REVIEW

Plant respiration under low oxygen

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Respiration is an oxidative process controlled by three pathways: glycolysis, the tricarboxylic acid (TCA) cycle, and oxidative phosphorylation (OXPHOS). Respiratory metabolism is ubiquitous in all organisms, but with differences among each other. For example in plants, because their high plasticity, respiration involves metabolic pathways with unique characteristics. In this way, in order to avoid states of low energy availability, plants exhibit great flexibility to bypass conventional steps of glycolysis, TCA cycle, and OXPHOS. To understand the energetic link between these alternative pathways, it is important to know the growth, maintenance, and ion uptake components of the respiration in plants. Changes in these components have been reported when plants are subjected to stress, such as oxygen deficiency. This review analyzes the current knowledge on the metabolic and functional aspects of plant respiration, its components and its response to environmental changes.

Key words: Electron transport chain, hypoxia, Krebs cycle, maintenance respiration.

INTRODUCTION

Plants are autotrophic organisms able to use solar radiation to split water molecules (H_2O) and reduce the carbon dioxide (CO_2) compounds that can finally be stored as insoluble polysaccharides (starch) or used directly in the synthesis of other compounds. In plants glucose is the main substrate for respiration. This process oxidizes carbohydrates through two principal pathways: glycolysis and the tricarboxylic acid (TCA) cycle. The products from these two pathways are CO_2 and the reduced compounds $NAD(P)H_2$ and $FADH_2$, which in turn are used for oxidative phosphorylation (OXPHOS), transferring their electrons to the terminal oxidase where O_2 acts as the final electron acceptor, producing high-energy phosphate bonds (ATP) (Millar et al., 2011; van Dongen et al., 2011). ATP represents the most efficient way to obtain energy for the synthesis of biomolecules and to maintain cellular structures, transport photoassimilates, uptake ions, assimilate N and S, regulate protein turnover and maintain electrochemical potential gradients across membranes in cells (Amthor, 2000).

Plant respiration has been widely studied, but despite this effort and the available new technologies, its mechanisms of regulation and control still require further elucidation. For instance, studies on the enzymatic functionality of glycolysis have determined the importance of phosphoglucomutase (PGM) in starch formation processes in both heterotrophic (root and seed) and autotrophic tissues as well as the role of hexokinases (HXK) and other enzymes such as the glucose signaling network (Sheen, 2014). Regarding the TCA cycle, some progress has been made in understanding how alternative pathways involving γ-aminobutyric acid (GABA) and the glyoxylate cycle operate, with special attention given to changes in the optimal conditions, in order to show the high level of plasticity in the response of the TCA cycle to environmental changes (Sweetlove et al., 2010). More details will be given in another section below.

On the other hand, research has been directed at finding new non-phosphorylates or alternative pathways for OXPHOS that allow energy to be dissipated. Alternative oxidase (AOX) is a protein associated with the inner mitochondrial membrane, it has been shown to be induced by a series of stress factors such as high and low temperatures, drought, and nutrient deficiency, among others (Moore et al., 2002). Furthermore, alternatives have also been found to the maintenance of the proton gradient in the mitochondrial matrix, which is performed through uncoupled proteins (UCP) that enables flows of protons to enter the matrix independent of ATP synthesis (Arnholdt-Schmitt et al., 2006). In turn, UCP would participate in the reduction of reactive oxygen species (ROS), a function also contributed to by AOX (Smith et al., 2004).

Respiration plays an important role in acclimation to different types of abiotic stress (water, temperature,

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photoinhibition, salinity, nutrient deficiencies, and hypoxia/anoxia, etc.), therefore many studies have focused on understanding the function, organization, and regulation of respiratory metabolism under unfavorable environments. These stresses usually result in changes in the energy requirements of plants, which in turn induce changes in respiratory metabolism as well as in other enzymes, electron transport, and redox gradient formation, among others. One important stress that affects respiration is partial deficiency (hypoxia) or absolute absence (anoxia) of oxygen. For instance, under hypoxic conditions alanine creates a link to glycolysis (de Sousa and Sodek, 2003). Moreover, under anoxia, fermentative lactate and ethanol pathways are activated and the rate of ethanol synthesis rises more than 5 fold as compared to normal conditions (Mancuso and Marras, 2006).

