

12 A 450-Million-Year History of Fire

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12.1 Introduction

Extinction and evolution have shaped the abundant life that we see on our planet today. This life owes its composition in no small part to the environmental conditions and forces existing on the Earth throughout its history. Fire is a considerable source of disturbance (Sugihara *et al.*, 2006). Moreover, the role that fire plays in influencing the Earth system over both short and long timescales is a subject of continued scientific research (e.g. Scott, 2000; Bowman *et al.*, 2009, 2011; see also Chapter 15, this volume). This chapter seeks to review the history of fire and show how it links to the environmental and evolutionary innovations that have led to the diversity of life on our modern planet.

Our planet is 4.54 billion years (Ga) old (Knoll, 2003), therefore our modern period, called the Holocene epoch, which began only c. 10 000 years ago, represents just a tiny fraction of the history of the Earth. Across this long tract of time Earth scientists can use the record of rocks and the fossils contained within them to read the history of Earth's past. The early Earth was not conducive to hosting life; the atmosphere had extremely high levels of carbon dioxide (CO₂) and contained barely any oxygen (Kastin, 2001; Berner *et al.*, 2003; Kump, 2010). The first fossil evidence of

life appears ~3.5 Ga; some of these early organisms are believed to have been photoautotrophic bacteria, or in other words, oxygen-producing blue-green algae (cyanobacteria) (Brasier *et al.*, 2006; Schopf, 2011; Schopf and Kudryavtsev, 2001; Schopf *et al.*, 2007; Wacey *et al.*, 2011). Via photosynthesis such organisms would have begun to 'breathe' life into our planet (Knoll, 2003; Schopf, 2011). By ~2.2 Ga this had transformed the chemistry of the Earth's atmosphere (Runnegar, 1991; Anbar and Knoll, 2002; C. Scott *et al.*, 2008). The newly oxygenated atmosphere enabled the evolution of more complex life (Dahl *et al.*, 2010; Kump, 2010) such that ~540 million years ago (Ma) planktonic algae had become diverse in the Earth's oceans (Knoll, 2011). One of the most important evolutionary innovations to occur was the migration of plants from the water to the land (Gensel, 2008). This occurred by 470 Ma, as evidenced by the occurrence of the spores of land plants in the fossil record (Wellman *et al.*, 2003; Steemans *et al.*, 2009; Wellman, 2010). Early vascular plants were tiny and leafless (e.g. *Cooksonia*, 425 Ma; Edwards, 1996; Edwards and Richardson, 2004). Between 395 and 300 Ma the Earth's flora diversified from small plants to a vegetation that included trees (Stein *et al.*, 2007; Gensel, 2008; Meyer-Berthaud and Decombeix, 2009). This time in Earth's

history can be referred to as 'The Greening of the Land' (Beerling *et al.*, 1998). As plants became widespread, particularly with large-leaved forest ecosystems in the Late Devonian/Early Carboniferous (350 Ma), oxygen concentrations increased in the Earth's atmosphere (Berner *et al.*, 2003; Dahl *et al.*, 2010) (Figure 12.1). The evolution of these new plant structures considerably influenced the Earth's climate and the atmosphere (Algeo and Scheckler, 1998). So how do the innovations of land plants, leaves and trees relate to the fire history of our planet? We must look to the fundamental controls on fire in order to understand their significance.

12.2 The Fundamental Requirements of Fire

In order for a fire to exist it requires three key elements, illustrated by the fire triangle shown in Figure 12.2. The fire triangle shows that fire requires an ignition source, a supply of oxygen and fuel in order that it can burn (Quintiere, 1998). The rise of oxygen, the appearance of the first land plants and the development of large volumes of fuel are shown on Figure 12.1. There has likely always been an ignition source for fires on our planet, i.e. lightning (Pyne *et al.*, 1996) (see Section 12.3 for other ignition sources). In order for ignition to occur a fire requires something to ignite. In the case of wildfires this first occurred with the evolution of adequate fuel (i.e. plants on the land) (Glasspool *et al.*, 2004). Finally, fire requires a supply of atmospheric oxygen (Quintiere, 1998; Van Wagtenonk, 2006; Cochrane and Ryan, 2009), the amount of which has varied throughout Earth's history (e.g. Berner *et al.*, 2003; Bergman *et al.*, 2004; see also Chapters 14 and 15). Therefore, only once atmospheric oxygen had reached suitable concentrations might fires have been present on the Earth (Scott and Glasspool, 2006). This rise in atmospheric oxygen, to suitable concentrations, is conveniently coupled to the diversification of land plants (fuel), such that from the onset of the invasion of the land by plants, fires not only had fuel but also sufficient oxygen to allow for the combustion

reaction. However, since this initial rapid rise, atmospheric oxygen concentration has fluctuated (e.g. see Figure 12.1) (Glasspool and Scott, 2010; see also Chapter 15) and therefore, because fire relies on oxygen, so too has the flammability of our planet (Belcher *et al.*, 2010a; Glasspool and Scott, 2010; Scott, 2010a; Scott *et al.*, *in press*).

12.3 Ignition: Lightning, Sparks, Volcanoes and Asteroids

Natural fires can be caused by spontaneous ignition, lightning, volcanic eruption, friction (Stott, 2000) and extraterrestrial impacts (Vasilyev, 1998). Spontaneous ignition can occur where the fuel is a good insulator of heat. For example, decaying organic matter in haystacks generates heat on decomposition and can reach temperatures sufficiently high to lead to spontaneous ignition (Stott, 2000). Fires can also ignite and burn for long periods of time underground in peat and coal deposits (see Chapter 2). Friction fires can be caused by rock falls and landslides, which can create sparks that may ignite nearby dry fuels. (Stott, 2000). Hot ash and ejected molten lava from volcanic eruptions may ignite nearby vegetation. Volcanic activity can potentially either ignite wildfires or entirely entomb and pyrolyse organic material in the case of pyroclastic flows (Scott and Glasspool, 2005; A.C. Scott *et al.*, 2008). Extraterrestrial impacts with the Earth surface and the atmosphere deposit significant energy that can ignite fires. For example, the Tunguska event in 1903, which is believed to have been a small cometary impact, delivered an air shock blast that flattened and may have ignited forest material (Vasilyev, 1998). However, by far the most important natural ignition source of fires is lightning strike, which is likely to have always existed on the Earth (Pyne *et al.*, 1996). There are currently 100 lightning strikes per second on our planet (Goodman and Christian, 1993). These, coupled with the correct weather conditions, can lead to ignition (e.g. Pyne *et al.*, 1996; Van Wagtenonk, 2006; Krawchuk and Moritz, 2011; see also Chapters 3, 4 and 6).

