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ORIGINAL PAPER

Metabolic scaling theory in plant biology and the three oxygen paradoxa of aerobic life

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Abstract Alfred Russell Wallace was a field naturalist with a strong interest in general physiology. In this vein, he wrote that oxygen (O_2), produced by green plants, is "the food of protoplasm, without which it cannot continue to live". Here we summarize current models relating body size to respiration rates (in the context of the metabolic scaling theory) and show that oxygen-uptake activities, measured at 21 vol.% O_2, correlate closely with growth patterns at the level of specific organs within the same plant. Thus, whole plant respiration can change ontogenetically, corresponding to alterations in the volume fractions of different tissues. Then, we describe the evolution of cyanobacterial photosynthesis during the Paleoarchean, which changed the world forever. By slowly converting what was once a reducing atmosphere to an oxidizing one, microbes capable of O_2-producing photosynthesis modified the chemical nature and distribution of the element iron (Fe), slowly drove some of the most ancient prokaryotes to extinction, created the ozone (O_3) layer that subsequently shielded the first terrestrial plants and animals from harmful UV radiation, but also made it possible for Earth's forest to burn, sometimes with catastrophic consequences. Yet another paradox is that the most abundant protein (i.e., the enzyme Rubisco, Ribulose-1,5-biphosphate carboxylase/oxygenase) has a greater affinity for oxygen than for carbon dioxide (CO_2), even though its function is to bind with the latter rather than the former. We evaluate this second "oxygen paradox" within the context of photorespiratory carbon loss and crop yield reduction in C3 vs. C4 plants (rye vs. maize). Finally, we analyze the occurrence of reactive oxygen species (ROS) as destructive by-products of cellular metabolism, and discuss the three "O_2-paradoxa" with reference to A. R. Wallace's speculations on "design in nature".

Keywords Alfred Russell Wallace · Design · Oxygen paradox · Photorespiration · Reactive oxygen species · Rubisco · Metabolic scaling theory · Wildfires

Introduction

Three and a half centuries ago, the British chemist Robert Boyle (1627–1691) observed that insects die when they are cultivated in a closed chamber, similar to the extinction of a burning candle. Accordingly, Boyle (1660) suggested that respiration and combustion may be related processes. Only 14 years later, the physician John Mayow (1645–1679) discovered that animals, such as house mice, likewise rapidly die in the absence of a flow of fresh air (i.e., in a closed glass container). He concluded that the air we breathe contains a life-supporting component that is transported via the blood stream and maintains the motions of muscles and the heart (Mayow 1674). However, it took 100 years of additional research efforts until the animal–plant relationships with respect to organismal gas exchanges were discovered (Höxtermann and Hilger 2007).

This article is a contribution to the Special issue Alfred Russel Wallace (1823–1913): The man in the shadow of Charles Darwin—Guest Editors U. Kutschera, U. Hossfeld.

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In a series of elegant experiments, the British scientist Joseph Priestley (1733–1804) elucidated a "mouse-peppermint" interaction that led him to conclude that, in the light, plants display a gas exchange pattern opposite to that of animals. Moreover, he argued that the green sessile organisms "improve" the bad air, so that animals can stay alive in a closed container (Priestley 1774, 1775). Later, the German botanists Julius Sachs (1823–1897) and Wilhelm Pfeffer (1845–1920) summarized the experimental evidence available at that time and concluded that green plants, like animals, are oxygen (O_2)-dependent (aerobic) organisms, although, in the presence of light, they release O_2 via photosynthesis, and, concomitantly, take up carbon dioxide (CO_2) (Sachs 1865, 1882; Pfeffer 1897/1904). However, Sachs and Pfeffer published their findings in German and their books were written for professional botanists and not for the general reader. As a result, their findings remained largely unknown outside the world of German plant physiologists. In contrast, the British naturalist Alfred Russell Wallace (1823–1913) was one of the first to write popular science books that covered not only natural history (the geographical distribution and evolution of animals, etc.), but also topics drawn from the much less comprehensible field of physiology (Fig. 1).

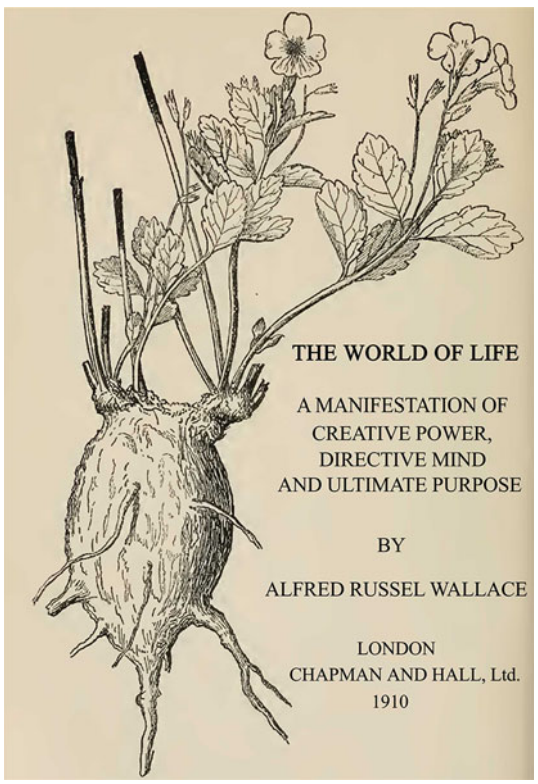

Fig. 1 The title page of Alfred Russel Wallace's book *The World of Life*, illustrated with the drawing of a plant, reproduced from chapter X of this monograph (adapted from Wallace 1910)

In this article, we first summarize the conclusions of Wallace (1903, 1910) concerning the significance of atmospheric oxygen for the life of animals and plants. We then describe the principles and methods for the analysis of organ-specific rates of cellular respiration in plants, and present unpublished data to illustrate our view of the metabolic scaling theory (Kutschera and Niklas 2011, 2012). Finally, we describe the three "oxygen paradoxa" of organic life and discuss the naturalistic "design argument" of Wallace (1903, 1910) in the light of more recent findings.

