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Carbon sources for the Palaeozoic giant fungus *Prototaxites* inferred from modern analogues

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A wide range of carbon isotope values in the Devonian fossil *Prototaxites* has been interpreted to support heterotrophy and the classification of *Prototaxites* as a giant fungus. This inference remains controversial because of the huge size of *Prototaxites* relative to co-occurring terrestrial vegetation and the lack of existing fungal analogues that display equally broad isotopic ranges. Here, we show wide isotopic variability in the modern saprotrophic fungus *Arrhenia obscurata* collected adjacent to shallow meltwater pools of a sparsely vegetated glacial succession in the Washington Cascades, USA. Soils collected specifically around the edges of these pools were up to 5‰ higher in $\delta^{13}\text{C}$ than adjacent soils consistent with C_3 origin. Microbial sources of primary production appear to cause these high $\delta^{13}\text{C}$ values, and the environment may be analogous to that of the Early Devonian landscapes, where *Prototaxites* individuals with extreme isotopic variance were found. Carbon isotopes are also compared in *Prototaxites*, Devonian terrestrial vascular plants, and Devonian algal-derived lake sediments. *Prototaxites* isotopic values show little correspondence with those of contemporaneous tracheophytes, providing further evidence that non-vascular land plants or aquatic microbes were important contributors to its carbon sources. Thus, a saprotrophic fungal identity is supported for *Prototaxites*, which may have relied on deposits of algal-derived organic matter in floodplain environments that were less dominated by vascular plants than a straight reading of the macrofossil record might suggest.

Keywords: saprotrophic fungi; carbon isotopes; fossil plants; Devonian vegetation

1. INTRODUCTION

Late Silurian to Late Devonian *Prototaxites* has puzzled scientists since its discovery (Dawson 1859). At up to 8 m tall (Hueber 2001), *Prototaxites* towered over the landscape, particularly before similar heights were first achieved by vascular plants in the Middle Devonian (Stein *et al.* 2007). Whether it should be classified as a land plant, alga, lichen or fungus has remained contentious for 150 years (Carruthers 1872; Church 1919; Jonker 1979; Hueber 2001). Despite allochthonous marine specimens (Schweitzer 1983), *Prototaxites* is well represented in non-marine deposits (Griffing *et al.* 2000; Hotton *et al.* 2001; Hillier *et al.* 2008) and is a land organism with the most recent anatomical work supporting a fungal interpretation (Hueber 2001). In subsequent geochemical research, the carbon isotope ($\delta^{13}\text{C}$) ratios of *Prototaxites* specimens were found to vary 11‰ within an individual locality and up to 13‰ overall (Boyce *et al.* 2007). The samples separated into two groups, a ^{13}C -enriched group between -16‰ and -19‰ and a ^{13}C -depleted group between -27‰ and -29‰ . This variability led the authors to suggest a heterotrophic origin for *Prototaxites* carbon—thus supporting a fungal interpretation—and to further suggest that the ^{13}C -enriched *Prototaxites* specimens assimilated carbon from non-vascular autotrophs possessing a carbon-concentrating mechanism, such as terrestrial microbial soil crusts or some hornworts (Smith & Griffiths 1996; Evans &

Belnap 1999). However, these authors did not identify any present-day fungal analogues for this large range of carbon isotope values.

Modern analogues are most likely to be found in environments that partially resemble the Early Silurian and Devonian landscapes where *Prototaxites* occurred, floodplains characterized by sparse and patchy vegetation (Griffing *et al.* 2000; Hotton *et al.* 2001; Hillier *et al.* 2008). Early successional systems developing after glacial retreat have some of the desired characteristics, and the simplified soil and vegetation structure lends itself to comparing carbon isotope patterns among the individual components. Here, we compared carbon isotope values among plants, ectomycorrhizal (symbiotic) fungi, saprotrophic fungi and soils from a sparsely vegetated glacial foreland at Lyman Glacier, Washington, USA as a possible analogue to Early Devonian landscapes. One of the saprotrophic genera collected, *Arrhenia*, is commonly associated with algae and mosses (Redhead *et al.* 2002), and thus appears probably to derive carbon from non-vascular plant sources. To constrain the possible isotopic fractionation between saprotrophic fungi and source carbon, we compiled results from culture studies with saprotrophic fungi.