Because of this concern, the objective of this review was to analyze the state of the art of plant respiration, both in terms of metabolism and from a functional point of view. For this reason, in the first part of this review, a comparative analysis of the major metabolic pathways of aerobic respiration in animals and plants is performed. Then, after analyzing recent advances in knowledge about the functionality of respiration in plants beyond its traditional role as an energy generating process, we discuss in particular its role in the synthesis of new compounds and in the maintenance of molecules and structures. Consideration is particularly given to functions under different kinds of stress. Finally, the response of different parts of the anaerobic respiration system to oxygen restrictions and the functionality of alternative metabolic pathways activated in plants when oxygen is restricted (i.e. during hypoxia) are discussed.

Overview of plant respiration

Respiration involves the participation of different processes responsible for the oxidation of glucose molecules for energy and C structures, either in the presence (aerobic) (Millar et al., 2011; van Dongen et al., 2011) or absence (anaerobic) of oxygen (Gupta et al., 2009). In the latter case, the most affected organ is the root, inducing partial oxidation strategies of substrates in order to continue to generate energy without oxygen (O_2). These strategies are called fermentation, which differentiate themselves by their end products: ethanol, lactic acid and alanine (Sousa and Sodek, 2002).

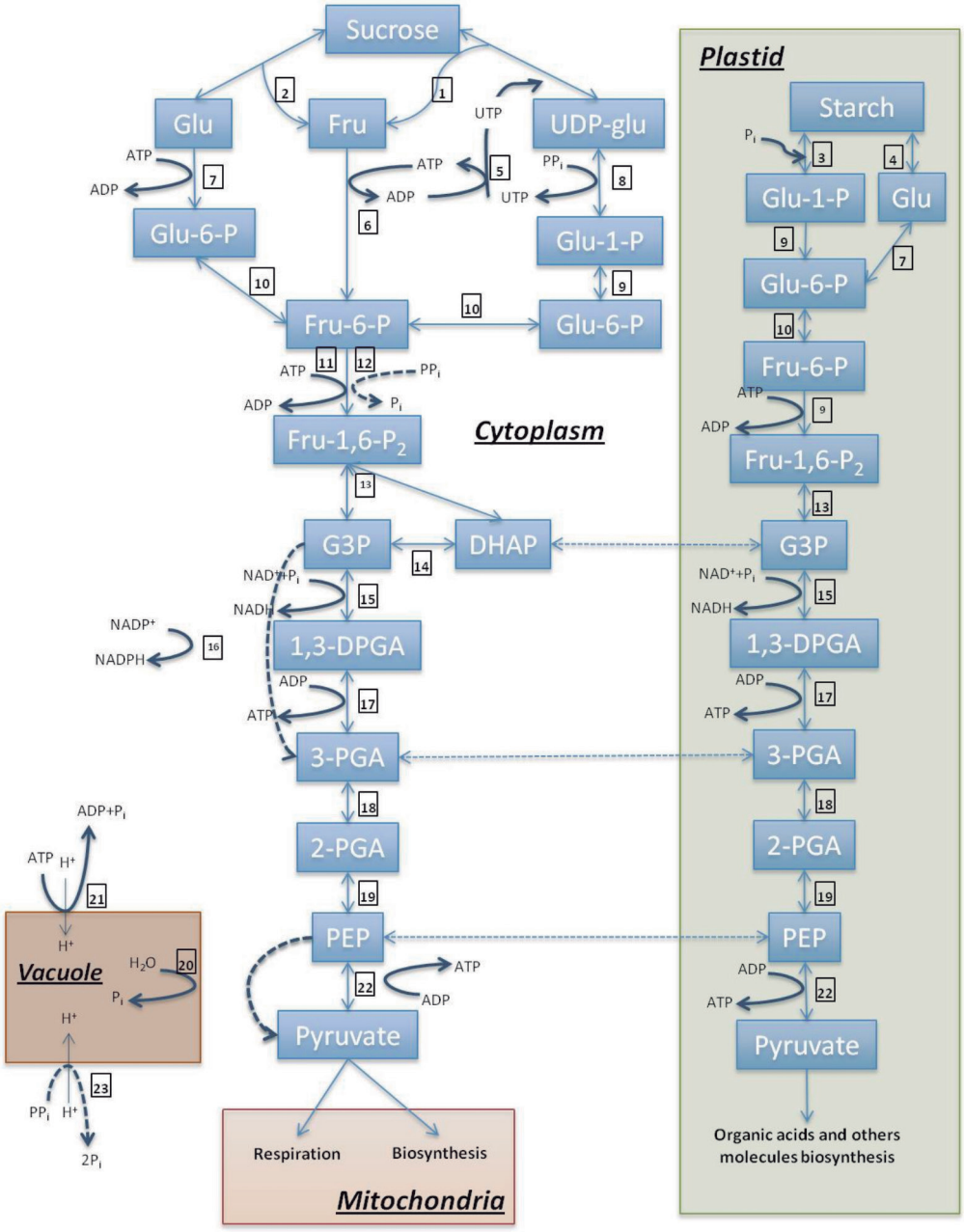
In the presence of O_2, substrates are completely oxidized to CO_2 and H_2O (van Dongen et al., 2011). This is done through three metabolic processes: glycolysis, the TCA cycle and the OXPHOS (Fernie et al., 2004). To these is added a fourth process; transport of the products of respiration. This corresponds to the movement of substrates and cofactors to facilitate the release of products throughout the cell (Millar et al., 2011). The operation of these processes is the most efficient way to obtain energy from complete oxidation of hydrocarbon substrates, both in plants and animals (Plaxton, 1996).