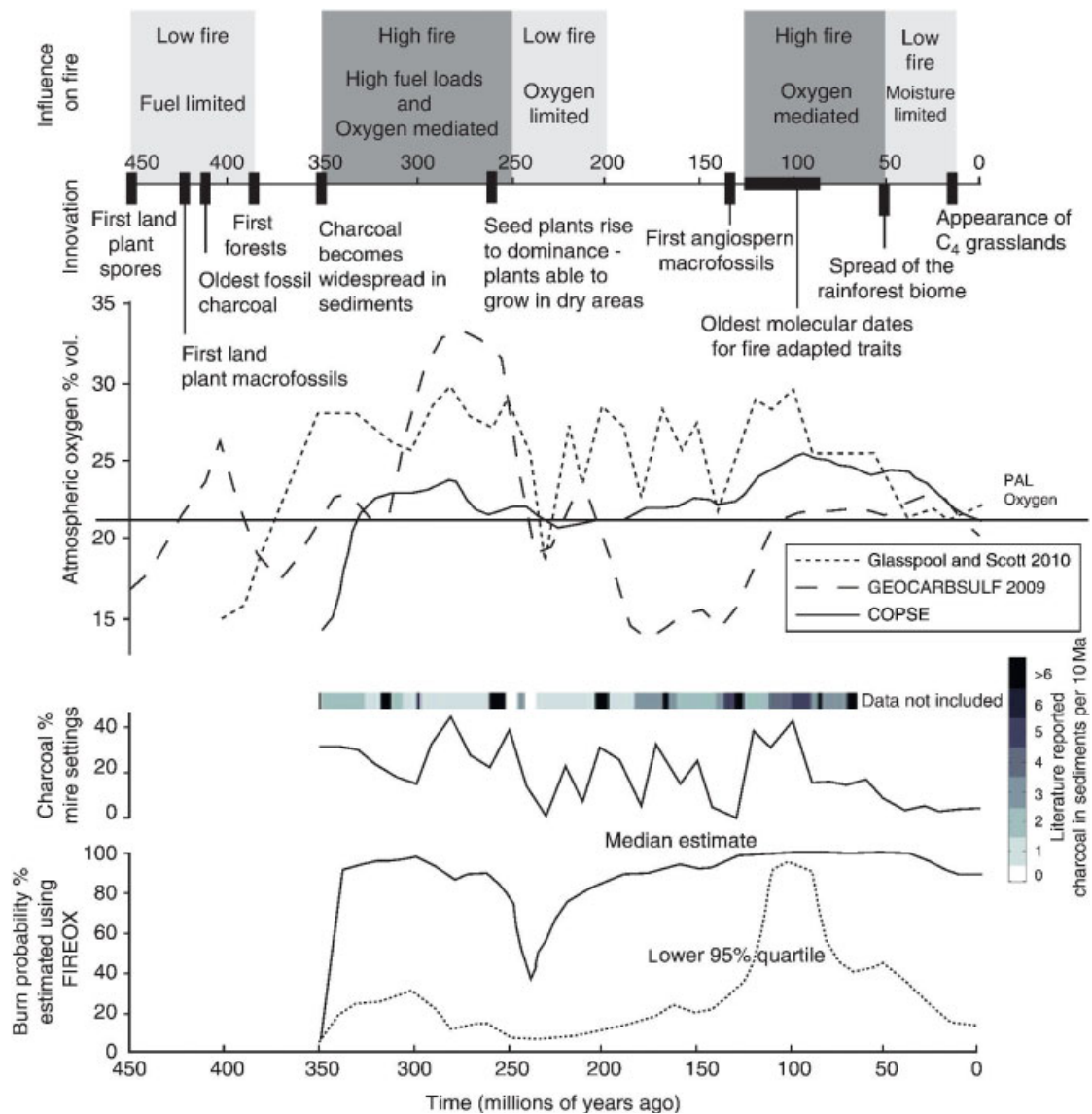


Fig. 12.1 Key evolutionary events in plants and estimates of fire activity and palaeoatmospheric oxygen for the past 450 million years of Earth history. Burn probabilities estimated using the FIREOX model (Belcher *et al.*, 2010a) based on COPSE palaeoatmospheric oxygen estimates (Bergman *et al.*, 2004). Charcoal (inertinite) records from mire settings from Glasspool and Scott (2010), published charcoal records from siliclastic sediments from Belcher and McElwain (2008). Palaeoatmospheric oxygen estimates from the GEOCARBSULF model of Berner (2009), the COPSE model of Bergman *et al.* (2004) and the oxygen proxy method of Glasspool and Scott (2010). PAL = present atmospheric level.

12.4 Air: Ancient Atmospheric Oxygen Concentration and the Flammability of our Planet

Laboratory experiments have been used to define the relationship between fire and atmospheric oxygen concentration (e.g. Watson, 1978; Watson *et al.*, 1978; Wildman *et al.*, 2004; Belcher and McElwain, 2008; Belcher *et al.*, 2010a; see also

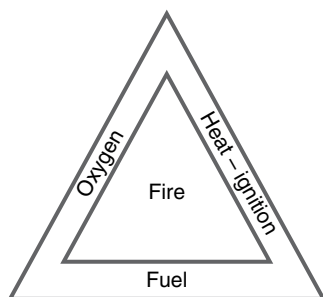


Fig. 12.2 The Fire Triangle (e.g. see Quintiere, 1998) – the basic elements required to allow ignition and sustained fire. Reproduced from Berner, R.A. (2009). © American Journal of Science.

Chapter 14). All reveal a general trend of increasing ease of ignition and more rapid fire spread rates with increasing concentration of oxygen in the atmosphere (e.g. Wildman *et al.*, 2004; Belcher *et al.*, 2010a; see also Chapters 14 and 15). Spread rates follow a near linear increase, whereas the ease of ignition (referred to as the relative probability of ignition by Watson and Lovelock in Chapter 14) plateaus at a point that is dependent on the moisture content of the fuel (see Chapter 14). It is likely that fires in natural plant material require a minimum concentration of 16% vol. of atmospheric oxygen in order to ignite and become self-sustaining (Belcher *et al.*, 2010a). The FIREOX model of Belcher *et al.* (2010a), which predicts burn probability as a function of atmospheric oxygen, reveals similar behaviour: burn probabilities remain low until atmospheric oxygen concentrations reach ~19% vol., then rapidly increase, slow again and plateau around 23% vol. (Figure 12.3). It is interesting that our atmosphere appears to have levelled across the most rapid change in burn probability, and this may speak volumes about the role that fires play in maintaining many aspects of the

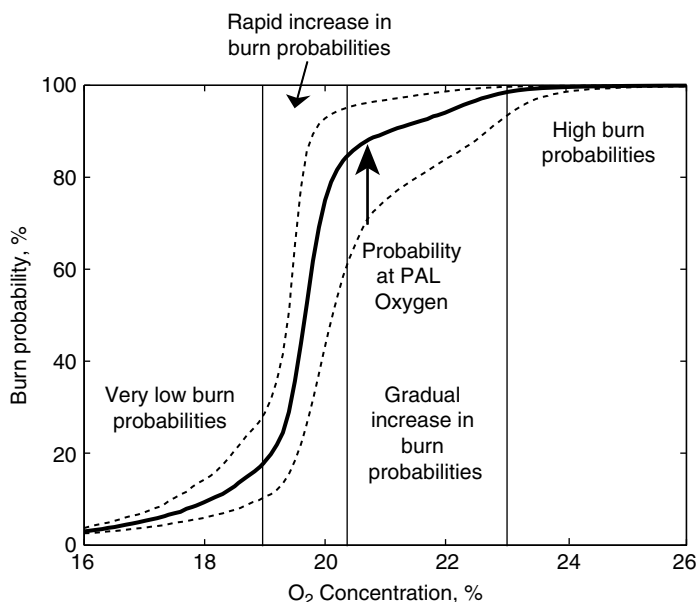


Fig. 12.3 Estimated burn probabilities as a function of atmospheric oxygen concentration according to the FIREOX model (modified from Belcher *et al.*, 2010a). PAL, present atmospheric levels.