2. MATERIAL AND METHODS

(a) Literature data compilation

Data on $\delta^{13}\text{C}$ values of terrestrial plants and *Prototaxites* from the Devonian were compiled from the following published sources: Beerling *et al.* (2002); Boyce *et al.* (2003, 2007),

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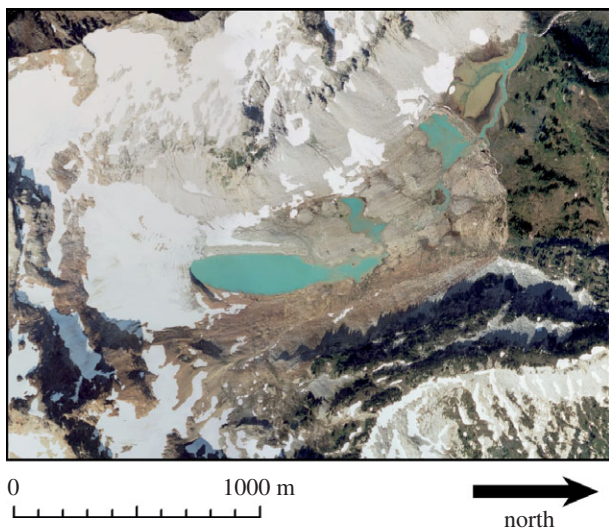


Figure 1. Aerial photo of the Lyman Glacier foreland. The glacier is at the left (south), the terminal moraine is at the right (north) with a stream outlet at the upper right. The sampling transect was along the western shore of the large lake. Image taken July 2006 for the US Geological Survey, High Resolution State Orthoimagery for Washington, 2008. Scale bar, 0–1000 m.

Jahren *et al.* (2003); Fletcher *et al.* (2004) and Peters-Kottig *et al.* (2006). Complete details are given in appendix A. To better constrain the potential isotopic relationship between fungi and source carbon in *Prototaxites*, literature values were also compiled from field and culture studies of modern fungi growing on complex substrates such as litter and wood.

(b) Modern data

(i) Site description

The study area is the foreland of Lyman Glacier. Lyman Glacier is at 48°10' N, 120°53' W, at an elevation of 1800 m in the Cascade Mountains of Washington, USA (figure 1). Sites were located 100, 300, 450, 600 and 750 m from the glacial terminus. The corresponding ages since glacial retreat were approximately 20, 40, 50, 60 and 70 years. The timing of glacial retreat has been determined from historical photographs and observations (Jumpponen *et al.* 1998, 2002). Individual sites were relatively heterogeneous and included both drier patches with vascular vegetation and more poorly drained areas of ephemeral water accumulation.

(ii) Sample collection

At each site, current-year foliage was collected from five plants of each of eight species if present. Tree and shrub species were generally less than 1 m in height. Species collected were *Luzula piperi* (Juncaceae), *Saxifraga ferruginea* (Saxifragaceae), *Luetkea pectinata* (Rosaceae), *Epilobium latifolium* (Onagraceae), *Abies lasiocarpa* (Pinaceae), *Salix phylicifolia* (Salicaceae), *Cassiope mertensiana* (Ericaceae) and *Phyllodoce empetriformis* (Ericaceae).

Fungal sporocarps were collected along the transect and the distance from the glacial terminus was recorded to the nearest 5 m. Fungi were identified to genus or species and classified as ectomycorrhizal (*Laccaria montana*, *Inocybe lacera* and *Cortinarius tenebricus*) or saprotrophic (*Arrhenia obscurata* and *Galerina* spp.). All fungi were basidiomycetes.



Figure 2. Soil was sampled in September 2009 at the Lyman Glacier foreland around 700 m from the glacial terminus, around shallow meltwater pools where *A. obscurata* commonly fruited. Photo: Ari Jumpponen.

At Lyman Glacier, *A. obscurata* commonly fruited in wet spots among mosses or on wet soil, often with algae on the soil surface (J. Trappe 1988–1999, personal communication). Five samples of relatively well-drained surface soils (top 5 cm) from each site were also collected. The sites were originally visited in late August 1999 for collections of soils, foliage and fungal sporocarps. During a later collection in early September 2009, soils were specifically collected around the edges of eight shallow meltwater pools 700 m from the glacial terminus (five samples per pool; an example is shown in figure 2). Pools 1–4 had no or very limited surrounding vegetation, whereas pools 5–8 were surrounded by early successional vegetation such as mosses and *Carex* (sedges). Additional details on site description and sample collection are in Hobbie *et al.* (2005).

