USE OF BOMB-^{14}C TO INVESTIGATE THE GROWTH AND CARBON TURNOVER RATES OF A CRUSTOSE LICHEN

BY

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ABSTRACT
The reliability of lichenometric dating is dependent on a good understanding of lichen growth rates. The growth rate of lichens can be determined from direct measurement of growing lichens or indirect methods by measuring lichens growing on surfaces of known age, although there are limitations to both approaches. Radiocarbon (^{14}C) analysis has previously been used in only a handful of studies to determine lichen growth rates of 2 species from a small area of North America. These studies have produced mixed results; a small amount of carbon turnover appears to occur in one of the species (*Caloplaca* spp.) previously investigated introducing uncertainty in the growth rate, while much higher carbon cycling occurred in another (*Rhizocarpon geographicum*), making the ^{14}C approach unsuitable for estimating growth rates in the species most commonly used in lichenometric dating. We investigated the use of bomb-^{14}C analysis to determine the growth rate of a different crustose species (*Pertusaria pseudocorallina*) common to Northern Europe. ^{14}C-based growth rates were considerably higher than growth rates of morphologically similar species based on direct measurement made at locations nearby and elsewhere in the UK. This observation strongly suggests that a degree of carbon turnover probably occurs in *Pertusaria pseudocorallina*, and that bomb-^{14}C analysis alone cannot be used to determine lichen age or absolute growth rates in this lichen species.

Keywords

Pertusaria pseudocorallina, Radiocarbon, Crustose lichen, Growth rate, Lichenometry.

Introduction

Lichenometry has proved to be a valuable method to date recently exposed surfaces. Examples of its application include establishing the age of glacial deposits (e.g. Matthews, 1975, 2005; Solomina and Calkin, 2003; Bradwell *et al*. 2006); examining rockfall and debris-flow frequencies (e.g. Bull *et al*. 1994; McCarroll, 1994; Winchester and Chaujar, 2002); reconstructing flood histories (e.g. Macklin and Rumsby, 2007) and dating archaeological features (e.g. Benedict, 2009). The technique makes use of the fact that following colonisation of a rock surface, crustose lichens grow slowly and radially and the size (e.g. diameter) of the lichen can be directly related to its age (e.g. Proctor, 1977; Clark *et al.* 2000; Bradwell, 2001). The technique is simple to apply, but the importance of the relationship between the age and size of the lichen is crucial to its accuracy as a dating technique. Debate still surrounds the best approach to relate lichen metrics to lichen age, with for example, the largest single lichen, the mean of several 'largest' lichens, the modelled mean of a 'population', and the gradient of the size-frequency distribution, all being used as age indicators (see Innes (1985) and Bradwell (2009) for critical discussions of these different techniques). Crucially, lichen growth rates vary with many factors including species and climate (temperature and available moisture), and therefore, for optimum use as a dating technique species-specific lichenometric dating curves need to be established for the climatic conditions relevant to the study area.

Lichenometric dating curves can be established using several approaches. Firstly, direct measurement of the same lichens over a period of time can be used (e.g. Proctor, 1977). However, due to the slow growth rate, observation can require many years and application of the curve to date much older surfaces will require extrapolation therefore increasing the uncertainty in age estimates. Another approach is to measure lichen size on independently dated surfaces (e.g. dated photographs or geomorphological features dated by historical records; e.g. Bradwell, 2001), however, such information will not always be available.

Clark *et al.* (2000) showed for the first time that the growth rate of a crustose lichen can be determined directly using radiocarbon (^{14}C) analysis. The approach relies on two factors; (i) the recent advent of accelerator mass spectrometry (AMS) that permits ^{14}C analysis of milligram-size samples, and (ii) the bomb-^{14}C spike created in the AD 1950s-60s by the atmospheric testing of nuclear devices. The latter produced a global ^{14}C tracer that in the atmosphere exhibited a concentration peak *c.* AD 1963 and subsequent decline. Carbon fixed from the atmosphere, such as in the photosynthetic parts of a lichen, since the mid-1960s can be precisely dated by matching the ^{14}C content to a record of atmospheric radiocarbon content (e.g. Levin *et al.* 2008).

In their pilot study, Clark *et al.* (2000) matched the pattern of declining ^{14}C content along a radial transect of a lichen to an atmospheric bomb-^{14}C record and determined that their single specimen of the crustose lichen *Caloplaca trachyphylla* from the Uinta Mountains, Utah, had an approximately linear radial growth rate of 1.48 mm/yr. In a second study, Bench *et al.* (2001) investigated the crustose lichen *Rhizocarpon geographicum,* the most commonly used species in lichenometry, using the bomb-^{14}C approach. However, growth rates could not be determined because the ^{14}C content of this species did not vary radially. According to numerous ^{14}C analyses on 3 different thalli the age of each portion of thallus along a transect from the centre to the edge apparently dated to approximately the same time. Bench *et al.* (2001) suggested that the pattern of lichen ^{14}C was a result of carbon cycling within the lichen, whilst accepting that other processes could equally affect the distribution of ^{14}C in a thallus, including translocation of carbon within the lichen and continued growth in the thallus centre as well as the perimeter. Returning to *Caloplaca trachyphylla,* following further bomb-^{14}C analyses of 7 thalli in Utah, Bench *et al*. (2002) concluded that a small amount (<10 % per yr) of carbon turnover was occurring in this species, thus providing important insight into the growth and biological functioning of crustose lichens.

Beazley *et al.* (2002) investigated the ^{14}C content of several species of pruinose lichens from south-western Texas and north-eastern Arkansas, USA. However, the purpose of their study was to test whether their lichen species incorporated carbon from the carbonate rock surfaces on which they occurred, and not to determine the growth rates of the lichens. Interestingly, the results of Beazley *et al*. (2002) were *not* consistent with the lichen obtaining carbon from the carbonate rock. ^{14}C has also been successfully used to investigate growth rate in a fruticose lichen from north-west Alaska, USA (Holt and Bench, 2008); furthermore, Daillant *et al.* (2004) assessed the utility of lichens to monitor radioactivity around nuclear installations using ^{14}C.

To our knowledge, the above studies comprise all the published work using bomb-^{14}C to investigate the growth or biology of lichens. The growth rate of only two species of crustose lichen have specifically been investigated, being restricted to a single area in arid continental North America (Utah). Here, we build upon these previous studies by describing an investigation into the use of bomb-^{14}C to determine the age, growth pattern, and carbon turnover of a common crustose lichen species in the British Isles – the first such study from a maritime climate, and the first conducted outside North America.

Methods

Sample collection and processing

A rock containing examples of the lichen *Pertusaria pseudocorallina* (Lilj.) Arnold, was recovered from a ruined dry stone wall, 110 m above sea level, near Lochearnhead, Perthshire, Scotland (Lat. 56.3764, Long. -4.2815; WGS84) on 25th June, 2003. The rock, a small mafic-rich dolerite (microgabbro) boulder, was photographed (Fig. 1), returned to the laboratory and stored in the dark (at *c*. 2^{o}C) until sampled.

