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# Investigation of the 'canopy effect' in the isotope ecology of temperate woodlands

M. Bonafini [a,b], M. Pellegrini [a,*], P. Ditchfield [a], A.M. Pollard [a]

[a] Research Laboratory for Archaeology and the History of Art, School of Archaeology, University of Oxford, South Parks Road, Oxford OX1 3QY, UK
[b] Department of Environmental Sciences, Università Ca' Foscari, Calle Larga Santa Marta 2137, 30123 Venezia, Italy

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ABSTRACT

Anomalously $^{13}C$-depleted carbon stable isotope values from closed forest ecosystems have been termed the 'canopy effect'. Originally this was ascribed to recycling of depleted carbon from forest floor decomposition of organic material, although others have suggested that it is equally likely to be due to variations in leaf-level processes in response to increased shade. This depletion in the heavier carbon isotope is passed on to woodland herbivores feeding within the forest environments. A similar isotopic depletion has also been reported in the archaeological literature from more open temperate woodland settings, but no measurements have been made on the plants at the base of the food chain in order to quantify the effect. In this study we attempt this by examining the carbon and nitrogen stable isotopic values of different species of grasses from a range of open to closed habitat settings within Wytham Wood, Oxfordshire, UK. We find a strong relationship between carbon isotopic depletion of plant tissue and lowered light intensity with an up to 5‰ shift between grass grown in open and closed locations. In order to follow this up the food chain, we also report data on wool from sheep grazing in open pastures near the Wood, and on fallow deer living within the woodland, but which turn out not to show a strong canopy effect, probably related to their feeding strategies. We conclude that there is indeed a strong 'canopy effect' in temperate woodland, probably related to differential light levels, but that not all apparently woodland-dwelling mammals show such an effect. We also show considerable isotopic variation at the base of the food chain, which should counsel caution when attempting to interpret dietary isotopes using mixing models.



## 1. Introduction

The effect of recycling carbon dioxide on the carbon isotopic composition of leaves in a forest environment was first systematically investigated by Vogel (1978). In a forest in Upper Bavaria, Germany, he noted that leaves of *Asperula* and *Oxalis* growing near the ground had a values of $\delta^{13}C = -31.4‰$ and $-31.5‰$ respectively, whereas leaves of *Larix* and *Fagus* gave values of $\delta^{13}C$ increasing from at $-31.2‰$ for those growing at 2 m to $-27.9‰$ at 19 m. He attributed this phenomenon to the presence near the ground of depleted carbon dioxide emanating from the decay of plant material in the leaf litter. Measurements of $CO_2$ collected from beneath an upturned barrel in a forest near Heidelberg gave $\delta^{13}C$ values of between $-15.0‰$ and $-22.4‰$ from June to August. This is substantially below the average atmospheric $CO_2$ value of c. $-7‰$, and suggests that the biogenic $CO_2$ might have a value approaching that of the humus itself at $\delta^{13}C = -27.0‰$, since the collected sample was a mixture of air and exhaled $CO_2$. He estimated that 15% of the $CO_2$ incorporated into leaves at a height of 2 m above the ground is from the soil in this particular forest environment.

An alternative explanation for this isotopic depletion has been proposed based on the work of Farquhar et al. (1982), who produced an equation to relate the carbon isotopic value of leaf tissue to the ratio of the $CO_2$ concentration in intercellular leaf spaces ($C_i$) and the atmospheric $CO_2$ concentration. Since $C_i$ is inversely related to light intensity, this model predicts that more shaded locations should produce vegetation with more negative $\delta^{13}C$ values (van der Merwe and Medina, 1991). In their seminal paper on the canopy effect in the Amazonian forest, van der Merwe and Medina (1991, 251) concluded that 'many observers have simply assumed that both alternatives may contribute to the canopy effect'. There is therefore a general assumption that carbon isotope depletion occurs in plants from forested environments, the degree of which is in some way proportional to forest density. Since plants are at the base of the food chain, any such depletion is expected to be transferred up the food chain.

* Corresponding author. Tel.: +44 1865 285204; fax: +44 1865 285220.
*E-mail addresses:* maura.pellegrini@rlaha.ox.ac.uk, maurapellegrini@tin.it (M. Pellegrini).

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The 'canopy effect' has now been widely invoked in archaeology to explain the observation of depleted $\delta^{13}C$ values in some animal bone collagen, attributed to depletion of vegetation $\delta^{13}C$ values in wooded or partially-wooded environments (e.g., Bocherens et al. 1995; Fizet et al. 1995; Rodière et al. 1996; Cerling and Harris, 1999; Bocherens et al. 1999; Iacumin et al. 2000; Drucker et al. 2000; Stewart and Lister, 2001; Krigbaum, 2003). The most extensive such consideration is that of Drucker et al. (2008), who studied isotopic values (from collagen or hair) in modern large herbivores from the boreal forest-steppe of Siberia, temperate forests of Dourdan (France), and the boreal forests of western Canada. This paper confirmed that 'the canopy effect observed in plants is passed on to their consumers', and concluded that the $-3‰$ shift in faunal collagen $\delta^{13}C$ values observed in the Late-Glacial–Early Holocene transition from a number of French sites was related to the differences in habitat. Although such depletion effects have been directly demonstrated in modern plant material from tropical Amazonia (van Der Merwe and Medina, 1989) and in other low latitude regions, they have been less well-studied in higher latitude temperate woodlands.

