Effects of branch length on carbon isotope discrimination in *Pinus radiata*

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Summary   Gas exchange was measured on a pruned *Pinus radiata* D. Don hedge and on a long-branch *P. radiata* tree near Hamilton, New Zealand, in spring 1993 when soil water content was close to field capacity. Foliage at the end of long branches (9.0 m) showed a marked drop in net photosynthetic rate and stomatal conductance as the saturation deficit increased, whereas foliage on short branches (0.5 m) showed little change. Mean foliage $\delta^{13}C$ was $-30.1‰$ for short branches and $-26.3‰$ for long branches.

Foliage $\delta^{13}C$ was correlated with branch length in two genetically improved *P. radiata* seedlots at four stocking densities. The multinodal seedlot had shorter branches and more ^{13}C-depleted foliage compared with branches and foliage from the long internode seedlot. There was a strong effect of stocking density on carbon isotope composition in both seedlots. We conclude that branch morphology affects foliage gas exchange properties and foliage carbon isotope composition.

Keywords: branch morphology, hydraulic conductance, productivity, stable carbon isotopes.

Introduction

Fractionation against the $^{13}CO_2$ molecule occurs during photosynthetic assimilation of CO_2 (Vogel 1980, O'Leary 1981). The extent of discrimination is moderated by the ratio of intercellular (C_i) to ambient (C_a) CO_2 concentrations (Farquhar et al. 1982). This ratio, in turn, reflects a combination of the rate at which CO_2 diffuses into the leaf, which is controlled by stomatal conductance (g_s), and the net rate of CO_2 assimilation (A). Environmental and physiological factors that influence A and g_s will be reflected in the isotopic composition ($\delta^{13}C$) of plant tissue (Farquhar et al. 1989). Analysis of $\delta^{13}C$ variability in plant tissue therefore has the potential to reveal information about physiological processes and environmental conditions at the time the carbon was assimilated (Mazany et al. 1980, Leavitt and Long 1991, Livingston and Spittlehouse 1993, McNulty and Swank 1995).

Interpreting stable carbon isotope data requires quantitative knowledge of the extent to which environmental and physiological factors contribute to total discrimination during photosynthetic assimilation. Waring and Silvester (1994) showed that branch length and branch aspect could explain up to 6‰ of the variability in $\delta^{13}C$ of *Pinus radiata* D. Don foliage. Although artificial manipulation of branch length by pruning produced evidence consistent with an increase in hydraulic conductance, it is not known whether natural differences in branch length would yield a similar result. Therefore, we investigated the physiological effects of branch length by comparing $\delta^{13}C$ of foliage from two genetically improved *P. radiata* seedlots that had been selected on the basis of different branching habits. Selection for long internodes tends to increase average branch size (diameter and length), whereas selection for a multinodal (short internode) branching habit decreases average branch size (Carson and Inglis 1988). We tested the hypothesis of Waring and Silvester (1994) that foliage from the multinodal seedlot would be more depleted in ^{13}C compared with foliage from the long internode seedlot.

Materials and methods

Short-branch hedge trees and long-branch trees

Gas exchange measurements and isotopic analysis were made on a *P. radiata* hedge (pruned, 0.5-m branches) and on a north-facing row of similarly aged, unpruned *P. radiata* trees (9-m branches) near Hamilton, New Zealand. It was assumed that pruning would not influence branch conductivity apart from the effect on branch length. A portable, open-flow infrared gas analysis system (PP Systems, Herts, U.K.) was used to measure gas exchange of current-year needles. Projected leaf area was estimated by measuring the length and width of the portion of the needles inside the leaf cuvette with digital calipers (Mitutoyo Corp., Osaka, Japan).

During gas exchange measurements, the photosynthetic photon flux density (PPFD) exceeded 1500 $\mu mol\ m^{-2}\ s^{-1}$ and the saturation deficit of the air reached 1.4 kPa. On the long-branch tree, measurements were made on a north-facing, fully exposed branch over the whole day. Measurements began on the hedged trees at around midday after the foliage became

exposed to direct sunlight. Because of the variability inherent in making instantaneous gas exchange measurements, several spot readings were taken from groups of similar needles over several minutes, with the mean recorded as one data point. Net assimilation rate (A), transpiration rate (E), stomatal conductance (g_s) and C_i were calculated according to the equations of von Caemmerer and Farquhar (1981).

