

## Variation in foliar $\delta^{13}\text{C}$ values within the crowns of *Pinus radiata* trees

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### Summary

Although herbaceous species generally show little within plant variation in  $\delta^{13}\text{C}$ , trees show large spatial and temporal differences. We found that the aspect of exposure and branch length accounted for up to 6‰  $\delta^{13}\text{C}$  difference within the foliage of individual trees of *Pinus radiata* D. Don. The foliage on branches 0.5 m in length was as much as 4‰ more depleted in  $^{13}\text{C}$  than foliage on 10-m long branches, and an additional 2‰ more depleted on the shaded side than on the exposed side. We confirmed that on clear days, relative branch hydraulic conductivity, defined as the ratio of transpiration to the water potential gradient, was much higher in short branches than in long branches. Stomatal conductance remained high in foliage on short branches during the day, whereas it declined progressively in long-branch foliage under similar conditions. These differences were sufficient to explain the observed variation in  $\delta^{13}\text{C}$  in foliage on long and short branches.

*Keywords:* carbon isotopes, hydraulic conductance, isotope fractionation, stomatal conductance, water potential.

### Introduction

The heavy stable isotope of  $^{13}\text{C}$  is discriminated against during photosynthetic uptake of  $\text{CO}_2$ . This depletion of  $^{13}\text{C}$ , as measured in the products of photosynthesis, is moderated by the rate at which  $\text{CO}_2$  diffuses into the leaf and the rate at which  $\text{CO}_2$  is fixed by RuBP carboxylase (Farquhar et al. 1982a). The average value of  $^{13}\text{C}$  depletion for  $\text{C}_3$  plants is approximately  $-27\text{‰}$ , and the wide range of values about this mean reflects the various degrees of stomatal control and water-use efficiency of plants. The accepted model for this process (Farquhar et al. 1988) predicts that any environmental stress limiting  $\text{CO}_2$  diffusion into leaves will lower the internal partial pressure of  $\text{CO}_2$  below normal, and result in photosynthetic products that are less depleted in  $^{13}\text{C}$ . Variation in  $\delta^{13}\text{C}$  among crop cultivars and other herbaceous species has been studied intensively, and differences in isotope ratio have been correlated with differences in water use efficiency (Farquhar et al. 1982b, Farquhar and Richards 1984).

The total range in  $\delta^{13}\text{C}$  variation within a given species of herbaceous plant is usually small. For example, less than a 2‰ difference was reported among four genera of grasses subjected to drought and irrigation (Johnson and Tiezen 1993). Trees, in contrast to annual plants, show large variations in carbon isotope abundance

both within individual plants and among species. Variations in  $\delta^{13}\text{C}$  of as much as 5‰ have been reported for cellulose extracted from annual rings (Craig 1954, Grinsted and Wilson 1979), within branches (Francey et al. 1985), and between neighboring trees of similar age (Leavitt and Long 1986), as well as among trees of different ages (Yoder et al. 1994). Irradiance is an important factor modifying  $\delta^{13}\text{C}$  in the foliage of huron pine in Australia (Francey et al. 1985), and there is little doubt that the same processes that control  $\delta^{13}\text{C}$  in herbaceous plants also operate in trees. Two major conclusions can be drawn from the existing literature concerning trees. First, cellulose in the growth rings of trees becomes less depleted in  $^{13}\text{C}$  as trees age (Jansen 1962, Francey and Farquhar 1982, Grootes et al. 1989). Second, there can be as much variation in  $^{13}\text{C}$  ratios of pure cellulose extracted from current foliage, twigs and wood as is observed between young and old trees (Leavitt and Long 1986).

Experimental designs to cope with the large variation in  $\delta^{13}\text{C}$  within trees have centered on pooling numbers of samples to provide values that express the weighted mean of the whole tree (Leavitt and Long 1984). Despite the apparent variation in values and difficulties in interpreting contemporary  $^{13}\text{C}$  ratios in trees, considerable weight is put on temporal changes in  $^{13}\text{C}$  abundance in tree rings as indicators of past climate change (Mazany et al. 1980, Becker et al. 1991). We have attempted to define the physiological factors operating within a tree that could give rise to the observed and unexplained variation in  $^{13}\text{C}$  abundance.

