Role of substrate on the dendroclimatic response of Scots pine from varying elevations in northern Scotland

A.K. Moir, S.A.G. Leroy, and S. Helama

Abstract: The influence of substrate was evaluated by comparing annual ring widths of Scots pine (*Pinus sylvestris* L.) with climate data at 13 new sites (five bog, three peat, and five soil), together with 17 previously studied soil sites in northern Scotland. Radial growth rates <1.0 and >1.5 mm·year^{-1} differentiate well between pine growing on bog and peat, respectively, highlighting the role of pine as a indicator of water levels in these environments. Scots pine chronologies from bog are shown to have a weak temperature–growth response and so limit potential in dendroclimatic reconstructions. However, correlation analysis shows temperature in January–February and July–August to be important determinants of the radial growth of Scots pine on soil. Moving correlation analysis indicates that the relationship between the radial growth of pine on soil near the altitudinal tree line and summer temperature (July–August) is time stable, despite an increase of temperature in northern Scotland. However, winter (January–February) temperature has become less limiting since the 1920s. Scots pine at some soil, bog, and peat sites have increased or developed correlation with October temperature since the 1940s, suggesting an extension of the growth season, particularly on the western coast of Scotland.

Résumé : L'influence du substrat a été évaluée en comparant la largeur des cernes annuels du pin sylvestre (*Pinus sylvestris* L.) aux données climatiques provenant de 13 nouvelles stations (cinq tourbières, trois tourbes et cinq sols) et de 17 stations précédemment étudiées au nord de l'Écosse. Des taux de croissance radiale inférieurs à 1,0 mm·an^{-1} et supérieurs à 1,5 mm·an^{-1} distinguent adéquatement les pins croissant respectivement dans les tourbières et les tourbes, ce qui met en évidence le rôle du pin comme indicateur de la hauteur de la nappe phréatique dans ces milieux. Les séries chronologiques du pin sylvestre établi dans les tourbières révèlent une faible réaction de croissance en fonction de la température et ont, par conséquent, un potentiel limité pour les reconstitutions dendroclimatiques. Cependant, une analyse de corrélation montre que la croissance radiale du pin sylvestre établi sur des sols est fortement liée aux températures de janvier à février et de juillet à août. Une analyse de corrélation mobile indique que la relation entre la croissance radiale du pin établi sur des sols près de la limite altitudinale des arbres et la température estivale (juillet et août) est stable dans le temps malgré une hausse de la température dans le nord de l'Écosse. Toutefois, la température hivernale (janvier et février) est devenue moins limitative depuis les années 1920. La corrélation entre la croissance du pin sylvestre établi sur certains sols, dans des tourbières et des tourbes et la température d'octobre s'est accrue ou s'est développée depuis les années 1940, ce qui indique un allongement de la saison de croissance, particulièrement sur la côte ouest de l'Écosse.

[Traduit par la Rédaction]

Introduction

The peatlands of northern Scotland are one of the largest and most intact areas of blanket bog in the world. *Pinus* pollen (Birks 1975) and widespread occurrence of subfossil trees (Moir et al. 2010) reveal abrupt fluctuations in the northern extent and altitude of pine woodland over the last 10 000 years. Moir et al. (2010) show that between 3200 and 3000 BC, Scots pine (*Pinus sylvestris* L.) expanded onto peatland, up to 60 km beyond its theoretical northern limit on soil, which in Scotland occurs just above Ullapool (Fig. 1). The apparent synchronicity of the fluctuations over large distance is often regarded as a sensitive response to climatic changes, but the precise nature of episodes of pine decline and climate change are not well defined (Tipping et al. 2007). Tree rings are an important source of information on past climate variability (Briffa et al. 2004), and their potential to extend climate-proxy data beyond the last ~150 years of meteorological records is well demonstrated (Jones et al. 2009). Control of annual growth by environmental factors, particularly climate, is strong and clearly discernable in areas where trees grow in marginal environments (Schweingruber et al. 1979). In such areas where tree growth has a high sensitivity to climate, dendroclimatological methods can be useful tools for revealing the dominant factors influencing radial growth (Fritts 1976).

Tree line and peatlands are two marginal environments of particular importance to dendrochronology and dendroclima-

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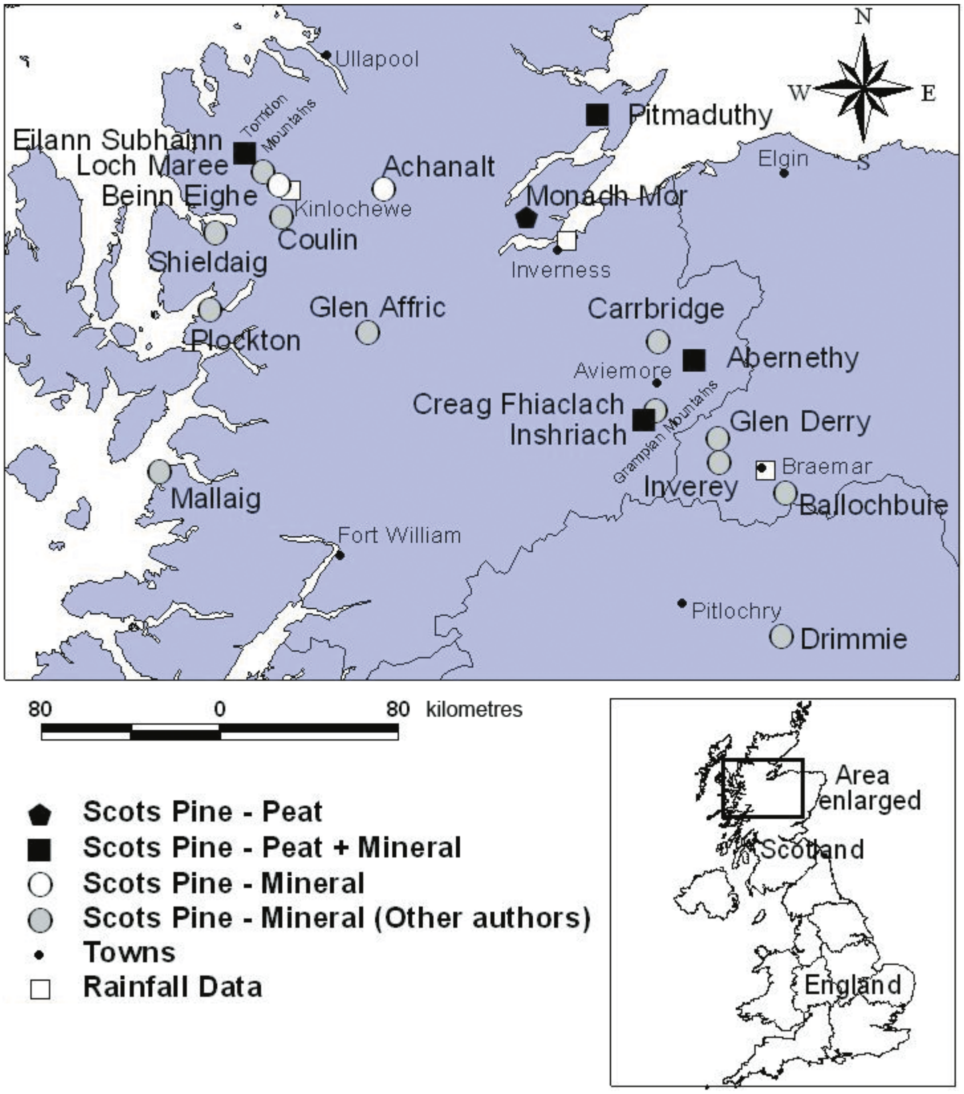
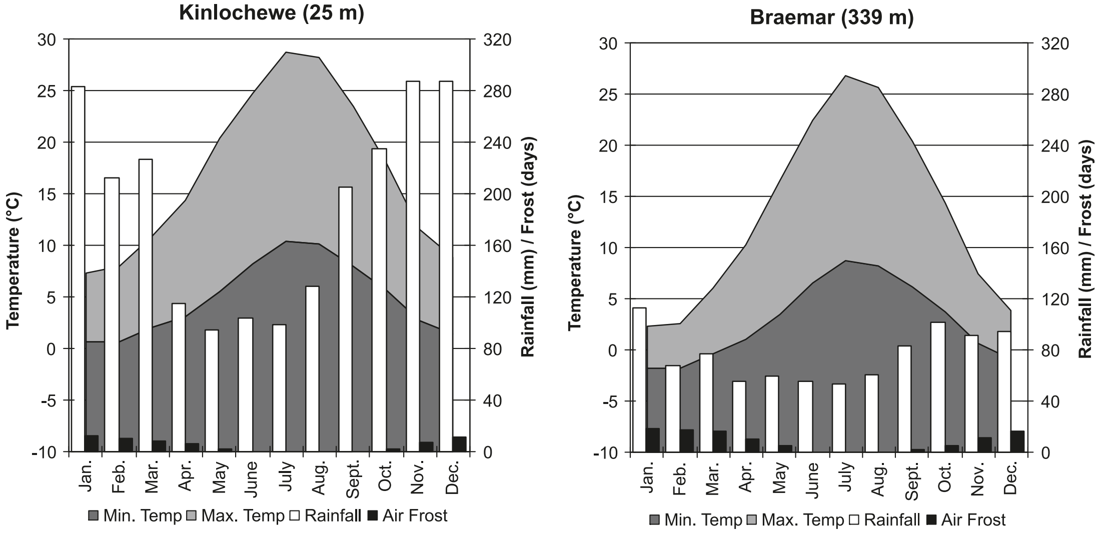
Fig. 1. Map of the locations of Scots pine (*Pinus sylvestris*) tree-ring chronologies developed in northern Scotland. Edinburgh, 90 km south of Pitlochry, is not shown.



tology. Tree line is defined here as the abrupt transition from trees to scrub vegetation (although isolated trees in favourable microsites may grow above the tree line). Forest line is the upper limit of land capable of supporting commercial forestry. However, these terms are often used synonymously elsewhere and are closely coupled boundaries. For its latitude, the tree line in Scotland is depressed (Körner 1998), this is probably due to the maritime climate and exposure to high winds (Tranquillini 1979) but also possibly due to management. Earlier investigations of the climatic controls on the radial growth of pine near the tree line in Scotland are similar to those across northern Europe in demonstrating strong control by July and August (summer) temperatures (Schweingruber et al. 1979; Hughes 1987). However, January and February (winter) temperatures have also been found to have positive correlation (Grace and Norton 1990; Fish et al. 2010), and the former authors emphasize that most physiological studies show the importance of winter conditions in limiting tree growth near its northern or altitudinal limit. Peatlands are an important environment for the growth and subsequent preservation of past pine across northern Europe, which appears associated with varying hydrological conditions (Eronen et al. 2002). Here we define peat as having a relatively low or absent water table and bog as having a high water table. Few dendroclimatic studies have been applied to pine on peatland, but studies in Russia and Sweden found little correlation between ring widths and either temperature or precipitation (Vaganov and Kachaev 1992; Linderholm et al. 2002).