Alfred Russell Wallace and oxygen as the food of protoplasm

Alfred Wallace was a polymath—a field biologist, a physiologist, a botanist, and an ecologist (Kutschera 2013). In his monograph *Man's Place in the Universe*, the 80-year-old naturalist defended his thesis that "Our earth is the only habitable planet … in the Solar System (and) the whole stellar universe" (Wallace 1903). In Chapter X, entitled "The essential characters of living organisms", he referred to the work of the British physiologist John S. Burdon-Sanderson (1828–1905) and quoted his definition of life: "The most distinctive peculiarity of living matter as compared with non-living is, that it is ever changing while ever the same". With reference to the publications of Thomas H. Huxley (1825–1895), Wallace (1903) argued that the physical basis of life is protoplasm. Thereafter, the botanist Wallace (1903) described the process of photosynthesis as follows: "The leaves of plants absorb carbonic acid gas from the atmosphere, and … chlorophyll, from which they derive their green color, has the power, under the influence of sunlight, to decompose it using the carbon to build up its own structure and giving out the oxygen" (Wallace 1903, p. 196–197). Based on these insights, the experienced ecologist argued that "We *could* have plants without animals; we could *not* have animals without plants" (Wallace 1903, p. 198).

With respect to the importance of oxygen, he wrote that "Plants as well as animals continually absorb oxygen from the atmosphere, … oxygen is … the food of protoplasm, without which it cannot continue to live" (Wallace 1903, p. 199). In Chapter XI, he summarized "The physical conditions essential for organic life". With respect to the gases of the atmosphere, he argued that "Oxygen is the one great essential for animal life" (Wallace 1903, p. 212). Finally, in Chapter XIII, entitled "The earth in relation to life: atmospheric conditions", the biologist summarized his views on general physiology as follows: "The physical basis of life—protoplasm—consists of the four elements, oxygen, nitrogen, hydrogen and carbon, and … both plants

and animals depend largely upon the free oxygen in the air to carry on their vital processes" (Wallace 1903, p. 213).

In his speculative Chapter XVI (entitled "Conclusion"), Wallace discussed "evolution versus design". On the one hand, he argued that "continuous evolution … must have occurred" (Wallace 1903, p. 216). However, on the other hand, he wrote "… it [evolution] is not in perfect harmony with this grandeur of design (if it be design), this vastness of scale …, that the material universe needed to produce this cradle of organic life, … of complexity, of beauty?" (Wallace 1903, p. 321). In his subsequent book, *The World of Life*, Wallace (1910) extended these considerations and provided further arguments for his "design proposals" (Fig. 1). We will discuss these speculations in the concluding section of this article and evaluate Wallace's concepts in the light of the ongoing "Intelligent Design (ID) debate" (Matzke 2010; Scott 2010). In his popular books, Wallace (1903, 1910) did not describe the discovery of oxygen and the methods to quantify metabolic activity. These topics are discussed in the next section.

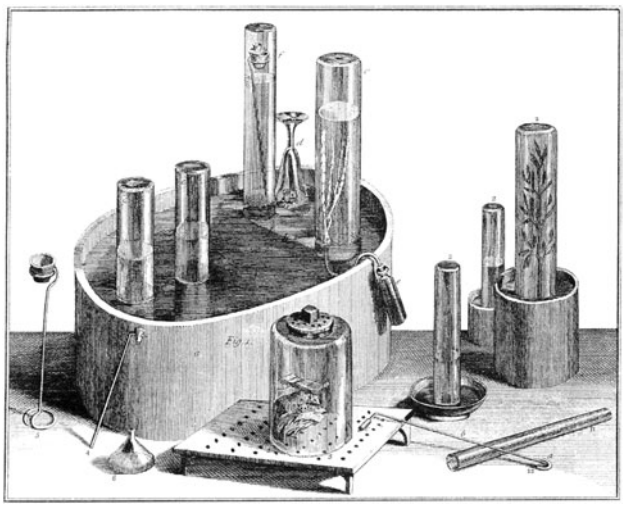

Fig. 2 The experiments of Joseph Priestley, which led to the discovery of the fact that atmospheric oxygen (O_2) is depleted in closed containers wherein a living animal (mouse, etc.) is kept, and the positive effect of green plants on the quality of the air (adapted from Priestley 1774)

From Priestley's different kinds of air to the oxygen electrode

As mentioned in "Introduction", the British chemist Joseph Priestley was a pioneer in the experimental analysis of the importance of air for animals and plants. Moreover, he was one of the discoverers of the chemical element oxygen (oxygenium) (O) (Schofield 2004). In this section, we briefly summarize the most important insights into the work of Priestley (1774, 1775), with special reference to his hypothesis concerning the negative effect of pure oxygen on living organisms (Fig. 2), and we summarize the principles for the quantification of oxygen uptake based on the use of O_2 electrodes.

In the first volume of his work entitled *Experiments and Observations on Different Kinds of Air*, Priestley concluded that "Plants are capable of perfectly restoring air injured by respiration" (Priestley 1774, p. 92). However, much deeper insights were articulated in the second volume of his important work. In section V, entitled "Miscellaneous Observations on the Properties of Dephlogisticated Air", Priestley proposed that oxygen may have a negative effect on humans and animals. Therein, Priestley wrote that "… as a candle burns out much faster in dephlogisticated air than in common air, so we (humans) might, as may be said, *live out too fast*, and the animal powers be too soon exhausted in this pure kind of air" … He concluded this section with the statement that "A moralist … may say that the air which nature has provided for us is as good as we deserve" (Priestley 1775, p. 101).

The simple methods used by Priestley (1774, 1775) (Fig. 2) were very much improved by Sachs (1865, 1882), Pfeffer (1897/1904), and other 20th century physiologists (e.g., Kleiber 1932, 1961). However, precise measurements of O_2 exchange in living systems were made possible only with the invention of the polarographic oxygen (O_2) electrode by Clark et al. (1953). The structure and mode of action of a typical "Clark oxygen electrode" are shown in Fig. 3a. Leland Clark (1918–2005) (Antioch College, Ohio) developed the oxygen electrode in response to the rejection of his manuscript dealing with his invention of a bubble oxygenator to be used in cardiac surgery. The rejection of the manuscript was based on the fact that, at the time, the oxygen tension in blood coming out of the bubble oxygenator could not be measured. Clark's oxygen electrode measures electron flow to oxygen as a result of oxidative phosphorylation (rendered as $O_2 + 2H^+ + 2e^- \rightarrow H_2O_2$). The electrode compartment is isolated from a reaction chamber by a thin Teflon membrane that is permeable to molecular oxygen and allows O_2 to reach a cathode, where it is electrolytically reduced. In turn, this reduction permits a current to flow. The potential difference generated by the process is proportional to O_2 activity, provided the solution is stirred constantly to minimize the effects of an unstirred boundary layer over the membrane (Walker 1990). A simple device to quantify the rate of O_2 uptake of living samples, such as leaf tips, is shown in Fig. 3b, and a representative measurement is depicted in Fig. 4. These data are discussed in the next sections.