(iii) Sample processing and isotopic analyses

Fungal and foliar samples were analysed for $\delta^{13}\text{C}$ on a Finnigan Delta-Plus isotope ratio mass spectrometer linked to a Carlo Erba NC2500 elemental analyser (Finnigan MAT GmbH, Bremen, Germany) located at the US Environmental Protection Agency, Corvallis, OR, USA. The internal standards for isotopic and concentration measurements were acetanilide and pine needles (NIST 1575). The average difference of duplicate samples was 0.2‰ for $\delta^{13}\text{C}$. Soils from 1999 were analysed for $\delta^{13}\text{C}$ at the Max Planck Institute for Biogeochemistry in Jena, Germany using a Finnigan Delta-Plus with acetanilide ($n = 9$, s.d. = 0.1‰) as the working standard. Soils from 2009 were analysed at the University of New Hampshire Stable Isotope Laboratory, with NIST 1515 (peach leaves), Underhill Bs (mineral soil), Underhill Oa (organic soil) and tuna as working standards.

3. RESULTS

Saprotrophic fungi were first collected at 270 m from the terminus of Lyman Glacier, whereas ectomycorrhizal

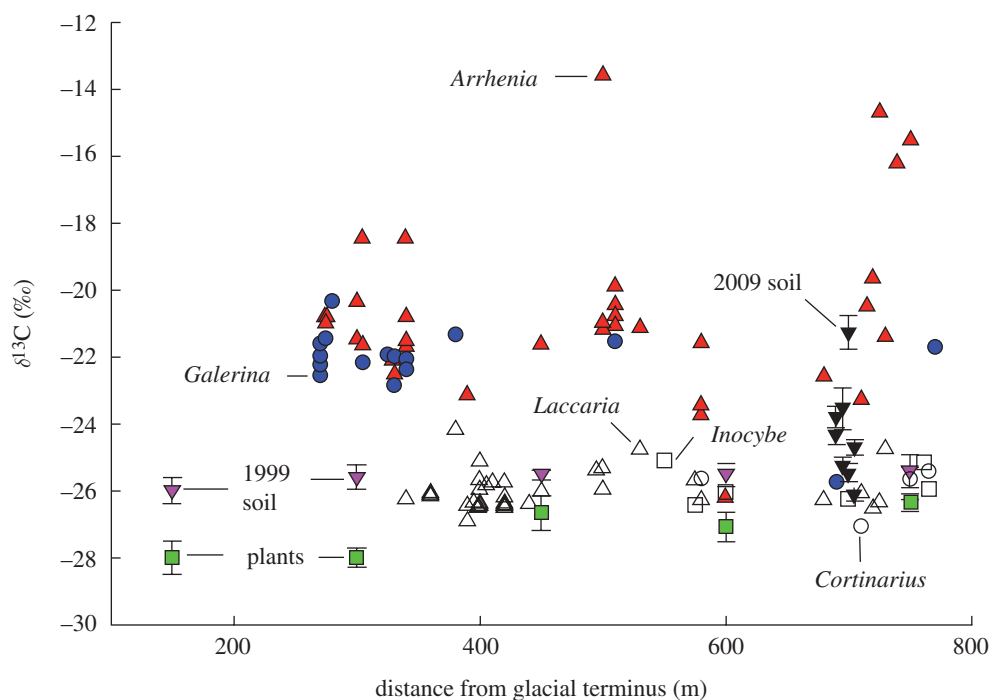


Figure 3. Carbon isotopes in ectomycorrhizal fungi, saprotrophic fungi, plants and soil at the Lyman Glacier foreland. Plants are shown as green squares, mineral soil collected in 1999 as upside-down pink triangles and mineral soil collected around meltwater pools in 2009 as upside-down black triangles, with standard errors indicated by error bars. Plants are means of eight species. Saprotrophic fungi are indicated by filled symbols: *Arrhenia*, red triangles; *Galerina*, blue circles. Ectomycorrhizal fungi are indicated by clear symbols: *Cortinarius*, triangles; *Inocybe*, squares; *Laccaria*, circles. Full data for plant species and soils are given in appendix B.

