

Fire and the spread of flowering plants in the Cretaceous

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Summary

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- We suggest that the spread of angiosperms in the Cretaceous was facilitated by novel fire regimes. Angiosperms were capable of high productivity and therefore accumulated flammable biomass ('fuel') more rapidly than their predecessors. They were capable of rapid reproduction, allowing populations to spread despite frequent disturbance.
- We evaluate the evidence for physical conditions conducive to fires in the Cretaceous. These included high temperatures, seasonally dry climate and higher atmospheric oxygen than current levels. We evaluate novel properties of angiosperms that contributed to rapid biomass accumulation, and to their ability to thrive in frequently disturbed environments. We also review direct evidence for Cretaceous fires.
- Charcoal mesofossils are common in Cretaceous deposits of the Northern Hemisphere. Inertinite, the charcoal component of coal, is common throughout the Cretaceous and into the Palaeocene, but declined steeply from the Eocene when angiosperm-dominated forests became widespread.
- Direct and indirect evidence is consistent with angiosperms initiating novel fire regimes, promoting angiosperm spread in the Cretaceous. Several traits are consistent with frequent surface fires. We suggest that forest was slow to develop until the Eocene, when fire activity dropped to very low levels. The causes and consequences of fires in the deep past warrant greater attention.

Introduction

The angiosperm radiation, one of the major episodes in the history of life, has long been the focus of intense research interest. From an ecological perspective, a key question has been how angiosperms rose to prominence from their beginnings in the Early Cretaceous (*c.* 135 million years ago (Ma)) to dominance in the tropics and a near-ubiquitous presence everywhere else by the end of the Cretaceous (65 Ma) (Crane & Lidgard, 1989; Lupia *et al.*, 1999). Unlike mammals, the ecological expansion of angiosperms cannot be attributed to extraterrestrial catastrophes wiping out competitors. Instead, it seems probable that their expansion was linked to key evolutionary innovations which promoted their spread in the environments of the time. From the fossil record, distinctive angiosperm features during their Cretaceous expansion were small stature (shrubs, herbs), high maximum photosynthetic rates, rapid

reproduction and small seeds. These are the attributes of ruderal species, weedy plants, in modern ecology (Grime, 1979; Taylor & Hickey, 1996; Wing & Boucher, 1998). How was it possible for weedy species to take over the world, displacing tall gymnosperm forests? In contemporary vegetation, ruderals thrive in highly disturbed environments, such as floodplains, and human-altered landscapes, such as abandoned fields. What promoted the worldwide spread of weedy plants in the Cretaceous? Here, we explore the hypothesis that angiosperms created novel fire regimes with positive feedbacks leading to more frequent fires, which further promoted their spread in Cretaceous landscapes. The angiosperm–fire cycle would have been most lethal for pre-existing vegetation where productivity was highest in open (sunlit), warm, low-latitude environments, creating fuels to support more frequent fires. As lower levels of atmospheric CO₂ promote the productivity of angiosperms relative to older lineages (Robinson, 1994;

McElwain *et al.*, 2005; Brodribb & Feild, 2010), we predict that angiosperm-fuelled fire regimes would be most effective at carving into older communities during a period of falling CO₂.

Fires are very widespread in the world today (Chuvieco *et al.*, 2008; Krawchuk *et al.*, 2009), and fire has also been common in the deep past (Harris, 1958, 1981; Chaloner, 1989; Scott, 2000; Scott & Glasspool, 2006). Fire is important in structuring contemporary world vegetation by maintaining extensive open vegetation where the climate has the potential to support closed forests (Bond *et al.*, 2005; Bowman *et al.*, 2009). It is also likely to have been important in structuring ecosystems in the deep past, but studies are still few (Scott, 2000, 2010; Pausas & Keeley, 2009). The influence of fire on the structure of vegetation and the dominant plant traits vary, depending on the fire regime. The fire regime is the characteristic pattern of fire frequency, severity (amount of biomass removed) and spatial extent (Gill, 1975; Bond & Keeley, 2005). Fire regimes depend on the synergy between external physical factors and the properties of vegetation. Changes in the fire regime can be brought about by changes in external conditions, such as climate, but also by changes in vegetation, such as changes in flammability or productivity, which influence the amount and accumulation of fuel. For example, the invasion of grasses into closed wooded habitats has initiated a 'grass fire cycle' in many parts of the world, triggering cascading changes in vegetation structure and composition from forest to open flammable grassy ecosystems (D'Antonio & Vitousek, 1992; Keeley & Rundel, 2005). The spread of invasive African grasses has even altered fire regimes of pyrophytic Australian savannahs, causing catastrophic ecosystem changes (Brooks *et al.*, 2004). Here, we consider the evidence for and against fire as a major factor promoting vegetation change and angiosperm spread in the Cretaceous.

Patterns of angiosperm spread

The oldest undisputed fossil angiosperms date from the Early Cretaceous (*c.* 135 Ma) (Friis *et al.*, 2006), although molecular dating analyses predict much earlier origins (217 Ma; Smith *et al.*, 2010). Angiosperm fossil floras increased in diversity from the Early Cretaceous, but were a minor contributor to the biomass of most vegetation until the mid-Cretaceous (Crane & Lidgard, 1989; Lupia *et al.*, 1999; Nagalingum *et al.*, 2002). From the Cenomanian (*c.* 100 Ma), angiosperms rapidly increased in ecological importance, whereas free-sporing plants (ferns, bryophytes) and nonconifer gymnosperms declined (Crane & Lidgard, 1989; Wing & Sues, 1992; Wing *et al.*, 1993; Lupia *et al.*, 1999). Early angiosperms were once thought to be forest trees, but early fossils were found in unstable, riparian settings and had a weedy nature (Stebbins, 1974; Hickey &

Doyle, 1977; Retallack & Dilcher, 1986; Royer *et al.*, 2010). Feild & Arens (2005) used modern descendants of early angiosperm clades to argue that the initial habitat was 'damp, dark and disturbed' and that the earliest angiosperms were 'xerophobic' (Feild *et al.*, 2009). If this was the case, it changed during the expansion phase of angiosperms. Smith *et al.* (2010), using molecular methods, estimated the origin of crown angiosperms to be 217 Ma, with the origin of the core angiosperm clade (monocots, magnoliids, eudicots) in the late Jurassic (*c.* 155 Ma) or possibly Early Cretaceous (< 144 Ma). All of the angiosperms that dominate modern ecosystems are from this core clade. The fossil evidence indicates that, until at least the mid-Cretaceous, angiosperms were understorey herbs, shrubs and small trees (Tiffney, 1984; Wing & Sues, 1992; Taylor & Hickey, 1996; Wing & Boucher, 1998). Gymnosperm trees persisted at higher latitudes forming woodlands with an angiosperm understorey (Spicer *et al.*, 1993). At lower palaeo-latitudes, in which angiosperms first reached dominance, several gymnosperm lineages went extinct, including the Benettitales and the conifer lineage Cheirolepidiaceae (Crane & Lidgard, 1989; Lupia *et al.*, 1999). The pattern of initial angiosperm spread at low latitudes and increasing ecological prominence by the Late Cretaceous is common to both North America (Lupia *et al.*, 1999) and Australia (Nagalingum *et al.*, 2002). Comparisons of diversity and abundance in the fossil record indicate that diversification preceded ecological abundance by several million years (Lupia *et al.*, 1999; far longer, *c.* 20–100 Ma, according to molecular dating; Smith *et al.*, 2010), with a surge in ecological abundance starting from the Cenomanian (100 Ma).