Water potentials of needles similar to those used in the gas exchange measurements were determined at intervals throughout the day with a pressure chamber apparatus (Scholander et al. 1965). Measurements were made within 1–2 min of needle excision.

After gas exchange and water potential measurements were made, the foliage samples were placed in paper bags, dried at 80 °C and analyzed for stable carbon isotope.

Long-internode and multinodal trees

A series of *P. radiata* growth trials were established in 1987 by the New Zealand Forest Research Institute (NZFRI). The NZFRI Silviculture/Breed Trial FR8, which is located in the Tahorakuri forest, near Broadlands in the central North Island, was planted with four genetically improved seedlots, including one long-internode and one multinodal seedlot, in a randomized incomplete block design with final stocking densities of 100, 200, 400, 500 and 600 stems per hectare (stems ha^{-1}). At age 5 years, the trees were pruned to leave 4 m of crown, except for trees in the plots stocked at 500 stems ha^{-1} which served as unpruned controls.

Each plot, replicated twice, consists of 16–32 trees and each plot is separated by at least two buffer rows. At age 6 years, stem diameter at breast height (DBH, 1.4 m) was measured for all trees and height measurements were made on 12 randomly chosen trees per plot. Needles for $\delta^{13}C$ analysis and nitrogen content were collected from the 12 trees measured for height in each plot. Thus, a random set of 12 trees across a range of sizes in each plot constituted an experimental group with two replicated plots for each seedlot and stocking density.

Needles were collected by means of extension clippers from the distal end of the lowest, north-facing branch on each tree. A northern aspect was chosen for maximum exposure to solar irradiation because shading influences foliage $\delta^{13}C$ (Ehleringer et al. 1986, Waring and Silvester 1994, Walcroft 1994). Following collection, the needles were dried at 80 °C, ground and analyzed by mass spectrometry for $\delta^{13}C$ and nitrogen.

For each sample branch, the height of the branch tip (a), the height at the branch connection to the main stem (b), and the horizontal distance (x) from the branch tip to the main stem were measured. Branch length (L) was calculated by the equation:

$$L^2 = (a - b)^2 + x^2, \qquad (1)$$

where it was assumed that the branch was straight.

Analyses of stable carbon isotope and nitrogen content

Samples were dried at 80 °C, ground to a homogeneous powder and then analyzed in a Europa Tracermass stable isotope analyzer (Europa Scientific Ltd., Cheshire, U.K.) connected to an automated elemental analyzer (Model NA 1500, Carlo Erba Strumentazione, Milan, Italy). Carbon isotope analyses were run against a CSIRO sucrose standard ($\delta^{13}C = -10.8‰$) and sample $\delta^{13}C$ was calculated relative to the Pee Dee Belemnite standard.

Calculation of carbon isotope discrimination

Daily assimilation-weighted values of C_i were calculated following the method of Francey et al. (1985). We assumed that net assimilation commenced at 0700 h (NZST) at the rate obtained for the first measurement and thereafter continued at that rate until a point in time halfway between the first and second measurements, and so on for the remaining measurements. Net assimilation was assumed to cease at 1900 h (NZST). Total photosynthesis for a period was calculated as the rate of photosynthesis for the period multiplied by the amount of time at that rate, and total daily net carbon assimilation was calculated as the sum of photosynthesis for all periods. The average daily assimilation-weighted C_i/C_a ratio was calculated as:

$$\overline{C_i/C_a} = (C_i/C_a)_1(A_1/A_T) + (C_i/C_a)_2(A_2/A_T) + \dots, \qquad (2)$$

where $(C_i/C_a)_1$ is the C_i/C_a ratio measured during the first period and A_1/A_T is the proportion of total daily photosynthesis estimated to have occurred during the first period, $(C_i/C_a)_2$ is the C_i/C_a ratio measured during the second period and so on.