fungi were first collected at 340 m. Means and standard deviations for taxa of saprotrophic fungi are: *A. obscurata* $-20.7 \pm 2.6\text{‰}$, $n = 34$; and *Galerina* $-22.1 \pm 1.0\text{‰}$, $n = 20$. Means and standard deviations for taxa of ectomycorrhizal fungi are: *C. tenebricus* -25.9 ± 0.8 , $n = 4$; *I. lacera* -25.8 ± 0.6 , $n = 6$; and *L. montana* $-25.9 \pm 0.6\text{‰}$, $n = 35$. The saprotrophic *Arrhenia* had some extremely ^{13}C -enriched values and a large overall range from -14‰ to -25‰ (figure 3). Overall, saprotrophic fungi at Lyman Glacier averaged 4.7‰ enriched in ^{13}C relative to co-occurring ectomycorrhizal fungi, with individual *Arrhenia* more than 10‰ enriched in ^{13}C relative to co-occurring ectomycorrhizal fungi. Of plants that could have supplied sugars to ectomycorrhizal fungi, the conifer *A. lasiocarpa* averaged -26.6‰ and the deciduous willow *S. phylicifolia* averaged -27.6‰ . There was about a 5‰ range in tracheophyte $\delta^{13}\text{C}$ overall, with highest values for the evergreen shrub *Cassiope mertensia* ($-24.9 \pm 0.3\text{‰}$ at 450 m) and lowest for the forb *L. pectinata* ($-29.8 \pm 0.2\text{‰}$ at 150 m) (complete data by location and plant species are given in appendix B). Overall, plant $\delta^{13}\text{C}$ averaged -27.2‰ , samples of the more well-drained soil occupied by these plants averaged $-25.6 \pm 0.7\text{‰}$ (s.d.) (range -25.4‰ to -26.0‰), and soils surrounding shallow meltwater pools averaged $-24.3 \pm 1.6\text{‰}$ (s.d.) (range -21.3‰ to -26.1‰). The two soil types differed significantly in average $\delta^{13}\text{C}$ (t -test: $p < 0.001$, d.f. = 60) and in variability of $\delta^{13}\text{C}$ (F -test: $p < 0.001$). Soil, plant and fungal $\delta^{13}\text{C}$ values for the Lyman forelands are shown in figure 3.

Carbon isotope patterns in Devonian *Prototaxites* are shown in figure 4 and are distinct relative to those of Devonian fossil plants. In particular, *Prototaxites* is distinguished from other fossils in the wide range of $\delta^{13}\text{C}$ values, with three samples clustering between -19.0‰ and -15.8‰ and the remaining eight samples clustering between -28.9‰ and -26.6‰ . Data compiled from the literature indicate that modern saprotrophic fungi are about 3‰ , enriched in ^{13}C relative to their substrates (table 1), but algal-derived lake sediments from Scotland (-31‰ to -34‰ , Stephenson *et al.* 2006) are the only Devonian samples so far found to be more depleted in ^{13}C than this second *Prototaxites* cluster.

4. DISCUSSION

The carbon isotope measurements in saprotrophic fungi at Lyman Glacier are remarkable for their wide range. Because no crassulacean acid metabolism plants, C_4 plants or hornworts are present at Lyman Glacier and the $\delta^{13}\text{C}$ of the C_3 plants collected ranged from -30‰ to -25‰ , alternate, non-tracheophyte sources of carbon must account for saprotrophic fungi of $\delta^{13}\text{C}$ greater than -20‰ . Analysis of nearby ectomycorrhizal fungi eliminates carbon within the plant-mycorrhizal symbiosis as a viable source for ^{13}C -enriched *Arrhenia*. Ectomycorrhizal (symbiotic) fungi incorporate transferred plant sugars, whereas saprotrophic fungi generally incorporate carbon derived from sugar polymers such as cellulose and hemicellulose (Hobbie 2005). In a global synthesis, saprotrophic fungi were enriched by

