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Silurian wildfire proxies and atmospheric oxygen

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ABSTRACT

The earliest evidence of wildfire is documented from two localities: the early mid-Silurian Pen-y-lan Mudstone, Rumney, Wales (UK), and the late Silurian Winnica Formation, Winnica, Poland. Nematophytes dominate both charcoal assemblages. Reflectance data indicate low-temperature fires with localized intense conditions. Fire temperatures are greater in the older and less evolved assemblage. These charcoal assemblages and others, new and previously documented, from the Silurian and earliest Devonian are compared to box models of atmospheric oxygen concentration ($p\mathrm{O}_2$). Based on modern charring experiments, these data indicate $p\mathrm{O}_2$ is divergent from the broad trends predicted by the COPSE-revisited and GEOCARBSULFOR models. Sustained burns require a minimum $p\mathrm{O}_2$ threshold of 16%, or ~0.75 present atmospheric level. This threshold was first met and, our charcoal data indicate, was exceeded in the mid-Silurian and then, later in the Silurian, attained again repeatedly.

INTRODUCTION

Atmospheric oxygenation has played a fundamental role in Earth systems since the Great Oxygenation Event (ca. 2.5–2.3 Ga; Bekker et al., 2004). Geochemical proxies indicate a soil-forming microbial cover, established by ca. 850 Ma (Kump, 2014), contributed to increasing atmospheric oxygen concentration ($p\mathrm{O}_2$). Atmospheric oxygen levels remained low until the mid-Ordovician advent of embryophytes, as evidenced by phytodebris (Wellman and Strother, 2015). These spore producers coexisted in a predominantly microbial biome (Wellman and Strother, 2015), where fungi acted as both decomposers and mycorrhizal symbionts, potentially accelerating the photosynthetic potential of embryophytes and green algae (Berbee et al., 2020). Nonvascular and vascular land plants evolved gradually in this landscape. The earliest vascular plant, *Cooksonia*, is preserved in the mid-Silurian (Wenlock, 433.4–427.4 Ma) rocks of Ireland (Edwards and Feehan, 1980) and the Czech Republic (Libertín et al., 2018). These diminutive (<10 cm high), leafless, dichotomously branched plants terminated in sporangia and grew alongside an enigmatic, globally distributed group, nematophytes.

Nematophytes vary from sub-millimetric to multi-meter-long structures (e.g., *Prototaxites*). All are united anatomically by aggregations of tubes and cuticles in a bound plant body. Their function and ecological role are unclear. Some are considered ascomycetes (fungi), and others are considered lichenized fungi (Wellman and Ball, 2021). If fungal, then nematophyte chitinous cell-wall chemistry would have differed from the cellulose, hemicellulose, and lignin of embryophytes. Most charring experiments focus on embryophytes (e.g., Belcher et al., 2010), though data exist from bracket fungi (Scott and Glasspool, 2005), with which *Prototaxites* has been compared (Boyce et al., 2007). Fungal cells must be charred at higher temperatures to produce the same reflectance values found in embryophytes (see the Supplemental Material[1]).

The geobiosphere was altered fundamentally through embryophyte diversification and feedbacks on Earth systems (Kenrick et al., 2012). Increased photosynthesis impacted the oxygen cycle, raising $p\mathrm{O}_2$ to near present atmospheric level (PAL) (Kump, 2014; Lenton et al., 2016). Agreement exists that terrestrialization impacted $p\mathrm{O}_2$, but no consensus exists as to the timing of its rise to near PAL. Predictions vary from the Neoproterozoic (>550 Ma; Och and Shields-Zhou, 2012) to the Phanerozoic (300 Ma; Krause et al., 2018). The Phanerozoic transition is marked by a switch from widespread marine anoxia to oxygenation (435–392 Ma; Dahl et al., 2010). However, for elevated $p\mathrm{O}_2$ to have persisted, a basic and continued change must have occurred to either increase the generation of free oxygen or decrease its sink (see Kump, 2014; Lenton et al., 2016). Evidence of fire (charcoal) is used as a proxy for $p\mathrm{O}_2$ (Glasspool et al., 2015) and provides an absolute minimum-burn threshold (Belcher and McElwain, 2008). Hence, fire is important for interpreting changes in atmospheric oxygenation.

