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The influence of leaf morphology on litter flammability and its utility for interpreting palaeofire

Claire M. Belcher[1]

[1] *wildFIRE Lab, Hatherly Laboratories, University of Exeter, Prince of Wales Road, Exeter, EX4 4PS, U.K.*

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Abstract

Studies of palaeofire rely on quantifying the abundance of fossil charcoals in sediments to estimate changes in fire activity. However, gaining an understanding of the behaviour of palaeofires is also essential if we are to determine the palaeoecological impact of wildfires. Here I utilise experimental approaches to explore relationships between litter fire behaviour and leaf traits that are observable in the fossil record. Fire calorimetry was used to assess the flammability of 15 species of conifer litter and indicated that leaf morphology related to litter bulk density and fuel load, which determined the duration of burning and the total energy released. These data were applied to a fossil case study which couples estimates of palaeolitter fire behaviour to charcoal based estimates of fire activity and observations of palaeoecological changes. The case study reveals that significant changes in fire activity and behaviour likely fed back to determine ecosystem composition. This work highlights that we can recognize and measure plant traits in the fossil record that relate to fire behaviour and therefore that further research is warranted toward estimating palaeofire behaviour as it can enhance our ability to interpret the palaeoecological impact of paleofires throughout Earth's long evolutionary history.

Introduction

Wildfires have shaped the evolutionary history of plants over millions of years, and play a key role in determining the spatial distribution of plant communities across our planet today [1]. It has long been known that plant species differ in flammability, and therefore that the composition of ecosystems strongly influences fire regime, which in turn feeds back to determine ecosystem composition. Our modern ecosystems exhibit a range of different fire regimes defined by the patterns of fire seasonality, frequency, size, spatial continuity, intensity, type (crown fire, surface fire or ground fire) and severity [US forestry service definition, 2013]. Because fire regime includes so many interlinked aspects of fire that we cannot yet estimate for the past, it is difficult to understand how palaeofire events link to palaeoecological change. Palaeofire studies typically rely on assessing the abundance of fossil charcoal in rocks and sediments [see 2 for a review], which allows

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*Author for correspondence (c.belcher@exeter.ac.uk).

palaeontologists to identify variations in fire activity [3]. It is also possible to study the fuel types that burned by observing the botanical affinities of fossil charcoals [2], and more recent research has shown that different plant types burned within the same fire likely experience different pyrolysis intensities as evidenced by variations in the reflectance properties of the charcoal created when studied using reflected light microscopy [4]. However, few palaeofire studies utilise either of these latter sources of information, focusing instead on estimating only the frequency component (changes in fire activity) of fire regime.

The behaviour of fires is critical to building an understanding of their ecological effects; therefore the ability to observe variations in aspects of palaeofire behaviour would be of key benefit to better understanding the effects of palaeofires on ancient ecosystems. Fire intensity and severity [see 5 for complete definitions] are strongly influenced by plant traits, which are readily observable in the fossil record. Plant traits influence fuel structure, and govern both the amount, and rate, of energy released from a fire, which in turn determines how much energy is transferred to the ground and other plants [6]. The behaviour of a fire, and the degree to which it is able to damage live, dead, litter and ground components of ecosystems determines ecosystem recovery, community composition, and or/change, as well as feedbacks to Earth surface processes [7-9] and Earth system processes [10].

Recent ecological research has begun to look for uniting patterns within plant traits, that may be independent of taxonomic affinity, and which transcend ecosystem specific fuel compositions, in order to define broad relationships that describe the flammability of plants [11-16]. Such approaches are logical because there are consistent interspecific variations in leaf traits across diverse ranges of ecosystems and dramatically different climates [17]. Such global trait based relationships show repeatable patterns in leaf structure/morphology, longevity, metabolism and chemistry [17] that can be considered part of a global leaf economic spectrum [18]. From their fossil remains, we know much about the types of plants that have grown throughout Earth’s history via reconstructions of plants and ecosystems [19]. Because fire behaviour relates strongly to fuel architecture, building an understanding of how plant traits influence fire, could allow coordination of key leaf traits that are consistent across major plant functional types, growth forms and biomes, to be used to explain aspects of fire behaviour in ancient ecosystems. Importantly, leaf size and morphology can be readily observed in leaf fossils; both these traits are known to impact litter flammability, and fire behaviour [11, 13, 14, 16].

Leaves form the most flammable part of a plant [15] because they are typically the first part of the plant to ignite and because they also often form easily ignitable litter. Litter beds are made of accumulated fine fuels, which conversely result in a thermally thick fuel. The most important fire properties of thick fuels are density, conductivity and specific heat [20], which decrease with bed bulk density, which describes the porosity of the fuel bed and impacts the rate at which energy is released. Bulk density is a function of the packing of a litter and therefore will relate to leaf morphology and hence leaf morphology, as observable in fossils leaves, should relate to litter bed energy release rate. However, this has not yet been explored using experiments linked to a fossil case study. In this study I build on leaf trait based approaches by undertaking controlled laboratory experiments using fire calorimetry that allowed the measurement of energy release (known as the heat release rate) from a selection of modern conifer litter fuels comprised of different leaf morphologies. These modern litters serve as analogies for key leaf morphotypes characteristic of Palaeozoic and Mesozoic conifer litters. These data are applied to assess the relationship between changes in fire activity and vegetation observed in rocks from the Triassic-Jurassic Boundary in East

Greenland [19, 21; 22]. The aim is to provide a case study which can be used to assess whether or not useful information an be gained from estimating palaeolitter fire heat release rate and whether this improves our ability to understand episodes of fire-driven palaeoecological change. My intent with this work is to provide a test bed to assess whether or not such approaches merit further study by the community towards developing their utility for interpreting the effects of palaeowildfires.

