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Review of plant evolution and its effect on climate during the time of the Old Red Sandstone

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ABSTRACT

A substantial decrease in atmospheric carbon dioxide (CO_2) concentration during the mid-Palaeozoic is likely to have been the consequence partially of the evolution of rooted land plants. The earliest land plants evolved in the Ordovician but these were small cryptophytes without any roots. Much of the evidence for the evolution of vascular plants comes from the Old Red Sandstone of South Wales and the Welsh Borderland. Plants with large rooting systems evolved during the Middle Devonian and resulted in an increase in chemical weathering of silicate rocks. This, in turn, caused a contemporaneous drop in atmospheric CO_2 concentration from approximately 25 times present concentration in the Cambrian to twice the present concentration by the late Carboniferous. The supposed mechanism for CO_2 removal from the atmosphere involves oceanic carbonate precipitation, enhanced by plant-enhanced chemical weathering of Ca and Mg silicates.

1. Introduction

The Old Red Sandstone symposium in Brecon was an excellent opportunity for taking stock of the current state of knowledge on late Silurian and early Devonian sediments, and what these tell us about that part of Earth's history. Some of the key developments in the evolution of terrestrialisation of plants and the chemical composition of our atmosphere happened during this time, and much of the evidence for these comes from contemporaneous rocks in southern Britain. The symposium was therefore a stimulus to provide a brief overview of the relationship between land plant evolution, atmospheric CO_2, and long-term climate change.

The current (April 2014) atmospheric CO_2 concentration (c_a) of 403 ppm at Mauna Loa (Keeling et al., 2015) is low compared to the remainder of the Phanerozoic. While c_a was generally below 1000 ppm during most of the Phanerozoic, prior to 390 Myr ago it largely exceeded 1000 ppm (Franks et al., 2014). The marked change in c_a happened during the Devonian and is thought to be the result of the evolution of land plants with complex rooting systems during the Middle Devonian (Baars et al., 2008), particularly the evolution of the earliest lycophytes with true roots (Gensel and Berry, 2001) heralding a new wave of vegetation of plants of diverse lineages, but with even more complex rooting systems in volume and depth (Raven and Edwards, 2001; Algeo and Scheckler, 1998) which led to the development of trees and forests (Stein et al., 2012).

2. Plant evolution

Microbial mats comprising cyanobacteria and green algae are hypothesised to have been among the first organisms to colonise the land (Edwards and Selden, 1993; Wellman and Strother, 2015), sometimes forming recurrent associations and distinct communities (Knoll, 1981). This suggests that the earliest vascular plants may have colonised a land surface with a biologically active soil cover and well-developed soils (Wright, 1985; LePage and Pfefferkorn, 2000).

While indirect evidence for the evolution of the first land plants comes from molecular studies (e.g., Heckman et al., 2001), the microfossil record indicates that it is likely that land plants originated in the middle of the Ordovician Period and that there was a major radiation of cryptospore-producing species during the latter part of the Ordovician. The earliest embryophyte spores are reported from the early Llanvirn of Bohemia (Vavrdova, 1984) and Saudi Arabia (Strother et al., 1996). Spore tetrads and cuticle-like sheets of cells are reported from Caradoc beds (Gray et al., 1982), and spore-containing plant fragments from Upper Ordovician rocks (Wellman et al., 2003). In the Llandovery, trilete monads appeared, which are typical of those produced by the free-sporing plants of the Devonian (Steemans et al., 1996; Wellman et al., 2000). Kenrick et al. (2012) recently explained the apparently late appearance of plant body fossils,

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compared to the spore record, with a bias in the rock record towards marine deposits prior to the Devonian.

The first megafossil evidence for the spore producers was in the Wenlock (Edwards et al., 1983; Edwards, 1993, 2000): isotomously branching, leafless axial plants with terminal solitary sporangia in uppermost Silurian and basal Devonian strata. Vegetation comprising these rhyniophytes and rhyniophytoids during this time probably grew in turf-like communities a few centimetres in height. The Lochkovian saw a major radiation of these axial plants as well as the appearance of lycophytes (Edwards and Davies, 1990). While there is little knowledge of below-ground structures, due to the size of the aerial shoot substantial below-ground structures would have been needed to anchor the plant adequately, and for sufficient nutrient and water uptake (Driese and Mora, 2001).

Throughout the Lower and Middle Devonian, successive radiations and competitive replacement occurred (Edwards and Davies, 1990; Berry and Fairon-Demaret, 1998), and overall plant diversity increased (Raymond and Metz, 1995). Having evolved no later than the Ludlow (Kotyk et al., 2002), the taller zosterophylls became more numerous in the Lochkovian.

