LAI with stand age although these increases were offset slightly by small, and statistically insignificant, differences in $V_{cmax}$, $J_{max}$, and $R_d$ with stand age. These carbon uptake estimates are lower than other published estimates from *Quercus* dominated hardwood stands at Harvard Forest (1300 g C $m^{-2}$ $yr^{-1}$, Barford et al. 2001) and Oak Ridge (1725 g C $m^{-2}$ $yr^{-1}$, Malhi et al. 1999). The differences in canopy carbon uptake between Black Rock Forest and these stands is likely due to differences in LAI which were greater at both Harvard Forest (3.2 $m^2/m^2$) and Oak Ridge (4.9 $m^2/m^2$) sites.

Biomass accumulation in northeastern forests was predicted to reach an equilibrium after 100 years by Bormann and Likens (1979). The high predicted GPP in the 135-yr old stand and the absence of a decline in wood production in the 95- and 135-yr old stands do not suggest that a saturation of carbon uptake in this forest. Similarly, an aggrading *Pinus strobus* forest exhibited continued carbon accumulation in woody biomass for 120 years after stand initiation (Hooker and Compton 2003). Since live wood biomass is the dominant sink in re-growing forests (Schlesinger and Lichter 2001), our study suggests that carbon sequestration in aggrading deciduous forests in the northeastern United States can continue for well over century after stand initiation.

The findings regarding age-related trends and differences between forests stands in estimates of $E_T$ and its maintenance and growth components, their proportion of GPP, or annual wood production observed in this study may be site specific. However, due to the paucity of studies that present data on woody tissue respiration and annual wood production or GPP in different aged stands, it is worthwhile to examine the trends in woody tissue respiration during stand development in this forest. Stand-level woody tissue respiration ($E_T$) and the proportion of GPP consumed by woody tissue respiration were similar in the 40- and 135-yr old stands, but not constant with stand age as $E_T$ and its proportion of GPP were ~50% greater in the 95-yr old stand. This decline in $E_T$ in the 135-yr old trees, despite significant accumulation of biomass, occurred due to the significantly lower rates of $CO_2$ efflux during both the growing season and dormant season.

Total woody tissue respiration also declined from 27-38 g C $m^{-2}$ $yr^{-1}$ in < 25 yr old *Pinus banksania* to 22-30 g C $m^{-2}$ $yr^{-1}$ in 63 yr old trees (Ryan et al, 1997) and

woody tissue respiration in a *Pinus contorta* chronosequence declined as reduced growth respiration in the older stands offset small increases in sapwood maintenance respiration (Ryan and Waring, 1992). However, it is important to note that woody tissue respiration may also increase during early stages of stand development as shown in this study between the 40- and 95-yr old stands. Similarly, stand-level woody tissue respiration was eight times greater in > 40 yr old *Populus tremuloides* stands than in ~25 yr old stands (Bolstad et al. 2005). In a fast-growing *Eucalyptus* plantation, woody tissue respiration and annual wood production were synchronized as both increased prior to canopy closure but each declined thereafter (Ryan et al. 2004). Our study suggests that changes in stand-level woody tissue respiration and wood production may not be coordinated in all forest stands as $E_T$, $R_M$, and their proportion of GPP in these *Q. rubra* stands increased sharply between the 40- and 95-yr stands, in contrast with the changes in stand-level wood production which declined by ~50% between these stands.

Our findings of a decline in $E_T$ and its proportion of GPP between the 95- and 135-yr old stands, despite an increase in LAI and GPP between these stands, is in contrast with the observations of Meir and Grace (2002) that stand-level woody tissue respiration and its proportion of GPP are positively correlated with LAI across a wide range of tree stands differing in species composition, climate, and phenology. Their relationship between stand-level woody tissue respiration and LAI was attributed to the general correlation between leaf area and sapwood area (Shinozaki et al, 1964; Mencucini and Grace, 1995). Our study indicates that this pattern may not be valid for differences in LAI related to stand development as the woody tissue respiration per unit sapwood volume is likely to change with stand age.

*Maintenance Respiration, Growth Respiration, and $r_g$*

The contribution of maintenance respiration ($R_M$) to total $CO_2$ efflux from woody stems and branches, calculated as either $E_T$ or $R_M + R_{G2}$, was estimated to increase with stand age as $R_M$ was 46-56% of $CO_2$ efflux in the 40-yr old stand, 53-76 % in the 95-yr old stand, and 75-78% in the 135-yr old stand. At the stand level, this trend is expected as a consequence of the increase in total woody biomass and sapwood volume with stand age and the decrease in growth respiration due to the decline in biomass production with stand age. This trend was also reported in *Pinus contorta* stands as maintenance respiration increased from 23 to 63% of woody tissue respiration in 40- and 240-yr old stands (Ryan and Waring 1992). In addition, maintenance respiration was found to be only 16-19% of total respiration in *Q. alba* saplings (Wullschleger et al. 1995) and 47-53% of total respiration in *Q. alba* trees in a 40 to 70 yr old forest (Edwards and Nelson 1996).

Estimates of $CO_2$ efflux due to growth respiration ($R_G$) differed depending on the method of calculation. Growth respiration derived from the mature tissue method ($R_{G1}$) were 0.8 and 2.4 times greater in the 40- and 95-yr stands, respectively, than estimates calculated from wood biomass production and growth coefficients derived from the construction cost of sapwood ($R_{G2}$). Interestingly, both methods produced similar estimates of $R_G$ in the 135-yr old stand. Similar results were reported in Edwards and Hanson (1996) where the use of construction cost-based coefficients underestimated growth respiration relative to the mature tissue method in *Q. alba* and *Acer rubrum*, but not in *Q. prinus*. Likewise, the growth coefficient ($r_g$) calculated in this study from the

relationship between the amount of carbon in newly constructed wood biomass and the amount of $CO_2$ efflux from stems attributable to growth processes (0.34 g C respired $g^{-1}$ C in new tissue) is higher than estimates derived from the construction cost of sapwood in *Q. alba* (0.23 g C $g^{-1}$ C, Wullschleger et al. 1997) and *Pinus ponderosa* (0.16-0.17 g C $g^{-1}$ C, Carey et al 1996). However, our estimate of $r_g$ is similar to those estimated using the mature tissue method in boreal forest species (0.25-0.76 μmol $\mu mol^{-1}$, Lavigne and Ryan, 1997).

Previous studies have hypothesized that the difference in estimates of growth respiration derived from construction cost-based growth coefficients and the mature tissue method are due to 1) inaccurate estimates of the cost of wood biosynthesis (Edwards and Hanson 1996), 2) underestimates of maintenance respiration by the mature tissue method due to correlations between maintenance respiration and growth rate (Lavigne and Ryan 1997), or 3) seasonal acclimation of the rate of maintenance respiration. The findings of McGuire and Teskey (2002) suggest that elevated estimates of growth respiration by the mature tissue method may result from the contribution of dissolved $CO_2$ in xylem sap to the observed $CO_2$ efflux from tree stems.