The experiments have been designed to study the nature of fires in leaf litters. This is because firstly, many fossil charcoal deposits are considered to be the result of litter fires [23] and secondly, because fires often start in litter because they can provide relatively dry extensive fuels loads in which individual leaves are easy to ignite, and the fuel tends to be well connected, enabling the fire to spread. Therefore producing estimates of the likely energy release rate of palaeolitter fires based on morphometric observations of fossil leaf assemblages would provide useful information about palaeofires. Previous high-resolution studies have shown that fossil leaf assemblages are considered to adequately represent forest-litter accumulations [24]. Such conclusions are supported by taphonomic observations of modern forests where leaf litter on tropical and temperate forest floors is typically derived from the surrounding 1000-3000m^2 of vegetation [25, 26]. Litter is generally easily degradable, therefore in order to be preserved in the fossil record leaf litter must be buried rapidly and without causing much fragmentation, implying that macrofossil remains are generally deposited within a basin's catchment area, and therefore fossil leaves likely reflect vegetation from a relatively local source [19]. Although it should be noted that careful spatial sampling is required in order to generate high-resolution macrofossil data suitable for detailed paleofloral reconstructions [19, 26] and also therefore be of any likely utility to palaeofire estimates. The Astartekløft site in East Greenland records a major floral change preserved in macrofossil leaves across the Triassic-Jurassic boundary global warming event [19, 21, 22]. This site preserves some >3000 fossil leaves that were census collected from laterally extensive sedimentary deposits, that has enabled reconstruction of the litter and the flora of the time. The Astartekløft site comprises eight fossiliferous horizons, termed plant beds that contain abundant well-preserved plant macrofossils [19, 21]. Plant beds 1, 1.5, 2 3 and 4 are considered Triassic in age and plant bed 5 represents the transition between the Triassic and the Jurassic periods [22, 27], whilst plant beds 6 and 7 are Jurassic in age (see figure 2 in 22). Plant beds 1 to 5 are interpreted as being crevasse splay deposits that preserve fossil leaves both as imprints and as intact fossil cuticle, in organic rich mudstones [19, 28]. Plant bed 6 appears to mark an alteration in the hydrological cycle [29] reflected by an increasingly moist and organic rich depositional environment where the plant fossils are preserved in an organic rich shale (Belcher 2009 field observations). Plant bed 7 represents an abandoned channel deposit [19]. The fossil leaves are interpreted to represent the *in situ* floodplain taxa, and the closed forests of the drier levees. The plant assemblages are considered to record a climate driven floral change that relates to a major phase of global warming that is apparent in plant beds 5 and 6 as indicated from the CO_2 record reconstructed using the stomatal method [30, 31].

Previous work on this site noted that the floral change, from a broad leaved conifer dominated assemblage to one dominated by narrow conifer leaves was coupled to a five-fold rise in charcoal abundance [22]. Live narrow leaved fuels have been found to ignite more rapidly than broad leaved conifer fuels, implying that a shift in ignitability may have in part been responsible for enhancing fire activity in the earliest Jurassic ecosystems at this location [22]. However, little is known about the behaviour of any resulting fires and whether this would vary according to the apparent morphological changes in the leaves that dominated the litter fuels or if any changes to fire behaviour may have fed back to driving the significant palaeoecological changes observed. As such this case study represents an excellent opportunity to explore the utility of assessing the potential palaeofire behaviour of ancient ecoystems.

Materials and Methods

Experiments were designed with the ultimate aim of interpreting the palaeofire litter fire behaviour in an ancient ecosystem from simple morphological observations of fossil leaves. In order to do this the relationships between major conifer leaf morphologies and their subsequent litter bed flammability was studied. In particular, the focus is on measurements that can be readily observed from fossil leaf assemblages such as, the morphology of shoots and individual leaves. To this end the flammable properties were tested of 15 species of conifer that shed either individual leaves or fragments of shoots. Conifers are the focus of the experiments because flowering plants had not yet evolved during the time period represented by the fossil case study. The morphotypes tested are shown in Table S1, these represent morphotypes that are commonly present in both Palaeozoic and Mesozoic aged conifer assemblages. I do not seek here to exhaustively test every possible ancient conifer morphotype but aim to test for broad patterns that might indicate that the area is worthy of further research. 7 of the species tested are broad morphological equivalents of the conifer leaf types found in East Greenland at Astartekløft. All leaf samples were collected from the Royal Botanic Gardens in Edinburgh. Whilst, ferns and cycads were important components of the Astartekløft flora, these forms are unfortunately too large for measurement of flammable properties in litter format in the fire testing apparatus used in this study. Monospecific conifer litters have been measured so that the results may be more simply translated to the general Palaeozoic and Mesozoic conifer fossil record which is a fair approach as it has been shown that litter flammability is typically driven by the most flammable components present in a leaf litter [32]. Therefore we anticipate that the conifer fuels, which are capable of forming high litter fuel loads, and often have high resin contents, would be expected to have the more signficant effect on the fire environment of the litters.

All litter samples were dried slowly at 50^{o}C for 6 days in an oven until all were less than 5% moisture before flammability testing enabling us to focus on the influence of leaf morphology rather than fuel moisture. Whilst, leaf morphology will impact fuel moisture [22], moisture must be driven off before ignition hence the testing of dry litter allowed us to best explore the resultant fire behaviour of each litter after ignition. Equal litter volumes were tested for each species and the resulting fuel load of each sample recorded. Leaf litter was placed in metal a mesh basket 15cm wide and of volume 368cm^{3} [33] and the basket filled according to the leaves natural packing density (the litter depth was 3 cm in all cases). Three baskets of litter were tested of each species. The baskets were placed in a cone calorimeter (following ASTM E1354), which was used to ignite and measure the flammable properties of the litters. The cone calorimeter uses a high power coiled "cone" shaped heating element to deliver a known flux of heat to the sample. The leaf litter samples were subjected to a heat flux of 30kWm^{-2} (within the typical range for flammability testing [20, 34]). Above the sample a spark pilot ignition was switched on at the same time as the sample was exposed to the heat source. This controlled laboratory set up, of heat and an ignition source, mimics the conditions surrounding a fuel sample when a wildfire approaches. The incoming fire begins to heat surrounding vegetation, as it does so it begins to decompose the constituent plant material such that first they release water vapour (removing any moisture) and then release volatiles and other thermal decomposition gases known as pyrolysate [20]. Once the rate of pyrolysate release is sufficient, the nearby fire (or spark in the laboratory tests) can cause ignition and a flame is established on the sample. The calorimeter part of the equipment monitors the amount of oxygen depletion in a flue positioned above the burning sample, where the heat released during combustion per unit mass of oxygen consumed is a constant [34]. The cone calorimeter enables the following aspects of fire behaviour to be measured for each sample: time taken for the samples to ignite [time to ignition - TTI (s)], the burn duration [the time from which the sample ignited to the point at which the flames extinguished (s)], the rate of and peak amount of energy released [peak heat release rate – pHRR (kW)], and the total amount of energy released [THR (kJ)] and the effective heat of combustion [EHoC (kJ/g)]. Together these generate a profile of heat released per unit time throughout the burns duration (e.g. Fig 1) and indicates the behaviour of the fire in each litter type. The cone calorimeter is a standard piece of equipment used in fire safety assessments and as such, tests are carried out according to the international standard, ASTM E1354 (http://www.astm.org/Standards/E1354.htm).