An increased understanding of the relationships between climate and pine growing on peatlands near the upper tree line in Scotland today is integral, both to interpreting past changes of pine woodland range and to managing its future. Two-thirds of land above the forest zone (6000 km^2) lies within the range of windiness and temperature conditions known to be tolerated by native pine (Hale et al. 1998), and Scotland's thriving forest industry aspires to expand woodland from 17% to 25% of land area by 2050 (Ray 2008). High-latitude mountain regions are those particularly sensitive to and worst affected by global warming (Intergovernmental Panel on Climate Change (IPCC) 2007) and hence important areas in which to investigate climatic proxies. A

Fig. 2. Meteorological records from Kinlochewe and Braemar (1971–2000).



well-known premise of tree-ring studies is that trees are more sensitive to temperature close to the tree line than at lower altitudes (Fritts 1976). Kullman and Öberg (2009) show that tree lines in the Swedish Scandes have recently increased in altitude by ~200 m. Therefore, a reduction of tree growth sensitivity to climate might be expected in some trees subsequently located further from the tree line. Reductions in sensitivity of trees have been reported to occur at some sites north of 55°N during the late 20th century (for a review, see D'Arrigo et al. 2008). To help our understanding of the effects of past and present climatic change on pine, this study compares the dendroclimatic response of pine growing today on peat, bog, and soil substrates using measurements of annual ring width. The stability of temperature and precipitation controls over the last century and a half on the radial growth of Scots pine near the tree line in northern Scotland is also investigated.

Background

Peatlands and climate

Bog vegetation is considered particularly sensitive to climate changes because it receives its water and nutrient supply from atmospheric precipitation. Although it has long been assumed that records of bog surface wetness reflect changes in precipitation and temperature, understanding and quantification of the relationships remains unclear (Charman 2007). Tree growth, size, and density on peat are, however, strongly associated with changes in the level of the water table (Mannerkoski 1991). Temperature may influence tree growth both directly through growth-season temperature and indirectly through regulation of the water table by evaporation (Mannerkoski 1985). Drainage of peatland is known to promote good tree growth, and major increases in pine on bog in response to drainage are well known from modern studies (Freléchoux et al. 2000). A lowering of the water table improves the aeration of the upper peat layers, increases soil temperature, and increases nutrient availability (Paavilainen and Päivänen 1995). Bogs in oceanic areas of the western British Isles are sensitive to past changes in effective humidity and provide more reliable archives of past climatic change than the *Sphagnum fuscum* dominated raised bogs in the more continental areas of northern Europe (Barber et al. 2004). In oceanic regions, with rainfall distributed throughout the year and relatively low summer temperatures, comparisons between reconstructed water table levels and meteorological records have shown that rainfall is the primary driver of peatland water table levels (Charman 2007). In turn, an important driver of precipitation and temperature variability at seasonal to decadal time scales in Scotland is the North Atlantic Oscillation (NAO) (Hurrell 1995).

Research area

Northern Scotland is greatly influenced by the presence of the Atlantic Ocean and Gulf Stream to the west, and consequently annual precipitation in Scotland ranges widely from 2000–2800 mm in the west to 900–1300 mm in the east (Fig. 2). The Torridon Mountains and Grampian Mountains (Fig. 1) force the prevailing southwesterly air from the Atlantic to rise, which can further amplify the difference between rainfall on their western and eastern sides. The ranges of daily and annual temperatures increase inland, away from the moderating influence of the sea (Fig. 2). Minimum temperatures are very dependent upon local topography, and marked differences can occur over relatively short distances. July and August are normally the warmest months, but few places in Scotland have more than one or two days in a year with temperatures greater than 25 °C (Parker 1985).

The western limit of Scots pine in northern Europe can be found at 5°38′W in Scotland (Ennos 1991). There are few remaining instances of complete tree line gradients in Scotland, but the present-day tree line is estimated at ~600–650 m near Aviemore (Miller and Cummins 1982) and at ~250 m near the west coast (Hale et al. 1998). The altitudinal boundaries between forest and treeless subalpine heath often occur as abrupt discontinuities; however, in Scotland, the "Krummholz" vegetation (characteristic of climatic tree lines) is often absent, presumably destroyed and kept suppressed by centuries of management practices such as burning and grazing blanket mire (Watson 1996). Hale et al. (1998) show that the maximum limit of forest line occurs at an accumulated temperature of 500 °C (threshold value +5 °C for growing degree days) and (or) a detailed aspect method scoring (DAMS) exposure value of 24. In the UK, DAMS is a widely used measure of wind exposure based on data collected using tatter flags (Quine and White 1994).

Scotland's climate is marginal for the growth of natural tree stands on bogs, except in the Eastern Highlands, where the more continental climate is favourable (MacKenzie and Worrell 1995). Bog woodland in the UK is a rare habitat. It has been broadly defined as areas of trees growing on peatlands where the high water table and low fertility restrict their growth. In continental Europe, a large proportion of bogs are naturally wooded (Moore 1984), but in the UK, this is uncommon (Ellenberg 1988). At Abernethy in Strathspey, which is one of the study sites, Legg et al. (2003) found Scots pine to be an almost ubiquitous constituent of wet heath, blanket mire, *Erica tetralix – Sphagnum papillosum* raised–blanket mire, and *Calluna vulgaris – Eriophorum vaginatum* blanket mire.

Materials and methods

Sampling and chronology building

Tree-ring chronologies were based on core samples, with the exception at Achanalt where ground-level sections were collected from the stumps of previously felled trees. Scots pines were sampled at Abernethy, Inshriach, Monadh Mor, and Pitmaduthy Moss by the Forestry Commission (Fig. 1). To compare the growth rates of trees on peatland and soil, soil-rooted Scots pine were also sampled at Abernethy, Achanalt, and Eilean Sùbhainn. The trees at Achanalt and Eilean Sùbhainn were sampled by the first author. Tree-ring data from earlier studies on soil-rooted Scots pine at 17 other locations were also obtained (Fig. 3).

Single increment cores were aimed to pass through the pith and to the far side of the tree, and both radii were measured. Cores were taken from 20–30 cm above ground, except at Eilann Sùbhainn where cores were taken from 40–80 cm above ground. Standard dendrochronological techniques were utilized for sample preparation, measurement, and dating (Stokes and Smiley 1968). Where the pith was not sampled, the numbers of missing rings to pith were estimated by using the curvature of the innermost measured rings (Villalba and Veblen 1997) and comparing them with concentric circles, spaced at either 1, 2, 3, 4, or 5 mm, on a acetate sheet. Other authors' data were sampled at 1.3 m, and as the pith offset was not known, an arbitrary 10 years was added for use in their age calculation. Cross matches between tree-ring series were reported using raw ring-width data and the standard Student's *t* value statistic (Fig. 4). In the British Isles, cross matching is usually based on the original CROS73 algorithm (Baillie and Pilcher 1973). This algorithm calculates the product movement correlation coefficient *r* and then uses it to calculate a value of Student's *t* to introduce a measure of significance in relation to the length of overlap. Pilcher et al. (1995) suggests that values greater than or equal to 4 be regarded as an acceptable match when cross matching pine.

Growth rates

Series of tree rings commonly contain age trend, caused by the general reduction of ring width as trees get progressively older and pass through the formative, mature, and senescent phases of growth (White 1998). Formative radial growth rates (defined here as the mean rate of growth over the first 55 years) are a more useful comparison than mean ring width because they are not influenced by differences between tree ages. For useful visual comparison between tree growth rates, age trend series for cumulative plots (Fig. 5) were produced. Cumulative plots align the tree-ring series from each tree according to the biological age of the rings (i.e., the number of years that the tree has been alive) and not the chronological age (i.e., the year in which the tree ring formed), which are then averaged to produce a mean for each site. This method greatly attenuates the yearly fluctuations in ring width due to environmental factors because of the chronological misalignment of the tree rings and helps emphasize the underlying biological age growth trend. Bog woodland has been defined as areas of trees growing on peatlands where the high water table and low fertility restrict their growth, so here we use high and low radial growth rates to distinguish between Scots pine probably growing on peats and waterlogged bog, respectively (Fig. 3).

Dendroclimatic analysis

In most dendroclimatic studies, it is usual to attempt to statistically remove age trend from individual tree-ring series to remove the areas of high and low growth in mean chronologies that are not associated with climatic change. This process is called standardization. Its aim is to prevent over-representation of wide-ringed series at the expense of narrow-ringed series, to remove other low-frequency variability assumed unrelated to climate (e.g., forest-stand disturbances), and to strengthen the common signal in the tree-ring data. Here, series were standardized before averaging, using ARSTAN software (Cook et al. 1990). Detrending was done with a negative exponential curve or linear regression, except where this method produced negative indices and then a 67% of series length spline with 50% frequency cutoff was applied. Only correlations in the year of growth were investigated, and therefore autocorrelation was removed from individual tree-ring series through autoregression modelling.

Chronology statistics were generated for the standardized series (Fig. 3). Mean sensitivity is a measure of the mean relative change between adjacent ring widths (Fritts 1976). Values greater than 0.30 are high and indicate that the tree-ring series are highly responsive to environmental factors; low values indicate weak interannual variance. Uncommon variance (noise) cancels in direct proportion to the number of series averaged. The expressed population signal (EPS) (Wigley et al. 1984) measures the degree to which the chronology correlates (or agrees) with the theoretical population chronology. The value of EPS ranges from 0 to 1, with 1 being the best possible value (the hypothetically perfect chronology).

To examine growth–climate relationships, dendrochronologists commonly use correlation functions as a statistical model to compute coefficients between tree-ring chronologies and monthly climatic variables (Blasing et al. 1984). These coefficients are univariate estimates of Pearson's product moment correlation. Correlation function analyses and moving interval correlation function analysis were performed using DENDROCLIM2002 software (Biondi and Waikul 2004), which computes correlation coefficients with 1000 bootstrapped samples and tests their significance at the 0.05%

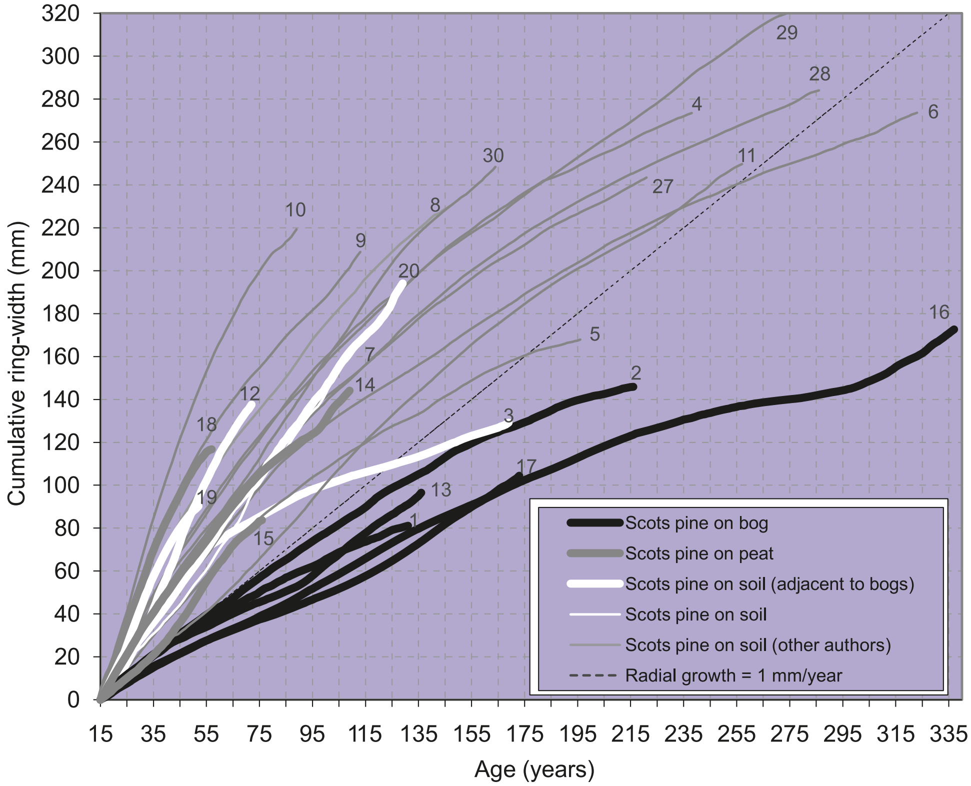
Fig. 3. Summary of Modern pine chronologies for Scotland. Shading denotes bog and peat sites. Latitude and longitude are expressed in decimal degrees (dec. deg.). Oceanicity: 1, hyperoceanic; 2, euoceanic; 3, hemioceanic (Birse 1971). Detailed aspect method scoring (DAMS), measure of wind exposure (© Crown copyright. All rights reserved Forestry Commission). Chronology statistics for the arstan standard chronology: MS, mean sensitivity; AR1, first-order autocorrelation; *R*(bt), between series correlation (≥0.35 in bold); EPS, expressed population signal (≥0.85 in bold). In the DAMS column, an asterisk (*) indicates that DAMS scores for the western Scottish seaboard maybe underestimated by 1.5 by the current model (1 September 2009) (Bill Rayner, personal communication). In the Short reference column, a dagger (†) indicates that the data are archived at the World Data Center for Paleoclimatology, Boulder, Colorado, USA.

