Fire ecology of the Carboniferous tropical zone

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Abstract

Fossil charcoal (fusain), indicating the occurrence of wildfire, is common in the Carboniferous rocks of North America and Europe. During the Carboniferous these regions lay on the southern margins of the Laurasian continent and within the tropical zone. This study examines the facies distribution and botanical identity of charcoal in order to investigate the influence of fire on Carboniferous tropical ecology. New data from charcoal-bearing units in eastern Canada, Poland and the British Isles are presented and synthesised with previously published data of charcoal occurrence. Tournaisian–Visean charcoal-bearing strata were deposited in volcanic, lacustrine, alluvial plain and coastal marine environments. In these deposits, charred floras are dominated by (pro?)gymnospermous plants, whilst uncharred (compressed or permineralised) floras are dominated by lycopsids. Uncharred lycopsid remains were probably derived from wetland communities growing close to the depocentres, whilst charred gymnospermous remains may have been sourced from well-drained extrabasinal settings. Based on the vertical distribution of charcoal layers in annually (?) laminated lacustrine deposits, it is estimated that fires occurred with high frequency, approximately every 3–35 years. Palaeoclimatic analysis indicates that southern Laurasia at this time was subject to a seasonal (monsoonal) tropical climate. Such environments today are characterised by tropical savannas with high fire frequencies, and Early Carboniferous fire-prone gymnospermous plant communities may have represented a comparable vegetation biome. Namurian–Stephanian charcoal-bearing strata were deposited in alluvial plain, coastal plain and coastal marine environments. Channelised sandstone units, interpreted as river channel deposits, contain charcoal derived from cordaitalean and conifers. This assemblage records fires in extrabasinal coniferopsid forests. Mudstone units containing coals are interpreted as the deposits of floodbasins and peat mires. Hollow uncharred lepidodendrid stumps occur in this facies and contain lepidodendrid charcoal in the stump bases and lepidodendrid, pteridosperm, coniferopsid and sphenopsid charcoal outside the stumps. This assemblage records fires in wetland lepidodendrid-dominated forests. Lepidodendrid trunks, comprising of a spongy parenchymatous core surrounded by dense periderm, became hollowed out during fire events. An estimate of fire frequency based on the vertical spacing of charcoal layers in coals implies that fires occurred every 105–1085 years in the peat mires. Palaeoclimatic analysis indicates that southern Laurasia was subject to a humid tropical climate during the Late Carboniferous. Such environments today are characterised by tropical rainforests where fires occur rarely, and Late Carboniferous communities may have represented a comparable biome. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

The ‘tropical zone’ is defined in this paper as the geographical region between the Tropic of Cancer (23.5°N) and the Tropic of Capricorn (23.5°S) in which the sun is directly overhead at noon for at least part of the year. During the Carboniferous the continental plates were grouped into two supercontinents; Laurasia straddled the tropical zone, and Gondwana dominated mid-to-high latitudes in the Southern Hemisphere (Scotese and McKerrow, 1990). This paper considers the influence of wildfire on the ecology of tropical vegetation growing in southern Laurasia. The occurrence of wildfire at this time can be recognised by the presence of charcoal (the inert residue of burned vegetation) incorporated into sedimentary and volcanic rocks (Scott, 1989). Early workers called this substance fusain and came to conflicting conclusions about its origin. However, recent chemical and physical studies have demonstrated unequivocally that fusain represents fossil charcoal (Jones and Chaloner, 1991). Charcoal is abundant in the Carboniferous rocks deposited on the southern margins of the Laurasian continent (now Europe and North America), indicating that wildfires were common in the palaeotropical zone (Robinson et al., 1997). In spite of their evident importance, wildfires have received little consideration in previous Carboniferous palaeoecological studies (Scott and Jones, 1994). Nothing is known about fire–climate–vegetation dynamics or fire frequency and only a little about which plant communities were prone to fire (Scott et al., 1986; DiMichele and Phillips, 1994; Scott and Jones, 1994).

