



Contribution of the earliest woody trees (lignophytes) to the greening of the continents

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The diversification of early terrestrial plants is characterized by an intense phase of morphological innovation during the Devonian that resulted in the evolution of a large variety of growth forms. Several unrelated taxa adopted the tree habit, a form characterized by its extended lifetime and the possession of a tall, vertical trunk. This evolution provided large-sized plants with functional advantages over smaller ones in terms of reproduction and light interception. From a biophysical point of view, this increase in stature was a challenge as it created new constraints in terms of biomechanical support and water transport. The various groups that evolved trees resolved these problems by adopting specific strategies in relation to their own evolutionary history and inherited traits. It is uncertain whether the evolution of the tree habit and of forests has directly promoted the diversification of the reproductive systems and the advent of the seed habit. But it created new niches, contributing to the diversification of the terrestrial floras and faunas. It may also have considerably impacted the biosphere and contributed to the dramatic decline of atmospheric CO₂ in the Late Devonian through the enhanced development of soils and changes in erosional and sedimentary processes. Understanding these interactions through a better assessment of the structure, development, functioning and evolution of early trees represents a new challenge for paleobotanists.

Here we provide a review of the earliest arborescent representatives of the lignophyte clade, paying special attention to the anatomical, morphological and developmental traits that may have contributed to their wide paleogeographical distribution in the Late Devonian and later on. These trees are the first ones in the history of vegetation to possess leaves as well as long-lived roots and branches. Their growth is three-dimensional by comparison to the essentially vertical growth of earlier trees. Using the material we collected from diverse North Gondwanan localities, we investigated the evolution and patterns of changes in the floras of arborescent lignophytes around the Devonian-Carboniferous boundary. New evidence indicates that (1) the time interval between the extinction of the progymnosperm (free-sporing) genus *Archaeopteris* that flourished in the Late Devonian and the diversification of a new tree flora in the Mississippian was short if any, and (2) that the majority of this renewed arborescent vegetation reproduced by seeds.