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DOES FUEL TYPE INFLUENCE THE AMOUNT OF CHARCOAL PRODUCED IN WILDFIRES? IMPLICATIONS FOR THE FOSSIL RECORD

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Abstract: Charcoal occurrence is extensively used as a tool for understanding wildfires over geological timescales. Yet, the fossil charcoal literature to date rarely considers that fire alone is capable of creating a bias in the abundance and nature of charcoal it creates, before it even becomes incorporated into the fossil record. In this study we have used state-of-the-art calorimetry to experimentally produce charcoal from twenty species that represent a range of surface fuels and growth habits, as a preliminary step towards assessing whether different fuel types (and plant organs) are equally likely to remain as charcoal post-fire. We observe that charcoal production appears to be species specific, and is related to the intrinsic physical and chemical properties of a given fuel. Our observations therefore suggest that some taxa are likely to be overrepresented in fossil charcoal assemblages (i.e. needle-shed conifers, tree ferns) and others poorly represented, or not preserved at all (i.e. broad shoot-shed conifers, weedy angiosperms, shrub angiosperms, some ferns). Our study highlights the complexity of

charcoal production in modern fuels and we consider what a bias in charcoal production may mean for our understanding of palaeowildfires.

Keywords: fuel type, wildfires, experimental, charcoal, fossil charcoal

Wildfires have been an important component of terrestrial ecosystems for the past 420 million years (Glasspool *et al.* 2004; Belcher *et al.* 2013). Despite the annual occurrence of conflagrations over approximately 3% of the terrestrial biosphere (Giglio *et al.* 2010), surprisingly little is known about fuel consumption and charcoal production in modern wildfires (Varner *et al.* 2015; Santín *et al.* 2016), which should lead us to question how much we actually know about the production of charcoal in palaeowildfires (i.e. Hudspith & Belcher 2017), and the extent to which fire alone can create a bias in the resulting charcoal we observe in the fossil record.

In modern ecosystems, plant litter and surface fuels are a major carrier of fires (Varner *et al*. 2015; Belcher 2016). Similarly, there is abundant evidence for charred surface fuels in the fossil record such as charred ferns, conifer needles, as well as charred flowers from early understory angiosperms (e.g. Harris 1958, 1981; Alvin 1974; Scott 2000; Collinson *et al.* 2000; Falcon-Lang *et al.* 2001; Van Konijnenburg-Van Cittert 2002; Friis *et al.* 2006; Falcon-Lang *et al.* 2016); however, many of these studies either utilise the exceptional preservation of charcoal for taxonomic identification only (i.e. early angiosperm flowers; Friis *et al.* 2006), or discuss fossil charcoal in the context of post-fire transport and/or taphonomic processes. Until now, with the exception of Hudspith & Belcher's (2017) work on charred flowers, there has been no discussion of how fire alone affects the potential for different plant genera/morphotypes, or even different plant organs, to survive as charcoal following palaeowildfires.

Before we can begin to understand the fossil record of fire, we first need to improve our understanding of charcoal production of modern surface fuels. To date, most experimental charcoal production, in relation to palaeontological studies, has used a muffle furnace to generate surface fuel reference charcoals (e.g. Jones *et al.* 1991; Lupia 1995; McParland *et al.* 2007). Yet a furnace is a temperature controlled environment operating under restricted atmospheric conditions, which does not capture the transient nature of a fire or the complex heat and mass transfer that occurs, and as such does not represent the complexities of charcoal production in real wildfire. To improve upon these approaches we have used combustion calorimetry (Babrauskas 2016) to experimentally produce charcoal from twenty taxa that represent surface fuels across a broad range of fuel types and growth habits (from conifers to ferns to weedy and shrub angiosperms) in order to question whether this spectrum of fuel types are equally likely to remain as charcoal post-fire. In contrast to furnace charring, calorimetry experiments do not operate under restricted atmospheric conditions and the fuel is exposed to a heat flux and allowed to ignite and burn in a controlled, representative environment (see Calorimetry experiments methods section for detail). Therefore the charcoal and ash produced using this method are a better representation of the combustion processes, and the charcoal that could be produced in a wildfire.

In addition to improving the experimental approaches that produce charcoal, we also need to consider that the atmospheric composition has also changed over geological timescales and how this in turn may have affected wildfire activity (Watson *et al.* 1978; Cope & Chaloner 1980; Wildman *et al.* 2004; Belcher & McElwain 2008; Belcher *et al*. 2010; Glasspool & Scott 2010). For example, during Periods where atmospheric oxygen reached superambient levels, we see evidence for enhanced wildfire activity, in the form of high fossil charcoal contents in sediments and coals (Belcher & McElwain 2008; Glasspool & Scott 2010). This is thought to be because superambient atmospheric oxygen greatly increases ignition probability (Watson *et al.* 1978; Belcher *et al.* 2010), as well as moisture of extinction (enabling wetter vegetation to burn) (Watson & Lovelock 2013). In order to test whether wildfires in superambient atmospheric oxygen conditions do indeed produce more charcoal, we tested species under the highest modelled superambient oxygen conditions that were thought to have occurred in the Cretaceous (peak 26 vol. % pO_2; Bergman *et al.* 2004; Mills *et al.* 2016).

Therefore, by producing charcoal under more representative, but controlled, laboratory conditions we aim to determine whether different plant types, and organs, are equally likely to remain as charcoal post-fire. Our experimental work will then be used to explore the extent to which fire alone may create a bias in the amount of charcoal that is produced, prior to any transportation, and before any additional taphonomic processes occur ahead of its incorporation into the fossil record. By considering how fire itself may lead to biases in the charred plant types and organs that are produced; we aim to improve our understanding of both the fossil record of charcoal, and palaeowildfires over geological timescales.

MATERIALS AND METHODS

Taxa studied

Twenty species were analysed, representing a range of surface fuel types. Twelve of the species were sampled from the botanical collection at the University of Exeter: *Buxus sempervirens, Rubus fruticosus, Urtica dioica, Asplenium scolopendrium Pteridium* sp., *Dryopteris* sp., *Dicksonia antarctica* (representing potential standing surface fuels) in addition to foliage/shed shoots of *Pinus radiata, Podocarpus salignus, Sequoia sempervirens, Cunninghamia konishii,* and *Cryptomeria japonica*. The remaining eight species (all representing standing understory surface fuels) were obtained from the University of Bristol botanic garden*: Drimys winteri, Laurus nobilis, Illicium* cf. *henryi, Sarcandra chloranthoides, Piper nigrum, Blechnum tabulare, Equisetum robustum,* and *Equisetum hyemale*. These species also represent different growth habits, from angiosperm shrubs (i.e. *Laurus nobilis*), weedy angiosperms (i.e. *Rubus fruticosus*) and ferns (i.e. *Pteridium* sp.), collectively representing a range of standing understory surface fuels. *Dicksonia antarctica* was selected as a sub-canopy component. For foliage from the canopy forming conifers, both live and recently senesced (hereafter termed dead) foliage was tested from a range of needle-shed (i.e. *Podocarpus salignus, Pinus radiata*) and shoot-shed (i.e. *Cryptomeria japonica, Cunninghamia konishii* and *Sequoia sempervirens*) morphotypes. All samples were oven dried at 50°C until they had attained a constant weight. Fully cured fuels were studied as these represent the most readily ignitable fuels in wildfires.

Calorimetry experiments

A 3 cm depth fuel bed was created for each species by filling a 15cm wide, 368 cm^3 porous metal mesh basket with a mix of foliar and vegetative material according to the natural packing density of the plant material (Belcher 2016) to ensure equal volume was analysed for each species. Leaf morphology affected packing density in the baskets, and wood, cones, *Equisetum* stems etc. have a greater mass than leaves. As such, start masses vary between species, resulting in each basket having an interspecific variation in bulk density (Table 1 in Hudspith *et al.* 2017), which is known to be an important component of leaf litter flammability (Belcher 2016). Bulk density of each fuel type was determined by dividing the sample mass by the volume of the metal mesh basket (Table 1 in Hudspith *et al.* 2017).