Were conditions conducive for fires in the Cretaceous?

Chaloner (1989) discussed the necessary preconditions for wildfire in the context of fossil charcoal. These were: growth of sufficient biomass to fuel the fire, periodic conditions dry enough for ignition to occur and for the fire to spread, climatic conditions conducive to lightning strikes to ignite the fire, and sufficient atmospheric oxygen to initiate and maintain a wildfire. The Cretaceous was a warm world (Spicer *et al.*, 1993; Sellwood & Valdes, 2006) and a model for a 'glasshouse world' (Beerling & Woodward, 2001). Lightning activity increases with air temperature (Williams, 1992; Price & Rind, 1994), and so lightning activity in the Cretaceous may have been similar to, or greater than, that in the modern world, and have extended to higher latitudes. Evidence from evaporites, clay minerals and tree rings indicates that, during the Cretaceous, there were extensive seasonally dry areas conducive to fires (Frakes, 1999; Beerling & Woodward, 2001; Finkelstein *et al.*, 2005). In deep time, atmospheric oxygen is an important factor

influencing the occurrence of fire (Robinson, 1989; Jones & Chaloner, 1991; Scott & Glasspool, 2006) and the moisture content at which fuels ignite and fires spread (Watson *et al.*, 1978; Wildman *et al.*, 2004; Belcher & McElwain, 2008). There are few proxies for oxygen in the fossil record and geochemical models used to predict palaeo-atmospheres produce widely divergent patterns (Berner & Canfield, 1989; Berner, 2001, 2009; Bergman *et al.*, 2004). Recent models predict that the Cretaceous had higher oxygen levels than the preceding Triassic (251–200 Ma) and Jurassic (200–145 Ma), peaking in the mid-Cretaceous (*c.* 100 Ma) and declining somewhat thereafter (Bergman *et al.*, 2004; Berner, 2009; see also Berner & Canfield, 1989). Oxygen levels were at least as high as present atmospheric levels and possibly exceeded 25% (Bergman *et al.*, 2004; Glasspool & Scott, 2010). Higher oxygen levels have been shown experimentally to promote fire spread through moister fuel types than contemporary vegetation (Watson *et al.*, 1978; Jones & Chaloner, 1991; Wildman *et al.*, 2004; Belcher & McElwain, 2008). Consequently, high palaeo-oxygen would have promoted fires under a wider range of weather conditions than today. Thus the physical preconditions were favourable for high fire activity throughout the Cretaceous, especially from the mid-Cretaceous. The availability of fuel would have been a significant constraint on how frequently fires occurred. Highly productive weedy angiosperms would have accumulated fuel rapidly, promoting shorter fire cycles where physical preconditions were met.

Did fires burn in the Cretaceous?

Global fire indicators

As the spread of angiosperms was ubiquitous and contemporaneous in both Northern and Southern Hemispheres (Lupia *et al.*, 1999; Nagalingum *et al.*, 2002), disturbance factors that opened forest and promoted angiosperm spread should also have had a global reach (Barrett & Willis, 2001). Fossil markers of wildfire activity are now well established (Scott, 2000, 2010). However, it is very likely that palaeo-fires have been under-reported because of the failure to recognize fossil proxies of fire activity (Scott, 2010). Palaeo-fires are identified from fossil charcoal (also known as fusain) (Scott, 1989, 2000, 2010; Jones & Chaloner, 1991), the maceral inertinite in coal (Scott & Glasspool, 2007) and geochemical proxies (polycyclic aromatic hydrocarbons) (Finkelstein *et al.*, 2005; Scott, 2010). Fossil evidence for wildfires shows that fires have been burning for > 400 Ma (Scott, 2000; Glasspool *et al.*, 2004). During the earlier history of terrestrial vegetation, fire activity was high in the Carboniferous (*c.* 360–300 Ma) (Falcon-Lang, 2000) and Permian (300–251 Ma), congruent with high atmospheric oxygen (Scott & Glasspool, 2006). Mesozoic (250–65 Ma) records of charcoal, inertinite and geochemical

proxies (polycyclic aromatic hydrocarbons) for wildfire have been collated recently by Belcher & McElwain (2008) and Glasspool & Scott (2010). These show that wildfires were burning throughout the Mesozoic, including the Cretaceous, contradicting some geochemical model predictions of oxygen levels too low to support wildfires over this period (Berner, 2006).

Inertinite is the charcoal fraction in coal deposits associated with wetland habitats – ‘mires’ (Scott & Glasspool, 2007). The inertinite content of coal provides a long, geographically widespread record of fire activity in mires over almost the entire history of terrestrial vegetation (Diessel, 2010; Glasspool & Scott, 2010). The inertinite record shows that fires were common in the Palaeozoic and helped shape Carboniferous and Permian ecosystems (Scott & Jones, 1994; Falcon-Lang, 2000; Scott, 2000). The mass extinction at the end of the Permian (251 Ma) terminated many Palaeozoic lineages, possibly including ancient fire-adapted elements. In the Mesozoic, fire activity was low in the early to mid-Triassic, increasing into the Jurassic (Belcher *et al.*, 2010), and quite common in parts of the Jurassic predating the spread of angiosperms (Harris, 1958; Scott, 2000; Scott & Glasspool, 2006). There are numerous records of fire in the Cretaceous, including many charcoali-fied fossils (Fig. 1). Belcher & McElwain (2008) reported higher fire activity in the Cretaceous than in the Triassic and Jurassic, with fires peaking in the Late Cretaceous (their Fig. 1b, in Supplementary Online Material). Their data are for overbank deposits, where angiosperms were most likely to flourish, rather than mires. The increase in fire activity is particularly marked when controlled for proxies of the availability of suitable rock sections for study (Belcher & McElwain, 2008). As wildfires long preceded the rise of the angiosperms, it is not the appearance of vegetation fires, but a change in the fire regime, that must be invoked as promoting their spread.