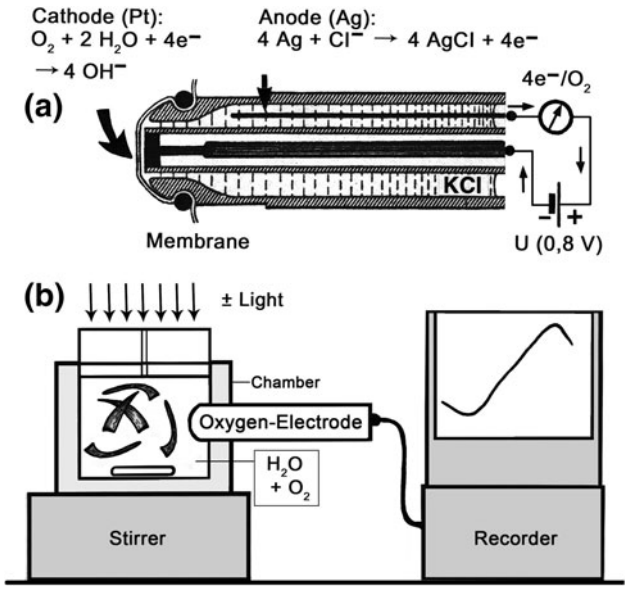

Fig. 3 Principle of the function of a polarographic oxygen (O_2) electrode, filled with potassium chloride solution, for determination of the O_2 concentration in water (**a**). A simple experimental setup for the quantification of the rate of oxygen uptake of pieces of plants (sample in transparent plexiglass container) (**b**) is based on the use of an O_2 electrode

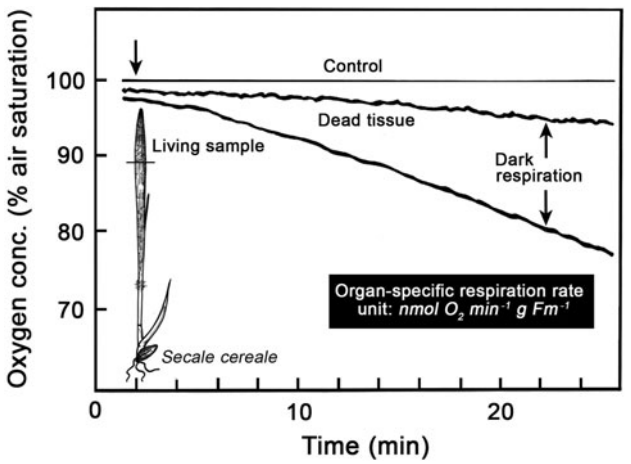

Fig. 4 Representative examples of oxygen (O_2)-depletion curves and the principle of calculation of organ-specific rates of O_2 uptake in darkness. Ten sections, 1 cm in length, were cut from the tips of green, 6-day-old rye (*Secale cereale*) seedlings (*inset*). The samples (leaf tips) were incubated in oxygen-saturated water (100 % O_2) and used to record the O_2 depletions with time, measured by use of a Clark-type electrode (see Fig. 3). Control: closed chamber without sample (25 °C)

Organ-specific respiration rates in animals and plants

Eighty years ago, the Swiss-American scientist Max Kleiber (1893–1976) reported that the basal metabolic rates of mammals scale approximately as the 3/4 power of body mass (Kleiber 1932). This scaling relationship is known as "Kleiber's law". However, it is more appropriately the "Pfeffer-Kleiber relationship", because it was the plant biologist Wilhelm Pfeffer, who had explicitly pointed out that "without respiration, there is no life" (Kutschera and Niklas 2009). Moreover, Pfeffer cogently argued for measuring the "specific rate of respiration" per unit "volume of O_2 consumed per h and g fresh mass" (Pfeffer 1897/1904), an idea that was later employed successfully by animal as well as plant physiologists (Glazier 2005) (Fig. 4).

In two recent research papers, we explored the Pfeffer–Kleiber relationship with respect to land plants, a monophyletic lineage of eukaryotic photoautotrophs that contain the same photosynthetic pigments as their closest living relatives, the green algae (Niklas 1997; Niklas and Kutschera 2009, 2010). In these studies, we used seedlings of sunflower (*Helianthus annuus* L.) as a model system to analyze the mechanisms of cellular and organ growth (Kutschera and Niklas 2007, 2011, 2012, 2013). To determine scaling relationships during germination and subsequent development of entire organisms, and for measurements of the changes in the organ-specific rates of cellular respiration in different parts of the juvenile plants, we employed seedlings that were raised for 6 days in darkness or white light, respectively.

Here, we describe our expanded metabolic scaling concept for land plants and illustrate the principles of this theory using data obtained from the primary leaves of rye (*Secale cereale*) seedlings (Fig. 4), which have been used previously to elucidate the mode of coleoptile development, and the mechanism of auxin-mediated organ growth (Kutschera et al. 2010a, Niklas and Kutschera 2012).

In order to determine the organ-specific rates of cell respiration, leaf sections measuring 1 cm in length were cut from the tip of 6-day-old rye seedlings raised for 3 days in darkness and thereafter irradiated for another 3 days with continuous white light. Ten sections were placed into the chamber of the oxygen-measuring device (Fig. 3b), and the change in O_2 concentration of the water (initial value: 100 %) was measured over the course of 20 min. Killed (frozen–thawed) samples were used as a control. As shown in Fig. 4, the organ-specific respiration rate of these green, de-etiolated leaf tips can be quantified and expressed in units of nmol O_2 min^{-1} g fresh $mass^{-1}$, as advised by Pfeffer (1897/1904).

The representative measurements shown in Fig. 5 document that 6-day-old etiolated samples lacking chlorophyll display the same rate of cell respiration as green leaf tips (232 ± 8 vs. 236 ± 6 nmol O_2 consumption min^{-1} g fresh $mass^{-1}$, respectively; $n = 6$ for both sets of experiments). Hence, the rate of oxygen uptake in darkness (cell respiration) is not affected by the greening response of the organ (i.e., chloroplast development, accompanied by the

accumulation of chlorophylls $a + b$ and carotenoids), at least in 6-day-old rye seedlings.

What remains of "Kleiber's law" with respect to the land plants?