It has been reported that there are differences in respiration according to species and plant tissue (Millar et al., 2011); for example, spinach leaf respiration is preferably performed at night, because during the day it is inactivated at low solar radiation intensities (10-50 μmol m^{-2} s^{-1}) (Atkin et al., 1998), presumably cause excess ATP from photosynthesis in chloroplasts (Atkin et al., 2004). However, for many years the effects of radiation on leaf respiration were studied without considering the effect of temperature. Thus, a study in eucalyptus plants showed that leaf respiration is highly dependent on both radiation and temperature, showing a high degree of inhibition of respiration at high temperatures and high radiation levels, which reduces the CO_2 ratio (provided by photosynthesis) that is respired (Atkin et al., 2000).

Likewise, root respiration can be altered by a variety of factors such as temperature (Rachmilevitch et al., 2006), salinity (Bernstein et al., 2013), heavy metals (Moyen and Roblin, 2013), drought (Jiménez et al., 2013), waterlogging and flooding (Liao and Lin, 2001); however, the availability of O_2 is what most affects root respiration (Gupta et al., 2009). This factor is key in respiration metabolism, because oxygen is the final electron acceptor in OXPHOS (Moller, 2001). Most of the energy (ATP) produced by root respiration is used for processes such as growth (van Iersel and Seymour, 2000; Thongo M'Bou et al., 2010), nitrate reduction, symbiotic N fixation (in legumes), the absorption of nitrate and other ions absorption by the roots (Poorter et al., 1991), protein turnover (De Visser et al., 1992; Bouma et al., 1994; Scheurwater et al., 2000), maintenance of the ion gradient and membrane potential (Veen, 1980; Bouma and De Visser, 1993) and waste mechanisms and production of heat through alternative pathways (Cannell and Thornley, 2000).

Glycolysis in plants

Glycolysis is an anaerobic pathway responsible for oxidizing sucrose (glucose in animals) to generate ATP, a reductant (NADH) and pyruvate (Millar et al., 2011; van Dongen et al., 2011). The universality of glycolysis is associated with its importance in adaptations to different environmental stressors, such as nutritional stress, temperature, drought, and anoxia, among others (Plaxton, 1996). In general, the transformation of glucose to pyruvate is performed through a series of reactions catalyzed by numerous enzymes (Figure 1) (Plaxton, 1996; van Dongen et al., 2011), which not only act as catalysts and energy metabolism regulators (Camacho-Pereira et al., 2009), but also as signal transducers in response to changes in the environment. For instance, it has been observed that the activity level of hexokinase (HXK) would correspond to a key component in the sugar signal detection. For example, it was determined that HXK (AtHXK1) regulates the signaling levels of sugar



Source: Author based on Plaxton (1996) and Plaxton and Podestá (2006).

Enzymes involved in each reaction are as follows: 1) sucrose synthase, 2) invertase, 3) phosphorilase, 4) α and β-amylase, 5) NDP kinase, 6) fructokinase, 7) hexokinase, 8) UDP-glucose pyrophosphorylase, 9) phosphoglucomutase, 10) phosphoglucose isomerase, 11) ATP-PFK, 12) PP_i-PFK, 13) aldolase, 14) triose phosphate, 15) and 16) glyceraldehyde-3-phosphate phosphorylated and non-phosphorylated, respectively, 17) phosphoglycerate kinase, 18) phosphoglyceromutase, 19) enolase, 20) PEP phosphatase, 21) H^+-ATPasa, 22) piruvate kinase, and 23) H^+-PP_iasa.

