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Towards an evaluation of the role of Mid Devonian forests in the development of the Earth System

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The development of tree form during the Middle Devonian (Eifelian and Givetian) is considered important because of its predicted profound effect on the Earth System. In order to be able to evaluate the impact of afforestation of the terrestrial environment, accurate whole plant concepts, reconstructions and growth models are a prerequisite. This paper will summarise both the considerable ongoing successes and important remaining gaps in our knowledge.

The main plant groups to evolve a tree habit in the Middle Devonian were the pseudosporochnalean cladoxylopsids, the archaeopteridalean progymnosperms and the bipolar lycopsids.

Amongst pseudosporochnaleans, the basic bauplan is for a swollen base with densely inserted narrow, long roots, a straight trunk and laterally inserted digitately divided branches bearing small, variously branched, unwebbed axial appendages. Fossils are known from Europe and the Americas. Spectacular new German specimens of Calamophyton (Mid Eifelian - Mid Givetian) demonstrate the whole plant from roots to trunk apex. Notable is the dense insertion of lateral branches. Pseudosporochnus (latest Eifelian - ?) includes bigger trunk material. Wattieza (Givetian - earliest Late Devonian) was a large tree with moderate sized specimens reaching 6-8 m height. Through time there is a clear trend of increase in maximum trunk diameters (and therefore height), decrease in density of lateral branch insertions on the trunk, and increasing three-dimensional morphological complexity of the (photosynthetic?) appendages. Basically monocauline, they had relatively short branches, and field evidence of the bases (Eospermatopteris) demonstrates the high density of individuals in Wattieza forests. Anatomically, structural elements (xylem tissues) are restricted to narrow strands which occupy a thin zone around the periphery of the trunk - much of the rest of the stem tissue is not lignified. Branches contain a much greater proportion of xylem tissues. Important issues regarding the impact of the plants on the Earth system include the large number of branches shed per individual (meaning a considerable depth of litter in a forest), and the size, depth and density of root penetration - only the depth cannot yet be determined.

Archaeopteridaleans are best known from the Late Devonian. Typically they had massive woody trunks, large long-lived lateral branches, and leafy ‘fronds’ attached to the branches which were abscised complete. However the early types of archaeopteridaleans, which appeared in the Givetian or earlier, lack detailed anatomical description and clear whole-plant concepts. Preliminary evaluation of new material from New York State, co-occurring with Wattieza, suggests that the ‘fronds’ may have been attached directly to relatively narrow trunks. We have no specimens to understand the rooting systems, neither do we have direct evidence for growth density.

Lycopsids are known to have achieved bipolar growth during the Middle Devonian. The most complete examples are from South China. Whole plant reconstructions show upright leafy trunks which branch at the top to give a crown of sparsely dichotomized leafy branches. At the base a dichotomizing rooting system is present where known, but rootlets are not thought to be present. Current whole plant reconstructions are based on small specimens, whereas more substantial fragmentary trunk material is relatively widespread. The rôle of lycopsids in the development of early forest ecosystems has yet to be properly evaluated.

At present therefore, pseudosporochnalean cladoxylopsids are the only group in which a series of relatively good whole-plant concepts is developed for the period spanning the Middle Devonian into the beginning of the Late Devonian. Further fieldwork with careful selection of localities may lead to equally spectacular success with the archaeopterdalean and lycopsid groups. This is highly desirable to constrain speculative models of Earth System

evolution during a critical phase of Earth history.