While contribution of $CO_2$ derived from xylem sap to stem $CO_2$ efflux would help to explain high values of $r_g$ derived from the mature tissue method and the difference between $E_T$ and $R_M + R_{G2}$ observed in the 40- and 95-yr old stands; in *Q. rubra*, there is only limited evidence that this is the case. For example, if interactions between dissolved $CO_2$ or xylem transport of $CO_2$ were responsible for the differences between $R_{G1}$ and $R_{G2}$, then the difference between the observed amount of carbon respired per gram of new biomass and that predicted from the release of only 0.23 g of carbon per gram of new

biomass would be correlated with the [$CO_2$] of xylem sap or the sap flux density within a given tree. We compared these differences with xylem [$CO_2$] and sap flux density data from (Chapter 5) and found no correlations. However, we have previously hypothesized that xylem [$CO_2$] and transport has little influence on stem $CO_2$ efflux in *Q. rubra* (Chapter 5). Therefore, xylem transport of $CO_2$ should still be investigated as a potential cause of differences in construction cost- and mature tissue method- based estimates of growth respiration in other tree species.

*Implications for Age-Related Decline in Wood Production*

The findings of this study are in contrast with the hypotheses concerning forest stand development supported by Odum (1956), Yoda et al. (1965), Kira and Shideii (1967), and Whittaker and Woodwell (1967) that the accumulation of biomass with stand age results in both an increase in woody tissue respiration and its proportion of GPP, thereby decreasing the carbon available for production of new biomass. For instance, stand-level woody tissue respiration ($E_T$) and the proportion of GPP consumed by woody tissue respiration did not increase consistently with stand age as $E_T$ and its proportion of GPP were similar in the 40- and 135-yr old stands, but not constant with stand age as $E_T$ and its proportion of GPP were ~50% greater in the 95-yr old stand. Stand-level maintenance respiration ($R_M$) was also similar in the 95- and 135-yr old despite large differences in stand sapwood volume. As stated earlier, our experimental design does not allow for rigorous statistical testing for the significance of the differences in $E_T$ or $R_M$ between stands and, accordingly, our results may be site specific. However, these findings are consistent with other studies discounting the role of increased respiration in

woody tissues in causing age-related declines in wood production (Ryan and Waring 1992; Ryan et al. 1997; Ryan et al. 2004).

Modern concepts of forest stand development include a peak in annual wood production that occurs early in stand development and is associated with canopy closure and high LAI (Ford 1982; Ryan et al. 1997; Smith and Resh 1999). After canopy closure, wood production, GPP, and LAI decline and foliage and stem biomass is redistributed into fewer and larger trees during stand self-thinning (Long and Smith 1992). Our findings indicate that that changes in the physiology of individual trees related associated with maturation do not correspond with the onset and magnitude of large declines in stand wood production (Smith and Long, 2001) and that wood production in individual trees can continue to increase decades after annual wood production of the stand declines (Assman, 1970) if microsite conditions are adequate. For instance, we observed no differences in stem physiology, as indicated by stem $CO_2$ efflux in the growing and dormant seasons, stem diameter increment, and respiratory potential (Chapter 4), between the 40- and 95-year old trees. In addition, foliar physiological traits were not significantly different between the 40- and 95-yr old trees (Griffin et al. *unpublished data*) and mean growth efficiency (annual biomass increment: tree leaf area) was not significantly different in any of the age-classes. This indicates that *Q. rubra* trees are highly conservative in their allocation to stem biomass, after age-related differences in foliage area are accounted for, throughout much of the tree's lifespan.

Forest development is also typically associated with a decline in GPP after canopy closure (Ryan et al. 2004) due to decreasing stand LAI (Smith and Long 2001) and other

changes in tree physiology related to maturation, such as hydraulic limitations to photosynthesis (Yoder et al. 1994), genetic effects (Greenwood, 1989; Ritchie and Keeley, 1994; Nooden and Guiamet, 1996), reduced photosynthetic capacity or leaf area due to nutrient limitations (Binkley et al. 1995) or mechanical abrasion with neighboring trees (Putz et al. 1994; Rudnicki et al, 2003). We observed some evidence of physiological changes in *Q. rubra* with maturation in stems, but only in the 135-yr old trees, as surface-area and sapwood volume based $E_5$ values suggest that respiratory activity was lower in the 135-yr old trees than the 95-yr old trees; however, no significant difference were observed between the 135- and 40-y r old trees. No variation in foliar physiological traits that would indicate changes in photosynthetic capacity, nutrient limitation, or hydraulic limitations with tree maturation was observed (Griffin et al, *unpublished data*).

In addition, we did not observe a decrease in LAI in contrast with many models of stand development as LAI actually increased by ~33% between the 40- and 135-year old stand. As a result, stand GPP was also predicted to increase slightly with stand age. This increase in LAI with stand age is in contrast with many chronosequence studies in coniferous trees and a few deciduous stands (*Prunus pennsylvanica*, Marks, 1974; *Eucalyptus regans*, Dunn and Conner, 1993) reviewed by Ryan et al. (1997)). However, other studies in deciduous forest chronosequences have observed no, or only a slight, declines in LAI with stand age (Brown and Parker, 1994). It is unknown whether the absence of a decrease in LAI and GPP with stand age in this study is due to site specific characteristics (such as regeneration of trees from sprout or coppices, slight differences in

site quality, or the emergence of well developed understory) or due to differences in stand development between coniferous and deciduous stands.

**Conclusions**

Our study verified that $CO_2$ efflux from respiration in woody stems and branches ($E_T$) is an important component of the carbon balance of temperate deciduous forests accounting for a flux to the atmosphere of 114-172 g C $m^{-2}$ $yr^{-1}$ and 10.3-16.9% of GPP. $E_T$ did not increase consistently with stand age supporting the conclusion that increases in woody tissue respiration with biomass accumulation in aging forests do not cause age-related declines in wood production. A substantial decline in wood production was observed between the 40- and 95-yr old *Quercus rubra* stands, however, wood production and canopy carbon uptake continued in the 135-yr old stand suggesting that carbon sequestration in aggrading eastern deciduous forests may continue for well over century after stand initiation.

**Table 1.** Stand characteristics for thee *Quercus rubra*- dominated stands located in Black Rock Forest in southwestern New York, USA. For tree age, woody biomass, and sapwood volume values represent means (± SE). Tree age estimates represent means from 12 trees on each study plot. Woody biomass and sapwood volume estimates represent means for all trees on each study plot using the allometric equations of Martin et al. (1998).

| Tree Age | Stems $ha^{-1}$ | Woody Biomass (kg) | Sapwood Volume ($m^3$) | % *Q. rubra* Biomass | % *Quercus sp.* Biomass | Stand Woody Biomass (t $ha^{-1}$) | Stand Sapwood Volume ($m^3$ $ha^{-1}$) |
|---|---|---|---|---|---|---|---|
| 38.8 (0.6) | 1400 | 71.1 (6.3) | 0.05 (0.004) | 60.8 | 86.8 | 63.0 | 50.7 |
| 93.0 (1.1) | 512 | 775.5 (137.3) | 0.47 (0.09) | 87.0 | 87.0 | 145.9 | 81.9 |
| 134.8 (3.3) | 622 | 1216.7 (262.9) | 0.74 (0.15) | 72.6 | 82.3 | 226.6 | 139.1 |

**Table 2.** Values for the parameters used in model of carbon uptake in the *Quercus* canopies. The parameters are expressed on a half-surface area basis. Values of $V_{cmax}$, $J_{max}$, and $R_d$ are from measurements at 20°C.