Results

In order to explore differences and/or similarities between the resultant fire behaviour for each litter morphotype the flammability parameters (time to ignition, pHRR, EHoC and THR Table S2) were combined using a principle components analysis (PCA) (Figure 2). The majority of the variance in the litter's flammability is explained by the first PC axis (81.85% Fig 2a). The relative loadings of this axis suggest that total heat release is the dominant fire behaviour character driving this aspect of the fire behaviour space (loading = -0.8967). PC axis 2 appears to be led by the duration of the burn (PC2 loading = -0.8965). The leaf-shed needle leaved litters appear to occupy a distinct region (Fig 2a region 1) of fire behaviour space. This group is characterised by low PC1 scores and widely ranging PC2 scores. Leaf-shed broad leaved morphotypes and small but thick scale leaved shoot shedding forms occupy intermediate PC1 scores and a narrower range of PC2 scores (region 2 on Fig 2a) and flat leaved shoot shedding morphotypes and those with large scale leaves are characterised by relatively high PC1 scores and a narrower range of PC2 scores (region 3 on Fig 2a). The clusters defined by the PCA were subsequently used to group the heat release rate profiles for each leaf litter morphotype and visually explore their fire behaviour characteristics (Figure 3). The region 1 heat release rate profiles are clearly distinctive, these litters sustain burning for longer than the others and release heat more steadily, such that they have a relatively low pHRR but that heat is released over a longer period. The litters of region 2 typically burn with a high pHRR, where the fire rapidly consumes the fuel leading to it burning intensely. The litters of region 3 burn rapidly but with low pHRR where the fire is only sustained for a short period.

de Magalhaes and Schwilk [14] found that leaf size influenced the bulk density of leaf shed needle leaf litters and that this impacted on their flammability. It is known that higher bulk density fuels support slower fire spread rates, firstly because more fuel must be pre-heated to ignition temperature in order for the fire to spread [35] and secondly because bulk density relates to variations in packing ratio which determines oxygen supply and heat transfer between particles [36]. Moreover, flaming time has been suggested to increase linearly with fuel load where a denser fuel bed provides more mass and therefore more flammable gases are available to support longer flaming times. It was therefore anticipated that the high bulk density fuels tested here would present a higher fuel load per equal volume of fuel and therefore would be expected to sustain a fire for longer leading to an overall greater total heat release. The litter fuel load was subsequently compared to the total heat release of the litters (Figure 4). A strong linear correlation was found between fuel load and total heat release

($r^2 = 0.74$). This relationship can is also apparent in the heat release rate profiles in Figure 3. The litters that characterised region 1 of the fire behaviour space have a mean bulk density of 0.086gcm^{-3}, the small flat needles allow the fuel to pack tightly together, leading to low aeration and a large amount of fuel per volume. These litters can be seen to sustain fires for the longest duration and slowly and steadily release heat from the dense fuel. This group released on average 248.46 kJ of energy for each basket of litter. The fuels in region 2 have a mean bulk density of 0.036gcm$^{-3,}$ here the large leaves or scale leaves pack much less densely as individual particles do not lie flat leading to a well-aerated fuel. Each particle itself however, holds a significant fuel load due to thick leaves and/or thick shoots leading to rapid burning with a high peak heat release rate. This group released on average 164.94 kJ of energy. The fuels in region 3 have a low bulk density of 0.018gcm^{-3}, the fuels are either relatively fine and/or loosely packed and well aerated. As such they represent a small fuel load that is well aerated so that what fuel there is rapidly releases heat but there is not sufficient fuel to lead to a sustained burn. Releasing on average 74.16 kJ of energy. The morphology of the leaves comprising the litter determines the bulk density of the fuel bed and its porosity and fuel load which in turn determines the rate of heat release from the litter, and for how long the fire will be sustained and the total amount of heat that the litter bed will release during combustion. Because leaf morphology can be related to the fire behaviour properties of the litter bed, such observations may be applicable and transferrable for consideration of palaeolitter fire behaviour in ancient ecosystems.

Discussion

Ecologists today may undertake fire severity surveys following major wildfires by documenting the nature of organic matter loss [e.g. see Table 1 in 5]. Fire severity indices have been shown to relate to fire intensity and residence time (together which account for total heat release) [37, 38]. Fire intensity and fire severity metrics have also been shown to correlate to ecosystems responses [39] where fire severity often determines ecosystem recovery and/or alien plant invasion [40], as well leading to below ground changes in flora and fauna [41]. Fire severity may further influence runoff and erosion. Higher severity fires can also enhance water run off due to enhancing water repellency in soils [8], as well as directly altering soil properties [7]. Therefore the ability to determine the likely intensity of palaeofires and the duration over which heat may have been delivered to the ground is of significant importance to palaeoecological interpretations. The analysis has indicated that the nature of litter determines the behaviour of a litter fire suggesting that useful information about fire severity might be gleaned from making observations of fossil leaves. However, it should be noted that factors that would be difficult to determine from the fossil record such as, climate (monthly-daily temperature changes), slope angle, wind and fuel moisture and litter depth would significantly alter the exact values of heat release values but not the shape of the heat release profiles that were observed on the laboratory setting. This makes fully quantitative estimates difficult, such that semi-quantitative assessments of aspects of palaeofire behaviour might most realistically be made for the past. To test this approach estimated changes in palaeofire behaviour were compared to the observed increase in palaeofire activity and floral shifts at Astartekløft in East Greenland.