Using the methods described in Figs. 3, 4 and 5, we determined the organ-specific rates of cell respiration in developing sunflower seedlings (Kutschera and Niklas 2011, 2012). We found that the metabolic rates of the cotyledons, cotyledonary hook, hypocotyl, and the roots of developing seedlings raised in darkness (skotomorphogenesis) and in white light (photomorphogenesis) differ by a factor of two to five, and are largely independent of light treatment. The organ-specific respiration rate (oxygen uptake min^{-1} g fresh $mass^{-1}$) of the cotyledonary hook, which consists of cells with densely packaged cytoplasm, is much higher than that of the hypocotyl, an organ that contains many more extensively vacuolated cells (ca. 480 vs. 120 nmol O_2 consumption min^{-1} g fresh $mass^{-1}$ in the hypocotyls of 3-day-old etiolated sunflower seedlings). Data for cell length, cell density, and DNA content further reveal that (1) cell elongation resulting in the opening of the cotyledonary hook is stimulated by white light on the inside of the curved organ, (2) respiration, cell density and DNA content are much higher in the hook than in the hypocotyl, and (3) organ-specific respiration rates and the DNA contents of tissues are statistically significantly correlated. We hypothesized that the metabolic heterogeneity of the plant body is a consequence of differences in the DNA content and the vacuolization of different cell and tissue types.

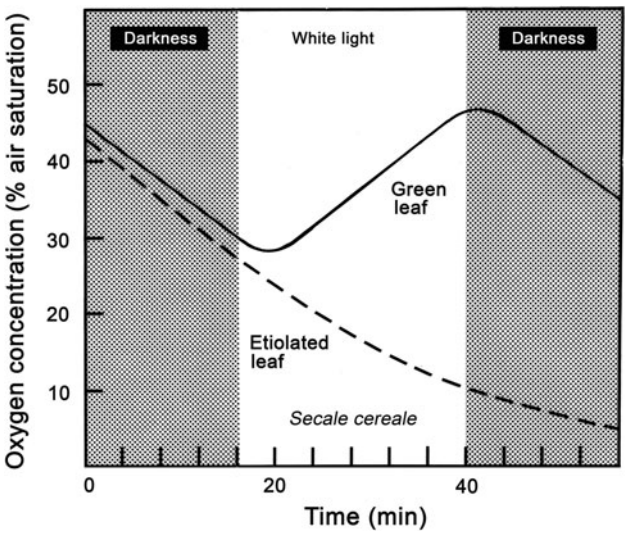

Fig. 5 Documentation of dark respiration and oxygenic photosynthesis in primary leaves of rye (*Secale cereale*) seedlings. Representative examples of oxygen (O_2)-depletion and O_2-enrichment curves, measured in water. Ten leaf sections, cut from green or etiolated rye seedlings, were incubated in darkness as described in Fig. 4. After 16 min, the chamber (Fig. 3b) was irradiated with continuous white light (100 µmol photons m^{-2} s^{-1}), and, after 40 min, again placed into darkness (25 °C)

The data reported here are consistent with this hypothesis. As a consequence, Kleiber's law, as deduced using the mammal body plan (Kleiber 1932, 1961) as a model system, cannot be applied to embryophytes without significant modification. In plants, we hypothesized that this "law" likely reflects a scaling relationship emerging from the manner in which the metabolically active protoplasmic contents of cells and tissues change over the course of ontogeny and across species with volumetrically different cell and tissue compositions. This hypothesis is consistent with a subsequent theoretical treatment of how cell surface-to-volume relationships are affected by external crenulations and internal surfaces, such as vacuoles (Okie 2013). It is also consistent with the notion that DNA content is a reasonably accurate reflection of mRNA and protein synthesis modulated by TOR feedback systems (see John et al. 2011).

In our oxygen-uptake experiments, water was saturated with a stream of air that contains the current level of ca. 21 vol.% of atmospheric O_2. However, as suggested by Wallace (1903, 1910), the living conditions for organisms on the planet Earth have changed over the course of geological time (millions of years). Today we know that, during the early evolution of life on Earth, this oxidizing atmosphere slowly developed, due to the metabolic activity of certain prokaryotic cyanobacteria-like microorganisms. This topic is discussed in the next section.

The evolution of the oxidizing atmosphere and its consequences

The available evidence indicates that Earth's earliest atmosphere was reducing and lacked measureable quantities of oxygen. The most ancient evidence of prokaryotic, presumably anaerobic, life forms is from the Paleoarchean (3,600 to 3,200 million years ago, mya). Circumstantial evidence suggests that microbially laminated stromatolites and filamentous (cyanobacteria-like) microbes may have been photosynthetic organisms (Schopf 1993, 2006, 2011). However, with the evolution of prokaryotes capable of oxygenic (i.e., O_2-producing) photosynthesis (indicated by cyanobacterial biomarkers and steranes dated between 2,700 and 2,600 mya), Earth's atmosphere slowly transitioned from a reducing to an oxidizing one (Fig. 6). This key event is indicated by a decline in banded iron (Fe) ore formations (i.e., laminated rock formations containing iron oxides); Fe is the fourth most common chemical element,

by mass, on the planet. Moreover, the gradual disappearance of detrital uraninite, siderite, and pyrite (all of which are unstable in aerated water), and changes in sulfur isotopes, which occurred between 2,450 and 2,200 mya, provide additional evidence for this transitioning in Earth's atmospheric composition (Schopf 2006, 2011; Johnson et al. 2013).

After the evolutionary development of the first eukaryotic cells via symbiogenesis (~1,800 mya), the ecological expansion of multicellular eukaryotes such as red (e.g., *Bangiomorpha*, ~1,200 mya), green (e.g., *Caryosphaeroides*, ~830 mya), and brown (e.g., *Vendotaenia*, ~540 mya) algae accelerated the oxygenation of the oceans and subsequently of the atmosphere (Niklas 1997; Kutschera 2009, 2011; Kutschera and Niklas 2004, 2005, 2008; Johnson et al. 2013; Noffke et al. 2013). This early form of "air pollution" resulted in the elimination of many ancient obligate anaerobic prokaryotes. While the descendants of the first forms of eukaryotic life continued to evolve and radiate during a two-billion year period to achieve global dominion, many forms of ancient organisms were driven to extinction or relegated to extreme microhabitats in the form of today's extremophiles (the Archaea; Cavalier-Smith 2010).