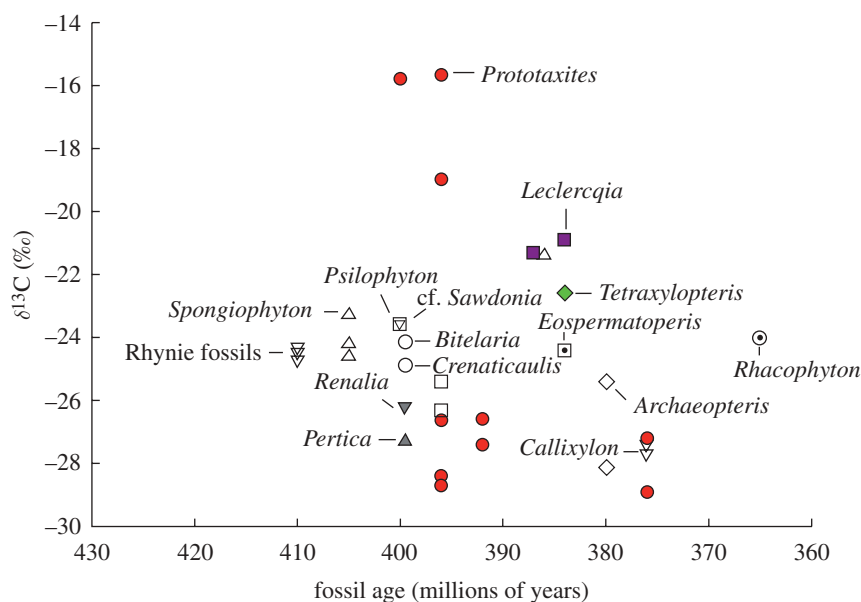


Figure 4. Carbon isotopes in terrestrial plant fossils and *Prototaxites* from the Devonian. Taxa represented are: *Prototaxites* (filled circles), *Spongiophyton* (upright clear triangles), *Psilophyton* (clear squares), *Leclercqia* (filled squares), *Callixylon* (upside-down clear triangles) and *Archeopteris* (clear diamonds). Other taxa are as indicated directly in the figure. Fossil details are in appendix A. The three indicated Rhynie fossils are *Aglaophyton major*, *Asteroxylon mackiei* and *Rhymia gwynne-vaughnii*.

Table 1. ^{13}C enrichment of fungi relative to substrates. $\epsilon_{\text{F-S}} = \delta^{13}\text{C}_{\text{Fungi}} - \delta^{13}\text{C}_{\text{Substrate}}$. (Standard errors are given when available. *Chaetomium globosum* is an ascomycete, all other fungi are basidiomycetes.)

substrate	organism	$\epsilon_{\text{F-S}}$ (‰)	reference
field studies			
wood	decay fungi	3.1	Gleixner <i>et al.</i> (1993)
wood cellulose	decay fungi	1.8	Gleixner <i>et al.</i> (1993)
litter	<i>Termitomyces</i> (termite fungi)	3–4	Tayasu (1998)
wood	decay fungi (20 taxa)	3.1 ± 0.2	Kohzu <i>et al.</i> (1999)
wood	decay fungi (five taxa)	3.5 ± 0.3	Hobbie <i>et al.</i> (2001)
culture studies			
<i>Fagus</i> wood	<i>Trametes versicolor</i>	3.5 ± 0.5	Kohzu <i>et al.</i> (1999)
<i>Fagus</i> wood	decay fungi (five taxa)	3.3 ± 0.4	Kohzu <i>et al.</i> (2005)
<i>Fagus</i> wood	<i>Chaetomium globosum</i>	1.6 ± 0.2	Kohzu <i>et al.</i> (2005)

1.1–3.5‰ in ^{13}C relative to co-occurring ectomycorrhizal fungi ($2.3 \pm 0.7\%$ s.d., mean of 23 studies (Mayor *et al.* 2009); global average, -22.9% for saprotrophic fungi and -25.3% for ectomycorrhizal fungi). By contrast, saprotrophic fungi at Lyman Glacier averaged 4.7% enriched in ^{13}C relative to co-occurring ectomycorrhizal fungi, with *Arrhenia* and *Galerina* averaging, respectively, 5.2% and 3.8% enriched in ^{13}C relative to co-occurring ectomycorrhizal fungi; the saprotrophic *Arrhenia* also varied more in $\delta^{13}\text{C}$ (s.d. of 2.6%) than *Galerina* or the ectomycorrhizal fungi (s.d. of 1% or less). Together, the isotopic values of the saprotrophic fungus *Arrhenia*, co-occurring ectomycorrhizal fungi and vascular plants indicate that the more ^{13}C -enriched *Arrhenia* require a carbon source other than vascular land plants. Fungi typically have a 3% enrichment in ^{13}C relative to their carbon sources (table 1), indicating that *Arrhenia* ranging from -26% to -14% are likely to have

consumed carbon sources that varied between -29% and -17% .

The glacial foreland at Lyman Glacier is pocked with shallow meltwater pools (figure 2). If the vascular plants at Lyman Glacier are insufficiently enriched in ^{13}C to account for some $\delta^{13}\text{C}$ values for *Arrhenia*, then aquatic photosynthesis in these pools is a probable source of ^{13}C -enriched carbon. Phytoplankton can vary widely in $\delta^{13}\text{C}$ depending on environmental conditions and can be quite enriched in ^{13}C if they possess a carbon-concentrating mechanism (Laws *et al.* 2002). The *Arrhenia* samples fruited around the fringes of these pools, suggesting that organic deposits derived from algae or cyanobacteria in these pools are probable additional sources for *Arrhenia*. The $\delta^{13}\text{C}$ values of the soils immediately surrounding some of these pools were as high as -21% (figure 3). Given the measured values for well-drained soils and C_3 vegetation of between -28% and -25% , higher

$\delta^{13}\text{C}$ values for most of the soils surrounding pools do not indicate an exclusively terrestrial C_3 origin, but rather some contribution of aquatically fixed carbon in these areas of ephemeral water cover. Similar ^{13}C -enriched values to those measured here have been reported previously for microbes from eutrophic lakes (Bontes *et al.* 2005; Xu *et al.* 2007) and hot springs (Jahnke *et al.* 2004). $\delta^{13}\text{C}$ values of -17‰ to -24‰ have also been reported in cyanobacteria or cyanobacterial lichens from rock outcrops and savannah soils, with the higher $\delta^{13}\text{C}$ values under wet conditions when the diffusion of CO_2 through water and CO_2 -concentrating mechanisms were most likely to be important for cyanobacterial photosynthesis (Ziegler & Lüttge 1998).

