Root suckering in a Triassic conifer from Antarctica: Paleoecological and evolutionary implications

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Abstract

• *Premise of the study*: Although root suckering and other types of sprouting are well studied in extant woody plants, little is known about the distribution of these traits at a macroevolutionary scale. Anatomically preserved fossil plants represent an excellent but understudied source of information of the distribution of sprouting behavior through time and across taxa.

• *Methods*: A block of silicified peat collected in the Middle Triassic Fremouw Formation at the Fremouw Peak locality, Central Transantarctic Mountains, Antarctica, contains a group of anatomically preserved roots of the fossil conifer *Notophytum krauselii* that bear young shoots. The specimen was prepared using the standard acetate peel technique and studied in reflected and transmitted light.

• *Key results*: Young sucker shoots bearing well-preserved leaves are produced in groups in some areas of the *Notophytum* roots.

• *Conclusions*: The production of root suckers in *Notophytum* indicates that some of the trees growing in polar forests during the Triassic could respond to environmental stresses by regenerating their vegetative structures and had the potential to reproduce vegetatively. The specimens also represent the first anatomical evidence of root suckering in any fossil seed plant, and its occurrence in an early putative podocarp supports the idea that this trait might be ancestral in at least some extant conifer families.

Key-words: conifer; Middle Triassic; sprouting; polar forest; root anatomy; vegetative reproduction

INTRODUCTION

Numerous modern woody plants produce root suckers. These shoots can increase the photosynthetic capacity of the plant and in some cases develop into new trunks (Del Tredici, 2001). They can be produced after environmental stresses or be part of the normal development in clonal species. Like all types of sprouting, the production of root suckers is common in angiosperms, but has been reported in a small number of conifer species (Del Tredici, 2001; Bond and Midgley, 2003). The only detailed anatomical description is that of buds developed on injured roots of hoop pine (*Araucaria cunninghamii*, Araucariaceae) (Burrows, 1990). Production of root suckers has also been documented for *Araucaria araucana* (Grosfeld et al., 1999) and *Agathis robusta* (Haley, 1957), one Podocarpaceae, and one Taxodiaceae (Bond and Midgley, 2003). Other conifer taxa are known to produce root suckers, but in the absence of detailed anatomical investigations, the distinction between collar and root sprouts often remains ambiguous. For example, the so-called root suckers of *Pinus echinata* are probably produced from the collar zone (Stone and Stone,1954). Similarly, the Wollemi pine (*Wollemia nobilis*, Araucariaceae) produces basal suckers but it is unclear if these are borne on the trunk or the roots (Hill, 1997).

Given the limited fossil data, our understanding of root suckering and other types of sprouting in gymnosperms and angiosperms at the macroevolutionary scale is currently based only on extant taxa (Bond and Midgley, 2003). Within the conifers, some authors (e.g., (Hill, 1997) have suggested that limited or absent sprouting is plesiomorphic.

Here, we document the production of young sucker shoots on roots of *Notophytum krausellii*, a Middle Triassic (245–230 Ma) conifer from Antarctica (Meyer-Berthaud and Taylor, 1991). The exceptional preservation of specimens in silicified peat allows for the observation of specific anatomical details, including the vascular connection between the sucker shoots and parent root, and the organization of young shoot apices. The Antarctic specimens not only provide new information on the biology of trees growing at high latitudes (70–75° S) during the Middle Triassic, but also represent the first anatomical evidence of root suckering in an extinct conifer.