The climate in this part of central Scotland is transitional between the mild maritime Atlantic west coast and the drier cooler east. Average annual rainfall (1971-2000) at nearby Loch Earn is *c.* 1500-2000 mm – considerably less than experienced in the mountains of northern Argyll (>3000 mm), only 30 km to the west, but more than twice that recorded 60 km to the east around the Firth of Tay. Rainfall around Loch Earn is spread evenly throughout all four seasons with 1 mm or more falling on 170 days per year, on average. Met station averages (between 1971-2000) show that Lochearnhead currently experiences a mean annual temperature range of 11.5°C, with mean July temperatures of 14.5°C and mean January temperatures of 3.0°C, and an average of 20-30 days of snow lie per year (www.metoffice.gov. uk).

The species *P. pseudocorallina* was chosen as it is commonly found across the British Isles and Scandinavia, particularly in coastal and upland areas and on acidic rocks. It is a greyish white unremarkable crustose species with an areolate morphology, granular or warty texture, rare apothecia, and a marginal hypothallus. Along with the closely related species *Pertusaria corallina*, this lichen was thought to be a promising contender for use in lichenometric dating owing to its ubiquity, climatic range and similar growth form to that of *Rhizocarpon* (Nienberg, 1926). Other equally promising crustose species with broadly similar characteristics and growth rates were also considered before this study was undertaken, most notably *Ochrolechia parella* (L.) Massal. and *Buellia canescens* (Dickson) Massal. However, *P. pseudocorallina* was preferred over these species for its ease of ^{14}C sampling owing to a lack of apothecia, relatively uniform thallus texture and simple morphology.

In the NERC Radiocarbon Facility, an approximately circular example of *P. pseudocorallina* measuring 45 x 37 mm in diameter was sampled for ^{14}C analysis: First, the entire rock surface was cleaned using compressed air and the thallus inspected under a microscope to check for contaminants. Consecutive samples of lichen were then cut along a transect (Fig. 1), using a scalpel, from the perimeter to the centre of the thallus, and placed in glass vials. Inbetween collection of a sample, the thallus was again dusted with compressed air and the scalpel cleaned using a hot flame. The minimum amount of sample that would provide sufficient material for ^{14}C analysis was removed to maintain the highest sampling resolution. Earlier tests on another *P. pseudocorallina* thallus on the same rock had been undertaken to establish that the moisture and carbon content of these lichens was *c.* 54 % and *c.* 45 %, respectively.

Each sample was washed in 0.5 M HCl to ensure there was no carbonate contamination. The samples were then combusted (900^{o}C) in sealed quartz tubes and the CO_2 cryogenically recovered. The volume of the CO_2 was measured and a sub-sample analysed on an isotope ratio mass spectrometer (VG Optima, Micromass, UK) for $\delta^{13}C$ ($^{13}C/^{12}C$ ratio in ‰ units relative to the standard Vienna Pee Dee Belemnite; VPDB). A further sub-sample was graphitised (Slota *et al.* 1987) and analysed for ^{14}C concentration by AMS at the Scottish Universities Environmental Research Centre (Freeman *et al.* 2007). Radiocarbon results were normalised to a $\delta^{13}C$ of -25 ‰ and expressed as %modern (Stuiver and Polach, 1977).

Following convention, measurement uncertainty for isotope concentrations are expressed as standard deviations.

Determination of age and modelling of carbon turnover

Anthropogenic disturbance of the atmospheric radiocarbon concentration over the last *c.* 50-100 years has resulted from i) the emission of large volumes of ^{14}C-free CO_2 through fossil fuel use, and ii) production of ^{14}C during atmospheric testing of nuclear weapons. The latter caused an approximate doubling of the global atmospheric ^{14}C concentration. Following a ban on atmospheric nuclear weapons testing, ^{14}C concentration in the atmosphere declined from a peak in *c.* AD 1963 as the ^{14}C excess was dispersed into other components of the carbon cycle (e.g. oceans) and through further dilution from continued emission of ^{14}C-free CO_2 from fossil fuels. The result was a global ^{14}C tracer (Levin and Hesshaimer, 2000; Fig. 2) which can be used to age carbon fixed from the atmosphere over the period of the bomb pulse by matching the ^{14}C content of the material under investigation to an atmospheric ^{14}C record (e.g. Levin *et al.* 2008). In the present study, we used the 'CaliBomb' software (Reimer *et al.* 2004) to age lichen samples using this approach, applying the northern hemisphere atmospheric ^{14}C record (Levin and Kromer, 2004; Levin *et al.* 2008) and using 1-yr resolution and 1-yr smoothing (Holt and Bench, 2008).

Determining the radial growth rate in a lichen by matching its ^{14}C content with the atmospheric ^{14}C record is not appropriate if the lichen carbon is either recycled or translocated following fixation. Bench *et al.* (2002) investigated carbon turnover in crustose lichens using a simple modelling approach, which we have also applied. The model calculates the transient ^{14}C concentration of a lichen over the period of the bomb pulse starting with the northern hemisphere atmospheric ^{14}C as the input, and assuming that each year a constant proportion of the lichen carbon is lost and replaced, based on the equation:

$$R_i = (1- T_o)R_{i-1} + T_o Y_i \qquad \text{Equation 1}$$

where R_i is the ^{14}C content (%modern) in the lichen at year *i*, T_o is the fraction of carbon turned over annually, and Y_i is the %modern of the atmosphere in the year *i*. We used the model to calculate the ^{14}C content of a lichen in the year of sampling (2003) assuming different fractional carbon turnover rates (Fig. 2). This allowed the initial year of lichen growth to be calculated, assuming different rates of carbon turnover.

Directly measured growth rates

In 2002-4, as part of a wider study into crustose lichen growth rates in Scotland, thalli of *Pertusaria* spp. and *Ochrolechia parella* were photographed at stable control sites in several localities across central Scotland (by TB). These lichens were revisited at intervals of 2 or 3 years and re-photographed to calculate absolute growth rates of different species in different settings over the intervening time. This work forms the basis of another study and will be described in full elsewhere, but some preliminary results are presented here in order to help constrain the ^{14}C dating of the *Pertusaria pseudocorallina* thallus. Precise lichen measurements along the horizontal axis and calculation of radial growth rates (RGR) were done using on-screen image processing software (Adobe Photoshop) broadly following the methodologies of McCarthy (2003) and Benedict (2008). Measurement accuracy is +/-0.05 mm using this technique. The exact measurement methodology is described in detail by Bradwell (in press, this volume) working with *Rhizocarpon geographicum* in NW Scotland.