Trees, because of their size and longevity, offer the opportunity for compartmentalization of processes and products in space and time. One result of compartmentalization is that the main stem of a tree offers less resistance to water movement than the branches (Richter 1973, Tyree 1988). Internal resistance to water flow should increase substantially as branches lengthen (Pothier et al. 1989). When transpiration approaches maximum rates on any branch, partial stomatal closure occurs, thus preventing irreversible cavitation in that branch (Tyree and Sperry 1988). Atmospheric water vapor deficits and light exposure are the two principal modifiers of stomatal aperture and, indirectly,  $^{13}\text{C}$  ratios. We hypothesized, therefore, that for any given species, the length and exposure of a branch should account for the majority of  $^{13}\text{C}$  variation reported in foliage and, by inference, annual growth rings.

## Methods

### *Site description*

All measurements were made in plantations in the North Island of New Zealand. At latitude 37°47' S, longitude 175°17' E, where the University of Waikato is located, the climate is maritime with rainfall well distributed throughout the year without extended periods of drought or frost. There is no significant air pollution in this area. Extensive plantings of *Pinus radiata* D. Don are available close to the campus in plantations, grown singularly and as pruned hedges. Under these growing conditions we sought sites where  $^{13}\text{C}$  discrimination in trees was unlikely to be influenced locally by fossil fuel consumption.

The experiments consisted of two major parts. First, we determined variation in  $^{13}\text{C}$  according to branch length and position on open-grown trees, and second, we made physiological measurements to assess stomatal conductance, photosynthesis and water tension on various sizes of branches exposed to comparable illumination throughout the day.

#### *Isotope measurements*

Duplicate carbon isotope measurements were made on three to four 1-mm segments taken from the center portion of needles collected from the current, but mature, fully exposed fascicles situated near the ends of branches. The needle segments were dried, sealed in aluminum foil, and analyzed for  $\delta^{13}\text{C}$  with a continuous flow combustion analyzer connected to a GC-MS (Europa Tracemass). All analyses were run against the CSIRO sucrose standard and recalculated in relation to the Pee Dee Belemnite standard, with variation in the analysis of less than 0.2%. Similar variation was observed between duplicate samples of foliage.

To document possible variation in  $^{13}\text{C}$  associated with aspect, we selected a 20-year-old, open-grown pine tree with 8–10-m long branches symmetrically arranged and with foliage accessible from the ground. We collected duplicate samples of foliage from the ends of eight branches representing different directions of exposure around the tree.

To document possible variation in  $^{13}\text{C}$  associated with branch length, we collected foliage from the lower branches of more than a dozen 12- to 20-year-old trees. Most trees were open grown so that separate samples from the predominantly sunny northwestern exposure and the less exposed southeastern aspect could be compared. In a few cases, collections were restricted to only one exposure because of shade cast by adjacent trees. Branches ranged in length from 0.5 to 10 m.

To assess the possible influence of tree height on  $^{13}\text{C}$  ratios, we collected exposed foliage from one tree growing as part of a hedge with branches pruned to 0.3 m in length up to a height of 6 m. We collected foliage samples at 1-m intervals from the base upward and included one sample from a 2.5-m long branch at a height of 7 m.

#### *Photosynthesis and stomatal conductance measurements*

We tested the hypothesis that branches of varying length and exposure would exhibit consistent differences in photosynthesis and stomatal conductance on the exceptionally clear day, December 18, 1991. On this day, photosynthetically active radiation (PAR) exceeded  $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$  between 0900 and 1700 h, and the vapor pressure deficit of the air remained above 2.5 kPa. Subsequently, the reported findings have been replicated (Walcroft 1994). Measurements of photosynthesis and stomatal conductance were made on current needles in a 1-l cuvette with a Li-Cor LI 6200 gas exchange system. Following the measurements, foliage was collected, stored in plastic bags in an ice chest, and returned to the laboratory for determination of projected leaf area with a Delta-T area meter.