Figure 1. Schematic representation of the glycolysis pathway and alternatives in vegetables. Continuous line represents glycolytic flux and broken lines represent alternatives.

in *Arabidopsis gin2* mutants under different lighting conditions. Normal growth was observed in control plants; however, in mutant plants (*gin2*/*hxk1*), growth was inhibited due to a reduction in cell expansion (Moore et al., 2003).

In turn, HXK activity in plants is related to the link between glycolysis and programmed cell death (apoptosis). Briefly, mitochondrial pathways of apoptosis are initiated by mitochondrial cytochrome *c* release (high control point of apoptosis initiation) into the cytoplasm

through pores in the mitochondrial permeability transition (MPT) in response to some stress (Kim et al., 2006). HXK is an integral component of MPT, through its interaction with porins (VDAC, Voltage-Dependent Anion Channel). When HXK binds to VDAC it interferes with the opening of MPT, inhibiting the release of cytochrome *c* into the cytoplasm and hence inhibiting apoptosis (Kim et al., 2006).

In animals, apoptotic activity has been attributed to the action of nuclear glyceraldehyde-3-phosphate dehydrogenase (GAPDH) on cultured neurons. Moreover, it has been observed that HXK mediates the signaling of sugars on the ABA pathway. The *gin1* mutant is allelic to *aba*, which has been found to act on an enzyme that catalyses the last step in ABA biosynthesis, indicating that HXK level mediates signaling by the ABA pathway (Rolland et al., 2002). In addition, protective functions against ROS have also been attributed to a mitochondrial HXK through the generation of ADP for OXPHOS, avoiding limitations in the synthesis of ATP during respiration and facilitating the release of hydrogen peroxide (Camacho-Pereira et al., 2009). While HXK is found in the mitochondria, there is also evidence to indicate the presence of HXK in the cell nucleus (Kim et al., 2006). This would indicate that HXK might be controlled at the level of glycolytic gene expression.

Although each enzyme involved in the glycolytic flux corresponds to a critical control point in respiration, it was observed that altering the activities of these enzymes caused only minor changes in respiration rates (Hajirezaei et al., 2006; Oliver et al., 2008). This indicates that there are other key points in the regulation of respiration. Studies in different organisms (bacteria and mammals) show that one of the key sites of regulation and control of respiration is at the level of pyruvate kinase (PK), which catalyzes the final reaction in the pathway using ADP and phosphoenolpyruvate (PEP) for ATP and pyruvate (Teusink et al., 2000). Likewise, in plants the situation is complex because there are various isoforms of the same enzymes, such as PK (Plaxton and Podestá, 2006).

Unlike other organisms, glycolysis in plants can be carried out in two different subcellular compartments, in the cytoplasm and plastids (chloroplast and amyloplast). This makes it difficult to analyze and understand, because it involves interactions and connectivity through highly selective transporters, together with the interactions of about 23 different enzymes (Plaxton, 1996; Muñoz-Bertomeu et al., 2010).

In animal cells studies have paid special attention to the spatial organization of glycolysis, because the physical concentrations of glycolytic enzymes may be associated with sites with high demand for ATP (Lu et al., 2001; Giegé et al., 2003) or other intermediates of glycolysis (Giegé et al., 2003; Fernie et al., 2004). A study in *Arabidopsis* established that the enzymes HXK, GADPH, and phosphofructokinase (PFK) were functionally associated with mitochondria (Giegé et al., 2003). Moreover, in bean (*Phaseolus vulgaris* L.) it was found that the enzymes 3-phosphoglycerate kinase (3-PGK), GAPDH, and aldose are associated with the nuclei and cytoskeletons of leaf cells, while in corn, 3-PGK and aldose are only associated with the cytoskeleton (Azama et al., 2003). The glycolytic flux is controlled by a cascade of reactions in which there are checkpoints on the pathway, such as HXK and PK activity, which can control glycolysis not only at the mitochondrial level but also from a posttranslational level.

Tricarboxylic acid cycle in plants

The tricarboxylic (TCA) cycle, also called the Krebs cycle in honor of its discoverer, is an essential metabolic pathway. It is located in the mitochondrial matrix where, by the oxidation of organic C substrates (pyruvate and/or malate), it releases CO_2 and provides reducing factors such as NAD(P)H and $FADH_2$, which are primary substrates for the synthesis of ATP in the electron transport chain in mitochondria (Fernie et al., 2004; Mailloux et al., 2007; Sweetlove et al., 2010) (Figure 2). In turn, the TCA cycle provides C skeleton components and precursors for the biosynthesis of secondary metabolites such as terpenes, amino acids, and fatty acids, among others (Plaxton and Podestá, 2006; Sweetlove et al., 2010).

