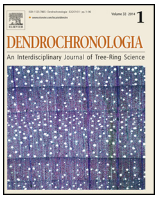
Dendrochronologia 33 (2015) 54–60

Contents lists available at ScienceDirect

Dendrochronologia

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



ORIGINAL ARTICLE

Effects of experimental stem burial on radial growth and wood anatomy of pedunculate oak

Paul Copini[a,*], Mathieu Decuyper[a], Ute Sass-Klaassen[a], Holger Gärtner[b], Frits Mohren[a], Jan den Ouden[a]

[a] *Wageningen University, Forest Ecology and Forest Management Group, P.O. Box 47, 6700 AA Wageningen, The Netherlands*
[b] *Swiss Federal Research Institute WSL, 8903 Birmensdorf, Switzerland*

ARTICLE INFO

Article history:
Received 21 September 2014
Accepted 15 December 2014

Keywords:
Dendrogeomorphology
Drift sand
Growth response
Quercus robur
Wood anatomy

ABSTRACT

In dendrogeomorphology, abrupt changes in wood anatomy are frequently used to date the exact year of burial and exposure events. However, few studies have addressed the precision and underlying mechanisms of these changes. In a field experiment, performed in a drift-sand area in the Netherlands, we buried the stems of mature pedunculate oak trees (*Quercus robur* L.) up to a height of 50 cm and analysed the responses in ring width and earlywood-vessel characteristics, while monitoring the course of temperature above and below the soil surface.

After 3 years of stem burial, we found no significant differences in ring width and earlywood-vessel characteristics between control and buried trees both above and below the burial level. Burial however strongly reduced temperature amplitude and the occurrence of sub-zero temperatures around the buried stems. All buried trees formed epitropic roots that grew upward into the new sediment layer, but no adventitious roots were formed on the buried stems. Irrespective of the burial treatments, we found that the mean ring width was largest at the original stem base and lowest at breast height. In contrast, vessel sizes were significantly larger at breast height compared with the stem base. Differences in vessel density barely differed between years and heights.

In our field experiment on mature pedunculate oak trees, the burial of stems by 50 cm of drift sand did not induce any local growth suppression or detectable changes in wood anatomy. As wood-anatomical changes in response to burial have previously been reported for trees that had formed adventitious roots, we stress the role of adventitious-root formation as a possible trigger behind the local changes in wood anatomy, reflecting a functional change of a buried stem towards a root. Based on our field experiment, it seems unlikely that years of shallow or moderate burial events ($\leq$50 cm) can be reconstructed using the wood structure of buried stems. As epitropic roots develop quickly after burial, dating such roots may potentially yield better estimates of burial events. Further research on the relation between adventitious root and changes in stem anatomy is needed to ascertain the precision of dating sand-burial events using tree rings.

Introduction

Dendrogeomorphology is a powerful tool to reconstruct geomorphic processes with high temporal resolution (Alestalo, 1971; Stoffel et al., 2010). This method is frequently used to ascertain erosion and accumulation rates or dynamics of sediment transport in many different ecosystems (e.g. Gärtner et al., 2001; Bodoque et al., 2005; Den Ouden et al., 2007; Stoffel et al., 2013). Transitions in ring width and vessel or tracheid-lumen size caused by burial or exposure have been used to date the exact year when such events occurred (Cournoyer and Bégin, 1992; Gärtner et al., 2001; Friedman et al., 2005; Stoffel et al., 2013). Normally, stems react to burial with reduced growth, whereas exposure of roots leads to the opposite (Fayle, 1968; Marin and Filion, 1992; Friedman et al., 2005; Matisons and Brūmelis, 2008). In conifers, exposed roots may develop tracheids that are reduced by 50% in the lumen area, whereas stems show a 50% increase in tracheid lumen after burial (Marin and Filion, 1992; Cournoyer and Filion, 1994; Gärtner et al., 2001). In broadleaved species, the response differs between diffuse-porous and ring-porous trees. Whereas

---

* Corresponding author. Tel.: +31 317 486355; fax: +31 317 486360.
E-mail address: Paul.copini@wur.nl (P. Copini).

http://dx.doi.org/10.1016/j.dendro.2014.12.001
1125-7865/

diffuse-porous species drastically increase vessel size after stem burial (Beakbane, 1941; Sigafoos, 1964; Fayle, 1968; Friedman et al., 2005), ring-porous species exhibit decreases in earlywood-vessel size (Knowlson, 1939; Cournoyer and Bégin, 1992; Friedman et al., 2005; Den Ouden et al., 2007). In addition, ring-porous species show the tendency to appear diffuse porous, or root like, after burial and shift back to ring-porous after exposure (Fayle, 1968; Cournoyer and Bégin, 1992; Den Ouden et al., 2007; Hitz et al., 2008).

