Forest Ecology and Management 260 (2010) 321–330

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

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

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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 (±36) years compared to 225 (±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.

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

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doi:10.1016/j.foreco.2010.04.017

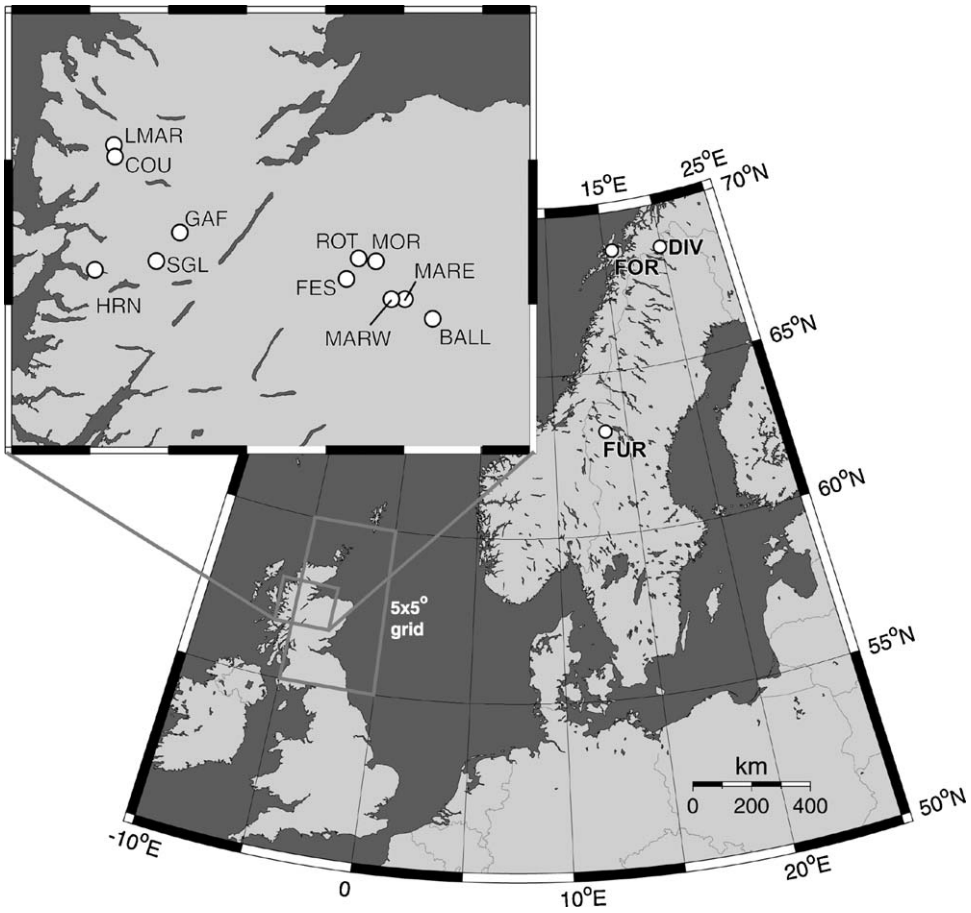

Fig. 1. Location map of Scottish and Scandinavian pine sites used in this study. Also shown is the $5^\circ \times 5^\circ$ temperature grid box used for correlation response function analyses (Brohan et al., 2006).

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 sample 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