In this paper, burned fossil plant specimens, represented by anatomically preserved charcoal fragments, are identified with the aid of a scanning electron microscope. The composition and site of growth of fire-prone plant communities are determined through a comparison of charred and uncharred taxa within the context of sedimentary facies (Falcon-Lang, 1998a). Analysis of charcoal occurrence in rocks with a distinct temporal framework (e.g. annually laminated lacustrine deposits or coals) at some localities is used to estimate fire frequency. All these data are integrated within a regional palaeoclimatic framework in order to present the first preliminary synthesis of the fire ecology of the Carboniferous tropical zone. New data, together with critically reviewed published data, are presented from sites in eastern Canada, central USA, Poland and the British Isles (Fig. 1).

2. Lower Carboniferous charcoal

2.1. Palaeoenvironmental framework

Charcoal-bearing localities in the British Isles and eastern Canada, ranging in age from late Tournaisian (Ivorian, 352 Ma) to late Viséan (Brigantian, 333 Ma), are considered in this section (Fig. 1b and c). These sequences were deposited in lacustrine/coastal plain settings within a series of strike-slip, graben/half graben that opened up on the southeastern margins of Laurasia in response to the northward convergence of Gondwana (Fig. 2a; Calder, 1998).

In the near-equatorial British province (palaeolatitude, 4–13°S; Scotese and McKerrow, 1990), the occurrence of palaeosols such as calcretes (Vanstone, 1996; Andrews and Nabi, 1998), xero-rendzinas (Wright, 1983) and vertisols (Wright, 1990), schizohaline lagoonal facies (Leeder, 1974), playa-lake evaporites (Belt et al., 1967) and gymnosperm woods containing growth rings (Falcon-Lang, 1999a,b) provide strong evidence for marked seasonal variations in annual rainfall. In the eastern Canadian province, which lay closer to the margins of the tropical zone (palaeolatitude, 6–20°S; Scotese and McKerrow, 1990), calcrete palaeosols (Hamblin and Rust, 1989), laminated lacustrine sediments (Hamblin, 1992) and sequences of playa-lake evaporites (Belt et al., 1967) indicate that an even more pronounced seasonality in rainfall prevailed there. Tropical rainfall seasonality was probably caused by monsoonal circulation (Falcon-Lang, 1999a).

2.2. Clastic floodbasin deposits

As a consequence of this seasonally dry climate, many Early Carboniferous clastic floodbasins were well drained and were dominantly colonised by
Fig. 1. Location details of charcoal-bearing units described in this study. Closed circles indicate Lower Carboniferous sites; open circles indicate Upper Carboniferous sites. (a) Central USA, (b) Eastern Canada, (c) British Isles and (d) Southern Poland.

gymnospermous forests (Falcon-Lang, 1999a). For example, at Kingswater, northern England (Upper Border Group, late Viséan), large in situ stumps of the arborescent pteridosperm *Pituis* are preserved (Long, 1979). At another floodbasin sequence, Weaklaw, southern Scotland (Strathclyde Group, late Viséan), in situ stumps of *Pituis* again occur together with the remains of pteridosperms and ferns (Galtier et al., 1994). In addition, Vanstone (1993) has described rhizoconcretions from calcrete palaeosols from Guides Farm, northern England (late Viséan), which Falcon-Lang (1999a) interpreted as having been formed by (pro)gymnospermous forests. Charcoal is not encountered in any of these seasonally dry floodbasin units. However, it is known that charcoal breaks down under similar semi-arid conditions in present-day Australia, which perhaps explains its absence in these Carboniferous deposits (Skjemstad et al., 1996).

2.3. Volcanically influenced deposits

Volcanic activity was an important part of the landscape of Early Carboniferous northern Britain, a consequence of back-arc spreading in this region (Leeder, 1987). Charcoal occurs commonly in volcanic palaeoenvironments (Scott, 1990). At Kingswood, southern Scotland (Strathclyde Group, late Viséan), charcoal layers in lacustrine deposits often directly overlie thin pyroclastic units, suggesting that some of these
flora are dominantly gymnospermous (Bateman and Rothwell, 1990; Bateman and Scott, 1990).