Order	Site name (transect)	Latitude (dec. deg.)	Longitude (dec. deg.)	Altitude (m)	Ocean-icity	DAMS	Site type	Mean depth of peat (m)	No. of trees sampled/cross matched	Chronology	Mean ring width	Mean formative growth rate (mm/year)	Chronology span	MS	AR1	Common interval	*R* (bt)	EPS	Short reference
1	Eilean Subhainn — A	57.69	-5.49	50	1	11	Wooded bog	0.35	14/9	ESBE-9	0.93	0.92	1869-2005	0.21	0.58	1880-1960	**0.45**	0.80	This paper
2	Eilean Subhainn — B	57.69	-5.49	50	1	12	Wooded bog	0.84	13/12	ESDB-12	1.00	0.99	1790-2005	0.20	0.75	1880-1960	**0.41**	**0.85**	This paper
3	Eilean Subhainn — C	57.69	-5.49	50	1	11	Soil prone to flooding		13/13	ESDG-13	0.85	1.77	1837-2005	0.20	0.73	1882-1960	0.27	0.72	This paper
4	Loch Maree	57.65	-5.42	100	2	12	Soil		8/8	LCHMAREE	1.00	2.17	1756-1978	0.16	0.53	1880-1960	**0.55**	**0.90**	Hughes et al. 1984 †
5	Beinn Eighe	57.62	-5.36	300	2	20	Waterlogged soil		17/10	BNAA-10	1.03	1.44	1809-1989	0.17	0.46	1880-1960	0.25	0.76	Barlow 1990
6	Coulin	57.55	-5.35	250	2	13	Soil		11/11	COULIN	1.18	1.68	1671-1978	0.14	0.67	1880-1960	**0.35**	**0.85**	Hughes et al. 1984 †
7	Achanalt	57.61	-4.94	130	2	13	Soil		8/7	ACHA-7	1.80	1.51	1893-2004	0.17	0.71	1995-1960	0.31	0.73	This paper
8	Shieldaig	57.52	-5.62	10	1	14*	Mineral/sloping		11/11	SHIELDAG	2.06	2.56	1847-1978	0.12	0.67	1880-1960	**0.45**	**0.89**	Hughes 1987 †
9	Plockton	57.35	-5.63	100	1	12*	Soil		13/12	PLOCKTON	2.40	3.03	1879-1976	0.13	0.60	1880-1960	**0.42**	**0.90**	Schweingruber et al. 1979 †
10	Mallaig, Loch Morar	57.00	-5.84	100	1	14*	Soil		13/10	MALLAIG	3.55	3.83	1903-1976	0.14	0.52	1880-1960	0.28	0.80	Schweingruber et al. 1979 †
11	Glen Affric	57.30	-5.00	300	2	22	Soil		13/13	GLNAFRIC	1.04	1.03	1735-1976	0.15	0.83	1880-1960	**0.38**	**0.89**	Hughes et al. 1984 †
12	Pitmaduthy — B (D1)	57.77	-4.07	100	2	12	Soil		6/6	PITM-M2	2.36	2.55	1938-1999						This paper
13	Pitmaduthy — A (S1)	57.77	-4.07	100	2	12	Wooded bog	—	12/12	PITM-M1	0.83	0.85	1875-1999	0.22	0.72	1880-1960	0.24	0.80	This paper
14	Monadh Mor — A	57.55	-4.36	200	2	13	Wooded peat	0.75	6/6	MONM-M1	1.67	1.85	1906-1999	0.16	0.61	1922-1960	**0.35**	0.76	This paper
15	Monadh Mor — B	57.55	-4.36	200	2	13	Wooded peat	0.75	4/4	MONM-M2	1.33	1.38	1934-1999						This paper
16	Abernethy — B (T1+S1)	57.24	-3.68	220	3	13	Wooded bog	4.86	22/22	ABEA-22	0.50	0.69	1694-2000	0.21	0.66	1880-1960	0.26	**0.87**	This paper
17	Abernethy — C (T3)	57.24	-3.68	220	3	13	Wooded bog	4.66	23/21	ABEC-21	0.69	0.66	1838-2000	0.19	0.77	1880-1960	0.30	**0.86**	This paper
18	Inshriach — A (S1)	57.11	-3.88	300	3	13	Cutover peat	0.35	7/3	INSH-M1	2.97	2.89	1953-1999						This paper
19	Inshriach — B (D1)	57.11	-3.88	300	3	13	Soil		6/2	INSH-M2	2.35	2.31	1958-1999						This paper
20	Abernethy — D (D1+D2)	57.24	-3.68	220	3	13	Soil		10/9	ABED-9	1.75	1.75	1882-2000	0.18	0.83	1955-1960	n/a	n/a	This paper
21	Carrbridge	57.28	-3.83	270	3	14	Soil/managed		13/13	CFG-13	1.46	—	1880-1979	0.13	0.61	1896-1960	**0.35**	**0.87**	Grace and Norton 1990
22	Creag Fhiaclach — F	57.13	-3.84	280	3	12	Waterlogged soil		11/11	CFF-11	1.57	—	1880-1979	0.13	0.52	1880-1960	0.31	0.76	Grace and Norton 1990
23	Creag Fhiaclach — E	57.13	-3.84	400	3	12	Soil/sloping		11/9	CFE-9	0.72	—	1880-1979	0.17	0.44	1880-1960	0.28	0.78	Grace and Norton 1990
24	Creag Fhiaclach — D	57.13	-3.84	450	3	12	Soil/sloping		11/11	CFD-11	0.48	—	1880-1979	0.16	0.64	1880-1960	**0.50**	**0.92**	Grace and Norton 1990
25	Creag Fhiaclach — A	57.13	-3.84	500	3	12	Soil/sloping		15/15	CFA-15	1.09	—	1880-1979	0.14	0.51	1880-1960	**0.38**	**0.90**	Grace and Norton 1990
26	Creag Fhiaclach — B	57.13	-3.84	550	3	12	Soil/sloping		10/10	CFB-10	1.03	—	1880-1979	0.15	0.64	1880-1960	**0.47**	**0.88**	Grace and Norton 1990
27	Glen Derry	57.07	-3.59	400	3	16	Soil		13/13	GLENDERRY	1.36	1.94	1773-1978	0.13	0.42	1880-1960	**0.42**	**0.90**	Hughes et al. 1984 †
28	Inverey	57.02	-3.58	500	3	13	Soil		13/13	INVEREY	1.23	1.99	1706-1976	0.13	0.73	1880-1960	0.33	**0.86**	Schweingruber et al. 1979 †
29	Ballochbuie	56.95	-3.32	380	3	19	Soil		11/11	BALLOCHB	1.38	2.22	1712-1978	0.13	0.58	1880-1960	**0.41**	**0.88**	Hughes et al. 1984 †
30	Drimmie	56.63	-3.35	200	2	12	Soil/flat		12/12	DIMMIE	1.88	1.94	1828-1976	0.17	0.69	1880-1960	**0.44**	**0.89**	Hughes 1987 †

Fig. 4. Cross matching between tree-ring chronologies from bog. Only *t* values over 3.5 are shown; *t* values were calculated using CROS74 (Baillie and Pilcher 1973). Shading denotes bog and peat substrate sites.

Order	File names	Area	Altitude (m)	Substrate	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1	ESBE-9	NW	50	Bog	7.1	6.2		5.5			3.9																						
2	ESDB-12	NW	50	Bog		7.2		4.4	6.1	4.3	5.1	5.0		4.2										4.2			3.6	3.5					3.8
3	ESDG-13	NW	50	Soil				3.7	3.6		3.7																						
4	LCHMAREE	NW	100	Soil				6.1	6.5	3.8	5.1	6.6		5.5			4.2							4.1	3.9	5.7	4.1	4.3	4.6	6.7	5.6	5.2	4.4
5	BNAA-10	NW	300	Soil					6.2	3.7	5.8	5.7		4.7												5.0		3.5	3.6	3.6			4.5
6	COULIN	NW	250	Soil								4.9		5.6										4.2		6.1	4.3	4.8	3.8	7.5	8.2	6.1	
7	ACHA-7	NW	130	Soil								6.9																					
8	SHIELDAG	NW	12	Soil								4.3		4.4											6.1	4.2		4.6	4.3	4.4			3.5
9	PLOCKTON	NW	100	Soil										4.8																3.5			
10	MALLAIG	NW	100	Soil										4.6																4.5			4.1
11	GLNAFRIC	NW	300	Soil																				7.5	6.9	8.1	6.0	9.0	6.9	8.7	6.2	6.0	
12	PITM-M2	SE	100	Soil																													
13	PITM-M1	SE	100	Bog													7.7																
14	MONM-M1	SE	200	Peat															4.3														
15	MONM-M2	SE	200	Peat																													
16	ABEA-22	SE	300	Bog																17.1				5.7				3.7					
17	ABEC-21	SE	300	Bog																				5.1				3.7					
18	INSH-M1	SE	300	Peat																		5.2											
19	INSH-M2	SE	300	Soil																													
20	ABED-9	SE	300	Soil																													
21	CFG-13	SE	270	Soil																					6.4	4.8	5.1	6.4	5.5	5.4	4.3	7.4	4.6
22	CFF-11	SE	280	Soil																						5.4	5.4	7.4	7.7	5.8	4.7	7.0	3.9
23	CFE-9	SE	400	Soil																							9.1	10.9	7.5	8.0	8.3	8.9	6.6
24	CFD-11	SE	450	Soil																								11.4	9.1	5.9	6.0	7.2	5.1
25	CFA-15	SE	500	Soil																									15.8	9.3	7.9	10.1	4.7
26	CFB-10	SE	550	Soil																										6.4	7.1	8.2	4.1
27	GLNDERRY	SE	400	Soil																											12.6	13.4	4.5
28	INVEREY	SE	500	Soil																												11.9	
29	BALLOCHB	SE	380	Soil																													4.5
30	DRIMMIE	SE	200	Soil																													

Fig. 5. Cumulative plots of age trend series showing growth rates <1.0 mm·year^{-1} for Scots pine (*Pinus sylvestris*) on bog and >1.5 mm·year^{-1} for Scots pine on soil and peat. (See Fig. 3 for order numbers shown.)



level. A 10-month analysis period extending from January to October of the year of growth was selected. Residual tree-ring chronologies were used with monthly means of temperature and precipitation as predictors, as residual chronologies proved to yield more climatic information and minimized autocorrelation. Monthly temperature series for the Scottish Mainland (Jones and Lister 2004), together with the nearest climate station rainfall data at either Braemar, Edinburgh, Inverness, or Kinlochewe, were used in this analysis (Fig. 1). The short rainfall record for Kinlochewe was extended using data from Achnashellach (14 km to the south) and Portree (58 km to the west). Missing values and homogeneity of climate data were achieved using ANCLIM and PROCLIMDB software (methods as described in Štěpánek et al. 2009).

