gebiology　WILEY

# Minimum levels of atmospheric oxygen from fossil tree roots imply new plant–oxygen feedback

Fredrik Sønderholm[1]　ID　|　Christian J. Bjerrum[1,2] ID

[1]Department of Geosciences and Natural Resource Management, University of Copenhagen, Copenhagen K, Denmark

[2]Nordic Center for Earth Evolution, Department of Geoscience and Natural Resource Management, University of Copenhagen, Copenhagen K, Denmark

**Correspondence**
Fredrik Sønderholm, Department of Geosciences and Natural Resource Management, University of Copenhagen, DK-1350 Copenhagen K, Denmark.
Email: frso@ign.ku.dk

**Funding information**
Department of Geosciences and Natural Resource Management, University of Copenhagen

## Abstract

The appearance and subsequent evolution of land plants is among the most important events in the earth system. Plant resulted in a change of earth surface albedo and the hydrological cycle, as well as increased rock weatherability thereby causing a persistent change in atmospheric $CO_2$ and $O_2$. Land plants are, however, themselves dependent on $O_2$ for respiration and long-term survival, something not considered in current geochemical models. In this perspective, we highlight two aspects of land plants' dependency on $O_2$ relevant for the geobiological community: (a) fossil root systems can be used as a proxy for minimum levels of past atmospheric $O_2$ consistent with a given fossil root depth; and (b) by identifying a positive feedback mechanism involving atmospheric $O_2$, root intensity, terrestrial primary production and organic carbon burial. As an example, we consider archaeopterid fossil root systems, resembling those of modern mature conifers. Our soil–plant model suggest that atmospheric $O_2$ with 1 *SD* probably reached pressures of $18.2 \pm 1.9$ kPa and $16.8 \pm 2.1$ kPa by the Middle and Late Devonian, respectively, that is $86 \pm 9\%$ and $79 \pm 10\%$ of the present-day 21.2 kPa.

**KEYWORDS**
devonian, earth atmosphere, feedback mechanisms, $O_2$, plants, roots

## 1 | INTRODUCTION

The appearance and subsequent evolution of land plants (Embryophytes) arguably is among the biggest revolutions of the earth system. Land plants originated as small and bryophyte-like vegetation during the middle Cambrian to Early Ordovician (~515–470 Ma) (Morris et al., 2018; Rubinstein et al., 2010). Trilete spores from the Late Ordovician suggest that vascular plants had evolved by that time; however, vegetation was still small and had limited interaction with the underlying rock due to miniscule rooting systems (Dahl & Arens, 2020 and references therein). It was not until Early Devonian that land plants really increased in height and extended their root systems in depth to more than few centimetres (Algeo

& Scheckler, 1998; Dahl & Arens, 2020). In the Middle Devonian Period, trees appear which by the end of the Period (~360 Ma) had evolved into forested ecosystems of modern complexity (Algeo & Scheckler, 1998). By this time, terrestrial vegetation reached deeply into the interior of the continents, and most likely constituted a significant fraction of the global biomass similar to that of today, where land plants are estimated to account for more than 80% by weight (Algeo & Scheckler, 1998; Bar-On et al., 2018). The transition from a barren to a green planet changed earth's albedo through ground cover and cloud distribution, intensified the hydrological cycle, and increased rock weatherability and net primary productivity (NPP). All of these changes impacted earth's climate and atmospheric composition (Beerling & Berner, 2005; Dahl & Arens, 2020; Rosing et al., 2010).

Because of land plants significant total mass proportion of the biosphere and impact on the geo- and atmosphere, they have been incorporated into several biogeochemical models through parameterization of various feedback mechanisms (see, e.g. Bar-On et al., 2018; Bergman et al., 2004; D'Antonio et al., 2020; Lenton et al., 2018). In example, a classic hypothesis proposes that increasing atmospheric $CO_2$ increases the NPP of land plants, resulting in increased organic carbon burial which reduces atmospheric $CO_2$ (Berner, 1999). The feedback mechanism is negative as it dampens an initial change. Recent treatments suggest that the negative feedback involving land plants and deep rooting systems is more complex resulting in an increase weathering feedback strength, thereby lowering the atmospheric $CO_2$ needed to achieve a given equilibrium weathering flux (D'Antonio et al., 2020; Ibarra et al., 2019). Another identified negative feedback mechanism involves $O_2$: where increasing atmospheric $O_2$ reduces NPP of land plants through increased photorespiration (the Warburg effect), which results in reduced production of $O_2$ (Lenton & Watson, 2000; Yiotis et al., 2017). Here, we highlight a coupling between atmospheric $O_2$ and land plants that have not been addressed explicitly in a geological context: Land plants require $O_2$ for long-term survival where insufficient $pO_2$ in soils limit plant root respiration and nutrient uptake, thereby limiting primary productivity (Geigenberger, 2014; Päpke et al., 2014; Waisel et al., 2002).

Plants harvest solar energy through photosynthesis, by consuming water and $CO_2$, and generating carbohydrates and $O_2$. Although a waste product of this process, $O_2$ is essential for the energy-rewarding aerobic respiration, which allows plants to utilize the harvested solar energy as ATP. Energy from respiration in the form of ATP is used for biosynthesis (growth), cellular maintenance and active transportation of essential elements like N, P and K in the root system (Atkin & Tjoelker, 2003; Waisel et al., 2002). Of the carbohydrates produced each day by plants, it is estimated that ~1/3 is respired in their root systems (Waisel et al., 2002). In contrast to the aerial part of the plant, $O_2$ can become very scarce in the root system, even under today's relatively high atmospheric $pO_2$ of 21.2 kPa, because of the lower gas diffusivity and high rates of respiration in soils by microbes and roots, as well as the low solubility in water (Armstrong & Drew, 2002; Brady, 1990). However, although the $pO_2$ of the modern, well-mixed atmosphere displays only limited variation over the course of a year to thousands of years, the atmospheric $pO_2$ can vary considerably over millions of years. On such longer timescales, it is important to consider the effect that $O_2$ variation may have had on vegetation via the rooting system in the past. Consequently, attempts at modelling the composition of the atmosphere through time, for example Krause et al. (2018), Lenton et al. (2018) and Schachat et al. (2018), should incorporate the effect of low atmospheric $pO_2$ on plant NPP and long-term survival.

In this perspective, we hope to: (a) illustrate how fossil root systems can be used to provide minimum levels of atmospheric $pO_2$ in the geological past, which can be used to evaluate existing $O_2$ models (see, e.g. Krause et al., 2018; Lenton et al., 2018; Schachat et al., 2018); and (b) present a positive feedback mechanism involving $pO_2$, root intensity (defined here as root respiration per square metre), plant NPP and organic carbon burial. We do this by highlighting present knowledge among biologist and soil scientist on plant root respiration and soil aeration and applying it in a geological context.