Earth system (e.g. Bergman *et al.*, 2004; see also Chapter 15).

The influence of variations in atmospheric oxygen on fire activity can be observed in the fossil record of charcoals. In Figure 12.1 it can be seen that the abundance of fossil charcoal and therefore fire activity has varied considerably throughout Earth history (e.g. Chaloner, 1989; Scott and Glasspool, 2006; Belcher and McElwain, 2008; Glasspool and Scott, 2010; Belcher *et al.*, 2010a). The most directly comparable charcoal records between geological periods are those from mire ecosystems (e.g. Glasspool and Scott, 2010). This is because peat-forming mire environments require that groundwater must remain throughout the year above or close to the ground surface; therefore, because these are high-moisture environments, the potential impact of different climatic regimes between sites will be minimized. Moisture content of fuel is also a key factor in ignition (e.g. Pyne *et al.*, 1996; Van Wagten donk, 2006; Cochrane and Ryan, 2009; see also Chapters 3, 4 and 6), and this is again more comparable between mire sites than between other ecosystems. Peaks in the abundances of charcoal occur during the Carboniferous (350–300 Ma) and Permian (300–250 Ma) and throughout much of the Cretaceous (130–65 Ma) (Glasspool and Scott, 2010; Brown *et al.*, 2012). Conversely, lows are recorded during the earliest Triassic, the earliest Jurassic, the earliest Cretaceous and the Eocene to Holocene. Several of these highs and lows appear to be explainable by variations in the concentration of oxygen in the ancient atmosphere (Glasspool and Scott, 2010; Belcher *et al.*, 2010a). This is also indicated by the burn probabilities estimated by the FIREOX model of Belcher *et al.* (2010a), which used only ancient atmospheric oxygen concentration as the driver of ecosystem flammability. The periods during which, in the FIREOX model, fluctuations in atmospheric oxygen concentration appear to have been a major driving force in causing variations in flammability of the Earth's ecosystems are the Carboniferous–Permian (350–250 Ma; high O₂), the early Triassic (250–230 Ma; low O₂), the majority of the

Cretaceous (from ~130 Ma; high O₂) and the Paleocene (65–55 Ma; high O₂). During both the Carboniferous–Permian and the Cretaceous, modelled atmospheric oxygen concentrations exceeded 25% vol. (the present level is 20.9% vol.) (Bergman *et al.*, 2004; Glasspool and Scott, 2010; see also Chapter 15) This leads to the FIREOX model estimating burn probabilities exceeding 95% if a source of ignition is present. This is well matched by the high abundance of charcoal in the fossil record (Belcher and McElwain, 2008; Scott, 2000, 2010; Glasspool and Scott, 2010; Brown *et al.*, 2012). It is likely that atmospheric oxygen concentrations were slightly lower during the earliest Triassic than in the present day (Bergman *et al.*, 2004; Glasspool and Scott, 2010) causing the lowest burn probabilities during the past 350 Ma (~40% chance of a fire spreading if an ignition source is present), matching well the low abundance of charcoal in rocks of this age.

Not all of the fluctuations observed in the charcoal record throughout the Triassic, Jurassic and earliest Cretaceous appear to have been driven by variations in atmospheric oxygen content. The large peaks observed in charcoal abundance during these times appear consistent with the modelled atmospheric oxygen concentrations, which yield burn probabilities of ~80–90% in the FIREOX model. However, not all the lows in charcoal abundance appear to match low burn probability based on oxygen concentration. This is either because the resolution of oxygen models (and therefore the FIREOX model) are insensitive to some levels of fluctuation or because other factors that influence fire activity are driving these variations. For example, climatic variation is an additional factor that has influenced ancient fire activity (Bowman *et al.*, 2009, 2011; Krawchuk *et al.*, 2009; Belcher *et al.*, 2010b; Krawchuk and Moritz, 2011; Uhl *et al.*, 2012), although at superambient concentrations of atmospheric oxygen (i.e. >21% vol.) climatic variations become less important at controlling the spread of fire. Variations in fuel will be discussed in the following section. It is without doubt, therefore, that atmospheric oxygen

concentration is not the only influence on fire activity (e.g. Krawchuk and Moritz, 2011; see also Chapters 3, 4, 6 and 11). However, there do appear to be periods in the Earth's history where both the models of fire activity (e.g. FIREOX) and the fossil record of charcoal imply that variations in atmospheric oxygen concentration have been an important driver of ecosystem flammability in the past.

12.5 Fuel: Past Vegetation Changes and Fire

Fuel type is of key importance to fire (e.g. Pyne *et al.*, 1996; Van Wagtenonk, 2006; Krawchuk and Moritz, 2011; see also Chapters 4 and 6). Evolution, extinction, extirpation and changes in the types of plants growing at a given location have influenced fire activity on our planet throughout its history (Scott, 2000; Pausas and Keeley, 2009). Different modern ecosystems have different flammable characters (Sugihara *et al.*, 2006; Fites-Kaufman *et al.*, 2006; Van Wagtenonk *et al.*, 2006; Bowman *et al.*, 2009; Keeley *et al.*, 2011a). For example, wildfires are generally infrequent in forests that contain leaves with high moisture contents and where the leaves have relatively coarse dimensions (e.g. large leaves); whereas flammable ecosystems are typically characterized by leaves with low moisture contents and fine plant parts (e.g. small or narrow leaves) with a fuel-surface-area-to-air ratio optimized to propagate a fire (Bond and van Wilgren, 1996; Bond and Midgley, 2012). Therefore the shifting of biomes and contractions and expansions of plant ranges have the ability to change the flammability of regions of our planet according to the types of plants that dominate in different locations. Moreover, fire has played a key role in driving evolutionary innovations within our ecosystems (Pausas and Keeley, 2009; Bond and Scott, 2010; Keeley *et al.*, 2011b; He *et al.*, 2012) and indeed continues to shape and maintain them today (Bond and Keeley, 2005; Bond *et al.*, 2005; Bowman *et al.*, 2009, 2011; Midgley and Bond, 2011).