MATERIAL AND METHODS

Notophytum krausellii was initially described from stems and roots with a podocarpaceous type of wood preserved in silicified peat from the Middle Triassic Fremouw Peak locality (Fremouw Formation), Central Transantarctic Mountains, Antarctica (Meyer-Berthaud and Taylor, 1991). Additional information on the *Notophytum* plant comprises leaf anatomy, including cuticle characters, and possibly ovulate cones and a seed with a well-preserved embryo (Axsmith et al., 1998; Escapa et al., 2010; Schwendemann et al., 2010). The present description is based on a silicified peat block (#11,160) from the Fremouw Peak locality containing several well-preserved *Notophytum* roots producing sucker shoots. Serial acetate peels were made using standard techniques (Galtier and Phillips, 1999). Selected zones of the peels were mounted with Eukitt® on microscope slides for observation and imaging. Images were taken using a Leica (Leica Microsystems GmbH, Wetzlar, Germany) DC500 digital camera attachment on a Leica MZ16 stereomicroscope and on a Leica DM5000 B compound microscope. The peat block, corresponding peels and slides are deposited in the Division of Paleobotany, Natural History Museum and Biodiversity Institute, University of Kansas collections (KUPB), under specimen number 11,160, slide numbers 24,016 – 24,021 and 26,556 – 26,587.

DESCRIPTION

The permineralized peat block contains a group of large decorticated *Notophytum* roots characterized by diarch protosteles and a significant amount of secondary xylem with numerous growth rings (figure 1a). Lateral roots of various sizes occur around the main roots (figure 1a). Two types of vascular traces to lateral organs occur in the secondary xylem of the roots. The first type are small, diarch, and protostelic root traces (figure 1b).The other type has a conspicuous eustele with a parenchymatous pith about 0.4–1.3 mm in diameter; this configuration corresponds to the vascular supply of sucker shoots (figure 1a, 1c). These traces occur in groups in some zones of the roots (figure 1a), have an oblique-to-horizontal course in the secondary xylem of the parent root, and cross several growth rings (figure 1a, 1d). Although the bark of parent roots is absent, some sucker shoots remained attached by their vascular tissues and protrude into the surrounding matrix. Apical portions of shoots are also anatomically preserved and these show the organization of young leaves in a compact spiral (figure 1d-f). The youngest leaves are about 1 x 0.3 mm in longitudinal section and partly enclose the apical meristem (figure 1e-f). The mesophyll of young leaves is made up of mostly round to isodiametric parenchyma cells. Older leaves are sometimes displaced or not preserved (figure 1e-f), but the vascular tissues are differentiated and form a central strand (figure 1g). Leaf epidermal patterns are similar to mature leaves of *Notophytum* (Axsmith et al., 1998), with a single layer of rounded cells usually filled with dark contents (figure 1e-g). Isolated *Notophytum* buds occur around the roots (figure 1g) and most likely correspond to the apices of sucker shoots produced at a lower level.

DISCUSSION

Anatomically preserved fossil plants such as the ones described here represent an exceptional source of information on sprouting behavior in extinct taxa. With tissues preserved, it is possible not only to look for the production of sprouts, but also to indicate where in the plant they were produced (trunk, branches, collar zone, roots). Nevertheless, information of this type in extinct seed plants and in their putative progymnosperm ancestors remains very limited. Epicormic sprouts have been reported on trunks of (1) *Archaeopteris* (Trivett, 1993), a Devonian progymnosperm that some phylogenetic analyses interpret as sister to the seed plants (Rothwell and Serbet, 1994), (2) a Permian glossopterid gymnosperm from Antarctica (Decombeix et al., 2010), and (3) the Permian-Triassic conifer *Woodworthia arizonica* (Creber and Collinson, 2006). Several Mesozoic cycads, including *Antarcticycas schopfii*, also from the Middle Triassic of Antarctica, produced bulbils (Smoot et al., 1985; Hermsen et al., 2009), adventitious buds that are part of normal development or a response to trunk damage. To the extent of our knowledge, the present paper is the first report of anatomically preserved root suckers in an extinct seed plant. The implications of this important discovery are twofold.