Previous research undertaken on the Astartekløft site has indicated a five-fold rise in fire activity in response to a climate driven shift from a prevalance of broad-leaved taxa to a predominantly narrow-leaved assemblage [22]. This intepretation focused predominantly on the ignition properties of fresh leaf material and concluded that broad-leaved morphotypes were less ignitable owing to that fact that they required greater pre-heating to drive off the larger amount of water held in each leaf. Thus narrow leaves were found to ignite faster than broad leaves. It was proposed that fire activity was enhanced during periods where the flora was dominated by more easily ignitable morphotypes. This interpretation is consistent with the palaeofire record for the site where the shift to narrow leaf morphologies corresponds to an increased abundance of fossil charcoal. Belcher et al., [22] did not consider whether there may have been major changes in the behaviour of palaeofires across the event.

The data used in the following analysis of the Astartekløft flora is taken from the Belcher et al., [22] database (see Table S1 in [22]) that included only those plant fossils that could assigned to a 10cm sub bed within each of the plant beds census collected by McElwain et al., [19]. The main canopy and litter forming plants at Astartekløft are the broad leaved, predominantly leaf shedding conifer genus *Podozamites*, the narrow/needle-leaved, shoot shedding conifer genus *Stachyotaxus*, the needle leaved predominantly leaf shedding conifer genus *Elatocladus* and several ginkgo genera (including *Ginkgoites*, *Czekanowskia*, *Baera* and *Sphenobaeria*) are also present at Astartekløft, although are not dominant at the point of ecological change [19, 21, 22]. Fossils of *Podozamites* can be found as exceptionally preserved leaves attached to shoots, but occur more commonly as individual leaves and in fossils that preserve the base of the leaves a short petiole can be observed [21, Belcher field observations], suggesting that this plant shed leaves to form litter. *Stachyotaxus* is predominantly found as intact shoots [21] that appear visually similar to *Sequoia sempervirens* in morphotype (although are not believed to be related), and has spirally arranged inserted leaves with constricted leaf bases. The leaves are not scale morphotypes. *Stachyotaxus* has been described as forming leaf litter matts of shoots at Astartekløft when abundant [19]. *Elatocladus* is less abundant at Astartekløft however, appears as the dominant litter former in plant bed 6. The genus is known from both leafy twigs and detached needles from much of the Mesozoic [42]. In Greenland it is often found as sparingly branched twigs (a few centimeters long) that show elliptical leaf scars and faint furrows at the points where leaves would have been inserted [21]. The leaves are petiolate and this genus is often represented in assemblages by twigs, individual leaves, leaf fragments and cuticle fragments from macerated rock samples [21]. *Elatocladus* therefore appears to have been a leaf-shedding conifer. In figure 2b the plants that have leaf morphologies representative of those found at Astartekløft are shown on the PCA. This is the same PCA as in figure 2a but with the other plants removed from the plot to highlight those representative of Astartekløft. The leaf morphologies that characterise the plants beds that correspond to the main phases of ecological change observed at Astartekløft [e.g 19] fall into different areas of the fire behaviour space (Fig 2b). The Triassic aged plants beds 3, 4 and 5a that see the onset of the rise in atmospheric CO_2, fall into the area of fire behaviour space characterised by litter fires that rapidly release a large amount of heat (e.g. heat release profiles characteristic of Region 2 group shown on figure 3). The earliest Jurassic litters (plant bed 5b) fall into the polygon with the the highest PC1 scores which have heat release rate profiles that have low peak heat release rates and where energy release from the litter bed is only sustained for a short period (e.g region 3 litters on figure 3). Finally the morphotypes found in plant bed 6 fall into the region of lowest PC1 scores which corresponds to leaf litter morphologies that are able to support sustained periods of heat release (region 1 on figure 3). This suggests that there was not only a change in fire activity across the Triassic-Jurassic boundary at Astartekløft but likely also a significant shift in fire behaviour, driven by transitions to new litter fuels.

Four distinctive fire-vegetation phases can be observed in the Astartekløft section (figure 5). Each phase is marked by a change in: (1) the dominant leaf morphotypes of the forest canopy and the major litter forming components of the flora [19, 22], (2) the abundance of fossil charcoal found in each plant bed [22] and (3) palaeolitter fire behaviour, based on the dominant leaf morphotypes in the litter, which together describe broad changes in fire regime. The phases are interpreted based on the vegetation phases defined by [19].

Phase 1 (plant beds 1, 1.5 and 2), no single taxon dominates the canopy or sub canopy elements (i.e. the assemblages can be considered macroecologically even) [19], but broad-leaved morphotypes are the most common [22]. Canopy fuels consisted of broad-leaved conifers including *Podozamites* and ginkgos, whilst cycads and ferns formed the subcanopy and ground cover. The ecosystem is suggested to have been similar in nature to the *Agathis* dominated ecosystems of New Zealand and Australia, with additional podocarps and a cycad understory (e.g. *Lepidozamia hopei* would be an analogue) [19]. Fire activity is generally uncommon, based on the low levels of charcoal found in the rock samples.

Phase 2, (plant beds 3, 4 and 5a), species richness is observed to decline and the mid canopy habit (not shown on figure 12) is eradicated, with a local extinction of erect bennetites and cycads [19]. Ginkgos also disappear from the assemblages, whilst at ground level dipterid ferns are replaced with osmundaceous ferns [19]. The canopy habit and likely litter fuels remain dominated by the broad-leaved conifer *Podozamites* until the very latest Triassic (plant bed 5a) where the narrow-leaved shoot-shedding conifer, *Stachyotaxus* becomes an important component [22]. The fire regime appears to constitute low frequency, but high intensity fires, based on a dominance of 89% broad leaf conifer leaf shed litter.

Phase 3 (plant bed 5b), the earliest Jurassic ecosystem is characterised by depressed generic richness and eveness, and the most compositionally distinctive vegetation of the entire Rhaetian and Hettangian interval [19], and is dominated by narrow-leaved shoot-shedding conifers [22]. There is limited evidence for major understory plants, with ferns as well as cycads and bennettites being limited in abundance [19]. This phase has the highest abundance of charcoal in the section, and more typical background levels of charcoal implying that the fire regime consisted of periods of low frequency fires and a period of high frequency fires, in both cases fires were likely of low intensity fires, due to the dominance of shoot shed narrow non-scale leaved conifer litter.

