



Contents lists available at ScienceDirect

## Forest Ecology and Management

journal homepage: [www.elsevier.com/locate/foreco](http://www.elsevier.com/locate/foreco)

## Exploring for senescence signals in native scots pine (*Pinus sylvestris* L.) in the Scottish Highlands

T. Fish<sup>a</sup>, R. Wilson<sup>b,\*</sup>, C. Edwards<sup>c</sup>, C. Mills<sup>b</sup>, A. Crone<sup>d</sup>, A.J. Kirchhefer<sup>e</sup>,  
H.W. Linderholm<sup>f</sup>, N.J. Loader<sup>g</sup>, E. Woodley<sup>g</sup>

<sup>a</sup> Pearce Consulting Services, LLC, 401 Diamond Drive, Huntsville, AL 35806, USA

<sup>b</sup> School of Geography & Geosciences, University of St. Andrews, St. Andrews, FIFE, KY16 9AL, Scotland, UK

<sup>c</sup> Forest Research, Northern Research Station, Roslin, EH25 9SY, UK

<sup>d</sup> AOC Archaeology, Loanhead, Midlothian, EH20 9SY, UK

<sup>e</sup> Department of Arctic and Marine Biology, University of Tromsø, NO-9037 Tromsø, Norway

<sup>f</sup> Department of Earth Sciences, University of Gothenburg, SE-40530 Gothenburg, Sweden

<sup>g</sup> Department of Geography, Swansea University, Swansea, SA2 8PP, UK

### ARTICLE INFO

#### Article history:

Received 4 December 2009

Received in revised form 12 April 2010

Accepted 19 April 2010

#### Keywords:

Scots pine

Dendrochronology

Senescence

Ring-width

Scotland

### ABSTRACT

The main aim of this project was to explore whether the pine trees in Glen Affric (GAF), one of the more extensive pine woodlands in the northern Scottish Highlands, are, on average, reaching a senescent stage which could ultimately be detrimental to the sustainability of the pine woodland in this region under present management conditions. This aim was realized by (1) comparing the mean stand age of the GAF trees to other pine woodlands around Scotland, (2) exploring whether there was a significant pre-death trend in ring-width series from naturally dead trees and (3) assessing whether a notable change in response of tree growth to climate was noted as a function of age which could indicate that trees were entering a state of senescence.

The average age of the GAF pine trees is 236 ( $\pm 36$ ) years compared to 225 ( $\pm 55$ ) years for Scotland as a whole and comparing the GAF data to older pine trees around Scotland suggests that the current mature trees should remain healthy for at least the next century. We also note no significant pre-death trend in ring-width time-series measured from recently dead standing trees. Intriguingly, however, there is a consistent weakening in the response of the pine trees to temperatures through the 20th century. Despite younger trees showing, on average, a stronger response to temperatures, they show the greatest temporal instability in response. This response change is likely not related to tree senescence and ongoing research is exploring this phenomenon in more detail.

© 2010 Elsevier B.V. All rights reserved.

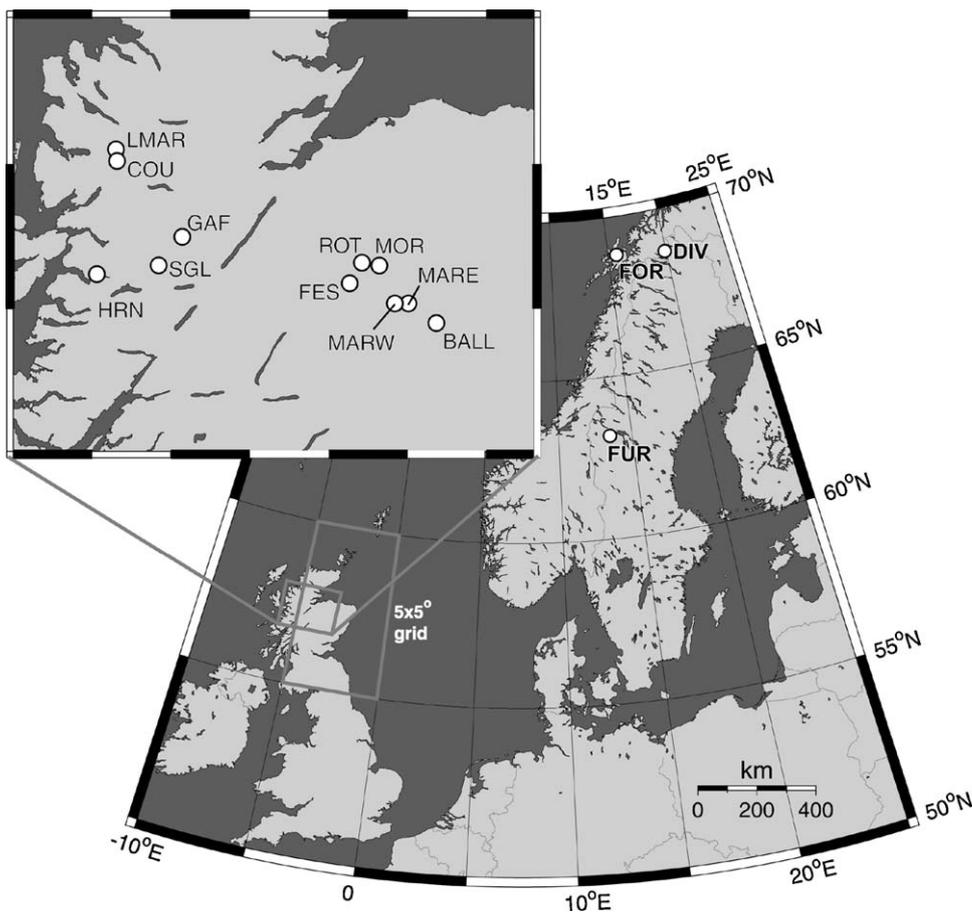
### 1. Introduction

Scots pine (*Pinus sylvestris* L.) is the only commercial conifer species to occur naturally in Great Britain and the only extensive pine woodlands to be found are located in the Scottish Highlands (Steven and Carlisle, 1959), where the coverage of pine was much more extensive in the past. The original Caledonian forest in Scotland included several tree species, particularly oak, birch, alder, as well as pine. The southern regions of Scotland were comprised of mixed deciduous woodlands, while pine was found mostly in the Highlands and northern regions (Steven and Carlisle, 1959). From 8800 to 4400 years BP, pine became widespread throughout much of mainland Scotland, and became the dominant tree type in the north. The expansion of pine reached its peak at around 5000 years

BP although in some areas a decline of the species had already started which accelerated over the millennia due to climate change and human impact (Bennett, 1995).

Today, only remnant patches of the original Caledonian pine forest remain and most of these are in a semi-natural state (Smout et al., 2005). These remaining woodland patches are protected by government policy and non-intervention management (i.e. only deer protection and some fire prevention are allowed) with the intention that they should be self-sustaining in perpetuity (Edwards et al., 2008). However, it is not clear if the present forests are indeed self-sustaining as there is little evidence of regeneration and many of the woodlands have an age structure dominated by trees of 200–300 years in age (on average) which may be close to their natural age of death. In Scotland, pine trees have been reported to live, typically, to a maximum age of approximately 300 years (Steven and Carlisle, 1959; Nixon and Cameron, 1994; Mason et al., 2004) although some individuals are known to exceed 400 years. The death of the old cohorts, of course, would not be a problem if a sufficient number

\* Corresponding author. Tel.: +44 01334 463914; fax: +44 01334 463949.  
E-mail address: [rjsw@st-andrews.ac.uk](mailto:rjsw@st-andrews.ac.uk) (R. Wilson).