The isotopic composition ($\delta^{13}C_p$) of foliage on the long and short branches was estimated by the model of Farquhar et al. (1982):

$$\delta^{13}C_p = \delta^{13}C_a - a - (b - a)(C_i/C_a), \qquad (3)$$

where $\delta^{13}C_a$ denotes the isotopic composition of source air (assumed to be $-8‰$), a is the fractionation due to differential diffusion in air of the two isotopes (theoretically determined as 4.4‰), and b is the fractionation that occurs during the carboxylation reaction (usually 27‰).

Results

Short-branch hedge trees and long-branch trees

Saturation deficit reached a maximum of 1.4 kPa by midafternoon on the day gas exchange was measured (Figure 1). As the saturation deficit increased, g_s of long-branch foliage was reduced from 100 to 20 mmol m^{-2} s^{-1} by midafternoon and was accompanied by a reduction in A from 8.5 to 3 μmol m^{-2} s^{-1} (Figure 2). In contrast, foliage on the short-branch hedge had high g_s (150–200 mmol m^{-2} s^{-1}) and A (11–13 μmol m^{-2} s^{-1}), both of which remained relatively constant over the afternoon (Figure 2).

The differences in g_s and A between short- and long-branch foliage were reflected in differences in C_i. In long-branch foliage, C_i declined from around 200 μmol mol^{-1} in the morning to around 120 μmol mol^{-1} by late afternoon, whereas it
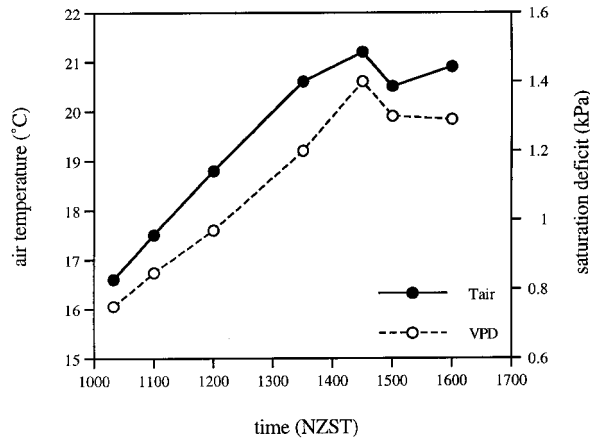
Figure 1. Variations in diurnal air temperature and atmospheric vapor saturation deficit recorded at the hedge site on the day gas exchange was measured.
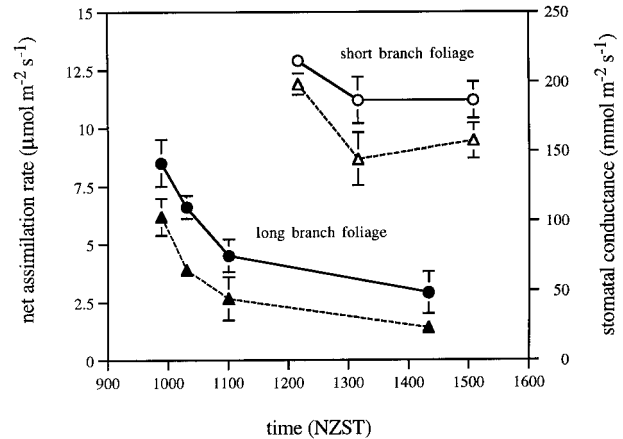

Figure 2. Diurnal course of mean net photosynthetic rate (circles) and stomatal conductance (triangles) in foliage from long- (closed symbols) and short-branch (open symbols) *Pinus radiata* trees (bars indicate standard deviation, $n = 5$).

remained at around 215 µmol mol^{-1} throughout the afternoon in short-branch foliage (Table 1). Transpiration rate followed a similar pattern to g_s being greater in short-branch foliage than in long-branch foliage. Transpiration rate declined over the afternoon in the long-branch foliage, whereas it remained relatively constant in the short-branch foliage (Table 1).