Results

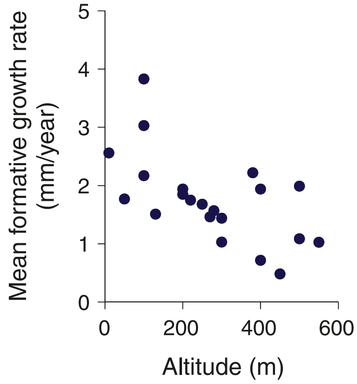
New Scots pine tree-ring chronologies were developed for five bog, three peat, and five soil substrate sites. Seventeen chronologies developed by earlier workers on soils were included to help contrast relationships between trees growing on different substrates (Figs. 1, 3). Sites are ordered consistently throughout this paper broadly from northwest (NW) to southeast (SE) areas, but with consideration to substrate and altitude.

Growth characteristics

Scots pine from new soil sites at Abernethy (D), Achanalt, Eilean Sùbhainn (C), Inshriach (B), and Pitmaduthy (B) have formative radial growth rates comparable with those from previous studies on this substrate (Figs. 3, 5). With the exception of pine at Glen Affric, which is the most exposed site sampled, with a DAMS of 22, pine on soil show formative growth rates of ≥1.5 mm·year^{-1} and an exponential decrease in ring width related to age. Pine from five bog substrate sites at Abernethy (A and C), Eilean Sùbhainn (A and B), and Pitmaduthy (A) show low formative radial growth rates of ≤1 mm·year^{-1} and a lack of age-related exponential decrease in ring width. Chronologies established from Scots pine on adjacent soil and bog sites at Abernethy, Eilean Sùbhainn, and Pitmaduthy contrast the low radial growth rates achieved on bog, which is attributed to the high water table and poor nutrient status, these factors being closely related (Larcher 1995). Scots pine from peat substrate sites at Inshriach (B) and Monadh Mor (A and B) have formative radial growth rates similar to those achieved by pine on soil sites. Growth rates achieved from pine on cutover peat at Inshriach (A) are even higher than those on the adjacent soil. A high water table is likely to account for the low radial growth of pine on bog. This suggests the radial growth of pine may be used to differentiate between moribund (inactive or non-peat-forming) peat and active bog. No exponential decrease in ring width related to age was seen in pine on the peat sites.

Excluding pine from bog sites, formative radial growth is found to be significantly lower at higher sites (Fig. 6). There are too few sites to make a clear comparison between the NW and SE areas. Nevertheless, comparing both areas, pine growing on soil in the NW show the highest formative radial growth rates (>2.56 mm·year^{-1}) at three sites under 100 m altitude and with low exposure (DAMS ≤ 14) and the lowest growth rates (<1.70 mm·year^{-1}) at two sites over 300 m and with high exposure (DAMS ≥ 20). In the more continental

Fig. 6. Scatterplot (r = –0.61).



SE area, a formative growth rate of 2.22 mm·year^{-1} at Ballochbuie highlights that reasonable growth rates are achievable at high-altitude (380 m) and high-exposure (DAMS = 19) sites in more southerly locations.

Chronologies

Cross matching of raw tree-ring chronologies shows that the highest similarities occur between geographically adjacent trees growing on the same substrate (Fig. 4). The higher cross-matching values tend to occur between higher elevation sites. This indicates that common growth forcing of environmental factors increases with altitude (i.e., tree growth at these sites becomes less complacent). Scots pine growing on active bog and soil in the NW cross match reasonably, but in the SE, cross matching is almost entirely absent. The two chronologies developed from pine growing on bog substrate at Eilann Sùbhainn and Abernethy cross match well within their respective sites, but there is no cross matching between the two sites or the pine on bog at Pitmaduthy Moss. The Pitmaduthy Moss chronology, however, does cross match (t = 7.7) with pine growing on peat some 30 km away at Monadh Mor.

Mean sensitivities range from 0.12–0.20, 0.16, and 0.19–0.23, respectively, at soil, peat, and bog substrate sites (Fig. 3). This shows that the relative change in ring widths from one year to the next (high-frequency signal) is higher for pine on bog. First-order autocorrelation, a measure of the influence of the previous year's growth on the current year (Fritts 1976), does not appear to be influenced by substrate. Values of EPS ≥ 0.85 suggested by Wigley et al. (1984) as being a sign of a reasonably strong climate signal are not met in all chronologies, which indicates that greater replication would be desirable for future analysis. Nevertheless, correlation analysis with climatic data shows that chronologies from Creag Fhiaclach with EPS values as low as 0.76 can achieve results consistent with chronologies with values greater than 0.85. Between-series correlation less than 0.35 reveals that there is considerable individual variability between the trees, and this is particularly evident in the chronologies developed from bog in the SE. The low-frequency growth patterns were characterized by relatively high variance at bog sites and considerably lower variance at peat and soil substrate sites (Fig. 7). Low-frequency growth patterns, particularly over decadal to bidecadal scale, are common between the bog chronologies developed at Eilann Sùbhainn and Abernethy but not between these and the other sites.

Water table level

Scots pine on bog show the lowest radial growth rates at Abernethy and the highest at Eilann Sùbhainn (Fig. 3). Decadal length variations at Pitmaduthy suggest that the site has been affected by changes in the level of the water table. One cause may have been peat cuttings that were visible at both bog and peats sites (with the exception of Eilann Sùbhainn) but were of unknown date. The chronology from Monadh Mor (A) (MONM-M1) has a formative growth rate of 1.85 mm·year^{-1}, which reduces to 0.94 mm·year^{-1} in the 1980s. This is likely to correspond to the water-table rise known to have occurred before the 1990s. The chronology from the soil site at Eilann Sùbhainn shows formative radial growth rates comparable with those of other pine on this substrate in the area, but a sudden reduction occurs from AD 1905.

Growth–climate relationships

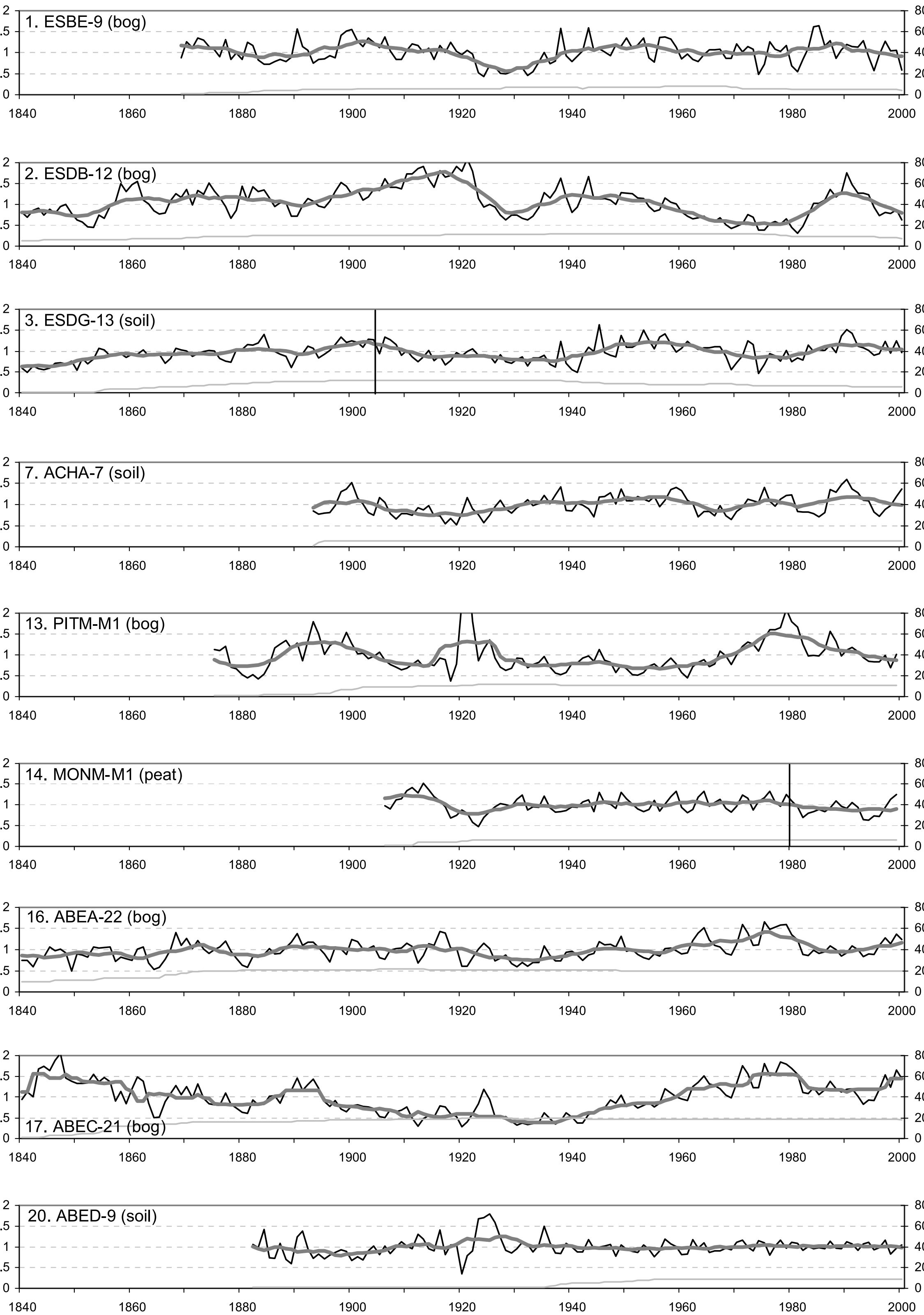
The temporal changes of dendroclimatic relationships were examined by means of moving interval correlation function analysis. The use of base lengths of 30, 40, 50, 60, 70, 80, and 90 years were compared (not shown), and an 80-year base length was selected. The strength of short-term relationships between tree-ring and climate data could often be increased by using shorter base lengths, but this was often at the loss of temporal stability, and the use of a longer base length precluded examination of the possible changes. Because of the differences between the date spans of the chronologies and changes in some relationships after the 1920s, an 80-year period between AD 1881 and AD 1960 was selected for common comparisons between the series. This common period was used except where the length of the tree-ring data necessitated a shorter period. Correlations between the ring width of pine from soil sites and climate data are summarized in Fig. 8. This shows that winter (January and February) and summer (July and August) temperatures are the most important determinants of ring width. These relationships are positive in both the NW and the SE but are stronger at the higher altitude sites in the SE. Negative correlation between ring width and August precipitation occurs only in the SE. In sharp contrast, all these relationships are absent from Scots pine growing on bog. Moreover, a positive correlation between ring width and October temperature occurs in pine on soils and bog in both the NW and the SE (and on the only peat site analysed in the SE), although this relationship is absent from all the soil sites above 270 m in the SE. Moving correlation functions (summarized only in Fig. 8) identify that at some sites, there is less correlation between tree-ring indices and October temperature from around the 1940s, but correlation with February temperature increases or develops from the 1920s (Fig. 9).

Discussion

Formative radial growth

Formative radial growth rates under 1.00 mm·year^{-1} are used here to distinguish between Scots pine probably growing on waterlogged bog and those growing on peats (Fig. 5).