**Fig. 1.** Location map of Scottish and Scandinavian pine sites used in this study. Also shown is the  $5^{\circ} \times 5^{\circ}$  temperature grid box used for correlation response function analyses (Brohan et al., 2006).

of younger trees are already in place to replace the trees that are approaching death (Mason et al., 2004). This, however, is not the case for some pine woodlands which are relatively even-aged and reflect regeneration after earlier clear cutting events in the 18th and 19th centuries (Smout et al., 2005). Therefore, as many of the pine trees in Scotland could theoretically be approaching their natural age of death, tree senescence and its contribution to final mortality is an important issue for research.

The response of trees to environmental conditions may also vary over time since trees undergo physiological changes as they age. As well as the influence of climate, ring-width patterns, when related to age and size, are also commonly affected by competition between the trees and any disturbances a woodland may experience (Cook, 1990). Peñuelas (2005) also noted that slow-growing trees tend to live longer as a result of durability and strength due to minimizing 'maintenance and repair costs'.

It has been postulated that multi-aged forest stands produce trees that respond to climate fluctuations in different ways, depending on their age or size, and older trees (>200 years) can show a greater response to climate than younger trees. This was shown for Scots pine at the central Scandinavian Mountain tree line (Linderholm and Linderholm, 2004), as well as for European larch (*Larix decidua*) and Swiss stone pine (*Pinus cembra*; Carrer and Urbinati, 2004), all of which showed age as a partially controlling factor to tree response and productivity. Conversely, Szeicz and MacDonald (1995) found that younger white spruce trees (*Picea glauca*) in northwestern Canada have a stronger response to climate than older trees. However, Wilson et al. (2004) showed no differential response between young and old trees, so long as sam-

ple replication in the differing age classes was high, when studying moisture sensitive Norway spruce (*Picea abies*) trees at low elevations in the Bavarian Forest region of Germany. Similar results, contrasting with the findings of Carrer and Urbinati (2004), were also noted by Esper et al. (2008) who studied Swiss stone pine in the central Alpine region.

The issue of whether age or size is the more dominant influence for senescence is difficult to determine because the two factors cannot be entirely separated from one another (Carrer and Urbinati, 2004). Pennisi (2005) and Martínez-Vilalta et al. (2007) contend that the size of the tree, and not just the age, plays the most important role. They speculate that this could be due in part to the decline in the efficiency of water-conducting cells as the tree grows taller. This is known as the hydraulic limitation hypothesis and basically suggests that it becomes more difficult for the tree to pull water up to the top of the canopy, as it grows, due to friction. This lack of water at the top of the canopy causes a loss in photosynthetic ability and a resultant decline in growth (Magnani et al., 2000; Pennisi, 2005; Mencuccini et al., 2005). It is possible that stable isotopic analysis of the tree-ring series may provide a means for testing these hypotheses as both carbon assimilation and plant water-use may preserve an isotopic signal in the resulting tree ring which relates to canopy/hydraulic processes (McCarroll and Loader, 2004, 2005).

Recent research has been conducted in Scotland on woodland stand structure to assess the effects of management and climate on differing age groups and size distributions of pine woodlands. Edwards and Mason (2006) found that Glen Affric (Fig. 1), a woodland located within the northern Highlands, has recently suffered

**Table 1**

Locations and summary statistics for all pine sites utilized in this study. The mean stand age values utilise pith-offset estimates.

Country	Site name	Site codes	Latitude	Longitude	Elevation (m)	Chronology period	Mean stand age (years)	Standard deviation of ages	Number of trees
Scotland	Glen Affric	GAF	57.15°N	4.56°W	250–350	1709–2002	236	35.5	95
	Glen Affric (dead)	GAFD	57.15°N	4.56°W	250–350	1704–1996	203	47.8	19
	Ballochbuie	BALL	56.58°N	3.19°W	300–500	1589–2003	283	54.9	38
	Mar Lodge (west)	MARW	57.01°N	3.34°W	420–530	1629–1992	241	52.3	45
	Mar Lodge (east)	MARE	57.01°N	3.30°W	400–550	1680–1992	251	35.4	20
	Glenmore	MOR	57.08°N	3.40°W	410–450	1740–2006	219	45.9	17
	Rothiemurchus	ROT	57.09°N	3.47°W	300	1841–2006	148	31.2	17
	Glen Feshie	FES	57.05°N	3.52°W	480–540	1811–2006	157	22.5	24
	Southern Glens	SGL	57.09°N	5.05°W	240–370	1459–2001	355	89.9	25
	Loch Hourn	HRN	57.07°N	5.28°W	90–240	1802–2007	191	21.8	10
	Coulin	COU	57.32°N	5.21°W	250	1671–2007	239	48.7	28
	Loch Maree	LMAR	57.31°N	5.20°W	100	1735–2006	188	49.7	13
	Sweden	Furuberget	FUR	63.10°N	13.30°E	650	1406–1927	132	32.5
Norway	Forfjorddalen	FOR	68.47°N	15.43°E	50–170	1412–1995	257	110.5	14
	Dividalen	DIV	68.38°N	19.52°E	260–400	1474–1972	337	131.8	8

an abundance of natural tree mortality (34 stems ha<sup>-1</sup>). They suggested that the amount of dead standing trees found among the older living trees indicates that the natural mortality may be due to competition between trees of the same population as they age and grow larger. However, like most other Scottish pinewoods, Glen Affric has, in the past, been managed for timber and subjected to intensive grazing by feral and domestic animals (Beaumont et al., 1995), and therefore non-climatic factors (e.g. felling) may have also influenced the growth rates within this region. Few studies have been conducted on senescence rates in Scots pine woodlands and this study will assess stand ages and tree response changes throughout Scotland to examine whether tree age could be a factor in the current pine die-off observed in Glen Affric.

## 2. Data and methods

### 2.1. Living tree ring-width data

The ring-width (RW) data used in this study are from 11 locations in the Scottish Highlands (Fig. 1; Table 1). These sites represent a northwest/southeast transect from Loch Maree and Coulin in the northwestern Highlands to Ballochbuie in the southeastern Highlands, including the main study region of Glen Affric, as well as additional sites within the Cairngorms National Park and southern Highlands and the oldest identified pine stand in the Southern Glens.

Seventy-two samples were crossdated and measured from tree core samples taken by Forest Research (UK Forestry Commission) from Glen Affric, the primary study area, in 1996. These data were further supplemented by 13 trees from a previous dendroclimatic study in Scotland conducted by Hughes et al. (1984) and Hughes (1987), as well as a more recent sampling of ten trees by the University of Swansea in 2003. The final Glen Affric living RW composite chronology (hereafter denoted by GAF) is derived from 95 trees.

A composite ring-width record was derived for the Ballochbuie pine woodland (hereafter BALL) to the southeast of Mar Lodge (Fig. 1), using data from trees sampled in the 1970s (11 trees; Hughes et al., 1984) and 2004 (27 trees; Mills, 2006).

In 1993 two hundred single tree core samples were taken by Forest Research from four sites within Mar Lodge Estate (southwest Cairngorms): Glen Derry, Glen Luibeg, Dubh Ghleann and Glen Quoich. For each site, ten of the oldest cores were dated and measured by the primary author. Due to their close proximity and similarity in site elevation and ecology, the Glen Derry and Glen Luibeg measurements were combined, deriving a western Mar Lodge composite (hereafter MARW), as were Dubh Ghleann and

Glen Quoich in the east (hereafter MARE). These data were also supplemented using RW data from the Hughes et al. (1984) study's earlier sampling of Glen Derry and Inverey, which were incorporated into the MARW and MARE data-sets. The final number of sampled trees in the MARW and MARE data-sets were 45 and 20, respectively.