Bench-scale combustion experiments in ambient atmospheric oxygen were undertaken using the iCone calorimeter (Fire Testing Technology, East Grinstead, UK) in the wildFIRE Lab, at the University of Exeter (refer to ISO 5660-1:2015). Cone calorimetry represents a benchmark in testing the flammability of a wide range of materials (Babrauskas & Peacock 1992; Dibble *et al.* 2007). The fuel sample is exposed to a radiant heat flux (similar to radiant heating ahead of a wildfire). We selected 50 kW/m^2 as this likely represents the lower range of heat fluxes experienced in a wildfire (50-250 kW/m^2) (Silvani & Morandini 2009; McAllister *et al*. 2012). This radiant heating causes the fuel to thermally decompose and generate volatile gases (pyrolysate), which mixes with air above the sample, generating a flammable mixture. A spark igniter is used to ensure piloted ignition such that once the pyrolysate release is sufficient, the flammable gas-air mixture ignites. The heat release rate (HRR) is continually calculated throughout the experiment, using oxygen consumption calorimetry (Babrauskas 2016). Samples were analysed in duplicate or triplicate depending on plant material availability (refer to Table 1 in Hudspith *et al.* 2017 for detail). The samples were removed from the cone calorimeter after flaming had ceased and the calculated heat release had returned to zero. Time to ignition (TTI), test duration, total heat release (THR), and the rate of CO release (in g/s) were also recorded (Fig. 1).

In order to better understand how the burning dynamics of each fuel influenced the amount of charcoal remaining at the end of each test; each CO production curve was examined (two end members are illustrated in Fig. 1). CO generation has been shown to well represent the different stages of fuel combustion (c.f. Schemel *et al.* 2008). And as charcoal is produced during the pyrolysis stage of combustion i.e. the stage at which the fuel is thermally decomposed to produce flammable volatile gases that are consumed by the flames, it might be assumed that samples with a longer flaming phase would produce more charcoal. We can see this in the CO production curve for *Cryptomeria japonica* dead foliage in Fig. 1A, where CO production shows a small initial increase at ignition (Fig. 1A), then stabilises during flaming combustion (Fig. 1A). Then, once the flame is naturally extinguished (flameout) oxygen is able to reach the sample surface and combustion of the charcoal itself occurs (char oxidation), producing ash, and dramatically increasing CO production further (Fig. 1A; Schemel *et al.* 2008). However, the fuel beds tested were a mixture of materials (leaves and their attached woody parts), which along with the morphology of the leaves, and their varied shoot arrangement, caused differences in the porosity (bulk density) between the fuels tested (as would be the case in the natural world). This has resulted in considerable variation in CO production between the species tested, as illustrated in Fig. 1B, where the arrangement of *Sarcandra chloranthoides* leaves on each shoot have resulted in a more open, higher porosity fuel bed (compared to the flatter scale leaves, and higher woody component in the *Cryptomeria japonica* dead foliage sample in Fig. 1A). When burned, a high porosity fuel bed creates a large surface area for oxygen diffusion, meaning that smouldering and flaming can co-occur (Torero 2013), consuming charcoal and producing ash, even in the flaming phase (as illustrated in Fig. 1B). In both cases the main phase of CO production (> 0.005 g/s in this study) is able to indicate that char oxidation is occurring, regardless of fuel type, porosity, or whether a flame is still present (Fig. 1) (Schemel *et al.* 2008); thus enabling semi-quantitative discrimination between duration of charcoal production and charcoal consumption (producing ash) that occurred in each test (Fig. 1).

The experiments run under superambient atmospheric oxygen conditions used the FM Global Fire Propagation Apparatus (FPA) (Tewarson 2008), at BRE Centre for Fire Safety Engineering, at the University of Edinburgh (UK). Samples were removed once flaming had ceased. This apparatus enables the composition of the experimental atmosphere to be altered (c.f. Hadden *et al.* 2013). A mixture of nitrogen and oxygen was combined to generate a 26 vol. % superambient oxygen environment that was allowed to flow through and around the sample at a flow rate of 150 L min^{-1}. The top surface of the sample was exposed to a uniform radiant heat flux of 50 kW/m^2 (comparable to the ambient iCone calorimeter experiments), but generated by 4 infrared heaters (refer to ASTM E2058-2013a), instead of an electric coil heater. Samples were tested in duplicate depending on plant availability (refer to Table 2 in Hudspith *et al.* 2017 for detail).

Charcoal and ash analysis

Photographs of the resulting ash and charcoal were processed using the open source scientific image processing program ImageJ (Rasband 2013). Images were processed according to standard procedure outlined in the ImageJ manual. Each image was converted to an 8-bit greyscale image, whereby the brightness levels of the red (R), green (G) and blue (B) components are each represented as a number from decimal 0 to 255. A histogram of pixel values was created for each image (Figure 1A in Hudspith *et al.* 2017) and all values were copied. A manual threshold was then applied to each image to determine a cut-off greyscale value for the pixels that were observed to represent charcoal, which could uniformly be applied to every sample in this study. A value of ≤ 50 was determined based on the analysis of each image, and assuring that all charcoal particles were being captured at that maximum value (see example in Figure 1B in Hudspith *et al*. 2017). Default thresholds were then applied to each image to give a maximum grey-scale value for the ash in each sample (Figure 1C in Hudspith *et al.* 2017). All pixel values higher than the predetermined maximum ash value (i.e. the background paper; Fig. 2) were deleted. All remaining values >50 therefore represent the amount of ash in each image, and all values ≤ 50 represent the amount of charcoal. The latter were then converted to a char percentage, which was then normalized according to the start mass to give a char mass fraction (Tables 1-2 in Hudspith *et al*. 2017). The resulting char mass fractions therefore provide a semi-quantitative approximation of the amount of charcoal and ash remaining post-burn.

RESULTS

Experimental charcoal production under ambient oxygen conditions

All the taxa tested represent equal volumes of cured, single species fuel beds, exposed to identical heat flux and ignition conditions. Yet, all show a wide variation in the amount of charcoal produced (char mass fractions) between species, and even between replicates of the same species (Fig. 3). The fuels tested were then grouped into growth habits for analysis.

Within each growth habit grouping (Fig. 3): *Pinus radiata, Podocarpus salignus* (conifer) *Dicksonia antarctica* (sub-canopy), *Buxus sempervirens* (shrub angiosperm), *Piper nigrum* (weedy angiosperm), *Blechnum tabulare, Asplenium scolopendrium* (ferns), and *Equisetum* spp. (marginal fluvial) produced the most charcoal. And the remaining shrub species, weedy angiosperms and ferns (Fig. 3) produced the least.

Within the conifers, the needle-shed morphotypes *P. radiata* (live and dead foliage) (Fig. 2G-H) and *P. salignus* (dead foliage) (Fig. 2E) produced considerably more charcoal by the end of the test than any of the shoot-shed conifers (Figs 3, 4).

It is clear that the different species generate different proportions of charcoal; therefore it is important to consider whether this can be attributed to something intrinsic in the fuels themselves, or whether leaf traits and their relationship to fuel bed structure could in part be influencing their combustion behaviour. For example, larger/broader leaves create more open and well ventilated, low bulk density litters (Scarff & Westoby 2006; Belcher 2016) which appear to cause earlier initiation of char oxidation (i.e. destruction of char by solid fuel oxidation) in these fuel types, consuming charcoal and generating ash (as in Fig 1A). Indeed, we observed that the fuels with the lowest bulk densities (such as ferns and weedy angiosperms, and some shrubs (Fig. 1B)) experienced the greatest proportions of charcoal consumption (Fig. 5B), with char oxidation being initiated even during flaming combustion (see CO curve in Fig. 1B), which likely accounts for their low charcoal yields at the end of the test (Fig. 5C). In contrast, the high bulk density fuels (Fig. 5A) result in a higher fuel load (Belcher 2016) meaning the pyrolysate release is greater, and more heat is released overall (Fig. 5A), as well as a flame that covers the sample surface for longer durations (Fig. 1A; Table 1 in Hudspith *et al.* 2017). Consequently, oxygen cannot penetrate far below the surface during flaming, and the lower layers are protected from char oxidation, resulting in comparatively higher charcoal yields at the end of these tests (Fig. 5).