Fig. 7. Standardized tree-ring indices. Thick grey line, 11-year running mean; vertical broken lines, fires; vertical solid line, probable water-logging. Lower lines indicate sample size over time (right *y* axis). ES, Eilann Sùbhainn; AB, Abernethy.



These figures are likely to be applicable to peatland sites ≤ 300 m, but the radial growth on soils can also fall below 1.00 mm·year^{-1} at sites ≥ 400 m as the tree line is approached. Such low radial growth rates in trees are indicative of stressful environmental conditions as ring widths ≤ 0.50 mm·year^{-1} are considered minimal in most tree species

Fig. 8. Summary of the significant correlation function elements shown for ring-width indices against monthly temperature and precipitation for the period 1881 to 1960 and over a moving interval range. The details of bog and peat sites are shaded. Only correlation coefficients significant at a level of $p < 0.05$ are shown (except where zeros are shown to enable the underlining of values to indicate significant correlation persistent over ≥50% of the range examined by moving interval analysis); bold values denote months also showing significant response coefficients. Correlation common interval is 1881–1960 (80 years) except for ACHA-07 (1894–1960), MALLAIG (1904–1960), MONM-M1 (1907–1960), and ABED-09 (1883–1960). Persistant signals = significant for 50% or greater of range. Correlation selected common interval is 1881–1960 (80 years) except for ACHA-07 (1894–1960), MALLAIG (1904–1960), MONM-M1 (1907–1960), and ABED-09 (1883–1960). Substrate: shaded, peat; no shading, mineral. Regions: NW, northwestern Scotland; SE, southeastern Scotland. Temperature data: SMT, Scottish Mainland Temperature. Rainfall data: KIN, Kinlochewe; INV, Inverness; BRA, Braemar; EDI, Edinburgh. JFM, January, February, and March; JJA, June, July, and August. Using residual chronologies developed from ARSTAN.

				Temperature												Precipitation										Changes in correlation with temperature		
Order	Pine chronology + brief description	Region and climate data	Moving interval range (window, in years)	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	JFM	JJA	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	1920s	1930s	1940s
1	ESBE-09 — Eilean Subhainn (50 m)	NW/SMT/KIN	1881-2002 (80)										0.17				0.28	0.22										> Oct.
2	ESDB-12 — Eilean Subhainn (50 m)	NW/SMT/KIN	1881-2002 (80)										0.21					0.24										
3	ESDG-13 — Eilean Subhainn (50 m)	NW/SMT/KIN	1881-2002 (80)										0.00			0.22		0.00					**0.23**				> Oct.	
4	LCKMAREE — Loch Maree (100 m)	NW/SMT/KIN	1881-1978 (70)	0.27					0.24	0.24	0.27		**0.31**	0.28	0.29											< Jan.		
5	BNAA-10 — Beinn Eighe (300 m)	NW/SMT/KIN	1881-1989 (80)	0.27	0.26				**0.23**				0.22	0.32												> June/Oct.		
6	COULIN — Coulin (250 m)	NW/SMT/KIN	1881-1978 (70)						0.27		0.27				0.23													
7	ACHA-07 — Acanalt (130 m)	NW/SMT/KIN	1894-2002 (80)				0.28			0.34	0.25		0.30		0.32													> Oct.
8	SHIELDAIG — Shieldaig (12 m)	NW/SMT/KIN	1881-1978 (70)	0.25	0.30	0.35							0.30	0.33	0.21	0.27	0.26	0.26										
9	PLOCKTON — Plockton (100 m)	NW/SMT/KIN	1881-1976 (70)															**0.23**										
10	MALLAIG — Mallaig (100 m)	NW/SMT/KIN	1904-1976 (50)																									
11	GLNAFRIC — Glen Affric (300 m)	NW/SMT/KIN	1881-1976 (70)	**0.42**	0.30									**0.43**				0.19								< Feb.		
13	PITMM-1 — Pitmaduthy (100 m)	SE/SMT/INV	1881-1994 (80)										0.00									**-0.19**					> Oct.	
14	MONMM-1 — Monadh Mor (200 m)	SE/SMT/INV	1907-1994 (70)				0.27				0.29	0.28	0.36		0.27							-0.24	-0.24					
16	ABEA-22 — Abernethy (300 m)	SE/SMT/BRA	1882-2000 (80)										0.00				0.19				0.00				0.00			> Oct.
17	ABEC-21 — Abernethy (300 m)	SE/SMT/BRA	1882-2000 (80)						-0.23				0.00								**0.23**				0.00	> Oct.	< June	
20	ABED-09— Abernethy (300 m)	SE/SMT/BRA	1882-2000 (80)	**0.37**	0.28									**0.37**										0.18				< Feb.
21	CFG-13 — Carrbridge (270 m)	SE/SMT/BRA	1881-1979 (80)		0.22							**0.30**								0.22								
22	CFF-11 — Creag Fhiaclach (280 m)	SE/SMT/BRA	1881-1979 (80)	**0.35**	**0.36**	0.25					0.20			**0.43**							0.26		-0.30					
23	CFE-09 — Creag Fhiaclach (400 m)	SE/SMT/BRA	1881-1979 (80)	**0.35**	0.25	0.21	0.21			**0.41**	0.26			**0.37**	**0.38**				0.22			-0.21	-0.28			< Feb.		
24	CFD-11 — Creag Fhiaclach (450 m)	SE/SMT/BRA	1881-1979 (80)	**0.33**	**0.27**					0.27				**0.37**	0.21				0.21				-0.24				< Jan./Feb.	
25	CFA-15 — Creag Fhiaclach (500 m)	SE/SMT/BRA	1881-1979 (80)	**0.33**	0.25					0.24	0.19			**0.36**	0.24							-0.25	-0.23				< Jan./Feb./July	
26	CFB-10 — Creag Fhiaclach (550 m)	SE/SMT/BRA	1881-1979 (80)	**0.37**	0.27									**0.38**									-0.24			< Feb.		
27	GLENDERRY—Glen Derry (400 m)	SE/SMT/BRA	1881-1978 (70)		0.23		0.18			0.26	**0.37**			**0.26**	0.37								**-0.20**					
28	INVEREY — Inverey (500 m)	SE/SMT/BRA	1881-1976 (70)					**0.21**		**0.22**	0.30				0.28													
29	BALLOCHB — Ballochbuite (380 m)	SE/SMT/BRA	1881-1978 (70)		**0.30**	0.28				0.21	0.19			**0.28**	0.22			-0.23					-0.23			< Mar.		
30	DRIMMIE — Dimmie (200 m)	SE/SMT/EDI	1881-1976 (70)	0.31	**0.45**	0.30							0.27	**0.46**													< Jan.	

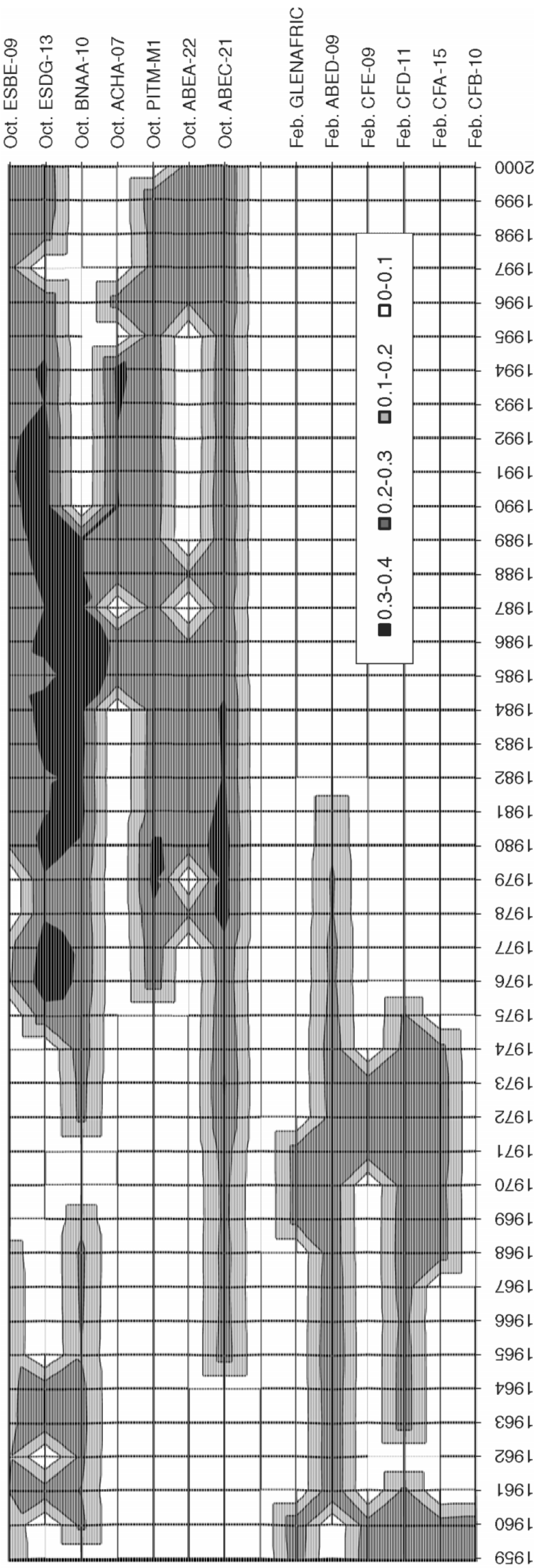


Fig. 9. Contour map showing decreasing February and increasing October temperature correlation values against ring-width indices, using a moving 80-year base length. Only the last years of the interval for coefficients significant at a level of $p < 0.05$ are shown. Note that the range only extends to 1979 for the Creag Fhiaclach data (CFA-15, CFB-10, CFD-11, and CFE-09).

(White 1998). Cores taken from Scots pine growing on blanket bog in Strathnaver Forest have been found to have, on average, two missing rings between AD 1952 and AD 2005 (A.K. Moir, unpublished). Narrow and missing rings indicate that Scots pine on bog in northern Scotland survives within a narrow ecological margin. The absence of the gradual reduction in ring width normally associated with age is suggested to be the result of these marginal conditions for growth, although few of the trees in this analysis were over 150 years of age, which is the age at which growth slowed in Scots pine on bog in Sweden (Ågren and Zackrisson 1990). A similar absence of age trend has been found in subfossil pine from Scotland (Moir et al. 2010).