Charcoal constrains $p\mathrm{O}_2$ in the range ∼0.7–1.4 PAL (Belcher et al., 2010). Its earliest occurrence is synchronous with a Silurian–Devonian shift of the molybdenum-isotope record (Dahl et al., 2010). Intervals, such as the Devonian "charcoal gap", exist where charcoal data are scarce (Fig. 1; Scott and Glasspool, 2006; Lu et al., 2021). Another such interval is the Silurian. Three widely used $p\mathrm{O}_2$ box models (GEOCARBSULF: Berner, 2009; COPSE-revisited: Lenton et al., 2018; GEOCARBSULFOR: Krause et al., 2018) support a steep $p\mathrm{O}_2$ rise to a peak initiated in the mid-Ordovician. A steep decline is predicted beginning in the Lochkovian (Krause et al., 2018, their figure 3). The rise is linked to the spread of cryptogamic cover (Lenton et al., 2018) and is consistent with reports of fire through this interval (Glasspool et al., 2015).

We report charred phytoclast (Gastaldo, 1994) remains from the Homerian and Ludlow (mid- to late Silurian) extending the burn record back 10 m.y. We used data from the Pen-y-lan Mudstone at Rumney, Wales (UK), and the Winnica Formation at Winnica, Poland (Fig. 1; see the Supplemental Material), to examine $p\mathrm{O}_2$ box models. We demonstrate that $p\mathrm{O}_2$ reached sufficient levels to sustain wildfire in the mid- to late Silurian and that it implies elevated concentrations.

RESULTS

Rumney

Nematophytes and *Pachytheca* (Fig. 2B) dominate the organic residues of the Rumney specimen morphotypes (Table S5 in the Supplemental

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[1] Supplemental Material. Localities and age assignments, observations on charcoal, methods, Figure 3 locality details, data tables, and supporting figures. Please visit https://doi.org/10.1130/GEOL.S.19878280 to access the supplemental material, and contact editing@geosociety.org with any questions.

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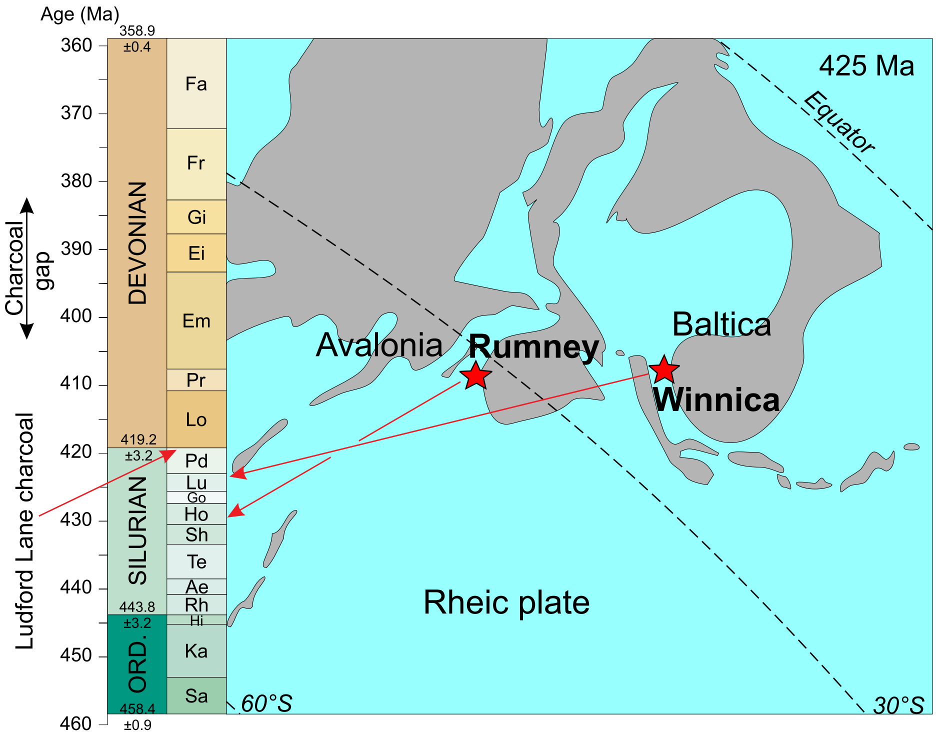