However, variations in bulk density cannot explain the entirety of charcoal production (Fig. 5C). Two diverging trends of charcoal production can clearly be observed in the data. The first trend (labelled 1 in Fig. 5C) includes: shrubs, (predominantly) shoot-shed conifer live and dead foliage, and *Equisetum robustum*. For these species, the longer the duration of char oxidation, the lower the yield of charcoal at the end of the test. In contrast, the second trend (labelled 2 in Fig. 5C) includes: ferns, weedy angiosperms, some shrubs, live and dead needle-shed foliage, *Dicksonia antarctica* and *Equisetum hyemale.* These fuels have low to medium bulk densities (Fig. 5B), yet show a wide variation in charcoal production (Fig. 5C), with needle-shed conifers and *Dicksonia antarctica* in particular generating unexpectedly high charcoal yields even at high relative proportions of solid fuel/char oxidation. This implies that for certain species bulk density-driven combustion behaviour cannot explain the entirety of charcoal production, and instead it must relate to the intrinsic physical and chemical properties of the fuel, as well as the heat transfer environment.

Experimental charcoal production under superambient oxygen conditions

The majority of species produced less charcoal under superambient test conditions (Fig. 6). Eleven of the taxa tested produced considerably less charcoal: all needle- and shoot-shed conifers (both live and dead foliage), *Dicksonia antarctica*, *Buxus sempervirens*, *Laurus nobilis*, *Illicium* cf. *henryi*, and *E. robustum*. However, five of the species showed ranges in char mass fractions that overlap for both test conditions (Fig. 6). For *Drimys winteri*, *Rubus fruticosus*, *Pteridium* sp., *Dryopteris* sp., this is likely because they produced little charcoal under either test conditions (Fig. 6), which may be attributed to their low bulk density, and rapid initiation of oxidation, consuming charcoal and producing mainly ash (Fig. 5B).

Overall, we generally observe less charcoal and greater ash production in our experiments under superambient oxygen conditions because solid-phase oxidation is initiated more rapidly (Torero 2013), resulting in more rapid consumption of the charcoal even under short test durations, compared to ambient conditions (as observed by Hadden *et al*. (2013)).

Post-burn ash colour after both ambient and superambient oxygen calorimetry experiments

Interestingly, we note that the ash colours produced by each fuel in this study varied widely from white, to orange, and light to dark grey (Tables 1-2 in Hudspith *et al.* 2017). It has previously been assumed that ash colour depends on combustion completeness and fire temperature (c.f. Bodí *et al.* 2014). However, for each species tested we observed more complete combustion under superambient (compared to ambient) test conditions (Fig. 6; Tables 1-2 in Hudspith *et al.* 2017), yet the ash colour visually appears to be the same for each species after both test conditions (Tables 1-2 in Hudspith *et al.* 2017). Therefore suggesting that ash colour variations are likely caused by species specific variations in ash chemistry (Vassilev *et al.* 2010), not combustion behaviour.

DISCUSSION

Charcoal production of different fuel types: Considerations for the charcoal fossil record

By experimentally producing charcoal from twenty species of surface fuels we have shown that charcoal production is a more complex process than has previously been appreciated by palaeontologists (Figs 2-6). Collectively, it appears that fuel type (structure and chemistry), fuel arrangement (bulk density) (Fig. 5B), combustion behaviour (Fig. 5A; Tables 1-2 in Hudspith *et al.* 2017), and the duration of solid fuel oxidation (char consumption) (Fig. 5C), and even the atmospheric composition (Fig. 6), all influence the amount and nature of charcoal that remains following a fire.

The heterogeneous mix of foliage and vegetative material in each sample also likely contributed to the variation in char mass fractions at the end of each test (Fig. 3). For example, the porous nature of leaves alone increases the surface area for oxygen diffusion, meaning that for some samples smouldering and flaming co-occurred (Fig. 1B; Torero 2013), producing charcoal and ash contemporaneously, but also differentially between fuel types. It is clear that certain plant organs such as fine woody fuels (Fig. 2D), cones (Fig. 2C), flowers (Hudspith & Belcher 2017), *Equisetum* stems, and certain leaves (e.g. *Podocarpus salignus* (Fig. 2E), *Pinus radiata* (Fig. 2G), *Dicksonia antarctica* (Fig. 2I), *Blechnum tabulare*) were more likely to remain as charcoal post-fire. The enhanced charcoal production of these plant organs is likely attributed to their chemical composition. Fuels with high lignin contents (i.e. woody fuels, cones) produce considerably more charcoal than those rich in cellulose (i.e. leaves) (Mackay & Roberts 1982), as cellulose and hemicellulose pyrolyze quickly at lower temperatures, whereas lignin is not only more resistant to thermal decomposition, but it also occurs over a broader temperature range (Yang *et al.* 2007). Whereas the enhanced charcoal production seen in other plant organs may be explained by a combination of factors. For example, the dead conifer needles in this study produced high bulk density fuel beds (Fig. 5A-B), which when coupled with the high lignin and/or tannin contents of individual needles, likely contributed to their enhanced charcoal production (c.f. Grootemaat *et al.* 2015). For other species, the accumulation of substantial quantities of inorganic constituents, such as high silica contents in *Equisetum* (and to a lesser extent *D. antarctica*) (Guntzer *et al.* 2010) may have provided some insulating properties during combustion by delaying the release of pyrolysis products (as seen in modern silicon-based fire retardants) (Lowden & Hull 2013), resulting in high charcoal yields for these species. Consequently, these observations suggest that fuel chemical composition also plays a role in charcoal production.

The preferential survival potential of woody fuels as charcoal in this study, may also in part explain why gymnospermous wood appears to be the most commonly identified charcoal type in the fossil record (Scott 2010; Brown *et al.* 2012; Belcher *et al.* 2013). However, it is not surprising that fossil wood charcoal is so readily identifiable given that the majority of previous experimental charcoal production (furnace experiments) and fossil charcoal literature primarily describe charred wood (c.f. Scott 2010 and references therein). Yet wood is not the only fuel source in wildfires, and many of the characters used to identify wood charcoal i.e. cell wall homogenization (Jones & Chaloner 1991; Scott 2010) do not apply to say charred seeds, leaves or flowers. Whilst post-burn charcoal inventories for modern forest fires (i.e. Santín *et al.* 2015) show that down wood and bark (from upright trees) constitute a major proportion of the charcoal that is produced overall, some of the biomass from needles and the forest floor are also converted to charcoal (Santín *et al.* 2015). It therefore seems unlikely that wood charcoal was favourably produced at the expense of all other fuel types in palaeowildfires. The apparent reduced abundance of other charred plant parts in the fossil record may also in part be due to the fact that much wildfire-derived charcoal is transported to some extent post-fire, and different charred plant organs can become separated (Nichols *et al*. 2000) meaning charred wood may not be associated with other charred plant organs. The charcoal fossil record is therefore not only affected by the preferential production of certain charcoal types by fire (as explored here), but will be further subjected to taphonomic and sampling biases that favour larger, and more easily recognisable, charred wood samples.

Despite this apparent sampling bias in favour of charred wood, charred surface fuels have been documented from Mesozoic charcoal assemblages, and these include: charred fern fragments (Harris 1958, 1981; Alvin 1974; Scott 2000; Collinson *et al.* 2000; Van Konijnenburg-Van Cittert 2002), conifer shoots and needles (Falcon-Lang *et al.* 2001; Friis *et al.* 2006; Falcon-Lang *et al.* 2016), and early angiosperm flowers and seeds (Friis *et al.* 2006). The fossil record therefore not only contains evidence of charred surface fuels, but also further highlights that certain plant organs, even of extinct genera, appear to have produced more charcoal in palaeowildfires than others.