New sites were sampled in 2007 from Glenmore (hereafter MOR, 17 trees), Rothiemurchus (hereafter ROT, 17 trees), and Glen Feshie (hereafter FES, 24 trees), located at the northwestern edge of the Cairngorm Mountains. As the elevation, aspect and site ecologies of these sites are quite different, these three sites were not composited together.

To complete the Scottish southeast to northwest transect (Fig. 1), 25 trees were also included from the Southern Glens (hereafter SGL), where the oldest known pine stand exists from Scotland (Mills, 2005; Woodley, in preparation). The addition of these samples provides an important comparative data-set due to the longevity of the trees. To the west of the SGL site, we also include ten trees from Loch Hourn (hereafter HRN).

Finally, from the Northwest Highlands we used RW data from Coulin (hereafter COU), combining 11 trees analysed by Hughes et al. (1984) as well 17 trees sampled in 2006/2007, and Loch Maree (hereafter LMAR), combining nine trees sampled by Hughes et al. (1984) and four trees sampled in 2007.

### 2.2. Dead tree ring-width data

As well as the living tree ring-width data, disks were taken from 19 dead standing trees in 2007 in Glen Affric (hereafter GAFD; Table 1) to provide an idea of the age and growth rates of the pine trees at death in this region. To evaluate potential ages of pine trees at death from regions outside of Scotland, we also used data from naturally dead trees from Scandinavia. Ten dead trees were collected from Furuberget, Sweden (hereafter FUR) in the central Scandinavian Mountains. In Norway, 14 dead trees were collected from Forfjorddalen (hereafter FOR) and eight dead trees from Dividalen National Park (hereafter DIV). In all cases, dead samples were only used if the measured rings extended to the outer edge of the tree. In many cases bark was still present, although the possibility of erosion of some outer rings where bark was not present cannot be excluded. Fig. 2 presents the distribution of death dates for each location. The date ranges for the Scandinavian sites cover both the 19th and 20th centuries while the GAFD samples are dated only to the 20th century, which likely reflects the relative rapidity of pine tree rot in Scotland compared to Scandinavia and the relatively recent abundance of mortality at this location. Overall, the death dates are randomly dispersed and are likely not related

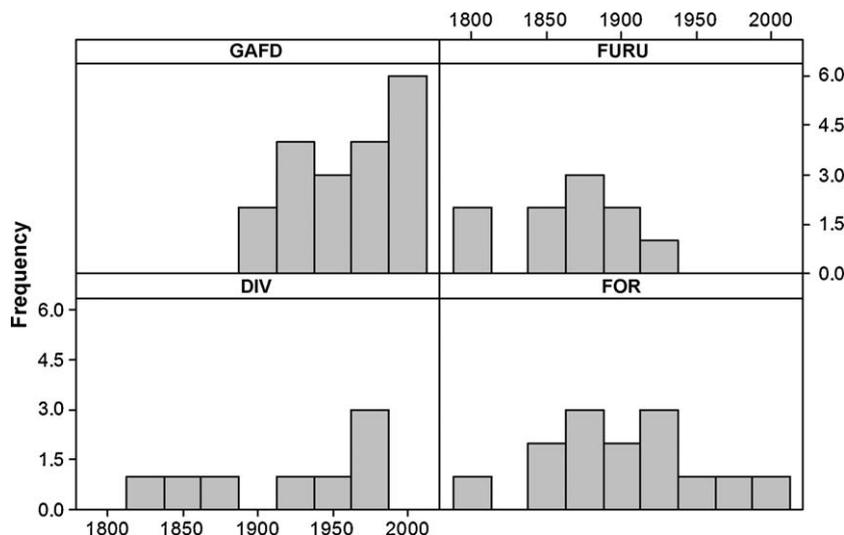


Fig. 2. Distribution of death dates for the dead samples from GAF, FURU, DIV and FOR.

to a stand-wide pathogenic attack or response to extreme climate events.

### 2.3. Sample and data processing

Standard dendrochronological techniques were utilized for sample preparation, measurement and dating (Stokes and Smiley, 1968). To allow for more realistic estimates of tree ages, the number of missing rings (the so-called 'pith-offset') between the first ring measured and the 'missed' pith at the centre of the tree were estimated by using the curvature of the innermost measured rings (Villalba and Veblen, 1997) and comparing them to concentric circles with different radii, ranging from 0.5 to 5 mm, on acetate sheets.

The dead samples from Glen Affric, Furuberget, Dividalen and Forfjorddalen were used to identify whether there was a significant common 'trend' in growth rates as the trees neared death. Aligning the series relative to the year of death, before averaging, results in a mean curve of growth rates leading up to death and may provide information on anomalous changes in growth prior to death. Accepting the possibility that any pre-death growth trend may be negative in nature, the raw data needed to be detrended so that the biological age trend did not mask any potential pre-death trends. However, detrending can cause biases in the resultant index series (Melvin and Briffa, 2008) leading to artificial positive or negative trends. To address this possibility, different detrending methodologies were employed to assess how such methodological choices affect the results. The detrending methods used were a fixed 200-year spline (Cook and Peters, 1981) and a modified negative exponential function (Cook and Briffa, 1990). Experimentation was also made with and without power transformation (Cook and Peters, 1997) of the data prior to using these two detrending procedures. We also employed the use of regional curve standardisation (RCS) which theoretically can capture variability at time-scales longer than the mean length of the samples (Briffa et al., 1996; Esper et al., 2003).

### 2.4. Growth/climate analysis

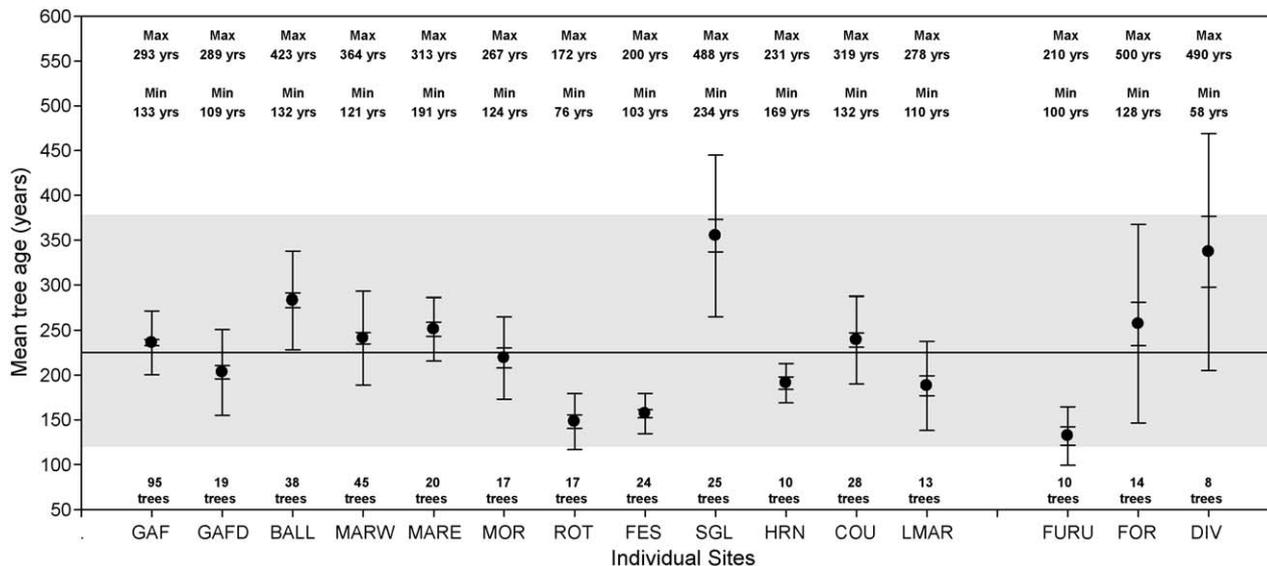
To ascertain whether there is a significant response change with increasing tree age, correlation response function analysis was undertaken for each of the 11 living Scottish site chronologies. The raw RW data for each composite data-set were detrended using a 200-year spline (Cook and Peters, 1981), after appropriate power