First, these *Notophytum* roots indicate that some of the arborescent gymnosperms growing at high latitudes during past episodes of greenhouse climate had the potential for vegetative regeneration, even if there was severe damage to their above-ground parts. With this mechanism, they may have had the capacity to spread vegetatively. This type of clonal growth is important in many extant plants, not only in colonizing new environments, but also in regenerating after environmental disturbances, even at high latitudes (e.g., Homma et al., 2003). Paleogeographic reconstructions indicate that during the Middle Triassic the Central Transantarctic Mountains were located at about 70–75° S paleolatitude (Parrish, 1990). Although living under a highly seasonal light regime, the fossil plants from Fremouw Peak were taxonomically diverse and represent almost every group of seed plants known in the Mesozoic (see list in Taylor and Ryberg, 2007). Studies of tree rings (Taylor and Ryberg, 2007) and of a contemporaneous *in situ* forest from nearby Gordon Valley (Cúneo et al., 2003) show that trees grew faster than in extant boreal forests, and that tree density was equivalent to that of some modern temperate forests. The presence of fusinized plant remains in the permineralized peat (Hermsen et al., 2009), the depositional setting of the peat (Taylor et al., 1989), and the presence of *phi* layers in roots (Millay et al., 1987) suggest the occurence of both fires and floods, disturbances that favors sprouters in extant ecosystems (Bond and Midgley, 2001). It is unknown whether the unique environmental conditions experienced by the Triassic polar forests might have given an advantage to sprouters, but the possibility that they were more abundant than in extant high-latitude forests needs to be investigated at a larger scale and taken into account when modeling the dynamics of past (and future) polar forests.

The presence of root suckers in *Notophytum* is also noteworthy from an evolutionary point of view. It indicates that the ability to produce root suckers existed in some conifers during the Triassic, close to the time when modern families arose (e.g.,Kelch, 1998; Escapa et al., 2010). This supports the idea that basal sprouting in conifers is probably not a recent adaptation as suggested by some authors (Hill, 1997), but rather a primitive trait expressed in only a few extant taxa. While no studies have investigated the distribution of sprouting in conifers on a large phylogenetic scale, it is also interesting that *Notophytum* displays several characteristics of the Podocarpaceae and was assigned to that family (Meyer-Berthaud and Taylor, 1991; Axsmith et al, 1998). Today, Podocarpaceae s.l. (i.e., including *Phyllocladus;* Kelch, 1998), along with Araucariaceae, are the conifer families in which basal sprouting is most frequent and the only two with well-documented root suckering. Future paleobotanical investigations of anatomically preserved plants will certainly provide additional information on the distribution of sprouters within extinct and extant seed plant clades and their importance in past ecosystems.

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Figure 1.

Anatomy of silicified *Notophytum krauselii* roots with root suckers from the Middle Triassic of Antarctica (specimen 11,160).

(a) Transverse section of a large root showing growth rings and vascular traces to lateral roots and sucker shoots. Scale bar = 1 cm. Peel Ctop#2.

(b) Vascular trace to a lateral root. Scale bar = 0.5 mm. Slide 26,566 (peel A#21)

(c) Vascular trace in the same root as (b), showing the parenchymatous pith of a sucker shoot. Scale bar = 0.5 mm. Slide 26,566 (A#21)

(d) Transverse section of parent root (below, with growth rings) with longitudinal section of an emerging young sucker shoot, showing both the vascular connection and young leaves around the apex of the shoot. Scale bar = 2 mm. Slide 26,571 (Bbot#1α)

(e) Detail of the apex of the shoot illustrated in (d) Scale bar = 0.5 mm. Slide 26,571 (Bbot#1α)

(f) Vascular tissues of a sucker shoot (bottom) connected to the parent root (left); note shoot apex protruding into the peat (to the right of S). Scale bar = 1 mm. Slide 26,563 (A#15)

(g) Transverse section of an isolated bud found close to a large root. Note shoot in center with surrounding young leaves. Scale bar = 1 mm. Slide 26,586 (Ctop#4)

Legend: L: young leaves; LR: lateral root; R: main root; S: vascular traces to sucker shoot

Figure 1

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