Palaeophytogeography of Ordovician–Silurian land plants

CHARLES H. WELLMAN1*, PHILIPPE STEEMANS2 & MARCO VECOLI3,4
1Department of Animal and Plant Sciences, University of Sheffield, Alfred Denny Building, Western Bank, Sheffield S10 2TN, UK
2Paléobotanique, Paléopalynologie, Micropaléontologie (PPM), University of Liège, Batiment B-18, allée du 6-Août, 4000, Liège-1, Belgium
3Université Lille 1, UMR 8217, FRES 3298 CNRS ‘Géosystèmes’, Villeneuve d’Ascq F-59655, France
4Present address: Biostratigraphy Group, GLTSD, Saudi Aramco, Dhahran, 31311 Saudi Arabia
*Corresponding author (e-mail: c.wellman@sheffield.ac.uk)

Abstract: A database of all reported Ordovician–Silurian land plant megafossil and dispersed spore assemblages has been assembled. For each assemblage a list of taxa has been prepared and its location plotted on new palaeocontinental reconstructions. These new data compare the distribution of the earliest land plants with respect to palaeophytogeographical differentiation and various patterns of taxonomic diversity and morphological disparity. Our analyses include new quantitative assessments.

Supplementary material: Appendix consisting of an abridged version of our dispersed spore database is available at: http://www.geolsoc.org.uk/SUP18680

The aim of this contribution is to review the palaeophytogeography of the earliest land vegetation in conjunction with newly created palaeocontinental reconstructions established for the Ordovician and Silurian. It is anticipated that this exercise will shed new light on the distribution of vegetation over this interval, in addition to providing an independent test of the new palaeocontinental reconstructions. Palaeocontinental reconstructions are mainly based on evidence from palaeomagnetism and the distribution of marine fossils. However, dispersed plant spores are by far the most common type of continental fossil, and provide an independent line of evidence useful in palaeocontinental reconstruction that is often neglected. They have the potential to provide both latitude and longitude constraints.

The Ordovician–Silurian time interval is of great interest regarding land plants as it witnessed their origin and subsequent diversification as they successfully colonized the land. The palaeophytogeography of the earliest land plants has been regularly reviewed over the years. However, the analysis presented herein differs from most previous attempts in that it: (1) integrates both the megafossil and dispersed spore fossil records of early land plants (with both at the species level); (2) considers the adaptive radiation and dispersal of land plants quantitatively in terms of measures of dispersed spore palaeophytogeographical distribution, taxonomic diversity and morphological disparity; and (3) utilizes the most comprehensive dispersed spore database hitherto constructed. Many previous reviews have been restricted to the very meagre plant megafossil record (e.g. Edwards 1990; Raymond et al. 2006). Reviews of the more extensive dispersed spore record have tended to be rather general in approach (e.g. Richardson 1996; Steemans 1999, 2000; Wellman & Gray 2000). Some reviews have considered both fossil records (e.g. Edwards & Wellman 2001; Gensel 2009; Steemans et al. 2010a), but these have been little integrated and none considered both plant megafossils and dispersed spores at the species level. We hope that our new analysis, combining both fossil records at the species level and utilizing new palaeocontinental reconstructions, will shed new light on the spatial/temporal (i.e. palaeophytogeographical/evolutionary) distribution of the earliest vegetation. In addition we present preliminary quantitative data on dispersed spore palaeogeographical distribution, taxonomic diversity and morphological disparity. These data are critical to our understanding of early land plant palaeophytogeography as they demonstrate the nature of the adaptive radiation and palaeogeographical dispersal of early land plants.

The early land plant fossil record

Plants leave two fossil records: a plant megafossil record and a dispersed spore fossil record. The plant megafossil record consists of fossils of a significant portion of the actual plant. For the earliest land plants it is very incomplete and is highly biased (e.g. Edwards 1990). These plants were generally diminutive and either lacked, or contained limited, recalcitrant tissues. Thus they were highly unlikely to be preserved. In fact there are only 23 localities where Ordovician–Silurian land plants have been reported (see Table 29.1). The early land plant record is also highly biased. First, it favours plants that contain recalcitrant tissues (e.g. sterome). Many of the earliest land plants are believed to have been ‘bryophyte-like’ in construction and completely lacked recalcitrant tissues, while even some of the Protracheophytes contained very little recalcitrant tissue (e.g. the Rhynie chert plant Aglaophyton). Consequently, they are only preserved in extremely rare cases of exceptional preservation. Second, terrestrial strata are uncommon in the Ordovician–Silurian. In fact all of the known Silurian plant megafossil assemblages are allochthonous and from near-shore marine strata. Thus plants that lived near the sea, or alongside water courses that drained into the sea, are probably over-represented. Third, rare cases of exceptional preservation skew the megafossil record (see the discussion below concerning the charcoalified early land plants from the Pridoli of the Anglo-Welsh basin).

In contrast to the plant megafossil record, the early land plant dispersed spore fossil record is abundant (supplementary material) and less biased. This is because Ordovician–Silurian land plants were most likely all free-sporing homosporous plants that relied on wind to distribute their spores. Free-sporing homosporous plants: (1) produce small isospores in vast numbers; (2) have the ability to disperse these small spores long distances by the vectors of wind and water, so they commonly accumulated in...
Table 29.1. Ordovician–Silurian land plant megafossil assemblages (after Edwards & Wellman (2001) and Edwards & Richardson (2004) with updates). Locality codes refer to those plotted on the palaeogeographical base maps. Pinnastracous qianensis is now considered to represent the roots of a younger, possibly Permian, plant that penetrated into Silurian strata (Edwards et al. 2007) and is omitted from this review.

