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Didier Bert, Jean-Luc Dupouey, S. Leavitt. Long-Term increasing WUE revealed by δ13C in tree-rings.. International Seminar on " Causes and consequences of accelerating tree growth in Europe ", May 1998, Nancy, France. 1 p., 1998. hal-02836720

HAL Id: hal-02836720
https://hal.inrae.fr/hal-02836720

Submitted on 7 Jun 2020

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LONG-TERM INCREASING WUE REVEALED BY $\delta^{13}C$ IN TREE RINGS

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INTERNATIONAL SEMINAR ON " CAUSES AND CONSEQUENCES OF ACCELERATING TREE GROWTH IN EUROPE". NANCY, FRANCE 18-19 MAI 1998.

INRA Institut National de la Recherche Agronomique 1998

The isotopic composition of tree rings carries an integrated annual record of environmental conditions, in particular temperature and precipitation. However, models of carbon discrimination during carbon fixation show that C3 plants are not passive recorders: the carbon isotopic variations are subjected to strong physiological control through leaf gas exchange regulation (Francey and Farquhar 1982). Therefore, records of carbon discrimination in tree-ring cellulose could be used to study past variations of the ecophysiology of silver fir (*Abies alba* Mill.), a common conifer in European mountains, over the last century (Bert et al., 1997).

PRINCIPLE

The isotopic composition is measured by mass spectrometry and expressed in reference to the PDB standard:

$$\delta^{13}C\ ‰ = \left(\frac{\frac{^{13}C_{sample}}{^{12}C_{sample}}}{\frac{^{13}C_{PDB}}{^{12}C_{PDB}}} - 1\right) \times 1000 \qquad (1)$$

A typical value for air in 1990 was $\delta^{13}C_{air} \approx -8‰$ therefore the discriminations in the C3 plants give typical values $\delta^{13}C_p \approx -22‰$ to -34‰. This carbon discrimination is expressed as (δ_a is $\delta^{13}C_{air}$ and δ_p is $\delta^{13}C_{plant}$):

$$\Delta‰ = \frac{\delta_a - \delta_p}{1 + \delta_p} \qquad (2)$$

Models of discrimination (Farquhar et al., 1982) show that Δ is related to the ratio between the internal gas phase pressure of CO_2, P_i, and the atmospheric partial pressure, P_a:

$$\Delta = a - d + (b - a)\frac{P_i}{P_a} \qquad (3)$$

In addition, net photosynthesis, A, measured as CO_2 uptake, and leaf conductance to CO_2, g_c, are linked by Fick's law:

$$A = g_c (P_a - P_i) \qquad (4)$$

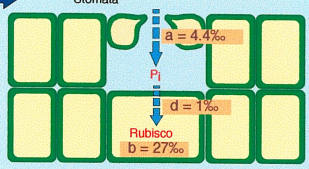
Given that, g_w, the leaf conductance to water vapor, is 1.6 g_c, and using equations (3) and (4), discrimination can be related to the intrinsic water-use efficiency "WUE" (Ehleringer et al. 1993) by:

$$\Delta = a - d + (b - a)\left(1 - \frac{1.6}{P_a}\left(\frac{A}{g_w}\right)\right) \qquad (5)$$

There are two stable-carbon isotopes in the atmosphere...

- $^{12}CO_2$ 98.9% (light isotope)
- $^{13}CO_2$ 1.1% (2.2% heavier molecule)

...and 3 main levels of discrimination against ^{13}C during photosynthesis



Result : less ^{13}C in the wood than in the air

Direct and indirect atmospheric estimates of δ_a are now available; therefore, equations (2, 5) can be used in order to study long-term changes of Δ and thus of intrinsic water-use efficiency from measurements of δ_a and δ_p.

This *intrinsic* WUE is part of the WUE of the whole plant which depends also on leaf to air water gradient, the *environmental* component.

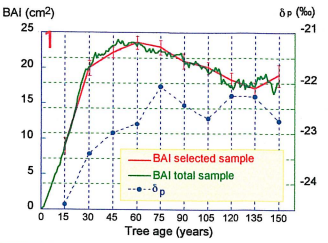
However, the wood formed when the tree was young is significantly more ^{13}C depleted than wood formed at later stages of tree life. Thus, an adequate sampling scheme has to be designed to distinguish such an 'age' effect and the effects of environmental changes on Δ.

TREE-AGE EFFECT ON δ_p

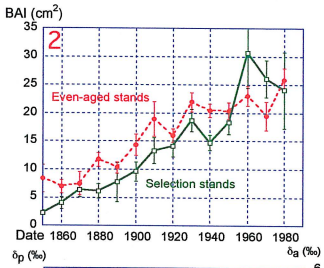
We confirm the existence of an 'age' trend, independent of any long-term environmental changes (Fig.1). This δ_p pattern could be attributed to

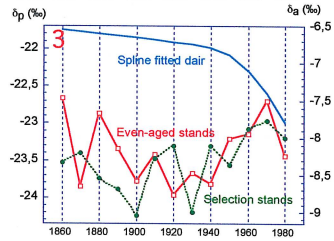
- internal age-related physiological factors
- changes of environmental factors associated with tree height, canopy closure and stand level competition (concentration of respired CO_2, soil moisture and light regime, etc.).