Many dendrogeomorphic studies have assumed that the wood-anatomical changes in response to burial or exposure events were caused by sudden changes in soil pressure, aeration, moisture, light, and/or temperature along buried stem parts (Fayle, 1968; Gärtner et al., 2001; Den Ouden et al., 2007). Especially temperature has been pointed out as a triggering factor (Richardson and Dinwoodie, 1960; Fayle, 1968; Gärtner et al., 2001). While studies generally assume an immediate response of tree stems to burial, few studies have explored the abruptness at which wood-anatomical changes occur after burial or exposure events and results are often inconsistent. Some studies indicate that trees respond to burial within the growing season following the event (Wieler, 1891; Gärtner et al., 2001; Friedman et al., 2005). Findings from other studies suggest that transitions in ring width and wood anatomy only occur in particular plant parts, most likely through mechanical constraints (Bannan, 1941; Fayle, 1968; Stokes and Mattheck, 1996; Heinrich and Gartner, 2008), or could be substantially delayed (Knowlson, 1939; Strunk, 1995).

In this study, we used a field experiment to study the effects of stem burial by drift sand over a period of 3 years on mature pedunculate oak (*Quercus robur* L.) trees. In line with previous findings (Friedman et al., 2005; Den Ouden et al., 2007), we hypothesised that burial of stems up to 50 cm would cause an immediate and significant reduction in ring width and vessel size as well as a shift from a ring-porous towards a more diffuse-porous wood structure within the growing season following the burial event. To assess the potential role of temperature (Richardson and Dinwoodie, 1960; Gärtner et al., 2001), we recorded the course of temperature above the soil surface and at various heights in the new sediment layers.

Materials and methods

Study site and experimental setup

Within the extensive drift-sand area ‘Loonse en Drunense Duinen’ in the Netherlands, we selected a site dominated by pedunculate oak (51.6508° N, 5.0991° E). In an area of 100 by 100 m, we randomly assigned 10 trees as controls and 10 trees for burial treatment. In March 2010 when the experiment was established, the 20 trees had a mean diameter at breast height (DBH, 130 cm) of 19.6 ± 3.4 cm (mean ± SD; $n = 20$) and a mean height of 11.4 ± 1.4 m and were all dormant. Around each of the 10 trees to be buried, we constructed a squared wooden enclosure of 2 m × 2 m × 0.6 m (length, width, height) with the tree in the centre (Fig. 1). We marked the 50 cm stem height around the entire circumference of the tree and then filled the enclosure up to 50 cm stem height with drift sand (fine grained sand) from the adjacent area. On four buried trees, we installed HOBO Pro temperature data loggers (Onset Corporation, Bourne, MA, USA) to record the temperature at 0 (original soil surface), 25, and 47 cm (both near the buried stem parts) as well as above the new soil surface at 75 cm. The loggers were installed on the north side of the trees. In two control trees, HOBO Pendant loggers (Onset Corporation, Bourne, MA, USA) were installed at the same heights. All loggers were synchronised and temperature was measured on an hourly basis.

Fig. 1. Setup of the field experiment in the ‘Loonse en Drunense Duinen’. Stems of mature pedunculate oak trees (*Quercus robur* L.) were covered by drift sand up to a stem height of 50 cm, before the onset of the 2010 growing season. The left arrow indicates one of the two temperature loggers that were installed to measure temperature at stem heights of 0, 25, 47, and 75 cm. The right arrow indicates one of the control trees.

Sampling and sample preparation

In November 2012, the buried trees were excavated and the north side of each trunk was marked. The formation of adventitious roots on buried stems and negative geotropic roots or epitropic roots, i.e., roots growing from the original root system upwards into the new sediment layer (Stone and Vasey, 1968; Alestalo, 1971), was noted. Next, all trees were felled, and stem discs were taken at stem heights of 12.5, 25, and 130 cm. Per stem disc, two radii with a tangential width of 1.5 cm were extracted from the north and south side of each disc. We avoided sampling in buttress zones in the discs. The surfaces of all radii were prepared with razorblades for tree-ring measurements and scanned using a high-resolution (1600 dpi) flatbed scanner (Epson Expression 10000 XL). We then cut transverse thin sections (20 μm) of the tree rings formed between 2007 and 2012 using a G.S.L.-1 sliding microtome (Gärtner et al., 2014). All thin sections were stained with a Safranin/Astrablue solution for 5 min. Following dehydration in graded series of ethanol (50–95–100%), the samples were rinsed with Roticlear®, mounted in Rotimount® (Carl Roth, Karlsruhe, Germany), and dried under pressure for 3 days. Photos were taken with a digital camera (DFC 320, Leica, Cambridge, UK) mounted on a microscope (DM2500, Leica, Cambridge, UK) using Leica imaging software (version 3.6.0). The photos were stitched together using PTGui software (v. 9.1.8, New House Internet Services B.V., Rotterdam, the Netherlands).

Measurements and analyses

To determine the age of the trees and for internal cross-dating, we measured the tree-ring widths using the WinDENDRO tree-ring image analysis software (version 2009b, Regent Instruments, Quebec, Canada). The tree-ring series were visually and statistically cross-dated using the programmes WinTSAP (Rinn, 1996) and COFECHA (Grissino-Mayer, 2001). To determine the potential effect of stem burial on tree-ring width and wood anatomy, we measured ring width (RW), earlywood width (EW), latewood width (LW) and earlywood-vessel area in the tree rings formed between 2007 and 2012 at the three sampling heights using ImageJ software (Rasband, 1997–2012). We measured all earlywood vessels larger than 30 μm in diameter. The first row of earlywood vessels was measured separately. To check the quality of vessel measurements,