| Locality | Age | Dating | Composition | Reference* |
|----------|-----|--------|-------------|------------|
| (K1) Oman | | Katian | Palynology (acritarchs, Chitinozoans) and field relations | Eohostimella heathana\(^a\) | Wellman et al. (2003) |
| (L1) Maine, USA | | Llandovery (?Telychian) | Invertebrates | Cooksonia sp. | Schopf et al. (1966) |
| (W1) Tipperary, Ireland | | Wenlock (Homarian) | Graptolites | Cooksonia sp. | Edwards et al. (1983) |
| (W2) Czech Republic | | Wenlock | Graptolites | Sterile rhyniophytes | Libertin et al. (2002) |
| (W3) Southern Bolivia | | Late Wenlock/Ludlow | Graptolites | cf. Cooksonia cambrensis | Toro et al. (1997) |
| (Lu2) Anglo-Welsh Basin | | Ludlow | Graptolites | Cooksonia pertoni | Edwards et al. (1979) |
| (Lu3) Northern Greenland | | Ludlow (?Ludfordian) | Graptolites | Salopella sp. | Edwards & Rogerson (1979) |
| (Lu4) Bathurst Island, Arctic Canada | | Ludlow | Conodonts | cf. Bathurstia sp. | Kotyk et al. (2002) |
| (Lu5) Victoria, Australia | | ?late Ludlow | Graptolites | Zosterophyllum sp. | | |
| (Lu6) Tarija, southern Bolivia | | Ludlow – ?early Pridoli | Field relations | Cooksonia sp. | Edwards et al. (2001) |
| (P1) Anglo-Welsh Basin | | Pridoli | Invertebrates | Stereotonia sp. | | |
| (P2) Anglo-Welsh Basin (Ludford Corner, Ludlow) | | Pridoli | Spores | cf. Cooksonia hemisphaerica | | |
| (P3) Anglo-Welsh Basin | | Pridoli | Invertebrates | Cooksonia pertoni | | |
| (P4) Anglo-Welsh Basin | | Pridoli | Spores | Hollandophyton colliculum | | |
| (P5) Anglo-Welsh Basin (Perton Lane, Hereford) | | Pridoli | Invertebrates | Salopella sp. | | |
| (P6) Anglo-Welsh Basin (Freshwater East, Pembrokeshire) | | Pridoli | Spore | Cooksonia cambrensis | Edwards (1979) |
| (P7) Anglo-Welsh Basin | | Pridoli | Spore | Cooksonia hemisphaerica | | |
| (P8) Anglo-Welsh Basin | | Pridoli | Spore | Cooksonia pertoni | | |
| (P9) Anglo-Welsh Basin | | Pridoli | Spore | Zosterophyllum sp. | Obrhel (1962), Schweitzer (1983), |
| (P10) Anglo-Welsh Basin (Little Wallop Hall, Shropshire) | | Pridoli | Invertebrates | Cooksonia sp. | Edwards & Rogerson (1979) |
| (P11) Northern Greenland | | Pridoli | Spores | Stereotoxidae Family | | |
| (P12) Northern Greenland | | Pridoli | Conodonts | Cooksonia sp. | Edwards et al. (2004) |
| (P13) Yunnan, China | | Pridoli | Graptolites | Cooksonia sp. | | |
| (P14) Yunnan, China | | Pridoli | Graptolites | Cooksonia sp. | | |
| (P15) Yunnan, China | | Pridoli | Graptolites | Zosterophyllum sp. | | |
| | | | | Zosterophyllum sp. | | |
| | | | | Lycopolis sp. | | |
| | | | | Glossopteris sp. | | |
| | | | | Eorhynia sp. | | |
| | | | | Lycopodolica sp. | | |
| | | | | Salopella sp. | | |
| | | | | Zosterophyllum sp. | | |

* For brevity only the most recent review of the flora is referenced.

\(^a\) Strother & Lenk (1983) suggested that Eohostimella represents an animal burrow rather than a plant although this was refuted by Gray (1984).
freshwater and near-shore marine environments suitable for sediment preservation; and (3) have spores with high fossilization potential because they have a resistant sporopollenin wall that serves to protect them during transportation. Despite the richness of the dispersed spore record, one must bear in mind that it too suffers from various biases. Thus plants that produced abundant spores (over producers) and those that lived near watercourses that readily transported their spores into sedimentary environments are over-represented (summarized in Steemans et al. 2007).

Critical to understanding the fossil record of early land plants is integrating the plant megafossil and dispersed spore fossil records. This is achieved primarily through studies of in situ spores that enable identification of spore-parent plant relationships. Studies of Ordovician–Silurian in situ spores are reviewed in Allen (1980), Gensel (1980), Fanning et al. (1988, 1991b), Balme (1995) and Edwards & Richardson (1996). Since these reviews, records of Ordovician–Silurian in situ spores have burgeoned, largely owing to work on the Late Silurian deposits of the Anglo-Welsh basin, including that on the exceptionally preserved charcoalified flora of Ludford Corner (e.g. Edwards et al. 1995, 1996, 1999; Edwards 1996; Wellman et al. 1998a). However, it remains the case that many taxa of Ordovician–Silurian spores (species and higher taxa including entire morphotypes) are not known in situ. While recent research suggests possible biological affinities at higher taxonomic levels for some groups (e.g. Emphanoid spores in Taylor et al. 2011), others remain totally unknown (e.g. patinate spores).

Understanding of plant spore relationships can also be gleaned from studies of spore wall ultrastructure. Spore wall development is often characteristic in different plant groups (summarized for extant homosporous plants in Brown & Lemmon 1990; Lugardon 1990) and thus can be used to infer the biological relationships of spores (e.g. Wellman 2004). Ordovician–Silurian studies of spore wall ultrastructure follow two modes of investigation. First, spore wall ultrastructure has been studied in plants containing in situ spores. Relevant studies are from Ordovician sporangia from Oman (Wellman et al. 2003) and Silurian sporangia from the Anglo-Welsh Basin (Rogerson et al. 1993, 2002; Edwards et al. 1995a, b, 1996, 1999; Wellman et al. 1998a), including those that are exceptionally preserved by charcoalification. Second, individual Ordovician–Silurian dispersed spores have been sectioned. These include various cryptospore morphotypes (Taylor 1995a, b, 1996, 1997, 2002) and trilete spores (Taylor 2003; Johnson & Taylor 2005). These studies have provided some evidence for possible relationships among the different spore morphotypes, particularly when considered in conjunction with information on in situ occurrence (most recently summarized in Edwards & Wellman 2001; Taylor 2000, 2001; Wellman 2004). Unfortunately, however, to date these studies have provided little definitive information regarding the biological affinities of the spore producers other than that some of the cryptospores have liverwort-like spore wall ultrastructure (e.g. Taylor 1995a; Wellman et al. 2003) and some emphanoid spores (i.e. Emphanisporites) may derive from a protraecophyte–hornwort clade (Taylor et al. 2011).