Phase 4 (early plant bed 6 = 4a late plant bed 7 = 4b), early phase 4a (plant bed 6) is dominated by narrow leaved morphotypes [22]. A high abundance of fern understory is apparent, making narrow-leaved ferns co-dominant with needle-leaved conifers [19, 22]. Fire regimes appear to have altered; fire frequency remains high, but litter assemblages appear to be dominated by narrow-leaf leaf-shed conifers, implying litter fires were of low peak intensity, but burned for a significant time. In this case the peak intensity of the litter fires would have been less important than the high total amount of heat delivered to the same area for a sustained period. These fires may therefore have been frequent, but also of a high severity. Late phase 4b (plant bed 7) sees the overall recovery of pre-event eveness and an increasingly diverse ecosystem [19]. Broad leaves dominate the assemblage, which is comprised mainly of two ginkgo morphotypes, one with highly dissected leaves (*Czekanowskia*), and another with broader lobes (*Ginkgoites*) [19, 22]. Fire activity dramatically falls again to similar levels as experienced in phase 1.

It should be noted that litter depth is not uniform across modern litter types or between ecosystems and as yet it is difficult to estimate palaeolitter depth. It is therefore important to consider the total amount of heat that might occur for a range of possible litter depths at Astartekløft in order to test the robustness of the interpretations. Because total heat release was found to increase linearly with fuel load the influence of changing the overall fuel load for each litter group is representative of variations in litter depth. The depth of the litter in the laboratory experiments was 3cm therefore the fuel load for each litter type was adjusted to be representative of 2cm, 1.5cm and 1cm litter depths. The equation that describes the linear relationship between fuel load and total heat release (Figure 4) was then used to create total heat release estimates for the different litter depths. The mean total heat release estimates for each litter group are shown in Table 1.

The group 1 litters best represent the vegetation of phase 4a (plant bed 6) at Astartekløft that is interpreted as experiencing frequent and high severity surface fires due to the sustain burning that high bulk density fuel allows. This group can be seen to have consistently high total heat release for a range of litter depths. The group 2 litters, that best represent phase 2 at Astartekløft and are interpreted as experiencing low frequency but high intensity rapidly burning surface fires, have the next highest total heat release across the range of litter depths. For the fires in phase 4a at Astartekløft to have a similar total heat release to those in phase 2 the fuel bed would have to be half the depth. Therefore, if half the litter depth were assumed, the total heat release could be similar however, the rate of heat release would still following the profiles indicated in figure 3. Such that in phase 4a surface litter fires would still release heat over a more sustained duration than those in phase 2 leading to longer duration heating of ground and surface fuels. Therefore due to the characteristics of the rate of heat release from litters that best represent the fuels at Astartekløft, variations in litter depth are unlikely to significantly alter the fire regimes described above and therefore their palaeoecological impact.

By combining morphometric observations of the dominant litter forming fossil leaves at Astartekløft with records of fossil charcoal abundance evidence for changes in palaeofire regime across the Triassic-Jurassic transition global warming event have been explored. Four distinctive fire regimes can be noted. Fire appears to be a minor component of ecosystems in the lower most and upper most plant beds. Both these fossil plant assemblages are diverse, ecologically even, and dominated by broad leaves. The transition between phase 1 and 2, as well as the entirety of phase 2, show a slight rise in fire activity. These would still be considered as infrequent, but it seems likely that when fires did occur that they were high intensity, quick burning flashy fires, as evidenced by the dominance of broad-leaved leaf shed conifer litter. Large and long needle morphotypes have also been correlated with high fire severity in modern coniferous ecosystems including enhanced crown scorch (from radiation heat from surface fires) and duff consumption [13]. The infrequent, but high intensity fires therefore may have been ecologically destructive, which may be explain the eradication of the mid canopy habit (cycads, bennettites) and ginkgo, due to heat induced necrosis of the leaves in the mid canopy by the high energy release from surface litter fires. Phase 3 occurs within the period of high CO_2 and sees a period with high fire frequencies [22]. The fires during phase 3 were likely of low intensity driven by a transition to narrow leaved shoot-shed fuels. It has been shown that large leaved gymnosperms burn more intensely than small leaved morphotypes [14] which accords with my laboratory experiments and interpretations, implying a likely switch from low frequency, high intensity fires to periods of both low frequency and high frequency fires both of which were of low intensity across the Triassic-Jurassic transition. Understory plants remain limited in abundance during phase 3 [19]. It may be that the recovery of the mid canopy plants from the previous regime of infrequent but intense fires, was prevented by a shift to a regime of frequent fires making new regrowth of subcanopy and understory elements impossible before the next fire occurred. This implies that shifts in fire regime, encompassing both the effects of changes in fire activity and fire behaviour throughout the sequence may have had important feedbacks on determining ecosystem composition at Astartekløft. Early phase 4 (plant bed 6) is characterised by frequent fires that may have also been of high severity, owing to the long period of soil heating that would be likely from slow moving litter fires. A fires impact in part relates to the temperatures reached in the forest floor and the duration of heating experienced by the vegetation, forest floor and underlying mineral soil [43]. Soil is the natural base for the growth of an ecosystem and is the primary factor responsible for ecosystem productivity and heat from wildfires can strongly influence the properties of both soil and ecosystems. Key factors that influence soil heating include the litter type and the composition of the duff layer. In a wildfire, be it in crown or surface fuels, most of the fires heat is directed upwards however, the transfer of heat to the soil is strongly dependent not only on the heat of the fire but importantly the duration of exposure. Less soil heating is experienced by a soil under a fast moving, high energy surface fire (such as those in phase 2) than in a low intensity, slow spreading fire (e.g. early phase 4), which have much longer residence times [44]. Plant bed 6 contains the highest proportion of ferns, which are often colonisers of frequently disturbed terranes. Fern spores are known to be capable of surviving significant surface heating and may also re-grow from underground rhizomes. Their success in this bed may relate to a high frequency and high severity fire regime that was otherwise incompatible with previously dominant taxa. However, it should be noted that bed 6 records a change in the environment of deposition to more swampy conditions at this location. It may be that the dominance of *Elatocladus* and ferns simply reflects this change, however, the high fire frequency, as evidenced by abundant charcoal, suggests that the environment was not too damp to suppress fire activity. Plant bed 7 is characterised by a dramatic fall in charcoal abundance that appears to coincide with falling CO_2 levels. Fire activity appears to have returned to levels similar to those seen in phase 1 ahead of the climatic deterioration. This decline in fire activity also seems to correspond to increasing diversity and ecological eveness.