2.4. Lacustrine deposits

Charcoal is particularly abundant in Early Carboniferous lacustrine deposits. At Horton Bluffs, Martock and Three Miles Plain, northeastern Nova Scotia (Horton Group, late Tournaisian), charcoal is dominated by (pro)gymnospermous material with rare lycopsids (Fig. 3a and b). This is in contrast to uncharred floras, which are lycopsid dominated. These data suggest that the remains of two distinct plant communities are mixed together in Horton Group lacustrine deposits: a fire-prone gymnospermous community and a lycopod-dominated community in which fire was a rare occurrence. Given that the occurrence of fire is strongly linked to edaphic drought (Beerling et al., 1998), it is likely that lycopod-dominated communities grew in wetland (possibly lakeside) niches, whilst fire-prone pteridosperm/ gymnosperm-dominated communities occupied well-drained sites.

A similar pattern is also found at several other charcoal-bearing lacustrine deposits. For example, at Kingwood, southern Scotland (Strathclyde Group, late Viséan), uncharred floras are dominated by lycopsids and gymnosperms, whilst charcoal is derived from gymnosperms, ferns and sphenopsids (Falcon-Lang, 1999a). At another Early Carboniferous lake deposit, East Kirkton, southern Scotland (Lower Limestone Group, late Viséan; Scott et al., 1994), a mixed plant assemblage is also present. Plant material is derived both from a (partly in situ) lake-margin lycopsid community, where fire was infrequent, and a fire-prone arborescent gymnosperm community (Scott et al., 1994). At Pettycur, southern Scotland (Strathclyde Group, late Viséan), uncharred floras are dominated by lycopsids and gymnosperms, whilst charcoal is derived from gymnosperms, ferns and sphenopsids (Falcon-Lang, 1999a). At another locality, Oxroad Bay, southern Scotland (Cementstone Group, late Tournaisian), lycopsids and gymnosperms locally occur as charcoal and are associated with floodbasin and volcanic mass-flow/base-surge deposits; uncharred
Fig. 3. Scanning electron photomicrographs of Early Carboniferous charcoal: (a)–(d) Nova Scotia; (e) and (f) Ireland. (a) Gymnospermous rachis, Three Miles Plain; (b) gymnospermous Rhodo-like pinnule, Three Miles Plain; (c) progymnospermous wood, reminiscent of Pityr, radial view, Blue Beach; (d) progymnospermous wood, tangential view, Blue Beach; (e) 'checking' in the tracheids of a pycnostylic gymnosperm wood, Creevagh Head; (f) growth ring in gymnosperm wood, transverse view, Creevagh Head.

nated by uncharred lycopsids, whilst the only charcoal illustrated by Scott and Rex (1987) from these localities is gymnosperm wood. In all these cases, pteridosperm/gymnosperm communities were considerably more fire prone than coeval lycopod-dominated communities. It is probable that all these gymnosperm/pteridosperm-dominated charcoal accumulations in Early
Carboniferous lacustrine deposits were derived from a dryland extra-basinal flora, whilst most lycopod material was derived from proximal wetland environments (Falcon-Lang, 1999a).

Crude estimates of Early Carboniferous fire frequency may be derived from lacustrine deposits at Martock, Nova Scotia (Horton Group, Late Tournaisian). Some of these units are micro-laminated, composed of sand-dominated lamina interbedded with algae-dominated lamina (lamina couplets). Distinct charcoal layers, representing discrete fire events, are found in these units and are vertically spaced six and 15 lamina couplets apart. Lamina couplets formed in most modern seasonal tropical lakes represent periods of deposition ranging from 0.5 to 2.36 years (Pilskaln and Johnson, 1991; Damnati et al., 1992; Talbot and Allen, 1996). Applying these modern values of sedimentation rate to the charcoal layer-spacing data, this implies a fire frequency in the order of 3–35 years for the Early Carboniferous gymnosperm-dominated plant community at Martock.