It is evident that the dating record of Ordovician–Silurian land plants includes an exceptionally preserved biota. The Ludford Corner locality in the Welsh Borderland is of Prudoli age and yields an assemblage of charcoalified plant mesofossils (Glasspool et al. 2004) in addition to assemblages of well-preserved spores. These fossils have enabled detailed anatomical investigation of Silurian plants washed into a shoreface–shallow marine environment (Jeram et al. 1990; Rogerson et al. 1993, 2002; Edwards et al. 1995a, b, 1996, 1999; Edwards 1996; Wellman et al. 1998a; Glasspool et al. 2004), including detailed studies of in situ spores and their wall ultrastructure, and comparison with coeval dispersed spore assemblages (Richardson & Lister 1969; Richardson & Rasul 1990).

The origin and early diversification of land plants

Numerous lines of evidence, from extant and fossil plants, suggest that the embryophytes (land plants) are monophyletic (summarized in Graham 1993; Kenrick & Crane 1997). There is very strong evidence, based on morphological and molecular studies, that land plants evolved from some form of charophycean green alga (e.g. Graham 1993; Karol et al. 2001; Qiu 2008). Thus it appears that land plants evolved from a charophycean green algal ancestor as an adaptive response to the invasion of the land (i.e. as they overcame the physiological problems associated with moving from an aquatic to subaerial existence). However, phylogenies of extant land plants are in a state of flux with various scenarios presented based on evidence from both morphological and molecular studies. Most concur that liverworts are the most basal group of living plants, with either the mosses, or more likely the hornworts, sister group to the vascular plants (e.g. Qui et al. 2006). Analyses consistently reveal that within the extant vascular plants lycopsids form a sister group relationship with all other vascular plants (e.g. Kenrick & Crane 1997).

The ‘liverwort basal’ hypothesis has led to suggestions that the earliest land plants were ‘liverwort-like’. This has been fuelled by fossil evidence of the earliest land plant that exhibit certain characteristic liverwort characters (Taylor 1995a; Edwards et al. 1995b; but see Edwards et al. 1999; Wellman et al. 2003; Graham et al. 2004). In reality, however, it is unclear exactly how closely related to modern liverworts these earliest land plants were. A taxonomically more realistic concept of stem group embryophytes is required. In fact the earliest convincing fossil evidence for liverworts of modern aspect is from the Middle Devonian (Herrick et al. 2008).

The fossil record for the earliest land plants consists of dispersed spores that first appear in the early Mid Ordovician ( Arenig/ Dapingian; Rubenstein et al. 2010; Wellman 2010). These dispersed spores occur in unusual configurations and are often called cryptospores. Similar cryptospore assemblages occur from the Dapingian to the Llandovery and are dominated by monads, dyads and tetrads that are either naked or envelope-enclosed. The envelopes may be variously ornamented. Occasionally the walls are ornamented with microgranula and/or are infrapunctate. Interestingly these latter forms appear to be confined to southeastern Gondwana and may represent the first evidence for palaeophytogeographical differentiation. However, the hypothesis of Gray (1993), that envelope-ornamentation indicated palaeophytogeographical differentiation, has now been discredited based on observation that the distribution of ornamented envelopes is essentially global. However, at the present state of knowledge, the question as to whether these Cambrian palynomorphs, represent true terrestrial or freshwater or terrestrial algae remains unresolved (Wellman 2003, 2010). Thus we prefer to take the Arenig/Dapingian cryptospore assemblages as the first undisputed evidence for land plants.

Gray (1985, 1991) and references therein made a convincing case for the land plant affinities of the Arenig/Dapingian cryptospores. She also made a case for the parent plants having liverwort-like physiology and ecology, but did not overstress a direct relationship with extant liverworts. Subsequent findings have strengthened the evidence for these spores deriving from land plants (e.g. Steemans et al. 2010a – evidence for sporopollenin walls) and a liverwort-like grade of organization for the
parent plants (Taylor 1995a; Edwards et al. 1995b, 1999; Wellman et al. 2003). Similar spore assemblages from the Dapingian to the Llandovery suggest that an uniform vegetation was present for some 30 myr. This vegetation is usually interpreted as consisting of ‘liverwort-like’ plants, which were presumably founder populations of ecological generalists. It is often considered that they would have been confined to damp environments because a film of water would have been required for reproduction. However, it is noteworthy that some extant bryophytes: (1) successfully reproduce in extremely dry environments by utilizing dew; (2) can survive in dry environments because they are homoiohydric; and (3) can tolerate high UV-B environments owing to the presence of UV-B screening phenolic compounds in their cells. Perhaps the earliest vegetation was more ecologically resilient and widespread than we anticipate. However, the upshot is that the aerial continental coverage of biotas is presently unknown. Presumably areas not colonized by the earliest land plants would have retained some form of simple microbial soil crust. However, even the simple and dimorphic earliest land plants would have begun to influence their environment in terms of development of a rudimentary soil (Boucot & Gray 2001).

During this time similar spore assemblages are reported globally from the equator to high latitudes, suggesting that the parent plants were palaeoecographically widespread. This is exactly what might be expected of the earliest land plants, interpreted as founder populations of ecological generalists tolerant of a wide range of ecological and climatic conditions. Widespread dispersal into what were essentially empty niches would have been particularly favourable (i.e. step-by-step dispersal through continents and long-distance dispersal across barriers). Such dispersal via spores would have been of prime importance, as would the ability to colonize a wide range of habitats and environments. Some dispersed spore assemblages occur at high latitudes and are intimately related to glacial deposits of the Hirnantian glaciations (e.g. from the Czech Republic (Vavrdova 1988) and South Africa (Gray et al. 1986)). This provides further evidence for cold tolerance among at least some of the parent plants. However, when interpreting parent plant palaeoecography based on dispersed spore record one should bear in mind that the similarity among the rather simple spore morphologies does not necessarily reflect similarity among the actual parent plants. The plants may have evolved differing morphology/anatomy but retained simple spores well adapted to their simple reproductive strategy.