12.5.1 The fossil record of fuel: reconstructing ancient vegetation

Ancient vegetation (fuel) histories are reconstructed using two key fossil types: (i) macrofossils of plants, and (ii) fossil pollen and spores. No fossil record is perfect and all fossils are subject to taphonomic effects, which may favour preservation of certain plant parts and certain plant types. Taphonomic bias affects both macrofossil and pollen and spore fossil assemblages and therefore influences the picture painted by reconstructions of ancient ecosystems. Studies of modern ecosystems have proved invaluable to our understanding of the plant macrofossil and pollen and spore records. For example the leaf litter of modern forests is known to well represent the nearby forest source (e.g. Dunwiddie, 1987; Burnham, 1989; Burnham *et al.*, 1992; Steart *et al.*, 2006). Mapped patterns of modern tree pollen percentages in temperate Europe and North America also correspond closely with tree abundance (e.g. Webb, 1974; Delcourt *et al.*, 1983, 1984; Prentice *et al.*, 1987). However, the record from tropical floras is less clear where variation is likely due to the dominance of insect pollination and hence limited pollen transport by wind or water (Faegri, 1966; Bush, 1995). The fossil record can be biased, for example in favour of taxa with high pollen productivity (Prentice, 1985) or leaves with a lower rate of decomposition (e.g. see Cornwell *et al.*, 2008). Other biases include those linked to the composition of plant tissues, for example favouring fruit walls and seed coats composed of a lignin-cellulose complex (Collinson, 2011). Even in modern sediment samples certain taxa may be represented better than others. For example, *Pinus* pollen is typically very abundant and relatively over-represents the abundance of *Pinus* trees in an area whilst taxa like *Acer* are typically under-represented (Jackson and Booth, 2007). Similar issues are known in the fossil record, where the same genera can be differently represented in macrofossils and pollen and spore assemblages. A good example is that of oaks (*Quercus*), hickory (*Carya*) and hazel (*Corylus*), which are often abundant in pollen and spore

assemblages but rare in macrofossil assemblages (Jackson and Booth, 2007). The converse is true for the firs (*Abies*), Douglas firs (*Pseudotsuga*) and larches (*Larix*) (Dunwiddie, 1987; Jackson and Booth, 2007).

Macrofossils and pollen and spores may also represent different source areas because pollen and spore assemblages can be derived from much greater distances than plant macrofossil assemblages. Pollen and spores can be transported thousands of kilometres by wind (Erdtman, 1943) whereas macrofossil assemblages might only be transported of the order of kilometres or much less (e.g. Gastaldo *et al.*, 1987). It is therefore generally accepted that pollen and spores represent regional to interregional vegetation, and macrofossils the vegetation of the more local area. For another example of the comparative sampling abilities of pollen and spores versus macrofossil plants see Mander *et al.* (2010). Despite these caveats the ancient history of plants is well represented in the fossil record and provides us with an exceptional picture of Earth's ancient ecosystems. In this chapter we place fire within these ancient vegetations and outline some key evolutionary events in Earth's history involving plants (fuel) in order to examine how these relate to Earth's fire history.

12.5.2 Fuelling early fires: the greening of the Earth

There could be no wildfires until a suitable fuel existed on land. The oldest evidence of wildfire is known from the Silurian (410 Ma) in the form of charred remains of a rhyniophytoid plant (a small leafless plant) (Glasspool *et al.*, 2004). This indicates that the first land plants were capable of being ignited and providing a small amount of fuel to carry a fire (Glasspool *et al.*, 2006). Between 395 and 360 Ma Earth's terrestrial flora evolved from small primitive plants to vegetation that included trees (Edwards, 1996; Meyer-Berthaud *et al.*, 1999; Edwards and Richardson, 2004; Meyer-Berthaud and Decombeix, 2009). This not only changed the face of the Earth and its atmosphere forever but allowed for large wildfires

to occur on our planet for the first time (Scott, 2000, 2010). During this time plants underwent major morphological innovations: they attained height, and leaves and wood evolved (Meyer-Berthaud *et al.*, 1999; Meyer-Berthaud and Decombeix, 2009). The first evidence of wood in the fossil record is from the middle Devonian (Algeo and Scheckler, 1998; Meyer-Berthaud *et al.*, 1999; Stein *et al.*, 2007) (~380 Ma). The evolution of wood represents the emergence of the first large fuel load able to sustain and carry a fire for a significant period. Therefore, until the evolution of woody shrubs and trees it is unlikely that fires would ever have been widespread (Scott and Glasspool, 2006). Interestingly the record of Devonian charcoals (Scott, 2000; Cresler, 2001) suggests that the spread of forest vegetation preceded evidence of extensive wildfires by ~20 Ma (Scott and Glasspool, 2006). This returns us to the fire triangle mentioned earlier (Figure 12.2), where it seems that during this early forest colonization phase (providing sufficient fuel) atmospheric oxygen concentrations may have been too low to support significant fires (e.g. ~18% vol.; Berner, 2009) (Figure 12.1). The FIREOX model predicts burn probabilities of just 10% at this concentration of atmospheric oxygen (Belcher *et al.*, 2010a). By the latest Devonian (~360 Ma) charcoal abundances increase (Scott and Glasspool, 2006) concurrent with a rise in the modelled concentration of atmospheric oxygen to ~19% vol. (Berner, 2009). From this period atmospheric oxygen concentrations continue to rise, indeed to attain superambient levels, until they decline at the end of the Permian (~250 Ma) (Bergman *et al.*, 2004; Berner, 2009). From the Devonian to Permian the Earth experienced, for the first time, sufficient oxygen and sufficient fuel to allow for large forest fires (Scott, 2000, 2009, 2010).

It might be hard to imagine a world without leaves. However, a huge gulf of time (40 million years) exists between the origin of land plants and the evolution of megaphyllous leaves (Beerling *et al.*, 2001). True leaves appear in the middle Devonian (380 Ma) (Beerling *et al.*, 2001; Beerling, 2007). It has been suggested that plants had the genetic toolkit to form leaves long before leaves

evolved. Early plants like *Cooksonia* (Edwards, 1996; Gensel, 2008) evolved in CO₂ concentrations 15 times higher than today. This meant that capturing CO₂ for growth was relatively easy. By the time the first forests with leafy crowns appear CO₂ concentrations had fallen by 90% (Edwards, 1998; Beerling, 2007). Plants with leaves better capture sunlight and increase their efficiency for gas exchange (absorption of CO₂) to promote their growth (Beerling *et al.*, 2001). It has been hypothesised that the high CO₂ and temperatures that prevailed prior to the evolution of leaves would have prevented their development. This is because the leaves would not have been able to lose heat rapidly enough, resulting in them reaching lethal temperatures (Beerling *et al.*, 2001).