The carbon isotopic range of saprotrophic fungi from this barren glacial foreland approximate the range of values reported from Devonian *Prototaxites* and this locality may provide a modern analogue of an Early Devonian landscape with sparse vascular vegetation. The ^{13}C -enriched values seen in some *Prototaxites* fossils (figure 4) require consumption of an autotrophic substrate with a carbon-concentrating mechanism (Boyce *et al.* 2007). In addition to the previously suggested sources of microbial soil crusts and hornworts, the Lyman Glacier ecosystem indicates that microbial photosynthesis from ephemeral terrestrial pools is an additional substrate possibility for ^{13}C -enriched *Prototaxites*. In Lower Devonian sediments of the Gaspé Peninsula, vascular plants were found in facies indicative of moist environments including levees and swampy areas. By contrast, *Prototaxites* was prevalent in channel fills that contained material transported from more proximal areas of the floodplain (Griffing *et al.* 2000; Hotton *et al.* 2001) that were likely to have been more sparsely infiltrated by vascular plants. Rooting structures from the Lower Devonian of the Anglo-Welsh Basin have recently been interpreted as those of *Prototaxites* involved in the consumption of exopolymeric substances, dissolved organic carbon in sediment pore fluids, and cyanobacterial and algal wall material deposited in ephemeral pools caused by seasonal flooding (Hillier *et al.* 2008). Our analysis of the modern analogue *Arrhenia* supports such an interpretation.

The ^{13}C -depleted and ^{13}C -enriched populations of *Prototaxites* had been interpreted, respectively, as consistent with a C_3 tracheophyte substrate and as requiring a non-tracheophyte alternative with a carbon-concentrating mechanism (Boyce *et al.* 2007). However, the approximately 3‰ enrichment of modern saprotrophic fungi in ^{13}C relative to their substrates (table 1) suggests that non-tracheophyte alternatives may also contribute to the carbon sources of the more ^{13}C -depleted *Prototaxites* samples as well. The more ^{13}C -depleted *Prototaxites* samples correspond poorly with the actual isotopic values of fossils of vascular plants and their close relatives, both locally (Boyce *et al.* 2007) and globally (Peters-Kottig *et al.* 2006) (figure 4), as the plant fossils are consistently too enriched in ^{13}C to be the exclusive carbon source for *Prototaxites*. In the Late Devonian, isotopic values of local *Callixylon* (progymnosperm wood) and *Prototaxites* overlap, but the 3‰ offset expected

with the consumption of a woody substrate would require plants to be more ^{13}C -depleted than observed. Similarly, in the Early Devonian, *Prototaxites* did not overlap in $\delta^{13}\text{C}$ with local vascular plant fossils and had minimal overlap with a larger compilation of Early Devonian vascular plants (figure 4).

One recent report suggested that *Prototaxites* fossils represent rolled up liverwort mats, with the broad range in *Prototaxites* $\delta^{13}\text{C}$ indicating variable degrees of mixotrophy in early liverworts (Graham *et al.* 2010). Although $\delta^{13}\text{C}$ patterns in *Prototaxites* cannot distinguish between heterotrophic contributions from liverworts or fungi, the evidence strongly suggests that liverwort mats are unlikely to form the anatomical features reported from *Prototaxites*. For example, the layering of *Prototaxites* trunks forms concentric rings rather than spiral rings in transverse section, anatomical structures frequently pass through multiple layers, no sediment is entrained between layers and the tissue is composed of tubes regularly oriented along the long axis of the trunk. These observations are consistent with the growth increments in a coherent organism but are not consistent with a rolled up mat (see Hueber (2001) for a comprehensive review of *Prototaxites* anatomy).