2.5. Fluvio-estuarine deposits

Units interpreted to represent fluvio-estuarine channel facies are common in Tournaisian-Visean sequences in Britain (Graham, 1996) and dominantly contain gymnospermous fossil plant remains (Scott and Rex, 1987). For example, at Craigleith Quarry, Edinburgh (late Visean; now infilled), abundant permineralised logs (>15 m long) belonging to the pteridosperm *Pitus* have been documented from units that may represent braided(?) river deposits (Witham, 1831). Charred plant fossils are also common and gymnosperm dominated. For example, at Creevagh Head, North Mayo, Ireland (Moyny Limestone Formation, early Visean), estuarine channel deposits contain abundant fragments of gymnosperm wood charcoal (Falcon-Lang, 1999b) that appear to have been derived from trees with slender trunks and moderate stature (Falcon-Lang, 1999b). Some of the wood fragments exhibit ‘checking’, a feature produced due to the wood drying out during drought (Fig. 3e). Others exhibit tree-rings indicating growth on well-drained soils and under seasonally dry climates (Fig. 3f; Falcon-Lang, 1999b).

At a further three localities, Shalwy Point, Muckros Head and Rinn Point in Donegal, Ireland (Shalwy Formation, early Visean), estuarine channel deposits bearing charcoal are also present. These contain, in roughly equal proportions, the charred axes of herbaceous lycopods and the wood of arborescent gymnosperms (Nichols and Jones, 1992). Finally, at Blue Beach, northeastern Nova Scotia (Horton Group, late Tournaisian), charcoal occurs in meandering fluvial channel deposits and consists largely of gymnospermous wood, some of which is reminiscent of *Pitus* (Fig. 3c and d), and a few fragments of lycopsid periderm.

2.6. Summary of Early Carboniferous fire-prone ecosystems

Early Carboniferous volcanic, lacustrine, fluviial, estuarine and floodbasin facies contain abundant charcoal. Charred floras are dominantly gymnosperms and were sourced from fire-prone communities that may have grown on well-drained soils outside the wetland depocentres. In addition, unstable volcanic environments may have been primarily colonised by fire-prone zygopterid fern communities. Fire in well-drained environments appears to have occurred with great frequency. Natural fire return intervals (NFRIs), i.e. the length of time between fire events at a single geographical site, are estimated to be in the order of 3–35 years. In contrast, uncharred floras contain a much higher proportion of lycopod material; this was probably sourced from plant communities living close to, or within, the wetland basinal environments where fires were uncommon.

3. Upper Carboniferous charcoal

3.1. Palaeoenvironmental framework

Charcoal-bearing units in Europe and North America, ranging in age from Namurian B (321 Ma) to Stephanian (290 Ma), are considered in this section (Fig. 1a–d). These sequences were deposited in lowland alluvial/coastal plain environments that extended over much of southeastern Laurasia during the Late Carboniferous (Fig. 2b; Calder, 1998).
At this time, more humid climates prevailed over the region compared with those of the Early Carboniferous. For example, in Britain (palaeolatitude, 1°N to 11°N; Scotese and McKerrow, 1990), the occurrence of widespread coals, with only intermittent well-drained palaeosols, indicates that humid to seasonally humid tropical climates prevailed (Broadhurst et al., 1980; Besly and Fieelding, 1989). In eastern Canada and the USA (palaeolatitude, 3°S to 5°S; Scotese and McKerrow, 1990), the occurrence of coals, interpreted as the product of rheotrophic mires, together with vertisols and calcretes, indicates that here the climate was seasonally humid (Calder, 1994, 1998). The transition from seasonal to more humid tropical palaeoclimates between the Early and Late Carboniferous is attributed to the formation of the equatorial Hercynian–Appalachian Mountain Chain during the Namurian. This would have caused orographic lifting of air masses and the fixation of the Intertropical Convergence Zone (ITCZ) close to the equator (Rowley et al., 1985; Wright, 1990), resulting in the breakdown of monsoonal circulation.