Wood is much less flammable than leaf and shoot material. This is because leaves are thermally thin and therefore easy to heat to ignition temperatures. For example, crown fires that pass rapidly through a forest typically burn leaves and small branches, yet the main trunks of the trees remain (Scott, 2010). Therefore, the innovation of leaves likely promoted a more easily ignitable vegetation but also one in which fires could spread rapidly from plant to plant and between plant parts, for example from leaves to small woody parts, allowing a wildfire to take hold. Moreover, leaf falls would have created a considerable build-up of fuel on the ground. The most commonly ignited fires today are those in grass, leaf litter and low-lying shrubby fuels (Pyne *et al.*, 1996; Van Wagtendonk, 2006; Scott, 2010). Therefore the evolution of leaves created a large new fuel source of dead, dry and decaying plant material that could carry a fire. As different tree species evolved with different leaf types, including different volatile and moisture contents, so diverse fire regimes would have been found across the planet.

12.5.3 The rise to dominance of the seed plants

At the same time as forests first spread, the planet underwent major changes such that by the Permian (300 Ma) the Earth's continents were reorganized into a single landmass, known as the

supercontinent Pangea (Ziegler, 1990). This vast single landmass meant that large areas of the land experienced a continental climate similar to that observed in the land-locked central areas of the United States and Africa today (Rees *et al.*, 1999, 2002). By the middle-late Permian many areas saw an increasingly arid climate (Rees *et al.*, 1999, 2002). Glasspool and Scott (2010) indicate that at this time the charcoal content of coals was greater than 40% (see Figure 12.1), implying high levels of fire activity (e.g. Hudspeth *et al.*, 2012), which may be related to increasingly dry fuel loads and/or to the near maximum modelled levels of atmospheric oxygen concentration. Many areas on the planet today burn during a distinct dry season suggesting that this increase in fire activity may be evidence of seasonally arid conditions during this time.

Until the Permian, spore-bearing plants had dominated Earth's ecosystems (DiMichele *et al.*, 2001). Such plants require free water available on the surface in order to reproduce (Bateman *et al.*, 1992; Bateman and DiMichele, 1994). The increasingly arid conditions across large areas of the planet during the Permian did not provide a favourable environment for such plants (DiMichele *et al.*, 2001). It was during this time that plants using seeds to reproduce rapidly diversified (DiMichele *et al.*, 2001). The seed habit requires no external water for sexual reproduction and the seed provides protection and nutrients for the developing embryo (Willis and McElwain, 2002). Seed plants rose to dominate the planet and by the upper Permian (260 Ma) 60% of the Earth's flora was dominated by seed-bearing plants (gymnosperms) (DiMichele *et al.*, 2001). Of importance is the evolution of gymnosperm conifers, such that by the Permian a group of scale-leaved conifers became dominant (the Walchian conifers) (Looy, 2007). These trees first evolved during the early Pennsylvanian (315 Ma) where they grew in drier environments (Falcon-Lang *et al.*, 2009) that were prone to fire (Scott, 1974; Scott and Chaloner, 1983; Scott *et al.*, 2010). These new trees spread into the lowlands as the climate changed during the late Carboniferous and Permian (DiMichele *et al.*, 2001). In the Carboniferous the cordaites (another

group of gymnospermous trees and the sister group to conifers) may have lived in drier upland settings that were prone to wildfire (Falcon-Lang and Scott, 2000). Large plants were now able to colonize many different land areas (e.g. lowlands to dry uplands) meaning that wildfires could now occur in many areas of the planet (Scott and Glasspool, 2006). Moreover, these plants formed ecosystems that were adapted to survive in drier conditions creating fuel loads with an enhanced chance of ignition (see, e.g., Chapter 4). By the end of the Triassic five families of conifers had evolved that still have a widespread distribution today: the Pinaceae, Taxaceae, Cupressaceae (including Taxodiaceae) Araucariaceae and the Podocarpaceae (Miller, 1999; Willis and McElwain, 2002). Several of these families, particularly the Pinaceae, form part of our modern world's flammable ecosystems (Van Wagtenonk and Fites-Kaufman, 2006). Some species within these ancient families exhibit so-called fire-adapted traits today (e.g. Schwillk and Ackerly, 2001; Keeley *et al.*, 2011b; He *et al.*, 2012; see also Chapter 7), the development of these traits appears to be linked to fire where fire has provided the evolutionary driving force that required some conifers to adapt in order to survive on an increasingly flammable planet (Pausas and Keeley, 2009) (see also Section 12.5.8 and Chapter 7).

12.5.4 'Prairies' before grasslands: ferns and fire

Savanna ecosystems are one of the planet's most frequently burned ecosystems today (Bond and Keeley, 2005). However, this ecosystem did not appear until the Miocene (~8 Ma) (e.g. see Section 12.5.7) (Beerling and Osborne, 2006; Edwards *et al.*, 2010; McInerney *et al.*, 2011; Stromberg, 2011). In times before the grasses evolved and spread to form savanna and prairie ecosystems, ferns may have filled a similar flammable niche (Scott, 2000; Collinson *et al.*, 2000). Extensive ancient communities of ferns have sometimes been termed 'fern prairies' in the literature (Collinson *et al.*, 2000; Collinson, 2001, 2002). These 'fern prairies' are well known from

Cretaceous floras and are often associated with disturbed terrains (Wing *et al.*, 1993). Collinson *et al.* (2000) reported a fern charcoal-dominated fossil assemblage, which they interpreted as being derived from a low-diversity fire-prone vegetation that formed a 'savanna' and/or prairie on a fire-prone coastal floodplain.

Abundant charcoaled fern remains can be found in western Europe in the Wealden part of the lower Cretaceous (Harris, 1981; Batten, 1998; Gomez *et al.*, 2012; Brown *et al.*, 2012 and references cited therein). This fern community was periodically subject to desiccation and therefore vulnerable to the spread of fire (Alvin, 1974). The ferns probably grew on low banks without trees adjacent to the floodplain of a river such that they formed something analogous to a modern bracken-covered (the fern *Pteridium*) heath (Batten, 1998). Observations by the authors (M.E.C. and A.C.S.) after modern heathland fires in Surrey, United Kingdom, indicate that bracken burns easily, the above-ground parts being often completely destroyed. Bracken also recovers quickly (within a few weeks) by sprouting new fronds from rhizomes below the ground surface. Moreover, shed fern fronds decompose slowly (more slowly than gymnosperm and angiosperm remains) (Cornwell *et al.*, 2008) implying that ferns are capable of forming a relatively large volume of both dead and live fuel. Returning to the English Wealden-aged ferns Harris (1981, p. 56) writes:

In the wet season the herbaceous ferns flourished. As it dried they produced and dispersed their spores and finally the leaves withered, just as grass savanna does today. I imagine, but without evidence, that the wet season began with high winds and electric storms and if dry, a lightning strike preceded the first heavy rain it would start a fire, as it does today, and the fire would spread widely.