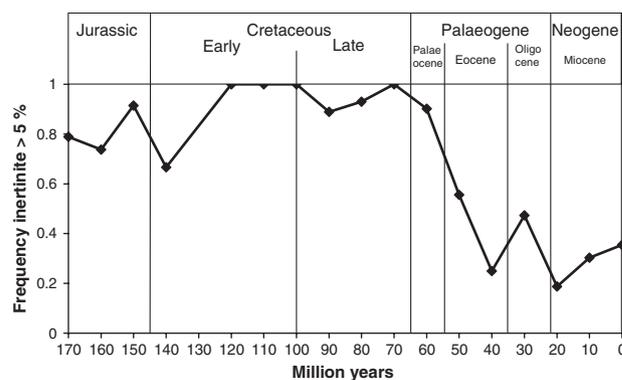


Fig. 1 Frequency of localities with inertinite exceeding 5% of coal macerals over time. The 5% threshold approximates the average charcoal content of contemporary mires. Data are sparse (< 10 records) from 140–125 million years ago (Ma) and 115–95 Ma. Data ex Glasspool & Scott (2010).

Fires continued to burn after the Cretaceous–Palaeogene (K–Pg) event (65 Ma = old Cretaceous–Tertiary (K/T)) and into the Palaeocene (Scott *et al.*, 2000b; Belcher *et al.*, 2003, 2005). However, the inertinite record shows an abrupt decline in mire fires in the Eocene (from *c.* 56 Ma) (Fig. 1) (see also Collinson *et al.*, 2007) and charcoal is rare in non-mire settings (Scott, 2010). Mire fire activity remained very low through the Cenozoic, with some signs of increased activity from the late Miocene/Pliocene (*c.* 10 Ma) to the present (Fig. 1; Diessel, 2010; Glasspool & Scott, 2010). During this period, when the modern biota began to assemble, wildfire activity measured by inertinite reached nearly its lowest level as plants first spread onto land! If fires were important in structuring world vegetation, this apparent decrease in fire activity should have triggered major vegetation change. By analogy with modern vegetation, a reduction in fires would have led to the replacement of Late Cretaceous/Palaeocene pyrophytic shrublands and open woodlands by closed forests wherever the climate was warm enough and wet enough (Bond *et al.*, 2005). Major changes in vegetation did indeed occur from the Palaeocene into the Eocene with the widespread expansion of forest, including tropical rainforests, consistent with reduced fire activity (Collinson, 1990, 2000; Willis & McElwain, 2002; Burnham & Johnson, 2004). Later, in the Neogene, the opening up of forested landscapes and the initial spread of grasslands were more likely because of the onset of cold dry conditions (Strömberg, 2005). Charcoal records from marine deposits (which record a much wider general record of fire) in the North Pacific show a massive increase in fire activity from the late Miocene (Fig. 2), which has been linked to the expansion of pyrophytic vegetation (Keeley & Rundel, 2005). This increased fire activity is not reflected in the inertinite record which is formed in mire habitats (Fig. 1). Glasspool & Scott (2010) interpreted this

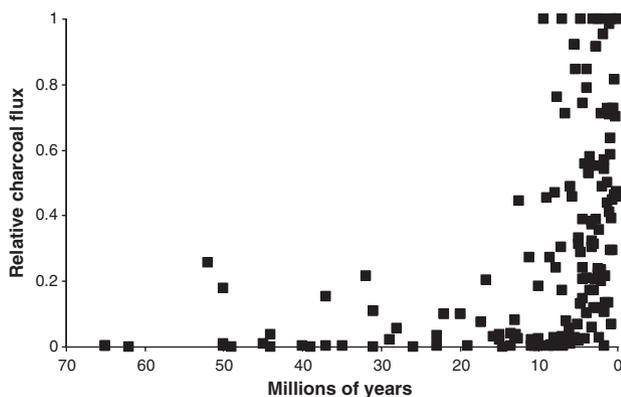


Fig. 2 Charcoal fluxes (relative to maximum flux) in the North Pacific as a measure of vegetation fires through the Cenozoic. Data are from seven marginal and two central deep sea drilling sites listed in Table 2 in Herring (1985). To compare across sites, fluxes are shown as proportions of the maximum flux for each site.

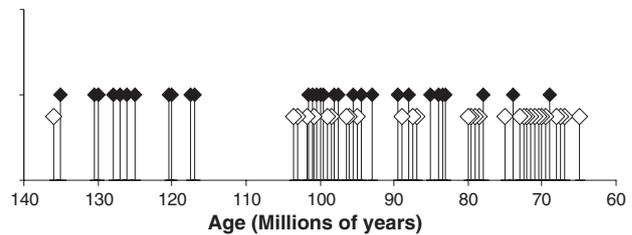


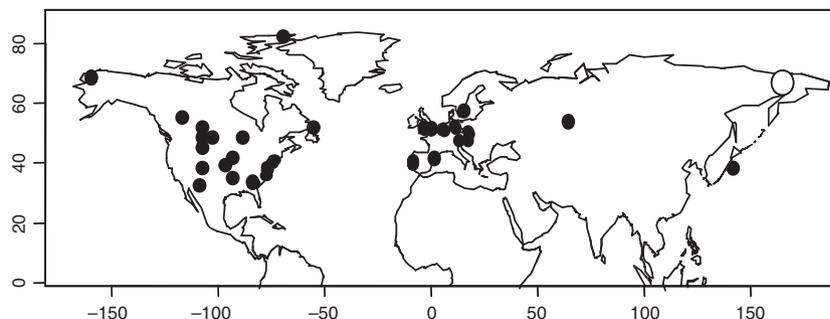
Fig. 3 Ages (millions of years) attributed to Cretaceous sites with evidence of wildfire. Closed symbols, sites with charcoalified mesofossil flowers and vegetative organs; open symbols, general charcoal. See Appendix A1 for sources.

reduction of fire in mire systems to indicate close to modern atmospheric oxygen levels and thus no promotion of increased fire. There is clearly a need for more Cenozoic data on upland fire activity to better interpret the factors influencing the emergence of modern vegetation.

Local fire indicators

There is abundant direct evidence, in the form of charcoal, that fires burnt vegetation containing angiosperms in the Cretaceous (Fig. 3). The most remarkable examples are three-dimensionally preserved flowers, first discovered by Friis in a Late Cretaceous locality in southern Sweden (Friis & Skarby, 1981). Ancient fires preserved the fine detail of charcoalified flowers, fruits, seeds and other organs of angiosperms, together with co-occurring gymnosperms and free-sporing plants (Friis *et al.*, 2000; Schönenberger, 2005; Scott, 2010). Since the initial discovery, similar charcoalified floras from the Cretaceous have been reported from many localities in Europe and eastern North America (Crane & Herendeen, 1996), with additional discoveries in Central Asia (Frumin & Friis, 1999), Japan (Takahashi *et al.*, 2008) and Antarctica (Eklund, 2003) (Fig. 4). Charcoalified fossil flowers are typically small (in the range of a few millimetres) and are categorized as mesofossils, as distinct from megafossils (larger structures such as leaves, branches and stems) or microfossils (pollen and spores). The ancient post-burn localities yielding these fossils have produced most of what we know about Cretaceous angiosperm flowers (Friis *et al.*, 2006), supplemented by rare compression fossils whose preservation is unrelated to fire (e.g. Crato Formation of Brazil; Mohr & Friis, 2000). All currently known charcoal mesofossil localities are from mid to high palaeo-latitudes, mainly from the Northern Hemisphere, but also from Antarctica (Gondwana; Eklund, 2003) (Fig. 4). They span from the Early Cretaceous (Barremian–Aptian of Portugal, 130–115 Ma; Friis *et al.*, 2000) to the Late Cretaceous (Maastrichtian) of Europe and North America (Crane & Herendeen, 1996; Friis *et al.*, 2006). The Early Cretaceous Wealden floras of southern Britain were dominated by open-habitat ferns and Bennettitales