From the Mid Ordovician hilate spores and trilete spores first appear in the dispersed spore record (Steemans et al. 2009). The hilate spores and trilete spores are the product of dissociation of dyads and tetrads, respectively. At first these are confined to southern Gondwana (Steemans et al. 2009). However, they subsequently spread into Avalonia, then into Euramerica, and finally into Baltica. Steemans et al. (2010a, b) trace their dispersal around the globe. It is generally considered that trilete spores derive from vascular plants (or their immediate ancestors; see discussion in Gray 1985 and online supporting material in Steemans et al. 2009). Thus it would appear that vascular plants (or their immediate ancestors) may have evolved in Gondwana before subsequently migrating beyond this continent and colonizing the rest of the globe. Where they appear they initially remain a subsidiary element of spore assemblages. However, by the Late Silurian (Wenlock) they begin to increase in quantity, diversity and disparity, presumably as the vascular plants underwent an adaptive radiation (Gray 1985, 1991; Richardson 1996; Steemans 1999, 2000; Strother 2000; Wellman & Gray 2000). The same pattern is seen in hilate spores. However, their affinities are more controversial. In situ studies demonstrate that at least some derive from polyporangiates (Wellman et al. 1998b; Habgood 2000) including some that possessed stomata (Habgood 2000).

Throughout the Late Silurian trilette and hilate spores continue to proliferate in terms of abundance, taxonomic diversity and morphological disparity. At the same time envelope-enclosed cryptospores virtually disappear (although they occur sporadically and rarely until the Early Devonian). Other cryptospores morphotypes persist but are generally subsidiary components of dispersed spore assemblages, although they may dominate locally (the ‘Wellman effect’ of Steemans 1999). Presumably the plants that produced trilete spores (vascular plants and their immediate ancestors) and hilate spores (?polyporangiates ?protracheophytes?) underwent an adaptive radiation and outcompeted the more primitive ‘liverwort-like’ cryptospore-producing plants that were thus relegated to the ecological ‘nooks-and-crannies’ unoccupied by the vascular plants, where they presumably have remained as bryophytes to the present day (with a later secondary diversification as ephiphytes once arborescence evolved).

The change from cryptospore to hilate/trilette spore dominance is a major global event in the dispersed spore record. Increasing trilette/hilate spore diversity most likely reflects the adaptive radiation of vascular plants as they begin to expand their range and exploit new habitats. Presumably there was an increase in community species packing related to increasing diversity and evolutionary innovations (crudely measured by our preliminary measures of disparity – see later) evidenced by an apparent increase in diversity despite greater complex ecology (see, for example, the contrasting models proposed by Wellman et al. 2000b and Edwards & Richardson 2004). During this time the first significant plant megafossil record appears (Table 29.1). The beginnings of phytogeographical differentiation become apparent in both the megafossil (e.g. Raymond et al. 2006) and dispersed spore (e.g. Steemans et al. 2010a, b) records.

The dispersed spore fossil record clearly illustrates the nature of the adaptive radiation of vascular plants and their competitive replacement of the bryophyte-like plants. Clear patterns have been demonstrated in terms of palaeoecographical spread, taxonomic diversity and morphological disparity (see below). Unfortunately, these patterns are far less apparent in the Ordovician–Silurian land plant megafossil record owing to the frustrating paucity of data. Indeed a number of mysteries remain. For example, the presence of the large lycopsid Baragwanathia from the Ludlow of Australia remains an enigma. The Ludlow age is now generally agreed to be secure, and consequently explanations for their anomalous size require something other than incorrect age assignment. Perhaps they represent either an extreme case of endemism, or they have strongly divergent morphology owing to unusual ecology (e.g. they were aquatic plants), or our fossil record of plant megafossils is simply too incomplete to represent the entire spectrum of Silurian plant life (after all, only 23 plant megafossil assemblages are reported from the entire Silurian).

The nature of the early land plant adaptive radiation

It is evident from the previous discussion that the earliest land plants rapidly colonized the globe forming vegetation that appears to have been cosmopolitan and is considered to have comprised diminutive and simple plants at a ‘liverwort-like’ grade of organization. The presence of similar spore assemblages over the next 30 million years suggests a period of stasis dominated by this simple vegetation. This period of stasis was shattered by the competitive replacement by vascular plants and their immediate ancestors that subsequently underwent an adaptive radiation. Understanding of this major event is based on patterns displayed by the dispersed spore and plant megafossil records.

There is a long history of plotting the temporal distribution of Ordovician–Silurian plant megafossils (e.g. Banks 1980; Chaloner & Sheerin 1979; Richardson & Edwards 1989) and dispersed spores (e.g. Richardson & McGregor 1986; Richardson & Edwards 1989; Richardson 1996; Gray 1993; Wellman & Gray 2000; Steemans 2000; Beck & Strother 2001, 2008). These data have
biostatigraphical utility, in addition to informing us of the evolutionary sequence of events of the adaptive radiation of early land plants. Both fossil records demonstrate the displacement of the ‘bryophyte-like’ flora by vascular plants following their origin and subsequent adaptive radiation. This essentially involves the origin of polysporangiate protracheophytes and their diversification into the traditional (i.e. non-cladistic) rhynephyte, zosterophyll, lycopsid and trimerophyte groupings. For information on recent cladistic re-evaluation of these groupings see Kenrick & Crane (1997).