Needle water potential in both the long- and short-branch foliage followed a pattern of a morning maximum, a midday minimum followed by an afternoon increase (Table 1). Absolute water potential values were greater in short-branch foliage than in long-branch foliage, and the difference in water potentials between short- and long-branch foliage was highest at midday (0.35 MPa) and least during the morning and afternoon (around 0.2 MPa).

The carbon isotope composition of short-branch foliage was 3.8‰ more depleted in ^{13}C than that of long-branch foliage (Table 1). The average daily assimilation-weighted value of

C_i/C_a for long-branch foliage was 0.505, which corresponds to a photosynthate δ^{13}C of −23.8‰. For short-branch foliage, the daily assimilation-weighted C_i/C_a was 0.631, which corresponds to a photosynthate δ^{13}C of −26.7‰, i.e., 2.9‰ more ^{13}C depleted than for long-branch foliage.

Long-internode and multinodal trees

The minimum difference in branch length between long-internode and multinodal seedlots occurred at a stocking density of 200 stems ha^{-1} (0.20 m) and the maximum difference (0.81 m) occurred at 400 stems ha^{-1} (Figure 3). Foliage from the multinodal trees was significantly ($P < 0.05$) more ^{13}C depleted than foliage from the long-internode trees at all stocking rates despite differences in branch length of less than 1 m between seedlots (Figure 4). Maximum difference in isotopic composition occurred at a density of 400 stems ha^{-1} (0.6‰) and the

Table 1. Mean (± standard deviation) of several physiological parameters as well as foliage carbon isotope composition measured in foliage from short- and long-branch radiata pine trees. All differences between short- and long-branch trees were significant ($P < 0.001$, Student's t-test).

| Variable	Time of day	Short branch	Long branch
Length (m)		0.5	9.0
Intercellular CO$_2$ (µmol mol^{-1})	Morning	–	205 (13.4)
($n = 3$)	Midday	216 (13.1)	162 (33.7)
	Afternoon	215 (18.0)	120 (16.8)
Transpiration rate (µmol m^{-2} s^{-1})	Morning	–	1.09 (0.22)
($n = 3$)	Midday	2.87 (0.30)	0.93 (0.22)
	Afternoon	2.53 (0.25)	0.42 (0.10)
Needle water potential (MPa)	Morning	−0.92 (0.01)	−1.15 (0.04)
($n = 3$–11)	Midday	−1.45 (0.07)	−1.81 (0.10)
	Afternoon	−1.43 (0.06)	−1.60 (0.08)
Assimilation-weighted $\overline{C_i/C_a}$		0.631	0.505
Calculated δ^{13}C (‰)		−26.7	−23.8
Measured δ^{13}C (‰) ($n = 7$–11)		−30.1 (0.75)	−26.3 (0.86)
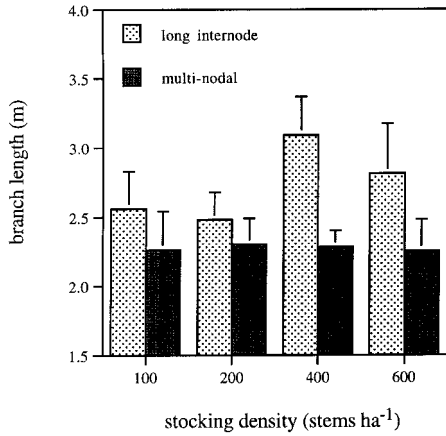
Figure 3. Mean length of the lowest north-facing branch from trees of long-internode and multinodal *Pinus radiata* seedlots grown at various stocking densities (bars indicate standard error, $n = 24$).
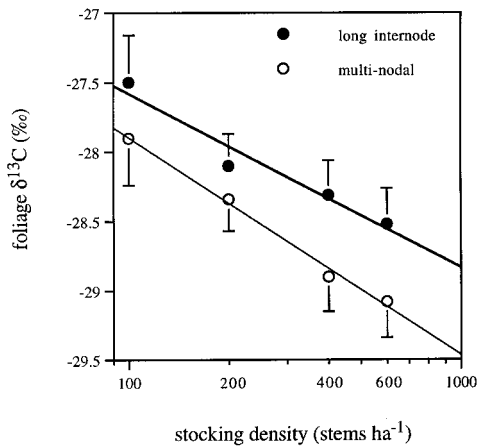

Figure 4. Mean $\delta^{13}C$ of foliage from trees of long-internode and multinodal *Pinus radiata* seedlots plotted on a linear scale against stocking density on a logarithmic scale (bars indicate standard error, $n = 24$).

minimum difference occurred at 200 stems ha^{-1} density (0.3‰).