Fig. 4 Localities with evidence for Cretaceous wildfires in the Northern Hemisphere (excluding mires). There are very few localities where Cretaceous charcoal has been reported in the Southern Hemisphere (Antarctica, Patagonia in Argentina and Queensland in Australia). See Appendix A1 for sources.



assembled into a frequently burnt 'fern prairie' (Harris, 1981; Collinson *et al.*, 2000). The reproductive structures of the seed ferns (Bennettitales) have been interpreted as analogous to serotinous structures in modern plants, insulating seeds from the flames, and releasing them once the fire has passed (Harris, 1981). The somewhat younger (Barremian–Aptian) floras of Portugal and the North American Potomac Group sequence have yielded abundant and diverse charcoalified angiosperm flowers mixed with burnt organs of nonangiosperms (ferns, gymnosperms, mosses) and even insects (Herendeen & Skog, 1998; Schönenberger, 2005; Friis *et al.*, 2006).

In a study that helps to reveal the kinds of fires that produced angiosperm mesofossils, Scott *et al.* (2000a) analysed the taphonomy of a modern heathland fire in England. Charcoalified flowers, fruits, wood and leaves resembled those of Cretaceous mesofossil floras. The heathlands burnt from a rapidly spreading surface fire with flames no greater than 2 m high, so that taller trees (*Pinus sylvestris*, *Betula pendula*) survived the fire. Severe, high-intensity, canopy fires would be more likely to destroy fine structures, preserving only larger segments of wood. Scott *et al.*'s study suggests that the mesofossil floras of the Cretaceous were burnt in low-intensity surface fires. Modern analogues would be shrublands or shrub/herb mixtures with or without an emergent layer of fire-tolerant (thick-barked) trees.

In summary, there is widespread direct evidence for surface fires of relatively low-intensity burning Cretaceous vegetation fuelled by angiosperms. Angiosperms did not initiate vegetation fires or even surface fire regimes. Similar fire regimes also occurred in the Early Cretaceous fuelled by open-habitat ferns (fern prairies; Harris, 1981; Collinson *et al.*, 2000). The gymnosperms characteristic of these habitats (Bennettitales, Cheirolepids) were among the first to go extinct as angiosperms spread (Crane & Lidgard, 1989). These fern prairies would be particularly suitable for early colonization by fast-growing weedy angiosperms. The spread of angiosperm-fuelled fire regimes into closed forest habitats would have been a slower process. It is interesting to note that ferns, such as bracken (*Pteridium aquilinum*), remain prominent components of some modern flammable vegetation, especially in wetter habitats (Gliessman, 1978).

Angiosperms would be better able to colonize drier habitats, recruiting from seeds rather than spores and without the constraint of a free-living gametophyte.

Cretaceous angiosperm traits and fire

High productivity and fuel accumulation

High productivity and rapid regeneration rates would be prerequisites for angiosperms to create novel fire regimes with positive feedbacks leading to more frequent fires, which further promoted angiosperm spread. The angiosperm fire cycle would have been most lethal for pre-existing vegetation, where productivity relative to nonangiosperms was highest. There has been considerable recent interest in the ANITA grade of early angiosperms and their ecophysiological properties. Feild *et al.* (2009) emphasized the 'xerophobic' nature of extant members of early angiosperm clades which live in 'damp, dark and disturbed' habitats. The growth forms predominant in the mid-Cretaceous expansion phase of angiosperms, however, were fast-growing, 'weedy' plants capable of rapidly colonizing disturbed areas (Stebbins, 1974; Tiffney, 1984; Taylor & Hickey, 1996; Wing & Boucher, 1998). The physiological basis for rapid growth and high productivity (rapid fuel accumulation) has been convincingly shown to be rooted in angiosperm innovations in the hydraulic system (Boyce *et al.*, 2009; Brodribb, 2009; Brodribb & Feild, 2010). Besides vessels, angiosperms have much higher maximum leaf vein densities than any nonangiosperm lineage (Boyce *et al.*, 2009; Brodribb & Feild, 2010). As much as 80% of the resistance to water flow from the soil to the leaf is in the last few millimetres from the vein endings to the stomata. High vein densities reduce this distance and facilitate rapid water transport in a transpiring leaf. Both theoretical models and empirical data show that vein densities are linearly related to maximum photosynthetic rates. Brodribb & Feild (2010) showed a threefold increase in vein density during the early evolution of angiosperms, which they predict would have increased maximum photosynthetic uptake of CO₂ by 174% during angiosperm radiation. For modern-day O₂ and CO₂, this change in vein densities would result in more than a

doubling of maximum photosynthetic rate for Late Cretaceous angiosperms. By contrast, fern and gymnosperm vein density showed no change through the Cretaceous (Brodribb & Feild, 2010).

To reach their high photosynthetic potential, angiosperms require optimal growth conditions, including open, sunlit habitats, adequate nutrients and water, and sufficient atmospheric CO₂. Thus, rapid fuel accumulation sufficient to change fire regimes would be most likely where growing conditions allow angiosperms to operate at A_{\max} (the light-saturated rate of CO₂ assimilation). This leads to the prediction that angiosperms would have been most successful in open habitats and not in the understorey of shady conifer forests. High nitrogen requirements (Berendse & Scheffer, 2009) associated with high A_{\max} are more likely to be met following disturbance by fire or herbivores than in the undisturbed litter of conifer forests. High photosynthetic rates should be expressed in leaf properties, including low leaf dry mass per area. Royer *et al.* (2010), using the petiole diameter and leaf area of Potomac Group (110–105 Ma) macrofossils, estimated that leaf dry masses per area were low for angiosperm species (< 125 g m⁻²; mean, 76 g m⁻²) compared with gymnosperm species (> 240 g m⁻²; mean, 291 g m⁻²). These differences are consistent with a 'weedy' habit for early flowering plants.