3.2. Peat mire deposits

Geographically and temporally, the deposits of peat mires (coals) dominate the sediment fills of most Late Carboniferous tropical basins. Permanently submerged central areas of the peat mires were colonised by monotypic stands of Lepidophloios. In contrast, marginal mire environments, characterised by emergent soils and elastic influence, supported a more diverse flora, dominated by lepidodendrids (Sigillaria, Lepidodendron and Paralycopodites), pteridosperms, tree ferns and sphenopsids (DiMichele and Phillips, 1994). Charcoal occurs abundantly in Late Carboniferous in situ permineralised stumps representing the remains of mixed-age, sigillarian (lepidodendrid) forests (Falcon-Lang, 1999c). The stumps are hollow and contain a dense, basal deposit composed of charred fragments of sigillarian periderm and parenchymatous tissues. Scattered around the outside of the stumps, lepidodendrid charcoal (periderm, secondary wood and leaves; Fig. 4b, c, e and f) is also present, together with the charred remains of medullosan pteridosperms.
Fig. 4. Scanning electron photomicrographs of Late Carboniferous charcoal, Joggins, Nova Scotia. (a) Dadoxylon-type pycnoxylic gymnospermous wood; (b) lepidodendrid periderm; (c) sclariformly thickened lepidodendrid wood; (d) manoxylc medullosan pteridospermous wood; (e) fragments of lepidodendrid leaf; (f) sclariformly thickened vascular strand in the lepidodendrid leaf shown in (e).

(Fig 4d), cordaitaleans and sphenopsids. Sigillarian trees were composed structurally of a central woody stele and a peripheral parenchymatous cortex, surrounded by a thick, woody periderm (Eggert, 1961). Falcon-Lang (1999c) interpreted these charcoal-stump associations at Joggins to have been formed by crown fires that tunneled out the parenchymatous central axis of the trunk. Charcoal then progressively fell off the remaining charred trunk cylinder, forming a dense
layer within the stump base and a diffuse layer around the outside. Similar lepidodendrid stump-charcoal assemblages have also been noted at Clifton, New Brunswick (Clifton Formation, Westphalian C), and Sydney, Nova Scotia (Sydney Mines Formation, Westphalian D), by Falcon-Lang (1999d). In addition, charred lepidodendrid roots have been described from the base of a coal seam at Sydney, Nova Scotia (Sydney Mines Formation, Westphalian D). This indicates that fires in peat mires were not restricted to aerial portions of the forests, but also locally burned the subsurface (Falcon-Lang, 1998a). Additional evidence for Late Carboniferous peatland ground fires has recently been presented by Petersen (1998).

Estimates of fire frequency in Late Carboniferous mires may be ascertained by examining the vertical spacing of charcoal layers in coals. For example, White et al. (1994) recorded 24 discrete charcoal layers in their analysis of the 144 cm thick Backpit Seam, Sydney, Nova Scotia (Sydney Mines Formation, Westphalian D), on average one charcoal layer every 6 cm. Hasquebard (1998) presented petrographic data from a further ten seams in the same Sydney region; in these coals the charcoal layers were spaced 10.9 to 22.2 cm apart. Estimates of the amount of time represented by Carboniferous coal seams have been calculated using data from modern peat accumulation rates and compaction coefficients (Stach et al., 1982; Broadhurst and France, 1986). Measurements of modern peat accumulation rates range from around 1 mm a⁻¹ in the subtropical reed swamps of Florida to 3–4 mm a⁻¹ in the equatorial swamp forests of Southeast Asia (Stach et al., 1982). Carboniferous bituminous coals, like those of Eastern Canada, have probably undergone an approximately seven-fold compaction since the peat accumulation, as indicated by the degree to which coal laminae are wrapped around uncompacted coal balls (Stach et al., 1982). Taken together, these data suggest that 1 year of Carboniferous peat accumulation is represented by 0.14–0.57 mm of coal. Applying these values to the charcoal spacing data above (6–22.2 cm), NFRIs for these Carboniferous peat mires may have been in the order of 105–1585 years.

3.3. Clastic floodbasin deposits

Charcoal is also found in mudstone units, interpreted as the deposits of clastic floodbasins. At Czerwionka, southeastern Poland (Orezeze Beds, Upper Mudstone Series, Westphalian B; Liptiarski, 1998), two examples of lepidodendrid stumps occur rooted in green mudstone units. One of these contains a dense basal deposit entirely composed of charred lepidodendrid periderm and parenchymatous tissue. Charcoal-bearing lepidodendrid trunks, 2 m high, rooted in grey-green floodbasin deposits have also been described from Joggins, Nova Scotia (Joggins Formation, Westphalian A) by Scott (1998) and Falcon-Lang (1999c). These two examples represent in situ lepidodendrid forest fire profiles similar to those described above; lepidodendrid fires were evidently not restricted to the peat mires, but also extended into clastic floodbasin regions.