## 2 | METABOLIC PATHWAYS

Plants consume carbohydrates in the mitochondria through several pathways, the most important ones being cytochrome-c oxidase (COX), alternative oxidase (AOX) and anaerobic fermentation. The COX pathway and AOX require $O_2$, whereas fermentation can function under anaerobic conditions. COX is the preferred pathway and has the largest ATP yield with 36 ATP generated for every glucose molecule ($C_6H_{12}O_6$) respired (Hopkins, 1999). In addition, it has a very high affinity for $O_2$, $K_m^{COX} = 0.01$ kPa, meaning that the energy production rate from this pathway is only halved at $O_2$ pressures of 0.01 kPa (Figure 1a; Armstrong et al., 2009, and references therein). The ATP yield from AOX is much smaller than that from the COX pathway (0–12 ATP generated for every glucose molecule respired), with the majority of the energy being lost as heat (Hopkins, 1999). The AOX affinity for $O_2$, $K_m^{AOX} = 0.13$ kPa, is also 1 order of magnitude lower than that of COX (Figure 1a; Armstrong et al., 2009, and references therein). Plants can also gain energy through fermentation under anoxic conditions, that is when soils become flooded. The ATP yield from fermentation is, however, very small with only two ATP being generated for every glucose molecule consumed. The energy yield of fermentation is insufficient to power nutrient uptake and growth and can only prolong the period of plant survival under anoxic conditions (Kozlowski, 1985). Furthermore, the anaerobic fermentation process cannot continue for a long time, as the ethanol produced through the reaction is a toxic waste product (Crawford, 1992). Consequently, $O_2$ is needed for sufficient root respiration and long-term plant survival and growth. The $O_2$ uptake is mainly secured in two ways: (a) through radial diffusion from the soil air into the root; and (b) through longitudinal diffusion via the intercellular gas space continuum of the cortex (Armstrong & Drew, 2002). Dissolved $O_2$ entering through water uptake and pressurized gas flow are thought to be of only minor importance, although the latter can be important in specific species (Armstrong & Armstrong, 2009; Armstrong & Drew, 2002). In the archaeopterid fossils studied, here the pressurized gas flow is, however, not important as their root systems have been described as woody which effectively inhibits the longitudinal transportation of $O_2$ (Armstrong & Beckett, 1985). The well-being of plants in relation to $O_2$ traditionally is monitored in two ways, by the Critical Oxygen Pressure for Respiration, and Critical Oxygen Pressure for Extension.

## 3 | CRITICAL OXYGEN PRESSURE FOR RESPIRATION

The critical oxygen pressure for respiration (COPR) is the $O_2$ pressure below which respiration is reduced. Here, focus will be on the
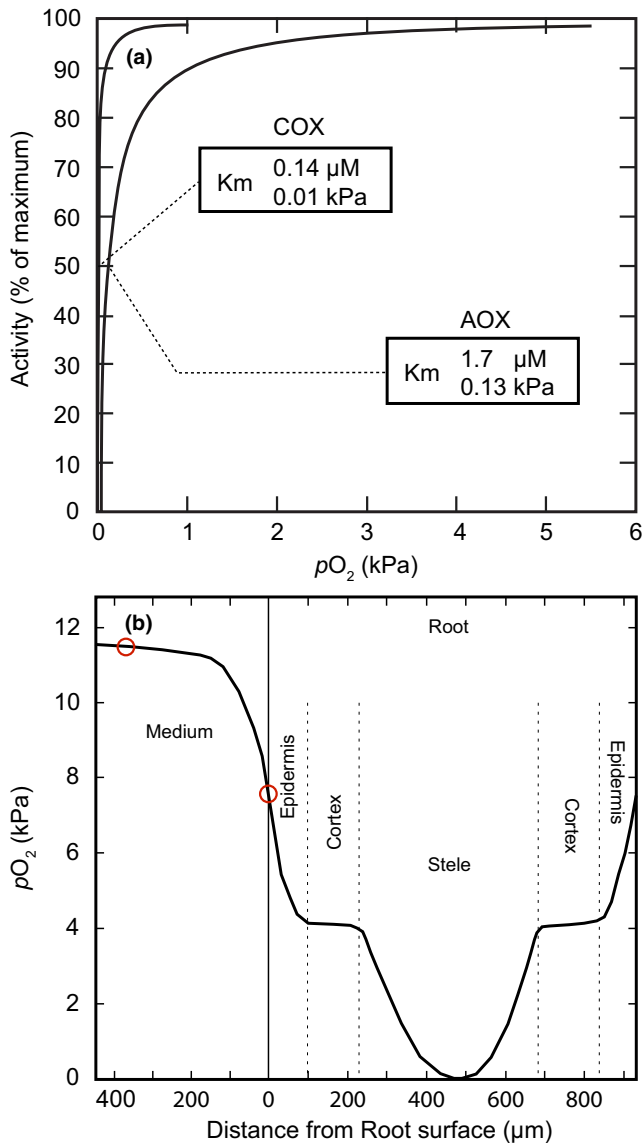
**FIGURE 1** Respirational Pathways & COPR. (a) Oxygen dependent activity of Cytochrome C oxidase (COX) and Alternative oxidase (AOX). Activity of both COX and AOX is only significantly affected at $O_2$ concentration below 1 kPa. (b) Conceptual $O_2$-profile through root segment. Whole-root respiration significantly decreases only when anoxia spreads within the root, as COX is the main respirational pathway and has a very high affinity for $O_2$ (see a). The critical oxygen pressure for respiration (COPR) is measured at the root surface or in the surrounding medium (red circles) at the point when anoxia first spread within the root. Adapted from Armstrong et al. (2009)

root system, as this is the part most likely to experience anoxia. The value of COPR depends on where the measurement is taking place. At a cellular level, respiration is not significantly affected except at an extremely low $O_2$ pressure as the major respirational pathway, COX, has a very high affinity for $O_2$ (Figure 1a). Whole-root respiration will only be seriously impaired when anoxia begins to spread within the root, usually from the centre (Figure 1b). The COPR is usually determined either at the root surface or in the surrounding

medium where $pO_2$ has stabilized—the difference in COPR between these two sites can be quite significant (Figure 1b). In experiments with sterile medium, the difference is due to respiration in root hairs (Armstrong & Drew, 2002). Under natural conditions, the difference also results from microbial respiration which tends to be more pronounced in the rhizosphere surrounding the root than elsewhere in the soil (Armstrong & Drew, 2002). The COPR for roots in natural soils will therefore be larger than the COPR reported in some literature. For several modern plant species, for example Banana, Pea, Corn, Tomato and more, the aerobic respiration is essential for biosynthesis, maintenance and nutrient uptake, which would be affected by even a small decrease in atmospheric $pO_2$ (Armstrong & Drew, 2002; Armstrong et al., 2009; Ben-Noah & Friedman, 2018; and references therein). With $pO_2$ declining further below the COPR, energy production can become insufficient to satisfy root extension.

## 4 | CRITICAL OXYGEN PRESSURE FOR EXTENSION

The critical oxygen pressure for extension (COPE) is the $O_2$ pressure below which a halt in root extension is observed. The value of COPE depends on the place of measurement (within the root or in the surroundings), as well as on the kind of extension considered (Armstrong et al., 2009). Experiments on apple seedlings have shown that initiation of new roots from an existing root system requires soil-air $pO_2$ above 12 kPa, whereas the extension rate of existing roots is not affected before the $pO_2$ decreases below 10 kPa, while limited extension is observed at pressures down to 5 kPa $pO_2$ (Boynton et al., 1938). Such experiments are supported by observations in nature, where severe reduction in growth has been reported at soil-air $pO_2$ below 10 kPa for various conifers and for *citrus* (Kozlowski, 1985, and references therein). The reduction in natural systems is probably due to slowed extension of existing roots and the inability to initiate new roots. In general, tree roots require soil-air $pO_2$ above 10 kPa for optimal growth in the short term (Kozlowski, 1985), whereas long-term plant survival seems to require soil-air $O_2$ pressures of at least 12 kPa (Boynton et al., 1938). In summary, emerging plants need to initiate new roots, whereas mature plants need to constantly renew their root systems when old roots are lost to disease or consumed by fauna. How atmospheric $pO_2$ relates to COPE and long-term plant survival depends on the characteristics of the soil, at least for plants that rely on soil-air $O_2$ for root respiration.