CO₂ starvation through the Cretaceous has been suggested as a significant driver of taxonomic diversification and ecological radiation of the angiosperms (Robinson, 1994; McElwain *et al.*, 2005). The assumption is that CO₂ concentrations were high in the Early Cretaceous (three to more than seven times modern CO₂), declining to levels perhaps similar to contemporary CO₂ by the end of the Cretaceous. McElwain *et al.* (2005) assembled pollen data to show that angiosperms increased in importance in local floras with declining CO₂, whereas pteridophytes decreased. They suggested that hydraulic innovations allowed angiosperms to cope better with the physiological drought imposed by lower atmospheric CO₂. Unfortunately, levels of atmospheric CO₂ through the Cretaceous are uncertain (Kuypers *et al.*, 1999; Berner & Kothavala, 2001; Fletcher *et al.*, 2008), although the trend of decreasing CO₂ through to the Cenozoic is fairly robust (Pagani *et al.*, 2005). The dramatic increase in angiosperm maximum vein densities during the mid- to Late Cretaceous (Brodribb & Feild, 2010) is consistent with declining CO₂ from the mid- to Late Cretaceous (Fletcher *et al.*, 2008). The implication is that major advances in the productivity of angiosperms vs nonangiosperms were only realized from the mid-Cretaceous.

In summary, recent advances in the ecophysiological understanding of plant hydraulics have revealed the basis for the high productivity of Cretaceous angiosperms and the environmental context in which it is most likely to be expressed. There are strong similarities to the evolution of

the C₄ photosynthetic pathway and the spread of C₄ grasses in the late Miocene (*c.* 8 Ma). Whereas the key vegetative innovation of angiosperms was the physics of water transport, the key innovation of C₄ photosynthesis in the Cenozoic was biochemical. Both innovations show greatest relative photosynthetic advantage at low CO₂ (Ehleringer *et al.*, 1997; Sage, 2004; Osborne, 2008; Brodribb & Feild, 2010) and under high-light conditions (Sage & McKown, 2006). Low CO₂ has also been implicated in the decline of trees under frequent disturbance (Bond *et al.*, 2003), because of the slower recovery rates of saplings and resprouting trees relative to grasses and shrubs. The synergy between fire and growth forms that are productive under low CO₂ may have promoted angiosperm expansion in the Cretaceous in a biological revolution much earlier than that of C₄ grasses (Beerling & Osborne, 2006).

Low stature

Frequent surface fires favour low-stature plants that can recover quickly after a burn. Analyses of the axis diameter of angiosperm woods in the Cretaceous show that angiosperm trees were very rare until near the end of the Cretaceous. Extensive fossil wood collections from North America (Wheeler & Baas, 1991) and Europe (Philippe *et al.*, 2008) show a lack of angiosperm trees during the major expansion phase of angiosperms. Large angiosperm trees were present in the Late Cretaceous, but were still rare in most assemblages (see review by Wing & Boucher, 1998; Oakley & Falcon-Lang, 2009; Wheeler & Lehman, 2009), and continued to be so into the Palaeocene. Angiosperm forests only became widespread from *c.* 56 Ma in the Eocene (Willis & McElwain, 2002; Burnham & Johnson, 2004; Philippe *et al.*, 2008). The scarcity of fossil evidence of tall angiosperm trees in the Cretaceous is all the more striking given their abundance in the Eocene. Charcoal records from both mire and nonmire environments show that fires were common through the Palaeocene, but dropped to low levels from the Eocene (Fig. 1) (Diessel, 2010; Glasspool & Scott, 2010). Thus, the global fire record is consistent with high fire activity in the Cretaceous supporting shrubby or herbaceous 'savannah-like' vegetation (without grasses) dominated by angiosperms or ferns in low-lying sites.

Diaspore size and dispersal

The small diaspore size of Cretaceous angiosperms contrasts with much larger seeds from the Eocene (Tiffney, 1984; Wing & Tiffney, 1987). Small seed size has been interpreted as indicating open sunlit habitats in the Cretaceous, with larger seeds in the Eocene indicating the appearance of tall, shady forests (Eriksson, 2008) or large trees (Moles *et al.*, 2005). Cretaceous angiosperm seeds were not only small, but also usually abiotically dispersed (Tiffney, 1984;

Collinson & Hooker, 1991; Eriksson, 2008). Abiotic dispersal is common in contemporary pyrophytic shrublands, such as chaparral and Cape fynbos, whereas animal-dispersed fruits dominate in adjacent closed forests (Keeley, 1991; LeMaitre & Midgley, 1992). The prevalence of abiotic dispersal in pyrophytic shrublands has been attributed to selection for dispersal in time (dormant seedbanks), rather than in space, as fires create large homogeneous regeneration gaps. By contrast, animal dispersal is selected where suitable safe sites for regeneration are small and patchy, such as in forest gaps (Keeley, 1991; LeMaitre & Midgley, 1992). The small seeds and abiotic dispersal characteristics of Cretaceous angiosperms are consistent with low, flammable vegetation.

Fire adaptations

A number of reproductive and vegetative plant traits are considered to be fire adaptations, with different traits in different fire regimes (Pausas *et al.*, 2004; Bond & Keeley, 2005). Some features of fossil plants have been interpreted as fire adaptations, such as serotiny in Bennettitalean seed ferns (Harris, 1981). Pausas & Keeley (2009) provided a guide to the traits characteristic of different fire regimes that might be apparent in the fossil record. These included cone retention (serotiny), indicative of crown fire regimes, thick bark, indicative of emergent trees in surface fire regimes, and organs that facilitate post-burn sprouting. Fire-adaptive traits have hardly been explored in the fossil record or in phylogenetic studies of clade diversification (but see Simon *et al.*, 2009 for a phylogenetic analysis of the origins of Brazilian savannahs). There are difficulties in doing so because a trait can seldom be unequivocally attributed to selection by fire (Bond & Keeley, 2005). However, if fires were important in angiosperm spread, we would predict that gymnosperm trees emerging above the angiosperm layer would have a thick bark to insulate against low-severity surface fires. Conifers with thin bark should be associated with fire-free localities with low angiosperm abundance (or with crown fires and serotiny) (Schwilk & Ackerly, 2001).

Many modern shrubs and juvenile trees survive fire by resprouting, often using stored reserves to facilitate rapid sprouting (Bond & Midgley, 2003). Wheeler & Lehman (2009), in a discussion of unusual features of Cretaceous dicot wood, noted the common occurrence of large amounts of storage tissue. They suggested that storage 'might aid in rapidly replacing cropped foliage, and be valuable for wound response', and might also facilitate stump sprouting if a tree was 'toppled by large herbivores', such as dinosaurs. We suggest that vegetation fire was a major additional factor selecting for storage tissue in Cretaceous woody dicots, facilitating post-burn resprouting (see also Verdaguer & Ojeda, 2002; Pausas & Keeley, 2009).