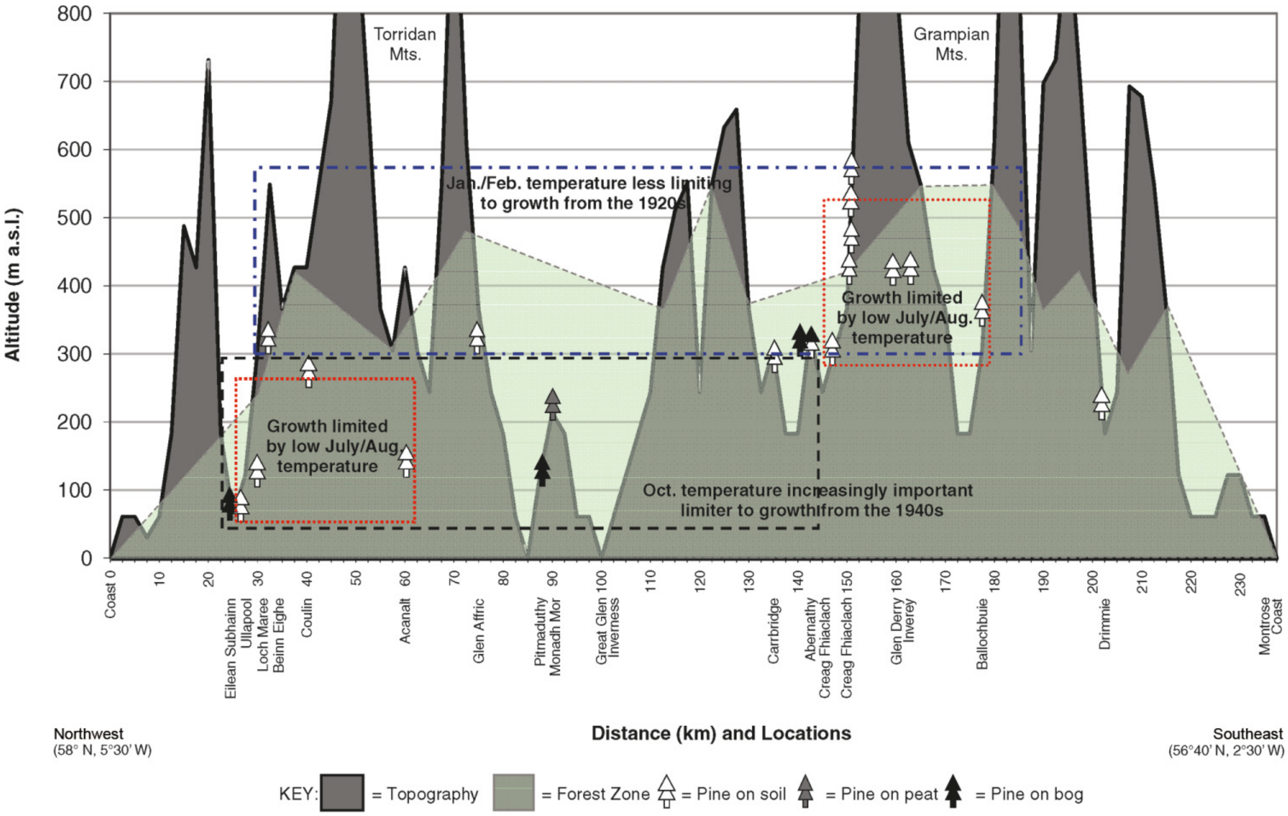
Climate–growth response in summer

As might be expected, the summer radial growth of pine on soils is correlated with temperature mainly in July and August, although this extends to June at three sites in the NW (Fig. 8). Warm summer months lead to increased radial growth, indicating that neither temperature nor moisture limit tree growth. Pines on soil show increases in both cross matches between chronologies and correlations with July–August temperature associated with sites at 57°N and ≥300 m altitude, which is in accord with earlier studies that found radial growth near the tree line to be limited by low summer temperature (Schweingruber et al. 1979; Hughes 1987). The weaker response shown with summer temperature in pine under ~300 m (Figs. 8, 10) is likely to be due to the sites being beneath the tree line, where growth is less limited because temperatures are higher, and therefore correlations with these months are expected to diminish (Fritts 1976). The radial growth of Scots pine on soil in the SE is inversely influenced by August precipitation. Both the lack of correlation between August temperature and rainfall ($r = 0.049$) and significant response coefficients displayed at some sites (Fig. 8) suggest that this relationship is not an artefact of an inverse relationship between the climate data. In cool humid regions where precipitation is greater than 1000 mm·year^{-1}, rainfall is unlikely to limit the growth of Scots pine on normally drained sites (Tranquillini 1979). The association between low rainfall in August and increased radial growth is therefore likely to be an indirect effect, where low rainfall corresponds with increased sunshine and therefore enhanced photosynthesis (Fritts 1976). August is an important month for pine because the current year's foliage is in full activity and has its maximum potential for assimilation (Linder and Flower-Ellis 1992). Near the tree line, Scots pine has a short growing season, and in this environment, low temperature and (or) low sunshine in August become a significant limiting factor of radial growth. Correlations between summer temperature and radial growth extend to June at three sites in the NW, indicating a longer growth season in this more oceanic area. Summer temperature was not found to be a limiting factor of the radial growth of pine on bog, but because the sites were at 300 m altitude or less (Fig. 10), this might be expected.

Climate–growth response in autumn

Temperature in October is newly shown here to be correlated with the radial growth of pine growing on bog, peat, and soil substrate. This positive relationship is attributed

Fig. 10. A summary of significant and positive temperature restrictions on the radial growth of Scots pine (*Pinus sylvestris*) on a northwest–southeast transect of northern Scotland. Topography and forest line (based on upper limits of woods) taken from 1 : 2 500 000 scale ordnance survey in 1999. July and August, summer; January and February, winter; October, longer growth season; forest zone, land capable of supporting commercial forestry. The bottom of each pine tree symbol represents the height of the site. The sites shown are within 30 km of the transect, except Coulin and Glen Affric, which are 35 and 50 km to the southwest, respectively.



here to a temperate maritime climate potentially extending the season of cambial growth, which is consistent with the absence of relationship from higher altitude sites, both in the NW and SE. From the 1930s to the 1940s, this correlation develops on bog sites $\leq$ 300 m in the SE and becomes increasingly significant at bog and soil sites $\leq$ 300 m in the NW (Fig. 8). The increased correlation between tree growth and temperature (Fig. 9) corresponds well with the known 1 °C increase of temperature in Scotland, which has caused a four-week increase in the length of the growing season and a more than 25% reduction in the number of days of frost between AD 1961 and AD 2004 (Barnett et al. 2006). Earlier research shows that the temperate maritime climate of northwestern Scotland can promote a relatively long June to October period of cambial growth in pine on soil (Schweingruber et al. 1979; Hughes 1987). In late autumn, exposure to nighttime low temperatures below 0 °C may limit radial growth by causing damage to photosystems, which can lower rates of photosynthesis for several days (Öquist and Huner 1991). A lack of correlation between radial growth and September temperature may be explained by the lack of frost days able to act as a limiting factor in this month (Fig. 2). The increasing correlation between radial growth and October temperature may not have been identified in more recent dendroclimatic studies because the monthly window of analysis typically only extends to August or September of the current year.

Climate–growth response in winter

Temperature in January and February is shown to be an important determinant of the radial growth of pine on soil in Scotland (Fig. 8). Correlations are good at high-altitude sites, but stronger and clearer at $\leq$300 m altitude sites (Fig. 10), where radial growth is not also limited by summer temperature. Correlation with these months at lower altitude sites (Shieldaig and Drimmie) suggests that this relationship is not restricted to proximity to the tree line. Although previous workers have typically selected sites near the tree line to investigate the correlations between summer temperature and ring width, correlations with winter temperature have been shown (Tuovinen 2005; Helama et al. 2005). Similarly to this study, Helama et al. (2005) find positive dendroclimatic correlation in high-latitude sites for Scots pine, with decreasing correlativity towards the south (i.e., toward a milder and warmer climate).

The physiological mechanism between the radial growth of Scots pine and winter temperature remains unclear. Grace (1990) shows that cuticular transpiration is unlikely to cause frost drought. Instead, Grace and Norton (1990) attribute the conspicuous winter browning of Scots pines needles observed at the tree line to mechanical abrasion from wind and wind-born particles disrupting the epidermis. Because buds in Scots pine form the previous season (Kozlowski et al. 1991) and old needles substantially contribute to photosynthesis (Linder and Troeng 1980), winter wind damage could reduce the potential biomass production throughout the subsequent growing season. Furthermore, gales in Scotland are especially common in January and February. However, root hardening is less than that of needles or shoots (Sutinen et al. 1996), and root injuries by low winter temperatures could also be a cause. Havranek (1972) showed strong linear correlation between low root zone temperature and growth. The sharp contrast shown here of a strong positive correlation between winter temperature and pine on soil and its absence in Scots pine on peat and adjacent bog sites suggest differences between the root zone temperatures. It is hypothesized that roots in bogs are less susceptible to cold damage. Few studies have investigated the penetration depth of frost in peat soils. Rossi et al. (2007) found similar air temperature thresholds for xylogenesis between high-altitude conifer sites but different soil temperature thresholds, although they do not attempt to explain the differences by soil types. Furthermore, by reducing soil heat flux, a closed forest canopy has a negative affect on its root zone temperature and creates cold soils that impair root activity (Ballard 1972). As the tree canopy is usually denser on surrounding soils than on bog, additional differences in the root zone temperature between the two substrates may occur. Trees on peat and bog may also be more sheltered by their low-lying location and (or) taller and denser tree cover on surrounding soils, making them less susceptible to damage from wind but more susceptible to frost.

Climate–growth response on peatland

The influence of climate on Scots pine growing on peat is only briefly discussed because only the Monadh Mor chronology was of sufficient length to perform correlation analysis. Scots pine at Monadh Mor show correlations with temperature and precipitation in summer and autumn that are similar to those seen in pine on soil. This is in accord with Linderholm (1999), who found that drainage of bog alters the growth response of pine to climate to resemble those on soil. Pine on cutover peat at Inshriach cross match well (t = 5.2) with neighbouring pine growing on soil, but perhaps due to disturbances such as fire and or peat cutting, the chronologies do not cross match with other pine chronologies from soil in the region. Where tree-ring series from numerous trees within a well-defined ecological area cross date, they attest to a common annual climatic signal. However, a weakness of this study is that a number of the chronologies developed have relatively weak signal strength (nonoptimal EPS, Fig. 3). The possible effects to the growth–climate response due to the low level at which some cores were taken (i.e., below 1.3 m) have not been assessed, but tree rings from subfossil stumps have previously been used to extend temperature reconstructions. Large sample sizes from peatlands are recommended to help improve the signal strength and therefore the correlations with climate.

Changes in water levels

The climate correlations shown here demonstrate that temperature in specific months is an important determinant of annual variation in the radial growth of Scots pine on soil and peat in northern Scotland. We show that although monthly levels of precipitation rarely correlate with annual ring width, waterlogging is probably the primary restriction on the radial growth of pine on bog. Charman (2007) found that changes in bog water table level had a linear response to annual rainfall deficit over the previous 5–10 years. The growth rates of pine on bog are shown here to be susceptible to decadal-scale fluctuations (Fig. 7) that are likely to correspond to changes in water table level. The failure of regional cross matching between the well-replicated bog pine chronologies developed at Eilann Sùbhainn and Abernethy may be caused by variations in water level, although climate differences cannot be entirely discounted despite the short 135 km distance between the sites. Scots pine chronologies from bog are shown here to have limited use in dendroclimatic reconstructions of monthly temperature due to a weaker climate–growth response than pine growing on mineral substrate and soil. The weaker climate–growth response is in agreement with a previous regional study on pine in Sweden (Linderholm et al. 2002), but this study made no differentiation between possible (inactive) peat and (active) bog sites. Our results highlight that the radial growth rates of pine on peatlands are potentially sensitive to a lowering of the water table and that climate–growth response may increase when the water table is lowered.

Other disturbances in a variety of forms (not always known) may influence these results. Although the pine growing on soil at Eilann Sùbhainn were not waterlogged at the time of sampling, it is the only chronology to show a sudden and sustained change of growth rate (Fig. 5), and the site is on the shore of Loch Maree, which the Scottish Natural Heritage states is subject to dramatic fluctuations in water levels (Fig. 11). Flooding of a tree can be harmful, especially during the growing season, due to the high oxygen requirement of actively growing roots (Kozlowski 1982). The sustained reduction in the radial growth of pine at this site after AD 1905 together with growth reduction (in the space of a couple of years) affecting pine progressively further from the shoreline indicate that they may be attributable to rises in loch level. The correlation relationship between these pine trees and temperature also resembles that of bog pine (Fig. 8), which suggests that pine on soil can develop responses to climate similar to those on bog when affected by flooding.