It seems that climate driven changes in vegetation composition influenced both fire activity and palaeolitter fire intensity and severity across the Triassic-Jurassic boundary in East Greenland. The changes to palaeolitter fire behaviour, which are based solely on the dominant litter fuels, likely had the ability to feedback into determining ecosystem composition as they appear to have caused significant alterations to the abundance of understory plants at Astartekløft. As such, this case study suggests that similar approaches might be of utility to building a better understanding of the role that changes in fire regime may have played in palaeoecological changes documented in Earth's ancient ecosystems.

Additional Information

Authors' Contributions
CMB designed the experiments. CMB undertook the experiments and analysed the data. CMB wrote the manuscript.

Competing Interests
'I have no competing interests'

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Figure Captions

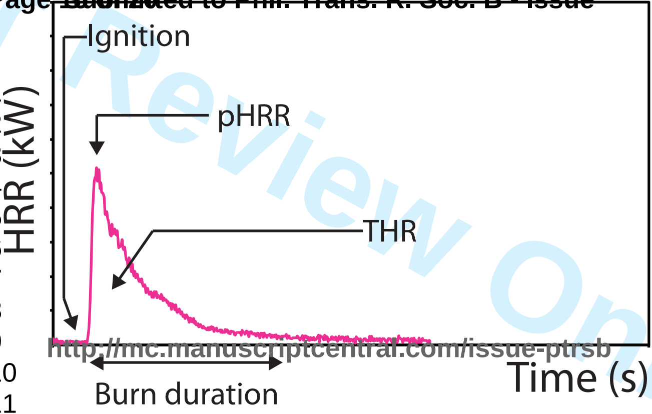
FIGURE 1 – Example labelled Heat Release Rate (HRR) profile showing position of ignition, peak Heat Release Rate (pHRR), Burn Duration and Total Heat Release (THR).

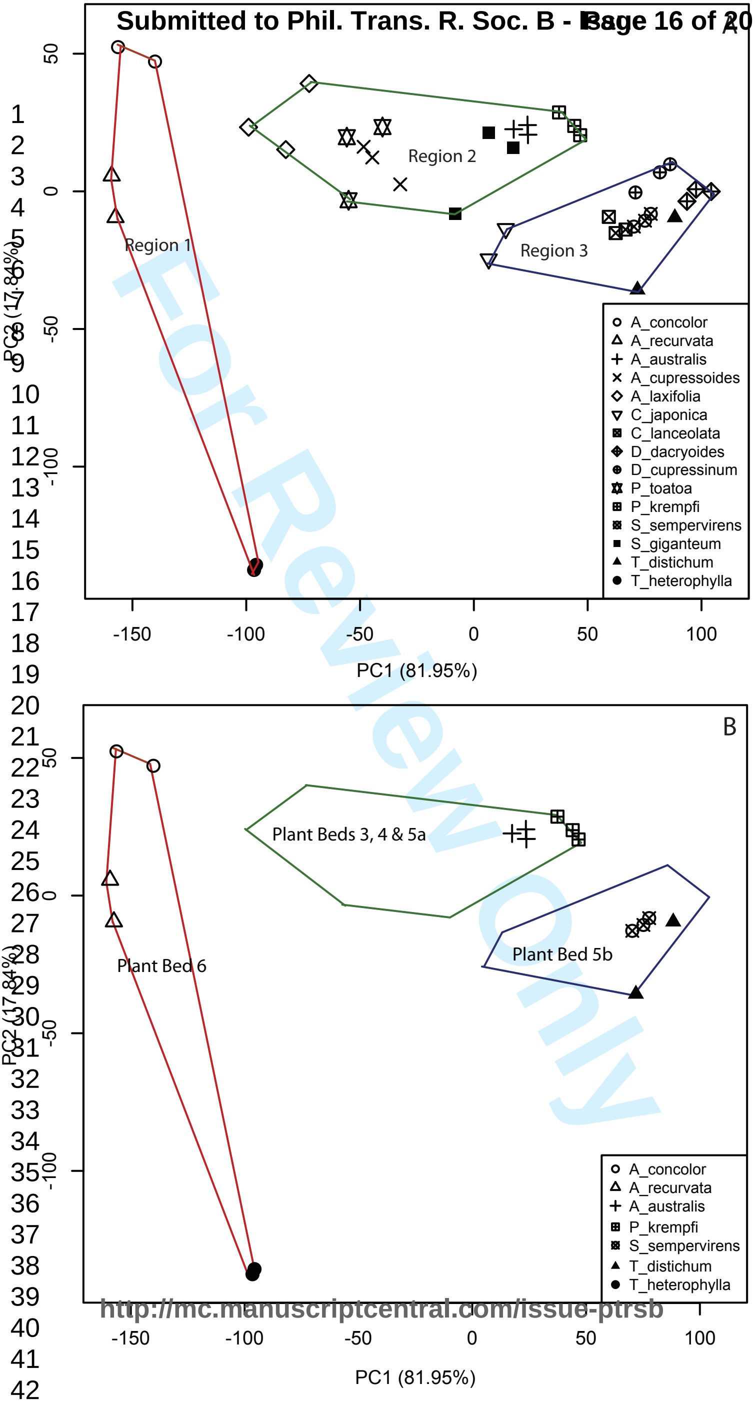
FIGURE 2 – Scatterplots showing the results of Principle Components Analyses (PCA) of the flammability data (TTI, Burn Duration, pHRR, EHoC and THR). A) shows PC axis 1 and 2 for all the species tested B) PC axis 1 and 2 with only species relevant to Astartekløft, East Greenland remaining on the plot.