Fire and forests

If novel fire regimes promoted the spread of flammable open communities rich in angiosperms, then other taxa that prefer open, rather than closed, forest understorey environments should also have been favoured unless outcompeted by angiosperms. Ferns, conifers and bryophytes that favour open, disturbed habitats should be associated with angiosperm spread rather than closed forest taxa. This prediction is at variance with studies claiming significant diversification of forest clades in the Cretaceous. Schneider *et al.* (2004), for example, used phylogenetic analyses to show that some fern lineages, and particularly polypods, diversified after angiosperm diversification in the Cretaceous 'under the shade of angiosperm forests'. They noted that many polypod ferns live in shaded habitats and some have a novel photoreceptor conferring ecological advantages under low-light conditions. A subsequent phylogenetic study explicitly analysed the pattern of epiphytic fern radiations, arguing that epiphytes would only have diversified in forests (Schuettpelz & Pryer, 2009). Their analysis showed that epiphytic ferns only began to diversify in the Eocene, consistent with the majority of fossil evidence indicating that angiosperm forests only became widespread in the Eocene (Tiffney, 1984; Willis & McElwain, 2002; Collinson & Hooker, 2003; Burnham & Johnson, 2004). More analyses are needed to resolve the origins of closed forest vs open habitat biota in the Cretaceous.

There are few good fossil data sources from palaeo-equator and low latitudes in the Cretaceous. Although there is very little fossil evidence for the presence of angiosperm-dominated tropical forests in the Cretaceous, there is also very little evidence for their absence (Burnham & Johnson, 2004). Some studies have inferred Early to mid-Cretaceous origins of tropical forests from phylogenies of living angiosperm groups (e.g. Davis *et al.*, 2005; Wang *et al.*, 2009). However, the earliest unequivocal fossil record of a neotropical rainforest is from the Palaeocene (*c.* 58 Ma) (Wing *et al.*, 2009). The family composition of this Colombian fossil flora matches that of extant neotropical rainforests, although the diversity is much lower. Wing *et al.* (2009) suggested that the low diversity and generalized patterns of insect herbivory indicate a recent assembly of the forest biome following a major extinction and changes in floral composition after the K–Pg event (65 Ma).

In the modern world, landscapes dominated by flammable vegetation often contain patches of fire-sensitive forests in refugia in which fires seldom burn. Such fire refugia may have been the cradle of angiosperm forests in the Cretaceous. However, it is surprising that fossil floras from riparian sites lack angiosperm trees, as such sites are often occupied by fire-sensitive riparian forest today. Forests did occur in the Cretaceous, but at high latitudes very different from today. Instead of tundra, gymnosperm forests extended

to near the poles (Wing *et al.*, 1993; Beerling & Woodward, 2001). Lower productivity and shorter growing seasons should favour less frequent, less severe fires and longer fire-return times because of slow fuel accumulation and, possibly, less frequent ignitions. The result would be that gymnosperm trees would persist at high latitudes just as they do today in areas of low angiosperm productivity (Bond, 1989).

Contemporary legacies of fiery beginnings

What, if any, legacy is there of ancient fiery origins of angiosperms? One would expect a bimodal origin of taxa that thrive in modern flammable ecosystems. Some should have ancient roots from angiosperms that evolved in the fires of the Cretaceous landscapes. Many others should have much more recent origins (late Miocene or even younger), coinciding with the increased fire activity of the last few million years (Fig. 2), especially those associated with highly flammable C_4 grassy ecosystems. C_4 grasses first appeared in the Oligocene (*c.* 33 Ma), but only became prominent as a global biome from the end of the Miocene (*c.* 8–9 Ma; Ehleringer *et al.*, 1997; Osborne, 2008; Passey *et al.*, 2009). Woody clades succeeded in colonizing Brazilian savannahs from adjacent biomes only in the last 4–10 Ma (Simon *et al.*, 2009). We would predict that some clades characteristic of pyrophytic shrublands (Californian chaparral, Cape fynbos etc.) might have ancient Cretaceous origins, with more recent diversification associated with Plio-Pleistocene increases in fire activity. This assumes that the few data on low fire activity in the Cenozoic are real and global in extent.

A second legacy of fiery origins may be the occurrence of butenolide-stimulated seed germination (Flematti *et al.*, 2004; Light *et al.*, 2009). Butenolide is a constituent of smoke. Many plants in crown fire systems, such as chaparral

and fynbos, have smoke-stimulated seed germination (Keeley & Fotheringham, 2000). However, the butenolide response of seeds is very widespread among angiosperms, including species (lettuce!) that do not occur in fire-prone habitats (Pausas & Keeley, 2009). Is the butenolide response an ancient physiological legacy of fire-stimulated germination in Cretaceous angiosperms?

Discussion

We suggest that the spread of angiosperms in the Cretaceous was promoted by the development of novel fire regimes linked to the evolution of novel, highly productive (and flammable) plants. Within the limits of physical constraints on fire occurrence, Cretaceous angiosperms would have initiated a positive feedback analogous to the grass–fire cycle (D’Antonio & Vitousek, 1992). Fast-growing angiosperms would not only compete with regenerating gymnosperms, but would also rapidly accumulate fuel. More fuel would promote more frequent fires, which would help to maintain open habitats in which rapid growth traits of angiosperms would be most favoured, promoting rapid fuel accumulation etc. (Fig. 5). Similar processes underlie the replacement of forests by invasive grasses in the modern world (D’Antonio & Vitousek, 1992), and probably promoted the spread of C_4 grassy biomes in the past (Keeley & Rundel, 2005; Beerling & Osborne, 2006). Frequent fires would have altered the vegetation structure and composition by both increasing the mortality rates of fire-damaged trees and reducing the recruitment rates of slow-growing tree seedlings and saplings (Fig. 5; showing feedback loops) (e.g. Beerling & Osborne, 2006). The effect would be to create more open sunlit conditions favouring plants with the angiosperm innovations of high photosynthetic rates (Brodribb *et al.*, 2007; Brodribb & Feild, 2010), rapid maturation (Verdu, 2002) and rapid reproduction

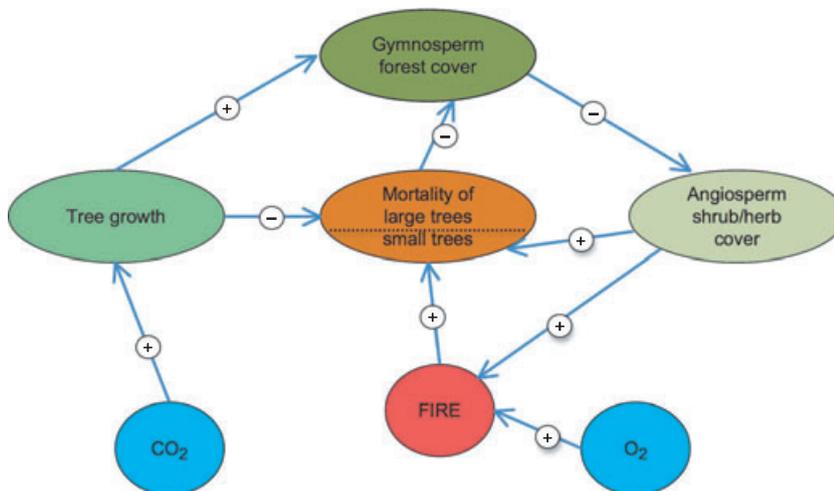


Fig. 5 The Cretaceous angiosperm–fire cycle showing the processes influencing the opening of gymnosperm-dominated forests and the incursion of low-growing angiosperms.

relative to gymnosperms (Bond, 1989). Gymnosperms and free-sporing plants would be negatively impacted by both the high disturbance frequency and competition from angiosperms in the regeneration phase (Bond, 1989). Fire would be most effective in maintaining open vegetation (promoting 'weedy' angiosperms) where the regrowth rates of trees were slow relative to understorey shrubs and herbs.