Figure 1. Silurian paleogeography with Rumney (Wales, UK) and Winnica (Poland) localities plotted against International Geological Congress (IGC) time scale version 2021.7 (Cohen et al., 2013). Abbreviations: Ord.—Ordovician; Sa—Sandbian; Ka—Katian; Hi—Hirnantian; Rh—Rhuddanian; Ae—Aeronian; Te—Telychian; Sh—Sheinwoodian; Ho—Homerian; Go—Gorstian; Lu—Ludfordian; Pd—Přídolí; Lo—Lochkovian; Pr—Pragian; Em—Emsian; Ei—Eifelian; Gi—Givetian; Fr—Frasnian; Fa—Famennian.

Material). Vitrinite from eight samples of the 314.71–316.3 m borehole interval (Rumney Borehole, drilled to 317.39 m by the British Geological Survey in 1978; 51°30’23.9"N, 3°08’18.6"W) indicate a mean random reflectance of $R_o = 1.08\%$ (medium to high volatile bituminous A), and that from 15 clasts of the 316.3–317.39 m interval indicate $R_o = 1.10\%$; the mean of both data sets is $R_o = 1.10\%$.

Fire-impacted reflectances range from near those of vitrinite to as high as $R_o = 5.61\%$; 20 samples have $R_o \geq 2\%$. Charred fragments indicate fire temperatures (T) ranging from *w*410–*w*730 °C or *g*440–*g*940 °C (calibrated against wood [prefix *w*, Equation S1 in the Supplemental Material] and the fungus *Ganoderma* [prefix *g*, Equation S2]; Table S6). The mean temperature (mT) of 48 phytoclasts is *w*490 °C (*g*540 °C). Recorded temperatures are greater than those at Winnica. The temperature range has a long, sparsely populated positive skew. Thirteen (13) specimens record $T >$ *w*500 °C (*g*540 °C), five record $T >$ *w*600 °C (*g*750 °C), and three record $T >$ *w*700 °C (*g*900 °C) (Table S5). The $T >$ *w*/*g*500 °C specimens are *Pachytheca*, nematophytes, or prototaxodioids (where specimens cannot be differentiated between *Prototaxites* and *Nematasketum*, we term them “prototaxodioids”, e.g., Fig. 2A). The $T >$ *g*700 °C materials are prototaxodioids or detritus of probable prototaxodioids.

Winnica

The majority of phytoclasts from Winnica (specimens collected in ca. 2013 from small outcrops on either side of the Słupianka stream near Winnica, in the Kielce region of Poland; 50°52’24.5"N, 21°6’16.5"E) are nematophytic (79%); none are demonstrably tracheophytic (Table S5). Taxa include undifferentiated prototaxodioids (*Nematasketum* or *Prototaxites*), nematothalloids (including *Nematothallus* or *Tristratothallus*; Fig. 2C), and aggregates of different-sized tubes (Fig. 2D; Table S5). In incident light, fossils differ in color (brown to matte-black gradient) and luster, and exhibit characteristics of charring (see the Supplemental Material). Scanning electron microscopy and reflected light microscopy confirm these observations (Table S5). Vitrinite in strew mounts indicate $R_o = 0.93\%$ (high volatile bituminous A; Teichmüller, 1987). Of the phytoclasts with anatomy, 32 had $R_o \geq 2\%$ (maximum 4.78%) which, if attributable to rank maturation, approaches that of meta-anthracite (Teichmüller, 1987). However, this charcoal burned at predominantly low temperatures; 82 specimens calibrated against both wood and *Ganoderma* indicate a mT of *w*480 °C (*g*520 °C) (see Tables S1–S6 and Figs. S2–S5B). The greatest T recorded in a specimen is *w*640 °C (*g*820 °C), while 30% of the samples record $T \geq$ *w*500 °C (*g*540 °C) (Table S5).