Climatic change at the tree line

In northern Scotland, the positive correlation shown here between radial growth and summer (July and August) temperature is consistent with the view that summer temperature limits the radial growth of pine near the tree line in northern Scotland. Assuming a lapse rate of 0.6 °C per 100 m of altitude, where tree line is limited by summer temperature, pine would be expected to vertically advance by about 200 m per degree. Pine found at altitudes greater than 800 m near Aviemore (French et al. 1997) corroborate such an increase in tree line. This is consistent with a 200 m increase in tree line (particularly evident in wind-sheltered and steep concave slopes) in Sweden, concomitant with a 1.4 °C increase in temperature (Kullman and Öberg 2009). Correlation between summer temperature and radial growth occurs in pine at 300–500 m altitude in the SE and at 50–250 m altitude in the NW (Fig. 10). This suggests a ~200 m wide altitudinal window of temperature correlation that lowers to the west and is concomitant with the known lowering of the tree line from SE to NW, although additional sites would be required to help confirm this relationship. The lowering of the tree line be-

Fig. 11. Waterlogged Scots pine (*Pinus sylvestris*) trees on the shore of Loch Maree. (Photo by John Allen.)

tween the SE and NW areas is unlikely to be accounted for by the 75 m altitude decrease expected by the 1° difference in latitude between the areas (Körner 1998). Pines on the coast in the NW show the highest and lowest formative radial growth rates over a 300 m difference of altitude. This contrast is difficult to attribute to variation in summer temperature and therefore is expected to be related to the influence of winter temperature, which is shown here to be an important limiter of radial growth.

Moving response analysis shows no significant change in the radial response of pine to summer temperature, indicating that the region is not affected by divergence (D'Arrigo et al. 2008). Similar findings were evident for high-latitude pines in Finland where radial growth was shown to have reacted positively to summer temperatures over the past three centuries (Helama et al. 2004). However, the correlation between February temperature and radial growth is shown to be reduced at sites above 300 m altitude since the 1920s. Correlations with October temperature at both soil and bog sites in both the NW and SW areas have also changed and show an increased influence on growth at soil sites ≤ 300 m in the NW since the 1940s. These changes are concomitant with warmer winters and increases in the length of the growing season, which are maximal at coastal areas and minimal in mountainous areas (Barnett et al. 2006). Our study suggests that the radial growth of pine at the tree line in northern Scotland is responding to changes in winter temperature rather than summer temperature but that there is little evidence for overall increases in radial growth rates.

Future research

Although the physiological mechanism between radial growth and winter temperature remains unknown, root damage and (or) wind exposure are suggested as two possible causes — the latter of which has been identified as a control on tree line in an earlier study (Hale et al. 1998). Körner (1998) emphasises the unknown effects of root zone temperature on tree growth but recognises that they could be critical to the tree line. Further research on the relationships between radial growth with other meteorological data such as wind speed, grass minimum or soil temperatures, and NAO is suggested to help clarify the physiological mechanisms between winter temperature and radial growth in pine and to help understand their effects on levels of tree line. Although not examined here, other studies have found correlations between earlywood (Tuovinen 2005) and latewood (Schmitt et al. 2004) ring measurements, which also indicates the potential to help differentiate between the response of tree rings to winter and summer temperature.

The growth–climate relationships examined in this study are likely to be complicated by co-varying environmental factors. A trend of higher temperature increasing tree growth and raising tree line is likely to be opposed by increases in precipitation and wind. Barnett et al. (2006) show that between AD 1914 and AD 2004, it has become 20% wetter, while a 1.0 °C temperature increase since the 1960s is unevenly spread, extending the length of growing season by two months in coastal areas, but reducing it by up to eight days in a few upland areas. Furthermore, the NAO (a measure of pressure differences between Iceland and the Azores) has strengthened particularly in the winter (Hurrell 1995), and this is not only likely to directly affect tree growth through exposure to stronger westerly winds, but also to cause variations in winter temperature and rainfall. Today spontaneous oceanic Scots pine forests are only distributed in Scotland and western Norway (Øyen 1998), and the pattern of upper forest line between the two countries is very similar. As Linderholm et al. (2003) find strong connections between radial growth of Scots pine in winter and NAO on the western coast of Norway, similar potential from pine in

Scotland might be expected and is indicated by the use of Scottish tree-ring data in the reconstruction of a winter NAO index (Cook et al. 2002).

Chronologies from earlier studies (see Fig. 3) end in the 1970s, preventing comparisons with the last 30 years of climate data. Some resampling of earlier sites is now underway (Fish et al. 2010), and this should help extend comparisons with climate data to present day. The establishment of additional soil sites particularly at altitudes >300 m in the NW and <300 m in the SE might also be considered worthwhile to help clarify and predict the possible effects of temperature change on radial growth rates near the tree line in northern Scotland.

Analysis of Scots pine from a peatland site of known drainage history and a comparison of the Eilean Sùbhainn pine with loch level are currently underway. Apart from changes in water table levels, substrate, and the altitudinal differences of the sites, we cannot rule out that some of the dendroclimatic differences originate from the high genetic diversity of the pines (Wachowiak et al. 2010). This also remains as an interesting future prospect to be tested.

Conclusions

Although Scots pine chronologies from bog are shown here to have limited use in dendroclimatic reconstructions of monthly temperature due to a weaker climate–growth response, the annual radial growth rates of pine on peatlands are hypothesized to correspond with water table level and may provide an important indicator of water levels in peat and bog.

Temperature in January–February and July–August are both important determinants of the radial growth of Scots pine on soil sites in northern Scotland. Root damage and (or) wind damage are suggested as potential mechanisms for the relationship between ring width and winter temperature.

Moving correlation analysis indicates that the relationship between the radial growth of pine near the altitudinal tree line and summer temperature (July–August) is time stable, despite an increase of temperature in northern Scotland. However, the radial growth of pine has become less limited by winter (January–February) temperatures since the 1920s. Scots pine at soil, bog, and peat sites have developed or increased their correlation with October temperature since the 1940s (Fig. 9). This suggests that the growing season of pine has extended, particularly in the commercial zone of forestry on the western coast.

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References

Ågren, J., and Zackrisson, O. 1990. Age and size structure of *Pinus sylvestris* populations on mires in central and northern Sweden. J. Ecol. **78**(4): 1049–1062. doi:10.2307/2260951.

Baillie, M.G.L., and Pilcher, J.R. 1973. A simple cross-dating program for tree-ring research. Tree-Ring Bull. **33**: 7–14.

Ballard, T.M. 1972. Subalpine soil temperature regimes in southwestern British Columbia. Arct. Alp. Res. **4**(2): 139–146. doi:10.2307/1550397.

Barber, K.E., Zolitschka, B., Tarasov, P., and Lotter, A.F. 2004. Atlantic to Urals — the Holocene climatic records of mid-latitude Europe. *In* Past climate variability through Europe and Africa. Vol. 6. Developments in paleoenvironmental research. *Edited by* R.W. Battarbee, F. Gasse, and C.E. Stickley. Springer, Berlin.

Barnett, C., Hossell, J., Perry, M., Procter, C., and Hughes, G. 2006. A handbook of climate trends across Scotland. Scotland and Northern Ireland Forum for Environmental Research, SNIFFER Project CC03. pp. 1–62.

Biondi, F., and Waikul, K. 2004. Dendroclime2002: a C++ program for statistical calibration of climate signals in tree-ring chronologies. Comput. Geosci. **30**(3): 303–311. doi:10.1016/j.cageo.2003.11.004.

Birks, H.H. 1975. Studies in the vegetational history of Scotland. IV. Pine stumps in Scottish blanket peats. Philos. Trans. R. Soc. Lond. **270**(905): 181–226. doi:10.1098/rstb.1975.0007.

Birse, E.L. 1971. Assessment of climatic conditions in Scotland. 3. The bioclimatic sub-regions. The Macaulay Institute for Soil Research, Aberdeen.

Blasing, T.J., Solomon, A.M., and Duvick, D.N. 1984. Response functions revisited. Tree-Ring Bull. **44**: 1–15.

Briffa, K.R., Osborn, T.J., and Schweingruber, F.H. 2004. Large-scale temperature inferences from tree-rings: a review. Global Planet. Change, **40**(1–2): 11–26. doi:10.1016/S0921-8181(03)00095-X.

Charman, D.J. 2007. Water deficit variability controls on peatland water-table changes: implications for Holocene palaeoclimate reconstructions. Holocene, **17**(2): 217–227. doi:10.1177/0959683607075836.

Cook, E.R., Briffa, K.R., Shiyatov, S.G., and Mazepa, V. 1990. Tree-ring standardization and growth-trend estimation. *In* Methods of dendrochronology: applications in the environmental science. *Edited by* E.R. Cook and L.A. Kairiukstis. Kluwer Academic Publishers, Dordrecht.

Cook, E.R., D'Arrigo, R.D., and Mann, M.E. 2002. A well-verified, multiproxy reconstruction of the winter North Atlantic Oscillation Index since A.D. 1400. J. Clim. **15**(13): 1754–1764. doi:10.1175/1520-0442(2002)015<1754:AWVMRO>2.0.CO;2.

D'Arrigo, R.D., Wilson, R., Liepert, B., and Cherubini, P. 2008. On the 'divergence problem' in northern forests: a review of the tree-ring evidence and possible causes. Global Planet. Change, **60**(3–4): 289–305. doi:10.1016/j.gloplacha.2007.03.004.

Ellenberg, H. 1988. Vegetation ecology of Central Europe. Cambridge University Press, Cambridge, UK.

Ennos, R.A. 1991. Genetic variation in Caledonian pine populations: origins, exploitation and conservation. *In* Genetic variation in European populations of forest trees. *Edited by* G. Muller-Starch and M. Ziehe. Sauerlander's Verlag, Frankfurt. pp. 235–249.

Eronen, M., Zetterberg, P., Briffa, K.R., Lindholm, H.W., Meriläinen, J., and Timonen, M. 2002. The supra-long Scots pine tree-ring record for Finnish Lapland: Part 1, chronology construction and initial references. Holocene, **12**(6): 673–680. doi:10.1191/0959683602hl580rp.

Fish, T., Wilson, R., Edwards, C., Mills, C., Crone, A., Kirchhefer, A. J., Linderholm, L., Loader, N.J., and Woodley, E. 2010. Exploring for senescence signals in native Scots pine (*Pinus sylvestris* L.) in the Scottish Highlands. For. Ecol. Manage. **260**(3): 321–330. doi:10.1016/j.foreco.2010.04.017.

Freléchoux, F., Buttler, A., Schweingruber, F.H., and Gobat, J.-M. 2000. Stand structure, invasion and growth dynamics of bog pine (*Pinus uncinata* var. *rotundata*) in relation to peat cutting and drainage in the Jura Mountains, Switzerland. Can. J. For. Res. **30** (7): 1114–1126. doi:10.1139/cjfr-30-7-1114.

French, D.D., Miller, G.R., and Cummins, R.P. 1997. Recent development of high-altitude *Pinus sylvestris* scrub in the northern Cairngorm Mountains, Scotland. Biol. Conserv. **79**(2–3): 133–144. doi:10.1016/S0006-3207(96)00104-8.

Fritts, H.C. 1976. Tree rings and climate. Academic Press, New York.

Grace, J. 1990. Cuticular water loss unlikely to explain tree line in Scotland. Oecologia (Berl.), **84**(1): 64–68. doi:10.1007/BF00665596.