Further examples exist in the fossil record that suggest that ferns have long been able to tolerate, and perhaps even take advantage of, disturbance caused by fire (Scott and Galtier, 1985; Scott, 2000, 2010). In the very latest Paleocene high fern spore abundances have been recovered that

correlate with a high episodic abundance of fossil charcoals some of which are fern rachides (Collinson *et al.*, 2007, 2009). This suggests that at this time ferns provided a significant volume of fuel for fires and that they were able to actively spore enabling recolonization following the fire event. Charred fern material is also evident in Australian Miocene coals (see Collinson, 2002, and references therein). The Yallourn coal seam contains fern charcoal across 1 km of its length indicating extensive fern communities that were dominated by *Gleichenia*. This fern is suggested as growing on an open shrubby moor with fern thickets in areas frequented by fire. The distribution of the modern relative *Gleichenia dicarpa* appears to be strongly influenced by fire, and typically occurs in patches of burned wet sclerophyll forests (see Collinson, 2002, and references therein). To conclude, ferns have been able to tolerate fire-prone environments throughout a large portion of Earth's history, likely linked to their ability to rapidly colonize or recolonize disturbed terranes. Moreover, ferns form an easily dryable and easily ignitable fuel, likely supporting greater fire frequencies and aiding expansion of open habitats prior to the evolution of modern grass-dominated savanna and prairie ecosystems.

12.5.5 A weed-fuelled invasion: fire and the spread of the angiosperms

The Cretaceous period (145–65 Ma) might be more famous for seeing the demise of the non-avian dinosaurs during its final phases; however, it also witnessed the birth of the dominant plant group in our world today – the flowering plants, or angiosperms (Friis *et al.*, 2011). According to Bond and Scott (2010) the success of these may be partially ascribed to fire.

The oldest undoubted angiosperm fossils are from the Early Cretaceous (Friis *et al.*, 2006, 2011), some 300 Ma years after the first vascular plant colonized the land (Edwards, 1996). Angiosperms rapidly increased in ecological importance, becoming diverse by ~100 Ma (Crane and Lidgard, 1989; Lidgard and Crane, 1990; Friis *et al.*, 2011). Angiosperms dominate our modern

flora, accounting for some 300 000 species, with forms ranging from small herbaceous plants through to large rainforest trees. The earliest angiosperms are believed to have been understorey herbs, shrubs and small trees (Tiffney, 1984; Taylor and Hickey, 1996; Royer *et al.*, 2010; Friis *et al.*, 2011). Estimates of leaf mass per area (LMA) from several North American fossil angiosperm floras reveal that the early angiosperms have a low LMA, half that of gymnosperms growing at the same time (Royer *et al.*, 2010). Based on the extant relationship between LMA and leaf economic traits this suggests that early angiosperms were likely fast-growing and weedy with short-lived leaves (Royer *et al.*, 2010). Density of the veins on angiosperm leaves increases throughout the Cretaceous (Brodribb and Field, 2010). Increased vein densities support increased water transport through transpiring leaves, which can be linearly related to photosynthetic rate. By the Late Cretaceous angiosperms had likely doubled their maximum photosynthetic rate (Brodribb and Field, 2010). These interpretations suggest that early angiosperms were capable of higher productivity than their gymnosperm and fern neighbours. During this time atmospheric levels of CO₂ fell, which has been suggested as enhancing the success of the angiosperms because they would most likely have had a productivity advantage over other plant types at the time (Bond *et al.*, 2003; McElwain *et al.*, 2005). Other key angiosperm innovations, many of which confer competitive advantage over gymnosperms (e.g. rapid life cycle, double fertilization, specializations of pollination biology), are discussed by Friis *et al.* (2011). Nevertheless an intriguing question remains regarding the details of how the world's gymnosperm forests were replaced by ones dominated by angiosperms.

It has been suggested that frequent fires in the highly flammable Cretaceous (from ~130 to 65 Ma), a period where models estimate relatively high atmospheric oxygen concentrations and burn probabilities (see Figure 12.1), may have opened up new ecological niches facilitating the spread of fast-growing angiosperm invaders into forests cleared by fire (Bond and Scott, 2010;

Brown *et al.*, 2012). Fire-prone ecosystems cover ~40% of the modern Earth (Bond *et al.*, 2005), where fire regime controls several of our planet's major biomes (grasslands, Mediterranean shrubland and boreal forests). In these areas frequent or severe fires replace trees with shrublands or grasslands promoting expansion of flammable, ecosystems (Bond *et al.*, 2005). The angiosperms had greatly diversified by around 100Ma and attained a near ubiquitous global presence between 100 and 65 Ma (Friis *et al.*, 2006, 2011); this well matches the period of high burn probabilities as predicted by FIREOX (Figure 12.1). It seems likely that this new, highly flammable, world began to clear patches of gymnosperm forest. Within these patches angiosperms invaded and, with their rapid life cycle and high productivity, out-competed slower-growing and slower-reproducing gymnosperms. This would also have potentially created a new positive feedback on ecosystem flammability. It has been argued that these weedy, easily dryable fuels would have been more ignitable (e.g. Van Wagendonk, 2006; Bond and Scott, 2010); however, whether or not a small angiosperm leaf or a small herbaceous fern is truly more intrinsically flammable under the same environmental conditions remains debated. Nonetheless the suggestion is that the early angiosperms may have been able to accumulate new fuel for fires rapidly and were also potentially highly flammable. Bond and Scott (2010) suggested that this created an early angiosperm-fire cycle analogous to the modern grass-fire cycle. Flammable grasses have increased the frequency of fires in some modern ecosystems (e.g. savanna) where woody plants (e.g. trees) are unable to cope with such frequent disturbance (Bond and Keeley, 2005) (see Section 12.5.7). This has caused ecosystems previously dominated by trees to become open flammable grasslands (Bond and Keeley, 2005). Hence, it is proposed that invading weedy angiosperms enhanced flammability, so that fires cleared patches of woodland allowing angiosperms to further expand into the newly opened areas. Fire therefore is suggested as providing a friendly foe, aiding the expansion of the angiosperms.

12.5.6 Early angiosperm-dominated tropical rainforest and possible fire suppression

Typically modern angiosperm-dominated tropical rainforests do not naturally burn as often as other biomes (Cochrane, 2003, 2009). As we mentioned in Section 12.5.5, angiosperms have greater vein densities than their gymnosperm counterparts. Vein density is linearly related to the leaves' ability to conduct water and so high vein densities allow for high transpiration rates in angiosperms (Brodribb and Field, 2010). Tropical rainforests rapidly transpire water taken from the soil back into the atmosphere and greatly increase rainfall, and today ensure high seasonal levels of precipitation in the tropics. High rainfall and high fuel moistures suppress fire activity. During the Eocene, which included the Early Eocene Climatic Optimum greenhouse interval (Zachos *et al.*, 2008), there was a considerable latitudinal expansion of vegetation types similar to the modern angiosperm-dominated tropical and paratropical rainforests such that these biomes extended up to 45–55° palaeolatitudes North and South (e.g. Collinson, 2000; Collinson and Hooker, 2003; Burnham and Johnson, 2004; Smith *et al.*, 2008; DeVore and Pigg, 2010; Pigg and DeVore, 2010; Collinson *et al.*, 2012). The Eocene also has much reduced charcoal in mire settings compared to the preceding Paleocene and Cretaceous (Glasspool and Scott, 2010) and it is possible that this is, at least in part, a consequence of widespread rainforest biomes that suppressed fire. Some support for this hypothesis comes from a study of a single mire setting across the Paleocene-Eocene Thermal Maximum (PETM) in southern United Kingdom, where charcoal is extremely abundant in the late Paleocene but almost disappears in the Eocene coincident with a hydrological change and increased rainfall (Collinson *et al.*, 2009). Further anecdotal evidence comes from the author's own research (M.E.C.), in which multiple Eocene plant mesofossil assemblages have been studied by sieving methods but none contains noticeable charcoal – a striking contrast, for example, to those from the Cretaceous (reviewed in Brown

et al., 2012). More detailed quantitative studies of Eocene charcoal occurrences are needed to investigate this possible link between widespread rainforests and fire suppression.