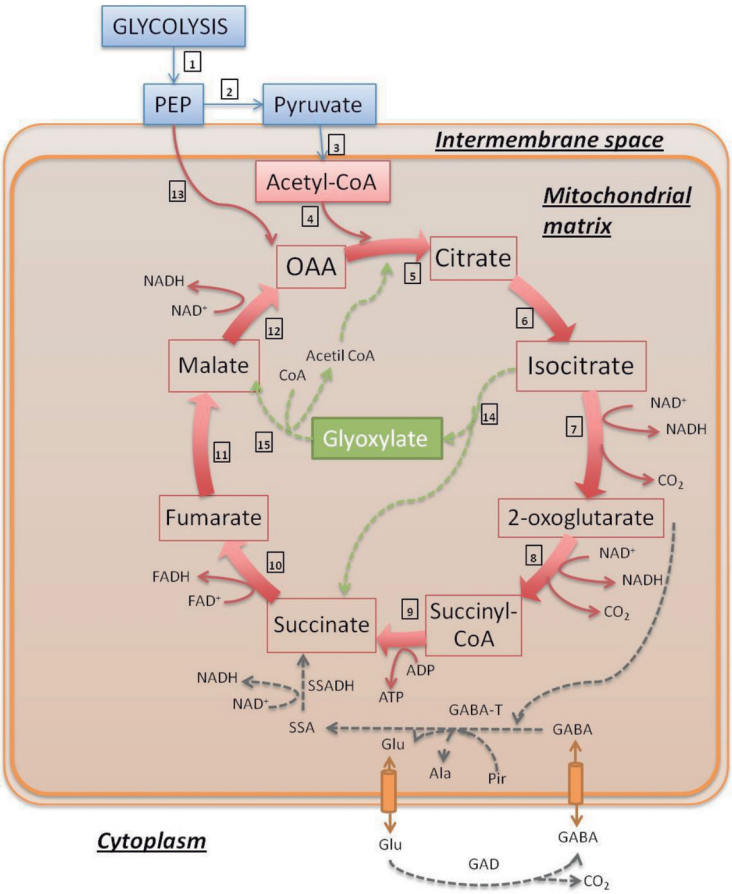
The TCA cycle begins with the reaction between acetyl CoA and oxaloacetate (OAA), yielding tricarboxylic acids that are oxidized and decarboxylated through a series of reactions in which CO_2 molecules are released. At the end of the cycle, OAA is regenerated for re-condensation with acetyl CoA, restarting the cycle (Figure 2) (Mailloux et al., 2007; Sweetlove et al., 2010).

One of the main differences between the TCA cycle in plants and animals is the energy molecule generated during the processing of succinyl CoA to succinate. While ATP is produced by succinyl CoA synthase in plants, in animal cell there are two isoforms, GTP-specific succinyl CoA synthase (G-SCS) and ATP-specific succinyl CoA synthase, which generate guanosine-5'-triphosphate (GTP) from guanosine diphosphate (GDP) and ATP from ADP, respectively (Johnson et al., 1998).

Another feature associated with the TCA cycle in plants, but not found in other organisms, is related to the significant activity of NAD-dependent malic enzyme (NAD-ME) or malate oxidoreductase, responsible for catalyzing the oxidative decarboxylation of malate to pyruvate, finally allowing complete oxidation of malate (Jenner et al., 2001).

Pathways associated with the TCA cycle in plants

There are several alternative pathways in the TCA cycle, which give some flexibility against environmental changes or simply in the choice of which compounds to biosynthesize (Sweetlove et al., 2010). For instance, γ-aminobutyric acid (GABA) was long considered just a



Source: Author based on Ryan et al. (2001) and Studart-Guimaraes et al. (2007).

PEP: Phosphoenolpyruvate, OAA: oxaloacetate, SSA: succinyl semialdehyde, SSADH: succinyl semialdehyde dehydrogenase, GABA: γ-aminobutyric acid, GABA-T: γ-aminobutyric acid transaminase, GAD: glutamate decarboxylase, Glu: glucose, Ala: alanine, Pir: pyruvate.
Enzymes involved in each reaction are as follows: 1) enolase, 2) pyruvate kinase, 3) pyruvate dehydrogenase, 4) coenzyme A, 5) citrate synthase, 6) aconitase, 7) isocitrate dehydrogenase, 8) 2-oxoglutarate dehydrogenase, 9) succinyl CoA synthase, 10) succinate dehydrogenase, 11) fumarase, 12) malate dehydrogenase, 13) phosphoenolpyruvate carboxylase, 14) isocitrate lyase, 15) malate synthase.