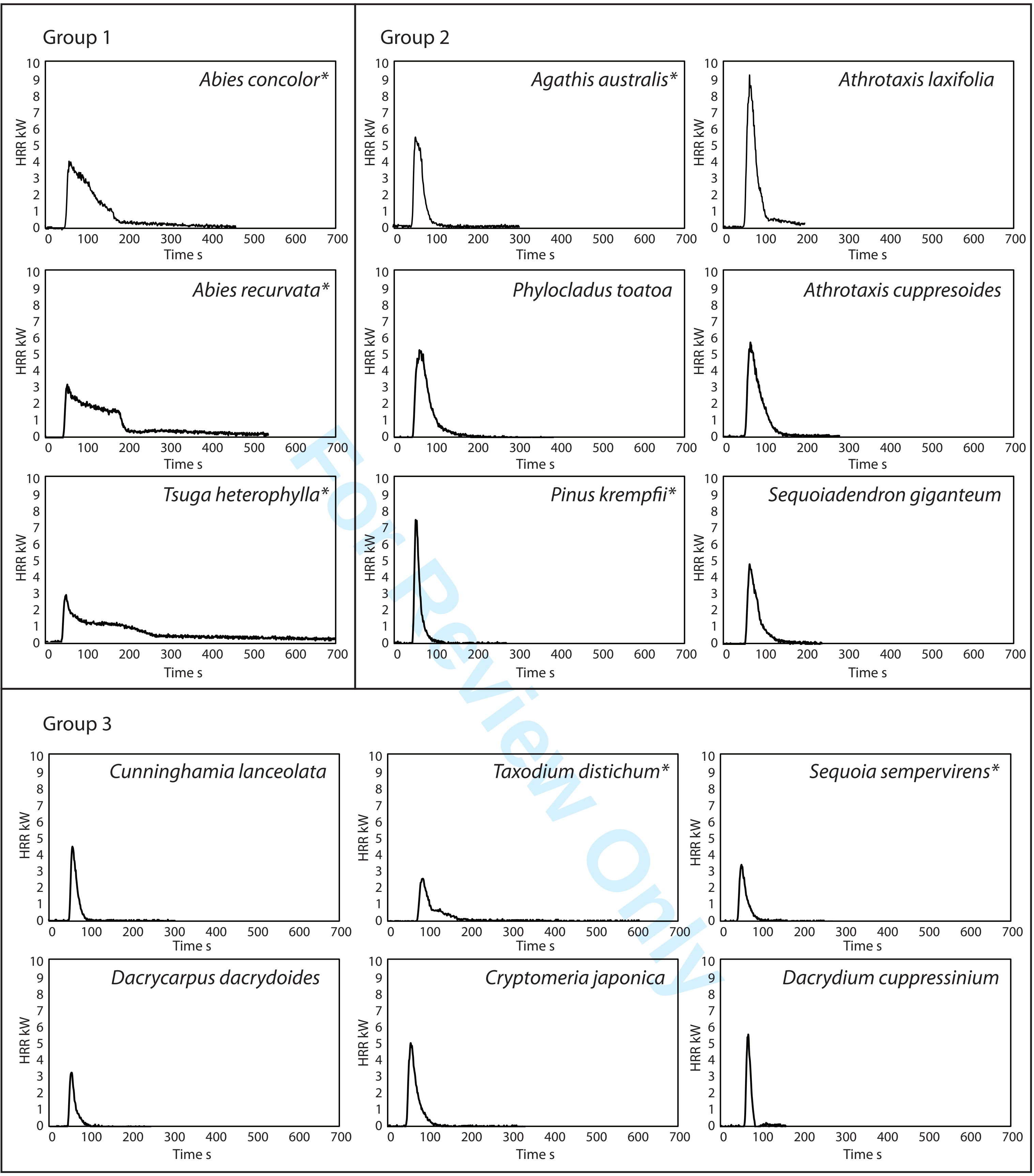
FIGURE 3 – Heat Release Rate Profiles for the conifer species tested grouped according to the results of the Principle Components Analyse; each group corresponds to the Region of the same number outlined on Figure 2A. Species shown with a *are morphotypes representative of fossil leaves found at Astartekløft, East Greenland.

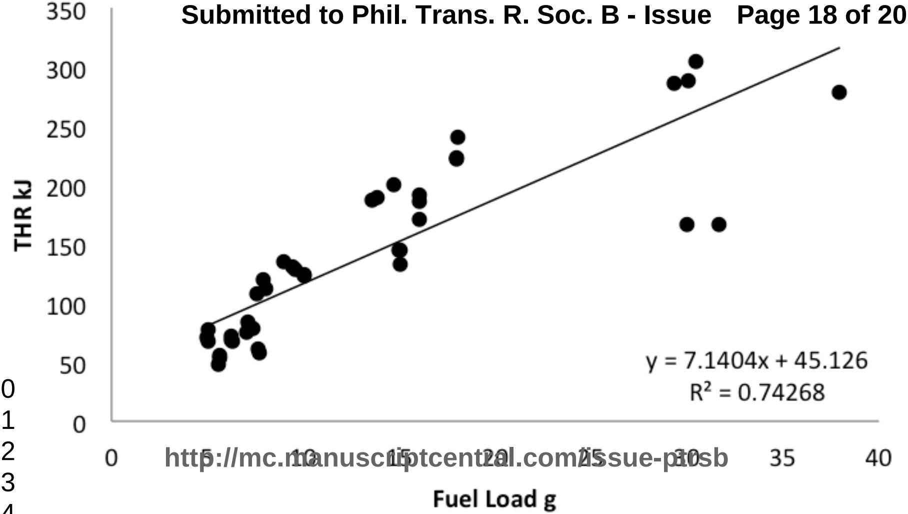
FIGURE 4 – Scatterplot of Fuel Load versus Total Heat Release (kJ) from the flammability experiments.

FIGURE 5 - Schematic of changes to major canopy and litter forming morphotypes across the Triassic-Jurassic Boundary at Astartekløft, East Greenland with changes in charcoal abundance (fire activity) and estimates of palaeolitter fire behaviour. All HRR profiles are shown at the same scale. Log and charcoal abundance modified from [22], floral data taken from [22], HRR profiles from this study.