DISCUSSION

Fire plays a multifaceted role in Earth history. Increasing Paleozoic pO_2 was integral in metazoan evolution and radiation (Lenton et al., 2014). Pinpointing the timing of thresholds for sustaining life on land is critical to understanding the biosphere. Elevated pO_2 allows aerobes to prosper through the enzymatic combustion of organics, though free radicals are deleterious. Cyanobacterial nitrogenase is particularly sensitive to oxygen and may have driven the early symbiotic evolution of cyanobacteria (e.g., *Nematothallus,* a lichenized fungus; Wellman and Ball, 2021), notably if pO_2 was elevated (Rikkinen, 2017). Fire data (Fig. 3) are indicative of pO_2 elevated to or above PAL at points from the Wenlock to earliest Devonian. Elevated pO_2 may justify the proliferation of lichenized fungi documented from the latest Silurian.

Fire had a strong effect on pO_2 through actions on weathering, runoff, erosion, and organic carbon burial, affecting phosphorous input to oceans (Kump, 2014). Several coarse-resolution pO_2 box models explore when such thresholds might have been attained (e.g., Brand et al., 2021). The charcoal record contributes to understanding when pO_2 reached this threshold.

Latest Silurian fire was documented first from Ludford Lane, Welsh Borders (Glasspool et al., 2004; Fig. 3). However, material shown by Niklas and Smocovitis (1983, their figures 20 and 22–25) from the Massanutten Sandstone, Passage Creek, Virginia (USA), may be charred (this and other localities are discussed in the Supplemental Material). If confirmed, this record would extend fire activity to the early Llandovery (ca. 441 Ma; Tomescu et al., 2009). Other Silurian and earliest Devonian (e.g., North Brown Clee Hill; Glasspool et al., 2006) charcoal exists in the Welsh Borders, and these and more regional data are herein confirmed (Fig. 3; see the Supplemental Material discussion). Our Rumney and Winnica data add to this record, pushing the fire threshold back to at least the early Wenlock (ca. 430 Ma).

High-amplitude carbon isotopic excursions, including the Wenlock to Přídolí, indicate the global carbon cycle was more frequently and severely perturbed during the Silurian than during any other Phanerozoic period (Frýda et al., 2021). Given the carbon and pO_2 feedbacks (Lenton et al., 2018), pO_2 oscillations could be expected due to the scale of carbon perturbations. The general trends of pO_2 models (Fig. 3; GEOCARBSULF: Berner, 2009; COPSE-reloaded: Lenton et al., 2018; GEOCARBSULFOR: Krause et al., 2018) are roughly comparable. These models have coarse resolution, and predictions of pO_2 are typically binned at 10 m.y. intervals. Hence, such binning cannot resolve high-frequency events such as the global carbon cycle perturbations predicted by Frýda et al. (2021). Conversely, single-point data, such