Figure 2. Schematic representation of tricarboxylic acid cycle (TCA) in plants. Red line: TCA cycle, green line: glyoxylate cycle, gray line: GABA route.

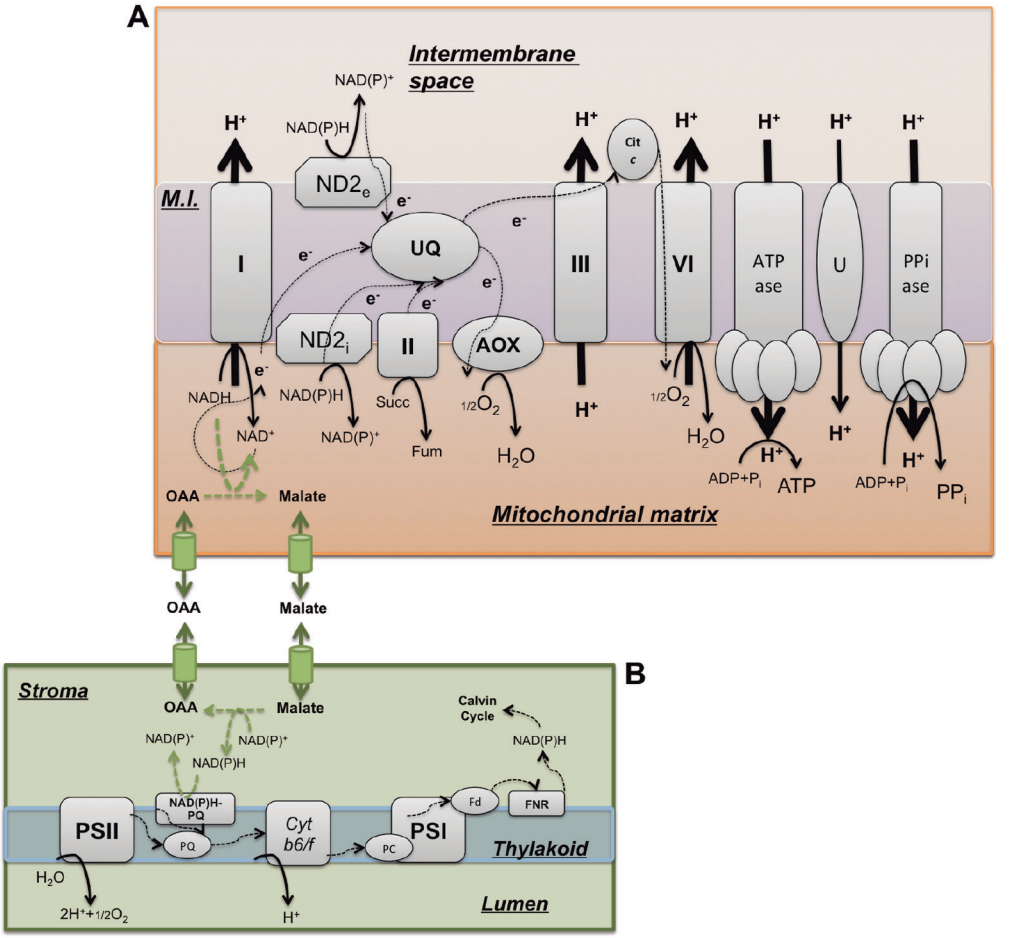
metabolite in plants with an unclear function; however, at present there is evidence to indicate that GABA plays a major role in C metabolism in response to stress (Bouché and Fromm, 2004). As shown in Figure 2, the GABA pathway is composed of three enzymes; glutamate decarboxylase (GAD), a cytoplasmic enzyme, and two mitochondrial enzymes called GABA transaminase and succinic-semialdehyde dehydrogenase (GABA-T and SSADH, respectively), present both in animals and plants (Bouché and Fromm, 2004; Sweetlove et al., 2010). In plants, it has been observed that GABA pathway responds quickly to environmental changes, e.g. it is stimulated under conditions of cold, salinity (Kinnersley and Turano, 2000), and anoxia (Aurisano et al., 1995). The role of GABA pathway in plants is still unclear because studies on this pathway are relatively new. However, it could be that GABA pathway is linked to many abiotic stress responses (Kinnersley and Turano, 2000). Unlike in plants, in mammals GABA clearly functions as a molecular neurotransmitter in the brain (Bouché and Fromm, 2004).