Results

^{14}C analysis and calibration

Details of the location and size of samples used for ^{14}C analysis are presented in Table 1. The minimum requirement of > 0.5 mg C was recovered in all samples from an area of at least 0.2 cm^2. The ^{14}C concentration of the samples generally increased along the transect away from the perimeter (Table 2), with all samples unambiguously containing bomb-^{14}C. Contrary to our expectations, the sample with the highest ^{14}C content was not from the central part of the thallus. Unfortunately, one sample (sample 4; 5-9 mm) failed during processing, and therefore could not be analysed for ^{14}C. Table 2 also gives the age range for the lichen carbon following calibration of the ^{14}C results using the 'CaliBomb' software. Two calibrated age ranges were possible for each sample, due to the rising and falling parts of the atmospheric bomb-^{14}C curve, however, the calibration peak area value (CPAV; a measure of the likelihood that a particular result falls within each age range) indicated that, in all cases, the most recent age range was more likely. All samples therefore most likely dated to AD 1998-2003.

When excluding sample 6, the calibrated age results plotted against the radial distance produced a linear correlation (Fig. 3), with the oldest sample apparently dating to between 1998 and 2000. The sample from the perimeter was dated the youngest with the calibrated age period (June 2002 to August 2003) overlapping with the date of sample collection (June 2003).

Based on the calibrated age values, the RGR along the transect between the perimeter and the oldest sample (total distance = 16.5 mm) was 4.1 mm/yr. However, assuming that the most ^{14}C-enriched sample (sample 5) represented the oldest part of the lichen would suggest that the pattern and rate of radial growth was not symmetrical, and therefore a much higher RGR was implied across the diametrically opposite radius of the thallus (6.8 mm/yr).

Comparison with directly measured growth rates

Table 3 summarises the preliminary results of the growth rate measurements. Average radial growth rates of 12 healthy, non-competing thalli of *P. pseudocorallina*/*P. corallina* (30-60 mm in diameter) at 3 sites in central Scotland were found to be 0.50-1.20 mm/yr between 2003 and 2009, assuming equal growth in all years. Note that owing to difficulties differentiating between these 2 species in the field all thalli are referred to as *P. (?pseudo)corallina* (Table 3). *Ochrolechia parella* at the same sites was found to be growing at a similar but slightly faster rate of *c.* 0.8-2.0 mm/yr.

Modelling lichen carbon turnover

Applying the carbon turnover model of Bench *et al.* (2002) made little difference to the age of the samples, except for the most ^{14}C-enriched sample (sample 5; Fig. 4). For sample 5, annual turnover rates for lichen carbon of at least 3 % per yr made a difference to the calendar age of the sample (Fig. 5). The estimated age of sample 5 increased when turnover rates were greater, with for example, a carbon turnover of about 10 % per yr suggesting that the sample dated to *c.* AD 1996, i.e. 2-4 yrs older than assuming no carbon turnover at all (Fig. 5). Consequently, as a higher rate of carbon turnover was assumed, the estimated lichen RGR declined (Fig. 6). The maximum annual carbon turnover rate was calculated to be *c.* 20 % per yr, because when the model used rates in excess of this, it did not predict values that were compatible with the ^{14}C value of the measured sample. This implied a maximum date for sample 5 of AD 1973, giving minimum radial increments of between 0.5 and 0.9 mm/yr (Fig. 6). However, when the analytical uncertainty in the ^{14}C determination was considered, there was a large increase in the uncertainty of the estimated age of the oldest sample at higher rates of annual carbon turnover (Fig. 4), suggesting that even lower rates of radial growth were possible (Fig. 6).

Discussion

Directly measured growth rates

Direct measurements gave radial growth rates for *P. pseudocorallina*/*P. corallina* at 3 sites in central Scotland of 0.50-1.20 mm/yr between 2003 and 2009, while *Ochrolechia parella* at the same sites was found to be growing at similar but slightly faster rates of *c.* 0.8-2.0 mm/yr. The only other growth rate study of *P. pseudocorallina* or *P. corallina* in the UK is by Dr. R. A. Armstrong (unpub), referred to in Armstrong and Bradwell (this volume; Table 1). Armstrong's study of 10 thalli in maritime North Wales recorded RGR of 0.85-1.45 mm/yr for *P. corallina* over 12 months. Collectively, these data, the only direct measurements of growth in this species carried out to the authors' knowledge, suggest that typical RGR in central Scotland is likely to be between 0.5 and 1.5 mm/yr. We would not expect RGR to exceed 3.0 mm/yr as that would be beyond even the fastest growing crustose species in extremely favourable UK settings (Armstrong and Bradwell, this volume).

^{14}C analysis and calibration

Calibration of the radiocarbon content of the sample from the lichen perimeter gave a date range of June 2002 to August 2003. The period covers the date of sample collection (June 2003) and, given that visual appearance suggested the lichen was healthy and actively growing, the observation is consistent with the lichen fixing carbon with a contemporary ^{14}C signature. Contrary to our expectations, the sample that represented the geometrical centre of the lichen did not yield the oldest age, suggesting that lichen growth was not symmetrical.

Lichen ^{14}C content generally increased towards the thallus centre, showing that the time elapsed since the carbon was fixed was greatest towards the centre of the lichen. i.e. the ^{14}C results were broadly consistent with radial growth outwards from the thallus centre. This pattern is similar to observations on *Caloplaca trachyphylla* reported by Clark *et al.* (2000), but is different to results from Bench *et al.* (2001) who found no relationship between ^{14}C age and radial distance in *Rhizocarpon geographicum*.

The apparent 'age' of the oldest part of the lichen in this study is estimated from the calibrated ^{14}C results to be 4 years. This is definitely an underestimate of the true age because (i) there will have been some crustal thickening during the initial growth of the lichen (Proctor, 1977) and, (ii) because the ^{14}C result for the oldest sample represented an average age over an increment of 3 mm of the lichen thallus. Assuming an initial growth rate of 1 mm/yr, the oldest part of the lichen may be up to *c.* 3 years older than suggested by the bomb-^{14}C age of the oldest sample. A higher sampling resolution may have enabled the oldest part of the thallus to be better constrained in terms of age and location, however, this was not possible due to the need to provide sufficient sample material for ^{14}C analysis.

Assuming no carbon turnover, the ^{14}C results suggest that the RGR was *c.* 4 mm/yr along the short axis of the lichen. Proctor (1977) reported maximum RGR for *Buellia canescens* (now known as *Diploicia canescens*) of *c.* 2.3 mm/yr, in the favourable climate of Devon, southern England; in a similarly conducive maritime setting, Armstrong has reported maximum RGR of 1.5 mm/yr in *Ochrolechia Parella*; 2.1 mm/yr in *Buellia aethalea*; and 3.0 mm/yr in *Rhizocarpon reductum*. As yet no-one has reported natural crustose lichen growth rates in excess of 3 mm/yr (with the exception of studies where added nutrients or anthropogenic pollution promoted rapid growth). If we assume that due to the sampling resolution issues discussed above that we underestimated the date of initial lichen growth by 2-3 years, then the ^{14}C-derived RGR reduces to 2.4-4.6 mm/yr. These rates are still considerably higher than those directly measured for this species in this climate (this study; Armstrong and Bradwell, this volume), or similar crustose species elsewhere in the British Isles (e.g. Sowter, 1950; Proctor, 1977; Armstrong, 2005).