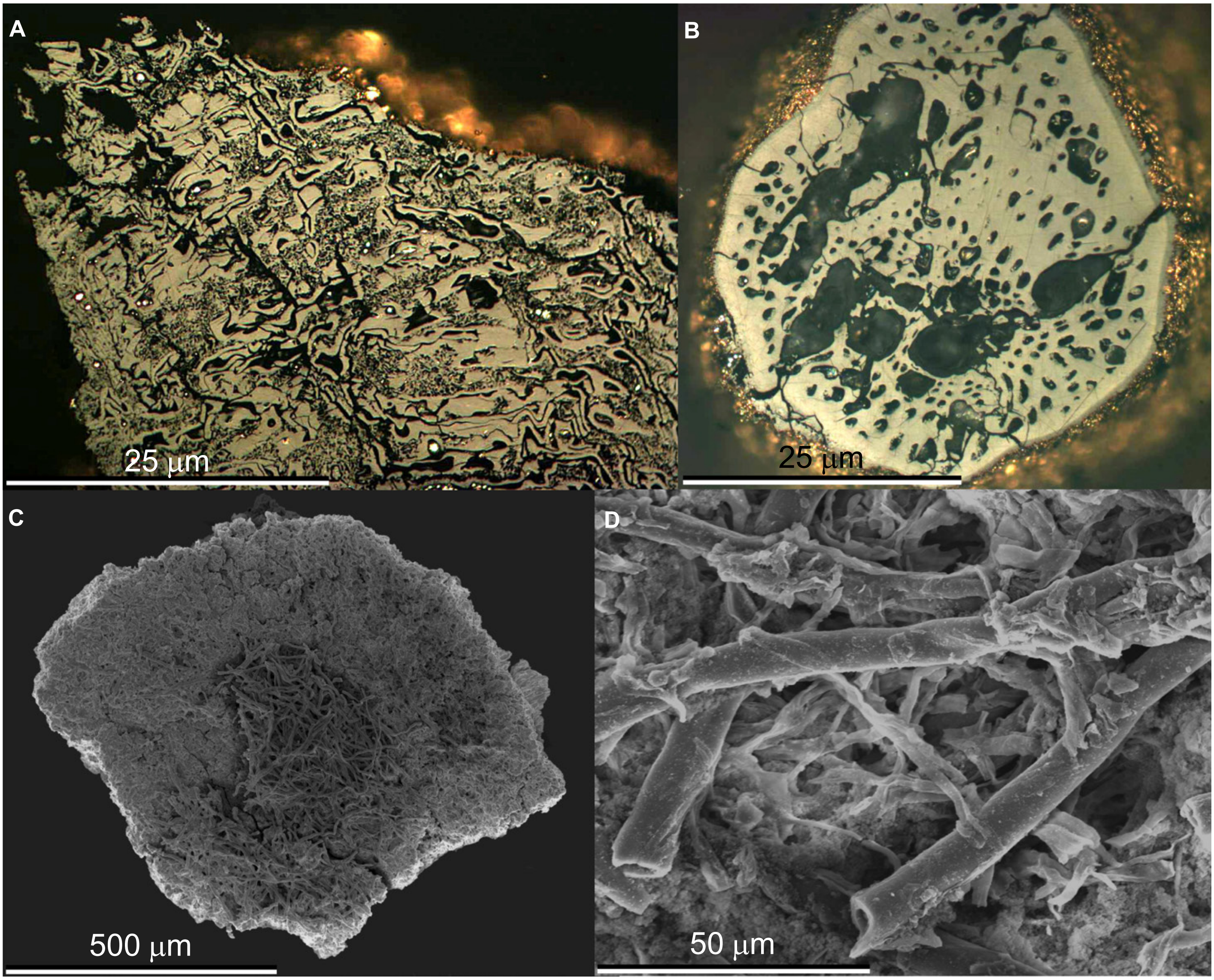

Figure 2. Select charred phytoclasts: Rumney (Wales, UK) nematophytes in reflected light (A,B) and scanning electron microscopy images of nematophytes from Winnica (Poland) (C,D). (A) High reflectance and brittle fracture in *Prototaxites*. (B) Outer cortex of *Pachytheca*. (C) Trilayered nematophyte cf. *Tristratothallus*. (D) Aggregation of small and large tubes.

as individual fire events, do not disprove model predictions at their broad 10 m.y. scale, though they do not preclude high-frequency fluctuations. However, fire regime data across longer intervals can cast doubt on model predictions. The data herein begin to establish this regime.

Box models show discrepancies in predictions of Late Ordovician to Early Devonian pO_2 amplitude. During this interval, the COPSE-reloaded model's best estimate predicts $pO_2 < 15\%$, a level discordant with the record of Silurian and earliest Devonian fire at this time (Fig. 3). For a dry natural fuel, a 16% pO_2 threshold is required for ignition and self-sustaining combustion (Belcher et al., 2010). The record of fire is also discrepant with the GEOCARBSULFOR model's best estimate (Krause et al., 2019), which models pO_2 at 420 Ma $<18\%$, a predicted threshold for the ignition and support of small fires but only where rainfall is "very low" and/or the fuel "seasonally very dry" (Belcher et al., 2010). Fire is not precluded at $pO_2 <18\%$ but, given the diminutive and hydrophilic nature of the Silurian fuel, it is highly unlikely. Early Homerian charcoal from Rumney and from the Gorstian of Nant Cwm-Ddu, Wales (under preliminary investigation; see the Supplemental Material), representing a time when *Baragwanathia* was an embryophytic "giant" (Gensel et al., 2020), is more incongruent with pO_2 predictions for this earlier interval, which fall at or below 15% (Lenton et al., 2018; Krause et al., 2019; cf. Belcher et al., 2010, their figures 2 and 4). At Rumney, the proportional volume of charcoal recovered from a marine setting indicates the extensive propagation of fire. This is concordant with pO_2 levels that approached PAL earlier than the latest box models predict (Lenton et al., 2018; Krause et al., 2019) and are in line with GEOCARBSULF (Berner, 2009).