Roots, combined with a fully integrated vascular system, were essential to the evolution of large plants, enabling them to meet the requirements of anchorage and the acquisition of water and nutrients (Boyce, 2005). Roots evolved independently in several major clades of plants, and rapidly acquired and extended functionality and complexity (Kenrick and Strullu-Derrien, 2014). Root-like structures were identified in Lower Devonian zosterophylls and lycophytes (Gensel et al., 2001; cf. Gensel and Berry, 2001). *Aglaophyton* and other Rhynie plants have subterranean axes bearing rhizoids (Raven and Edwards, 2001), and root traces were found in Emsian fluvial sediments (Elick et al., 1998). True roots probably evolved independently in the lycophytes and the euphyllophytes (which include all extant vascular plants other than lycophytes; Raven and Edwards, 2001). By the Upper Devonian, root-like structures penetrated almost a metre into the substrate (Raven and Edwards, 2001).

Increasing plant diversity resulted in the emergence of the progymnosperms in the Middle Devonian, and of the sphenopsids (equisetopsid) and fern (polypodiopsid) clades in the Upper Devonian (Edwards, 1998; DiMichele and Phillips, 2002). The subsequent radiation of the pteridosperms in the latest Devonian completed the establishment of the four major clades which were to dominate the vegetation throughout the Carboniferous (Edwards, 1998). The final vegetation phase of the Palaeozoic followed in the drier times of the Permian, when seed plants, particularly conifers, replaced arborescent free-sporing plants (Gray, 1993).

3. Plants of the ORS in South Wales

The stratigraphical record of palynomorphs precedes the record of macroscopic plant remains partly because of the nature of the rock record during the early part of the Palaeozoic, when significant changes in the proportions of terrestrial and marine rocks are thought to open and close taphonomic windows on to macrofossil and palynomorph evidence (Kenrick et al., 2012) and partly in changes in the preservation potential of the plants themselves (Edwards et al., 2014).

Research on the Anglo-Welsh Basin, a small region on the southern margin of the Old Red Sandstone continent, provides a detailed regional picture of the evolution of plant life on land. These sediments are the best in the world for a more or less uninterrupted sequence through the Upper Silurian (Pridoli) to Lower Devonian (Pragian), with an excellent biostratigraphical framework. Although direct fossil evidence of cryptophytes comes from only two sites, there is an extensive and well-documented record of dispersed spores for the region (Edwards et al., 2014). The relatively localized area between South Wales and the Welsh Borderland is of particular importance. Early plant remains have been recovered for almost 200 years from rocks spanning the transition from marine Upper Silurian into fluvial Lower Devonian, with the first published records by Murchison (1839). Following Lang's seminal study in the 1930s (Lang, 1937; Croft and Lang, 1942), work on early Devonian plant material from this area received detailed attention chiefly by Edwards (e.g., Edwards, 1970, 1979; Edwards and Rogerson, 1979; Edwards et al., 1992, 1995; Edwards and Richardson, 1974, 2000; Fanning et al., 1992). Other

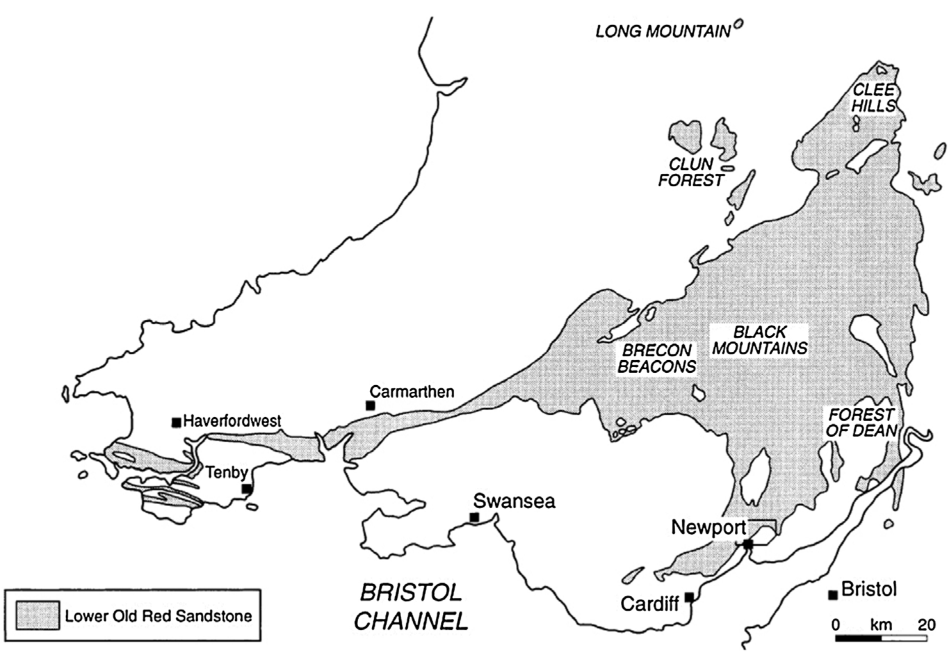

Fig. 1. Outcrop of the Lower Old Red Sandstone in the Anglo–Welsh Basin, after Wellman et al. (2000). Reproduced with kind permission by The Royal Society.

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