Differences in branch length between the two seedlots were correlated with differences in foliar $\delta^{13}C$ at each stocking density, indicating an effect of branch length on foliage physiology and carbon isotope discrimination. An isotopic branch length coefficient was calculated by dividing the difference in foliage $\delta^{13}C$ at each stocking density by the respective difference in branch length. Coefficients at each stocking density varied between 0.75‰ m^{-1} at 200 stems ha^{-1} and 1.37‰ m^{-1} at 400 stems ha^{-1} (Table 2). The coefficient for the pruned hedge trees and long-branch trees was 0.45‰ m^{-1} (Table 2) (cf. Waring and Silvester 1994).

There was a negative logarithmic relationship between foliage $\delta^{13}C$ and stocking density in both the long-internode ($r^2 = 0.95$) and multinodal ($r^2 = 0.99$) seedlots (Figure 4). Foliage from trees of both seedlots planted at 600 stems ha^{-1} had an

Table 2. Isotopic branch length coefficients calculated for genetically selected *Pinus radiata* trees differing in mean branch length and foliage carbon isotope composition. Coefficients are also shown for the branch length and isotopic differences between artificially pruned hedge trees and unpruned trees.

Treatment	Isotopic branch length coefficient (‰ $\delta^{13}C$ m^{-1})
Genetically selected trees	
100 (stem ha^{-1})	0.78
200 (stem ha^{-1})	0.75
400 (stem ha^{-1})	1.37
600 (stem ha^{-1})	1.00
Artificially pruned trees	
This study	0.45
Waring and Silvester (1994)	0.33

isotopic composition almost 1‰ more ^{13}C depleted than that of foliage from trees of their respective seedlot planted at 100 stems ha^{-1}. Foliar nitrogen concentration was not significantly affected by branch length or stocking density (Figure 5).

Discussion

We observed an effect of branch length on needle physiology and carbon isotope composition in *P. radiata*. Sprugel et al. (1991) reviewed the extent to which differences in branch characteristics influence subtending foliage and concluded that branches are somewhat autonomous with respect to water, despite continuity of the water column, because of a vascular constriction at the branch–stem junction. Thus, differences in branch conductivity (e.g., with branch length) will be reflected in physiological differences in the foliage.

Variations in water potential and g_s within tree crowns have been described (Scholander 1965, Waring and Cleary 1967, Hellkvist et al. 1974). Hinckley and Ritchie (1970) found branches in the lower crown of a 8-m tall *Abies amabilis* Dougl. ex J. Forbes. tree had water potentials up to 0.6 MPa
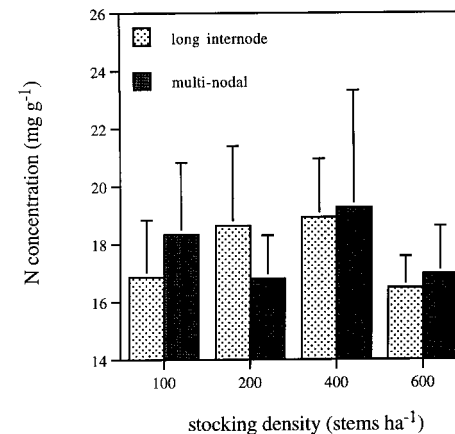

Figure 5. Average nitrogen concentration (expressed on a dry weight basis) of foliage from long-internode and multinodal trees grown at four stocking densities (bars indicate standard deviation).

lower than branches near the top. This finding is not consistent with the hydrostatic gradient but it is consistent with a branch length effect, assuming branches in the lower crown are longer than those near the top. We found that water potential in long-branch foliage was lower than in short-branch foliage (i.e., foliage on pruned branches) reflecting a lower conductance in long branches. Lower foliage water potential may result in an enhanced stomatal sensitivity to saturation deficit, and hence a lower average g_s, which is apparent in the gas exchange data. The reduction in C_i that accompanied the decline in photosynthesis over the day (Figure 1, Table 1) may reflect an increase in stomatal limitation of photosynthesis (Farquhar and Sharkey 1982).