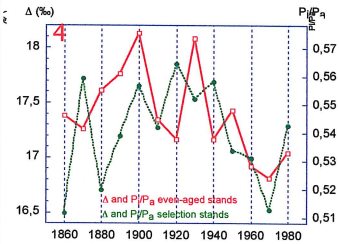
This aging effect has to be taken into account when comparing the stable-carbon isotope content of rings formed at different tree ages.

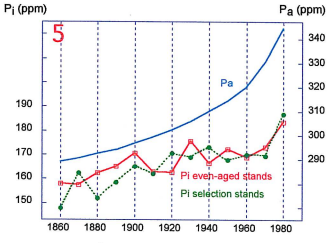


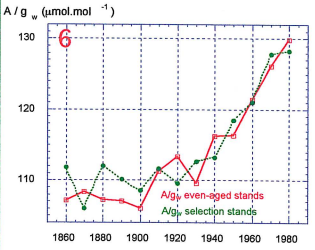
LONG-TERM CHANGES











The basal area of tree rings formed at the age of 40 increased after circa 1860 (Fig.2). The mean BAI is significantly different for the two types of stands but δ_p values showed no significant difference (Fig.3).

δ_p should have paralleled δ_a if the plant fractionation was not affected by any long-term environmental changes. Actually, the variations of δ_p and δ_a were very different after 1930s (Fig.3).

Discrimination Δ kept constant before the 1930s and significantly decreased afterwards (Fig.4). The P_i/P_a ratio followed the same changes (Eq.3, Fig.4), which allows to reconstruct the P_i variation because P_a is known (Fig.5).

During the period 1930-1980, P_i increased slower than P_a and the intrinsic water-use efficiency significantly increased 30% (Fig.6).

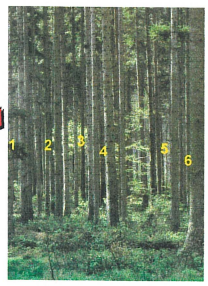
Our observation of an *in situ* increase of intrinsic WUE of a forest tree species is a first upscaled confirmation of similar observations made in controlled experiments (CO_2 increase, temperature etc.).

However, we are faced with the difficulty of ascribing this observed ecophysiological change in the forest to the effect of improvement of silvicultural methods or macroclimatic changes, increasing atmospheric CO_2 concentration, atmospheric deposition of nitrogen, etc.

SAMPLING SILVER FIRS IN THE JURA MOUNTAINS



208 plots
6 firs per plot
1 core per tree



Dendroecological study (Bert, 1992)

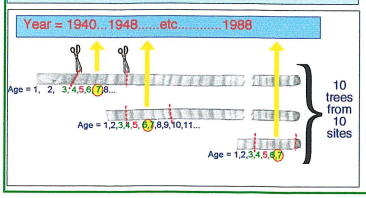
Sampling tree rings for "age effect" study

150 years of stand life were studied with 15-yrs steps. Bias of δ_p measurements was limited:

- studied tree ring pooled with its 4 neighbors;
- studied age reached between 1940 and 1988;
- site effects averaged by choosing ten trees at different locations.

For each studied age, ten tree-ring pentads were ground together and one δ_p value was measured.

Example for 5-yr-old:

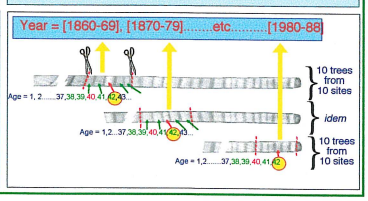


Sampling tree rings for "long term" study

Ten trees which reached 40-yrs-old during the time period were selected per decade (1860-69... 1980-88).

The tree-ring pentad of 38 to 42-yr-old was extracted from each core. The 10 pentads were ground together and one δ_p value measured for each decade.

Selection forests and even-aged forests revealed different increasing BAI long-term trends (Fig.2) and the sampling process was repeated for both.



CONCLUSION

The studied variations have important implications for the use of carbon isotope ratios in tree rings as a palaeorecorder of past environments.

The long-term component is better suited for the reconstruction of year-to-year deviations of climatic parameters from their long-term average (Dupouey et al. 1993).

The relationship between the isotopic composition of tree rings and climatic parameters is often calibrated during the recent period of rapid environmental changes. It may perhaps not be directly applicable to previous time periods, at least for the reconstruction of absolute climatic values.

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