A number of workers have undertaken taxon counts on Ordovician–Silurian dispersed spores to demonstrate the nature of the adaptive radiation of vascular plants (e.g. Richardson & Lister 1969; Knoll et al. 1984; Steemans 1999, 2000; Strother 2000; Beck & Strother 2001). Similar curves have been generated for plant megafossil data (e.g. Niklas 1977, 1978; Knoll et al. 1979, 1984; Niklas et al. 1980, 1983; Raymond & Metz 1995). Obviously far fewer and less palaeogeographically widespread records are available from the plant megafossil compared with dispersed spore database. New dispersed spore diversity curves, based on the data from the supplementary material, are presented in Figure 29.1. These curves demonstrate a fairly consistent low abundance of dispersed spores (dominated by obligate cryptospores) during the Ordovician and earliest Silurian. There is a dramatic exponential increase in trilete spore diversity from small numbers in the Late Ordovician–Early Silurian through the remainder of the Silurian and into the Devonian. Hilate spore diversification in general mirrors that of trilete spores. However, they appear to begin diversifying prior to the trilete spores, and their diversification is more variable. After an initial diversification, there is a temporary reduction in diversity, followed by a rediversification, before a further reduction in diversity towards the end of the Silurian. Obligate cryptospores exhibit variable, but low, diversity throughout the Silurian.

Relatively few plant megafossil taxa have been described from the Ordovician–Silurian (see Table 29.1), and these data are skewed by the exceptionally preserved charcoalified biota of the Pridoli of the Welsh Borderland, to the extent that there is little value in plotting them.

Various workers have considered disparity (i.e. morphological diversity) of Ordovician–Silurian dispersed spores (Allen 1981; Richardson & Burgess 1999) and plant megafossil (e.g. Chaloner & Sheerin 1979; Banks 1981; Knoll et al. 1984). However, these analyses are non-quantitative except for Knoll et al. (1984). They scored plant megafossil characters and developed an ‘anatomical and morphological advancement score’. These showed an exponential increase in early land plant ‘anatomical and morphological advancement score’ in theLate Silurian–earliest Devonian. However, only one plant taxon was scored for the Ordovician–Silurian interval.

We have generated new diversity and disparity curves based on Silurian–Early Devonian (Lochkovian) dispersed trilete spores. We gathered data from three palaeogeographically distinct areas where there is a relatively complete succession of well-preserved dispersed spore assemblages: the Anglo-Welsh Basin of Avalonia, the Spanish Cantabrian Mountains of Peri-Gondwana and African sequences of southeastern Gondwana. We have restricted these initial analyses to trilete spores because: (1) trilete spores represent a discrete and easily recognized group that is probably monophyletic; (2) cryptospores are difficult to work with because their distribution appears to be fairly cosmopolitan but they are often lacking in near-shore marine deposits owing to ecological/transportation effects (Steemans et al. 2004); and (3) cryptospores were often overlooked in early works on Silurian dispersed spore assemblages.

Spore taxon diversity data was simply measured by assembling all the publications on Silurian spores from these locations and counting all reported trilete spore species from each biozone (the Spore Assemblage Biozones of Richardson & McGregor 1986 were used). The count was then plotted in the chronological midpoint of each biozone using the timescale of Gradstein et al. (2004) (although one must, of course, be aware that the biozones are of differing durations). Spore morphological disparity was measured in a similar way but by giving each trilete spore species a disparity score based on its morphological characteristics. Table 29.2 outlines the numerical scoring system. Average (mean) disparity for the spores reported from each biozone was then calculated. The generated trilete spore species diversity and disparity curves are illustrated in Figures 29.2 and 29.3 respectively.

The spore taxon diversity curve (Fig. 29.2) exhibits a general exponential increase in trilete spore species over the course of the Silurian and into the Devonian. Apparent reductions in diversity in the Pridoli of the Anglo-Welsh Basin and Lochkovian (Early Devonian) of North Africa are almost certainly a product of a paucity of strata and described assemblages in these regions at this particular time. It is evident from our database and palaeophytogeographical analysis (see later) that, although many spore taxa are common between the three areas, there are distinct differences. In fact Peri-Gondwana appears to be more closely associated with Southern Gondwana than with Avalonia: a not entirely unsurprising result. Interestingly, however, taxon numbers and pattern of diversification are similar in all three regions even though different taxa are involved.

The spore morphological disparity curve (Fig. 29.3) suggests a pattern of additive increase in trilete spore disparity over the course of the Silurian in all three regions. Again it is interesting that in all three areas disparity values and the pattern of disparity increase is similar even though different taxa are involved.

**Fig. 29.1.** Ordovician–Silurian dispersed spore diversity curve generated from the data presented in Appendix 1. Timescale is from Gradstein et al. (2004).
Table 29.2. Character scoring for spore disparity index

| 1. Amb shape | 2. Amb size | 3. Structure | 4. Tetral configuration | 5. Laesurae | 6. Proximal structural features | 7. Proximal ornament | 8. Distal structural features | 9. Distal ornament |
|--------------|-------------|--------------|------------------------|------------|--------------------------------|---------------------|------------------------|-----------------|
| Circular–subcircular–subtriangular (1); ellipsoid (monolet only) (1); triangular (2); triangular convex (3); triangular concave (3); triangular truncated (3) | 0–50 µm (1); 50–100 µm (2); 100–200 µm (3); >200 µm (4) | Crassitate (1); retusoid (2); patinate (2); cingulate (2); zonate (3); bilayered-perine or sloughing outer layer (3); camerate (4) | Trilete (1); monolet (2) | Simple (1); prominent lips (2) | None (1); interradial papillae (2); thickening associated with trilete mark (2); thinning associated with trilete mark (2); radial ribs (2); radial ribs and thickening associated with trilete (4) | Laevigate (1); irregular murornate (2); irregular apiculate (2); irregular fovea (2); regular murornate (3); regular apiculate (3); regular reticulate (3); regular foveolate (3); biform (4); complex elements (4) | None (1); circular thickening (2); infrastructure (proximal and/or distal) (2); annular thickening (3) | Laevigate (1); irregular murornate (2); irregular apiculate (2); irregular fovea (2); regular murornate (3); regular apiculate (3); regular reticulate (3); regular foveolate (3); biform elements (4); reticulate with extended intersections (4); complex elements (e.g. gnarl-in-tipped) (5) |

Each spore is scored for each of the nine morphological components listed above. These are summed to provide the 'spore disparity index'. Scores within each of the nine morphological components are intended to reflect morphological complexity, rather than order of appearance in the fossil record. We have attempted to consider their complexity within a developmental context (i.e. how easy they are to construct in terms of exospore development).