*Determination of branch hydraulic conductance*

In the laboratory, saturated hydraulic conductivity of detached branches was measured under steady state conditions of  $300 \mu\text{mol m}^{-2} \text{s}^{-1}$  PAR at  $25^\circ\text{C}$  with a vapor pressure deficit of 1.5 kPa and unlimited water supply. A constant transpiration rate could be maintained for over 2 h with either tap water or distilled water. We first removed all bark from the lower 10 cm of the cut branch, then cut a clean surface and plunged the end of the branch into boiling water for at least 60 s. The boiling water killed resin-producing parenchyma cells, which was essential to keep the cut surface clean. Organic solvents were not appropriate as they would injure the foliage when transported through the vascular system. The boiling process also released most trapped gases and, as a result, increased the conducting properties to near maximum (< 5% increase in flux observed when boiling was extended to 5 min). A beaker was placed under the submerged branch end, and the branch was fastened into a ring stand positioned above a weighing balance. The weighing balance was programmed to record the loss of water from the beaker in  $\text{ml min}^{-1}$  at 1-min intervals. A specially designed pressure chamber was used to measure xylem water potentials on individual needle fascicles with a precision of 0.2 MPa. Branch hydraulic conductance was calculated as the ratio of flux ( $\text{mmol m}^{-2} \text{s}^{-1}$ ) to the water potential gradient (MPa). In the field, the water potential difference between predawn and daytime readings defined the gradient.

Because of difficulties in driving off all trapped gases from the 10-m long branches even after submerging cut branch ends in boiling water for more than 20 min, we sought an alternative approach that allowed for less than fully saturated xylem and could be related to measurements made on intact branches of varying length. In the field, we selected branches of varying length and, after preparing the cut bases as previously described, fastened them in an upright position with each of the severed ends suspended in a beaker of water of known weight. At hourly intervals, a battery-operated precision balance was placed under each beaker and the weight loss recorded since the last weighing. At the same time, water potential and gas exchange measurements, required to estimate stomatal conductance, were made on a few fascicles of current foliage at the branch tips. A relation between flux measured on the whole branch and transpiration from a few fascicles was then established. On intact branches we made only gas exchange measurements and determined the water potential gradient by subtracting the hourly recordings made during the day from predawn measurements ( $-0.35$  MPa) made when dew was on the foliage. Branch hydraulic conductance, representing the flux from more than a square meter of projected foliage area, and the relative branch hydraulic conductance, determined from transpiration measured on a few fascicles within the gas exchange cuvette, were linearly related ( $r^2 = 0.77$ ). In obtaining the correlation, we wanted as large a range in hydraulic conductance as possible. We were not concerned whether cavitation was induced naturally or by a source of water not fully deaerated.

## Results

Branch aspect had a significant influence on  $\delta^{13}\text{C}$  values. The general pattern observed on three separate trees matched that illustrated in Figure 1, showing  $\delta^{13}\text{C}$  values above  $-27\text{‰}$  on the most exposed northerly aspects and values below  $-30\text{‰}$  on the least exposed SE aspect from a tree with 8–10-m long branches.

Sampling of needles from trees with 0.5 to 10-m long branches representing extremes in exposure showed  $^{13}\text{C}$  enrichment varied consistently and linearly with branch length (Figure 2). Ten-meter long branches showed up to 4‰ enrichment in  $^{13}\text{C}$  compared to 0.5-m long branches regardless of the aspect of exposure.

Branch length, rather than branch height, appeared to be the major contributor to variation in  $\delta^{13}\text{C}$  as demonstrated by the finding that foliage sampled at the ends of 0.3-m long pruned branches collected from heights of 1 to 6 m from a hedged pine had values of  $-29.8\text{‰}$  to  $-30.5\text{‰}$ , respectively (Figure 3). Significant changes in  $^{13}\text{C}$  enrichment occurred only above the pruned level at 7 m where branches reached a length of 2.5 m. Based on these comparisons of  $^{13}\text{C}$  variation in foliage collected from the ends of branches of various lengths, aspects and heights, we inferred that the shorter a branch and the less its exposure to solar radiation, the more favorable should be its water relations. Physiological measurements made in the morning and afternoon of a clear day confirmed that water relations were more favorable for foliage on short shaded branches than on long exposed branches (Figure 4).