It seems highly likely that, in this study, lichen growth rates derived using the bomb-^{14}C approach are overestimates. There are at least three processes that could occur within the thallus that would lead to the age of the lichen being underestimated, and therefore the growth rate overestimated. Firstly, carbon could continue to be fixed within the central part of the thallus as well as the perimeter. However, this is considered to be unlikely as the density (mg C cm^{-2}) of the lichen would be expected to be greatest in the centre and decline outwards. No such pattern was observed (Table 1). Secondly, recycling of carbon could occur within the lichen, as postulated by Bench *et al.* (2001) for *Rhizocarpon geographicum*. However, this is also considered unlikely in the present study because we did find a trend of increasing ^{14}C content towards the centre of the lichen, and the perimeter sample had an identical ^{14}C content to the contemporary atmosphere (consistent with fixation of contemporary carbon). Our results differ from those of Bench *et al.* (2001) which showed no consistent gradient in ^{14}C content in transects from the centre to perimeter of the lichen, and where carbon recycling was concluded; though their investigations concerned *Rhizocarpon geographicum*, a different species to the one used in our study. Thirdly, carbon turnover (i.e. decomposition and fixation of carbon) could have occurred in the lichen thallus, thus introducing more recent carbon (with slightly lower ^{14}C content, thus decreasing the ^{14}C content of the oldest part of the thallus) without causing further significant crustal thickening. This explanation seems the most likely in the present study, and was therefore investigated using a simple model of carbon turnover described by Bench *et al.* (2002).

Modelling showed that a carbon turnover of less than 3 % per yr had no effect on the age of the oldest sample and therefore the annual RGR (Figs. 5 and 6). However, modelling also showed that a turnover of more than *c.* 20 % per yr was not possible. Therefore, even allowing for up to 20 % annual carbon turnover, we can constrain the growth rate to between *c.* 0.5-4.1 mm/yr, for one radial axis of the *Pertusaria pseudocorallina* lichen under study (Fig. 6). Direct measurements of growth rates in this species have shown that RGR >2.0 mm/yr are not to be expected; hence we can confidently reject rates above this value.

In their study, Bench *et al.* (2002) suggested the *Caloplaca trachyphylla* specimens they examined had annual carbon turnovers of *c.* 4.5 % because at this level the relationship between radial position and lichen age was most linear (i.e. growth rate was linear). Using the same criteria would suggest that the higher growth rates we calculated are better estimates for our *Pertusaria pseudocorallina* specimen, and therefore that no, or very little, carbon turnover was occurring; when the fraction of carbon turnover is increased the oldest sample is made relatively older than the other samples, causing lower growth rates but a non-linear relationship between age of lichen sample and radial position (Fig. 4). However, selecting the carbon turnover rate based on the linearity of the growth rate may not be suitable criteria for our sample because there is compelling evidence to suggest that growth rates of some crustose lichens conform to a parabolic model, with slow growth rates in early development, accelerating to a maximum, before gradually declining in larger thalli (e.g. Proctor, 1977; Armstrong, 1983; Benedict, 2008). The form of this growth curve and the size at which optimum growth rates occur is probably species specific, but in several species of crustose lichen Armstrong (2005) showed a growth rate peak at between 25-50 mm (e.g. *B. aethalea*, *R. geographicum*, *R. reductum*). In *Rhizocarpon geographicum* this growth rate peak was also found to occur between 25-50 mm in 3 separate studies (Armstrong, 1983; Bradwell and Armstrong, 2007; Benedict, 2008). In fact, a linear relationship between growth rate and lichen size is rarely reported in carefully conducted long-term field experiments.

Using a 10 % carbon turnover rate yields a radial growth rate for our specimen of *Pertusaria pseudocorallina* of *c.* 2.4 to 4.0 mm/yr, and using a 15 % turnover, this reduces to *c.* 1.8 to 3.1 mm/yr. This latter range is similar to the optimum growth rates for healthy thalli of the same size and species in this climate, as reported from direct measurements (this study; and Armstrong and Bradwell, this volume). The minimum RGR that we calculated from bomb-^{14}C results assuming a carbon turnover of *c.* 20 % was between 0.5 and 0.9 mm/yr (Fig. 6) and is within the expected radial growth range, inferred from direct measurements. The suggestion is that the annual carbon turnover in this species is between 15 % and 20 % per yr. This is considerably more than the 3-6 % turnover deduced by Bench *et al*. (2002) for thalli of *Caloplaca trachyphylla*, which therefore may indicate that the extent of carbon turnover varies with different species of lichen.

The main aim of this study was to investigate the utility of bomb-^{14}C analysis of a lichen in order to determine the relationship between its size and age, a necessity if the species is to be used in lichenometric applications. Bomb-^{14}C analysis has revealed useful information – confirming the radial pattern of growth in this lichen, and implying that growth is not necessarily symmetrical. However, uncertainties associated with the estimated growth rate probably mean that the value of the current study is limited in its implications for lichenometry. A large contribution to the uncertainties in the estimated growth rate was due to the high level of carbon turnover implied from the ^{14}C results. Carbon turnover appears to be species dependent, suggesting that bomb-^{14}C analysis may be of more value in other lichen species than in *Pertusaria* spp. In addition, use of bomb-^{14}C analysis to determine lichen growth rates would greatly benefit from recent technological advances in ^{14}C analysis of smaller samples and higher precision measurements.

Conclusions

This study provides the first example of the use of bomb-^{14}C analysis to determine the radial growth and carbon turnover rates of a crustose lichen outside North America. The uncorrected ^{14}C derived radial growth rates for our specimen of *Pertusaria pseudocorallina* from central Scotland was calculated to be *c.* 4-7 mm/yr, which is notably higher than our direct measurements for this species in central Scotland, and higher than previous growth rates for this and similar species in the British Isles, reported by others. The results probably indicate that carbon turnover occurs within the crustose lichen *Pertusaria pseudocorallina*, as has been shown for the crustose species *Caloplaca trachyphylla* (Bench *et al.* 2002). However, our study suggests that carbon turnover is in the range of 15-20 % per year – much higher than previously deduced.

Bomb-^{14}C analysis is potentially a valuable technique for determining the growth rate of lichens, but its utility for lichenometric applications also requires a knowledge of site-specific growth rates. Better constrained growth rates should be possible using larger (older) lichen specimens on surfaces of known age, but as shown in the current study, reliable growth rate derivation will also require much better estimates of the rate of carbon turnover, if any, in the lichen being studied.

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Table 1. Details of samples used for radiocarbon analysis including radial distance (relative to geometrical centre), area sampled and carbon content.

Sample no.	Radial distance (mm)	Mid-point (mm)	Area sampled (cm^2 ±0.05)	Carbon content (mg ±0.05)	Density (mg C cm^2)
1	16 - 20	18.0	0.48	1.01	2.10
2	13 - 16	14.5	0.27	1.44	5.34
3	9 - 13	11.0	0.28	2.01	7.17
4	5 - 9	7.0	0.32	1.44	4.49
5	2 - 5	3.5	0.24	0.82	3.44
6	-2 - +2	0.0	0.30	1.44	4.79

Table 2. Radiocarbon content of samples and calibration of results. Age ranges and their associated probability are shown for each sample. Calibration was performed with 'CaliBomb' software using the radiocarbon datasets of Levin and Kromer (2004) and Levin *et al.* (2008). CPAV (calibration peak area value).