The presence of free atmospheric oxygen (O_2) eventually resulted in the ozone (O_3) layer, which made it possible for plants to colonize the land during the early Paleozoic (~430 mya) without experiencing the negative effects of intense ultraviolet (UV) radiation (Wellman et al. 2003; Niklas and Kutschera 2009, 2010; Niklas and Spatz 2012). The presence of oxygen also made the evolution of multicellular animals possible, which invaded terrestrial habitats ca. 380 mya (Koch and Britton 2008; Kutschera and Elliott 2013). Thus, the evolution of oxygenic photosynthesis dramatically and irreversibly changed Earth's ecosystems and permitted the development of multicellular complexity (Koch and Britton 2008) (Fig. 6).

However, during the Phanerozoic, Earth's atmosphere oxygen levels nevertheless fluctuated and are reported to reach a maximum at approximately 280 mya (late Carboniferous), and a minimum at approximately 180 mya (Berner 2009) (Fig. 7). This fluctuation has had a profound effect on terrestrial ecosystems for two reasons. First, the occurrence of fire, which requires a minimum of 13 % the present-day atmospheric oxygen level (PAL, i.e., ca. 21 vol.% O_2), affects carbon sequestration and, second, charcoalified plant material is much less easily broken down than un-charcoalified material (Schmidt and Noack 2000). Thus, the presence of charcoal, which is a proxy for fire, is an indirect measure of atmospheric oxygen concentrations equal to or exceeding the 13 % PAL, which established an ecological mechanism to sequester atmospheric carbon dioxide. The oldest charcoalified plant remains are reported from the Late Silurian (Prídolí) (Glasspool et al. 2004). However, an analysis of the occurrences of charcoal in progressively younger strata, which track models of PAL fluctuations (Fig. 7), indicates that fires first became widespread in the Middle Mississippian and became ecologically important in the Permian (Scott and Glasspool 2006).

The occurrence of wildfires throughout the history of terrestrial organisms is well documented, notably during the late Carboniferous (oxygen maximum of >30 vol.% O_2), when giant insects existed, and even moist plant material was flammable. These catastrophes, which were induced by lightning and the result of high atmospheric O_2

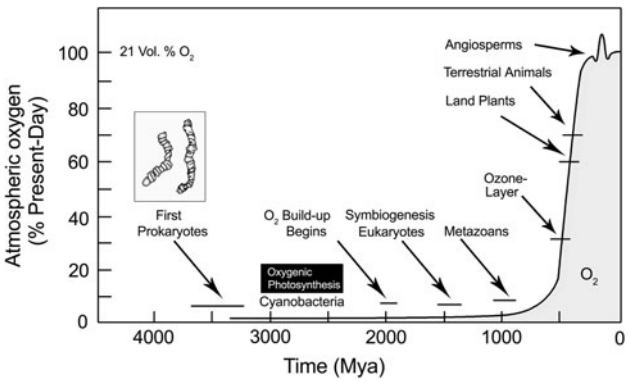

Fig. 6 Changes in the concentration of atmospheric oxygen (O_2) over the past 3,500 million years, and key events in the history of life on the Earth. The oldest known prokaryotic filamentous microfossils that resemble extant cyanobacteria are shown in the *inset*. Note that the early atmosphere was rich in nitrogen gas (N_2) and carbon dioxide (CO_2). Today, the atmosphere consists of ca. 78 vol.% N_2, 21 vol.% O_2 and 0.04 vol.% CO_2. Rubisco, the key enzyme of photosynthetic CO_2 fixation, evolved in ancient cyanobacteria concomitant with the "invention" of oxygenic photosynthesis. *Mya* millions of years ago

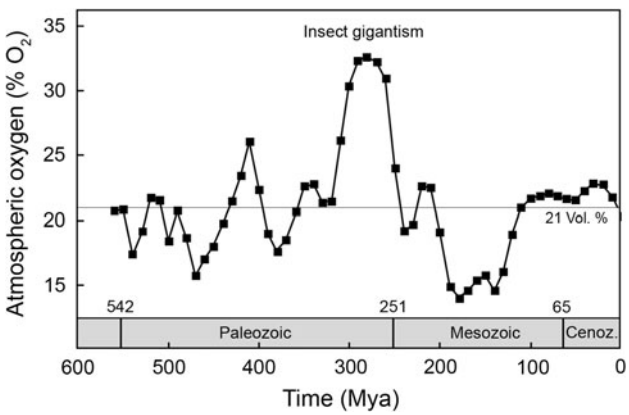

Fig. 7 Changes in the concentration of atmospheric oxygen (O_2) over the past 540 million years, based on revised calculations. Note that during the late Carboniferous the O_2 level reached a maximum of ca. 32 vol.%, concomitantly with the occurrence of giant insects (adapted from Berner 2009). *Mya* millions of years ago

levels, had devastating effects on biotas. The occurrence of destructive wildfires is one of three "paradoxa" of O_2-dependant life. It is obvious that fluctuations in atmospheric oxygen concentrations over the past 500 mya (Fig. 7) have had noticeable and significant effects on the evolution of organisms inhabiting terrestrial ecosystems, as well as the dynamics of Earth's geochemical cycles (Scott and Glasspool 2006; Koch and Britton 2008; Bowman et al. 2009).

Another, negative effect of high atmospheric oxygen levels (ca. 13–30 vol.% O_2, the so-called "fire window") is the occurrence of the phenomenon of photorespiration in the majority of plants. This topic is discussed next.

Photorespiration: atmospheric oxygen and reduced crop yields

Seedlings of rye (*Secale cereale*) have been used for the analysis of auxin-induced growth and their related developmental processes for many years (Kutschera et al. 2010a; Kutschera and Niklas 2012). Here, we document the occurrence of oxygenic photosynthesis in seedlings of this important crop plant. A representative experiment with etiolated vs. green leaf tips, cut from 6-day-old rye seedlings, is depicted in Fig. 5. The samples were incubated in air-saturated water and the changes in oxygen concentration were recorded over a period of 46 min. In etiolated leaf tips, a steady decline in O_2 concentration was observed, which was independent of light treatment. This is in contrast to the situation in de-etiolated (green) samples: upon irradiation with white light, net O_2 consumption rapidly stops and is converted into an accumulation of O_2 in the surrounding water, i.e., oxygenic photosynthesis is activated (average rate 226 ± 8 nmol O_2 production min^{-1} g fresh $mass^{-1}$, $n = 6$). When the light is again turned off, oxygen production ceased and cell respiration continued at the same rate as before (234 ± 6 nmol O_2 consumption min^{-1} g fresh $mass^{-1}$, $n = 6$) (Fig. 5).