Both bryophytes and aquatic algae without carbon-concentrating mechanisms can be ^{13}C -depleted relative to C_3 vascular plants (Raven *et al.* 2000; Jahren *et al.* 2003; Fletcher *et al.* 2004). For example, algal-derived lake sediments from the Middle Devonian, ranging from -31‰ to -34‰ , are much lower in $\delta^{13}\text{C}$ than any Devonian tracheophyte fossils (Stephenson *et al.* 2006). Because their preservational potential is low, the diversity of bryophyte-grade land plants in the Devonian is likely to have been higher than the macrofossil record would suggest (Hotton *et al.* 2001; Boyce 2010). The most ^{13}C -depleted *Prototaxites* specimens suggest that bryophytes and algae could have provided an important contribution to *Prototaxites* carbon sources throughout the Devonian, including after the advent of the first vascular plant forests. Given that neither ^{13}C -enriched nor ^{13}C -depleted populations of *Prototaxites* are consistent with the exclusive consumption of vascular plants, we conclude that bryophytic and algal alternatives to vascular plants were even more important as carbon sources for *Prototaxites* than previously hypothesized. By linking carbon isotope patterns in both ancient *Prototaxites* and modern *Arrhenia* to that of aquatic-derived photosynthesis, our results strengthen the suggestion by Hillier *et al.* (2008) that sedimentary deposits of cyanobacterial or algal-derived organic matter from ephemeral water bodies were probably important substrates for the subterranean hyphal network of *Prototaxites*.

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APPENDIX A

Carbon isotope signatures of plants and *Prototaxites* from the Devonian given in figure 4. The estimated age is also given.

fossil taxon	age (Ma)	error (Ma)	sample type	$\delta^{13}\text{C}$ (‰)	s.e. (‰)	experimental error (‰)	notes	reference
<i>Aglaophyton major</i>	410		axes	-25.7				Boyce <i>et al.</i> (2003)
<i>Archaeopteris jacksonii</i>	380	2	leaves and axes	-28.1	0.5		$n = 2$	Beerling <i>et al.</i> (2002)
<i>A. macilenta</i>	380	1	leaves and axes	-25.4				Beerling <i>et al.</i> (2002)
<i>Asteroxylon mackiei</i>	410		axes	-24.9				Boyce <i>et al.</i> (2003)
<i>Bitularia dubjanskii</i>	399.5		cuticles	-24.1				Peters-Kottig <i>et al.</i> (2006)
<i>Callixylon newberryi</i>	376		wood	-27.7		0.1		Boyce <i>et al.</i> (2007)
<i>C. newberryi</i>	376		wood	-27.4		0.2		Boyce <i>et al.</i> (2007)
<i>Crenatacaulis verruculosus</i>	399.5		coalified tissue	-24.9				Peters-Kottig <i>et al.</i> (2006)
<i>Eospermatopteris erianus</i>	384	1	axes	-24.4				Beerling <i>et al.</i> (2002)
<i>Leclercqia complexa</i>	384		cuticles	-20.9				Peters-Kottig <i>et al.</i> (2006)
<i>L. complexa</i>	387	2	leaves and axes	-21.3	0.09		$n = 3$	Beerling <i>et al.</i> (2002)
<i>Pertica varia</i>	399.5		cuticles	-27.3				Peters-Kottig <i>et al.</i> (2006)
<i>Prototaxites loganii</i>	400			-15.8		0.1		Boyce <i>et al.</i> (2007)
<i>P. loganii</i>	396			-28.4		0.5		Boyce <i>et al.</i> (2007)
<i>P. loganii</i>	396			-28.7		0.1		Boyce <i>et al.</i> (2007)
<i>P. loganii</i>	396			-26.6		0		Boyce <i>et al.</i> (2007)
<i>P. loganii</i>	396			-26.6		0		Boyce <i>et al.</i> (2007)
<i>P. loganii</i>	396			-19		0.1		Boyce <i>et al.</i> (2007)
<i>P. loganii</i>	396			-15.7		0		Boyce <i>et al.</i> (2007)
<i>P. southworthii</i>	376			-28.9		0.1		Boyce <i>et al.</i> (2007)
<i>P. southworthii</i>	376			-27.2		1.0		Boyce <i>et al.</i> (2007)
<i>Prototaxites</i> spp.	392			-26.6		0		Boyce <i>et al.</i> (2007)
<i>Prototaxites</i> spp.	392			-27.4		0.5		Boyce <i>et al.</i> (2007)
<i>Psilophyton forbesii</i>	400	2	axes	-25.4				Beerling <i>et al.</i> (2002)
<i>Psilophyton forbesii</i>	396	2	axes	-26.3				Beerling <i>et al.</i> (2002)
<i>Psilophyton princeps</i>	396		axes	-23.6		1.4		Boyce <i>et al.</i> (2007)
<i>Renalia hueberi</i>	399.5		cuticles	-26.2				Peters-Kottig <i>et al.</i> (2006)
<i>Rhacophyton ceratangiium</i>	365	3	axes	-24				Beerling <i>et al.</i> (2002)
<i>Rhynia gwynne-vaughnii</i>	410		axes	-24.2				Boyce <i>et al.</i> (2003)
coal (of cf. <i>Sawdonia</i>)	400			-23.5		0.4		Boyce <i>et al.</i> (2007)
<i>Spongiophyton minutissimum</i>	405		cuticle	-23.3			$n = 6$	Fletcher <i>et al.</i> (2004)
<i>S. minutissimum</i>	405		bulk	-24.6			$n = 12$	Fletcher <i>et al.</i> (2004)
<i>S. minutissimum</i>	405		thalli	-24.2 ^a			$n = 96$	Jahren <i>et al.</i> (2003)
<i>S. namum</i>	386		cuticle	-21.4			$n = 2$	Fletcher <i>et al.</i> (2004)
<i>Tetraxylopteris schmidtii</i>	384		cuticles	-22.6				Peters-Kottig <i>et al.</i> (2006)