## 5 | SOIL-AIR OXYGEN

Well-drained and aerated soils are important for optimal plant growth as most plants obtain $O_2$ for respiration radially from the soil air (Armstrong & Beckett, 1985). Soils, however, in general experience reduced $O_2$ and enriched $CO_2$ levels because of respiration by plant roots and microbes, and because of diffusional resistance between soil and atmosphere (Brady, 1990). Consequently, $O_2$
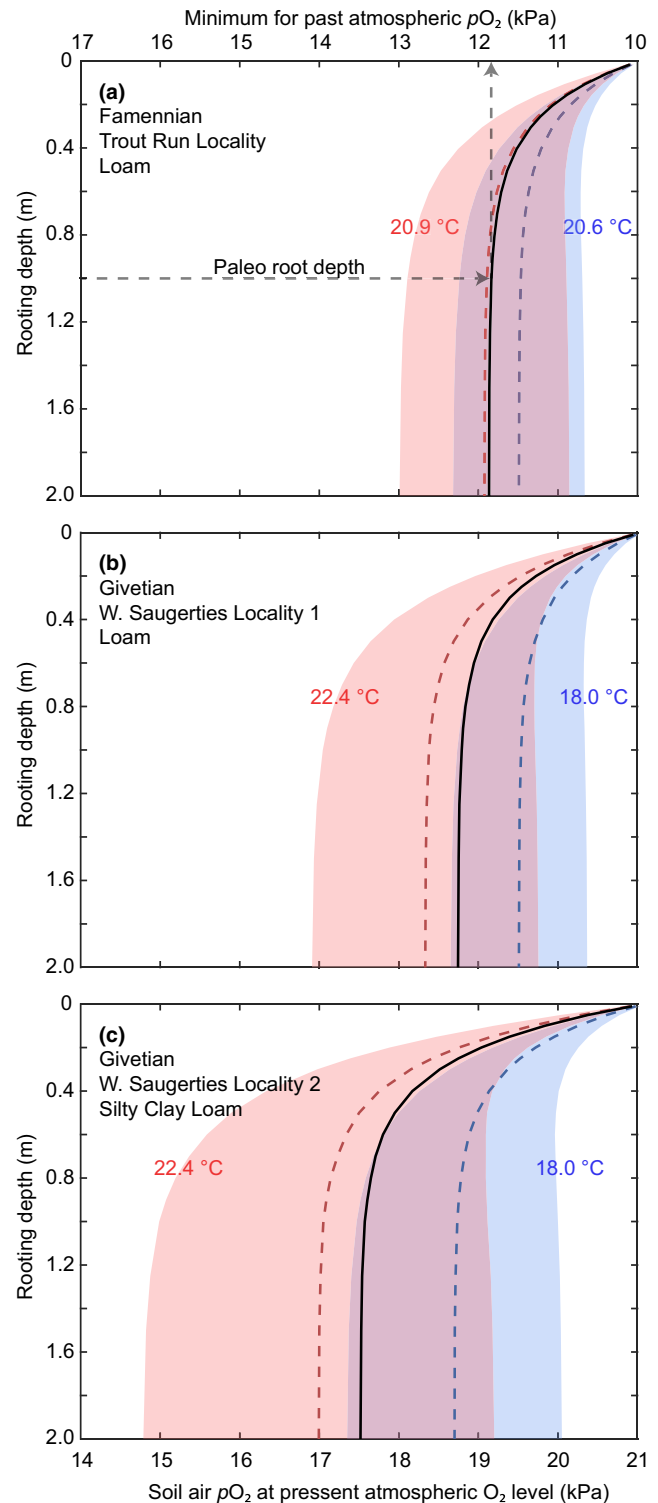
**FIGURE 2** Modelled soil $O_2$-profiles and minimum for past atmospheric $pO_2$. Modelled soil $O_2$ profiles of three palesol-outcrops with fossil archaeopterid root systems to a depth of 1 m (a, c) and 1.5 m (b). Solid black lines are the median of all model calculations for each palesol-locality. Dashed lines are medians with one standard deviation for surface temperatures at two adjacent GCM grid points of paleogeographic relevance (Supplementary Information). Lower horizontal axis is modelled soil-air $pO_2$ at present atmospheric $O_2$ level. The difference between atmosphere and soil gives the drawdown of $O_2$. The upper horizontal axis is modelled minimum of past atmospheric $pO_2$ needed for long term survival, where the oxygen drawdown have been added to the 10 kPa minimum where conifer like root systems experience a severe reduction in growth



pressures decrease with soil depth, and the resulting $O_2$ profiles are further influenced by several factors such as lithology (soil type), soil respiration rate and water content (Armstrong & Drew, 2002).

Soil respiration constitutes an $O_2$ sink caused by respiration of both roots and microbes, including the important symbiotic arbuscular mycorrhiza fungi, which at least dates back to the Early Devonian Period (Quirk et al., 2015; Remy et al., 1994). Root respiration is usually dominant, but its effect decreases rapidly with depth as root intensity and $pO_2$ decline (Ben-Noah & Friedman, 2018). Additionally, microbial respiration is more pronounced towards the surface where the content of organic matter is higher, but this type of respiration is largely independent of $pO_2$ and is not affected except at pressures very close to zero (Ben-Noah & Friedman, 2018). Increasing temperatures increases microbial and root respiration resulting in a lower $O_2$ pressure in the soil (Figure 2). Consequently, soil-air $pO_2$ may decline with depth to values unsustainable for most plants or for optimal growth if diffusional resistance is too high as well.

Today, water content is the most important factor influencing soil $O_2$ profiles, because the water displacing soil air contains only 1/30 of the $O_2$ in air and has diffusivities that are 10,000 times lower (Armstrong & Drew, 2002). The diffusion rate of $O_2$ is therefore effectively 300,000 times lower in soil water, meaning that soil-air $pO_2$ can decrease dramatically under heavy rains or become entirely depleted in a matter of hours to days during and after floods (Armstrong & Drew, 2002; Crawford, 1992). The increased diffusional resistance of $O_2$ in water is why well-drained soils are important for most plants, which in part is controlled by lithology or soil type.

Lithology affects the soil $O_2$ profile through the effects of porosity and the interconnectivity and tortuosity of pore spaces (cf. Brady, 1990; Breecker et al., 2009; Wynn et al., 2005). The higher the porosity and interconnectivity of the pore spaces, the better the diffusion (as well as the drainage), and with increasing diffusivity, soil-air $pO_2$ will be higher. For example, the decrease in $pO_2$ with depth will be more pronounced in a silty clay loam than in a sandy loam which is apparent in one-dimensional soil-$O_2$ models, and from carbon-isotope measurements of pedogenic carbonates (Figure 2b,c; Bartholomeus et al., 2008; Wynn et al., 2005). Such models build on a long tradition of modelling crop production in the agronomic sciences and have been applied in regional and global models (Bartholomeus et al., 2008; Campbell, 1985; Cook, 1995; Cook & Knight, 2003; Fierer et al., 2006; Jackson et al., 1996; de Willigen & van Noordwijk, 1987). Here, the modelled $O_2$ profiles are modelled by randomly sampling probability distributions of parameters other than soil type which are poorly known for fossil soils (Table S1).

The three factors mentioned here, *that is* soil water content, respiration rate and lithology, have a prominent effect on soil $O_2$

profiles. These controlling factors may locally be ever changing as changes in weather and river paths redistribute sediments and water. However, on a longer time scale, global soil aeration based on these three factors may be considered to be relatively constant and is probably only to some degree affected by major changes in seawater level and the hydrological cycle.

On a geological time scale, the atmospheric $pO_2$ becomes an important factor for soil $O_2$ profiles. With declining atmospheric $pO_2$, soil-air $pO_2$ would decrease globally and soils would eventually become anoxic at shallower depths. Even small changes in atmospheric $pO_2$ would have consequences for plants whose value of critical $O_2$ pressure for respiration (COPR) is relatively high, thereby affecting root respiration even in well-drained and porous soils. This would result in a decrease in root penetration depth and reduce the amount of soil and rock volume that can be exploited by plants. Consequently, a decrease in atmospheric $pO_2$ would mean that a larger fraction of soils would become inaccessible to plants requiring high soil-air $pO_2$, and these would be displaced by plants better adapted to sub- and anoxic soil conditions. Such changes in the floral pattern would impact the influence of terrestrial plants on the earth system, as adaptation to sub- and anoxic soil conditions should decrease primary productivity.