Most Rumney data indicate low-temperature fire ($\bar{x}$ [mean]: R_o 2.31% = *w*490 °C; Table S6), but 30% of the inertinite is calculated to have formed at > *w*500 °C, and 6% at > *w*700 °C. Calibration of fire temperature using data from Hudspith et al. (2014; Tables S3–S4) increases this to 79% > *w*500 °C, 11% > *w*800 °C, and 4% > *w*900 °C. Experimental charring of the chitinous bracket fungus *Ganoderma* (Scott and Glasspool, 2007; Table S2), compared with composite lignin-rich data from Scott and Glasspool (2005; Table S1), indicates that this fungus requires higher burn temperatures (40–85 °C greater) to generate comparable reflectance values (Table S5). At Rumney, the highest reflectances are recorded in fragmented nematophytes.

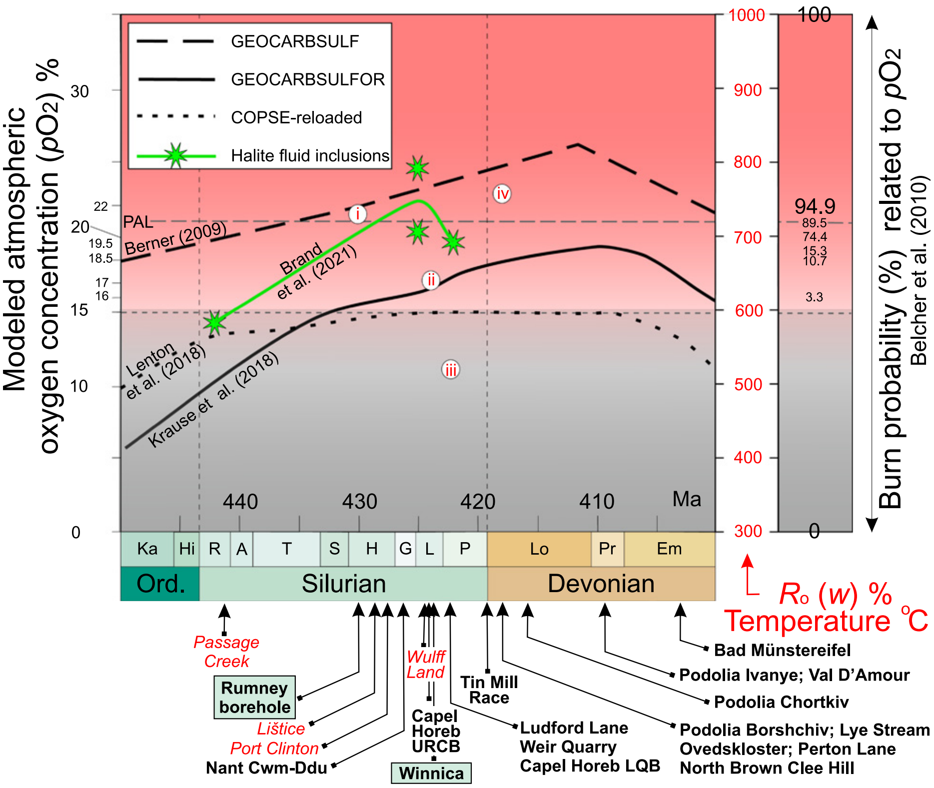

Figure 3. Silurian–Devonian charcoal plotted against three common models of Paleozoic pO_2 and back-calculated measurements (green line) of pO_2 in halite fluid inclusions. pO_2 (%) and probability of ignition and sustained burn of plant matter are after Belcher et al. (2010). Temperatures using Equation S1 (see footnote 1) (calibrated against wood [*w*]) are applied to vitrinite reflectance (R_o %). Localities (see the Supplemental material [see footnote 1]) where charred phytoclasts are observed are labeled in black, unconfirmed localities are labeled in red. White circles indicate maximum fire temperature from R_o % at Rumney (Wales, UK), *w*730 °C (i); Winnica (Poland), *w*640 °C (ii); Ludford Lane (Welsh Borders), *w*520 °C (iii); and North Brown Clee Hill (Welsh Borders), *w*760 °C (iv) (Table S6). Abbreviations: PAL—present atmospheric level; A—Aeronian; Dev.—Devonian; Em—Emsian; G—Gorstian; H—Homerian; Hi—Hirnantian; Ka—Katian; L—Ludfordian; Lo—Lochkovian; LQB—Long Quarry Beds; Ord.—Ordovician; P—Přídolí; Pr—Pragian; R—Rhuddanian; S—Sheinwoodian; T—Telychian; URCB—Upper Roman Camp Beds.

Early Homerian fire temperatures > *g*700 °C may seem improbable due to the impoverished potential embryophyte fuel load. However, very high reflectances for nematophytes, a group with demonstrable fungal and lichenized-fungal affinities (Wellman and Ball, 2021), lend support that these temperatures were attained.

Trends for pO_2 based on Silurian halites suggest atmospheric levels rose then fell between 442 and 422 Ma (Brand et al., 2021; Fig. 3). Back-calculated measurements for pO_2 at 442 Ma are 14.3% ± 1.7%; at 425 Ma, 20.4% ± 6.6% and 24.7% ± 3.7%; and at 422 Ma, 19.8% ± 2.1%. The charring events at Winnica (Ludlow, ca. 424 Ma; mT = *w*480 °C; Table S6) and Ludford Lane (Přídolí, ca. 423 Ma; R_o 1.03%–2.74%; $\bar{x}$ = 1.67%; mT = *w*450 °C; Table S6) align with these data. The occurrence of fire in the Gorstian at Nant Cwm-Ddu also aligns with these data. The locally intense early Silurian burns are discordant with the coarse amplitudes of GEOCARBSULFOR (Krause et al., 2018) and COPSE-reloaded (Lenton et al., 2018) through this time interval.