The glyoxylate cycle is another pathway associated with the TCA cycle in plants, defined as a modification of the TCA cycle (Figure 2) (Kornberg and Madsen, 1958). In turn, it has mainly been associated with lipid metabolism in seeds of oil plants (Eastmond and Graham, 2001). In general, the difference between glyoxylate cycle and TCA cycle is that the first avoids two points of decarboxylation and allows the generation of acetyl CoA through β-oxidation of fatty acids, giving rise to succinate, which is then incorporated into the mitochondria to generate OAA, which will go directly toward the synthesis of sucrose by gluconeogenesis (Eastmond and Graham, 2001).

In oil seeds, the most important source of storage supply is lipids, which are used by the glyoxylate cycle to maintain growth and respiration of the seed. For example, in *Arabidopsis* seeds, lipids are stored in cotyledons that show marked *icl* and *mls* gene expression coding for isocitrate lyase and malate synthase, respectively, two key enzymes in the glyoxylate cycle (Eastmond and Graham, 2001). Light plays an important role in post germination growth, it being observed in mutants of *Arabidopsis (icl)* that a reduction in the activity of isocitrate lyase inhibits lipid breakdown and strongly reduces the growth of hypocotyl (Eastmond et al., 2000). In seedlings, the glyoxylate cycle plays a key role in growth because it is involved in lipid metabolism through the ß-oxidation of fatty acids (Finkelstein and Gibson, 2002). This oxidation produces two-C units of acetyl-CoA capable of entering the glycolate cycle. Sugar (sucrose) is the ultimate product of this process, being the primary form in which reduced C is translocated from the cotyledons to the growing seedling tissues (Taiz and Zeiger, 1991).

Oxidative phosphorylation in plants

Oxidative phosphorylation (OXPHOS) (Figure 3) is the pathway in which oxidation of NADH and $FADH_2$, which are produced during the TCA cycle, occurs. Here, the electrons resulting from oxidation are transferred through protein complexes (I, II, III, IV) inserted in the inner mitochondrial membrane ad on to O_2, which acts as a final electron acceptor, finally reduced in the form of H_2O (Bailey-Serres and Voesenek, 2008; Sweetlove et al., 2010). The electrochemical potential produced in



Source: Author based on Peltier and Cournac (2002) and Bauwe et al. (2010).

OXPHOS abbreviations: I: cytochrome I or NADH dehydrogenase, $ND2_i$, $ND2_e$, NAD(P)H dehydrogenase type II internal and external, respectively, II: cytochrome II or succinate dehydrogenase, UQ: ubiquinone, AOX: alternative oxidase; III: cytochrome c reductase or cytochrome bc_1, IV: cytochrome c oxidase or COX, ATPase: ATP synthase, U or UCP: uncoupling protein, PP_iasa: pyrophosphate synthase.
Chlororespiration abbreviations: OAA: oxaloacetate, PSII: photosystem II, PQ pool of plastoquinone, Ndh or NAD(P)H-PQ, NAD(P)H dehydrogenase complex or NAD(P)H-plastoquinone oxidoreductase, respectively, Cyt *b6/f*, cytochrome *b6/f*, PC: plastocyanin, PSI: photosystem I, Fd: ferredoxin, FNR: ferredoxin $NADP^+$ reductase.

Figure 3. Schematic representation of oxidative phosphorylation (OXPHOS) (A) and chlororespiration (B).

the inner mitochondrial membrane is the force that drives ATP synthesis (Millar et al., 2011).

In plants, studies have focused on finding alternative pathways to the conventional OXPHOS pathway of the electron transport chain. For example, the participation of certain alternative pathways that involve proteins associated with complex I (Rasmusson et al., 2004) and AOX (Moore et al., 2002) has been proposed (Figure 3). However, non-phosphorylation pathways do not contribute to the generation of the inner-membrane proton gradient (Fernie et al., 2004). To overcome this deficiency in the proton gradient, plants have a strategy developed from uncoupling proteins (UCP) embedded in the inner mitochondrial membrane (Smith et al., 2004; Arnholdt-Schmitt et al., 2006). Uncoupling proteins activity can enhance the transfer of protons into the mitochondria by controlling the rate of production of superoxides, and may even have some control over the TCA cycle, because increases in the UCP content can increase the rate of conversion of pyruvate to citrate (Smith et al., 2004).