## 6 | ADAPTATION TO LOW OXYGEN

Two mechanisms allow plants to adapt to low soil-air $O_2$ pressures: the reduction of $O_2$ consumption through decreased respiration and the enhancement of $O_2$ availability through decreased diffusional resistance. Adaptation of the respirational pathways, COX and AOX, should have little influence. The two enzymatic pathways have a very high affinity for $O_2$ meaning that respiration is only affected when $O_2$ basically is absent. A higher affinity for $O_2$ would therefore not have any significant effect. The former mechanism is still the subject of debate, as it is unclear whether such reductions in respiration rate are due to $O_2$ limitations, or whether respiration is being actively down-regulated by the plant itself (Päpke et al., 2014). Regardless of this, reduced respiration results in less ATP being produced and this negatively impacts primary productivity by impeding several essential plant functions such as carbohydrate translocation and nutrient and water uptake (Geigenberger, 2014). As for the latter mechanism (decreased diffusional resistance), plants can enhance the amount of $O_2$ available to their roots through adaptations in root porosity and shape, where adaption strategy differs between non-wetland and wetland plants. Roots of wetland plants cannot obtain $O_2$ from the anoxic soil, but transport it from the shoot to the root via aerenchyma (intercellular air canals) (Armstrong & Beckett, 1987). The development of aerenchyma is, however, not an unmitigated benefit. Aerenchymatous roots have remarkably large diameters and low ratios of root surface area to biomass, impairing nutrient uptake per unit biomass (Lambers et al., 2008). Non-wetland plants lack aerenchyma, meaning that $O_2$ transport from shoot to root is very limited, and root woodiness (e.g. lignification) may disrupt this path

completely (Armstrong & Beckett, 1985). Non-wetland plants therefore require $O_2$ from the soil, the availability of which can be enhanced by developing thinner roots with increased porosity, which would decrease the diffusional resistance from root surface to centre (Armstrong & Beckett, 1985). However, such porosity increase would also decrease the plant capability of carbohydrate storage and transportation, thereby limiting root respiration, resulting in a reduced primary productivity overall. Consequently, plants would likely be able to adapt to lower atmospheric $pO_2$, but such adaptation would negatively impact plant root respiration and primary productivity, and likely be recorded in the fossil record as changes in root morphology.

## 7 | USING FOSSIL ROOT SYSTEMS TO CONSTRAIN ATMOSPHERIC $pO_2$

Fossil root systems can serve as proxies for atmospheric $pO_2$ levels in the geological past, because the morphology of root systems is dependent on soil-air $pO_2$ and hence the atmospheric composition. It, however, requires the associated soil type, soil and air temperature, soil respiration, as well as soil moisture content to be taken into account as this affects the drawdown of $O_2$ within the soil. Furthermore, it requires the fossil root systems and the palaeosol to be preserved in such a degree that root traces or casts can be tracked, near continuously, from palaeosol surface to root tip (apex). This approach is exemplified in the following by considering the archaeopterid fossils of deeply penetrating root systems found at three different outcrops: The Famennian (372.2–358.9 Ma) Trout Run outcrop and the Givetian (387.7–382.7 Ma) W. Saugerties outcrops 1 and 2 (Driese et al., 1997; Mintz et al., 2010).

The well-studied archaeopterids were some of the most important forest-forming trees during the Devonian Period (Algeo & Scheckler, 1998; Meyer-Berthaud et al., ,1999, 2013). They could reach more than 25 m in height and measure more than 1.5 m in diameter at the base (Meyer-Berthaud et al., 2013). Archaeopterids are recognized as the earliest known modern tree, with stems and root systems resembling those of modern conifers (Kenrick & Strullu-Derrien, 2014; Meyer-Berthaud et al., ,1999, 2013). Because of their woody root systems, the archaeopterids were restricted to obtain $O_2$ from the soil air towards root respiration. Accordingly, the here studied palaeosols have been described as being well-drained to seasonally wet (Driese et al., 1997; Mintz et al., 2010).

The drawdown of $O_2$ within the paleosols at the different outcrops is estimated by applying a one-dimensional soil–root model with a few modification (cf. Table S1–S4; Bartholomeus et al., 2008; Bjerrum, 2021). The soil types, used in the soil–root model, are determined based on palaeosol descriptions and the classification scheme from the U.S. Department of Agriculture (Supplementary Information; Brady, 1990; Driese et al., 1997; Mintz et al., 2010; Wösten, 1997; Wösten et al., 2001). The temperature of surface air and soil as well as soil moisture content is obtained from published results of a coarse resolution Devonian climate model-setup

building on the intermediate complexity coupled Earth System model CLIMBER-3α (Table S5; Brugger et al., 2019; Montoya et al., 2005). Paleogeographical locations are based on the PALEOMAP (Figure S4; Scotese, 2016). Modern day values for the soil respiration dependent on temperature with a $Q_{10}$ of 2. Yapp and Poths (1994) suggest, based on geochemical analysis of Upper Ordovician Goethite, that pre-vascular soil respiration probably reached modern day levels. We have therefor assumed that soil respiration in the Middle and Late Devonian Period could reach similar levels, where the biosphere resembled the present much more. Other poorly known parameters are randomly re-sampled from global representative probability distributions during 2000 model evaluations (Table S2). Because of uncertainty in the position of the continents during the time intervals, two paleogeographical locations were used for each of the outcrops, resulting in two $O_2$ profiles mostly affected by temperature (Figure 2). The $O_2$ drawdown between soil and atmosphere was determined from the modelled soil $O_2$ profiles as the $pO_2$ difference between the atmosphere and the median of all the model calculations (Table 1; Figure 2).

Based on the observed lithology, Devonian Climate Model data and the fact that the fossilized root systems are analogous to those of modern mature conifers (Driese et al., 1997; Kenrick & Strullu-Derrien, 2014; Meyer-Berthaud & Decombeix, 2007; Meyer-Berthaud et al., 2013), inferences can be made regarding both soil air and atmospheric $pO_2$ when the trees were living. Adaptation to low $O_2$ is limited to respirational demand and morphology. We therefore suggest that archaeopterid roots systems of the Middle–Upper Devonian (388–359 Ma) would have required soil-air $O_2$ pressures of 10 kPa comparable to those required by their morphologically similar modern analogues (here modern conifers), assuming a similar respirational demand (Kozlowski, 1985). Severely reduced growth is not viable for long-term survival as the trees, like today, would have been supplanted (Crawford, 1992). We can therefor provide a strict

minimum for atmospheric $pO_2$ by adding the drawdown of $O_2$ between soil and atmosphere to the 10 kPa $pO_2$ (Table 1; Figure 2). In example, a minimum for atmospheric $pO_2$ of 11.9 ± 1.1 kPa (1 SD) can be obtained for the Famennian by adding the modelled soil $O_2$ drawdown of 1.9 ± 1.1 kPa (1 SD) for the paleo root depth of 1 m in loam, to the 10 kPa $pO_2$ where growth of the archaeopterid with conifer-like root systems will be severely reduced (Table 1; Figure 2a). For the Givetian, a minimum atmospheric $pO_2$ level of 13.6 ± 2.2 kPa (1 SD) is estimated based on archaeopterid paleo root depth of 1 m in silty clay loam (Table 1; Figure 2c).

The minimum levels of atmospheric $pO_2$ derived from the minimum $O_2$ requirement for growth as presented in Table 1 are rather conservative low estimates—probably too conservative. If soil conditions were severely reducing growth of the archaeopterid trees, these would most likely, as today, have been supplanted by other better adapted plants or trees (Crawford, 1992). In that sense, it is more relevant to calculate to what atmospheric $pO_2$ level optimal growth can occur. The minimum $O_2$ requirements for optimal growth have here been calculated with the one-dimensional soil–root model where only results fulfilling optimal growth have been accepted where the respiration factor is $\eta = 5$ (cf. Table S1–S5; Bartholomeus et al., 2008). These calculations resulted in minimum atmospheric $pO_2$ requirements for optimal growth at 18.2 ± 1.9 kPa (1 SD) for the Givetian and 16.8 ± 2.1 kPa (1 SD) for the Famennian (Table 1; Figure 3; Figures S1–S3).