In cereal plants characterized by the ancient mode of C3 photosynthesis (ca. 90 % of all angiosperms) (Fig. 6), such as rye (*Secale cereale*), wheat (*Triticum aestivum*), oats (*Avena sativa*), and barley (*Hordeum vulgare*), crop yields of 2.0–2.8 t/ha have been obtained (Fig. 8). This is in contrast to maize (*Zea mays*), a major C4 crop, which provides yields of up to 4.8 t/ha (Fig. 9) (FAO 2007). This difference in dry matter accumulation is to a large extent due to the fact that C3 plants display a high rate of photorespiration. This wasteful process (ca. 25 % loss of assimilated CO_2 at 25 °C) is largely suppressed in the leaves C4 species such as maize (Kutschera and Niklas 2006; Kutschera et al. 2010b; Sage and Zhu 2011; Parry et al. 2013). The occurrence of photorespiration is the consequence of the rise in atmospheric O_2 level over the past 800 mya (Fig. 6).

This strange phenomenon can be described as the "Rubisco-Oxygen paradox". Ribulose-1,5-biphosphate carboxylase/oxygenase (Rubisco) is a chloroplastic enzyme that is involved in the first step of carbon dioxide (CO_2) fixation, i.e., the very abundant leaf protein Rubisco catalyzes the carboxylation of the CO_2-acceptor ribulose-1,5-biphosphate. However, this enzyme has a much higher affinity for oxygen (O_2) than for carbon dioxide (CO_2) (Raven 2013). When oxygen is provided as a substrate, the products of Rubisco's oxygenase catalysis are phosphoglycolate and 3-phosphoglycerate. Phosphoglycolate is recycled through a series of reactions called photorespiration (light-dependent O_2 uptake/CO_2 release), which occur in mitochondria and peroxisomes. Phosphoglycolate is converted into one molecule of carbon dioxide and one molecule of 3-phosphoglycerate, which can enter the Calvin cycle. At ambient atmospheric CO_2 levels (21 vol.% O_2, see Fig. 6), the ratio of carboxylation to oxygenation is roughly 4:1 (Kutschera and Niklas 2006; Parry et al. 2013). This inefficiency reflects the fact that Rubisco evolved at the time when oxygenic photosynthesis originated, and thus when atmospheric O_2 levels were extremely low, and CO_2 levels were high (Fig. 6). Since Rubisco lies at the heart of the chemical reactions of chloroplastic CO_2 fixation, modifications of its molecular architecture would be lethal. Over time, however, oxygenic photoautotrophs have

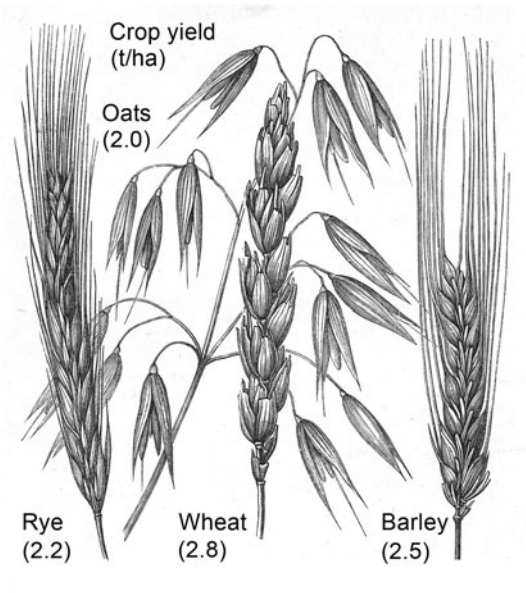

Fig. 8 Average crop yields in cereals that were grown in Europe. Rye (*Secale cereale*), oats (*Avena sativa*), wheat (*Triticum aestivum*) and barley (*Hordeum vulgare*) are C3 plants with an ancient mode of photosynthesis that is characterized by photorespiration (data from FAO 2007)

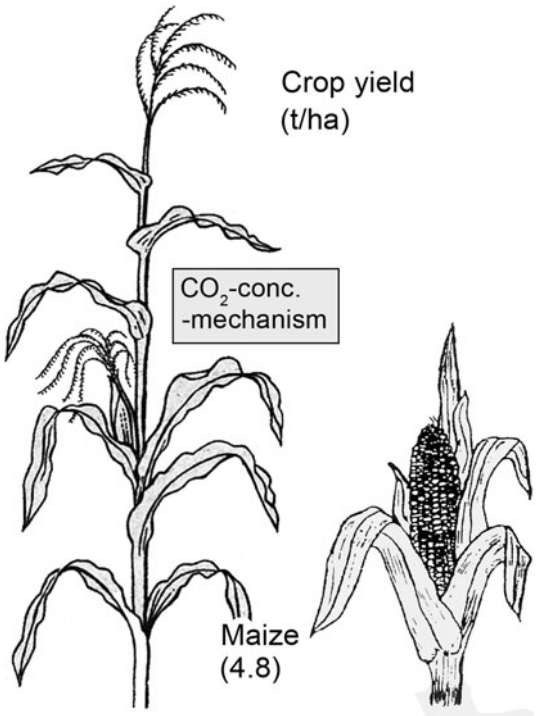

Fig. 9 Maize (*Zea mays*) is a C4 photosynthesizer that displays almost no photorespiration, due to the presence of a specialized mechanism for CO_2 concentration around the chloroplastic enzyme Rubisco. Therefore, it has a higher capacity to fix CO_2 and to produce larger starch-rich kernels, compared with those of the C3 plants depicted in Fig. 8 (data from FAO 2007)

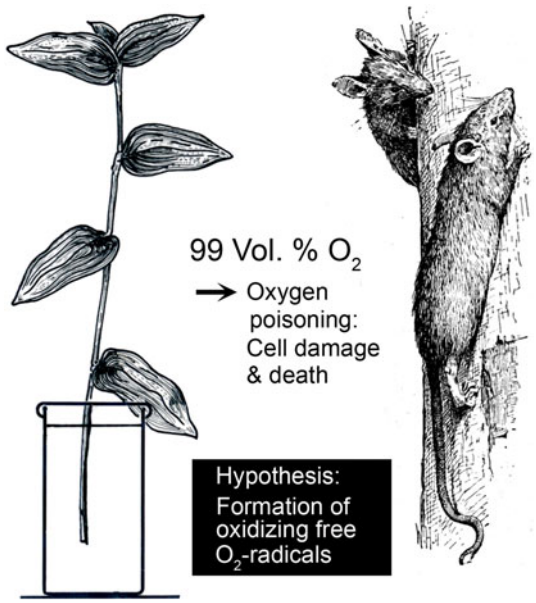

Fig. 10 Summary of the experiments that led to the discovery of oxygen poisoning in the cells of plants (*Tradescantia* sp.) and house mice (*Mus musculus*). The hypothesis (*black box*) published in 1954 was later confirmed by numerous independent studies

evolved modes of increasing CO_2 concentrations around Rubisco, resulting in a drastic reduction of photorespiration. These include C4 carbon fixation in some evolutionary "modern" cereals, such as maize (Fig. 9), and crassulacean acid metabolism in crop plants, such as the cactus (*Opuntia*) and the pineapple (*Ananas*) (Sage and Zhu 2011; Parry et al. 2013; Raven 2013).