Sample. No.	Publication code	^{14}C content (%Modern ±1σ)	$\delta^{13}C_{V\text{-}PDB}$ ±0.1 ‰	Calibrated one sigma range	CPAV
1	SUERC-2754	107.61 ± 0.29	-22.0	1953.64(Aug) - 1953.94(Dec)	0.17
				2002.43(Jun) - 2003.62(Aug)	0.83
2	SUERC-2755	107.91 ± 0.29	-22.0	1953.75(Oct) - 1954.06(Jan)	0.19
				2001.96(Dec) - 2003.11(Feb)	0.81
3	SUERC-2756	108.23 ± 0.33	-21.2	1953.87(Nov) - 1954.18(Mar)	0.17
				2001.40(May) - 2002.70(Sep)	0.83
5	SUERC-2759	109.77 ± 0.29	-22.1	1954.45(Jun) - 1954.76(Oct)	0.13
				1998.41(May) - 2000.29(Apr)	0.87
6	SUERC-2760	108.70 ± 0.29	-22.2	1954.05(Jan) - 1954.36(May)	0.16
				2000.67(Sep) - 2002.01(Jan)	0.84

Table 3. Axial measurements of *Pertusaria* spp. from 3 sites in central Scotland, taken in 2003/2004 and again in 2009. Measurement accuracy is +/-0.05 mm.

Location (lat., long. WGS84) [and time of first measurement]	Lichen species[1]	Diameter (at t=0)[2]	Diameter in June 2009	Total growth during measurement period (mm)	Average radial growth[3] (mm/yr)
Killin (56.4638, -4.3220)	*P. (?pseudo)corallina*	33.45	41.65	8.20	0.82
[May 2004]	*P. (?pseudo)corallina*	32.80	40.20	7.40	0.74
	P. (?pseudo)corallina	54.35	63.40	9.05	0.91
	P. (?pseudo)corallina	38.00	46.80	8.80	0.88
	P. (?pseudo)corallina	40.45	50.95	10.50	1.05
	P. (?pseudo)corallina	45.90	53.50	7.60	0.76
Bridge of Orchy (56.5174, -4.7720)	*P. (?pseudo)corallina*	32.90	44.80	11.90	1.19
[May 2004]	*P. (?pseudo)corallina*	38.25	47.75	9.50	0.95
	P. (?pseudo)corallina	47.95	59.15	11.20	1.12
Comrie (56.3784, -3.9817)	*P. (?pseudo)corallina*	60.35	68.15	7.80	0.65
[June 2003]	*P. (?pseudo)corallina*	56.55	62.50	5.95	0.50
	P. (?pseudo)corallina	55.75	61.75	6.00	0.50

Notes:

1 – *P. corallina* and *P. pseudocorallina* could not be differentiated in the field.

2 – Diameter along horizontal axis at time of first measurement (June 2003 or May 2004). See Fig. 1 for example of axial measurement.

3 – Total growth divided by the number of years elapsed gives diametral growth rates; converted to radial growth rate by dividing by 2.

FIGURE CAPTIONS

Fig. 1. Photograph and schematic diagram showing the axial dimensions of the *Pertusaria pseudocorallina* thallus and location of samples used for ^{14}C analysis.

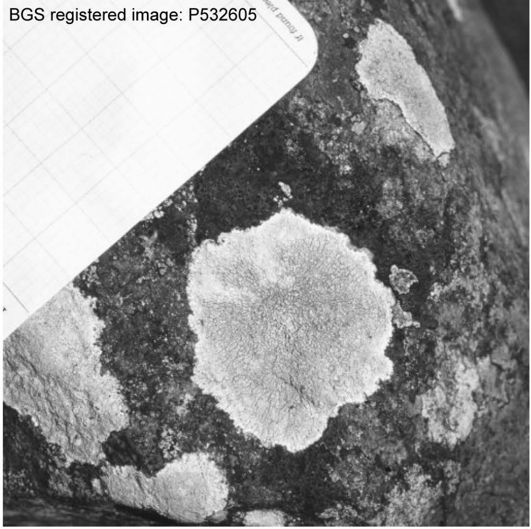
Fig. 2. Northern hemisphere atmospheric radiocarbon concentration 1950 to 2003 (Levin *et al.* 2008) and modelled radiocarbon concentration of lichen in 2003 assuming different rates of annual carbon turnover.

Fig. 3. Relationship between age (determined from bomb-^{14}C content) and radial distance, for *Pertusaria pseudocorallina* lichen. The data point at 0 cm has been omitted from the regression. X-error bars represent distance occupied by sample relative to geometric centre of the thallus, y-error bars represent 1 σ bomb-^{14}C calibrated age range.

Fig. 4. Calibrated age of samples from the thallus of a *Pertusaria pseudocorallina* lichen based on bomb-^{14}C content assuming different rates of fractional carbon turnover per yr. F=0 assumes no carbon turnover and is equivalent to results presented in Fig. 3. Error bars represent the possible age range based on the 1 σ uncertainty of the ^{14}C measurements. Using this approach, when f=0.20, a maximum age for the sample at 3 cm could not be determined.

Fig. 5. Calculated year of earliest growth for the *Pertusaria pseudocorallina* thallus in the present study based on bomb-^{14}C measurements, assuming different rates of fractional carbon turnover per yr. Year of growth is rounded to the nearest whole year. Error bars represent the possible age range based on the 1 σ uncertainty of the ^{14}C measurements. Using this approach, when f=0.20, a maximum age could not be determined.