Our experiments demonstrate that fire alone creates a clear bias in the amount and nature of the charcoal it produces, with certain species such as, needle-shed conifers, *D. antarctica* foliage, and *Equisetum* spp. producing more charcoal than shoot-shed conifers, shrub and weedy angiosperms and some fern species. Consequently, the latter surface fuels may therefore be underrepresented in the charcoal fossil record because the charcoal that is produced is rapidly destroyed and converted to ash, meaning that these species leave limited charred remains post-fire, so they have a reduced likelihood of being represented as charcoal in the fossil record. This is well illustrated with the conifer foliage tested in these experiments, for example, the needle-shed morphotypes *Pinus radiata* (live and dead foliage) (Fig. 2G-H) and *Podocarpus salignus* (dead foliage) (Fig. 2E) produce greater proportions of charcoal than any of the shoot-shed conifers tested (Figs 3, 4), suggesting the potential for a charcoal production bias in favour of needle-shed conifers, irrespective of whether the conifer leaves are broad and flat (*Podocarpus salignus*) or thin needles (*Pinus radiata*), in the charcoal fossil record. Indeed, although rarely reported, charred needles are more commonly observed in fossil charcoal assemblages compared to other charred leaf morphologies (i.e. Falcon-Lang *et al.* 2001; Hudspith *et al.* 2015). Therefore, despite the abundance of leaf impressions in the fossil record (Greenwood 1991), broader leaf morphologies, which produce lower bulk density well aerated litter fuels, are more likely to be completely consumed during wildfires and converted to ash. The low production of charcoal from these fuel types therefore severely limits their potential to become incorporated into the charcoal fossil record.

The most commonly reported clearly identifiable and widely reported charred surface fuel type to date in the fossil record are fern fragments (Harris 1958, 1981; Alvin 1974; Scott 2000; Collinson *et al.* 2000; Van Konijnenburg-Van Cittert 2002). Their relative abundance in the charcoal fossil record is not surprising given that ferns had attained near extant diversity by the Late Cretaceous (Watkins & Cardelús 2012) and were dominant understory components throughout a large part of the Mesozoic (Van Konijnenburg-Van Cittert 2002), and were therefore also major carriers of fire (Scott 2000; Collinson *et al.* 2000). Interestingly our experiments indicate that not all fern genera produce equal proportions of charcoal, with *Pteridium* sp. and *Dryopteris* sp. producing far less than *B. tabulare,* or *D. antarctica* (Figs 3, 6) thus suggesting that charcoal production biases may have also existed within fossil fern genera. This is supported by the fossil record as most of the previously reported fern charcoal derives from only two families, Gleicheniaceae and Matoniaceae (the latter including *Weichselia*) (Harris 1958, 1981; Alvin 1974; Watson & Alvin 1996; Van Konijnenburg-Van Cittert 2002). In fact, *Weichselia* charcoal is often the only fuel type preserved, despite evidence suggesting it grew alongside other ferns, conifers, lycopods and bryophytes (Watson & Alvin 1996). Does this therefore mean that the surrounding vegetation was not as flammable? Or has the charcoal from these other fuel types been transported/ preserved in a finer fraction/ not as easily identifiable? Or conversely, based on the results we have presented here, have the other fuel types been more completely combusted (resulting in the production of ash, not charcoal), whilst the inherent fuel properties of *Weichselia* resulted in its enhanced production during, and survival as charcoal following, fires. It is not possible to explore all these factors in the fossil record, however, *Weichselia* is known to have generated high fuel loads from its growth habit in fern heaths/ prairies (Alvin 1974), and it also exhibited xeromorphic leaf adaptations such as thickened pinnules and cuticles (Harris 1958; Alvin 1974; Watson & Alvin 1996; Van Konijnenburg-Van Cittert 2002) both of which alone could potentially result in higher charcoal production during fires. As in this study, where ferns with leathery (i.e. *B. tabulare*), or thick (i.e. *D. antarctica*) fronds showed some of the highest survival potentials as charcoal (Fig. 3). It therefore appears that charcoal production is also tied to some aspects of the intrinsic structural and chemical properties of the fuel, and considerations of plant phytochemistry certainly warrant further investigation in the future when considering charcoal production.

Reconciling high charcoal contents from geological Periods with superambient oxygen atmospheres

Superambient oxygen conditions, such as those experienced during the Cretaceous Period (Mills *et al.* 2016), resulted in enhanced wildfire activity (Belcher *et al.* 2013) as is evidenced by the high fossil charcoal contents at this time (Brown *et al.* 2012). Yet, in our superambient oxygen experiments we show that many species contradictorily produced less charcoal at the end of the test (Fig. 6). This supports previous findings by Hadden *et al.* (2013), who also show that enhanced charcoal consumption occurs when atmospheric oxygen concentrations are progressively increased. We should note however, that it is difficult to directly compare our ambient oxygen experiments, undertaken using the iCone calorimeter, with our superambient oxygen experiments using the FPA. This is because in order to alter the atmosphere in the FPA experiments, the samples were subjected to a flow of N_2 and O_2 gas, which caused increased air movement across the samples during the superambient experiments. However, it is encouraging that our results are similar to those observed by

Hadden *et al.* (2013), which were undertaken in equal flow conditions across both ambient and superambient atmospheric compositions.

Nonetheless, some species in our superambient oxygen experiments still produced considerable quantities of charcoal (Fig. 6), and similarly to our ambient oxygen iCone experiments, certain plant organs i.e. wood (Fig. 2D), and some leaf morphologies (Fig. 2H,J) were more likely to remain as charcoal post-burn than others. Further highlighting that even under superambient oxygen conditions certain plant organs will likely be overrepresented in the charcoal fossil record whereas: shoot-shed conifer foliage, weedy and shrub angiosperm foliage, and some ferns (Fig. 6) may be poorly represented, if at all.

Both these results and those of Hadden *et al.* (2013) indicate that higher concentrations of atmospheric oxygen lead to lesser amounts of charcoal remaining post-burn, which seems at odds with the fossil record, where we see increased abundances of fossil charcoal (Belcher & McElwain 2008; Glasspool & Scott 2010; Belcher *et al*. 2010) in Periods where numerical models estimate elevated atmospheric pO_2 vol. levels occurred (e.g. Bergman *et al.* 2004; Berner 2009; Mills *et al*. 2016). This might be reconciled by considering that although each fire in a high oxygen world must produce less charcoal, fire frequency itself must have been significantly increased owing to the ease of ignition, and rapid spread of fires (Belcher & Hudspith 2016). Therefore this increased fire activity, which also potentially may have produced larger burned areas, might account for the higher abundance of charcoal found in the fossil record during these Periods. It is also likely that fuel moisture played a role, because under higher oxygen concentrations increasingly wetter fuels can burn (Watson & Lovelock 2013), and spread rates and fire intensity were both found to be higher for wet fuels as atmospheric oxygen increased, compared to those ignited under ambient conditions (Belcher & Hudspith 2016). In order to reconcile our observations with the charcoal fossil record, future experiments should seek to study the influence of charcoal production across a range of fuel moistures and atmospheric oxygen concentrations.

Charcoal production might also in part be related to atmospheric-driven shifts in net primary productivity (NPP), decomposition rates, and their relationship to fuel bed structure. For example, postulated higher than present day NPP in the Mesozoic (Beerling 2000) would have created higher litter fuel loads, that experienced slower decomposition rates (conifer, fern and basal angiosperm litters), compared to eudicot litter (Liu *et al.* 2014). The potential for deep litter beds ought to imply higher bulk density, resulting in longer flaming durations (Grootemaat *et al.* 2015) which may have led to higher charcoal production (Fig. 5B) during Cretaceous wildfires. Consequently, multiple factors are capable of altering the dynamics of fires, fire regimes, and therefore the production of charcoal, during Periods of superambient atmospheric oxygen.