The facts summarized in the previous sections show that high levels of O_2 (≥21 vol.%) can cause devastating wildfires and result in photorespiration in C3 plants (and thus losses in crop yields), phenomena we may call the first and second "oxygen paradoxa". In the following section, we describe the third paradox of aerobic life on Earth—the fact that almost all organisms depend on O_2 (as pointed out by Wallace 1910), but that activated oxygen is a potentially toxic substance for much of a cell's normal metabolism (Davies 1995).

Reactive oxygen species and cell damage

Six decades ago, a research team analyzed the effect of diatomic oxygen (O_2) on cell structure and metabolism in land plants (*Tradescantia* sp.) and mammals (*Mus musculus*). When these life forms were treated with pure oxygen (99 vol.% O_2), cell and tissue damage occurred and the organisms died (Gerschman et al. 1954). The basic findings of this discovery of "oxygen poisoning" are summarized in Fig. 10. Moreover, the authors of this seminal study pointed out that, even at ambient O_2 levels (ca. 21 vol.%) (Fig. 7), oxygen may be destructive to cells. Gerschman et al. (1954) attributed these effects to "the formation of oxidizing free radicals". The current status of our knowledge of this third "O_2-paradox" is summarized as follows.

It has long been known that all animals and plants depend on atmospheric oxygen (Sachs 1865, 1881; Pfeffer 1897/1904; Wallace 1903, 1910; see Armstrong and Beckett 2011; Lane and Martin 2010 for recent discussions of this topic). However, in its activated state, atmospheric O_2 is a potentially mutagenic free radical (it has two unpaired electrons) that required the evolution of antioxidant reactions with the appearance of organisms capable of cellular respiration and oxygenic photosynthesis (Davies 1995; Halliwell 2006). In addition, hydrogen peroxide (H_2O_2) can be produced in moist air as a result of ultraviolet light (UV)-mediated O_2 activation. In this regard, the formation of solid banded iron ores (see above) was critical to the survival of many early life forms, since ferrous iron (Fe^{2+}), dissolved at high concentrations in Earth's first oceans, was a sink for oxygen, which was toxic to many ancient forms of prokaryotes. However, Fe^{2+} ions can rapidly react with hydrogen peroxide (H_2O_2) to form

hydroxyl radicals, a process called Fenton chemistry (i.e., $Fe^{2+} + H_2O_2 \rightarrow Fe(III) + OH^{\bullet} + OH^{-}$, where the superscript [•] denotes a free radical), which is toxic to most modern-day organisms. Hydrogen peroxide was probably abundant in Earth's early oceans because, in the absence of an ozone layer, UV light photochemically reacts with H_2O to form H_2O_2. Thus, the first organisms capable of oxygen production must have had some method to deal with the effects of O_2 and H_2O_2.

What might these methods have been? One is suggested by Olson and Blankenship (2004) who postulated that the evolutionary precursor to photosystem II employed not H_2O as a source for electrons, but H_2O_2 as a substrate, and only later evolved the ability to split water (see Johnson et al. 2013 for a more recent hypothesis). Be that as it may, insufficient energy dissipation in modern-day chloroplasts can lead to the formation of the chlorophyll triplet state (i.e., the condition when two electrons in chlorophyll have parallel spins). The triplet state can transfer excitation energy to ground-state O_2 (i.e., the form of oxygen in which both unpaired electrons have parallel spins) to form the singlet state of O_2 (denoted as "singlet oxygen", $^1O_2$), which is toxic because it can oxidize chlorophyll and trigger cell death. The evolution of carotenoids, which are found in cyanobacteria as well as eukaryotic photoautotrophs (embryophytes), likely provided a means to quench the triplet state of chlorophyll and even $^1O_2$ itself (Young 1991; Apel and Hirt 2004).

Plant and animal mitochondria reduce only ca. 98 % of the O_2 they consume into water (H_2O) by means of cytochrome oxidase. As a result, they have to cope with ca. 2 % of toxic, partially reduced oxygen (ROS, reactive oxygen species, such as superoxide, hydrogen peroxide and hydroxyl radicals). These ROSs are produced in mitochondria (Fig. 11), chloroplasts, and peroxisomes, where they act as aggressive mutagenic radicals and cause cellular damage, notably under conditions of stressful environmental conditions (e.g., shortage of water) (Apel and Hirt 2004; Gill and Tuteja 2010). Since it is impossible to add two electrons to O_2 at the same time (Halliwell 2006), cytochrome oxidase removes one electron from each of its four reduced cytochrome *c* molecules (oxidizing them to ferric cytochrome *c*) and adds the four electrons to O_2 to give rise to H_2O. This biochemical "design error" is one reason why mitochondria produce toxic ROS (Fig. 11). It should be noted that plant and animal mitochondria contain uncoupling proteins in their inner membrane that act as anti-oxidants. However, this "damage-control" mechanism is far from perfect (Apel and Hirt 2004; Gill and Tuteja 2010).

The literature on the negative effects of ROS on cell structure and function, inclusive of the involvement of mutagenic O_2 radicals in disease, senescence, aging and death in microbes, animals and plants, is vast. The reader is referred to Decker and van Holde (2010), Torres (2010), Green et al. (2011), Hamilton et al. (2012), Halliwell and Gutteridge (2007), Khanna-Chopra (2012), Lane (2011), Marchal and Van der Leyden (2000), Managhan et al. (2009), Nunnari and Snomalainen (2012), Schloss (2002), Shokolenko et al. (2009), Tanaka et al. (2012), and Widder (2010) for detailed information on additional aspects of this third "O_2-paradox".