12.5.7 Fire – a victory for grasses: evolution of C_4 photosynthesis and the evolution of the savanna ecosystem

The most recent major plant group to appear on our planet is the grasses (Jacobs *et al.*, 1999; Edwards *et al.*, 2010; Stromberg, 2011). The first grasses evolved in the Late Cretaceous (Stromberg, 2011), as evidenced by the occurrence of pollen and macrofossil remains of grasses in northern South American, northern Africa and India. By the Eocene grasses had attained a near global distribution (Stromberg, 2011). These early grasses used the C_3 photosynthetic pathway. Throughout the world today, tropical and subtropical savannas and grasslands are dominated by grasses that use the C_4 photosynthetic pathway (Keeley and Rundel, 2005). C_4 photosynthesis is a variation on the C_3 pathway and provides these grasses with a competitive advantage in environments where light and temperature are not highly limiting on carbon uptake (Ehleringer and Monson, 1993; Osborne, 2011). This in part explains their success in parts of the world with a warm growing season such as is experienced in climates dominated by summer rain (e.g. Africa) (Keeley and Rundel, 2005). Isotopic evidence from pollen grains reveals that this new photosynthetic pathway had evolved by the earliest Oligocene (30 Ma) (Urban *et al.*, 2010); however, the C_4 savanna ecosystem itself appears to have developed somewhat later ~7–8 Ma (Cerling *et al.*, 1993; Beerling and Osborne, 2006; Edwards *et al.*, 2010).

The C_4 photosynthetic pathway also has increased photosynthetic efficiency in conditions of low atmospheric CO_2 concentrations (Beerling and Osborne, 2006; Osborne, 2011). Falling CO_2 levels in the Oligocene are suggested to have led to the evolution of the C_4 photosynthetic pathway, and the geologically rapid expansion of the savanna ecosystem in the Miocene may have been a result of further falling CO_2 levels (see

Beerling and Osborne, 2006, and references therein). This idea, although logical, is not necessarily well supported (e.g. see Edwards *et al.*, 2010). The earliest evidence for C_4 photosynthesis appears when atmospheric CO_2 levels were relatively high in the earliest Oligocene (Urban *et al.*, 2010), and CO_2 proxy records reveal no decrease in CO_2 during the period of grass expansion in the Miocene (e.g. Pagani *et al.*, 1999; Pearson and Palmer, 2000; Royer *et al.*, 2010). These factors suggest that something other than variations in atmospheric CO_2 likely played a role in the evolution of, and latterly the worldwide expansion of, the C_4 savanna ecosystem.

In our modern world fire is a strong predictor of the global distribution of the savanna ecosystem (Staver *et al.*, 2011). Fires occur typically every 2–3 years in these ecosystems (Hoffmann *et al.*, 2002). It has been suggested that many modern savannas now occur in areas that are wet enough to support forest ecosystems and that the savannas in these areas established themselves during drier periods in Earth history (Desjardins *et al.*, 1996; Pausas and Keeley, 2009). Fire maintains these savannas where otherwise moisture and climate would allow tree cover to prevail (Bond and Keeley, 2005). Patterns of fire, tree cover and climate in these areas show that fire functions as a positive feedback in modern savanna ecosystems: (i) by suppressing tree cover and (ii) because low tree cover promotes fire spread (Staver *et al.*, 2011, and references therein; Edwards *et al.*, 2010).

Beerling and Osborne (2006) have suggested that the success of C_4 savanna ecosystems likely involves a series of positive feedbacks that link both fire and climate. Their proposed systems analysis suggests that fire initiated, and has since sustained, the C_4 savanna biome. They suggest that the starting point was the death of trees during drought periods that left forest gaps into which C_4 grasslands spread. Much like in the angiosperm invasion scenario (see Section 12.5.5) these grasses rapidly acquire biomass in the wet season and hence provide abundant fuel in the dry season (Keeley and Rundel, 2005). This starts the self-promotion of grass spread into a forested

ecosystem by decreasing fire return intervals causing tree mortality followed by replacement by grasses (Cochrane and Ryan, 2009). Loss of forest cover, however, also causes major changes to the hydrological cycle, and, as an example, Amazon forests supply 88% of their own rainfall via evapotranspirational recycling (Cochrane, 2003, 2009). Loss of trees therefore slows evapotranspiration and cloud formation reducing regional precipitation (Beerling and Osborne, 2006, and references therein). Deforestation by enhanced fire return intervals therefore has the potential to impact climate causing a longer dry season and further enhancing fuel susceptibility to fire (Cochrane, 2003), leading to increased tree mortality and thus supporting further grass invasion (Beerling and Osborne, 2006).

The potential positive feedbacks do not stop there, because fires themselves have the ability to influence weather and climate (Artaxo *et al.*, 2009). Smoke aerosols influence cloud formation by increasing the number of cloud droplets. This tends to make precipitation less frequent and such lack of early precipitation can lead to the development of more violent convective storms (Andreae *et al.*, 2004; see also Chapter 13). Lower rainfall ought to further enhance tree mortality by increased drought; moreover, violent convective storms with little rain have a high chance of increasing ignition potential. Monitoring of recent fires in the Amazon (Artaxo *et al.*, 2009; Cochrane, 2009) and during the Yellowstone fires of 1988 has shown that large volumes of smoke from forest fires suppress cloud formation. Moreover, thick smoke plumes block out sunlight and prevent it from reaching the ground. This slows down evapotranspiration on the ground causing the air to become drier (see, e.g., Chapter 13). Meanwhile the darker smoky air above the fires absorbs sunlight. All these phenomena combined lower the moisture content of the air and reduce cloud formation. It therefore appears that large fires, at least, can exacerbate dry periods providing a positive feedback that further increases tree mortality and enhances large dry fuel loads that might be subject to future ignition events. The formation of pyroclouds (convective

smoky clouds) above large fires often causes intense thunderstorms, increasing lightning ignition potential and igniting further fires (Beerling and Osborne, 2006; see also Chapter 13). Hence fires can influence both weather and climate in favour of further fire events. Fire therefore seems well linked to the evolution of the C_4 savanna ecosystem and continues to maintain it on our planet today.