| Symbol | Definition | Month | Value | | | Units | Source |
|---|---|---|---|---|---|---|---|
| | | | 40-yr Stand | 95-yr Stand | 135-yr Stand | | |
| $L$ | Leaf Area Index | | 2.34 | 2.67 | 2.87 | $m^2\ m^{-2}$ | W. Bowman and R. Carson (unpublished data) |
| $W_{max}$ | Maximum root-zone water storage | | 75.1 (8.7) | 109.5 (19.0) | 144.8 (18.0) | Mm | W. Bowman (unpublished data) |
| $W_{min}$ | Minimum root-zone water storage | | 15.8 (1.9) | 21.8 (3.3) | 22.5 (4.6) | Mm | W. Bowman (unpublished data) |
| $V_{cmax}$ | Maximum rate of RuBP carboxylation | May-July | 43.8 (3.3) | 38.2 (2.7) | 33.7 (2.6) | $\mu mol\ m^{-2}\ s^{-1}$ | K.Griffin et al. (unpublished data) |
| | | August-October | 35.9 (5.4) | 30.0 (3.1) | 36.8 (2.4) | $\mu mol\ m^{-2}\ s^{-1}$ | K.Griffin et al. (unpublished data) |
| $J_{max}$ | Maximum electron transport rate at saturating irradiance | May-July | 81.6 (5.0) | 66.9 (4.0) | 74.4 (3.7) | $\mu mol\ m^{-2}\ s^{-1}$ | K.Griffin et al. (unpublished data) |
| | | August-October | 69.1 (13.3) | 64.1 (7.1) | 78.6 (8.3) | $\mu mol\ m^{-2}\ s^{-1}$ | K.Griffin et al. (unpublished data) |
| $R_d$ | Rate of respiration during the day | May-July | 1.54 (0.11) | 1.32 (0.12) | 1.52 (0.06) | $\mu mol\ m^{-2}\ s-1$ | K.Griffin et al. (unpublished data) |
| | | August-October | 1.21 (0.12) | 1.29 (0.05) | 1.31 (0.12) | $\mu mol\ m^{-2}\ s^{-1}$ | K.Griffin et al. (unpublished data) |
| $\alpha$ | Quantum efficiency of electron trsnsport | | 0.22 | 0.22 | 0.22 | mol E mol $quanta^{-1}$ | Turnbull et al. (2002) |
| $\beta$ | Convexity of J/Irradiance relationship | | 0.66 | 0.66 | 0.66 | | Turnbull et al. (2002) |
| $a$ | Parameter related to intercellular $CO_2$ concentration | | 4 | 4 | 4 | | Whitehead et al. (1996) |
| $g_{s0}$ | Residual conductance at light compensation point | | 10 | 10 | 10 | $mmol\ m^{-2}\ s^{-1}$ | Whitehead et al. (1996) |
| $D_s$ | Sensitivity of stomatal conductance to air saturation deficit | | 1001 | 1001 | 1001 | $mmol\ m^{-2}\ s^{-1}$ | D. Tissue and V. Engel (unpublished data) |

**Table 3.** Stem $CO_2$ efflux rates at 15 ºC ($E_{15}$, μmol $CO_2$ $m^{-3}$ $s^{-1}$) for three *Quercus rubra* stands measured at three times during the year in Black Rock Forest in southwestern New York, USA. The two sets of June-July values for Sites 1 and 3 represent data collected in 2002 (first value) and 2004 (second value). September measurements were made in 2002 while November-December values were collected in 2004. Standard errors of the means are given in parentheses. Different letters within rows adjacent to listed values indicate statistically significant differences at $P < 0.05$ based on *post hoc* analysis of least significant difference of means after a two-way ANOVA. Factor effects were significant for tree age ($P < 0.01$), time of year ($P < 0.01$), and the interaction between age and time of year ($P < 0.05$).

| Stand Age | June-July | September | November-December |
|---|---|---|---|
| 40 | 105.2 (19.6)[a], 125.3 (12.1)[a] | 55.0 (5.3)[b] | 34.3 (4.3)[b] |
| 95 | 119.3 (9.9)[a] | | 38.4 (5.5)[b] |
| 135 | 57.7 (5.9)[b], 40.6 (11.2)[b] | 33.5 (4.1)[b] | 22.4 (4.0)[b] |

**Table 4.** Modeled $CO_2$ efflux parameters derived from fitted temperature response curves (Eq. 1) as a function of tree age and time of year in *Quercus rubra* trees from Black Rock Forest, NY. $E_{20}$ is the stem $CO_2$ efflux rate at the base temperature (20 ºC) used to fit Eqn. 1 to the $CO_2$ efflux-temperature data measured during June-July 2004. $E_5$ is the stem $CO_2$ efflux rate at the base temperature (5 ºC) used to fit Eqn. 1 to the $CO_2$ efflux-temperature data measured during November-December 2004. $A_o$ is a modeled parameter describing the shape of temperature response of $CO_2$ efflux. Values shown are means (standard error); for 40 yr trees, n = 9; for 95 yr trees, n = 8; for 135 yr trees, n = 4. Significance of factor effects for tree age are indicated by the *P*-value. Different letters within rows adjacent to listd values indicate statistically significant differences at $P < 0.05$ based on least significant difference of means.

| | **Growing Season** | | | **Dormant Season** | | | |
|---|---|---|---|---|---|---|---|
| | 40 yr | 95 yr | 135 yr | 40 yr | 95 yr | 135 yr | **ANOVA Statistics** |
| $E_{20}$ (μmol $CO_2$ $m^{-3}s^{-1}$) | 167.5 (8.8)[a] | 148.9 (9.8)[a] | 64.7 (5.7)[b] | - | - | - | $P < 0.01$ |
| $E_5$ (μmol $CO_2$ $m^{-3}s^{-1}$) | - | - | - | 18.9 (2.2)[a] | 21.0 (1.8)[a] | 11.3 (2.4)[b] | $P = 0.04$ |

**Table 5.** Modeled $CO_2$ efflux parameters derived from fitted temperature response curves (Eq. 1), respiratory potential and nitrogen concentration of inner bark and sapwood tissues as a function of tree height in three *Quercus rubra* trees from Black Rock Forest in southwestern New York, USA. $E_{15}$ is the $CO_2$ efflux rate at 15 ºC calculated from the fitted $CO_2$ efflux-temperature response curves during the two weeks in late September 2004. $A_o$ is a modeled parameter related to the overall energy of activation. Values shown are means (± SEM). Different letters within columns represent statistically significant different values at $P < 0.05$ based on paired t-tests for $E_{15}$ and $A_o$ and one-way ANOVAs for respiratory potential and nitrogen concentration.

| Tree Position | $E_{15}$ (μmol $CO_2$ $m^{-2}$ $s^{-1}$) | Ao (kJ mol $K^{-1}$) | Inner Bark Respiratory Potential (nmol $O_2$ $g^{-1}s^{-1}$) | Sapwood Respiratory Potential (nmol $O_2$ $g^{-1}$ $s^{-1}$) | Inner Bark Nitrogen Concentration (g g-1) | Sapwood Nitrogen Concentration (g g-1) |
|---|---|---|---|---|---|---|
| Branches | 0.59 (0.9)[a] | 27.5 (2.8)[a] | 1.13 (0.18)[a] | 0.26 (0.02)[a] | 0.43 (0.02)[a] | 0.21 (0.01)[a] |
| Mid Stem | 0.60 (0.4) | 29.8 (7.4) | 0.88 (0.04)[a] | 0.27 (0.10)[a] | 0.38 (0.03)[a] | 0.21 (0.01)[a] |
| Lower Stem | 0.78 (0.6)[a] | 18.7 (5.3)[a] | 1.05 (0.10)[a] | 0.31 (0.04)[a] | 0.42 (0.02)[a] | 0.29 (0.02)[b] |