Fig. 6. Calculated radial growth rate for the short and long axis of the *Pertusaria pseudocorallina* thallus in the present study based on bomb-^{14}C measurements and assuming different rates of fractional carbon turnover per yr. Error bars represent the possible range in growth rate based on the 1 σ uncertainty of the ^{14}C measurements. Shaded area represents the range in radial growth rates for *Pertusaria* spp. obtained from direct measurements of the diameter (horizontal axis) at the field sites (Table 3).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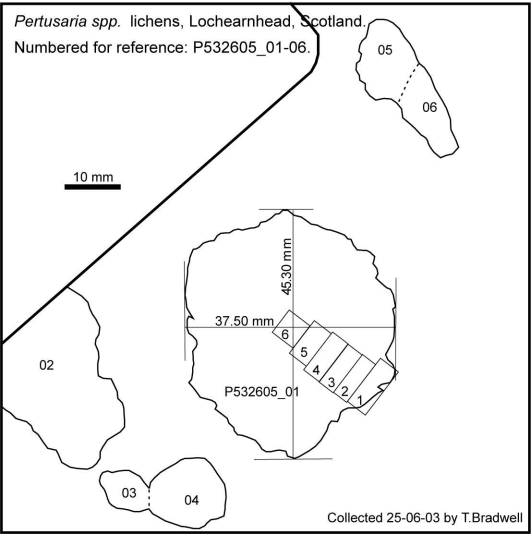
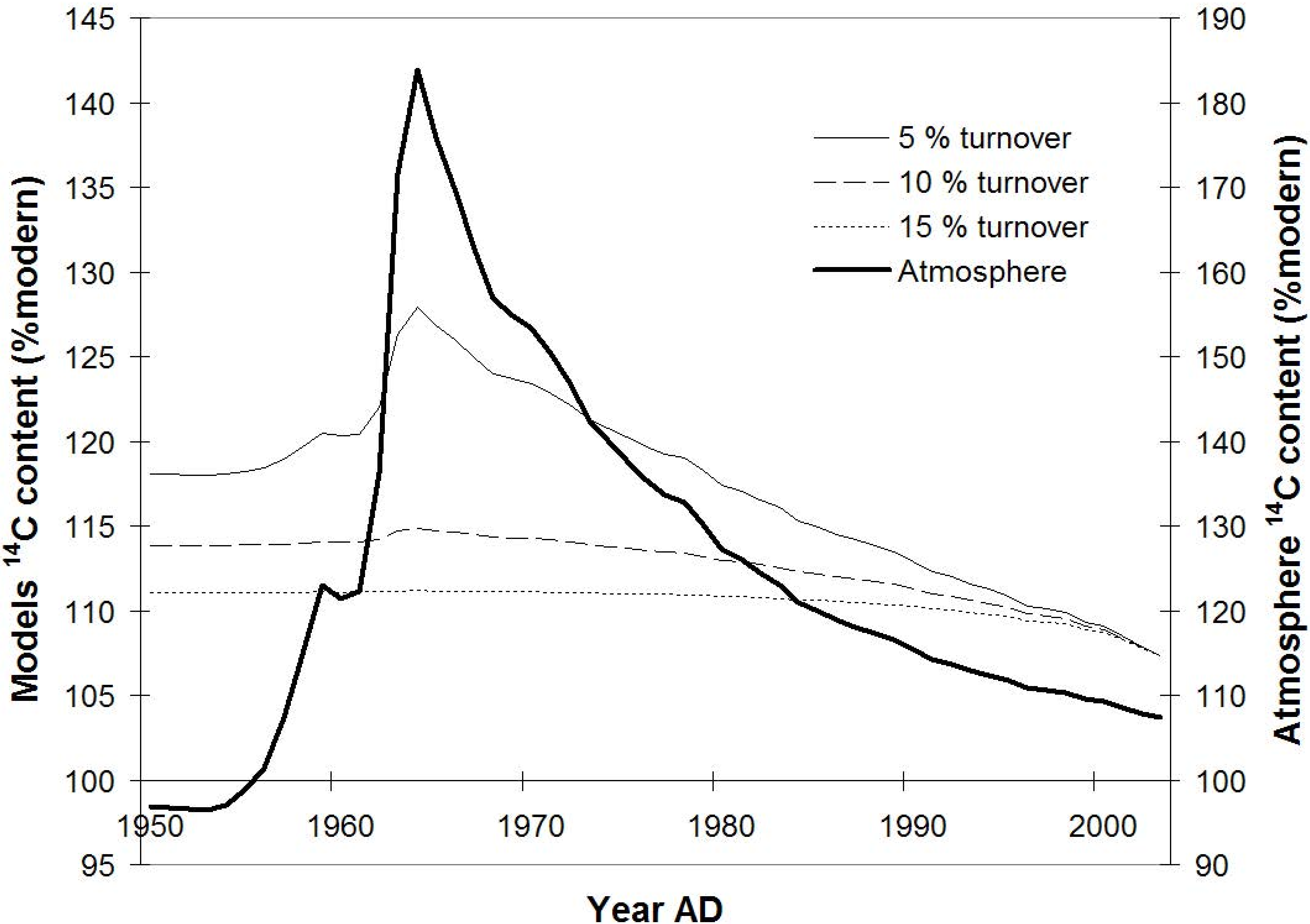
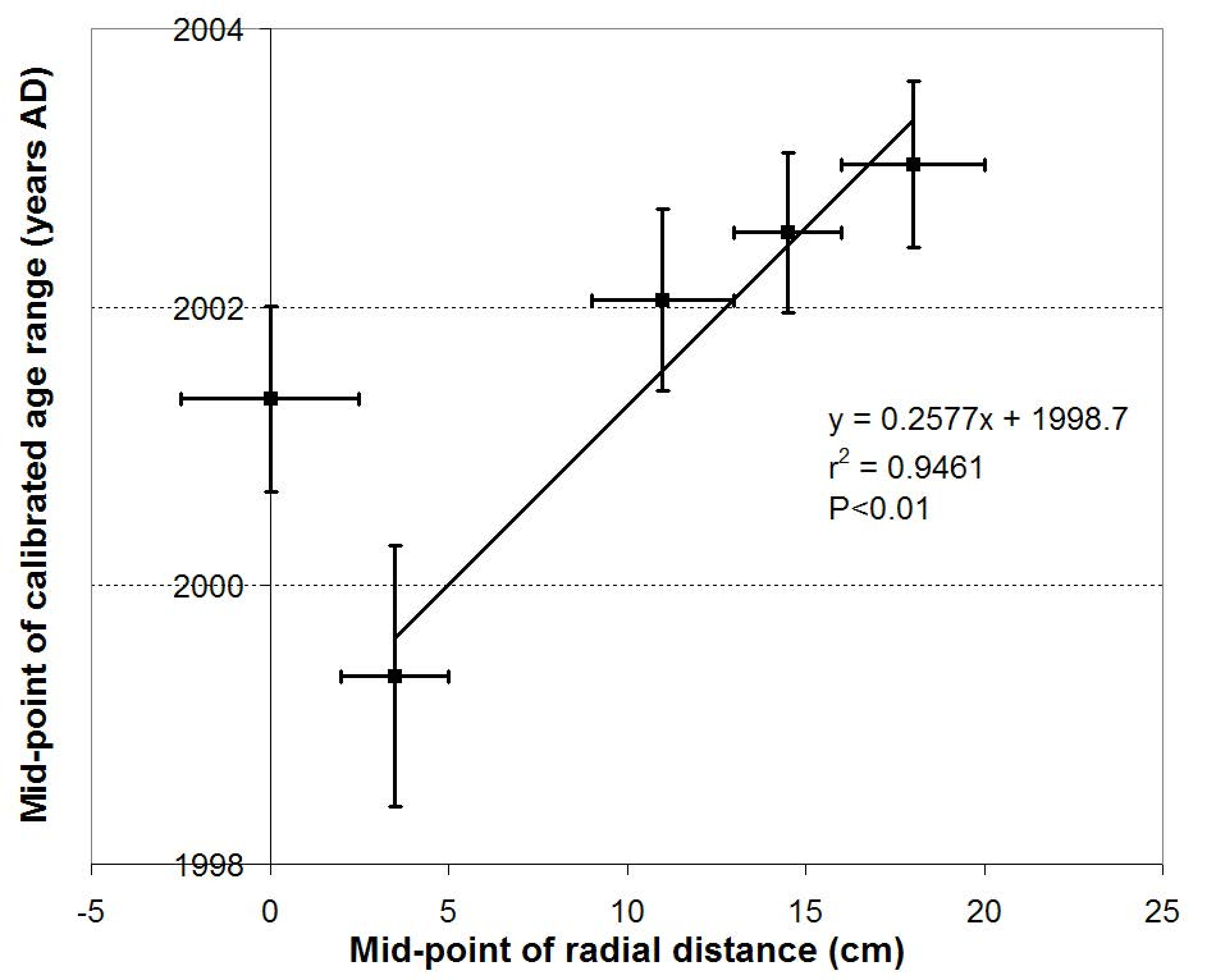
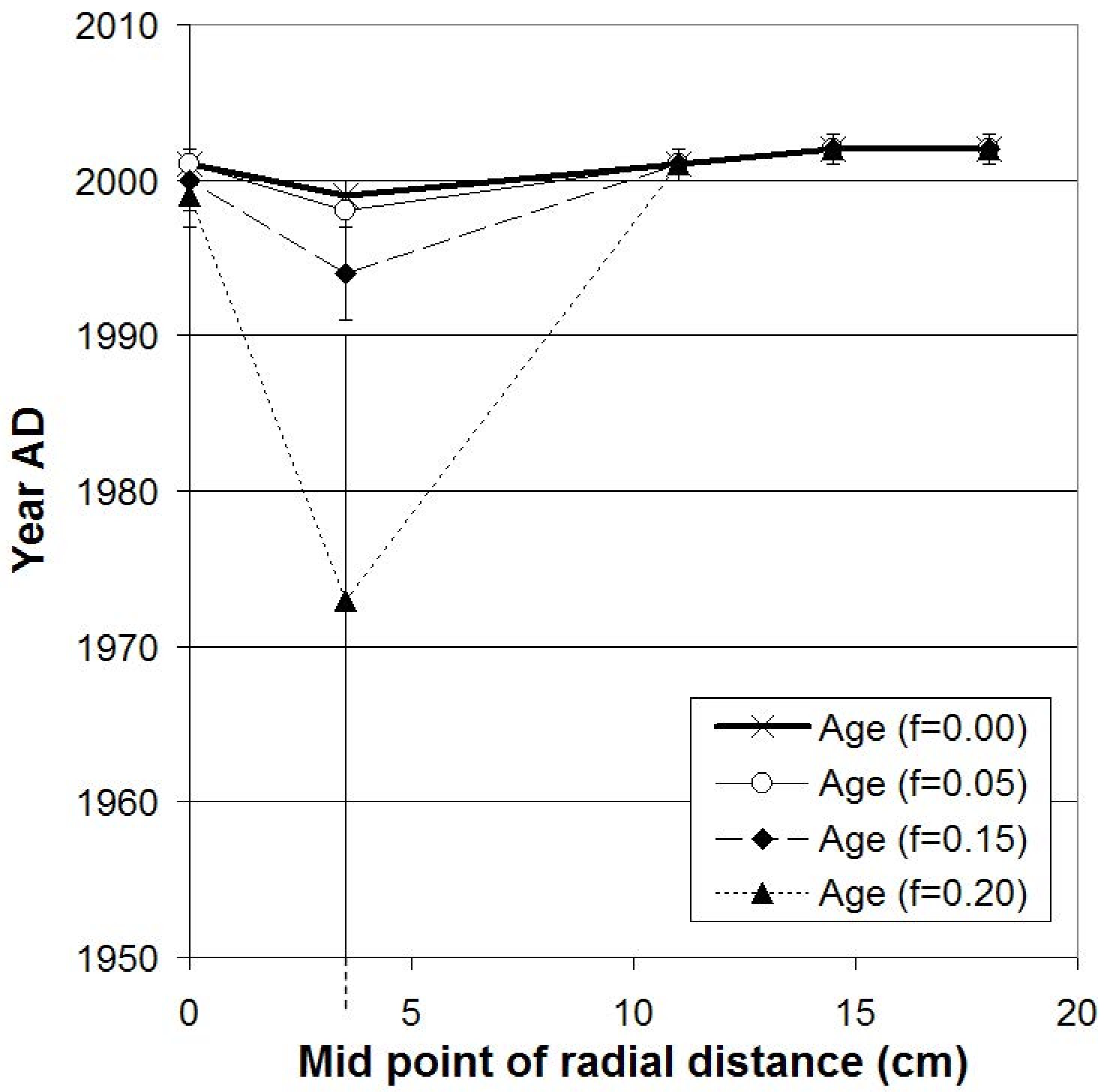