transformation (Cook and Peters, 1997), to reduce potential end-effect inflation of resultant indices. These chronologies were then empirically compared against monthly variables of gridded (Fig. 1) mean land temperatures (Brohan et al., 2006) in order to determine if there was a quantifiable response of the trees to climate. Analyses were undertaken over the period where common replication was at least five series. This restricted the outer date for analysis to 1978 as the LMAR chronology, originally sampled by Hughes et al. (1984), is only replicated by four trees after this date. The full period for analysis was AD1850–1978. This period was split into two equal parts (AD1850–1914 and AD1915–1978) to assess the temporal stability of the climate response identified. The 11 chronologies were also averaged together to assess the relationship of the Scotland-wide pine signal to climate.

To explore further the response of the pine trees to climate as a function of age, all the living pine RW data for Scotland were split into two age groups. Unfortunately, due to the sampling strategy of coring only older trees, and the fact that there is very little regeneration in many of the pine woodlands, only seven juvenile trees (<100 years) have been sampled. The two age groups are therefore termed "Mature" and "Old." The Mature group was defined as all trees <200 years old while the Old group included all trees >250 years in age. Trees aged 200–249 years old were excluded to ensure a significant split between the two age classes. The mean age of the Mature group is 161.5 years, while the mean age of the Old group is 291.1 years. The final age group composite series were made up of 106 and 163 series, and had a minimum replication of 20 series from 1823 and 1657 for the Mature and Old groups, respectively. A similar age group split was also undertaken using only the GAF data. As with the individual chronologies, the raw RW data for each age group composite data-set were detrended using a 200-year spline (Cook and Peters, 1981), after appropriate power transformation (Cook and Peters, 1997), and a mean chronology derived. Separate growth/climate analyses, as undertaken for the individual sites, were undertaken using these age-grouped chronologies.

### 2.5. Growth rates and cumulative tree diameter

Finally, to assess whether the GAF trees are, on average, in a reasonable state of "healthiness" with respect to growth rates and age, we transformed the RW data into measures of mean tree diameter as a function of age. The GAF data were first excluded from the Mature and Old groups described above. For each data-set (GAF, Mature and Old), the raw RW data were aligned by cambial age



**Fig. 3.** Mean tree ages of individual site chronologies. The horizontal line denotes the overall Scottish mean age of 225 years. The longer whiskers represent one standard deviation, while the shorter whiskers represent one standard error. Upper values show maximum and minimum trees ages for each site, while lower values denote number of trees sampled per site.

and mean growth curves derived by averaging the non-detrended data together. These data were summed from year to year to derive a cumulative plot of RW (in mm) as a function of tree age. These RW cumulative values were then transformed to mean tree diameter estimates as a function of tree age.

### 3. Results and discussion

#### 3.1. Mean stand ages

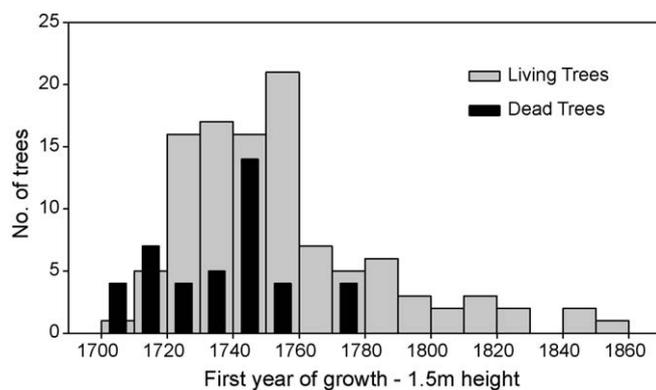
One of the aims of this study is to estimate, if possible, the age at which senescence begins in Scots pine in the Scottish Highlands. This required both the accurate ageing of the living trees as well as identifying the age of those trees that have recently died. These age estimates are detailed in Table 1 and Fig. 3. It should be noted that for the GAF, MARW and MARE sites, only the oldest samples were chosen for measurement, therefore biasing the sampled woodland age structure upwards for these sites. It is not known whether this was the case with the various Hughes sites (Hughes et al., 1984; Hughes, 1987) where the original sampling strategy is not detailed. However, the traditional approach for dendroclimatological sampling is to sample the oldest trees in a stand so it is likely that the strategy utilized by Hughes et al. (1984) would have maximized the mean stand age at the time of sampling. Another more potentially significant bias with the use of the Hughes et al. (1984) data, as well as the MARW and MARE data, is the fact that these sites were sampled in 1978 and 1993, respectively, and do not extend to the present. Since these trees may still be living, the age estimates derived for these stands may be slight underestimations of the present tree stand ages. To partly overcome this, we updated as many sites as possible for this study and these potential age biases are now well within the error ranges of the age estimates and have minimal effect on the final results.

Overall, the mean ages of the individual sites range from 148 ( $\pm 31$ ) years at ROT to 355 ( $\pm 90$ ) years at SGL, with an overall mean stand age across Scotland of 225 ( $\pm 55$ ) years (Fig. 3). ROT and FES are the youngest sites while SGL is clearly the oldest pine stand. Exceptionally old trees >350 years, however, are also found in BALL and MARW.

The main study site, GAF, has a mean stand age of 236 ( $\pm 36$ ) years. The mean age at death of the 19 dead trees sampled from the

Glen Affric region is 203 ( $\pm 48$ ) years. Although slightly lower than the mean age of the living trees, there is no significant difference, at the 95% confidence limit, between these mean values using a *t*-test. Fig. 4 plots the frequency of tree establishment for both the living and dead trees in Glen Affric. The median value of the first year of growth (measured at ca. 1.5 m approximately chest height) is 1748 and 1741, respectively, between the living and the dead trees, suggesting that the dead trees essentially represent the same population as the living trees but simply died earlier than the bulk of the trees in the region. This observation agrees with the results of Edwards and Mason (2006) suggesting that the natural mortality in Glen Affric may simply be due to competition between trees of the same population, although random deaths cannot also be excluded.

As one of the aims of this study was to address whether these recently dead trees may represent the beginning of a phase of mortality in the older growth trees in the Glen Affric region, we also compare the age of the Glen Affric trees at death with other naturally dead pine trees from Scandinavia. For these sites, the mean age at death was 132 ( $\pm 33$ ) years at FUR, 257 ( $\pm 111$ ) years at FOR and 337 ( $\pm 132$ ) years at DIV (Table 1 and Fig. 3), with the oldest tree (500 years old) located in FOR. In light of the overall greater mean tree ages noted for the living sites BALL and SGL and the dead samples from FOR and DIV, it therefore seems unlikely that the GAF



**Fig. 4.** Tree establishment histogram of the living and dead trees sampled from Glen Affric.

trees are close to their “natural” end of life, when only taking tree age into account, and the GAFD data appear to only represent individuals that have died ‘early’ within the local population due to inter-tree competition (Oliver and Larson, 1996).