In summary, if charcoal is being used as a tool for interpreting past wildfire activity, we should first consider that the amount of charcoal produced is clearly biased in favour of certain species, and plant organs, as shown in both our experiments (Figs 2-6) and the fossil record. Our findings demonstrate that in order to interpret palaeowildfire activity from fossil assemblages of charred surface fuels we (as a community) first need to: 1) improve our recognition of non-woody fossil charcoal in the field and when using microscopy in the laboratory. 2) Continue the application of novel experimental approaches in order to better understand charcoal production of different fuel types and plant organs; including further experiments that couple both enhanced atmospheric oxygen levels with varying fuel moisture contents. Our study also alludes to a potential relationship between plant chemistry and charcoal production, which requires further exploration. 3) Finally, we need to be mindful that not all surface fuels are equally likely to remain as charcoal post-fire, meaning that fire alone is capable of creating a charcoal production bias, even prior to any subsequent loss of material before it reaches the depositional environment and ultimately becomes incorporated into the fossil record.

CONCLUSIONS

We have used calorimetry to experimentally produce charcoal from twenty species that represent a range of surface fuels and growth habits. All species tested showed an interspecific variation in the amount of charcoal produced at the end of each test. We show that needle-shed conifers, *Dicksonia antarctica* foliage, and *Equisetum* spp. produced more charcoal than shoot-shed conifers, shrub and weedy angiosperms and some fern species under either ambient or superambient (26 vol. % pO_2) atmospheric oxygen conditions. We also observe that certain plant organs such as: fine woody fuels, cones, *Equisetum* stems, certain leaves (*e.g. Podocarpus salignus, Pinus radiata, Dicksonia antarctica, Blechnum tabulare*) appear to preferentially produce more charcoal, compared to the remaining foliage tested. Thus suggesting that charcoal formation in fine surface fuels is a more complex process than previously appreciated and such variation between species suggests that charcoal production must be closely tied, not only to combustion behaviour, but also to the intrinsic structural and chemical properties of a given fuel. We therefore suggest that future research directions consider the effect of plant chemistry on charcoal production and suggest further experimental approaches are required in order to better understand charcoal production under superambient atmospheric oxygen conditions. Further, in order to better understand past wildfire activity we (as a community) need to be better at scrutinising the types of charcoal that occur in the fossil record. Particularly as our experiments clearly demonstrate that different species, and even different plant organs, are not equally likely to remain as charcoal post-fire, and this must also be true for the vegetation that burned in palaeowildfires. Therefore, fire alone should be considered as an additional bias that affects the charcoal we observe in the fossil record, even before considering any other subsequent loss of material caused by post-fire transport, or other taphonomic processes. It is likely this combination of factors that has resulted in certain species potentially being overrepresented as charcoal in the fossil record (i.e. *Weichselia*), or conversely not represented at all. The potential for a charcoal production bias has not previously been considered; therefore these charcoal production experiments represent a preliminary step in trying to improve our understanding of the fossil record of fire.

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DATA ARCHIVING STATEMENT

Data for this study are available in the [Dryad Digital Repository]: http://datadryad.org/review?doi=doi:10.5061/dryad.g2fm2

REFERENCES

ALVIN, K.L. 1974. Leaf anatomy of *Weichselia* based on fusainised material. *Palaeontology*, **17**, 587-598.

ASTM E2058-2013a. Standard test methods for measurement of material flammability using a Fire Propagation Apparatus (FPA). *American Society for Testing Materials.* West Conshohocken, Pennsylvania, USA.

BABRAUSKAS, V. 2016. Chapter 28 the cone calorimeter. *In* Hurley, M.J. (ed.), *SFPE Handbook of Fire Protection Engineering – Fifth Edition*. Springer, New York, USA, 952-980 pp.

-------- PEACOCK, R.D. 1992. HRR. The single most important variable in fire hazard. *Fire Safety Journal*, **18**, 255–292.

BEERLING, D.J. 2000. Global terrestrial productivity in the Mesozoic era. *In* Hart, M.B. (ed.), *Climates: Past and present.* Geological Society, London, Special Publication, **181**, 17-32 pp.

Belcher, C.M. 2016. The influence of leaf morphology on litter flammability and its utility for interpreting palaeofire. *Philosophical Transactions of the Royal Society B*, **371**, 20150163.

-------- McELWAIN, J.C. 2008. Limits for combustion in low O_2 redefine paleoatmospheric predictions for the Mesozoic. *Science*, **321**, 1197–2002.

-------- HUDSPITH, V.A. 2016. Changes to Cretaceous surface fire behaviour influenced the spread of the early angiosperms. *New Phytologist*, DOI: 10.1111/nph.14264

-------- COLLINSON, M.E. and SCOTT, A.C. 2013. A 450-Million-year history of fire. *In* Belcher, C.M. (ed.), *Fire Phenomena and the Earth System: An Interdisciplinary Guide to Fire Science.* John Wiley and Sons, Chichester, UK, 229-249 pp.

-------- YEARSLEY, J.M., HADDEN, R.M., MCELWAIN, J.C. and REIN, G. 2010. Baseline intrinsic flammability of Earth's ecosystems estimated from paleoatmospheric oxygen over the past 350 million years. *PNAS*, **107**, 22448–22453.

BERGMAN, N.M., LENTON, T.M. and WATSON, A.J. 2004. COPSE: a new model of biogeochemical cycling over Phanerozoic time. *American Journal of Science*, **304**, 603-606. doi:10.2475/ajs.304.5.397.

BERNER, R.A. 2009. Phanerozoic atmospheric oxygen: New results using the GEOCARBSULF model. *American Journal of Science,* **309**, 603-606.

BODÍ, M.B., MARTIN, D.A., BALFOUR, V.N., SANTÍN, C., DOERR, S.H., PEREIRA, P., CERDÀ, A. and MATAIX-SOLERA, J. 2014. Wildland fire ash: Production, composition and eco-hydrogeomorphic effects. *Earth-Science Reviews*, **130**, 103-127.

BROWN, S.A.E., SCOTT, A.C., GLASSPOOL, I.J. and COLLINSON, M.E. 2012. Cretaceous wildfires and their impact on the Earth System. *Cretaceous Research***,** **36**, 162-190.

COLLINSON, M.E., FEATHERSTONE, C., CRIPPS, J.A., NICHOLS, G.J. and SCOTT, A.C. 2000. Charcoal-rich plant debris accumulations in the Lower Cretaceous of the Isle of Wight, England. *Acta Palaeobotanica (Suppl. 2),* 93–105 (for 1999).

COPE, M.J. and CHALONER, W.G. 1980. Fossil charcoal as evidence of past atmospheric composition. *Nature*, **283**, 647-649.

DIBBLE, A.C., WHITE, R.H. and LEBOW, P.K. 2007. Combustion characteristics of north-eastern USA vegetation tested in the cone calorimeter: invasive versus non-invasive plants. *International Journal of Wildland Fire,* **16**, 426-443.

FALCON-LANG, H.J., KVACEK, J. and ULICNY, D. 2001. Fire-prone plant communities and palaeoclimate of a Late Cretaceous fluvial to estuarine environment, Pecinov Quarry, Czech Republic. *Geological Magazine*, **138**, 563–576.

-------- COLLINSON, M. and MAGES, V. 2016. The oldest *Pinus* and its preservation by fire. *Geology*, **44**, 303-306.

FRIIS, E.M., PEDERSEN, K.R. and CRANE, P.R. 2006. Cretaceous angiosperm flowers: innovation and evolution in plant reproduction. *Palaeogeography Palaeoclimatology Palaeoecology*, **232**, 251–93.

GIGLIO, L., RANDERSON, J.T., VAN DER WERF, G.R., KASIBHATLA, P.S., COLLATZ, G.J., MORTON, D.C. and DeFRIES, R.S. 2010. Assessing variability and long-term trends in burned area by merging multiple satellite fire products. *Biogeosciences*, **7**, 1171–1186.

GLASSPOOL, I.J. and SCOTT, A.C. 2010. Phanerozoic atmospheric oxygen concentrations reconstructed from sedimentary charcoal. *Nature Geoscience,* **3**, 627-630.