Concurrent with the occurrences of fossil archaeopterid roots mentioned above is a so-called charcoal gap, stretching from the Early Devonian through the Early Carboniferous (Figure 3; Glasspool et al., 2015; Scott & Glasspool, 2006). The presence of charcoal in sediments is an independent proxy for the occurrence of fires, which require a certain pressure of atmospheric $O_2$. Fires cannot persist below 15 kPa $pO_2$, and the probability of combustion is low at $pO_2$ levels between 15 and 17 kPa; above 17 kPa, fires spread readily

**TABLE 1** Fossil tree roots' minimum atmospheric $pO_2$ requirements for long-term survival and optimal growth

| Locality | Age | Root depth (m) | Interpreted soil texture | Paleo Lat. (°S) | Soil temp.[a] (°C) | Drawdown of $O_2$ (kPa) | Minimum $pO_2$ (kPa) for | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | | | | | | | Long-term survival[b] | Optimal growth |
| Trout Run | Famennian | >1 | Loam | Combined | 22.4 ± 1.5 | 1.9 ± 1.1 | 11.9 ± 1.1 | 16.8 ± 2.1 |
| | | | | 33.75 | 21.7 ± 1.6 | 1.5 ± 0.8 | 11.5 ± 0.8 | 16.1 ± 1.9 |
| | | | | 26.25 | 22.8 ± 1.1 | 2.0 ± 1.0 | 12.0 ± 1.0 | 17.4 ± 1.9 |
| W. Saugerties OC1 | Givetian | 1.5 | Loam | Combined | 21.8 ± 2.6 | 2.3 ± 1.5 | 12.3 ± 1.5 | 17.1 ± 2.2 |
| | | | | 41.25 | 18.4 ± 2.2 | 1.5 ± 0.9 | 11.5 ± 0.9 | 15.6 ± 2.1 |
| | | | | 33.75 | 22.6 ± 1.2 | 2.6 ± 1.5 | 12.6 ± 1.5 | 17.1 ± 1.9 |
| W. Saugerties OC2 | Givetian | 1 | Silty Clay Loam | Combined | 21.0 ± 2.6 | 3.6 ± 2.2 | 13.6 ± 2.2 | 18.2 ± 1.9 |
| | | | | 41.25 | 17.9 ± 2.1 | 2.3 ± 1.3 | 12.3 ± 1.3 | 17.3 ± 1.8 |
| | | | | 33.75 | 22.1 ± 1.2 | 3.9 ± 2.1 | 13.9 ± 2.1 | 19.0 ± 1.6 |

Note: Data are ±SD.

Abbreviation: OC, Outcrop.

[a]Median during maximal soil respiration: October through December in the southern hemisphere.

[b]Based on the severe reduction in growth of modern conifers that experience soil-air $O_2$ of 10 kPa (Kozlowski, 1985).
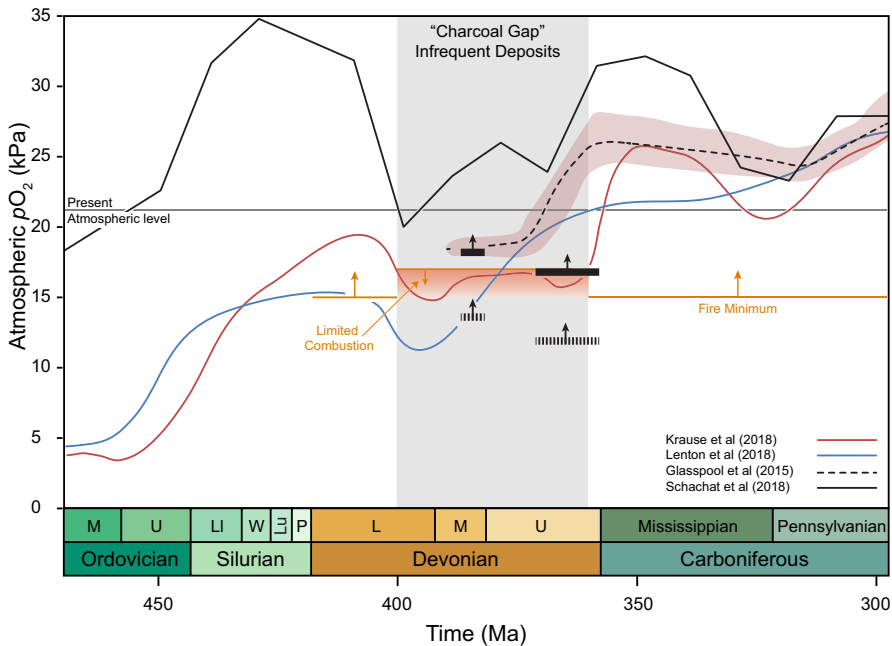
**FIGURE 3** Evolution of atmospheric $O_2$ through time. New minimum levels of atmospheric $pO_2$ based on the conifer-like fossil root system of archaeopterids: Bold black bars represent minimum atmospheric $pO_2$ for optimal growth, whereas stippled black bars represent minimum atmospheric $pO_2$ for long-term survival. Infrequent charcoal deposits or "Charcoal Gap" (grey box; Glasspool et al., 2015). Fire window (orange lines; Cope and Chaloner, 1980). Limited combustion between 15 and 17 kPa (grading orange box; Belcher and McElwain, 2008)

(Belcher & McElwain, 2008). Charcoal gaps have therefore been suggested to represent periods where levels of atmospheric $pO_2$ were insufficient to maintain fires (Scott & Glasspool, 2006). The Devonian charcoal gap in fact represents a period of infrequent charcoal deposits (Glasspool et al., 2015), and so the infrequent occurrences of charcoal have been suggested to represent a period with atmospheric $O_2$ pressures between 15 and 17 kPa, which would allow smouldering fires, but not make them extensive (Figure 3; Krause et al., 2018). However, the infrequent charcoal deposits could also be a result of limited fuel load (Glasspool et al., 2015). The diversification and worldwide appearance of the woody archaeopterid trees was not complete until the end-Devonian (Scheckler, 2006), and the vegetation before that is thought to have been patchy as it was confined to water-rich habitats (Algeo & Scheckler, 1998). Glasspool et al. (2015) therefore suggest that the infrequent charcoal deposits of the mid-Devonian are a result of an insufficient fuel load rather than an insufficient $O_2$ pressure, which is also supported by their inertinite-$O_2$ model suggesting atmospheric $O_2$ pressures of 18–19 kPa. This accords well with our observations from archaeopterid root systems, which indicate that atmospheric $pO_2$ levels during the Givetian (387.7–382.7 Ma) may have exceeded well above $13.6 \pm 2.2$ kPa (1 SD) for roots to extend down to 1 m in depth in a clay rich soil while not being severely reduced in growth. This is furthermore supported by the one-dimensional soil model which suggests atmospheric $O_2$ pressures of $18.2 \pm 1.9$ kPa (1 SD) as a minimum required for optimal growth.

Likewise, our model results can be used to evaluate long-term biogeochemical cycle models. For example, $O_2$ levels modelled by Krause et al. (2018) during the Givetian implicate reduced root respiration and plant growth, while the low $O_2$ levels modelled by Lenton et al. (2018) implicate severe inhibition of root respiration and higher plant growth (Figure 3). Consequently, our results only agree with some models that in the Givetian have relatively high

atmospheric $O_2$ that support optimal root respiration and plant growth of the studied archaeopterid trees (Glasspool et al., 2015; Schachat et al., 2018). During the Famennian, it is only the $O_2$ model by Krause et al. (2018) that to some extent results in reduced root respiration and plant growth.