Peñuelas (2005) noted that slow-growing trees tend to live longer as a result of durability and strength due to minimizing ‘maintenance and repair costs.’ As seen in Fig. 5, which plots mean tree diameter as a function of tree age for GAF and the Mature/Old age groups (excluding the GAF data), our data appear to agree well with this observation with the older trees generally expressing slower growth rates. What is crucial to note however, with respect to the GAF data, is that the mean tree diameter data for this location appear to track very closely the trend noted for the Old age group. This observation would imply that so long as pine tree growth rates continue at a similar rate, then the Glen Affric trees should remain, on average, in a generally healthy state for many more years.

### 3.2. Death-aligned time-series

To make an attempt to identify a possible senescence signal within the ring-width series, it was essential to look at only the dead material. The GAFD, FUR, DIV and FOR data all represent pine trees that have died naturally and provide a unique data-set to test whether any significant pre-death trends may occur. Fig. 6 shows the 200-year spline and negative exponential detrended versions (with and without a power transform (Cook and Peters, 1997)) as well as the RCS chronologies of the death-aligned data-sets for these sites. The wider range in error bars in the recent

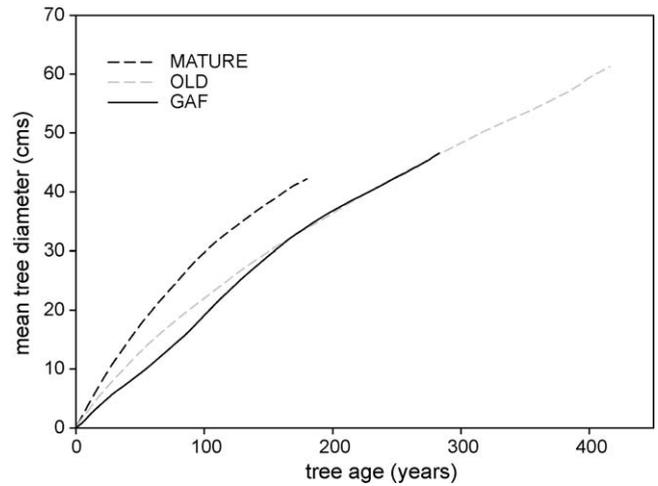


Fig. 5. Time-series of mean tree diameter (in centimetres) as a function of tree age for GAF, and the Mature and Old groups. Diameter estimates are only shown for tree ages represented by at least 5 trees.

period clearly highlights the end-effect sensitivity of detrending (Cook and Peters, 1997; Melvin and Briffa, 2008) and emphasizes the difficulty of extracting a possible pre-death trend signal from the decreasing biological age trend. Overall, there appears to be no significant indication of a decrease in growth rates for any of the sites using the different detrending methods. There is, how-

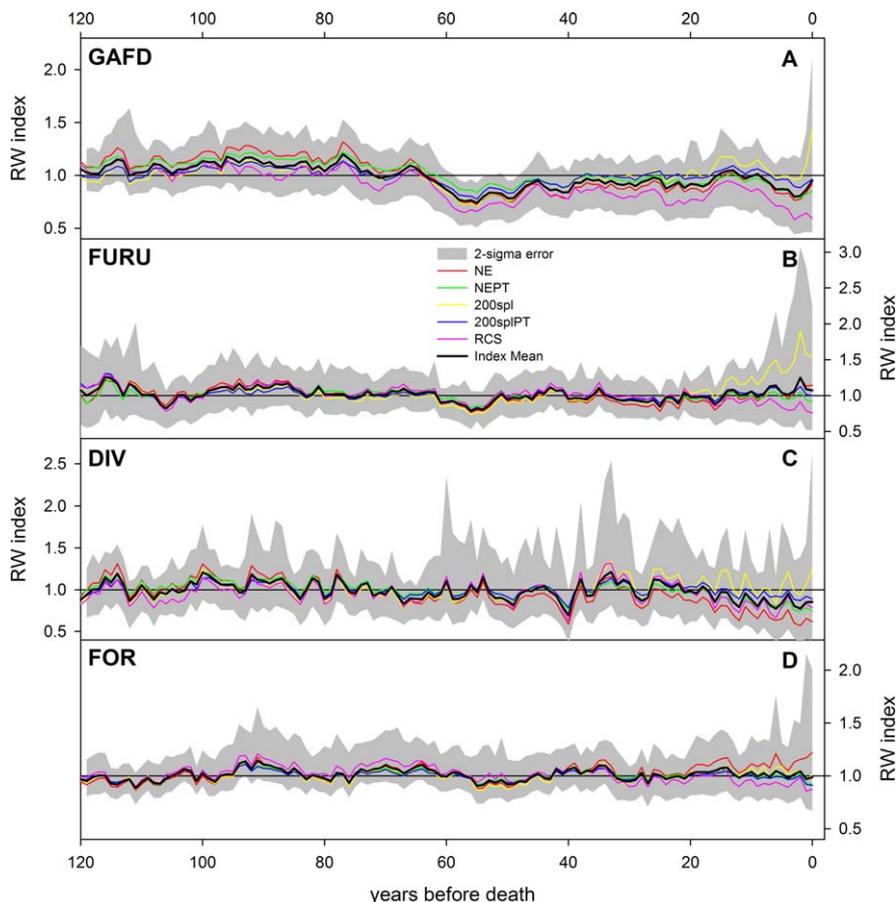
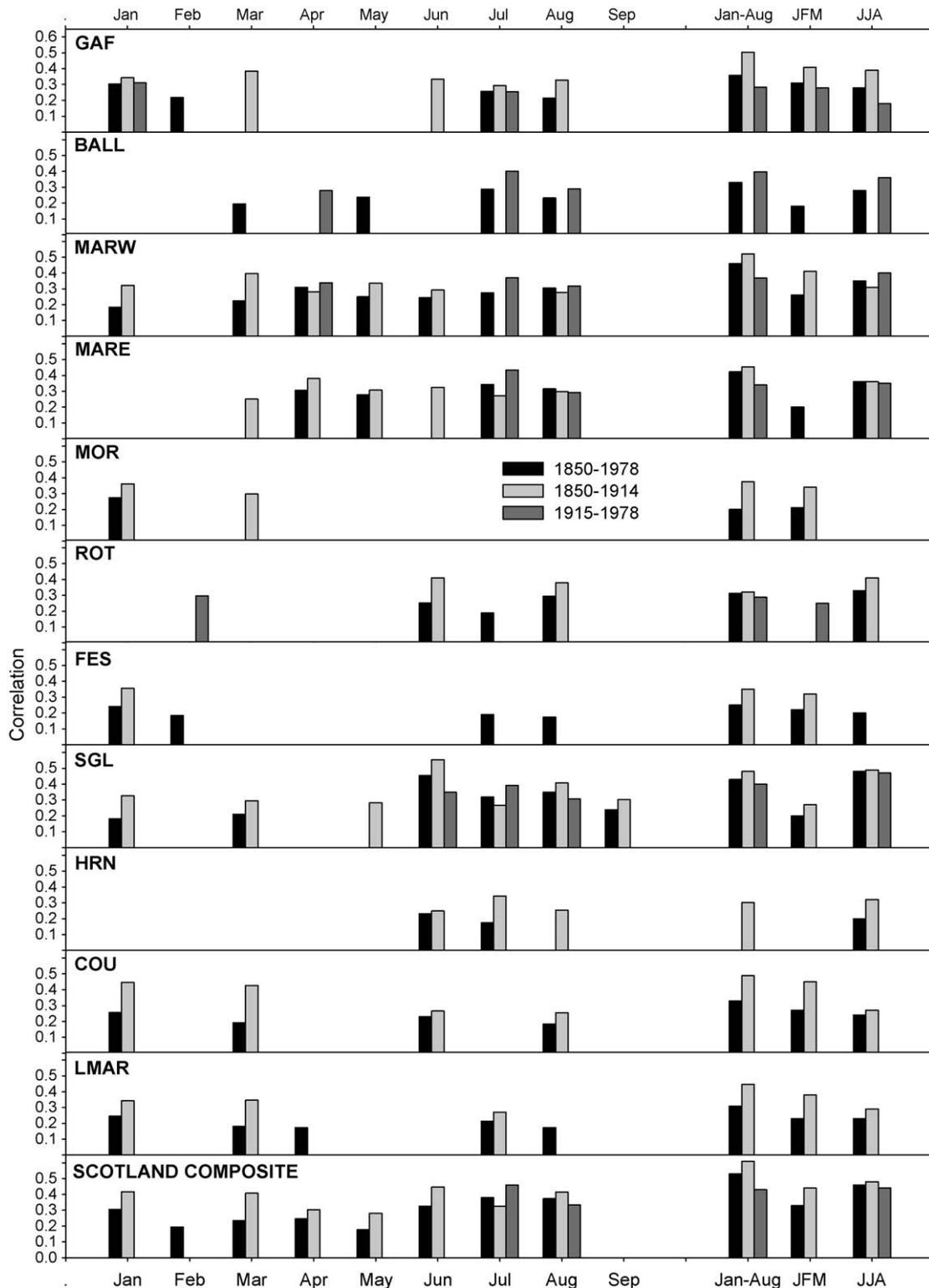