-------- EDWARDS, D. and AXE, L. 2004. Charcoal in the Silurian as evidence for the earliest wildfire. *Geology*, **32**, 381-383.

GREENWOOD, D.R. 1991. Chapter 7 - The taphonomy of plant macrofossils. *In* Donovan, S.K. (ed.)*, The Process of Fossilization*. Columbia University Press, 142 pp.

GROOTEMAAT, S., WRIGHT, I.J., VAN BODEGOM, P.M., CORNELISSEN, J.H.C. and CORNWELL, W.K. 2015. Burn or rot: leaf traits explain why flammability and decomposability are decoupled across species. *Functional Ecology*, **29**, 1486-1497.

GUNTZER, F., KELLER, C. and MEUNIER, J.D. 2010. Determination of the silicon concentration in plant material using Tiron extraction. *New Phytologist*, **188**, 902-906.

HADDEN, R.M., REIN, G. and BELCHER, C.M. 2013. Study of the competing chemical reactions in the initiation and spread of smouldering combustion in peat. *Proceedings of the Combustion Institute,* **34**, 2547-2553.

HARRIS, T.M. 1958. Forest fire in the Mesozoic. *Journal of Ecology*, **46**, 447-453.

-------- 1981. Burnt ferns from the English Wealden. *Proceedings of the Geological Association*, **92**, 47-58.

HUDSPITH, V.A. and BELCHER, C.M. 2017. Fire biases the production of charred flowers: Implications for the Cretaceous fossil record. *Geology*, doi:10.1130/G39093.1.

-------- BELCHER, C.M., KELLY, R. and HU, F.S. 2015. Charcoal reflectance reveals early Holocene boreal deciduous forests burned at high intensities. *PLoS one*, **10**, e0120835.

-------- HADDEN, R.M., BARTLETT, A.I. and BELCHER, C.M. 2017. Data from: Does fuel type influence the amount of charcoal produced in wildfires? Implications for the fossil record. *Dryad Digital Repository*. http://datadryad.org/review?doi=doi:10.5061/dryad.g2fm2

ISO 5660-1, 2015. Reaction-to-fire tests – Heat release, smoke production and mass loss rate – Part 1: Heat release rate (cone calorimeter method) and smoke production rate (dynamic measurement). International Organization for Standardization, Geneva, Switzerland.

JONES, T.P. and CHALONER, W.G. 1991. Fossil charcoal, its recognition and palaeoatmospheric significance. *Palaeogeography Palaeoclimatology Palaeoecology*, **97**, 39-50.

-------- SCOTT, A.C. and COPE, M. 1991. Reflectance measurements against temperature of formation for modern charcoals and their implications for the study of fusain. *Bulletin de la Société Géologique de France*, **162**, 193–200.

LIU, G., CORNWELL, W.K., PAN, X., CAO, K., YE, X., HUANG, Z., DONG, M. and CORNELISSEN, J.H.C. 2014. Understanding the ecosystem implications of the angiosperm rise to dominance: leaf litter decomposability among magnoliids and other basal angiosperms. *Journal of Ecology*, **102**, 337-344.

LOWDEN, L.A. and HULL, T.R. 2013. Flammability behaviour of wood and a review of the methods for its reduction. *Fire Science Reviews*, **2**, 1-19.

LUPIA, R. 1995. Paleobotanical data from fossil charcoal: an actualistic study of seed plant reproductive structures. *PALAIOS*, **10**, 465-477.

MACKAY, D.M. and ROBERTS, P.V. 1982. The dependence of char and carbon yield on lignocellulosic precursor composition. *Carbon*, **20**, 87-94.

McALLISTER, S., GRENFELL, I., HADLOW, A., JOLLY, W.M., FINNEY, M. and COHEN, J. 2012. Piloted ignition of live forest fuels. *Fire Safety Journal*, **51**, 33-142.

McPARLAND, L., COLLINSON, M.E., SCOTT, A.C., STEART, D.C., GRASSINEAU, N.V. and GIBBONS, S.J. 2007. Ferns and fires: experimental charring of ferns compared to wood and implications for palaeobiology, coal petrology and isotope geochemistry. *PALAIOS*, **22**, 528–538.

MILLS, B.J.W., BELCHER, C.M., LENTON, T.M. and NEWTON, R.J. 2016. A modelling case for high atmospheric oxygen concentrations during the Mesozoic and Cenozoic. *Geology*, **44**, 1023-1026.

NICHOLS, G.J., CRIPPS, J., COLLINSON, M.E. and SCOTT, A.C. 2000. Experiments in waterlogging and sedimentology of charcoal: results and implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **164**, 43–56.

RASBAND, W.S. 2013. ImageJ. U. S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/, 1997-2014.

SANTÍN, C., DOERR, S.H., PRESTON, C.M. and GONZÁLEZ-RODRÍGUEZ, G. 2015. Pyrogenic organic matter production from wildfires: a missing sink in the global carbon cycle. *Global Change Biology*, 21, 1621-1633.

-------- DOERR, S.H., KANE, E.S., MASIELLO, C.A., OHLSON, M., DE LA ROSA, J.M., PRESTON, C.M. and DITTMAR, T. 2016. Towards a global assessment of pyrogenic carbon from vegetation fires. *Global Change Biology*, **22**, 76-91.

SCARFF, F.R. and WESTOBY, M. 2006. Leaf litter flammability in some semi-arid Australian woodlands. *Functional Ecology*, **20**, 745-752.

SCHEMEL, C.F., SIMEONI, A., BITEAU, H., RIVERA, J.D. and TORERO, J.L. 2008. A calorimetric study of wildland fuels. *Experimental Thermal and Fluid Sciences*, **32**, 1381–1389.

SCOTT, A.C. 2000. The Pre-Quaternary history of fire. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **164**, 281–329.

-------- 2010. Charcoal recognition, taphonomy and uses in palaeoenvironmental analysis. *Palaeogeography Palaeoclimatology Palaeoecology*, **291**, 11-39.

SILVANI, X. and MORANDINI, F. 2009. Fire spread experiments in the field: Temperature and heat flux measurements. *Fire Safety Journal*, **44**, 279-285.

TEWARSON, A. 2008. SFPE Fire Protection Handbook Chapter 3-4: Generation of heat and gaseous liquid, and solid products in fires, fourth ed., National Fire Protection Association, Quincy, MA, USA 02269.

TORERO, J.L. 2013. An introduction to combustion in organic materials. *In* Belcher, C.M. (ed.), *Fire Phenomena and the Earth System: An Interdisciplinary Guide to Fire Science*. John Wiley and Sons, Chichester, UK, 3-13 pp.

VAN KONIJNENBURG-VAN CITTERT, J.H.A. 2002. Ecology of some Late Triassic to Early Cretaceous ferns in Eurasia. *Review of Palaeobotany and Palynology*, **119**, 113-124.

VARNER, J.M., KANE, J.M., KREYE, J.K. and ENGBER, E. 2015. The flammability of forest and woodland litter: A synthesis. *Current Forestry Reports*, **1**, 91-99.

VASSILEV, S., BAXTER, D., ANDERSEN, L. and VASSILEVA, C. 2010. An overview of the chemical composition of biomass. *Fuel*, **89**, 913-933.

WATKINS Jr, J.E. and CARDELÚS, C.L. 2012. Ferns in an angiosperm world: Cretaceous radiation into the epiphytic niche and diversification on the forest floor. *International Journal of Plant Sciences*, **173**, 695-710.

WATSON, J. and ALVIN, K.L. 1996. An English Wealden floral list, with comments on possible environmental indicators. *Cretaceous Research*, **17**, 5-26.

WATSON, A.J., LOVELOCK, J.E. and MARGULIS, L. 1978. Methanogenesis, fires and the regulation of atmospheric oxygen. *Biosystems*, **10**, 293-298.

-------- LOVELOCK, J.E. 2013. The dependence of flame spread and probability of ignition on atmospheric oxygen: an experimental investigation. *In*: Belcher, C.M. (ed.), *Fire Phenomena and the Earth System: An Interdisciplinary Guide to Fire Science*. John Wiley and Sons, Chichester, UK, 273-287 pp.

