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# CARBON CONTENT IN BRANCHES OF *Tsuga heterophylla* (RAF.) SARG

Maria Carolina O. Silva[1], Sabah H. Lamlom[2*] and Rodney A. Savidge[3]
[1]Planning Department, Western Forest Products Inc, Holberg, Canada
[2]Faculty of Arts and Science, University of Omar Al-Mukthar, Tobruk, Libya
[3]Faculty of Forestry and Environmental Management, University of New Brunswick, Fredericton, Canada
Corresponding author: E-Mail: nursing_omu_2008@yahoo.com

**ABSTRACT**

The goal of this study was to determine carbon (C) content in branch wood of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). Branch samples from 26 trees were obtained during summer 2005 from mature trees growing in northern Vancouver Island near Holberg, British Columbia, Canada. Two branches were taken per tree, one from the live-crown base and another from near the top of the live crown. By elemental analysis, mean C content of wood in tree-top branches was ~57.4% ± 0.8% and ranged from 55.7% to 58.8%. Mean C content for branch wood near the crown base was 57.6% ± 0.7% and ranged from 55.6% to 58.8%. Branch compression wood (Cw) yielded >58% C, approximately 2% more than was found in opposite wood (Ow). These are the highest C contents yet reported in wood of any tree species, and the findings point to the inadequacy of using 50% C in forest carbon modelling budgets.

**Keywords:** *Tsuga heterophylla*, carbon content, trees, trunk wood, branches, reaction wood, compression wood, opposite wood.

## INTRODUCTION

In mature forest trees, the main C storage organ is the trunk, but C also accumulates in bark, roots, branches, leaves and reproductive organs, albeit to a lesser extent than in the stem. Following the various ecophysiological paths of these ecosystem components, C is used for growth, stored as reserve material, exported through the translocation process, shed through abscission and released as volatile carbon molecules (Cooper, 1983; Savidge, 2001).

Accumulated evidence strongly suggests that one role of branches is to regulate wood formation in the trunk and root system over the entire growing season. An active union between a branch and the main stem assures a steady supply of nutrients and water to a branch, and the seasonal layer of wood produced in the branch is often continuous with that produced in the trunk. Foliage in branches produces photosynthate which upon reaching the trunk becomes available for distribution to other regions within the tree (Larson, 1969).

Branches add wood throughout their lifetime, although at a slower rate than stems. Cooper (1983) pointed out that branches, as C accumulators, are extensions of the stem, and that C content in branches arises through physiological processes, beginning within fixation of $CO_2$ during photosynthesis.

Many internal and external factors such as type, number, size, shape, physical structure, and chemical composition lead to variation in C content and distribution. Larson (1969) noted that the contribution of branches to tree biomass varies with growth conditions. For example, if the tree were open-grown there will be more branches than if it were stand-grown.

Growing conditions also influence the width of xylem growth rings and the proportions of early wood to late wood within growth rings. As a result, the relation between crown and different cambial regions on the stem is constantly altered by environmental conditions, the growth of the tree, and the tree's age (Larson, 1969).

Branches tend to be distributed more or less equally and at similar angle from the trunk axis throughout the tree crown. Any displacement from a branch's equilibrium position is attended by compression wood (Cw) formation in the branch. Usually, branches are displaced downward by their own weight or by agents such as snow and ice, and Cw in branches is usually located on their under side (Timell, 1986). Thus, it has long been considered that Cw is formed in stems and branches of conifers as a corrective response to bending (Timell, 1986; Fahn, 1990).

Numerous theories have been advanced to account for generation of longitudinal compressive stress in CW. It is well established that lignin content is elevated in Cw (Savidge, 2003). The lignin swelling theory is based on two principal points: 1) high correlation between lignin concentration and stress level, and 2) lignin deposition between cellulosic micro fibrils causing expansion of the cell wall and generating longitudinal compressive stress (Timell, 1987; Bamber, 2001).

Cw is formed in association with locally accelerated growth resulting in eccentric growth rings, and Cw appears to contain an abnormally large proportion of late wood in the region of fastest growth (Panshin and de Zeuuw, 1980). When Cw is obvious, cross sections showing the region of faster growth are red to red-brown in colour, much darker than normal wood, in agreement with the chemistry of Cw being different from that of normal wood (Panshin and de Zeuuw, 1980; Timell, 1986). The higher density of Cw is a consequence of its thicker cell walls (Panshin and de Zeuuw, 1980). Though CW is of higher density than normal wood, it is less elastic, dimensionally unstable and can fail without warning (Panshin and de Zeuuw 1980, Savidge 2003).