Fire has some analogies to large-vertebrate herbivory, particularly in the potential to open forests and create habitat for low-growing, sun-loving plants over extensive areas (Bond & Keeley, 2005). Our suggested role for fire in favouring 'weedy' plants by maintaining open habitats is similar to that proposed for dinosaurs by Bakker (1978). He noted a switch from high-browsing sauropod dinosaurs in the Jurassic to low-browsing (ornithischian) dinosaurs in the Cretaceous, and argued that the switch in browser height would favour fast-growing angiosperms. Trampling by dinosaurs ('dino-turbation') would also have helped open forests, especially where animals concentrated. The dinosaur hypothesis has recently been tested and found to be wanting as a general explanation for angiosperm spread, because of mismatches in the timing and coincidence of angiosperm abundance and low- vs high-browsing dinosaurs (Barrett & Willis, 2001; Butler *et al.*, 2009).

The notion that early angiosperms were weedy has been challenged (e.g. Feild & Arens, 2005). Our point is that the major expansion of angiosperms, especially during the mid-Cretaceous, was by flowering plants with the vegetative and reproductive attributes of fast-growing 'ruderal' forms (Taylor & Hickey, 1996; Wing & Boucher, 1998; Brodribb & Feild, 2010; Royer *et al.*, 2010). Angiosperms are extraordinarily diverse and have penetrated almost every habitat. They cover nearly the full range of vascular plant morphologies, including slow-growing gymnosperm-type attributes, fern-like epiphytes, desert succulents, etc. The sheer diversity of growth forms must account for much of their diversification and penetration of diverse habitats by the Late Cretaceous. However, angiosperms were not mere additions to Mesozoic vegetation. They also created new plant communities and displaced older free-sporing and gymnosperm clades, particularly at low latitudes. We suggest that fire was a major factor behind this process, as fast-growing ruderals were not only able to tolerate very frequent disturbance, but also to promote more frequent fires, whilst also outcompeting slower growing plants in regeneration gaps (Bond, 1989).

The palaeo-history of fire indicates that frequent fires and fire-adapted vegetation (e.g. fern prairies) already existed in Early Cretaceous landscapes (Collinson *et al.*, 2000). Environmental conditions of high oxygen content of the atmosphere, seasonal climates with a dry season and warm conditions favouring fires over wide latitudinal gradients helped to promote novel angiosperm-fuelled fire regimes. The principle of uniformitarianism is difficult to apply to

the Cretaceous world. The range of flammable leaf and stem morphologies of the modern world would have been quite different under high atmospheric oxygen with a much wider range of plant forms supporting the spread of fire (Belcher & McElwain, 2008). The considerable direct evidence of fires in Cretaceous vegetation in the form of mesofossils (Figs 3, 4) indicates that fires were not rare catastrophic events, but occurred as low-intensity surface fires analogous to those of many flammable formations today.

Bakker (1978) recognized that external disturbance agents would have favoured the ecological spread of angiosperms. Vegetation fires would work in analogous ways in helping to create gaps in closed forests, facilitating the growth of low-statured, shade-intolerant plants. Heavy dinosaur browsing and physical habitat trampling were probably also important in opening habitats, particularly in areas favourable for dinosaur herbivory. Berendse & Scheffer (2009) have recently suggested that differences in nutrient cycling between angiosperms and gymnosperms may have driven positive feedback cycles favouring the spread of angiosperms. Their hypothesis is contingent on open, well-lit conditions favouring plants with leaves with high tissue nutrient contents and rapid decomposition. Both fire and dinosaur activity could have facilitated these conditions.

Bakker's (1978) dinosaur hypothesis has been challenged for failing to account for the global pattern of angiosperm spread, as angiosperms colonized areas regardless of whether or not dinosaurs were present, or whether they were low- or high-necked feeders (Barrett & Willis, 2001; Butler *et al.*, 2009). The fire hypothesis could be subjected to a similar test. Nearly all the evidence for Cretaceous fires is from the Northern Hemisphere and mostly from eastern North America and Western Europe (Fig. 4). The only charcoal mesofossils reported from the Southern Hemisphere to date are from Antarctica (Eklund, 2003), with scattered reports of charcoal in other localities in Australia (Pole & Douglas, 1999) and South America (Passalia, 2007). However, the absence of evidence is not evidence for absence. Cues for recognizing burnt plants have only recently been well established (Scott, 2000, 2010). The fire hypothesis predicts that fires should have been as prominent in driving angiosperm spread in the Southern Hemisphere as in the north. The spatial and temporal patterns of angiosperm spread seem to have been similar in both hemispheres (Crane & Lidgard, 1989; Lupia *et al.*, 1999; Nagalingum *et al.*, 2002). If closer scrutiny of southern fossil floras fails to reveal evidence for frequent fires, the fire hypothesis cannot be construed as a general explanation for angiosperm spread in the Cretaceous, but only of regional importance.

Finally, we note the similarities in our suggested fire hypothesis for angiosperm expansion and the much later spread of the C₄ grassy biomes (Keeley & Rundel, 2005;

Beerling & Osborne, 2006; Osborne, 2008). Both were expansions of low-statured 'weedy' species with rapid photosynthetic rates in open, sunlit conditions. Both clades have greatest relative photosynthetic advantages over their competitors at low atmospheric CO₂ (Brodribb & Feild, 2010 for angiosperms; Ehleringer *et al.*, 1997 and Sage, 2004 for C₄ grasses). Both were characterized by long periods of diversification before their expansion to ecological prominence. Both required some external factor to escape the shade of forest trees. Aridity promoted the spread of C₄ grasses in some parts of the world (Strömberg, 2005), with fire being a major factor in more mesic settings (Bond *et al.*, 2005; Keeley & Rundel, 2005; Simon *et al.*, 2009). Both expansions implicate the introduction of novel fire regimes as a significant contributor to their ecological success. We believe that greater attention should be given to fire as a factor in vegetation history in the deep past (Bowman *et al.*, 2009; Pausas & Keeley, 2009). In addition to the need to document changing fire activity and changing fire regimes through time, there is the challenge of explaining why fire activity has changed over time and space and feedbacks to the Earth system.