At Swillington, Yorkshire, England (Coal Measures, Westphalian B), clastic splits in a coal seam contain large quantities of charcoal consisting of conifer, cordaitalean and pteridospermous leaves and Dadoxylon-type pycoxylar cordaitalean wood (Scott, 1978). In addition, volcanic airfall deposits associated with clastic floodbasin deposits at Kingswinford, West Midlands, England (Westphalian C) contain partially charred conifer-like stems (Galtier et al., 1992). It is unlikely that delicate leaf material preserved at Swillington would have been transported intact for long distances. Therefore, these allochthonous charcoal assemblages were probably derived from a variety of lowland settings within a few kilometres of the final site of deposition (Scott, 1978). These fire-prone gymnospermous communities probably occupied well-drained sites in the floodbasin or on top of the channel levees.

3.4. Fluvial channel deposits

Charcoal is abundant in Late Carboniferous river channel deposits. At Boss Point, Nova Scotia (Boss Point Formation, Westphalian A) up to
5.5 m thick, coarse-grained sandstone units occur, interpreted as the deposits of large, braided distributary channels in a delta top environment (Browne and Plint, 1994). They contain small (2–5 mm) charcoal fragments composed of *Dadoxylon*-type pycnoxylic cordaitalean wood (Falcon-Lang and Scott, 2000). At Joggins, Nova Scotia (Joggins and Springhill Mines formations, Westphalian A–B), up to 3.5 m thick, fine- to medium-grained sandstone units are present, interpreted as the deposits of anastomosing and meandering river channels in a coastal plain setting (Gibling, 1987). Charcoal fragments (1–2 cm in size) are abundant and comprised mainly of *Dadoxylon*-type pycnoxylic cordaitalean wood (Fig. 4a) together with rare wood charcoal fragments derived from early conifers (Falcon-Lang, 1999c). At Czerwionka, south-eastern Poland (Oreszce Beds, Upper Mudstone Series, Westphalian B), a 4 m thick sandstone unit, interpreted as the deposit of a large meandering fluvial channel occurs (Gradzinski et al., 1982). This contains rare 1–2 cm fragments of *Dadoxylon*-type pycnoxylic cordaitalean wood. At Clifton, New Brunswick (Clifton Formation, Westphalian C) a small (1.5–2 m thick), straight channelised sandstone unit cutting down into an underlying coal seam is exposed in low sea-cliffs. This is interpreted as a river channel that incised into a peat mire deposit during flood discharge (Leguin and Rust, 1982; Falcon-Lang, 1999a). It contains 1–2 cm lepidodendrid periderm charcoal attached to coal fragments (evidently reworked from the coal seam) together with rare (<1 cm) fragments of *Dadoxylon*-type cordaitalean wood. Large braided river channel deposits also occur at Clifton and contain a mixture of lepidodendrid periderm charcoal and pycnoxylic gymnosperm charcoal (Falcon-Lang, 1998a). At Sydney, north-eastern Cape Breton, Nova Scotia (Sydney Mines Formation, Westphalian D), there are multi-storey channelised sandstone units; these are interpreted as the fluvial channel deposits of up to 20 m deep palaeovalleys (Gibling and Bird, 1994). These contain common (1–2.5 cm) charcoal fragments of unidentified pycnoxylic gymnospermous wood.