Branch hydraulic conductance, estimated on fascicles of needles at the ends of 7-m long branches, showed a progressive decrease in mean values throughout the day, from the most exposed aspect (NW), through the W, to the least exposed aspect (SW). At 1400 h, up to a 50% drop in hydraulic conductivity was recorded on the intermediate (W) exposed branch that was unrelated to any significant change in

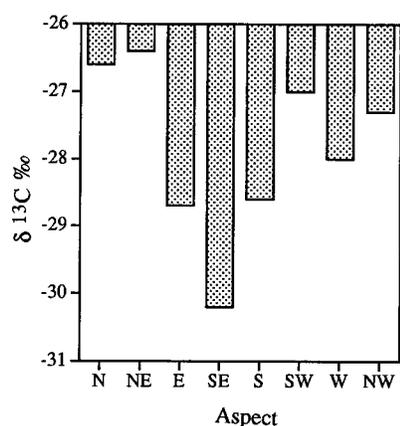


Figure 1. Values of  $\delta^{13}\text{C}$  for foliage of *Pinus radiata* varied by aspect. All foliage was mature and taken from branch tips of long (8–10 m) branches at similar height on one 20-year-old open-grown tree. The maximum  $^{13}\text{C}$  depletion occurred on foliage with least exposure to direct solar radiation (S to E);  $^{13}\text{C}$  was relatively enriched on the more exposed north and west aspects.

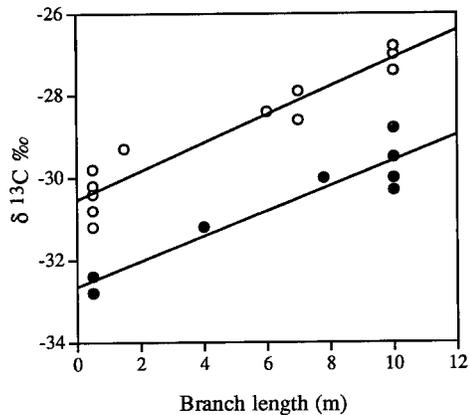


Figure 2. Values of  $\delta^{13}\text{C}$  for foliage of *Pinus radiata* from branches of different length and aspect. Foliage was taken from low branches on predominantly sunny NW (○) aspects and shaded SE (●) aspects. Long branches were sampled from several 12–20-year-old open-grown trees, whereas short branches were from hedged trees 12–14 years old.

water potential between branch exposures (–1.43 to –1.46 MPa). At 1400 h, the fully exposed long branches (W and NW) had photosynthetic rates of  $2 \mu\text{mol m}^{-2} \text{s}^{-1}$  and transpiration rates of  $1.5 \text{ mmol m}^{-2} \text{s}^{-1}$ , whereas the less exposed branch (SW) had values of  $14 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $3.8 \text{ mmol m}^{-2} \text{s}^{-1}$ , respectively. Near the same time, three samples from 0.25-m long branches on a NW-facing hedge had three times the hydraulic conductance of the fully exposed long branches (Figure 4). At 1500 to 1600 h, the three short branches exhibited photosynthetic rates of  $15.1 \pm 0.2 \mu\text{mol m}^{-2} \text{s}^{-1}$  and stomatal conductances of  $0.062 \pm 0.1 \text{ mmol m}^{-2} \text{s}^{-1}$  with water potentials

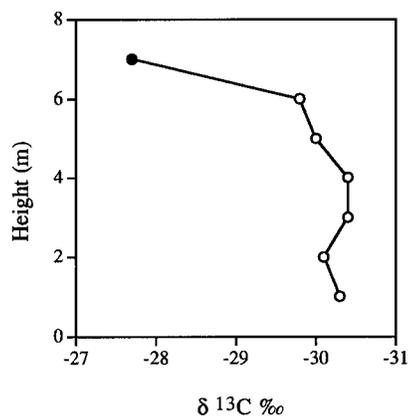


Figure 3. Values of  $\delta^{13}\text{C}$  for foliage of a trimmed *Pinus radiata* hedge at different heights and branch lengths. An exposed (NW facing) hedge was sampled at 1-m intervals from the base up to 6 m where trimming had ceased (○). Foliage from one 2.5-m long branch was analyzed above the pruned level at a height of 7 m (●). Each data point is a mean of two samples with less than 0.2‰ variation.