## 8 | AN $O_2$ OPTIMUM FOR PLANT GROWTH

Terrestrial vegetation and atmospheric $O_2$ is coupled through different mechanisms in various feedback mechanisms. Feedback mechanisms that dampen an initial change are negative and those that intensify are positive. Based on the existing literature, we find that the earth system possesses two overlooked positive feedback mechanisms involving atmospheric $O_2$ and root intensity (Figure 4). Firstly, following path A–C–E–F in Figure 4, we get the positive feedback mechanism where increasing atmospheric $pO_2$ increase root intensity, thereby increasing net primary productivity (NPP), carbon burial and atmospheric $pO_2$. Although, it should be mentioned that an increase in atmospheric $O_2$ could decrease the area of anoxic soils and thereby decrease the carbon storage potential. Secondly, by following path A–C–G–H–F in Figure 4, increasing atmospheric $pO_2$ increases root intensity, which increases NPP, thereby increasing plant induced weathering, ocean nutrient availability, marine NPP, carbon burial and finally atmospheric $pO_2$.

Already identified negative feedback mechanisms include the effects of photorespiration and fire. Following path B–D–E–F in Figure 4, an increase in the atmospheric $O_2$:$CO_2$ ratio increases photorespiration which decreases terrestrial NPP, thereby reducing carbon burial and atmospheric $pO_2$, ultimately reducing the $O_2$:$CO_2$ ratio (Beerling et al., 1998; Lenton & Watson, 2000). Fire exerts a negative feedback mechanism through the following path (I–J–E–F;

Figure 4): increasing atmospheric $pO_2$ increases widespread fires which reduce the standing terrestrial biomass of plants resulting in a reduced terrestrial NPP, carbon burial and production of $O_2$, leading to a lower atmospheric pressure of $O_2$ (Kump, 1988). However, this negative fire feedback mechanism functions only within the 'fire window' of 15–30 kPa $pO_2$. Below 15 kPa, fires cannot persist, and above ~30 kPa, fires spread so readily, even under moist conditions, that extensive forests will not be able to exist (Belcher & McElwain, 2008; Chaloner, 1989; Cope & Chaloner, 1980). Yet another negative feedback mechanism involves rock weathering (Lenton, 1998). Following path (B–D–E–F) or (I–J–E–F) in Figure 4,
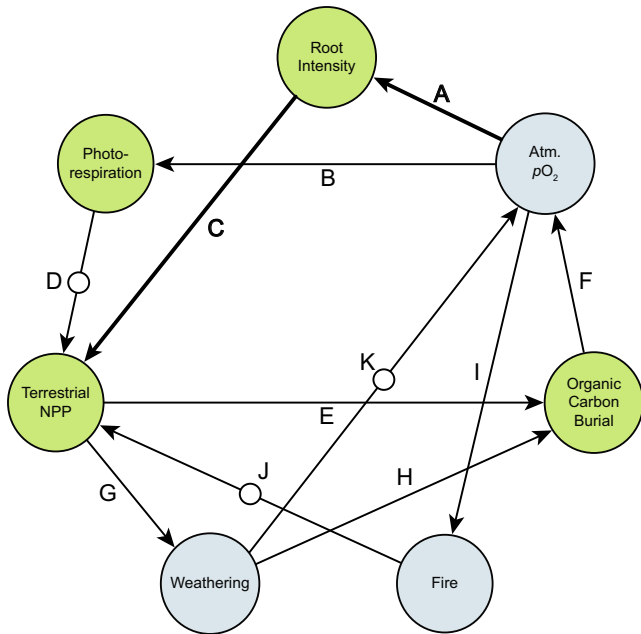


**FIGURE 4** Feedback diagram highlighting a subset of the many interactions between plants and atmospheric $O_2$. The straight arrows indicate a positive coupling between two factors, while arrows with a circle indicate a negative coupling. Green circles (biological factors) and blue (physical factors). Note: Two newly discovered positive feedback mechanisms (A–C–E–F and A–C–G–H–F; this study) are enabled by the previously overlooked couplings (A and C; marked by bold arrows) between atmospheric $pO_2$, roots and NPP. The two new couplings should be viewed in a grander scheme as they can affect other parts of a more complete feedback diagram (cf. Berner, 1999; D'Antonio et al., 2020; Lenton and Watson, 2000)

increasing $pO_2$ both results in increasing fire frequencies and photorespiration leading to lower plant NPP which reduces weathering and delivery of nutrients to the oceans, thereby reducing organic carbon burial and production of $O_2$. There exist a large number of other plant feedbacks previously described well (Berner, 1999; D'Antonio et al., 2020; Lenton & Watson, 2000). Here, we highlight a subset relevant for the present focus on oxygen feedback on plants. Our results should therefore be viewed in a grander scheme. However, by combining the positive and negative feedbacks, there may exist an $pO_2$ optimum for growth of terrestrial vegetation; high enough to secure well aerated conditions within the soils for the roots, but low enough to ensure a reasonable low photorespiration and limited fires.

The $pO_2$ optimum for growth and NPP is, however, dependent on rooting depth. Growth and NPP is only positively correlated with atmospheric $pO_2$ until the rooting system and the rhizosphere are sufficiently aerated; hereafter, there will be no benefit of increasing atmospheric $pO_2$. Therefore, an upper limit of atmospheric $pO_2$ exists for the positive feedback mechanisms and this upper limit depends on at what point full root aeration is reached. This in turn depends on existing plant species as deeper penetrating and more extensive rooting systems require a higher level of atmospheric $pO_2$ to be fully aerated. Today, forest ecosystems have the largest NPP per area, being more than double that of grass- and shrublands (Table 2; Melillo et al., 1993). The $pO_2$ optimum for forest ecosystems can therefore be used as a global $pO_2$ optimum for NPP. If forest ecosystems in general since the Mid to Late Devonian have had a similar minimum atmospheric $pO_2$ requirement for optimal growth, as suggested by our model results, there is a good chance that the global $pO_2$ optimum for NPP the last 400 million years would have been close to $18.2 \pm 1.9$ kPa (1 $SD$), although dependent on the mean temperature and intensity of the hydrological cycle (Table 1). Increasing temperatures and intensity of the hydrological cycle would results in a higher $pO_2$ optimum for NPP, because soil and root respiration would increase and diffusivity of $O_2$ would decrease.

The $pO_2$ optimum for NPP would also be dependent on atmospheric $CO_2$. For optimal NPP conditions, there need to be a balance between the production of carbohydrates in the canopy and consumption in the rooting system and elsewhere. The production of carbohydrates above ground increases with decreasing $pO_2$:$CO_2$ ratios (Beerling et al., 1998; Edwards & Walker, 1983; Yiotis et al., 2017). On the other hand, root respiration below ground decreases with lower

**TABLE 2** NPP of ecosystems (g C m$^{-2}$ year$^{-1}$)

| Vegetation | Boreal | | Temperate | | Tropical | |
|---|---|---|---|---|---|---|
| | Mean | Range | Mean | Range | Mean | Range |
| Forests | 206 | 173–238 | 624 | 465–741 | 985 | 871–1098 |
| Grass- and shrublands | N/A | N/A | 255 | 129–342 | 368 | 343–393 |
| Ratio | N/A | N/A | 2.45 | 1.36–5.74 | 2.68 | 2.22–3.20 |

*Note:* Data from Melillo et al. (1993).

Abbreviation: N/A, Not Available.

levels of soil-air $O_2$. This means that there for a giving concentration of $CO_2$ exists a $pO_2$ optimum for NPP. Low enough $pO_2$ to ensure a low $pO_2$:$CO_2$ ratio and thereby high carbohydrate production above ground, but at the same time high enough $pO_2$ to ensure that respiration of the translocated carbohydrates in the root system below ground can be met. By simultaneously increasing atmospheric $O_2$ and $CO_2$, it is possible to keep the $pO_2$:$CO_2$ ratio constant or even lower it while at the same time increasing soil-air $pO_2$, resulting in a higher production of carbohydrates above ground and a higher respiration capacity below ground. This increases the $pO_2$ level where the optimum for NPP is being reached while increasing the NPP at the optimum as well—vice versa for decreasing levels of atmospheric $CO_2$.