Studies of charcoal taphonomy in modern fluvial systems demonstrate that all these ancient river channels would have had the potential to transport charcoal from tens of kilometres away and, in the case of the palaeovalleys of Sydney, perhaps from hundreds of kilometres away (cf. Blong and Gillespie, 1978). Transported clasts of calcrite are associated with many of the charcoal-bearing channel deposits described here (Falcon-Lang, 1999c), which further implies that fire-prone coniferopod forests may have grown in well-drained environments (Goudie, 1983). In addition, recent work has suggested that some tree-sized cordaitaleans and conifers may have formed mesic forests in geomorphically sensitive upland terrains during the Late Carboniferous (Falcon-Lang, 1999a; Falcon-Lang and Scott, 2000). It is therefore concluded that the coniferopod charcoal may have been derived from extrabasinal cordaitalean/conifer fires, in some cases perhaps from upland environments deep within the hinterland.

3.5 Coastal marine deposits

Charcoal also occurs in Late Carboniferous coastal marine facies. For example, charcoal is present in Namurian B coastal marine units at Starwood, Staffordshire, England. Here floras are dominated by cordaitaleans and pteridosperm remains and contain some elements that are charred (Scott et al., 1997). In addition, numerous Late Westphalian/Stephanian localities in Kansas and Texas associated with near-shore marine and estuarine palaeovalley deposits contain charcoal (Baxter and Hartman, 1954; Cunningham et al., 1993; Mapes et al., 1997). Charcoal fragments are up to 5 cm in size and dominantly derived from walchian conifers, together with cordaitalean and pteridosperm material. In both these examples, palaeobotanic and taphonomic data indicate that these charcoal deposits were derived from fires in seasonal, well-drained upland communities (Scott et al., 1997; Mapes et al., 1997).

3.6 Summary of Late Carboniferous fire-prone ecosystems

Late Carboniferous lowland environments were dominated by widespread peat mires. In situ charcoal in these mire deposits attests to the rare occurrence of lepidodendrid-medullosan fires with
NFRIs in the order of 105–1085 years. Charcoal in elastic floodbasin deposits is mainly allochthonous and appears to have derived from fires in conifer, cordaitalean, and pteridosperm-dominated communities growing in the floodbasin or on nearby levées. Finally, river channel, estuarine channel and coastal marine deposits contain charcoal that probably has been transported from upland coniferous forest fires.

4. Discussion

4.1. Modern tropical fire ecology

Two main vegetation biomes characterise the modern tropical zone: everwet climatic zones support dense rainforests, whilst seasonally dry zones support closed semi-deciduous forests to open savannas (Walter, 1973). Fires occur in both these biomes and to differing degrees exert an important influence on their ecology (Goldammer, 1990). Fires occur with the lowest frequency in humid (>2500 mm a\(^{-1}\) rainfall) rainforests; estimates of NFRIs for such ecosystems range from 389 to 1540 years (Sanford et al., 1985; Saldarrriaga and West, 1986). Uhl et al. (1988) have demonstrated that this low fire-frequency is related to high fuel moisture content, not biomass density. Sufficient humidity to prevent fuels from drying out is usually maintained, even during periods of drought, due to high levels of evapotranspiration (Salati, 1987). When rainforest fires do occur, they are often associated with severe droughts, such as those linked to the El Niño Southern Oscillation (Goldammer and Seibert, 1990). Kauffman and Uhl (1990) noted that rainforest vegetation displays few adaptations to fire survival, implying that fire occurrence has always been rare in this ecosystem. In contrast, fire is a frequent phenomenon within seasonal tropical biotas where rainfall typically ranges from 200 to 1800 mm a\(^{-1}\) (Gillon, 1983). Grasslands predominate at the drier end of this rainfall gradient and are subject to NFRIs of 1 to 10 years (Lacey et al., 1982; Gillon, 1983), whilst semi-deciduous forests predominate at the wetter end and experience NFRIs of >90 years (Goldammer, 1992). Most plants in seasonal tropical savannas exhibit an array of fire-adaptive traits, indicating that fire has operated as an important selection pressure throughout the evolution of this biome (Gill, 1981).