**Table 6.** Annual estimates of wood production at both the tree and stand level for three *Quercus rubra* dominated stands in Black Rock Forest in southwestern New York, USA. Growth efficiency represents mean values for the ratio of woody biomass increment to tree leaf area. For tree-level variables, values represent means (±SE) where n = 12. Within columns, means with different subscripts differ significantly (One-way ANOVA, $P < 0.05$)

| Tree Age | Mean Diameter Increment (mm $tree^{-1}$) | Mean Woody Biomass Increment (kg $tree^{-1}$) | Relative Woody Biomass Increment (g $kg^{-1}$) | Mean Growth Efficiency ($kg^{-1}$ $m^{-2}$) | Stand Woody Biomass Production (Mg $ha^{-1}$) |
|---|---|---|---|---|---|
| 40 | 4.2 (0.4)$^{a}$ | 5.5 (0.8) | 75.5 (8.6) | 0.08 (0.01)$^{a}$ | 4.44 |
| 95 | 3.2 (0.4)$^{ab}$ | 21.6 (3.6) | 20.6 (2.3) | 0.09 (0.02)$^{a}$ | 3.00 |
| 135 | 2.7 (0.3)$^{b}$ | 28.3 (3.3) | 13.2 (1.8) | 0.08 (0.01)$^{a}$ | 3.02 |

**Table 7.** Annual carbon fluxes, per unit ground area, due to stand-level stem and branch $CO_2$ efflux ($E_T$), its maintenance ($R_M$) and growth ($R_{G1}$ or $R_{G2}$) components, and canopy carbon uptake (GPP) for three *Quercus rubra* stands located in Black Rock Forest in southwestern New York, USA.

| Tree Age | $R_M$ (g C $m^{-2}$) | $R_{G1}$ (g C $m^{-2}$) | $R_{G2}$ (g C $m^{-2}$) | $R_M + R_{G2}$ (g C $m^{-2}$) | $E_T$ (g C $m^{-2}$) | GPP (g C $m^{-2}$) | $R_M + R_{G2}$ (% GPP) | $E_T$ (% GPP) |
|---|---|---|---|---|---|---|---|---|
| 40 | 53.2 | 77.8 | 41.9 | 95.1 | 116.2 | 985.0 | 9.7 | 11.8 |
| 95 | 90.9 | 96.8 | 28.3 | 119.2 | 172.2 | 1010.0 | 11.8 | 17.0 |
| 135 | 89.6 | 26.5 | 28.5 | 118.1 | 114.1 | 1115.0 | 10.6 | 10.2 |

**Figure Captions.**

**Figure 1.** Allometric relationship between total aboveground wood biomass (stem wood, stem bark, and branches) and tree diameter at 1.3 m in *Quercus rubra*. Open circles represent trees sampled in Black Rock Forest in southwestern New York, USA. Solid line represents an allometric relationship presented in Martin et al. (1998), $\log_{10} y = -1.279 + 2.651(\log_{10} x)$, where x is diameter (cm) at 1.3 m and y is aboveground wood biomass (kg).

**Figure 2.** a) Relationship between micrometeorological tower air temperature and sapwood temperature in the 95-yr old *Q. rubra* stand during the day (open circles) and at night (closed circles). Solid lines represent least mean square regressions: Day- $y = 0.42x + 9.68$, $r^2 = 0.73$, $P < 0.01$; Night- $y = 0.62 + 7.01$, $r^2 = 0.65$, $P < 0.01$. b) Relationship between predicted sapwood temperatures, based on stand- and season-corrected air temperature data, and actual sapwood temperature. The solid line represents a 1:1 relationship.

**Figure 3.** Seasonal trends in stem $CO_2$ efflux at 15 ºC ($E_{15}$) in *Quercus rubra* from 40 (circles), 95 (squares), and 135 (triangles) yr old trees. Measurements were collected in the growing and dormant seasons of 2002 and 2004. $E_{15}$ values shown are means (± SE).

**Figure 4.** The relationship between sapwood thickness (mm) and the rate of branch $CO_2$ efflux ($E_{15}$) normalized to 15 ºC for three *Q. rubra* trees during the late September 2004. The solid line represents a least squares regression: $y = 39.21x + 0.2$, $r^2 = 0.59$, $P < 0.01$.

**Figure 5.** Seasonal trends in daily canopy carbon uptake and stand woody biomass increment for 40 (a), 95 (b), and 135 (c) yr old *Quercus* stands in Black Rock Forest in southwestern New York, USA. Seasonal trends in $CO_2$ efflux rates (per unit ground area) from woody stems and branches for the 40, 95, and 135 yr old stands are shown in (d), (e), and (f), respectively. Rates of $CO_2$ efflux from woody stems and branches ($E_T$, filled circles) were calculated by extrapolating discrete measurements of $E_{15}$ (shown in Figure 3) throughout 2004 by applying seasonal $A_o$ values to modeled changes in sapwood temperature and multiplying by stand sapwood volume. $CO_2$ efflux attributable to maintenance respiration ($R_M$, filled triangles) was estimated by extrapolating measurements of $E_{15}$ made during November/December 2004 throughout that year. Rates of $R_M + R_{G2}$ (open circles) were estimated by summing $R_M$ and $CO_2$ efflux attributable to growth respiration ($R_{G2}$) predicted from biomass increment and a growth coefficient derived from the construction cost of *Quercus* sapwood (Wullschleger et al. 1995).

**Figure 6.** The relationship between carbon incorporated into new wood biomass and amount of $CO_2$ efflux from stems attributable to growth processes in *Quercus rubra* trees. The solid line represents a growth coefficient ($r_g$) of 0.34 and was calculated by a least squares regression: $y = 0.34x + 0.43$, $r^2 = 0.71$, $P < 0.001$. The dashed line represents the relationship between new wood biomass and the growth-related $CO_2$ efflux predicted from a growth coefficient of 0.23.