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Appendix A1 Sources of Cretaceous charcoal records (Preserve, mode of preservation; Meso, 1, mesofossils present)

Age	~Ma BP	Locality	Preserve	Meso	Reference
Maastrichtian	65	Raton Basin New Mexico	Inertinite		Scott <i>et al.</i> (2000b)
Maastrichtian	67	Walbeck, Germany	Charcoal		Knobloch & Mai (1991)
Maastrichtian	67	Eisleben, Germany	Charcoal		Knobloch & Mai (1991)
Maastrichtian	67	Kossen Niedendorf, Austria	Charcoal		Knobloch & Mai (1991)
Campanian-Maastrichtian	69	Mira, Portugal	Charcoal	1	Friis <i>et al.</i> (2003)
Campanian-Maastrichtian	70	Flysh, Czech	Charcoal		Knobloch & Mai (1991)
Campanian-Maastrichtian	70	Vienna Flysh, Austria	Charcoal		Knobloch & Mai (1991)
Maastrichtian	70	Colorado, USA	Inertinite		Belcher <i>et al.</i> (2003)
Maastrichtian	70	Wyoming USA	Inertinite		Belcher <i>et al.</i> (2003)
Maastrichtian	70	Montana USA	Inertinite		Belcher <i>et al.</i> (2003)
Maastrichtian	70	North Dakota, USA	Inertinite		Belcher <i>et al.</i> (2003)
Maastrichtian	70	Saskatchewan, Canada	Inertinite		Belcher <i>et al.</i> (2003)
Maastrichtian	70	Saskatchewan, Canada	Inertinite		Belcher <i>et al.</i> (2003)
Campanian-Maastrichtian	74	Esguiera, Portugal	Charcoal	1	Friis <i>et al.</i> (2003)
Campanian-Maastrichtian	75	Canada boreal	Charcoal		Falcon-Lang <i>et al.</i> (2004)
Late Santonian	80	Antarctica	Charcoal	1	Eklund (2003)
Upper Santonian-Lower Campanian	80	South-Limburg, Netherlands	Charcoal		Knobloch & Mai (1991)
Upper Santonian-Lower Campanian	80	Aachen, Germany	Charcoal		Knobloch & Mai (1991)
Upper Santonian-Lower Campanian	80	Bakony Mts Hungary	Charcoal		Knobloch & Mai (1991)
Campanian	80	Santa Rita Mtns, Ariz	Diverse		Finkelstein <i>et al.</i> (2005)
Campanian	83	Neuse R cut-off, Goldsboro, N. Carolina, USA	Charcoal	1	Crane & Herendeen (1996)
Late Santonian - Early Campanian	83.5	Allon, Georgia, USA. See also Whitewater Creek nearby	Charcoal	1	Crane & Herendeen (1996)
Cenomanian-Maastrichtian	84	Asen, Sweden	Charcoal	1	Friis & Skarby (1981)
Santonian	85	Upatoi Creek, Georgia, USA	Charcoal	1	Crane & Herendeen (1996)
Upper Turonian-Santonian	87	Sth Bohemia Czech	Charcoal		Knobloch & Mai (1991)
Coniacian Santonian	89	Japan	Charcoal	1	Takahashi <i>et al.</i> (2008)
Turonian-Coniacian	89	Slezske, Czech	Charcoal		Knobloch & Mai (1991)
Turonian	89.5	Crossman, NJ, USA (Sayreville)	Charcoal	1	Crane & Herendeen (1996)
Cenomanian-Turonian	93	Rudnyy, northern Kazakhstan	Charcoal	1	Frumin & Friis (1999)
Cenomanian	95	Czech Republic, near Prague	Charcoal	1	Kvaček & Eklund (2003)
Cenomanian	95	Moravia, Czechoslovakia	Charcoal		Knobloch & Mai (1991)
Cenomanian	95	Mauldin Mtn, N. Maryland, USA	Charcoal	1	Crane & Herendeen (1996)
Cenomanian	96	West and Central Bohemia	Charcoal		Knobloch & Mai (1991)
Cenomanian	98	Bull Mountain, Maryland, USA	Charcoal	1	Crane & Herendeen (1996)
Late Albian	98	New Ulm, Minnesota, USA	Charcoal	1	Hu <i>et al.</i> (2006)
Albian - Cenomanian	98	Alaska, USA	Charcoal		Spicer & Herman (2001)
Albian - Cenomanian	99	Nebraska, Dakota formation	Charcoal		Upchurch & Dilcher (1990)
Albian	100	Spain east	Charcoal		Sender <i>et al.</i> (2005)
Albian	100	West Brothers Maryland, USA	Charcoal	1	Crane & Herendeen (1996)
Albian	100	Quantico Virginia, USA	Charcoal	1	Crane & Herendeen (1996)
Albian	100	Bank near Brooke, Virginia, USA	Charcoal	1	Crane & Herendeen (1996)
Albian	100	Puddledock, Virginia	Charcoal	1	Crane & Herendeen (1996)
Albian	100	Black Wolf, Ellsworth Kansas, USA	Charcoal		Wang (2004)
Albian - Cenomanian	101	Queensland, Australia	Charcoal		Pole & Douglas (1999)
Albian	103	British Columbia	Inertinite		Lamberson <i>et al.</i> (1996)
Late Albian	103	Patagonia Argentina	Charcoal		Passalia (2007)
Early Aptian	117	Dutch Gap, Virginia, USA	Charcoal	1	Crane & Herendeen (1996)
Early Aptian	117	Drewry's Bluff, Richmond Virginia	Charcoal	1	Crane & Herendeen (1996)
Barremian-Aptian	120	Catefica, Portugal	Charcoal	1	Friis <i>et al.</i> (1999)
Aptian - Albian	120	Nashville, Arkansas, USA	Charcoal		Axsmith (2006)
Barremian-Aptian	125	Buarcos, Portugal	Charcoal	1	Friis <i>et al.</i> (1999)
Barremian-Aptian	126	Torres Vedra, Portugal	Charcoal	1	Friis <i>et al.</i> (1999)
Barremian-Aptian	127	Fanalicao, Portugal	Charcoal	1	Friis <i>et al.</i> (1999)
Barremian-Aptian	128	Vale de Agua, Portugal	Charcoal	1	Friis <i>et al.</i> (1999)
Hauterivian-Barremian	130	Isle of Wight, UK	Charcoal		Collinson <i>et al.</i> (2000)
Hauterivian-Barremian	130	Bedfordshire, UK	Charcoal		Herendeen & Skog (1998)
Berriasian-Barremian	135	Purbeck S. UK	Charcoal		Watson & Alvin (1996)
Valenginian-Hauterivian	136	Nova Scotia Canada	Charcoal		Falcon-Lang <i>et al.</i> (2007)