4.2. Early Carboniferous savannas

From the above it is clear that rainfall seasonality and intensity exerts the largest impact on tropical fire ecology. Evidence documented here suggests that, during the Early Carboniferous, the operation of monsoonal circulation favoured the widespread development of seasonal tropical environments in Britain and eastern Canada. These settings were dominated by gymnospermous-dominated ecosystems that were subject to high-frequency fire events (NFRIs in the order of 3–35 years). Lycopsid-dominated plant communities only existed in narrow zones of waterlogged soils along the margins of standing water bodies. This phytogeographic reconstruction, however, is in contrast to previous biogeographical studies, which have suggested that during the Early Carboniferous a uniform flora dominated by arborescent lycopsids extended worldwide (Chalonier and Lacey, 1973; Chalonier and Meyen, 1973). These reconstructions, however, have been based on compression floras that are taphonomically biased towards those plants living in wetland deposition centres (Scott, 1979).

On the basis of high fire-frequency data and the xeromorphic character of the vegetation (Falcon-Lang, 1999a), Early Carboniferous gymnospermous plant communities are interpreted to represent seasonal tropical savanna-like biomes (Fig. 5a). A good parallel to Early Carboniferous southern Laurasia may be modern-day East Africa, where climate is characterised by uniform temperatures and low, seasonal rainfall (Nieuwolt, 1974). Here, well-drained soils are geographically widespread and support savanna vegetation. However, large freshwater lakes (such Lake Victoria) also occur and support narrow, dense zones of papyrus (non-savanna) vegetation on the waterlogged lake-margin soils (Lind and Morrison, 1974).
Fig. 5. Interpretation of Carboniferous fire ecology and phytogeography: (a) Early Carboniferous; (b) Late Carboniferous.
4.3. Late Carboniferous rainforests

During Late Carboniferous times, rather humid tropical climates prevailed over Britain, Poland, central USA and eastern Canada, which encouraged the growth of dense, luxuriant forests. Fire frequency in lowland peat mire environments appears to have been very low (NFRIs in the order of 105–1085 years), and these plant communities may have resembled modern tropical rainforests. Charcoal encountered in river channel deposits may have been sourced from higher-frequency fire events in upland or extrabasinal regions (Fig. 5b). Tropical montane or submontane zones often experience higher fire frequencies than coeval lowland vegetation because climate at altitude is more seasonal (Goldammer and Penafiel, 1990). It is possible that the same was true for Upper Carboniferous coniferopod upland vegetation; however, there is no obvious way to estimate fire frequency for these communities.

It is significant that estimates of NFRIs for Late Carboniferous lowland rainforests (105–1085 years) are closely similar to modern values (389–1540 years). This observation is in marked contrast to the results of numerical modelling by Beerling et al. (1998), who suggested that equatorial fire frequency in the Late Carboniferous well-drained habitats would have been in the order of 3–6 years, two to three orders of magnitude greater than the findings of this study. This exceptionally high fire frequency was predicted because they incorporated into their model a palaeoatmospheric oxygen concentration of 35%, derived from the atmospheric model results of Berner and Canfield (1989). These data may be partly reconciled in two ways. First, fire frequencies estimated here were for wetland peat mire environments and, therefore, are likely to be considerably lower than that for the coeval well-drained settings that Beerling et al. (1998) modelled. Second, atmospheric oxygen levels may have been considerably lower than those suggested by Berner and Canfield (1989).

5. Conclusions

(1) Charcoal is abundant in the Carboniferous sequences of Europe and North America, indicating that fire played a significant role in influencing the ecology of Carboniferous tropical plant communities. Changing climate appears to have exerted the largest impact on Carboniferous tropical fire ecology.

(2) Early Carboniferous tropical climates were seasonal, with at least one rainy season and one dry season each year. Gymnospermous plants were dominant in this tropical environment and were subject to high-frequency fire events (NFRIs in the order of 3–35 years). These fire-prone communities may have resembled modern seasonal tropical savannas.

(3) Late Carboniferous tropical climates were much more humid, with only a little seasonality in rainfall. In this environment, dense, lowland leptodendroid forests were geographically widespread and burned very infrequently (NFRIs in the order of 105–1085 years). Pteridosperm, cordaitalean and conifer vegetation appears to have dominated on channel levies and in upland terrains; these communities may have experienced higher fire frequencies. Late Carboniferous plant communities may have resembled modern humid tropical rainforests, where fire is extremely rare.

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