"Opposite wood" (Ow) is formed directly opposite Cw, i.e., at 180$^{o}$ around the circumference of a branch or leaning trunk from the Cw zone. Ow is distinct from Cw in colour, wood anatomy and growth ring width, and it also displays characteristics different from normal wood (Timell, 1986).

Less is known about Ow than Cw (Timell, 1973; Lee and Eom, 1988; Dadswell, 1958). Ow widths vary depending on whether they occur in early wood or late wood. Differences between Cw and Ow are most readily evident in the ultrastructure of their tracheids, and in the structure and chemical composition of their secondary cell walls (Timell, 1973, 1986). Tracheids of Cw tend to be more uniform and do not display the differences between early wood and late wood found in Ow. Furthermore, Cw and Ow differ chemically (Panshin and de Zeuu, 1980; Timell, 1973; Lee and Eom, 1988).

In order to have accurate estimates of total C content in any tree, and given that there is variation in C content within tree species, and in order to account for C in any forest stand, it has been suggested that total C content should be estimated by integrating each individual tree component (Savidge, 2001; Lamlom, 2005; Silva, 2012; Silva *et al*., 2012). In this study, branches from 26 old-growth western hemlock trees were sampled and the mean values of C content were investigated. Branch wood always contains reaction wood (compression and opposite wood) in conifers, therefore another objective of this study was to determine variation in C content between the two sides of the branch.

## MATERIALS AND METHODS

### Sample preparation for branches of western hemlock

In 2005, 52 branches were sampled from 26 felled old-growth *Tsuga heterophylla* (Raf.) Sarg. trees near Holberg (Vancouver Island), British Columbia, Canada. Two branches were randomly selected (in relation to cardinal direction and branch size) from each tree, one from the base of live crown (BLC) and another from near the top of the live crown (TLC). BLC was defined by an imaginary horizontal line at the bottom of the lowest live limb while TLC was within one meter of the highest point of the tree. Two disks were taken from each branch, one from the branch base and the other from near the branch apices. Thus, in total, 104 disks were investigated for C content.

The four sample disks from each tree were air dried for a week prior to shipping the samples to the University of New Brunswick laboratory. Disks were prepared for analysis and analyzed as previously described (Lamlom and Savidge, 2003; Silva, 2012; Silva *et al*., 2012).

Branches from eight of the 26 trees (tree numbers 1 to 8 in Figure-2) were also used to determine C content in compression wood (Cw) and opposite wood (Ow). Each of the eight branches was debarked and examined by unaided eye to identify the darker zone of Cw. A carefully cleaned rasp was used to produce fine particles of Cw and Ow from opposing sides of each branch, and a Wiley mill was used in order to obtain fine wood particles.

To homogenize the resulting particles, the wood powder was placed in liquid nitrogen within a mortar and ground with a pestle. The wood powders were processed and capped in glass vials, following the same procedure earlier described (Lamlom and Savidge, 2003) to determine C content.

### Statistical analysis

The mean and standard deviations of C content in branches of at least three replicate analyses per sample were calculated. When the standard deviation was greater than 0.7% (w/w), more replicates were analyzed. Mean C contents were plotted, each with its respective standard deviation (SD), and the standard error of the mean (SEM) was determined at 99% confidence (Figures 1 and 2).

## RESULTS

There was variation in C content within a tree and among trees (Figures 1A, 1B), but mean C contents for TLC and BLC samples were very similar. The mean C content for TLC branch wood of T. heterophylla was ~57.4% (w/w) with a standard deviation of ± 0.8% (Figure-1A). C content ranged from 55.7% ± 0.6% (SD) to 58.8% ±0.2% (SD) (w/w).

Mean C content for BLC branch wood was 57.6% with a standard deviation of ± 0.7% (Figure-1B). C content ranged from 55.6% ± 0.7% (SD) to 58.8% ± 0.2% (SD) (w/w). For TLC and BLC sampling positions, the SEM illustrates the dispersion of the sampling errors. The SEM (n=26) was 0.1 for the BLC branches (Figure-1B) and 0.2 for the TLC branches (Figure-1A).

Hydrogen contents in TLC and BLC branch woods ranged from 8.47% to 8.99% ±0.2%. Nitrogen was also analyzed, but its content never exceeded trace levels. Hydrogen and nitrogen were not further investigated in this study.