Fig. 6. (A) Death-aligned mean time-series for GAFD for the 120 years leading up to death. Five different detrending options were used. NE = negative exponential function, NEPT = negative exponential function with power transform, 200spl = detrending using a 200 year spline, 200splPT = detrending using a 200 year spline with power transform and RCS = regional curve standardisation. The black line represents the mean of the five detrending options. The bootstrapped error bars (Efron, 1987) are the widest range of uncertainty (95% C.L.) from all five versions; (B) as A but for FURU; (C) as A but for DIV; (D) as A but for FOR.



**Fig. 7.** Correlation response function analysis for each site, plus a composite series for Scotland derived by averaging all the individual site chronologies together. Analysis undertaken over the full (1850–1978) and split periods (1850–1914 and 1915–1978). Only correlations significant at the 95% C.L. are shown.

ever, an intriguing dip in growth for the GAFD data about 60 years before death. As the death dates of these trees were scattered mostly through the 20th century (Fig. 2), it is unlikely that this dip is related to a specific event and probably reflects the noisy nature of this analysis and that many more samples are needed for this type of analysis to be meaningful. DIV also appears to show a decreasing trend prior to death (accentuated in the NE

version), but this is not significant when the error bars (95% confidence limit) are taken into account. However, these data represent some of the oldest trees at death and these results, although non-significant, may imply a decrease in growth rates as the trees acquire extreme ages. The outer few decades of the oldest tree at the SGL site could not be measured as they were extremely narrow.

**Table 2**  
Number of series and relative percentage weighting of each site chronology in the Mature and Old age group Scotland composite series.

Mature	No. of series	% Weight per site	OLD	No. of series	% Weight per site
GAF	18	17.0	GAF	47	28.8
BALL	2	1.9	BALL	37	22.7
MARW	13	12.3	MARW	33	20.2
MARE	1	0.9	MARE	8	4.9
MOR	4	3.8	MOR	2	1.2
ROT	17	16.0	ROT	0	–
FES	22	20.8	FES	0	–
SGL	0	–	SGL	17	10.4
HRN	7	6.6	HRN	0	–
COU	10	9.4	COU	17	10.4
LMAR	12	11.3	LMAR	2	1.2

### 3.3. Growth/climate analysis

Fig. 7 presents the correlation response function analysis results for each individual Scottish pine RW chronology as well as for a Scotland-wide composite series. As would be expected with conifer trees growing in a high-elevation environment, mostly close to the upper tree-line, there is a general positive response to mean summer temperatures. What is perhaps not expected is that on average the trees correlate significantly with both winter and summer temperatures although for all sites, except GAF, MOR, FES and COU, correlations are higher against June–August temperatures than January–March. Grace and Norton (1990) also found significant correlations between ring-width indices and mean temperatures of the winter months in their study on Scots pine near the upper tree limits in the Cairngorm Mountains. They speculated that this could be due in part to a slight increase in winter photosynthesis because of warmer spells occurring during the winter, thus allowing more access to groundwater.

The response of the 11 living composite chronologies to temperature is highly variable between the different sites. The sites with weakest response are MOR, ROT, FES and HRN. The mean response of all the 11 living composite chronologies to January–August temperatures over the AD1850–1978 period is 0.36, with HRN showing no significant correlation and the strongest response being expressed by MARW ( $r = 0.46$ ). Of all the living sites, HRN has the lowest replication (10 trees) and the weak correlation response function results are therefore likely partly a result of weak signal strength. By averaging the 11 chronologies together to derive a Scotland-wide composite, the correlation to January–August temperatures increases to 0.53, suggesting that site-specific effects (ecological or management related), which could dominate individual sites, can be partly overcome by averaging many sites together.

The correlation values over the early and later (AD1850–1914 and AD1915–1978) periods, however, appear to show a general weakening in the response to temperature. This response change appears to be greatest for the JFM season where all sites show a loss in the response to winter temperatures through the 20th century. However, it should be noted that a decrease in response with summer (JJA) temperatures is also noted for GAF, ROT, HRN, COU and LMAR, while MOR and FES show little or no response to summer temperatures at all.

Is this loss in sensitivity to mean temperatures related to the aging of the trees, or to some other unknown cause? To test this, chronologies were derived for the Mature and Old age classes described earlier. Table 2 summarizes the relative weighting that each of the original individual chronologies has on the final Mature and Old age group series. The percentage weighting shows that there is a site bias in the Mature group to GAF, ROT and FES while the Old group is more weighted to GAF, BALL and MARW. The fact that the GAF data influence both sub-sets reflects the larger amounts of samples taken from this site and also indicates that such age groups may be derived for this location with reasonable replication.

**Table 3**

Correlations for the early (AD1850–1914) and late (AD1915–1978) periods between the age group chronologies and mean temperatures for the January–August, January–March and June–August seasons. Results shown for both the Scotland-wide age group chronologies as well as the GAF data. ns = denotes correlations not significant at the 95% confidence limit.