**Figure 1.**

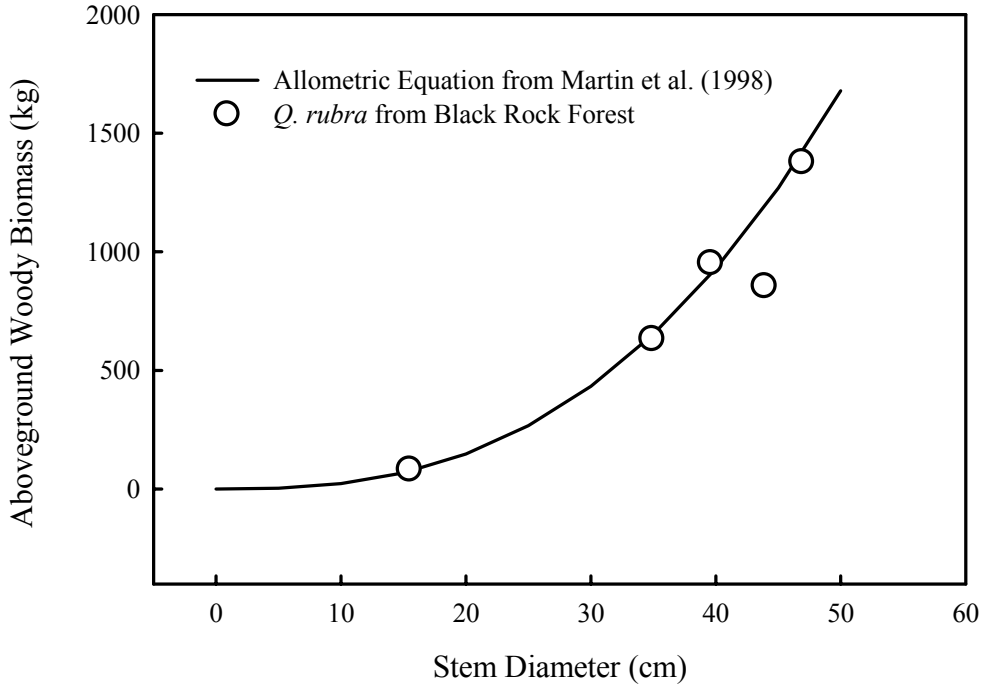
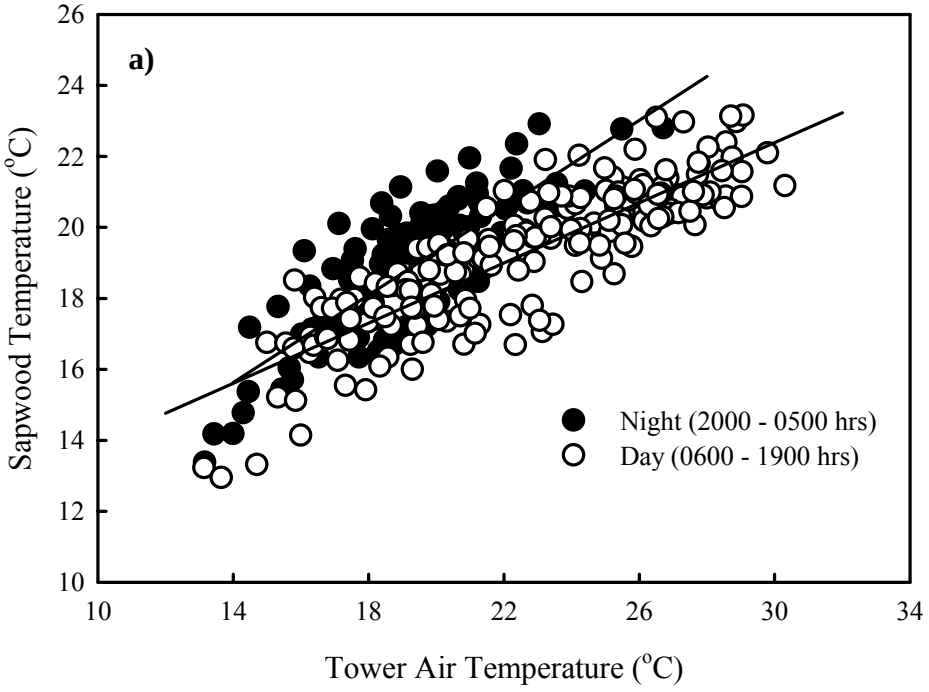

Allometric Equation from Martin et al. (1998)
Q. rubra from Black Rock Forest
Aboveground Woody Biomass (kg)
2000
1500
1000
500
0
0
10
20
30
40
50
60
Stem Diameter (cm)

**Figure 2.**


a)
Sapwood Temperature (°C)
Tower Air Temperature (°C)
Night (2000 - 0500 hrs)
Day (0600 - 1900 hrs)
10
12
14
16
18
20
22
24
26
10
14
18
22
26
30
34

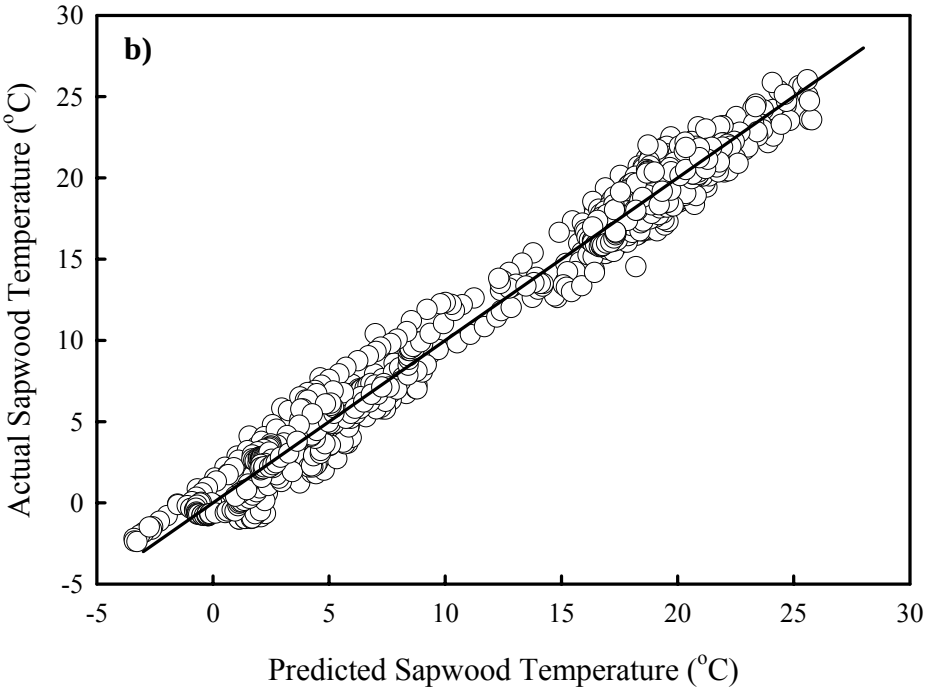

b)
Actual Sapwood Temperature (°C)
Predicted Sapwood Temperature (°C)
-5
0
5
10
15
20
25
30