Different stomatal responses between long- and short-branch foliage were also indicated by the daily assimilation-weighted values of C_i/C_a and in the calculated $\delta^{13}C$ values (Table 1). The calculated $\delta^{13}C$ values indicated that long-branch foliage was 2.9‰ less ^{13}C depleted than short-branch foliage; however, the calculated $\delta^{13}C$ values for long- and short-branch foliage were 2.5 and 3.5‰ less ^{13}C depleted than the corresponding measured values. The discrepancy between the calculated and measured $\delta^{13}C$ values arises because we estimated $\delta^{13}C$ values from assimilation over 1 day only when the combination of high irradiance and saturation deficit resulted in a lower C_i and less ^{13}C discrimination than the growing season average. Measured $\delta^{13}C$ values of whole-leaf tissue represent the effect of average environmental conditions on carbon assimilation over the life of the leaf.

Because the artificial pruning treatment may have confounded the effect of branch length on foliage physiology, we examined the effects of a more natural variation in branch length in genetically selected long-internode and multinodal *P. radiata* trees. Mean branch length of the long-internode seedlot was significantly greater than that of the multinodal seedlot, and long-internode foliage was less ^{13}C depleted than multinodal foliage. The average isotopic branch length coefficient was about 1‰ m^{-1} (Table 2), which is higher than the coefficients determined from measurements on hedge trees and long-branch trees.

Several papers have described genetic differences in carbon isotope discrimination among families or populations of annual crop species (e.g., wheat, Condon et al. 1987; peanut, Hubick et al. 1988; cowpea, Hall et al. 1990), and more recently, genetic differences have been reported among populations of two conifer species (e.g., *Pseudotsuga menziesii* (Mirb.) Franco, Zhang et al. 1993; *Larix occidentalis* Nutt., Zhang and Marshall 1994). Although many of these studies show a correlation between carbon isotope discrimination and water use efficiency, the physiological process underlying this relationship was not identified. Geber and Dawson (1990) correlated differences in gas exchange and isotopic discrimination with variation in leaf size and development in *Polygonum arenastrum* Boreau. We postulate that the genetic variation in $\delta^{13}C$ results from a difference in branch length influencing the physiological response of needles to the environment.

The negative logarithmic relationship between foliage carb-

on isotope composition and stocking density in each seedlot (Figure 4) may reflect the effect of an increase in leaf area index on self-shading in the lower crown. The attenuation of light through canopies due to absorption by foliage is generally exponential and can be approximated by a modification of Beer's law (Nobel 1991):

$$J = J_o/e^{kF}, \qquad (4)$$

where J is PPFD below the crown when LAI $= F$, J_o is PPFD incident on the canopy, and k is the foliar absorption coefficient. An increase in LAI with stocking rate would result in an exponential decrease in PPFD below the canopy. Photosynthesis in the lower crown will therefore be reduced at higher stocking rates resulting in an increase in C_i and greater ^{13}C discrimination.

It is possible that competition for water or nutrients may also have affected ^{13}C discrimination at different stocking densities. Although published evidence suggests a strong positive relationship between leaf nitrogen content and $\delta^{13}C$, we found no differences in foliar nitrogen concentrations between seedlots and stocking rates that could explain the trend in $\delta^{13}C$ with stocking density. It is unlikely that competition for water affected ^{13}C discrimination at different stocking densities because soil water content would tend to be reduced at higher stocking densities. A decline in soil water content would cause reductions in leaf water potential and g_s, leading to decreases in C_i and ^{13}C discrimination, and resulting in a positive relationship between $\delta^{13}C$ and stocking rate. Because the observed relationship was negative, we conclude that competition for nitrogen or water was not a determining factor in the relationship between stocking density and foliage $\delta^{13}C$.

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