Early land plant palaeophytogeography: previous analyses

Megafossils

Ordovician–Silurian land plant megafossil assemblages were first described in the 1930s (e.g. Lang 1937). Since this time there have been many attempts to plot their spatial/temporal distribution, with the most relevant obviously those postdating the realization of continental drift. Owing to the small number of reported assemblages most of these simply plot locations directly on palaeocontinental and/or palaeogeographical base maps of consecutive age. Edwards (1990) is an excellent example. More recently, as numbers of described assemblages has gradually risen, there have been attempts to use statistical techniques to analyse such data. For example, Raymond et al. (2006) utilized cluster analysis and correspondence analysis.

Edwards (1990) included a comprehensive review of Silurian early land plant megafossils. She reported 16 assemblages of plant megafossils and plotted their distribution on the Silurian continental reconstruction of Scotese. Edwards went on to discuss the problems of working with such a fragmentary database and stated that ‘the intention of this account is to emphasize the pitfalls when handling Silurian and Early Devonian megafossils, but is not meant to be critically destructive’. She emphasized problems of: (1) stratigraphical accuracy and precision; (2) recognition of facies bias; and (3) accuracy of identification and affinity. Although the number and palaeogeographical spread of described Silurian plant megafossil assemblages has increased significantly since Edwards’s review, owing in no small part to her own labours, these inherent problems persist. This must be borne in mind when making sweeping generalizations concerning Silurian plant palaeophytogeography, particularly as the database, improved as it is, remains woefully inadequate.

Raymond et al. (2006) reported on a detailed quantitative analysis of Silurian plant megafossils. They used a database containing 35 macrofloral assemblages reported as megafossil genera and morphological traits. The database was analysed using cluster analysis and correspondence analysis. They recognized four phyto-geographical units: (1) a North Laurussian unit (Bathurst Island); (2) a south Laurussian unit–SW Gondwana unit (Great Britain, Podolia and Bolivia); (3) a Kazakhstanian unit; and (4) a SW Gondwana unit (Australia).

Fig. 29.2. Newly developed Silurian–Early Devonian (Lochkovian) trilete diversity curve based on sequences in Avalonia (Anglo-Welsh Basin), Peri-Gondwana (northern Spain) and Northern Gondwana (Libya). Details of how the curve was constructed are outlined in the text.

Fig. 29.3. Newly developed Silurian–Early Devonian (Lochkovian) trilete disparity curve based on sequences in Avalonia (Anglo-Welsh Basin), Peri-Gondwana (northern Spain) and Southern Gondwana (Libya). Details of how the curve was constructed are outlined in the text and Table 29.2.

Dispersed spores

Ordovician–Silurian dispersed spore assemblages were first described in the late 1950s (e.g. Hoffmeister 1959). Since this time a huge literature has amassed with numerous assemblages (usually containing many different spore types) described from all over the globe (reviewed in Richardson & McGregor 1986;
Richardson 1996; Steemans 2000, 2001; Strother 2000; Wellman & Gray 2000). Plots of assemblage distribution are fairly common (e.g. Wellman 1996; Steemans et al. 2010a, b). However, owing to the magnitude of the database, attempts to plot the distribution of individual taxa in a thorough way are limited. At this point a note of caution is warranted. Historically many palynologists and their students have confined their research to (or at least concentrated it on) specific palaeogeographical areas. Thus taxonomies favoured by particular ‘palynology schools’ may be slightly different and confined to different palaeogeographical areas (see Marshall 1996). Obviously this can skew an analysis suggesting palaeogeographical differences when none exist.

Steemans et al. (2007) reviewed spore dispersal among early land plants. They concluded that long-distance dispersal was uncommon, but rare long-distance transportation events potentially could have resulted in successful establishment of populations. They also proposed that cryptospore-producers and trilete spore-producers had different dispersal and hence fossilization potential. They suggested that cryptospore-producers (‘bryophyte-like’ plants) inhabited restricted habitats (such as bogs and marshes) with little access to waterways and hence transportation to the sea. They considered that they were not climatically sensitive and were cosmopolitan. However they suggested that trilete spore-producers (vascular plants) were more widespread and inhabited a variety of habitats with access to waterways and hence the sea. However, they considered that they were climatically sensitive and hence restricted in distribution. Ecological models for the Ordovician–Silurian vegetation have been proposed by Wellman et al. (2001) and Edwards & Richardson (2004). These vary slightly in detail. Wellman et al. (2001) suggest that diminutive and short-lived plants (both bryophyte-like cryptospore-producing and vascular trilete spore-producing) inhabited unstable areas prone to flooding near water bodies, but with larger and longer-lived vascular plants inhabiting more stable areas away from water bodies liable to flooding. Edwards & Richardson (2004) suggest that cryptospore-producing plants became restricted to dry areas away from water bodies once vascular plants evolved and outcompeted them to colonize the more favourable damper areas near to water bodies.

**Early land plant palaeophytogeography: general principles**

What essentially governs the palaeogeographical distribution of the world flora at any given time is where plant taxa originate (centre of origin), and their ability to disperse and successfully colonize, counterbalanced by local, regional and ultimately total extinction. Local distribution is governed by the ability of individual species to occupy niches, which is essentially controlled by their tolerance of local environmental conditions (substrate, climate, water availability etc.) and their ability to co-exist with or outcompete other plants that already inhabit these environments.