WILDMAN Jr, R.A., HICKEY, L.J., DICKINSON, M.B., BERNER, R.A., ROBINSON, J.M., DIETRICH, M., ESSENHIGH, R.H. and WILDMAN, C.B. 2004. Burning of forest materials under late Paleozoic high atmospheric oxygen levels. *Geology*, **32**, 457-460.

YANG, H., YAN, R., CHEN, H., LEE, D.H. and ZHENG, C. 2007. Characteristics of hemicellulose, cellulose and lignin pyrolysis. *Fuel*, **86**, 1781-1788.

FIGURES

FIG. 1. Line graphs showing two end members in CO production and how this curve can indicate the burning dynamics of the different fuels tested. The grey shaded areas denote the proportion of each test where char oxidation (charcoal consumption) is occurring. In (A) CO production is stable during flaming and the rise in CO occurs far later, resulting in shorter duration of char oxidation, and more charcoal being left at the end of the test (*Cryptomeria japonica* dead foliage). In (B) the rise in CO production occurs during flaming and the test duration is dominated by ash-forming char oxidation (*Sarcandra chloranthoides*).

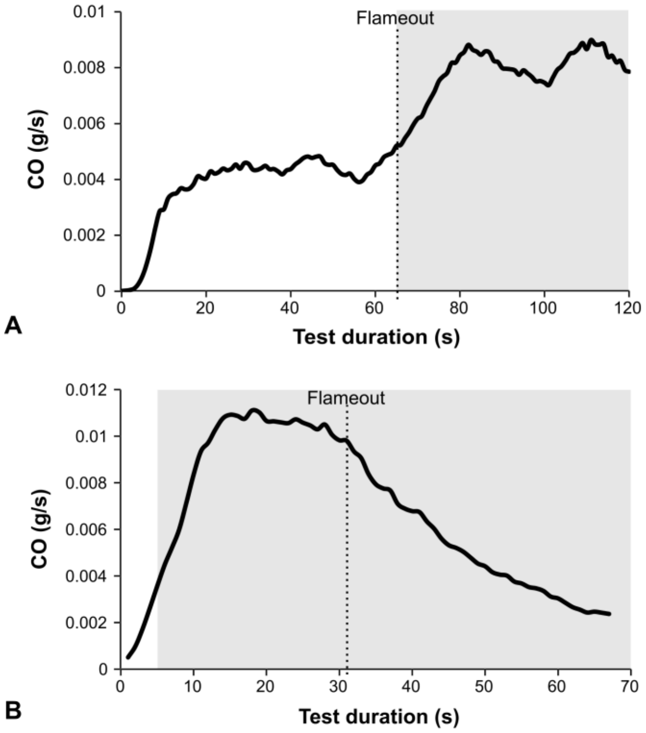

FIG. 2. 8 bit greyscale photographs used for image analysis, illustrating the interspecific variation in the percentage of charcoal and ash produced post-burn. Images are presented as comparative charcoal percentages between tests run under ambient atmospheric oxygen conditions using the iCone calorimeter: (A), (C), (E), (G), (I), and superambient 26 vol.% atmospheric oxygen using the FPA: (B), (D), (F), (H), (J). Image (A) *Pteridium* sp. (1%), (B) *Cryptomeria japonica* dead foliage (0%), (C) *Cryptomeria japonica* dead foliage (13%), (D) *Drimys winteri* (15%), (E) *Podocarpus salignus* dead foliage (42%), (F) *Asplenium*

scolopendrium (43%), and (G)-(H) *Pinus radiata* foliage (76% and 64%), (I)-(J) *Dicksonia antarctica* foliage (84% and 91%). Scale bar in all images is 40 mm.

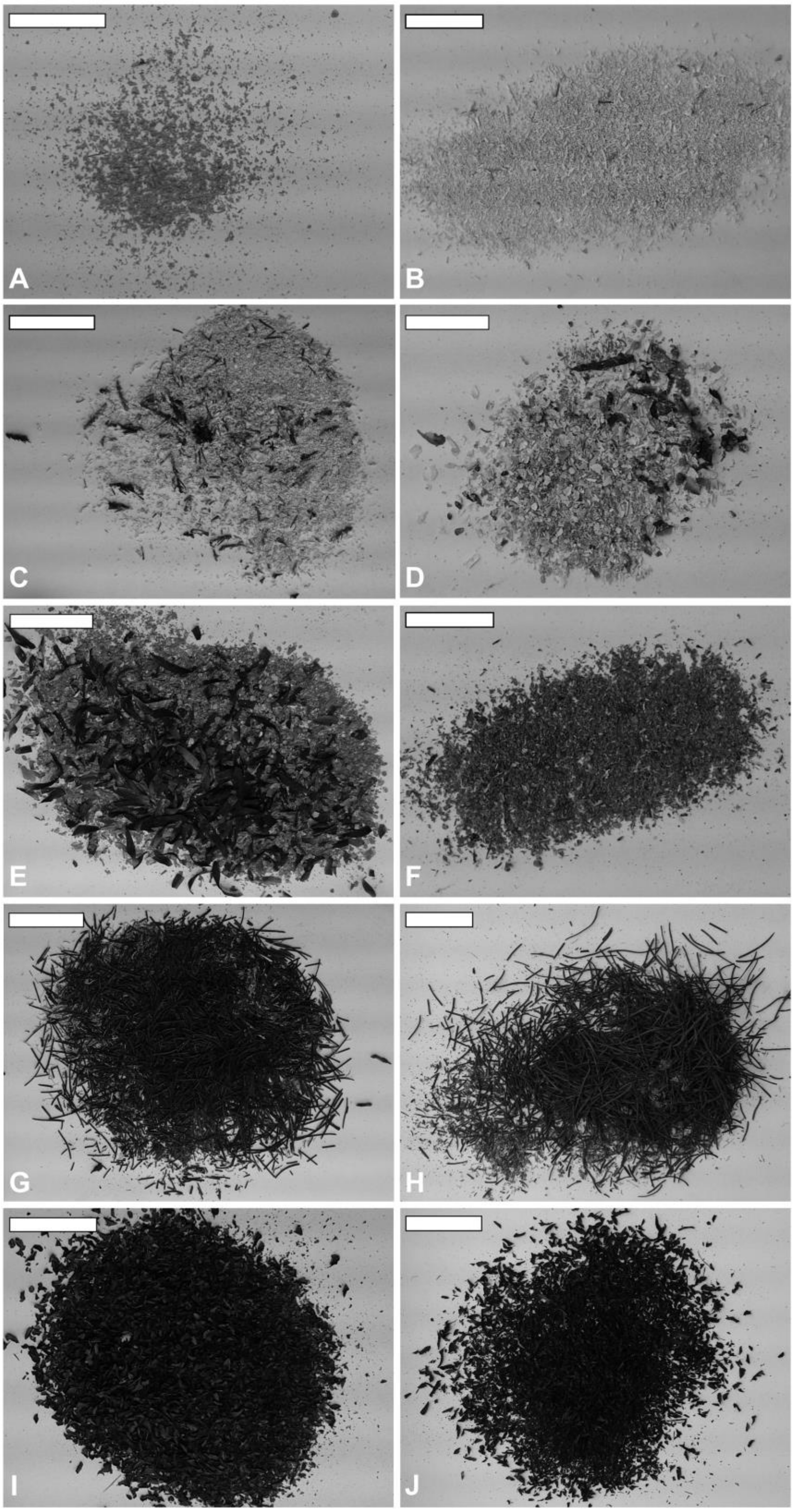

FIG. 3. Graph illustrating the range of char mass fractions for all fuel types and replicates studied under ambient oxygen conditions. Species are grouped according to growth habit.