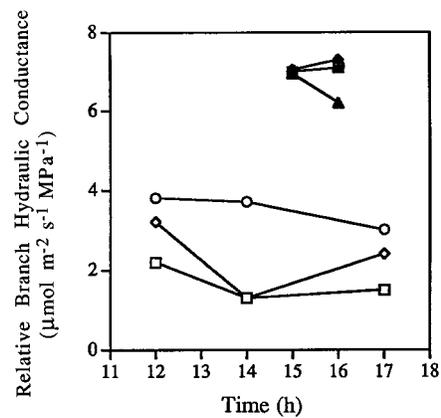


Figure 4. Relative branch hydraulic conductance estimates made on fascicles at the tips of three long (6 m) branches (open symbols) from SW (top), W (middle) and NW (bottom) exposures are compared with values observed on three short (0.25 m) intact (*in situ*) *Pinus radiata* branches with N exposure (closed symbols). Transpiration was measured in a 1-l cuvette, and needle water potentials were determined with a pressure chamber at predawn and during December 18, 1991, which was a clear day.

averaging  $-1.13 \pm 0.02$  MPa.

In narrow-leaved conifers such as *P. radiata*, the leaf and air temperatures are generally within a few degrees of each other (Riha and Campbell 1985). Because the water potential gradient did not vary significantly from the sunny to the shaded side of a tree (see data above), we assumed that differences in flux of water through branches must be related, under favorable conditions, to the amount of light available for photosynthesis. Gas exchange measurements showed a general increase in stomatal conductance with increases in photosynthetic rate that could explain how transpiration might initially be increased on the sunny side of trees compared to the shaded side. With continued exposure to high solar irradiance, however, hydraulic conductance decreased so that, overall, photosynthesis was closely coupled to changes in stomatal conductance (Figure 5).

## Discussion

The physiological data acquired from the one-day field experiment together with subsequent measurements provide evidence that differences in branch hydraulic conductance play a major role in explaining the observed variation in  $\delta^{13}\text{C}$  values in foliage on branches of varying lengths and exposure. If the main stem or root system were contributing significantly to an increase in resistance to the movement of water through the vascular system, we would have expected less variation in hydraulic conductance with aspect and branch length, and more variation with height. Tyree (1988) provides additional evidence that the branch system offers the major resistance to water flow through trees. Rapid diurnal changes in the hydraulic conductance of mature trees have been reported in similar situations where clear days

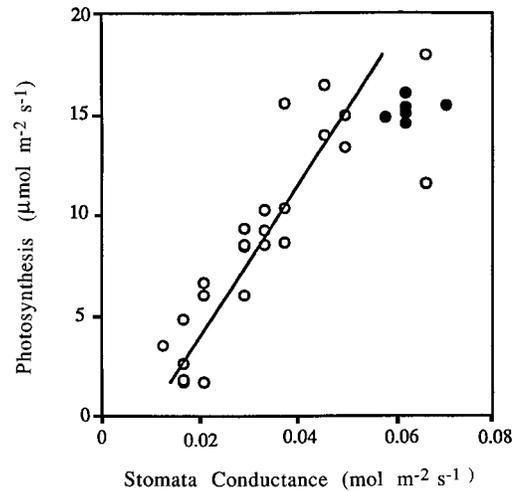


Figure 5. Relation between stomatal conductance and net photosynthesis for foliage from *Pinus radiata* during December 18, 1991. Measurements were taken on foliage fully exposed to radiation ( $> 1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) on long branches ( $\circ$ ) and short branches ( $\bullet$ ). All data were collected between 1100–1600 h from trees growing within a 400 m radius. A regression line is drawn for foliage on long branches only and shows leaves on short branches had significantly higher stomatal conductances than leaves on long branches.

followed a long period of cloudy wet weather (Waring and Running 1978, Whitehead et al. 1984). Partial recovery of embolized tracheids can occur overnight (Sobrado et al. 1992), although a longer period of cloudy wet weather is normally required (Chalk and Bigg 1956, Waring and Running 1978). On the North Island of New Zealand, temperatures are mild and precipitation is well distributed throughout the year. In such an environment, cavitation in xylem elements in sapwood should be minimal, resulting in branch length being the major contributor to variation in hydraulic conductance. Still, on long branches at the end of the day we found sapwood water contents at about 90% of saturation. If, in the morning, sapwood were saturated, the presumed change in water content would result in about a 25% reduction in hydraulic conductivity in accordance with studies done on spruce branches (Sellin 1991). In more extreme environments, where cavitation occurs more frequently, only a small fraction of sapwood remains functional throughout the year. This may contribute to a reduction in hydraulic conductance equal to or greater than that associated with branch length (Jeanne Panek, Oregon State University, personal communication).