**Figure 3.**

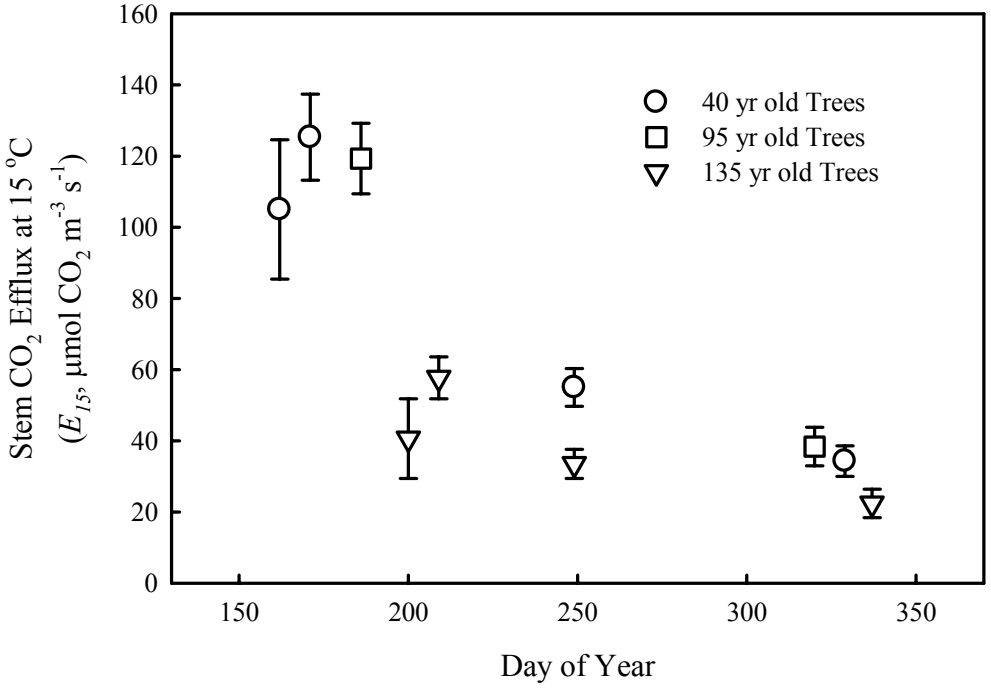

160
140
120
100
80
60
40
20
0
150
200
250
300
350
Day of Year
Stem $CO_2$ Efflux at 15 °C
($E_{15}$, μmol $CO_2$ $m^{-3}$ $s^{-1}$)
40 yr old Trees
95 yr old Trees
135 yr old Trees

**Figure 4.**

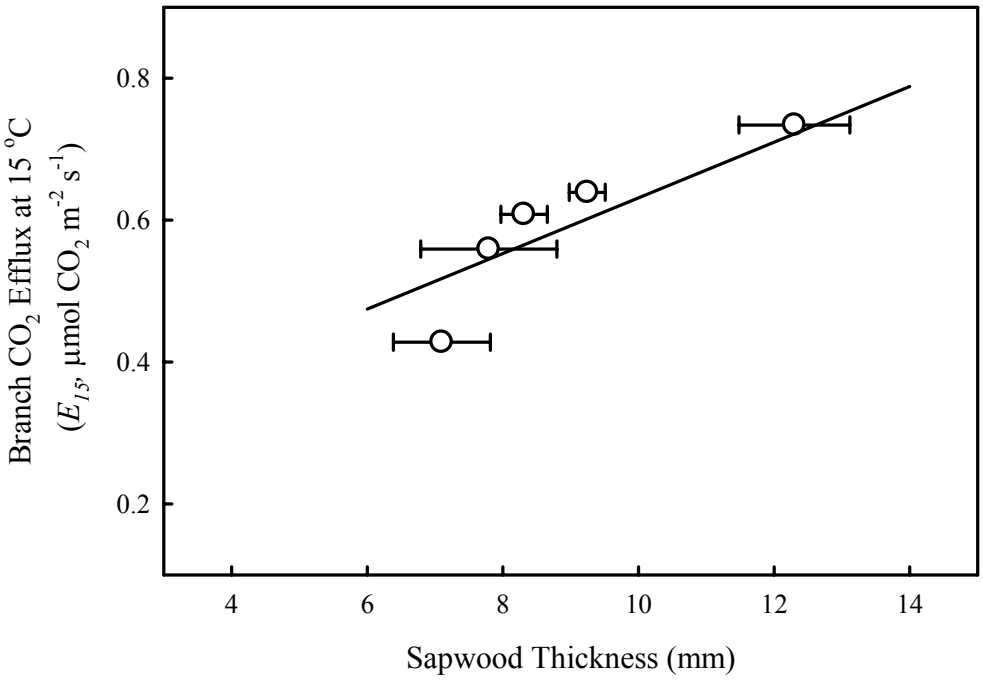

Branch $CO_2$ Efflux at 15 °C
($E_{15}$, μmol $CO_2$ $m^{-2}$ $s^{-1}$)
0.8
0.6
0.4
0.2
4
6
8
10
12
14
Sapwood Thickness (mm)

**Figure 5.**

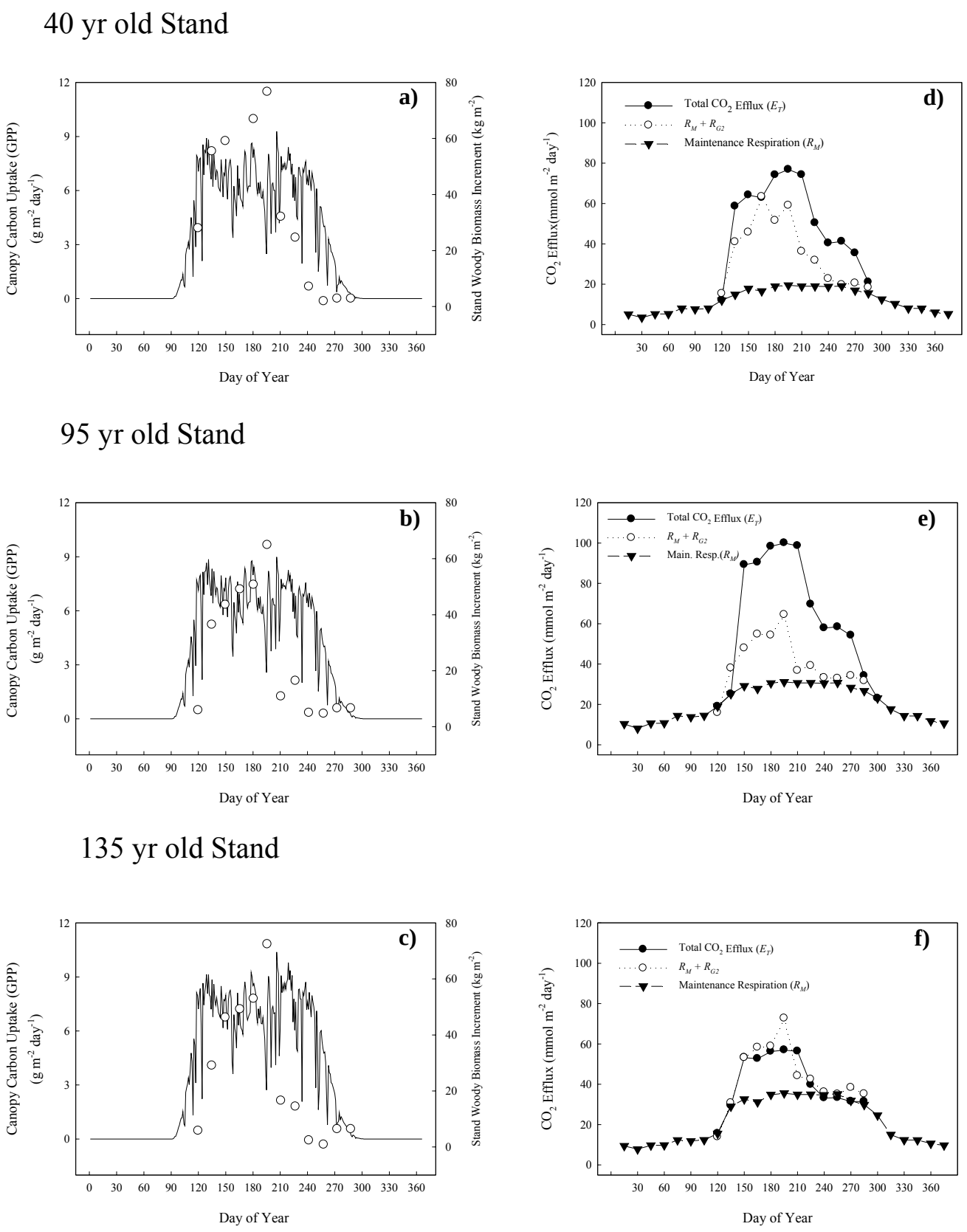
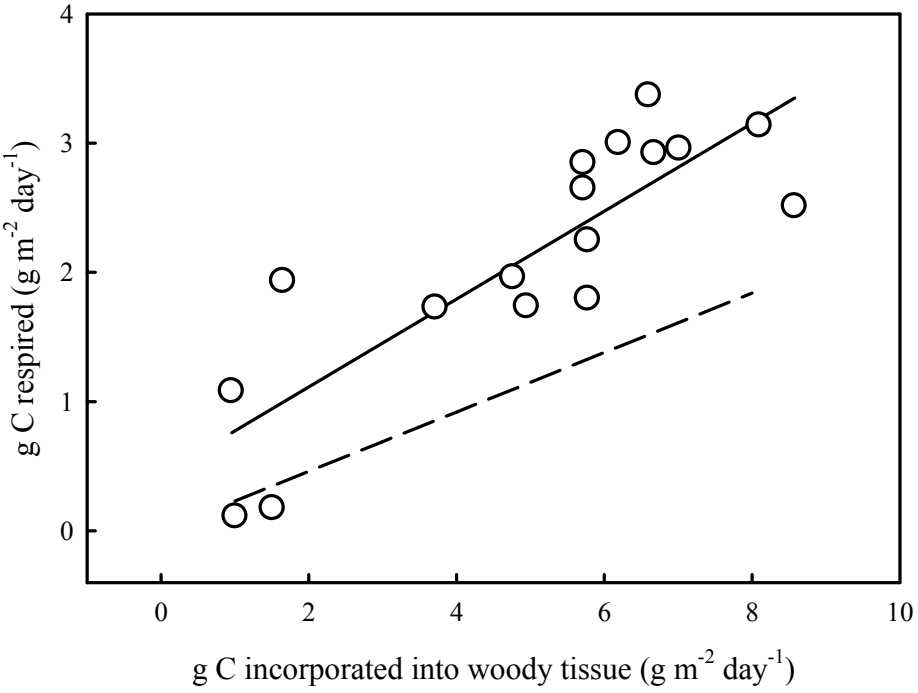