The mean C content of Cw based on analysis of eight trees was 58.1% ± 0.8% (w/w) for BLC branches and ~58.5% ± 0.6% (w/w) for TLC branches (Figures 2A, 2C). The SEM for TLC and BLC samples were 0.2 and 0.3 (n=8), respectively. The mean C content (w/w) in Ow was 56.7% ± 0.3% (SD) (w/w) for both TLC and BLC branches (Figures 2B, 2D). The SEM for both was 0.1 (n = 8).

Hydrogen contents in Cw and Ow ranged from 8.55% to 9.62%. Nitrogen was also analyzed, but its content never exceeded trace levels. Hydrogen and nitrogen were not further investigated in this study.

The data of Figure-2 indicate that Cw had higher C content than Ow regardless of branch position within the trunk.

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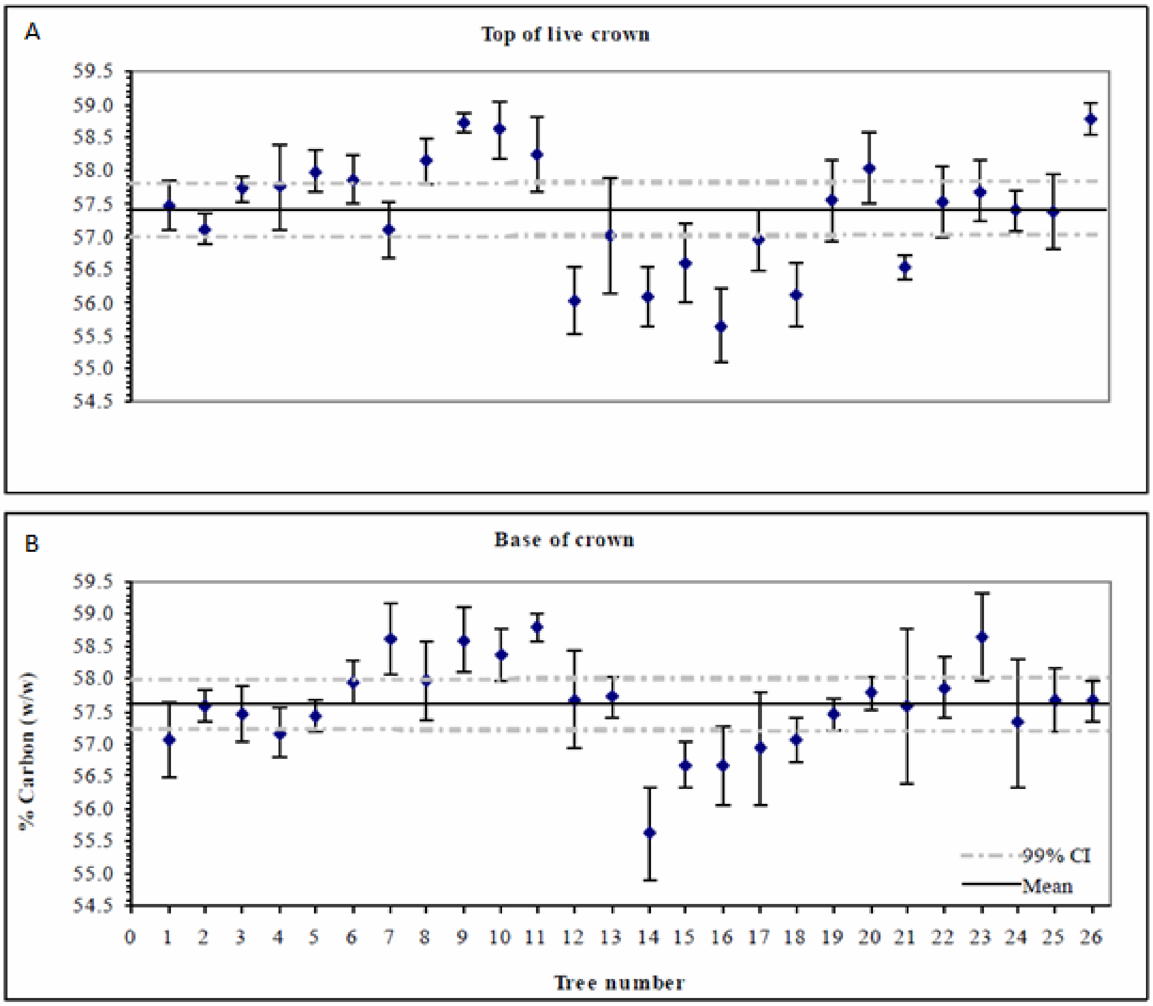