The Ordovician–Silurian situation regarding plant distribution presumably was initially rather simple. The first land plants essentially invaded an unoccupied niche (other than the microbial inhabitants of a pre-land plant world). Thus there was limited competition and suitable environments would soon have been colonized. This is particularly the case because the earliest land plants were almost certainly homosporous, producing prodigious quantities of isospores that would have easily been transported vast distances by wind and water (see Gray 1985). However, the early vegetation would soon have occupied suitable habitats and begun to modify the environment in terms of sediment stabilization and soil formation. Thereafter in order to colonize new areas plants had to invade new habitats or co-exist with/displace plants that already occupied a particular habitat.
Obviously the ecology of Ordovician–Silurian plants is critical. It is important to understand to what extent individual plant species were confined to particular habitats on the local (e.g. substrate specific) and regional (e.g. climatic tolerance) scale. This is one of the main factors governing the distribution of plants and whether they are cosmopolitan, endemic, etc. There is little firm evidence regarding this issue. However, it has been discussed and various scenarios proposed by Gray (1984, 1985), Wellman et al. (2000b), Edwards & Richardson (2004) and Steemans et al. (2007) among others.

At this juncture spore dispersal requires consideration. Based on the Ordovician–Silurian dispersed spore record it would appear that all plant groups of this time were homosporous with the vast majority of spores falling within the size range 20–40 μm.

**Fig. 29.5.** Ordovician palaeocontinental reconstructions plotting palaeogeographical distribution of dispersed spores. Data from Appendix 1.
although some were up to 70 μm in size. Optimum size for wind dispersal is 25 μm or less according to Mogensen (1981). Nonetheless, it is generally assumed that wind was the main agent of spore dispersal during the Ordovician–Silurian. In fact wind dispersal may have been easier during this time than at present because: (1) the vegetation was essentially ground hugging with no tall plants to impede transport out of the boundary layer and into wind currents at higher altitudes; (2) average surface wind strength may have been greater owing to the absence of large vegetation forming wind breaks; and (3) it has been calculated that total atmospheric pressure was higher than at present, resulting in a higher density of air (Berner 2006), and hence increased spore buoyancy. Thus although the vast majority of spores would have been deposited very close to parent plants (following the classic leptokurtic distribution), there would have been potential for long-distance transport.

A number of workers have suggested that long-distance transport is unusual among extant bryophytes and therefore by analogy early land plants (e.g. Van Zanten 1978; Van Zanten & Gradstein 1988; van Zanten & Pócs 1981). Long-distance transport requires high-altitude wind currents, which are damaging to spores owing to problems associated with dessication, frost and UV-B. Additionally, such wind currents are usually parallel to latitudes and never cross the equator. Spores need to settle in a suitable environment to successfully germinate, grow and reproduce to establish a new colony. To favour maximal fertility a bisexual gametophyte is required, but to prevent endemic assemblages it is important that genetic exchange between two localities occurs in both directions. Following the above arguments, basing palaeocontinental reconstructions on the shortest distances between miospore palaeogeographical distributions becomes the most parsimonious method (Steemans et al. 2007, 2010a, b; Spina & Vecoli 2009). However, we recognize that it is not possible to completely rule out the possibility that rare events over vast periods of geological time could permit colonization of new locations by long-distance transport of the bisexual spores of homosporous plants.

Early land plant palaeophytogeography: a new database and quantitative analysis

In this review we treat both plant megafossils and dispersed spores. For plant megafossils we provide an up-to-date list of all described

![Fig. 29.6. Silurian palaeocontinental reconstructions plotting palaeogeographical distribution of dispersed spores. Data from Appendix 1.](image-url)
Ordovician–Silurian plant megafossil localities (Table 29.1) and plot these on the new palaeogeographical plots (Fig. 29.4). For dispersed spores we have constructed an extensive database of all records of Ordovician–Silurian dispersed spore taxa. This database is too large to print in full in this paper and is available from the authors. A greatly condensed version of the database is presented in the supplementary material. The databases were assembled and analysed in 2011. The location of the most important reports has been plotted on the newly constructed palaeocontinental reconstructions (Figs 29.5 & 29.6). However, we have excluded a few brief reports where spores constitute only a small component of the palynomorph assemblage and/or are poorly age-constrained and/or are too poorly preserved or thermally mature to enable accurate identification. Furthermore, owing to the size of the Ordovician–Silurian dispersed spore record there are also problems concerning the quality of data in the database. Synonomy is probably rife and there are many published examples of incorrect identification. It is anticipated that over time continual re-evaluation of the dispersed spore record will eliminate much of this bad data. Our preliminary attempts are evident in the database we have erected provided in the supplementary material. Throughout this review the Geological Time Scale of Gradstein et al. (2004) is utilized.

The data on stratigraphical and palaeogeographical occurrences of Silurian miospore species have been treated by means of statistical analysis in order to quantitatively analyse the similarities among assemblages belonging to defined palaeogeographical areas. A total of 787 data points have been analysed; each datapoint represents the occurrence of a miospore species in a given stratigraphical interval and in a given palaeogeographical area. The stratigraphical subdivisions used correspond to the Silurian Series: Llandovery, Wenlock, Ludlow and Pridoli. The following palaeogeographical localities have been defined: ‘southwestern Gondwana’ (mainly North African localities); ‘Peri-Gondwana terranes’ (corresponding to Western Europe, Bohemia, etc.); Avalonia (British Isles, part of northern France); Arabian Plate (including mainly Saudi Arabia and adjacent areas such as Iran and Iraq); Laurentia (corresponding to North America); ‘Eastern Gondwana’ (South America: Argentina, Paraguay, Bolivia); Baltica (Sweden, Norway, Batic States, northern Poland), South China Plate (mainly

Fig. 29.6. Continued.
localities belonging to the Yangtze Platform); and ‘Northern Gondwana’ (North Africa); additionally South Africa is used as a separate palaeolocality, belonging to southern Gondwana.

In order to assess the similarities among the fossil assemblages, two methods have been used: cluster analysis and metric multidimensional scaling (MDS). Cluster analysis has been widely applied in the past for analysis of palaeobiogeographical patterns of different fossil groups, including palynomorphs (e.g. Fortey & Mellish 1992; Vecoli & Samuelsson 2001). However, when this method is applied to fossil biogeography using databases that might be affected by sample biases, limitations become evident because artefacts can easily arise that may result in unreliable or artificial clustering of sets of little similarity (Brayard et al. 2007). However, MDS is generally used in modern ecological studies and is considered among the most reliable methods in quantitative assessment of biogeographical patterns (e.g. Edinger et al. 2000). In both cases, the Jaccard index was used to calculate the ‘similarity’ (fraction of species shared) among assemblages; the Jaccard coefficient is among the most commonly used species similarity measures in extant biogeographical and ecological studies (e.g. Izsack & Price 2001; Condit et al. 2007). The linkage method used for cluster analysis was Ward’s method. Calculations and plotting of diagrams were performed using the ‘R’ freeware statistical package (http://www.r-project.org/) and the programming script was kindly provided by Professor Wolfgang Kiessling (Natural History Museum, Berlin).