40 yr old Stand
a)
d)
95 yr old Stand
b)
e)
135 yr old Stand
c)
f)
Canopy Carbon Uptake (GPP)
(g m-2 day-1)
Stand Woody Biomass Increment (kg m-2)
CO2 Efflux(mmol m-2 day-1)
CO2 Efflux (mmol m-2 day-1)
Day of Year
Total CO2 Efflux (ET)
RM + RG2
Maintenance Respiration (RM)
Main. Resp.(RM)

**Figure 6.**


4
3
2
1
0
0
2
4
6
8
10
g C respired (g m-2 day-1)
g C incorporated into woody tissue (g m-2 day-1)

## Chapter 7: Conclusion

In the Chapters 1 and 2 of this dissertation, the case was made that our understanding of woody tissue respiration would benefit greatly from research aimed at elaborating on the functional model of respiration by integrating the effects of other physiological characteristics and functions of tree stems on the $CO_2$ efflux from stems and branches. In particular, the movement of xylem sap through stems associated with transpiration and the presence of high $CO_2$ concentrations in the internal air spaces within wood and dissolved in xylem sap were identified as having the potential to strongly influence $CO_2$ efflux from stems and branches. Concurrent measurements of stem $CO_2$ efflux with sap velocity in *Dacrydium cupressinum* (Chapter 3) and with sap velocity and internal $CO_2$ concentration in *Quercus rubra* (Chapter 5) confirm that stem hydraulics can influence stem $CO_2$ efflux; however, the relationship between hydraulics and stem $CO_2$ efflux was found to vary both within- and between-species.

In contrast with many previous studies, diel variation in $CO_2$ efflux from woody stems in *D. cupressinum* was not well explained by sapwood temperature as $CO_2$ efflux often did not respond to, or declined during, coincident increases in temperature during the day. The absence of a strong relationship between stem $CO_2$ efflux and sapwood temperature resulted from xylem transport of $CO_2$ as stem $CO_2$ efflux was depressed during periods of sap flow compared to the efflux rate expected for a given stem temperature. It was estimated that xylem transport of $CO_2$ accounted for 10.6 % of woody tissue respiration over a 24 h period and 13-38% of predicted woody tissue respiration during periods of peak transpiration. In addition, storage of $CO_2$ in xylem sap also influenced stem $CO_2$ efflux and was estimated to be 15.8 and –12.1%, on average, of

woody tissue respiration during periods of maximum $CO_2$ transfer into and out of xylem sap. Between-tree variation in the magnitude of xylem storage of $CO_2$ was found to be determined by the volumetric water content of the sapwood. In *D. cupressinum*, high percentages of woody tissue respiration were attributable to both xylem transport and/or storage of respiratory $CO_2$ at certain times of the day. These estimates suggest that stem $CO_2$ efflux is strongly influenced by stem hydraulics in *D. cupressinum* and, as a result, there is uncertainty about the source of stem $CO_2$ efflux as this $CO_2$ may have been respired locally, in lower positions in the stem or roots, or in the soil.

Furthermore, $CO_2$ efflux from *D. cupressinum* in the growing season was not related to estimates of respiratory activity of the underlying wood such as wood respiratory activity and nitrogen content. Instead, the best predictor of between-tree variation in stem $CO_2$ efflux was sapwood density. This study is the first to observe correlation between stem $CO_2$ efflux and sapwood density. Interestingly, wood density may be linked to both xylem transport and storage $CO_2$ fluxes in woody stems as it has been found to be negatively correlated with wood water content (Meinzer, 2003) and sap velocity (Roderick and Berry 2001; Barbour and Whitehead 2003). Further research on other tree species and environments should be undertaken to determine if this linkage between the structural, hydraulic, and respiratory properties of tree stems is present in other tree species and uncover the mechanism underlying this relationship.

In contrast with this study's findings in *D. cupressinum*, variation in stem $CO_2$ efflux was strongly related to sapwood temperature in *Q. rubra* and was found to be related to local respiratory production of $CO_2$ during the dormant season, when rates of $CO_2$ efflux were correlated with inner bark respiratory potential, and the growing season,

when rates of $CO_2$ efflux were correlated with stem diameter growth. Some evidence for the effects of xylem $CO_2$ concentration or sap transport on stem $CO_2$ efflux was observed in *Q. rubra* but these interactions were not consistent across tree age classes and did not appear to be as significant as those observed in *D. cupressinum*. Stem $CO_2$ efflux was found to be positively correlated with xylem [$CO_2$] in young (40 yr old) *Q. rubra* trees, but not in the older age classes; in addition, $CO_2$ efflux was negatively correlated with sap flux density in the 95 and 135 yr old trees, but not in the youngest trees.