## 9 | CONCLUDING REMARKS

Plants, like nearly all other eukaryotes, need $O_2$ for long-term survival. $O_2$ is used for the aerobic respiration that provides plants with the energy needed for biosynthesis, cellular maintenance and nutrient uptake. The respiration rate of plant roots depends on the surrounding pressure of $O_2$, and the point at which the rate of respiration is negatively affected may be only a few kPa below pre-industrial atmospheric levels (21.2 kPa). If $O_2$ decreases below a certain threshold, the energy output from root respiration will be insufficient for prolonged plant survival. Previous work on the $O_2$ cycle has largely overlooked the importance of the $O_2$-dependent respiration rate and the minimum $pO_2$ requirements of plants. Nonetheless, these factors are highly relevant for biogeochemical models and can help to constrain atmospheric $pO_2$ through time. For example, the minimum $pO_2$ requirement for long-term plant survival can be used to determine minimum levels of atmospheric $pO_2$ through time: fossil conifer-like archaeopterid root systems from the Middle Devonian (388–383 Ma) may suggest that $O_2$ pressures exceeded well above $13.6 \pm 2.2$ (1 $SD$) kPa during this time, with our root model suggesting atmospheric $O_2$ minimum levels of $18.2 \pm 1.9$ kPa (1 $SD$) for optimal growth. The absence of large and deeply penetrating roots prior to the Middle Devonian may have been related to low atmospheric $O_2$ pressures, but it is just as likely that the early evolution of roots reflects structural plant evolution rather than available soil $O_2$. We have proposed a positive feedback mechanism involving atmospheric $pO_2$, root intensity and plant NPP that can be incorporated into biogeochemical models. Together with the negative feedback mechanisms of fire and the Warburg effect, the positive feedback should result in a $pO_2$ optimum for global NPP possibly near modern levels. The strength of the positive feedback, however, still needs to be quantified, through months-long physiological growth experiments with different plant groups, preferably at different stages of their life-cycle.

## ORCID

*Fredrik Sønderholm* https://orcid.org/0000-0002-5861-9549
*Christian J. Bjerrum* https://orcid.org/0000-0002-7804-1633

## REFERENCES

Algeo, T. J., & Scheckler, S. E. (1998). Terrestrial-marine teleconnections in the Devonian: Links between the evolution of land plants, weathering processes, and marine anoxic events. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *353*(1365), 113–130.

Armstrong, J., & Armstrong, W. (2009). Record rates of pressurized gasflow in the great horsetail, Equisetum telmateia. Were Carboniferous Calamites similarly aerated? *The New Phytologist*, *184*(1), 202–215.

Armstrong, W., & Beckett, P. M. (1985). Root aeration in unsaturated soil - A multi-shelled mathematical-model of oxygen diffusion and distribution with and without sectoral wet-soil blocking of the diffusion path. *The New Phytologist*, *100*(3), 293–311.

Armstrong, W., & Beckett, P. M. (1987). Internal aeration and the development of stelar anoxia in submerged roots - A multishelled mathematical-model combining axial diffusion of oxygen in the cortex with radial losses to the stele, the wall layers and the rhizosphere. *The New Phytologist*, *105*(2), 221–245.

Armstrong, W., & Drew, M. (2002). Root growth and metabolism under oxygen deficiency. In Y. Waisel, A. Eshel, T. Beeckman, & U. Kafkafi (Eds.), *Plant roots: The hidden half* (pp. 729–761). Marcel Dekker.

Armstrong, W., Webb, T., Darwent, M., & Beckett, P. M. (2009). Measuring and interpreting respiratory critical oxygen pressures in roots. *Annals of Botany*, *103*(2), 281–293.

Atkin, O. K., & Tjoelker, M. G. (2003). Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science*, *8*(7), 343–351.

Bar-On, Y. M., Phillips, R., & Milo, R. (2018). The biomass distribution on Earth. *Proceedings of the National Academy of Sciences*, *115*(25), 6506–6511.

Bartholomeus, R. P., Witte, J.-P.-M., van Bodegom, P. M., van Dam, J. C., & Aerts, R. (2008). Critical soil conditions for oxygen stress to plant roots: Substituting the Feddes-function by a process-based model. *Journal of Hydrology*, *360*(1–4), 147–165.

Beerling, D. J., & Berner, R. A. (2005). Feedbacks and the coevolution of plants and atmospheric $CO_2$. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(5), 1302–1305.

Beerling, D. J., Woodward, F. I., Lomas, M. R., Wills, M. A., Quick, W. P., & Valdes, P. J. (1998). The influence of carboniferous palaeoatmospheres on plant function: An experimental and modelling assessment. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *353*(1365), 131–139.

Belcher, C. M., & McElwain, J. C. (2008). Limits for combustion in low $O_2$ redefine paleoatmospheric predictions for the Mesozoic. *Science*, *322*(5899), 192.

Ben-Noah, I., & Friedman, S. P. (2018). Review and evaluation of root respiration and of natural and agricultural processes of soil aeration. *Vadose Zone Journal*, 17(1), 1–47

Bergman, N. M., Lenton, T. M., & Watson, A. J. (2004). COPSE: A new model of biogeochemical cycling over Phanerozoic time. *American Journal of Science*, 304(5), 397–437.

Berner, R. A. (1999). A new look at the long-term carbon cycle. *GSA Today*, 9(11), 1–6.

Bjerrum, C. J. (2021). *cjbjerrum/PaleoO2_RootSoil: First stable release of PalO2_RootSoil*. https://doi.org/10.5281/zenodo.4495296

Boynton, D., DeVilliers, J., & Reuther, W. (1938). Are there different critical oxygen concentrations for the different phases of root activity? *Science*, 88(2294), 569–570.

Brady, N. C. (1990). *The nature and properties of soils*. Macmillan Publishing Company.

Breecker, D., Sharp, Z., & McFadden, L. D. (2009). Seasonal bias in the formation and stable isotopic composition of pedogenic carbonate in modern soils from central New Mexico, USA. *Geological Society of America Bulletin*, 121(3–4), 630–640.

Brugger, J., Hofmann, M., Petri, S., & Feulner, G. (2019). *Model output for the publication: "On the sensitivity of the Devonian climate to continental configuration, vegetation cover, orbital configureation, $CO_2$ concentration and insolation"*. Stefan Petri's Publications.

Campbell, G. S. (1985). *Soil physics with BASIC: Transport models for soil-plant systems*. Elsevier.

Chaloner, W. G. (1989). Fossil charcoal as an indicator of palaeoatmospheric oxygen level. *Journal of the Geological Society*, 146, 171–174.

Cook, F. (1995). One-dimensional oxygen diffusion into soil with exponential respiration: Analytical and numerical solutions. *Ecological Modelling*, 78(3), 277–283.

Cook, F., & Knight, J. (2003). Oxygen transport to plant roots. *Soil Science Society of America Journal*, 67(1), 20–31.

Cope, M., & Chaloner, W. (1980). Fossil charcoal as evidence of past atmospheric composition. *Nature*, 283(5748), 647.

Crawford, R. (1992). Oxygen availability as an ecological limit to plant distribution. *Advances in Ecological Research*, 23, 93–185.

D'Antonio, M. P., Ibarra, D. E., & Boyce, C. K. (2020). Land plant evolution decreased, rather than increased, weathering rates. *Geology*, 48(1), 29–33.

Dahl, T. W., & Arens, S. K. (2020). The impacts of land plant evolution on Earth's climate and oxygenation state–An interdisciplinary review. *Chemical Geology*, 547, 119665.

de Willigen, P., & van Noordwijk, M. (1987). *Roots, plant production and nutrient use efficiency*. Universiteit te Wageningen.

Driese, S. G., Mora, C. I., & Elick, J. M. (1997). Morphology and taphonomy of root and stump casts of the earliest trees (Middle to Late Devonian), Pennsylvania and New York, USA. *Palaios*, 12(6), 524–537.