Although convincing, this and other papers have inferred an isotopic shift at the base of the food chain from measurements of faunal collagen values in open compared to forested environments, rather than by direct observation of the flora. The aim of this research is to directly assess the extent of isotopic variation in grass growing at different locations in temperate woodlands (Wytham Woods, near Oxford, England) as a function of time through the growing season, degree of shade, and climatic conditions in general. At the same time we have analyzed biological tissues (bone collagen from fallow deer and wool from sheep) from animals reared in the same area. We deliberately chose to analyze whole grass samples for carbon and nitrogen isotopes (rather than selecting specific components such as cellulose, lignin, etc.), as this is the dietary basis of the grazing animals. The results of this study provide a quantitative measure of the 'canopy effect' in the flora at mid to high latitudes, and the extent of isotopic shifts which might be expected in the food chain at these latitudes.

## 2. Wytham woods

The research area was Wytham Wood (51.460 N 1.200 W; UK National Grid SP 460 080), which is located to the west of Oxford (Fig. 1). The wood covers 415 ha at an altitude from 90 to 165 m A.M.S.L. and is part of the Wytham Estate, which is c. 980 ha in extent. The remaining part of the estate is farmland. The woods are now exceptional in lowland England since they encapsulate the range of both woodland and non-woodland habitats that were common prior to agricultural intensification. Approximately one-third of the area is ancient semi-natural woodland, which was historically managed as coppice with standards. Over the course of the last 100 years coppice management has been largely abandoned. Another third of the area is recent semi-natural woodland that has regenerated on arable, pasture or wood pasture sites in the last two hundred years. The remaining woodland area consists of a variety of plantations, some on ancient woodland sites, some on sites which were formerly open. The woods lies on neutral clay soils, ranging from thin, freely-draining rendzinas over Corallian limestone at the higher altitudes to poorly-drained deep clay soils at lower altitudes (Avery, 1980).

## 3. Materials and methods

A series of experiments were carried out to quantify the canopy effect on flora and fauna in temperate conditions:

1) Four native grass species were placed in canopy and open contexts, following a period in an unheated greenhouse for germination. They were harvested at set time intervals during the growing season (March to September), and measured for their carbon and nitrogen isotopic compositions.
2) Bone collagen from fallow deer *Dama dama* living within Wytham Woods was extracted and measured for its carbon and nitrogen isotopic compositions.
3) Wool from sheep reared in the pasture adjacent to Wytham Woods was collected and measured for its carbon and nitrogen isotopic compositions.

### 3.1. Measurement of $\delta^{13}C$ and $\delta^{15}N$ in four native grass species

The grass seed was bought from Emorsgate Seeds (http://wildseed.co.uk), a nursery specializing in autochthonous flower seeds and wild herbs from Great Britain, and grown in individual

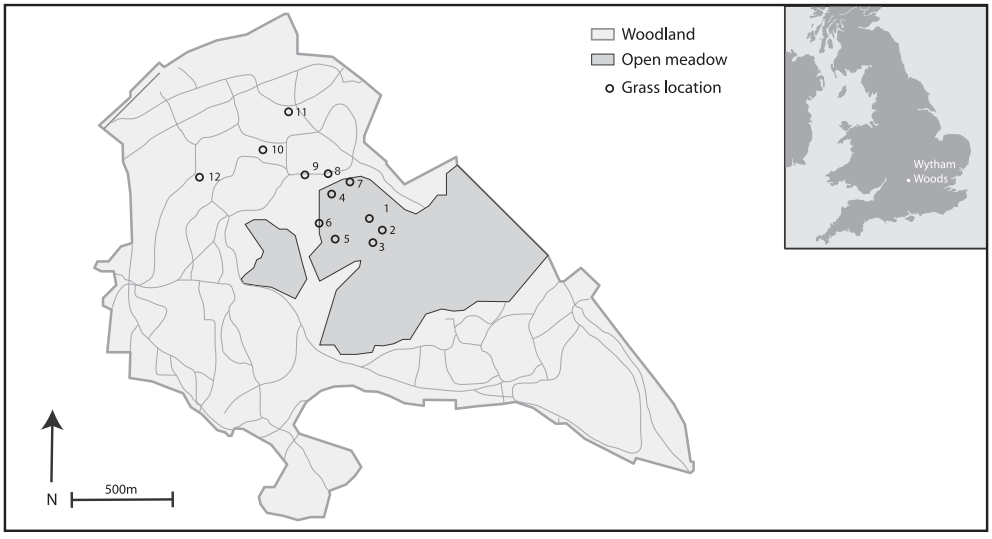


**Fig. 1.** Map of Wytham Woods, and location of placement of grass samples.