Pertusaria spp. lichens, Lochearnhead, Scotland.
Numbered for reference: P532605_01-06.
05
06
10 mm
45.30 mm
37.50 mm
6
5
4
3
2
1
02
P532605_01
03
04
Collected 25-06-03 by T.Bradwell



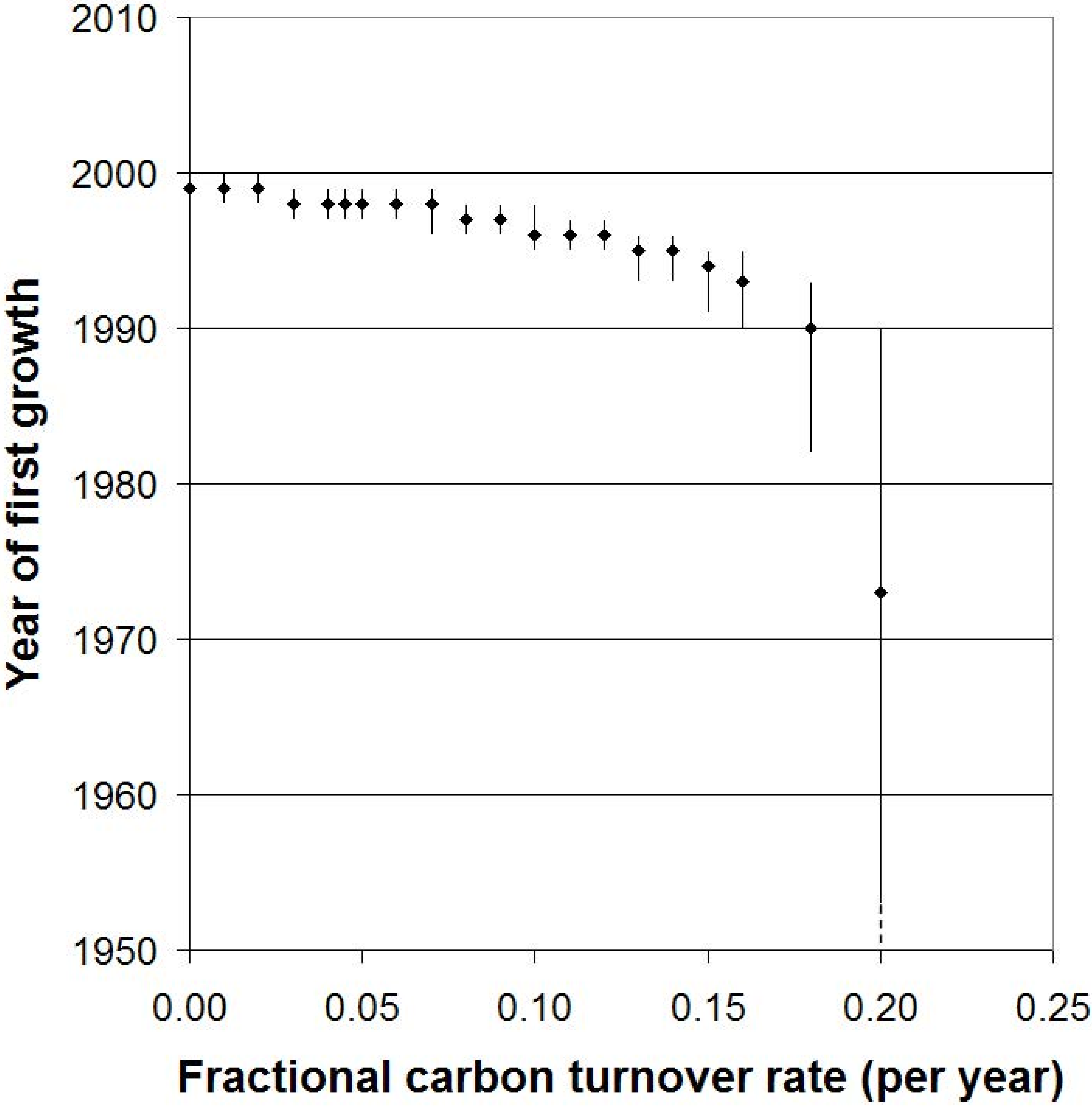
Models ^{14}C content (%modern)
Atmosphere ^{14}C content (%modern)
Year AD
5 % turnover
10 % turnover
15 % turnover
Atmosphere
145
140
135
130
125
120
115
110
105
100
95
190
180
170
160
150
140
130
120
110
100
90
1950
1960
1970
1980
1990
2000



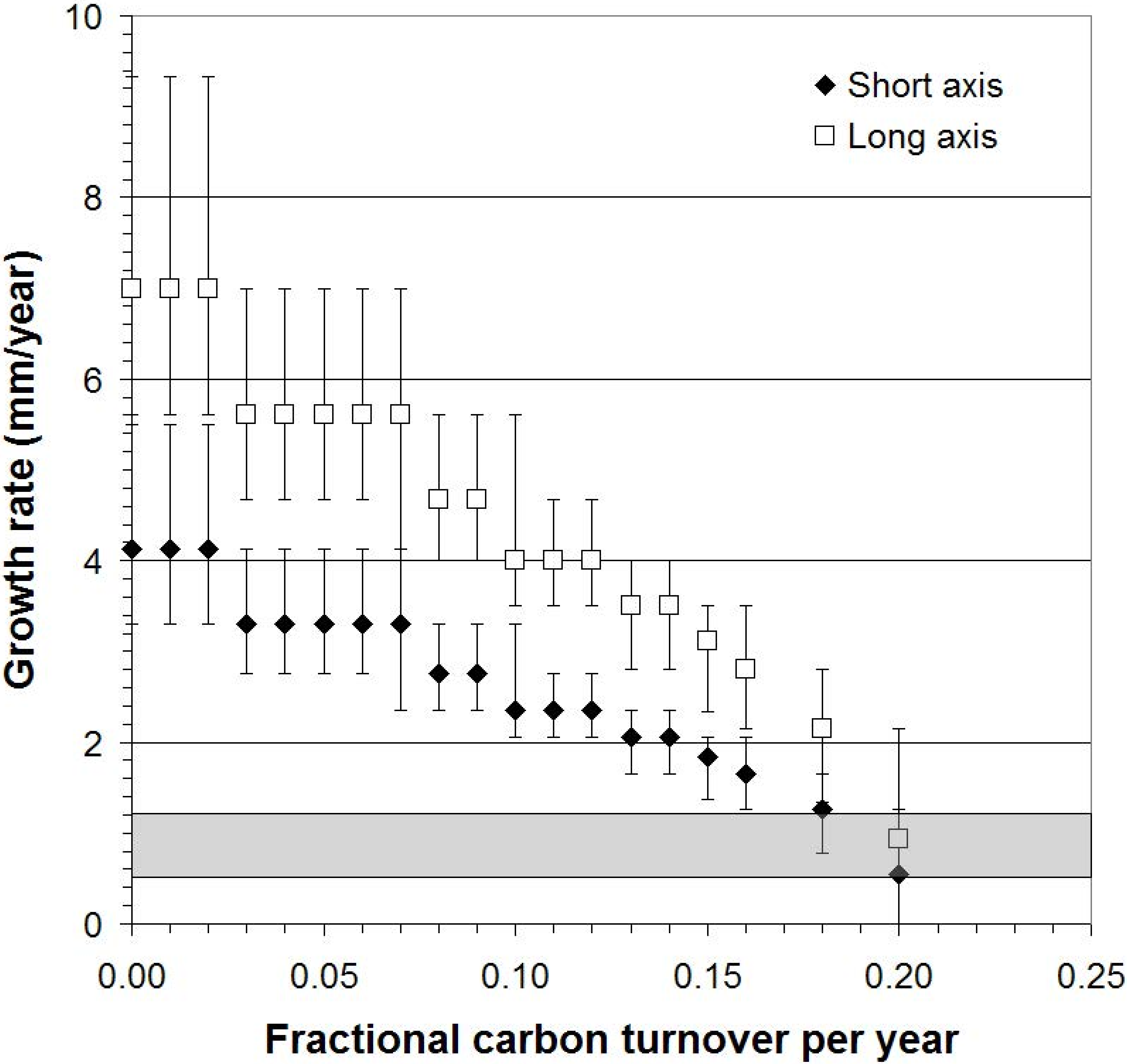
2004
2002
2000
1998
Mid-point of calibrated age range (years AD)
-5
0
5
10
15
20
25
Mid-point of radial distance (cm)
y = 0.2577x + 1998.7
r2 = 0.9461
P<0.01



2010
2000
1990
1980
1970
1960
1950
Year AD
0
5
10
15
20
Mid point of radial distance (cm)
Age (f=0.00)
Age (f=0.05)
Age (f=0.15)
Age (f=0.20)



Year of first growth
2010
2000
1990
1980
1970
1960
1950
0.00
0.05
0.10
0.15
0.20
0.25
Fractional carbon turnover rate (per year)



10
8
6
4
2
0
Growth rate (mm/year)
Short axis
Long axis
0.00
0.05
0.10
0.15
0.20
0.25
Fractional carbon turnover per year