Edwards, G., & Walker, D. (1983). *C3, C4: Mechanisms, and cellular and environmental regulation, of photosynthesis* (p. 541). University of California Press.

Fierer, N., Colman, B. P., Schimel, J. P., & Jackson, R. B. (2006). Predicting the temperature dependence of microbial respiration in soil: A continental-scale analysis. *Global Biogeochemical Cycles*, 20(3), 1–10.

Geigenberger, P. (2014). Adaptation of storage metabolism to oxygen deprivation. In J. T. Van Dongen, & F. Licausi (Eds.), *Low-oxygen stress in plants* (vol. 21, pp. 223–244). Springer.

Glasspool, I. J., Scott, A. C., Waltham, D., Pronina, N., & Shao, L. Y. (2015). The impact of fire on the Late Paleozoic Earth system. *Frontiers in Plant Science*, 6, 756.

Hopkins, W. G. (1999). *Introduction to plant physiology*, 2nd ed. John Wiley and Sons.

Ibarra, D. E., Rugenstein, J. K. C., Bachan, A., Baresch, A., Lau, K. V., Thomas, D. L., Lee, J.-E., Boyce, C. K., & Chamberlain, C. P. (2019).

Modeling the consequences of land plant evolution on silicate weathering. *American Journal of Science*, 319(1), 1–43.

Jackson, R., Canadell, J., Ehleringer, J. R., Mooney, H., Sala, O., & Schulze, E. D. (1996). A global analysis of root distributions for terrestrial biomes. *Oecologia*, 108(3), 389–411.

Kenrick, P., & Strullu-Derrien, C. (2014). The origin and early evolution of roots. *Plant Physiology*, 166(2), 570–580.

Kozlowski, T. (1985). Soil aeration, flooding, and tree growth. *Journal of Arboriculture*, 11(3), 85–96.

Krause, A. J., Mills, B. J. W., Zhang, S., Planavsky, N. J., Lenton, T. M., & Poulton, S. W. (2018). Stepwise oxygenation of the Paleozoic atmosphere. *Nature Communications*, 9, 1–10.

Kump, L. (1988). Terrestrial feedback in atmospheric oxygen regulation by fire and phosphorus. *Nature*, 335(6186), 152.

Lambers, H., Chapin, F. S. III, & Pons, T. L. (2008). *Plant physiological ecology*. Springer Science & Business Media.

Lenton, T. M. (1998). *Redfields green ocean: A geophysical model of marine nitrate, phosphate and atmospheric oxygen regulation*. University of East Anglia.

Lenton, T. M., Daine, S. J., & Mills, B. J. W. (2018). COPSE reloaded: An improved model of biogeochemical cycling over Phanerozoic time. *Earth-Science Reviews*, 178, 1–28.

Lenton, T. M., & Watson, A. J. (2000). Redfield revisited 2. What regulates the oxygen content of the atmosphere? *Global Biogeochemical Cycles*, 14(1), 249–268.

Melillo, J. M., McGuire, A. D., Kicklighter, D. W., Moore, B., Vorosmarty, C. J., & Schloss, A. L. (1993). Global climate change and terrestrial net primary production. *Nature*, 363(6426), 234.

Meyer-Berthaud, B., & Decombeix, A. L. (2007). Palaeobotany - A tree without leaves. *Nature*, 446(7138), 861–862.

Meyer-Berthaud, B., Decombeix, A. L., & Ermacora, X. (2013). Archaeopterid root anatomy and architecture: new information from permineralized specimens of famennian age from anti-atlas (Morocco). *International Journal of Plant Sciences*, 174(3), 364–381.

Meyer-Berthaud, B., Scheckler, S. E., & Wendt, J. (1999). Archaeopteris is the earliest known modern tree. *Nature*, 398(6729), 700.

Mintz, J. S., Driese, S. G., & White, J. D. (2010). Environmental and ecological variability of middle Devonian (Givetian) forests in Appalachian basin paleosols, New York, United States. *Palaios*, 25(2), 85–96.

Montoya, M., Griesel, A., Levermann, A., Mignot, J., Hofmann, M., Ganopolski, A., & Rahmstorf, S. (2005). The earth system model of intermediate complexity CLIMBER-3α. Part I: Description and performance for present-day conditions. *Climate Dynamics*, 25(2–3), 237–263.

Morris, J. L., Puttick, M. N., Clark, J. W., Edwards, D., Kenrick, P., Pressel, S., Wellman, C. H., Yang, Z., Schneider, H., & Donoghue, P. C. (2018). The timescale of early land plant evolution. *Proceedings of the National Academy of Sciences*, 115(10), E2274–E2283.

Päpke, C., Ramirez-Aguilar, S., & Antonio, C. (2014). Oxygen consumption under hypoxic conditions. In J. T. Van Dongen, & F. Licausi (Eds.), *Low-oxygen stress in plants* (vol. 21, pp. 185–208). Springer.

Quirk, J., Leake, J. R., Johnson, D. A., Taylor, L. L., Saccone, L., & Beerling, D. J. (2015). Constraining the role of early land plants in Palaeozoic weathering and global cooling. *Proceedings. Biological Sciences / The Royal Society*, 282(1813), 20151115.

Remy, W., Taylor, T. N., Hass, H., & Kerp, H. (1994). Four hundred-million-year-old vesicular arbuscular mycorrhizae. *Proceedings of the National Academy of Sciences*, 91(25), 11841–11843.

Rosing, M. T., Bird, D. K., Sleep, N. H., & Bjerrum, C. J. (2010). No climate paradox under the faint early Sun. *Nature*, 464(7289), 744–747.

Rubinstein, C. V., Gerrienne, P., De La Puente, G., Astini, R., & Steemans, P. (2010). Early middle Ordovician evidence for land plants in Argentina (eastern Gondwana). *The New Phytologist*, 188(2), 365–369.

Schachat, S. R., Labandeira, C. C., Saltzman, M. R., Cramer, B. D., Payne, J. L., & Boyce, C. K. (2018). Phanerozoic $pO_2$ and the early evolution of terrestrial animals. *Proceedings of the Royal Society B*, *285*, 1–9.

Scheckler, S. E. (2006). *Devonian forest expansion increased land-based trophic capacity and food web connections*. Geological Society of America, Abstracts with Programs, *38*(340).

Scotese, C. (2016). *PALEOMAP PaleoAtlas for GPlates and the PaleoData Plotter Program*. PALEOMAP Project.

Scott, A. C., & Glasspool, I. J. (2006). The diversification of Paleozoic fire systems and fluctuations in atmospheric oxygen concentration. *Proceeding of the National Academy of Sciences of the United States of America*, *103*(29), 10861–10865.

Waisel, Y., Eshel, A., Beeckman, T., & Kafkafi, U. (2002). *Plant roots: The hidden half*. Marcel Dekker.

Wösten, J. (1997). *Pedotransfer functions to evaluate soil quality, developments in soil science* (vol. 25, pp. 221–245). Elsevier.

Wösten, J., Veerman, G., de Groot, W., & Stolte, J. (2001). *Water Retention and Conductivity Characteristics of Upper and Deeper Soil Layers in the Netherlands*. Alterra Report, *153*.

Wynn, J. G., Bird, M. I., & Wong, V. N. (2005). Rayleigh distillation and the depth profile of 13C/12C ratios of soil organic carbon from soils of disparate texture in Iron Range National Park. *Far North Queensland, Australia: Geochimica Et Cosmochimica Acta*, *69*(8), 1961–1973.

Yapp, C. J., & Poths, H. (1994). Productivity of pre-vascular continental biota inferred from the Fe (CO3) OH content of goethite. *Nature*, *368*(6466), 49.

Yiotis, C., Gerald, C. E. F., & McElwain, J. C. (2017). Differences in the photosynthetic plasticity of ferns and Ginkgo grown in experimentally controlled low $O_2$: $CO_2$ atmospheres may explain their contrasting ecological fate across the Triassic-Jurassic mass extinction boundary. *Annals of Botany*, *119*(8), 1385–1395.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.