**Figure-1.** Mean percentage (w/w) C content of 52 branches (two branches sampled at TLC and BLC positions from each of 26 western hemlock trees) and standard deviations (error bars, based on at least six analyses) per branch. The horizontal solid line represents the overall mean. The 99% confidence interval attending the standard error of the mean is shown within the dotted lines. A: The mean C content for TLC branch wood of was ~57.4% ± 0.8%. C content ranged from 55.7% ± 0.6% to 58.8% ±0.2%. B: Mean C content for BLC branch wood was 57.6% ± 0.7%. C content ranged from 55.6% ± 0.7% to 58.8% ± 0.2%.

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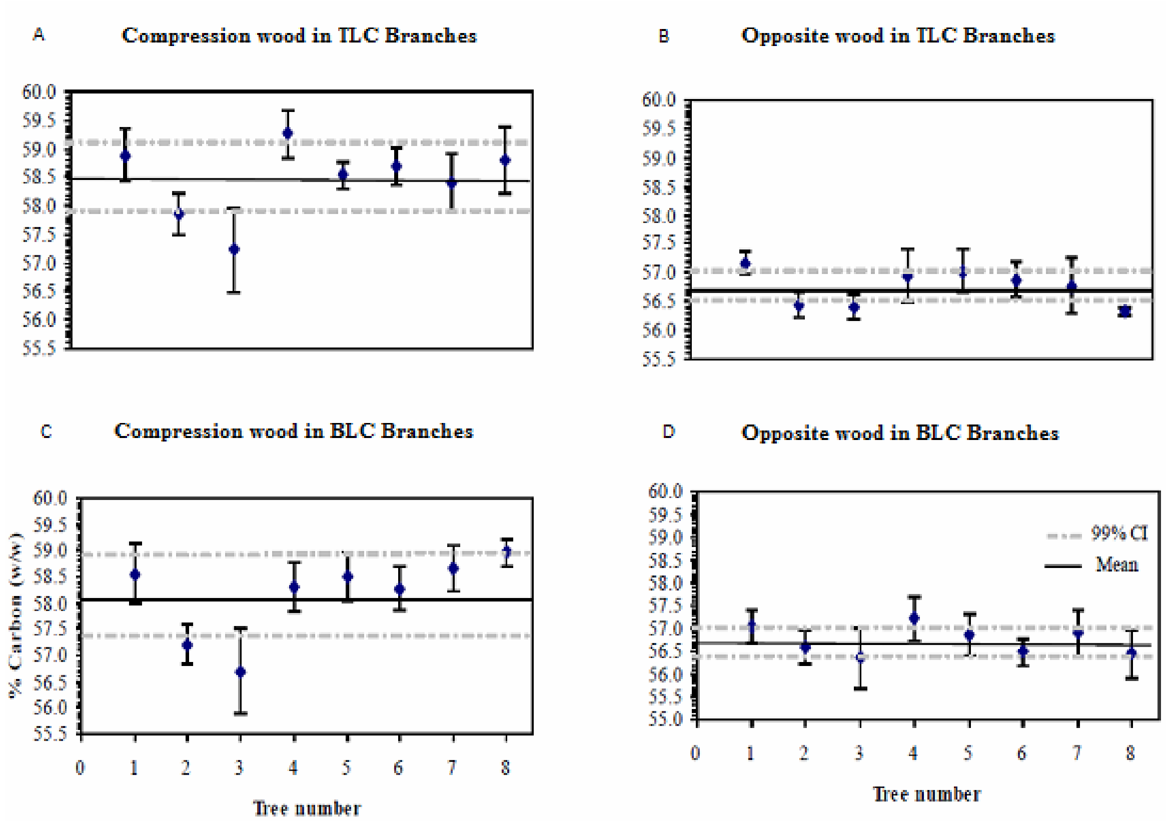


**Figure-2.** Mean percentage (w/w) C contents of branch compression wood and opposite wood at two branch positions, with standard deviations (error bars, n = 8). Horizontal solid lines represent the overall mean. The 99% confidence interval attending the standard error of the mean (SEM) is shown within the dotted lines. A: Mean C content of Cw in TLC branches was 58.1% ± 0.8%. B: Mean C content of Ow in TLC branches was 56.7% ± 0.3%. C: Mean C content of Cw in BLC branches was 58.5% ± 0.6%. D: Mean C content of Ow in BLC branches was 56.7% ± 0.3%.