^aRange -25.8‰ to -21.1‰.

APPENDIX B

Carbon isotope signatures for eight plant species along the Lyman Glacier foreland, \pm s.e. (n) and mineral soil (0–5 cm depth), as shown in figure 3. (Plant mean \pm s.e. is of species averages at each location.)

taxa	distance from glacial terminus (m)				
	$\delta^{13}\text{C}$ (‰)				
	150	300	450	600	750
<i>Abies lasiocarpa</i>	-26.4 \pm 0.3 (7)	-28.2 \pm 0.4 (7)	-25.1 \pm 0.5 (5)	-26.6 \pm 0.3 (5)	-25.6 \pm 0.4 (4)
<i>Cassiope mertensiana</i>	—	—	-24.9 \pm 0.3 (4)	-25.9 \pm 0.5 (5)	-25.2 \pm 0.1 (5)
<i>Epilobium latifolium</i>	-28.1 \pm 0.4 (2)	-28.4 \pm 0.6 (5)	-28.5 \pm 1.0 (2)	-27.5 \pm 0.2 (5)	-26.9 \pm 0.4 (5)
<i>Luetkia pectinata</i>	-29.8 \pm 0.2 (4)	-28.7 \pm 0.5 (4)	-27.7 \pm 0.2 (4)	-28.8 \pm 0.3 (6)	-27.2 \pm 0.5 (6)
<i>Luzula piperi</i>	-28.3 \pm 0.2 (5)	-26.8 \pm 0.4 (5)	-27.1 \pm 0.2 (6)	-28.9 \pm 0.5 (4)	-27.0 \pm 0.6 (4)
<i>Phyllodoce empetriformis</i>	-28.6 \pm 1.9 (2)	-28.0 \pm 0.5 (6)	-26.1 \pm 0.3 (6)	-26.4 \pm 0.3 (5)	-25.8 \pm 0.5 (5)
<i>Salix phyllicifolia</i>	—	-28.7 \pm 0.3 (5)	-27.2 \pm 0.4 (5)	-27.0 \pm 0.2 (9)	-26.5 \pm 0.3 (5)
<i>Saxifraga ferruginea</i>	-26.7 \pm 0.6 (5)	-27.0 \pm 1.0 (4)	—	-25.4 \pm 0.3 (4)	-26.5 \pm 0.7 (4)

(Continued.)

Appendix B. (Continued.)

taxa	distance from glacial terminus (m)				
	$\delta^{13}\text{C}$ (‰)				
	150	300	450	600	750
plant mean	-28.0 ± 0.5 (6)	-28.0 ± 0.3 (7)	-26.7 ± 0.5 (7)	-27.1 ± 0.5 (8)	-26.3 ± 0.3 (8)
mineral soil (1999) ^a	-26.0 ± 0.4 (5) ^b	-25.6 ± 0.3 (5)	-25.5 ± 0.1 (4)	-25.5 ± 0.3 (5)	-25.4 ± 0.5 (3)
mineral soil (2009) ^c					-24.3 ± 0.3 (40)

^a1999 soils were sampled from upland areas not adjacent to water.

^bSampled at 100 m.

^c2009 soils sampled adjacent to eight pools at 700 m; values for soils at individual pools were $-23.8 \pm 0.3\text{‰}$, $-23.5 \pm 0.6\text{‰}$, $-21.3 \pm 0.5\text{‰}$, $-26.1 \pm 0.2\text{‰}$, $-24.3 \pm 0.3\text{‰}$, $-25.2 \pm 0.3\text{‰}$, $-25.5 \pm 0.3\text{‰}$ and $-24.7 \pm 0.2\text{‰}$.

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