	Mature	Old	GAF Mature	GAF Old
January–August				
1850–1914	0.61	0.50	0.46	0.37
1915–1978	0.34	0.40	0.31	0.22 (ns)
Difference:	0.27	0.10	0.15	0.15
early and late				
January–March				
1850–1914	0.50	0.33	0.43	0.32
1915–1978	0.29	0.17 (ns)	0.35	0.23 (ns)
Difference:	0.21	0.16	0.08	0.09
early and late				
June–August				
1850–1914	0.43	0.42	0.31	0.31
1915–1978	0.24 (ns)	0.41	0.14 (ns)	0.23 (ns)
Difference:	0.19	0.01	0.17	0.08
early and late				

Table 3 summarizes the correlations between the resultant Mature and Old group chronologies against January–August, January–March and June–August mean temperatures. Overall, the strongest response to mean temperatures is noted for the Mature group trees, which is unexpected as this group is weighted to ROT and FES which individually show weak correlations to temperature (Fig. 7). The Mature group, however, shows the greatest weakening in the signal between the 1850–1914 and 1915–1978 periods. No significant weakening is noted for the Old group chronology against the summer season. To ensure that there was no bias due to the different weightings of the sites in both Scotland-wide age classes, this analysis was also performed using the age class chronologies from GAF (Table 3). As expected from the results shown in Fig. 7, the correlations with climate for the GAF data are weaker than with the Scottish-wide composites. However, the results are consistent in the fact that the Mature age group chronology show a stronger response than the old trees. This response change is consistent for both the winter and summer seasons.

## 4. Conclusion

Understanding senescence, and the environmental factors influencing the onset of senescence, is important in the overall understanding of woodland dynamics. The ability to determine when a tree is approaching death would be very useful in managing a woodland site and would allow forest managers to ensure that there are a representative number of immature trees already in place (Bigler and Bugmann, 2004; Wunder et al., 2008).

The main aim of this project was to explore whether the pine trees in Glen Affric were, on average, reaching a senescent stage in their lives which could ultimately be detrimental to the sustainabil-

ity of the pine woodland in this region under present management conditions. This aim was realized by (1) comparing the mean stand age and growth rates of the Glen Affric trees to other pine woodlands around Scotland, (2) exploring whether there was a significant pre-death trend in RW series from naturally dead trees in the region and (3) assessing whether a notable change in response of tree growth to climate was noted as a function of age which could indicate that trees were entering a state of senescence.

By using RW data from 11 locations (Fig. 1) around the Highlands of Scotland, the range in mean stand ages was from 148 ( $\pm 31$ ) years at ROT to 355 ( $\pm 90$ ) years at SGL, with an overall mean stand age across Scotland of 225 ( $\pm 55$ ) years (Fig. 3). GAF, with a mean stand age of 236 ( $\pm 36$ ) years is therefore about average in the Scottish context and it is thus conceivable that the current trees in Glen Affric may live for many more years and the dead trees noted in the region simply died as part of natural pine stand dynamics (Edwards and Mason, 2006).

In the analysis of RW series from naturally dead standing trees from Glen Affric and three sites in Scandinavia (Fig. 6), no significant “trend” in growth indices prior to death was identified. This time-series analysis was conducted on a site-by-site basis, utilizing data from a total of 57 trees. However, it is possible that (1) the amount of data used was too low to overcome the limitations of detrending end effects that might suppress or inflate the index values at the very period where any possible senescence signal would be observed and (2) the possible physical loss of outer rings from the surface of the dead trees due to weathering may remove relevant tree-rings for such an analysis. Such an approach may only prove useful for samples where the bark is preserved and still attached to the outer surface of the tree to ensure that no loss of outer rings has occurred.

Growth/climate analysis using the living tree-ring data identified that the dominant response of pine trees to climate is with both winter and summer mean temperatures although, unsurprisingly, the weighting of this response is stronger for the growing season. The climate response of pine trees appears to be quite variable between sites with the northwest Cairngorm (MOR, ROT and FES) and HRN sites expressing the weakest response with temperatures. The sites expressing the strongest climate responses are MARW and SGL.

The growth/climate analyses also showed, however, that the pine growth relationship with temperatures was weaker during the latter half of the 20th century, especially for the winter season. By dividing the RW data for the whole of Scotland into two age classes (Mature < 200 years; Old > 250 years), the growth/climate analyses indicate that, on average across the Scottish Highlands, while Mature trees express a stronger response with temperatures, the Old trees show a more stable response with temperatures, especially for the summer season. At this time, no definitive cause or causes for the response change in the Scottish pine chronologies can be identified, but it is unlikely to be related to changes in tree age as all sites appear to consistently express this weakening in response (Fig. 7). In recent years, similar observations have been made at many mid- to high-latitude conifer sites throughout the northern hemisphere, where trees have either expressed a weakening in response with temperature, or that ring-width or maximum density indices do not track local temperature trends over the last 30–40 years. This phenomenon, which is the subject of considerable research effort worldwide and may reflect a variety of factors including a non-linearity in tree response, site disturbance or an artefact of sampling/data analysis, has become known as the “divergence problem” (D’Arrigo et al., 2008; Wilson et al., 2007). However, at this time, further research is needed to explore this phenomenon in more detail with respect to the Scottish pine chronologies and is the focus of ongoing research in the region.

In conclusion, from the analyses presented herein, there appears to be no evidence for the living trees in Glen Affric to be close to death and they should remain, on average, in a generally healthy state for many decades to come (Fig. 5). It is likely that for many of the native pinewoods of Scotland, extensive clearance during the 18th and 19th centuries has adversely affected the age structure of the remnants of native woodland that remain. To this end, the woodland structure and senescence characteristics at Glen Affric may be regarded as one reflecting a recovering ecosystem and that the woodland has yet to reach its full age potential or climax age structure. There is currently only limited natural pine regeneration in the Glen Affric region. Consequently management strategies need to be implemented now to ensure that in ~100 years, a sufficient quantity of “natural replacement” will occur. This will be necessary to ensure that sufficient younger pine cohorts are established to replace the mature trees that will be naturally approaching death as the woodland continues its post-clearance recovery towards ecological maturity.

### Acknowledgements

RW, AK, NJL and EW are funded by the European Community under research contract 017008-2 MILLENNIUM. NJL also acknowledges support from the UK NERC NEB501504. CM and AC’s work on developing native chronologies for Scotland was funded principally by Historic Scotland, for cultural heritage applications, and supported by Forest Research. HL was funded by the Swedish research Council (VR). All of the Hughes data was obtained from the International Tree Ring Data Bank (ITRDB, [www.ncdc.noaa.gov/paleo/treering.html](http://www.ncdc.noaa.gov/paleo/treering.html)) while relevant pith-offset data were kindly provided by Dave Frank and Jan Esper of the Swiss Federal Research Institute WSL. CM is grateful to Glenn Iason of MLURI for loan of the Ballochbuie core samples. We are grateful to all the landowners and managers who gave access to their sites for sampling. Many thanks to Jan Esper and Brian Luckman whose reviews substantially improved the manuscript.