## DISCUSSIONS AND CONCLUSIONS

An earlier study (Silva *et al*., 2012) found that mean C content of western hemlock trunk wood was ~ 53.5% (w/w). In this current study, mean C content of western hemlock branch wood was approximately 4% higher than that in the bole, and branch compression wood with ~ 58% (w/w) C has approximately 2% more C than opposite wood. The C content of compression wood in western hemlock is, to our knowledge, the highest value yet found in wood of any tree species.

A 50% C content has been the most broadly promulgated value in forest modelling (Wenzel, 1970; Ajtay *et al*., 1979; Karchesy and Koch, 1979; Sedjo, 1989; Dewar and Cannell, 1992; Hollinger *et al*., 1993; Matthews, 1993; Thuille *et al*., 2000). For western hemlock forests in coastal British Columbia, Canada, their total C content clearly is elevated well above the 50% value and deserves special consideration in relation to carbon credits.

Based on our studies, the precedent of generalizing C content data in forest carbon models is questionable and should be re-examined in relation to identifying actual C contents of forests (Lamlom and Savidge, 2003; Lamlom and Savidge, 2006; Lamlom and Savidge, 2007; Lamlom, 2005). When a 50% conversion factor is used in C inventories, a 2% variation at the stand level could translate to a 10% to 25% error at the individual tree level (Houghton *et al*., 1985, Joosten *et al*., 2004). These errors are considerable and show the need to develop and improve existing relationships for estimating C content, especially when estimating at the stand level (Xing *et al*., 2005).

One of the major limitations for achieving accurate estimates of C content in forests is that, volume Tables used in forest inventory are valid only for inside-bark volume of merchantable-sized logs, i.e., for trunk wood. There are no data for the non-merchantable components (Savidge, 2001). Chard (2005) attempted to investigate non-merchantable biomass of western hemlock using known growth rates and merchantable volumes. In principle, such derived yield curves could be used to calculate total C content of western hemlock trees, and then compared to forest inventories to estimate the amount of C in forested stands. For instance, biomass for western hemlock trunk wood has density of 0.440g/cm$^3$. Once trunk biomass volume is known, it could be multiplied by the C content 53.5% (w/w) and the density of western hemlock trunk wood to determine the total trunk wood C content of a stand (Savidge, 2001; Lamlom and Savidge, 2006). However, our data show that this simplistic approach would be in error in relation to all wood within a tree, because like branch wood, juvenile (i.e., non-merchantable tree top) and root woods can be expected to have densities and C contents different from one another as well as from trunk wood. Clearly, juvenile, branch and root wood considerations remain to be adequately integrated into forest stand C estimates.

The anatomical and chemical differences intrinsic to wood arise despite the biological principle that the genetic constitution of cambium is constant throughout the tree (Savidge, 1996, 2000, 2003). The differences in C content between the bole and branches and even within opposite sides of a branch evidently have their explanation mainly in terms of intrinsic environmental differences that influence cambial growth and biochemical reactions within cambial derivatives as they mature into wood. In addition, we reported evidence that metabolism within mature wood also modified C content (Lamlom and Savidge, 2006, 2007).

C content in wood of branches was 4% higher than that of the bole. However, excepting the greater tendency for reaction wood (i.e., Cw and Ow) in branches, there is no obvious reason why branch wood should have properties of C metabolism and accumulation that set them apart from the trunk (Sprugel *et al*., 1991; Sprugel 2002). The elevated C content in Cw undoubtedly has some of its explanation in the higher lignin content combined with the higher amount of p-hydroxyphenyl lignin in Cw (Savidge 1996, 2000, 2001, 2003). However, Cw cannot be the full explanation for the overall increase in branch C content relative to that in western hemlock trunks, because our data indicate that Ow mean C content (56.5%) is also significantly higher than that of trunk wood, comparing branch and trunk wood in the identical trees (cf. Silva, 2012; Silva *et al*., 2012).

In conclusion, considerable additional research is needed in order to have accurate estimates of total C content in any tree, and given that there is variation in C content within tree species, C content should be estimated depending on each individual tree component. This will be the path to follow to account more accurately for the total C in any forest stand.

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