The MDS scatterplot of the Llandovery subset (Fig. 29.7a) shows considerable similarities among most of the palaeocontinents, as almost all miospore localities plot very close to each other, with the exception of South China and southern Gondwana (South Africa). The isolated position of these continents with respect to the main cluster is most probably a consequence of

Fig. 29.7. MDS scatter plot (a) and cluster diagram (b) for Silurian (Llandovery) dispersed spores. Details of methods are in the text.

Fig. 29.8. MDS scatter plot (a) and cluster diagram (b) for Silurian (Wenlock) dispersed spores. Details of methods are in the text.
sampling, since only impoverished assemblages are known in from the Llandovery of these two localities (a monospecific assemblage in South Africa, and only nine species described from South China). The cluster plot (Fig. 29.7b) also reflects this situation, with southern Gondwana (South Africa) and South China constituting a cluster of low similarity clearly distinct from the larger cluster formed by the rest of the localities. Note that data from Baltica are almost non-existent, with only rare tetrads reported from around the Ordovician–Silurian boundary from Gotland, Sweden (Le Hérisse 1989).

The MDS plot for the Wenlock (Fig. 29.8a) shows more scattering of the locality data points. However, an Avalonia–Peri-Gondwana cluster shows some similarity with Arabia and North Africa, and this group is clearly separated by a Laurentia–Baltica cluster. South America plots separately from the other two groups. The cluster diagram (Fig. 29.8b) basically recognizes the same groupings, with a first-order divergence between a North

![Fig. 29.9. MDS scatter plot (a) and cluster diagram (b) for Silurian (Ludlow) dispersed spores. Details of methods are in the text.](image)

Africa–Peri-Gondwana plus Avalonia–Arabia cluster and a Laurentia–Baltica (plus South America) cluster. The grouping of South America (a Gondwanan locality) with the Laurentia–Baltica cluster (which is somewhat inconsistent with the palaeogeographical reconstruction) could simply result from an artefact of the clustering method (see discussion above).

The Ludlow MDS plot (Fig. 29.9a) shows a significant degree of scattering of all localities, although South America, Peri-Gondwana and North Africa show some similarity and tend to cluster separately from the other palaeogeographical domains. Because of the large scattering of the data in the MDS plot, the cluster diagram for the Ludlow (Fig. 29.9b) must be interpreted with care, as the resulting clustering is not highly significant.

It should be emphasized that the first-order grouping of Laurentia with South America and Baltica with South China is based on datasets of very different sizes (much less data for South America and South China with respect to the large datasets

![Fig. 29.10. MDS scatter plot (a) and cluster diagram (b) for Silurian (Pridoli) dispersed spores. Details of methods are in the text.](image)
available for Baltica and Laurentia), which is very likely to introduce biases and errors in the geometrical clustering.

The Pridoli MDS diagram (Fig. 29.10) clearly highlights similarities among North Africa, Peri-Gondwana, South America and Avalonia. This group is clearly separated from a cluster formed by the Laurentia-South and Baltica cluster. Note also that no Pridoli occurrences are available for the Arabian Plate. The same grouping is almost exactly reflected in the cluster diagram.

Unfortunately it is very difficult to compare these analyses with those based on plant megafossils by Raymond et al. (2006) because dispersed spore assemblages have not been reported from two of their four phytogeographical units (Kazakhstan and SW Gondwana (Australian)). However, for both the Ludlow and Pridoli, dispersed spores do not appear to support Raymond et al.’s South Laurussian–SE Gondwana unit or the distinction between this unit and their North Laurussian unit.

As stated before, the palaeobiogeographical interpretation of the quantitative analysis of assemblage similarities must be undertaken with care because the available sample sets show high spatial heterogeneity and significant differences in sample size. It is evident that data are completely lacking for certain areas (e.g. Russia, Siberia, most of West Gondwana) and there is a concentration of data from North America, Europe, North Africa and the Middle East (especially Saudi Arabia). Baltica is also under-reported.

Interpretation of new database/analyses

In general, analysis of the newly assembled database/phytogeographical plots confirms the general picture of early land plant origins and diversification that has emerged over the last 40 years or so. However, its importance lies not in highlighting previously unrecognised patterns, but in quantifying and statistically analysing those patterns that were beginning to emerge from the ever increasing database.

Bear in mind the limitations described above, the data seem to indicate that, generally, during the entire Silurian, phytogeographical differentiation is decreasing progressively during this time period. Gondwana and North America/Baltica become closer longitudinally and also, but to a lesser extent, latitudinally. It is likely that these apparent contradictions are related to trilite sporoproducing plants becoming less climatically tolerant than the more primitive cryptospore-producing plants (e.g. Steemans 1999; Steemans et al. 2007).

Conclusions

The fossil record has much to inform us regarding the origin and adaptive radiation of land plants. As always, more data (i.e. more fossils increasing temporal and spatial coverage) are essential for improved interpretation. However, continual re-evaluation of the database is also imperative. This includes taxonomic revision, in addition to analysis of diversity, disparity, biogeography, etc., particularly as new methods and statistical techniques become available. However, key to successful interpretation of this fossil record as always involves understanding of its incompleteness and biases.

Plants and their spores are by far the richest fossil group from the continents. Potentially they provide invaluable data for palaeogeographical reconstructions in determining acceptable distances between continents to allow spores to colonize new areas. These constraints are especially important for longitudinal proximities between continents, but also, but to a lesser extent, for latitude. The early land plant fossil record is most satisfactorily explained by palaeocontinental reconstructions showing shorter distances between the continents.

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