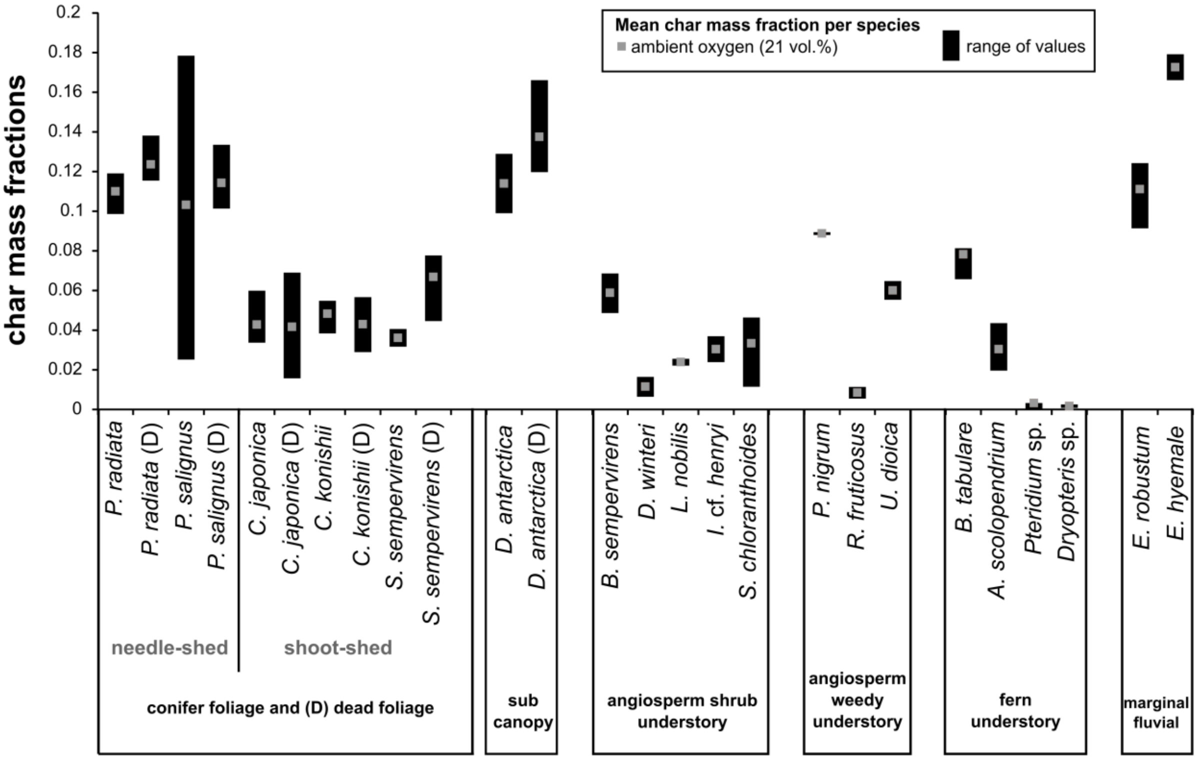

FIG. 4. Box and whisker plot of char mass fractions from the different conifer leaf morphotypes. Needle-shed species are *Pinus radiata* and *Podocarpus salignus.* Shoot-shed species are *Cryptomeria japonica, Cunninghamia konishii,* and *Sequoia sempervirens.* The box limits are the 25% and 75% quartiles, the central line in each box is the median and the whiskers are 1.58 times the interquartile range.

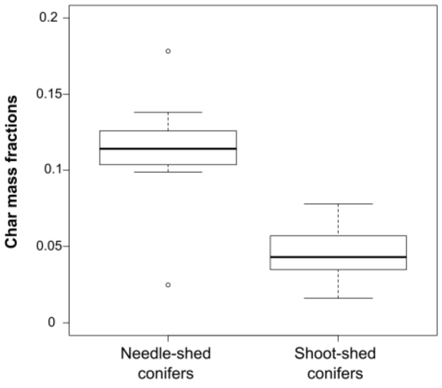

FIG. 5. Scatter plots showing relationships between (A) total heat released and bulk density. Proportion of each test duration (in %) where char oxidation is occurring, plotted against (B) bulk density, and (C) char mass fractions. Black arrows in (C) highlight the two divergent trends in the data. Fuel types are grouped according to growth habit in all plots.

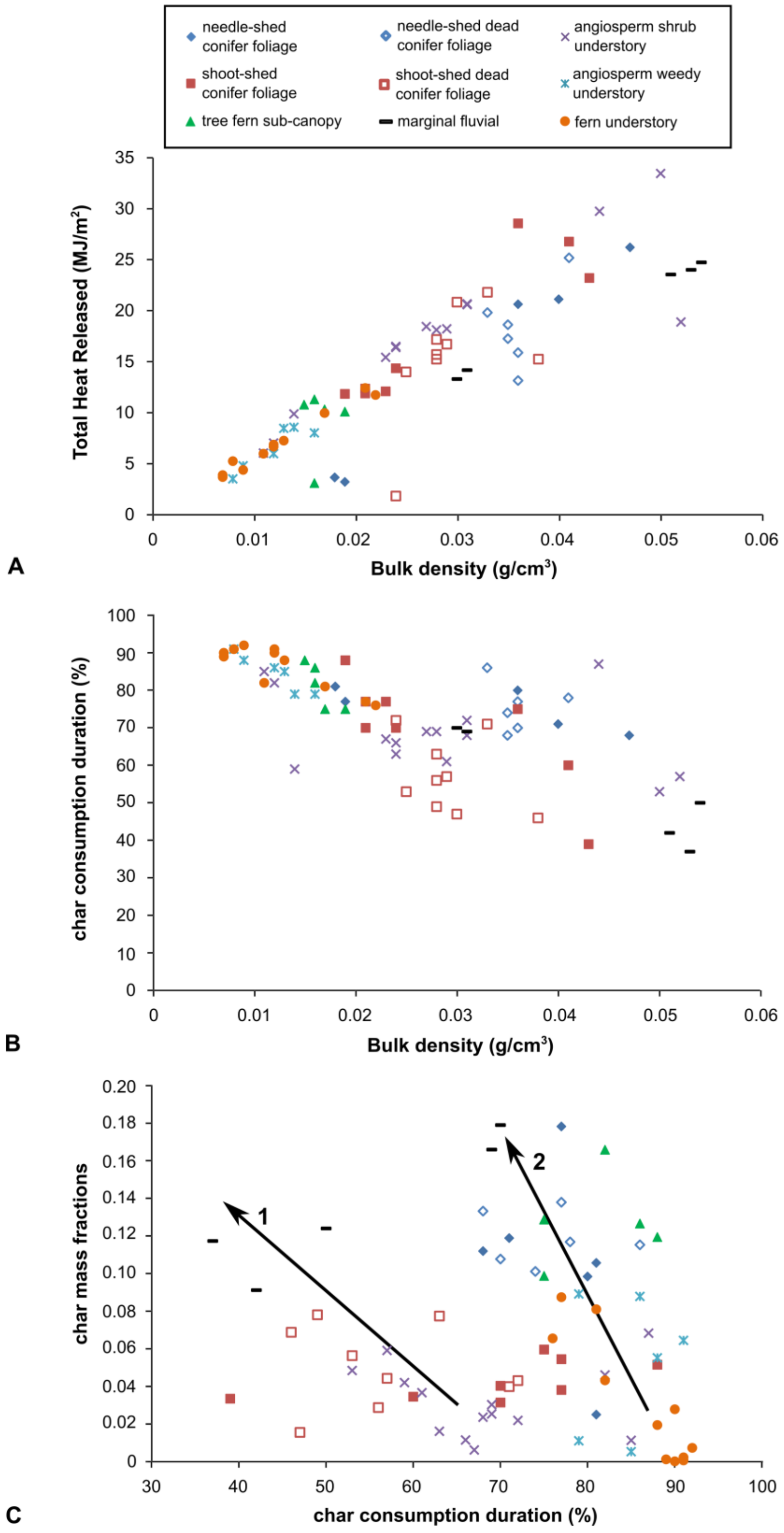

FIG. 6. Comparative graph illustrating the range of char mass fractions for all fuel types and replicates tested under both ambient and superambient oxygen conditions. Fuel types are grouped according to growth habit.