Grace, J., and 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**(3): 601–610. doi:10.2307/2260887.

Hale, S.E., Quine, C.P., and Suárez, J.C. 1998. Climatic conditions associated with treelines of Scots pine and birch in Highland Scotland. Scottish Forestry, **52**(2): 70–76.

Havranek, W. 1972. Über die Bedeutung der Bodentemperatur für die Photosynthese und Transpiration junger Forstpflanzen und für die Stoffproduktion an der Waldgrenze. Angewandte Botanik, **46**: 101–116.

Helama, S., Holopainen, J., Timonen, M., Ogurtsov, M.G., Lindholm, M., Meriläinen, J., and Eronen, M. 2004. Comparison of living-tree and subfossil ringwidths with summer temperatures from 18th, 19th and 20th centuries in northern Finland. Dendrochronologia, **21**(3): 147–154. doi:10.1078/1125.7865.00049.

Helama, S., Lindholm, M., Meriläinen, J., Timonen, M., and Eronen, M. 2005. Multicentennial ring-width chronologies of Scots pine along north–south gradient across Finland. Tree-Ring Res. **61**(1): 21–32. doi:10.3959/1536-1098-61.1.21.

Hughes, M.K. 1987. Dendroclimatology of *Pinus sylvestris* L. in the Scottish Highlands. *In* Applications of tree-ring studies: current research in dendrochronology and related subjects. *Edited by* R.G.W. Ward. BAR International Series 333.

Hurrell, J.W. 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. Science (Washington, D.C.), **269**(5224): 676–679. doi:10.1126/science.269.5224.676. PMID:17758812.

Intergovernmental Panel on Climate Change. 2007. Climate Change 2007: the physical scientific basis. Cambridge University Press, Cambridge, UK.

Jones, P.D., and Lister, D. 2004. The development of monthly temperature series for Scotland and Northern Ireland. Int. J. Climatol. **24**(5): 569–590. doi:10.1002/joc.1017.

Jones, P.D., Briffa, K.R., Osborn, T.J., Lough, J.M., van Ommen, T. D., Vinther, B.M., Luterbacher, J., Wahl, E.R., Zwiers, F.W., Mann, M.E., Schmidt, G.A., Ammann, C.M., Buckley, B.M., Cobb, K.M., Esper, J., Goosse, H., Graham, N., Jansen, E., Kiefer, T., Kull, C., Küttel, M., Mosley-Thompson, E., Overpeck, J.T., Riedwyl, N., Schulz, M., Tudhope, A.W., Villalba, R., Wanner, H., Wolff, E., and Xoplaki, E. 2009. High-resolution palaeoclimatology of the last millennium: a review of current status and future prospects. Holocene, **19**(1): 3–49. doi:10.1177/0959683608098952.

Körner, C. 1998. A re-assessment of high elevation treeline positions and their explanation. Oecologia (Berl.), **115**(4): 445–459. doi:10.1007/s004420050540.

Kozlowski, T.T. 1982. Water supply and tree growth. Part II. Flooding. Forestery Abstracts, **43**(3): 145–161.

Kozlowski, T.T., Kramer, P.J., and Pallardy, S.G. 1991. The physiological ecology of woody plants. Academic Press, San Diego, California.

Kullman, L., and Öberg, L. 2009. Post-Little Ice Age tree line rise and climate warming in the Swedish Scandes: a landscape ecological perspective. J. Ecol. **97**(3): 415–429. doi:10.1111/j.1365-2745.2009.01488.x.

Larcher, W. 1995. Physiological plant ecology. Ecophysiology and stress physiology of functional groups. Springer, Berlin, Heidelberg, New York.

Legg, C.J., McHaffie, H., Amphlett, A., and Worrell, R. 2003. The status of wooded bogs at Abernethy, Strathspey. *In* Restoring natural forest habitats. Highland Birchwoods, Munlochy. pp. 12–16.

Linder, S., and Flower-Ellis, J. 1992. Environmental and physiological constraints to forest yield. *In* Responses of the forest ecosystems to environmental ehanges. *Edited by* A. Teller, P. Mathy, and J.N.R. Jeffers. Elsevier Applied Science, London. pp. 149–164.

Linder, S., and Troeng, E. 1980. Photosynthesis and transpiration of 20-year-old Scots pine. Ecol. Bull. (Stockholm), **32**: 153–163.

Linderholm, H.W., 1999. Climatic and anthropogenic influences in radial growth of Scots pine at Hanvedsmossen, a raised peat bog, in south central Sweden. Geografiska Annaler Ser. A, **81**(1) 75–86.

Linderholm, H.W., Moberg, A., and Grudd, H. 2002. Peatland pine as climate indicators? A regional comparison of the climate influence on Scots pine growth in Sweden. Can. J. For. Res. **32**(8): 1400–1410. doi:10.1139/x02-071.

Linderholm, H.W., Solberg, B.Ø., and Lindholm, M. 2003. Tree-ring records from central Fennoscandia: the relationship between tree growth and climate along a west–east transect. Holocene, **13**(6): 887–895. doi:10.1191/0959683603hl671rp.

MacKenzie, N.A., and Worrell, R. 1995. A preliminary assessment of the ecology and status of ombrotrophic wooded bogs in Scotland. Scottish Natural Heritage Report No. 40.

Mannerkoski, H. 1985. Effect of water table fluctuation on the ecology of peat soil. Publ. 7, Department of Peatland Forestry, University of Helsinki, Helsinki, Finland.

Mannerkoski, H. 1991. Relation between tree roots and soil aeration on drained peatlands. *In* Peat and peatlands — diversification and innovation. *Edited by* J.K. Jeglum and R.P. Overend. Canadian Society for Peat and Peatlands, Quebec. pp. 109–114.

Miller, G.R., and Cummins, R.P. 1982. Regeneration of Scots pine *Pinus sylvestris* at a natural tree-line in the Cairngorm Mountains, Scotland. Holarct. Ecol. **5**: 27–34.

Moir, A.K., Leroy, S.A.G., Brown, D.M., and Collins, P.E.F. 2010. Dendrochronological evidence for a lower water table on peatland around 3200–3000 BC from sub-fossil pine in northern Scotland. Holocene, **20**(6): 931–942. doi:10.1177/0959683610365935.

Moore, P.D. 1984. The classification of mires: an introduction. *In* European mires. *Edited by* P.D. Moore. Academic Press, London. pp. 1–10.

Öquist, G., and Huner, N.P.A. 1991. Effects of cold acclimatation on the susceptibility of photosythesis to photoinhibition in Scots pine and in winter and spring cereals: a fluorescence analysis. Funct. Ecol. **5**(1): 91–100. doi:10.2307/2389559.

Øyen, B.-H. 1998. Scots pine forest in western Norway and some affinities with Scots pine forests in Scotland. Blyttia, **56**: 108–119.

Paavilainen, E., and Päivänen, J. 1995. Peatland forestry — ecology and principles. Ecological Studies, Springer-Verlag, Berlin. pp. 1–248.

Parker, J. 1985. The hazards of Scotland's climate. *In* Proceedings of the Joint Royal Scottish Geographical Society and Royal Meteorological Society Symposium, University of Stirling, June 1984: Climatic Hazards in Scotland. *Edited by* S.J. Harrison. Geo Books, Norwich, UK. pp. 9–14.

Pilcher, J.R., Baillie, M.G.L., Brown, D.M., McCormac, F.G., MacSweeney, P.B., and McLawrence, A.S. 1995. Dendrochronology of subfossil pine in the north of Ireland. J. Ecol. **83**(4): 665–671. doi:10.2307/2261634.

Quine, C.P., and White, I.M.S. 1994. Using the relationship between rate of tatter and topographic variables to predict site windiness in upland Britain. Forestry, **67**(3): 245–256. doi:10.1093/forestry/67.3.245.

Ray, D. 2008. Impacts of climate change on forestry in Scotland — a synopsis of spatial modelling research. Forestry Commission Scotland, Research Note 101.

Rossi, S., Deslauriers, A., Anfodillo, T., and Carraro, V. 2007. Evidence of threshold temperatures for xylogenesis in coniferes at high altitudes. Oecologia (Berl.), **152**(1): 1–12. doi:10.1007/s00442-006-0625-7.

Schmitt, U., Jalkanen, R., and Eckstein, D. 2004. Cambium dynamics of *Pinus sylvestris* and *Betula* spp. in the northern boreal forest of Finland. Silva Fenn. **38**(2): 167–178.

Schweingruber, F.H., Bräker, O.U., and Schär, E. 1979. Dendroclimatic studies on conifers from central Europe and Great Britain. Boreas, **8**(4): 427–452. doi:10.1111/j.1502-3885.1979.tb00438.x.

Štěpánek, P., Zahradníček, P., and Skalák, P. 2009. Data quality control and homogenization of air temperature and precipitation series in the area of the Czech Republic in the period 1961–2007. Adv. Sci. Res. **3**: 23–26. doi:10.5194/asr-3-23-2009.

Stokes, M.A., and Smiley, T.L. 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago and London.

Sutinen, M.-L., Mäkitalo, K., and Sutinen, R. 1996. Freezing dehydration damages roots of containerized Scots pine (*Pinus sylvestris*) seedlings overwintering under subarctic conditions. Can. J. For. Res. **26**(9): 1602–1609. doi:10.1139/x26-180.

Tipping, R., Ashmore, P., Davies, A., Haggart, B.A., Moir, A.K., Newton, A., Sands, R., Skinner, T., and Tisdall, E.W. 2007. Peat, pine stumps and people: interactions behind climate, vegetation change and human activity in wetland archaeology at Loch Farlary, northern Scotland. *In* Archaeology from the wetlands: recent perspectives. *Edited by* J. Barber, C. Clark, M. Cressey, A. Crone, A. Hale, J. Henderson, R. Housley, R. Sands, and A. Sheridan. Society of Antiquaries of Scotland, Edinburgh, WARP Occasional Paper 18. pp. 157–164.

Tranquillini, W. 1979. Physiological ecology of the alpine treeline. Springer, Berlin.

Tuovinen, M. 2005. Response of tree-ring width and density of *Pinus sylvestris* to climate beyond the continuous northern forest line in Finland. Dendrochronologia, **22**(2): 83–91. doi:10.1016/j.dendro.2005.02.001.

Vaganov, E.A., and Kachaev, A.V. 1992. Dendroclimatic analysis of the growth of pine in forest–bog phytocenoses of Tomsk Oblast. Lesovedenie, **6**: 3–10.

Villalba, R., and Veblen, T.T. 1997. Determination of total tree ages using increment core samples. Ecoscience, **4**: 534–542.

Wachowiak, W., Salmela, M.J., Ennos, R.A., Iason, G., and Cavers, S. 2010. High genetic diversity at the extreme range edge: nucleotide variation at nuclear loci in Scots pine (*Pinus sylvestris* L.) in Scotland. Heredity. doi:10.1038/hdy.2010.118. PMID: 20823905.

Watson, A. 1996. Internationally important environmental features of the Cairngorms, research, and the main research needs. Bot. J. Scotl. **48**(1): 1–12. doi:10.1080/03746609609480370.

White, J.E.J. 1998. Estimating the age of large and veteran trees in Britain. Forestry Commission Information Note 250.

Wigley, T.M.L., Briffa, K.R., and Jones, P.D. 1984. On the average value of correlated time-series, with applications in dendroclimatology and hydrometeorology. J. Clim. Appl. Meteorol. **23**(2): 201–213. doi:10.1175/1520-0450(1984)023<0201:OTAVOC>2.0.CO;2.