At present, in most tropical settings, phosphorus is the major limiting nutrient, while this role falls to nitrogen at higher latitudes (Du et al., 2020). The predominant drivers of these phenomena are mean annual temperature and precipitation, seasonality of temperature and precipitation (climatically driven), and soil-clay fraction (Du et al., 2020). The same criteria would have impacted our low-latitude Silurian sites (Fig. 1), where phosphorus could be predicted to have been the limiting factor on primary productivity. Fires would have mobilized phosphorus from the terrestrial to marine realms, promoting algal photosynthesis and increased levels of pO_2 (Kump, 2014). However, intense or frequent fires impact biocrusts in modern cold desert ecosystems, resulting in complete loss of the bacterial community and recovery times of decades for the pre-fire flora (Aanderud et al., 2019). In the Silurian, these crusts included cyanobacteria, algae, lichenized fungi, and early, diminutive embryophytes (Wellman and Ball, 2021). We propose that the locally intense burn temperatures, documented at Rumney in the early Homerian and to a lesser extent at Winnica in the Ludlow, demand levels of pO_2 equivalent to, or possibly above, PAL. At such levels, fires must have been a significant global phenomenon, having a strong negative effect on the photosynthetic biocrustose flora. It seems probable that the relationship between pO_2 and other Earth system processes continued throughout the Silurian until the development of a more embryophytically dominant flora.

CONCLUSIONS

Charcoal from early Homerian strata at Rumney, Wales, extends the earliest record of fire on Earth back a further 10 m.y. to ca. 430 Ma. The frequency of charcoal data from Silurian sequences indicates that fires were not rare but an established part of the terrestrial biome from at least the Wenlock onward. Compiling the reflectance data of our study with that of Ludford Lane (Welsh Borders; Glasspool et al., 2004) indicates the most intense Silurian fires occurred in the least-evolved ecosystems. The Devonian charcoal gap conforms to box-model forecasts of pO_2 decline to <16% prior to the Late Devonian rise of higher vascular plants. This coincidence may imply the feedbacks moderating pO_2 within the fire window differed in the Silurian. Our data further indicate that geochemical models for the Silurian still require refinement before they accurately reflect the amplitude of pO_2 at that time.

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