Recent studies describing significant interactions between stem $CO_2$ efflux and xylem $CO_2$ transport and storage have called into question the validity of scaling measurements of $CO_2$ efflux to the tree- or stand-level. However, this study's findings in *Q. rubra* indicate that measurements of stem $CO_2$ efflux are indeed related to the respiratory activity of underlying wood and suggest that deriving stand-level estimates of woody tissue respiration based on measurements of biomass production are valid for *Q. rubra* stands. An unresolved question emerging from this study's findings is why interactions with xylem transport of stem $CO_2$ efflux appeared to affect *D. cupressinum* more than *Q. rubra*. This may be due to differences in hydraulic anatomy and water relations between *D. cupressinum* and *Q. rubra* trees as the narrow radial width of sapwood and the low volumetric water flow typical of *Quercus* species may result in lower capacity for xylem transport of $CO_2$. If this hypothesis is correct, xylem transport of $CO_2$ may tend to have greater influence on stem $CO_2$ efflux in diffuse-porous and tracheid anatomy trees than in trees with ring-porous anatomy; old trees than young trees; and trees from hydric or mesic habitats versus trees from xeric habitats. For instance, in *Q. rubra*, the effects of xylem $CO_2$ transport on $CO_2$ efflux rates appeared to be greatest

in the oldest trees as there was 1) no correlation between stem $CO_2$ efflux and diameter growth, 2) a negative correlation between stem $CO_2$ efflux and maximum sap flux density and 3) low values of $A_o$ resulting from the modest response of stem $CO_2$ efflux to variation in sapwood temperature. However, in *D. cupressinum*, the proportion of $CO_2$ transported by the xylem sap relative to total woody tissue respiration did not increase with tree size or volumetric water flow.

This study's findings in *D. cupressinum* and *Q. rubra* suggest that interactions between sap flow and stem $CO_2$ efflux are common, but not ubiquitous, in forest trees. However, it is apparent that we have much to learn about the various conditions, such as species, tree age, xylem anatomy, or environment, in which xylem $CO_2$ concentration and transport are likely to confound estimates of respiration in woody stems and branches. Further research aimed at identifying these conditions and integrating tree water relations into studies of stem $CO_2$ efflux is likely to contribute to our understanding intra- and inter-specific variation in stem $CO_2$ efflux and improve our ability to scale stem $CO_2$ efflux to the tree- and stand-level.

Respiration in the woody stems of forest trees was found to be an important component of forest carbon budgets in both a lowland podocarp-angiosperm rainforest in New Zealand and an aggrading temperate deciduous forest in New York. Stem respiration in *D. cupressinum* accounted for an annual carbon flux to the atmosphere of 1.22-1.29 Mg C $ha^{-1}$ and consumed 6.7-7.2 % of forest GPP; whereas, stand-level estimates of woody tissue respiration in the three *Quercus* stands ranged from 114-172 g C $m^{-2}$ $yr^{-1}$ and accounted for 10.3-17.0 % of GPP.

Similar to previous studies, finding reliable predictors of between-tree variation in stem $CO_2$ efflux that are also scalable to the stand level was difficult in both *D. cupressinum* and *Q. rubra*. In both *D. cupressinum* and *Q. rubra*, robust linear relationships between stem $CO_2$ efflux and stem surface area, sapwood volume, and/or tissue nitrogen concentration were not observed and, as a result, mean rates of stem $CO_2$ efflux on both surface area and/or sapwood volume bases were used to scale-up to the stand level. In both *D. cupressinum* and *Q. rubra*, the respiratory potential in inner bark tissue was greater than that of sapwood; while, sapwood accounted for a greater proportion of woody biomass. These findings suggest that the difficulty in scaling $CO_2$ efflux to the tree- and stand-level is due, in part, to our inability to partition respiration into inner bark and sapwood components and scale these components to the stand-level separately.

The findings of this study contributed to our understanding of scaling measurements of stem $CO_2$ efflux to the forest stand-level in several ways. For example, previous studies (Stockfors 2000) have suggested that within-tree variation in sapwood temperature may significantly affect the accuracy of scaled-up estimates of stem respiration for both trees and whole stands. In this study, large within-tree gradients in sapwood temperature, up to 6º C, were observed in *D. cupressinum* trees with upper regions of the trees exhibiting greater maximum sapwood temperatures during the day than the lower stems and lower temperatures at night. However, the inclusion of these gradients will produce only small improvements in the accuracy of stand-level estimates of stem respiration due to 1) the opposing effects of day-time warming and night-time cooling on respiration in the forest canopy and 2) the small fraction of the respiring

woody biomass located in the canopy. This finding is consistent with studies of foliar photosynthesis and respiration that found within-canopy temperature gradients to be of little importance when scaling leaf physiological responses to the canopy level (Amthor 1994; Lloyd et al. 1995).

This study also found that estimates of stand-level woody tissue respiration in the *Q. rubra* stands differed depending on the method of calculation. For example, estimates of woody tissue respiration derived from the mature tissue method were 18 and 31% greater than estimates resulting from construction cost-based growth coefficients in the 40- and 95-yr old stands, respectively, but not in the 135-yr old stand. Similar results were reported in *Pinus ponderosa* (Carey et al. 1997), *Q. alba*, and *Acer rubrum* (Edwards and Hanson 1996) and have been attributed to inaccurate estimates of the respiratory cost of wood biosynthesis or maintenance respiration during the growing season. Another possible explanation is that elevated estimates derived from the mature tissue method may result from the contribution of $CO_2$ dissolved in the xylem sap to the observed $CO_2$ efflux. This hypothesis was not supported as there was no relationship between the [$CO_2$] of xylem sap within a given tree and the difference between the observed amount of carbon respired per gram of new biomass and that predicted from the construction cost of new biomass for that tree. However, this study has also indicated that the effects of xylem [$CO_2$] and transport on stem $CO_2$ efflux in *Q. rubra* are small. Therefore, xylem transport of $CO_2$ should still be investigated as a potential contributor to differences in construction cost- and mature tissue method-based estimates of woody tissue respiration in other tree species.

Previous studies (Meir and Grace 2002) observed that stand-level woody tissue respiration and its proportion of GPP are correlated with LAI. In contrast, this study's findings observed a decline in stand-level woody tissue respiration and its proportion of GPP between the 95- and 135-yr old *Q. rubra* stands, despite a slight increase in LAI and GPP between these stands. As a result, this study indicates that the correlation observed by Meir and Grace may not be valid for differences in LAI related to stand development as, in the case of *Q. rubra*, rates of woody tissue respiration may change with stand age.

This study's principle aim of integrating the effects of sap flow and the dissolved $CO_2$ concentration of xylem sap on $CO_2$ efflux from woody stems and branches has provided several important insights into the respiratory physiology of stems and branches at the tissue-, organ-, tree-, and stand-levels. However, due to the many experimental difficulties posed by tree stems, which are obviously quite challenging to access and manipulate due to their size and longevity, unresolved questions still remain at levels of organization raging from the a single respiring cell to the large expanses of temperate forests. In the study of organisms and ecosystems, robust understanding requires consideration of smaller levels of organization to provide mechanisms and larger levels of organization to provide context and significance (Allen and Hoekstra 1992). This study has endeavored to take this perspective and consider the complexity and the diversity of functions of tree stems. As a result, I hope that its findings will spark debate and research that will further our understanding of tree stems as integrated structures.

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