On a clear day, stomata open progressively as the opportunity for photosynthesis increases (cf. Meinzer 1982, Wong et al. 1985, Teskey et al. 1986). On a day with prolonged high irradiance and high humidity deficits, however, we observed significant decreases in the hydraulic conductance of long branches exposed to direct radiation for more than 3 h. These decreases were associated mainly with a reduction in stomatal conductance rather than with a change in water potential gradient

(Figure 4). In contrast, on short branches stomata remained open throughout the day (see stomatal conductance data and Figure 5) and photosynthetic rates remained high. Differences in stomatal behavior associated with branch length and aspect of exposure provide a mechanism to explain the  $^{13}\text{C}$  variation. In long branches stomatal closure induced by changes in the water conducting properties of wood should, if carboxylation capability does not change, reduce internal  $\text{CO}_2$  ( $C_i$ ) resulting in less depletion of  $^{13}\text{C}$  in the leaves, whereas in short branches, stomata remain open and  $C_i$  is relatively high, resulting in more  $^{13}\text{C}$ -depleted photosynthetic products.

The use of total leaf carbon in analyzing  $^{13}\text{C}$  and relating this to photosynthesis has some obvious advantages and some less obvious interpretational difficulties. With samples from whole leaves, the time required for processing is minimal and analysis may be made with an automated continuous flow mass spectrometer within 10 min of taking a leaf sample. Current photosynthesis, however, may not be well represented because carbon laid down in the leaf tissue may be the result of photosynthetic activities during leaf emergence, or possibly the result of mobilized reserves assimilated under varying environmental conditions, or both. We rationalized that our measurements on whole leaves were a good representation of general environmental responses because *P. radiata* photosynthesizes all year on the North Island of New Zealand. In such a case, we believe that carbon in needles most likely originates from photosynthesis in the shoot. Even in more extreme environments, most of the carbon in new foliage of coniferous species is the product of the foliated shoot itself, not imported (Webb and Kilpatrick 1993).

The  $^{13}\text{C}$  values in leaves integrate photosynthetic conditions over the period of leaf development and, to the extent that the products of photosynthesis remain in the leaf, the condition currently prevailing. The effects of exposure on  $^{13}\text{C}$  values have been previously reported (Farquhar et al. 1988) but the eccentric distribution of  $^{13}\text{C}$  about a tree (Figure 1) have not. Our understanding of these relationships is enhanced by the physiological interpretation shown in Figure 4 that demonstrates a difference in SW- and W-facing long branches that could easily explain the  $^{13}\text{C}$  differences observed in Figure 1.

The effects of branch length on hydraulic conductance (Figure 4) and  $\delta^{13}\text{C}$  (Figures 2 and 3) appear significant and provide a likely explanation for the so-called "age" effect in  $^{13}\text{C}$  ratios in wood. This age phenomenon, reported for whole wood and cellulose by Grinstead and Wilson (1979), shows that young wood is significantly more  $^{13}\text{C}$  depleted than older wood. The  $^{13}\text{C}$  values tend to flatten out and become consistent after 50 to 200 years, and have been attributed to uptake of respired  $\text{CO}_2$  or some age-related physiology. We postulate that this change could relate to branch length and may also explain the slowing down in growth of mature trees. This interpretation is supported by observations made by Yoder et al. (1994) who found a 20–30% reduction in the photosynthetic rates of old trees compared to young trees of ponderosa and lodgepole pine, with associated changes in  $\delta^{13}\text{C}$  of similar aged foliage. Young trees have a high proportion of short branches, and as the trees increase in height, they maintain a continuing production of short branches. When

height growth ceases, canopy branches elongate and most foliage is situated at the distal end of the branches. Thus, one would expect the wood of mature trees to reflect the higher resistance to water movement along these long branches and be significantly less depleted in  $^{13}\text{C}$  than the wood of immature trees.

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