12.5.8 Fire-driven evolutionary traits

Some modern plant species exhibit so called fire-adapted traits (e.g. Keeley *et al.*, 2011b; Schwilk and Ackerly, 2001; see also Chapter 7). The development of these traits appears to be linked to fire, where fire has provided the evolutionary driving force that required some plants to adapt in order to survive on an increasingly flammable planet (Pausas and Keeley, 2009). Linking evolutionary adaptations in individual plant taxa to fire is difficult; not only are fossils of putatively 'fire-adapted' taxa rare, but also coupling an evolutionary trait directly to fire based on the fossil record of, for example, serotinous cones, is at best challenging (Keeley *et al.*, 2011b). Recent studies have used the DNA of plants to provide molecular phylogenies in which traits that are currently common in 'fire-adapted' ecosystems can be correlated with best estimates of ancient fire regime and environmental parameters (Gagnon *et al.*, 2010; Crisp *et al.*, 2011; Midgley and Bond, 2011). Currently the oldest known fire adaptation, dated via molecular techniques, is that of the evolution of fire-protective thick bark in *Pinus* (He *et al.*, 2012). The Pinaceae are believed to have evolved ~240Ma but thick bark did not evolve until 126Ma (He *et al.*, 2012). Thicker bark, together with branch shedding and serotinous cones, evolved in *Pinus* somewhat later ~89Ma (He *et al.*, 2012). Thick bark and branch shedding are believed to be fire-adapted traits because both reduce fire damage, the former by increasing stem insulation from heat and the latter by deterring surface fires from reaching the crown. Serotinous cones are considered a fire adaptation (Fites-Kaufman *et al.*, 2006; Keeley

et al., 2011b) because these cones only release seeds on exposure to heat from a fire and therefore ensure reproductive success should the plant be killed by fire (He *et al.*, 2012; see also Chapter 7). The period 126–89 Ma is estimated to have seen an increase in atmospheric oxygen to super ambient concentrations (e.g. Bergman *et al.*, 2004; Berner, 2009; Glasspool and Scott, 2010), high predicted burn probabilities (Belcher *et al.*, 2010a) and high abundances of charcoal in the fossil record (Glasspool and Scott, 2010; Brown *et al.*, 2012) (see Figure 12.1). It seems likely therefore that fire-adapted traits in *Pinus* evolved during this most flammable period of Earth's history. It appears that fire likely provided a significant selective pressure driving the evolution of these traits (He *et al.*, 2012).

A high bark-to-wood ratio, i.e. thick bark, has been noted in lycopsid trees from the Carboniferous (e.g. Falcon-Lang, 2000; see also Chapter 15). This observation may indicate that this fire adaptation goes back to the Carboniferous (~350 Ma).

There are also many fire adaptations in flowering plants (see discussion in Chapter 7; see also Bond and Midgley, 2012). *Banksia* (Proteaceae) is endemic to Australia and famed for distinctive fruiting 'cones', which open only when subject to fire. Molecular phylogenies suggest that this innovation appears at the same time as the first appearance of *Banksia* (Carpenter *et al.*, 2010) in the Paleocene (c. 60.8 Ma), a time of continued high atmospheric oxygen concentrations and high burn probabilities (see Figure 12.1), such that He *et al.* (2011) suggested that *Banksia* was 'born to burn'. Other Australian plants also show fire-adapted innovations at this time. For example, Crisp *et al.* (2011) recently reported that the deeply buried epicormic resprouting strands of eucalypts (Australian Myrtaceae) have their origin in the Paleocene (~60 Ma). This timing further supports the idea that superambient oxygen initiated high fire frequencies, which provided a significant evolutionary forcing.

The subsequent history of *Banksia* reveals that the innovations of dead leaf retention (which enhances flammability and fire spread to the crown – thus ensuring heating of the serotinous

cone) and underground bud resprouting (aiding recovery following fire) appear in the Miocene between 26 and 16 Ma (Carpenter *et al.*, 2010). These innovations reveal an interesting coincidence with the increased abundances of grass pollen in Australia (Stromberg, 2011). By the Late Miocene sclerophyllous forests with a grassy understorey are believed to have been present (Stromberg, 2011). It may be that understorey grasses enhanced fire frequencies, driving selection favouring new adaptations necessary in *Banksia*. Looking at a similar time, Bytebier *et al.* (2011) have provided a molecular date for the evolution of fire-stimulated flowering of Cape orchids of 15–13 Ma (Miocene). A similar story occurs in South America's cerrado ecoregion, with several genera (e.g. *Andira* and *Mimosa*) appearing to diversify and develop strong adaptations to fire around 5 Ma at the same time that C₄ grasses spread across this area (Simon *et al.*, 2009). To summarize, it appears that there is good evidence for fire becoming increasingly important as a driver of selection for plant innovations throughout the past 126 million years of Earth history.

12.6 Summary

In this chapter we have attempted to present a broad history of our planet's flammability. We hope that we have shown how fire has played an important role in the evolution and maintenance of some of the Earth's major ecosystems and how interplay between fuel and past atmospheric composition has potentially influenced broad trends in fire activity.

Climatic change is also likely to have been a significant driving force in influencing fire activity throughout the past 450 Ma of Earth's history. We have touched little on this in our chapter, but it remains an important direction of future studies. Moreover, relationships between climatic changes and fire activity are discussed in Marlon *et al.* (2009), and in Chapters 11 and 13. Nonetheless we note that fire has been part of pre-Quaternary climate change events; examples include climatic change across the

Triassic-Jurassic Boundary (Belcher *et al.*, 2010b) and during the Paleocene-Eocene Thermal Maximum (Collinson *et al.*, 2007). As has the influence of seasonality and weather (Uhl *et al.*, 2012).

We have shown the significance of changes in atmospheric oxygen concentrations to altering fire activity. In high-fire worlds where oxygen levels were well above the present level of 20.9% it is probable that climate would play a less important role in controlling the occurrence and distribution of fire as significantly wetter fuel could burn compared with the present day.

Throughout Earth's long history fire has been both a driver for and a consequence of evolutionary innovations, and a consequence of variations in atmospheric composition. It is clear that the Earth's history would be very different if it were not for the relationships we have outlined between fire and the atmosphere (e.g. Scott and Glasspool, 2006; Belcher *et al.*, 2010a; see also Chapters 13, 14 and 15), fire and the evolution of plant life (e.g. Beerling and Osborne, 2006; Bond and Scott, 2010; Pausas and Keeley, 2009) and the role of fire in maintaining our ecosystems (e.g. Staver *et al.*, 2011; see also Chapters 6 and 7). These relationships highlight the strong coupling of fire to Earth system processes (e.g. Bowman *et al.*, 2009; Scott, 2009, 2010; see also Chapter 15) and the importance of recognizing the influence of fire on long-term and short-term biogeochemical cycles (e.g. Scott, 2010; see also Chapters 6, 8, 9, 13 and 15). To conclude, without fire life on our planet would simply not be as we know it to today.

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