Ignition
pHRR
THR
HRR (kW)
Time (s)
Burn duration


A
Region 1
Region 2
Region 3
PC2 (17.84%)
PC1 (81.95%)
50
0
-50
-100
-150
-100
-50
0
50
100
A_concolor
A_recurvata
A_australis
A_cupressoides
A_laxifolia
C_japonica
C_lanceolata
D_dacryoides
D_cupressinum
P_toatoa
P_krempfi
S_sempervirens
S_giganteum
T_distichum
T_heterophylla
B
Plant Bed 6
Plant Beds 3, 4 & 5a
Plant Bed 5b
PC2 (17.84%)
PC1 (81.95%)
50
0
-50
-100
-150
-100
-50
0
50
100
A_concolor
A_recurvata
A_australis
P_krempfi
S_sempervirens
T_distichum
T_heterophylla


Group 1
Abies concolor*
Abies recurvata*
Tsuga heterophylla*
Group 2
Agathis australis*
Athrotaxis laxifolia
Phylocladus toatoa
Athrotaxis cuppresoides
Pinus krempfii*
Sequoiadendron giganteum
Group 3
Cunninghamia lanceolata
Taxodium distichum*
Sequoia sempervirens*
Dacrycarpus dacrydoides
Cryptomeria japonica
Dacrydium cuppressinium
HRR kW
0
1
2
3
4
5
6
7
8
9
10
Time s
0
100
200
300
400
500
600
700


THR kJ
350
300
250
200
150
100
50
0
0
5
10
15
20
25
30
35
40
Fuel Load g
y = 7.1404x + 45.126
$R^2 = 0.74268$

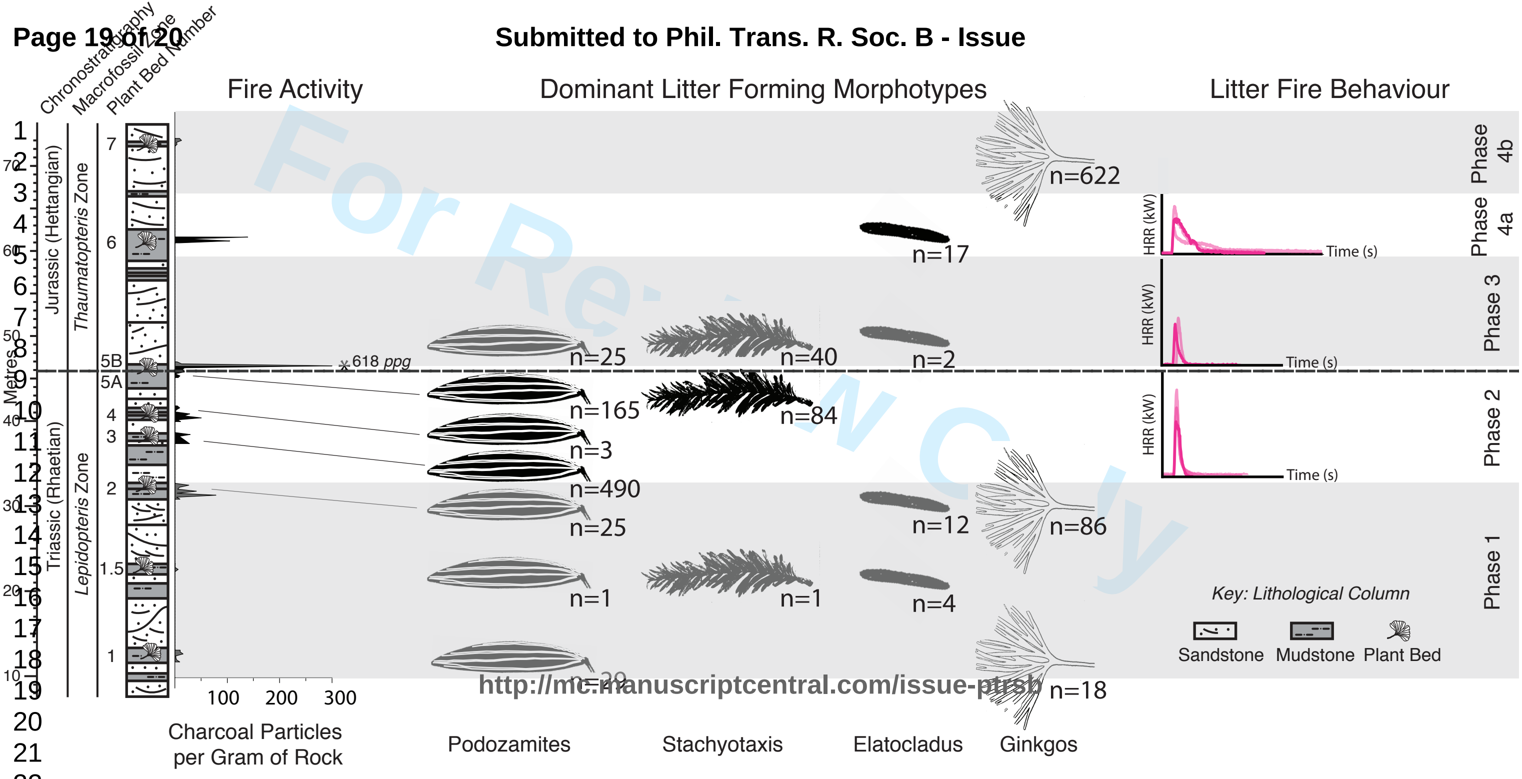

Chronostratigraphy
Macrofossil Zone
Plant Bed Number
Fire Activity
Dominant Litter Forming Morphotypes
Litter Fire Behaviour
Metres
70
60
50
40
30
20
10
Jurassic (Hettangian)
Triassic (Rhaetian)
Thaumatopteris Zone
Lepidopteris Zone
7
6
5B
5A
4
3
2
1.5
1
618 *ppg*
100
200
300
Charcoal Particles per Gram of Rock
n=622
n=17
n=25
n=40
n=2
n=165
n=84
n=3
n=490
n=25
n=12
n=86
n=1
n=1
n=4
n=29
n=18
Podozamites
Stachyotaxis
Elatocladus
Ginkgos
HRR (kW)
Time (s)
Phase 4b
Phase 4a
Phase 3
Phase 2
Phase 1
Key: Lithological Column
Sandstone
Mudstone
Plant Bed

Table 1: Total Heat Release (kJ) estimates for different litter depths per fuel group

Litter Depth	**1cm**	**1.5cm**	**2cm**	**3cm**
Group 1	120.27	157.85	195.42	248.46
Group 2	76.98	92.91	108.83	164.94
Group 3	61.14	69.14	77.14	74.15