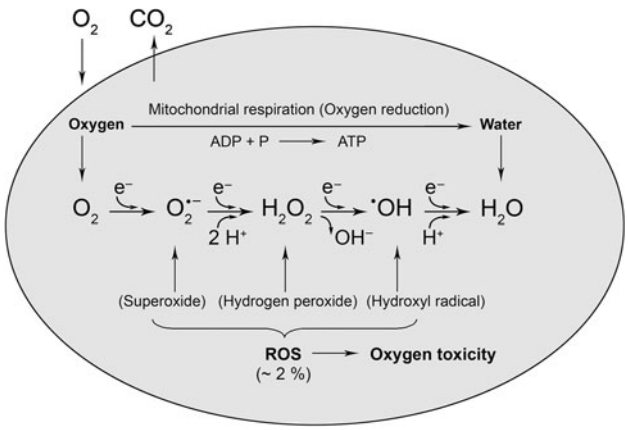

Fig. 11 Scheme illustrating the formation of reactive oxygen species (ROS) as side effect of the imperfect flow of electrons from molecular oxygen (O_2) to water (H_2O) (respiration) within mitochondria of animal and plant cells

Finally, it should be noted that ROS, at low intracellular concentrations, can act as signaling molecules, or may be involved in apoplastic cell-wall modifications (Apel and Hirt 2004; Schopfer and Liszkay 2006; Gill and Tuteja 2010; Kutschera and Wang 2012). However, when the organism experiences stressful conditions, which is the "real-world" situation, ROS exert negative effects, despite the evolution of the intracellular defense mechanisms reviewed here and elsewhere (Halliwell and Gutteridge 2007).

Conclusions: the three oxygen paradoxa and metabolic scaling

The so-called "oxygen paradox of aerobic life" (Davies 1995) refers to the fact that reactive oxygen species (ROS) cause cell damage and death in many organisms. In this article, we described two additional detrimental effects of O_2 on living organisms: the occurrence of wildfires, associated with the destruction of large populations of organisms or entire ecosystems (Bowman et al. 2009) and photorespiration, i.e., the reduction of CO_2 assimilation due to the inefficiency of the enzyme Rubisco in C3 plants (which makes up the vast majority of angiosperms) (Parry et al. 2013). These three features taken alone argue against

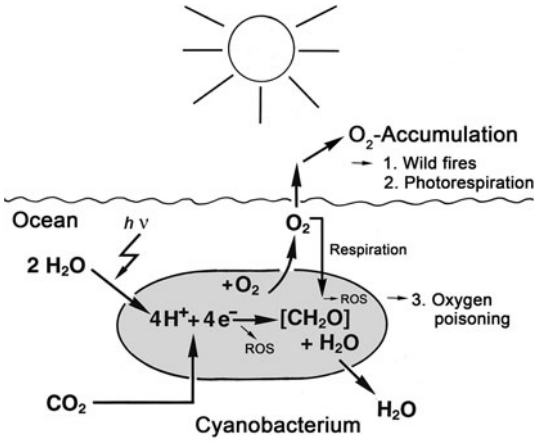

Fig. 12 The threefold oxygen paradox of aerobic life. Molecular oxygen (O_2) was released as a consequence of the evolutionary "invention" of oxygenic photosynthesis in ancient, marine cyanobacteria ca. 3,000 million years ago (see Fig. 6). As a result, a rise in O_2 concentration in the atmosphere occurred ca. 2,400 mya, so that today ca. 1/5 of the air consists of O_2 (about 21 vol.%). The accumulation of O_2 had three major negative effects on living organisms: *1* the induction of destructive wildfires; *2* the occurrence in photorespiration in C3 plants, a wasteful process that reduces crop yield; *3* the production of reactive oxygen species (ROS), resulting in O_2 poisoning, leading to cell damage

Wallace's naturalistic "design" thesis, which is articulated in his once very popular books *Man's Place in the Universe* and *The World of Life* (Wallace 1903, 1910). Therein, Wallace argued that nature manifests an "ultimate purpose" or "perfection" (Fig. 1), a thesis that was deduced from scientific data available at that time. Here we have shown that molecular oxygen, the "food of protoplasm" (Wallace 1903), is required for the maintenance of cellular respiration, but that it can (and often does) have three very negative consequences, i.e., the fueling of wildfires, the competition of O_2 for Rubisco, and the production of aggressive free radicals (ROS) (Fig. 12). These facts were unknown when Wallace (1903, 1910) published his speculations on "design" in living organisms, although Priestley (1775) had already suggested that O_2 may have negative effects on animals and humans.

The corrosive nature of oxygen, on the one hand, and its vital physiological necessity, on the other hand, remain one of life's great paradoxes—a dramatic example of the biological truism that organisms change their environment by the very act of living and evolving (Fig. 12). Moreover, it is a powerful argument against "Intelligent Design" in nature that has been largely ignored in debates on this topic (Matzke 2010; Scott 2010).

An additional insight into the data reviewed here is that plant respiration rates (determined as O_2 uptake in darkness) are not uniform throughout the living substance, even at the level of a single individual organism. Rather, respiration rates are seen to correlate with growth rates and with DNA content at the level of individual tissues or organs (Kutschera and Niklas 2011, 2012, 2013). This finding helps explain why features of the metabolic scaling theory remain contentious regarding body size and respiration rates. Empirical studies have shown that whole plant respiration rates correlate linearly with body size across small and juvenile plants, but scale, on average, roughly as the 3/4 power of body mass for larger, more mature plants (Niklas 1994, 2004; Price et al. 2010). A variety of hypotheses have been proposed to explain this shift in the scaling exponent. In our view, the most obvious explanation is that this shift reflects a change in the volume fraction of protoplasm with respect to that of the non-metabolically active content of individual plants. The gradual accumulation of cell wall materials resulting from primary and secondary tissues during the growth of woody plants necessarily leads to a gradual decline in the volume fraction of the respiring symplast, where the O_2-consuming mitochondria are localized (Fig. 11). A similar phenomenology can be posited for animals, since an increase in body mass is attended by the addition of non-respiring structural elements necessitated for locomotion, mechanical support, or defense (Glazier 2005; Okie 2013).

We therefore conclude that the shift in the volume fractions of living and "necro"-mass attending the growth and development of multicellular plants and animals provides a fertile ground for future research, particularly if it is studied with detailed measurements of cellular respiration at the level of individual tissues and organs.

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