### References

- Beaumont, D., Dugan, D., Evans, G., Taylor, S., 1995. Deer management and tree regeneration in the RSPB reserve at Abernethy forest. In: Aldhous, J.R. (Ed.), *Our Pinewood Heritage*. Forestry Commission, Royal Society for the Protection of Birds and Scottish Natural Heritage, pp. 186–195.
- Bennett, K.D., 1995. Post-glacial dynamics of pine (*Pinus sylvestris* L.) and pinewoods in Scotland. In: *Our Pinewood Heritage*. Bell & Bain, Glasgow.
- Briffa, K.R., Jones, P.D., Schweingruber, F.H., Karlen, W., Shiyatov, G., 1996. Tree ring variables as proxy climate indicators: problems with low-frequency signals. In: Jones, P.D., Bradley, R.S., Jouzel, J. (Eds.), *Climatic Variations and Forcing Mechanisms of the Last 2000 Years*. Springer-Verlag, Berlin.
- Brohan, P., Kennedy, J.J., Harris, I., Tett, S.F.B., Jones, P.D., 2006. Uncertainty estimates in regional and global observed temperature changes: a new dataset from 1850. *J. Geophys. Res.* 111, D12106, doi:10.1029/2005JD006548.
- Bigler, C., Bugmann, H., 2004. Predicting the time of tree death using dendrochronological data. *Ecol. Appl.* 14 (3), 902–914.
- Carrer, M., Urbinati, C., 2004. Age-dependent tree-ring growth responses to climate in *Larix decidua* and *Pinus cembra*. *Ecology* 85 (3), 730–740.
- Cook, E.R., Peters, K., 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-Ring Bull.* 41, 45–54.
- Cook, E.R., 1990. A conceptual linear aggregate model for tree rings. In: Cook, E.R., Kairiukstis, L.A. (Eds.), *Methods of Dendrochronology: Applications in the Environmental Sciences*. Kluwer Academic Publishers, Dordrecht, pp. 98–104.
- Cook, E.R., Briffa, K.R., 1990. A comparison of some tree-ring standardization methods. In: Cook, E.R., Kairiukstis, L.A. (Eds.), *Methods of Dendrochronology: Applications in the Environmental Sciences*. Kluwer Academic Publishers, Dordrecht, pp. 153–162.
- Cook, E.R., Peters, K., 1997. Calculating unbiased tree-ring indices for the study of climatic and environmental change. *The Holocene* 7 (3), 361–370.
- D’Arrigo, R., Wilson, R., Liepert, B., Cherubini, P., 2008. On the ‘Divergence Problem’ in northern forests: a review of the tree-ring evidence and possible causes. *Global Planet. Change* 60, 289–305.
- Edwards, C., Mason, W.L., 2006. Stand structure and dynamics of four native Scots pine (*Pinus sylvestris* L.) woodlands in northern Scotland. *Forestry* 79 (3), 261–277.

- Edwards, C., Taylor, S.L., Peace, A., 2008. Determining the Risk of Pinewood Deterioration Based on Tree Size (DBH), Structure and Regeneration Density Data. Contract Report for the Deer Commission, Scotland. Forest Research, Edinburgh.
- Efron, B., 1987. Better bootstrap confidence intervals. *J. Am. Stat. Assoc.* 82, 171–185.
- Esper, J., Cook, E.R., Krusic, P.J., Peters, K., Schweingruber, F.H., 2003. Tests of the RCS method for preserving low-frequency variability in long tree-ring chronologies. *Tree-Ring Res.* 59, 81–98.
- Esper, J., Niederer, R., Bebi, P., Frank, D.C., 2008. Climate signal age effects—evidence from young and old trees in the Swiss Engadin. *For. Ecol. Manage.* 255, 3783–3789.
- Grace, J., Norton, D.A., 1990. Climate and growth of *Pinus sylvestris* at its upper altitudinal limit in Scotland: evidence from tree growth-rings. *J. Ecol.* 78, 601–610.
- Hughes, M.K., Schweingruber, F.H., Cartwright, D., Kelly, P.M., 1984. July–August temperature at Edinburgh between 1721 and 1975 from tree-ring density and width data. *Nature* 308, 341–343.
- Hughes, M.K., 1987. Dendroclimatology of *Pinus sylvestris* L. in the Scottish Highlands. In: Ward, R.G.W. (Ed.), *Applications of Tree-ring Studies: Current Research in Dendrochronology and Related Subjects*, vol. 333. British Archaeological Reports International Series, pp. 91–106.
- Linderholm, H.W., Linderholm, K., 2004. Age-dependent climate sensitivity of *Pinus sylvestris* L. in the central Scandinavian Mountains. *Boreal Environ. Res.* 9 (4), 307–317.
- Magnani, F., Mencuccini, M., Grace, J., 2000. Age-related decline in stand productivity: the role of structural acclimation under hydraulic constraints. *Plant Cell Environ.* 23, 251–263.
- Martínez-Vilalta, J., Vanderklein, D., Mencuccini, M., 2007. Tree height and age-related decline in growth in Scots pine (*Pinus sylvestris* L.). *Oecologia* 150 (4), 529–544.
- Mason, W.L., Hampson, A., Edwards, C. (Eds.), 2004. *Managing the Pinewoods of Scotland*. Forestry Commission Publications.
- McCarroll, D., Loader, N.J., 2004. Stable isotopes in tree rings. *Quat. Sci. Rev.* 23, 771–801.
- McCarroll, D., Loader, N.J., 2005. Isotopes in tree rings. In: Leng, M.J. (Ed.), *Isotopes in Palaeoenvironmental Research*. Springer, The Netherlands, pp. 67–116.
- Mencuccini, M., Martínez-Vilalta, J., Vanderklein, D., Hamid, H.A., Korakaki, E., Lee, S., Michiels, B., 2005. Size-mediated ageing reduces vigour in trees. *Ecol. Lett.* 8, 1183–1190.
- Melvin, T.M., Briffa, K.R., 2008. A “Signal-Free” approach to dendroclimatic standardisation. *Dendrochronologia* 26, 71–86.
- Mills, C.M., 2005. Scottish native pine dendrochronology development: Glen Loyne Stage 3 report. Unpublished AOC Archaeology Report for Historic Scotland and Forest Research Agency.
- Mills, C.M., 2006. Scottish native pine dendrochronology development: a long chronology from Ballochbuie, Deeside. Unpublished AOC Archaeology Report for Historic Scotland and Forest Research Agency.
- Nixon, C., Cameron, E., 1994. A pilot study on the age structure and viability of the Mar Lodge pinewoods. *Scottish Forest.* 48 (1), 22–27.
- Oliver, C.D., Larson, B.C., 1996. *Forest Stand Dynamics*. McGraw-Hill, Inc., New York.
- Pennisi, E., 2005. Tree growth: the sky is not the limit. *Science* 310, 1896–1897.
- Peñuelas, J., 2005. Plant physiology: a big issue for trees. *Nature* 437, 965–966.
- Smout, T.C., MacDonald, A.R., Watson, F., 2005. *A History of the Native Woodlands of Scotland, 1500–1920*. Edinburgh University Press, 434 pp.
- Steven, H.M., Carlisle, A., 1959. *The Native Pinewoods of Scotland*. Oliver and Boyd, Edinburgh.
- Stokes, M.A., Smiley, T.L., 1968. *An Introduction to Tree-Ring Dating*. The University of Chicago Press, Chicago and London.
- Szeicz, J.M., MacDonald, G.M., 1995. Recent white spruce dynamics at the subarctic alpine treeline of northwestern Canada. *J. Ecol.* 83 (5), 873–885.
- Villalba, R., Veblen, T.T., 1997. Determination of total tree ages using increment core samples. *Ecoscience* 4, 534–542.
- Wilson, R.J.S., Esper, J., Luckman, B.H., 2004. Utilising historical tree-ring data for dendroclimatology: a case study from the Bavarian Forest, Germany. *Dendrochronologia* 21 (2), 53–68.
- Wilson, R., D'Arrigo, R., Buckley, B., Büntgen, U., Esper, J., Frank, D., Luckman, B., Payette, S., Vose, R., Youngblut, D., 2007. A matter of divergence—tracking recent warming at hemispheric scales using tree-ring data. *J. Geophys. Res. Atmos.* 112, D17103, doi:10.1029/2006JD008318.
- Woodley, E.J., in preparation. Reconstructing the climate of northern Britain using stable carbon and oxygen isotopes in tree rings. Ph.D. thesis, University of Wales Swansea.
- Wunder, J., Reineking, B., Bigler, C., Bugmann, H., 2008. Predicting tree mortality from growth data: how virtual ecologists can help real ecologists. *J. Ecol.* 96, 174–187.