In both plants and animals, once in the mitochondria, NADH and $FADH_2$ are oxidized in a complex called NADH dehydrogenase or complex I (Figure 3A), which initiates the transfer of electrons through OXPHOS. In plants this complex has 46 subunits, of which only 32 are similar to complex I proteins present in animals (Millar et al., 2011). A study in *Arabidopsis* showed that plants without complex I could still survive in association with a complex I protein called NAD(P)H dehydrogenase (Fernie et al., 2004). According to their position on the inner mitochondrial membrane, there are two kinds of NADPH dehydrogenase, internal and external ($ND2_i$ and $ND2_e$, respectively) (Rasmusson et al., 2004). The function of $ND2_e$ is related to the regulation of NADH and NAD(P)H reduced in the cytoplasm in response primarily to the cytoplasmic Ca concentration, while ND2i participates with substrates from the TCA cycle (Rasmusson et al., 2004).

Complex II (succinate dehydrogenase, SDH) is an enzyme shared between TCA cycle and OXPHOS (Figure 2 and 3). Succinate dehydrogenase has different functions depending on the tissue in which it is found. For example, some influence of SDH has been reported in leaves with phytochrome A, which controls the activity of SDH (Plaxton and Podestá, 2006). Complexes III and IV (cytochrome c reductase and cytochrome c oxidase (COX), respectively) correspond to the OXPHOS supercomplex, COX being a prime OXOPHOS terminal oxidase (Popov et al., 2010).

Despite COX, there is another terminal oxidase that is inserted in the inner mitochondrial membrane, called alternative oxidase (AOX) (Figure 3). Is was thought that AOX's function was to support the transfer of electrons when COX was at full capacity (van Dongen et al., 2011). Nevertheless, is known that both AOX and COX compete for electrons, because both are positioned at critical OXOPHOS control points (Lambers, 1982). Studies have elucidated a crucial role of AOX in protecting against ROS produced during oxidative stress (van Dongen et al., 2011), and it can also influence mitochondrial adaptability to different kinds of stress (Moller, 2001; Rasmusson et al., 2009), even expressing mitochondrial genes in a wide variety of environments. AOX acts against ROS as follows: AOX allows electron transfer from ubiquinone (UQ) to O_2, which high levels of reducing agents in the UQ pool can be dissipated through AOX, thus avoiding the formation of ROS (Polidoros et al., 2009).

Chlororespiration

In plants, it is possible for electron transport to O_2 to occur in the presence of light through thylakoidal membranes of chloroplasts, via chlororespiration (Figure 3) (Polidoros et al., 2009), distinct from photorespiration (Bennoun, 1982; Peltier and Cournac, 2002) and the Mehler reaction. The function of this process is to ensure supplies of ATP and NAD(P)H generated by glycolysis for converting starch into triose phosphate (D-glyceraldehyde phosphate or dihydroxyacetone phosphate) (Bauwe et al., 2010; Maurino and Peterhansel, 2010). Both chloroplasts and mitochondria share similar mechanisms and control components, e.g. the electron transport is carried out in the membrane and shares the same membrane components (cytochrome, ion-S proteins, quinones and ATPase) (Bennoun, 1982). Although there are no exclusive carriers of NAD(P)H in the thylakoidal membrane, this may be performed indirectly through OAA-malate ports which allow the transport of malate (Figure 3), being oxidized by NAD^+ to produce NADH in the chloroplast stroma (Bennoun, 1982). The ability to transport reducing agents through the inner chloroplast membrane means that it is in communication with the rest of the cell. There have been studies on the importance of environmental changes in chlororespiration, with an increase in the activity and expression of a protein complex called NDH (homologous to complex I) (Peltier and Cournac, 2002). This complex catalyzes the transfer of electrons from NAD(P)H to plastoquinones (Rumeau et al., 2005). According to some authors, this complex is key in chlororespiration because it has an NADH dehydrogenase function in mitochondria. In turn, the Ndh complex regulates the proton gradient produced in the stroma, suggesting a role in the control of oxidative stress produced in the chloroplast stroma (Rumeau et al., 2005).

Photorespiration

Unlike chlororespiration, photorespiration (also called the C_2 cycle) corresponds to an oxidation mechanism of C molecules (such as ribulose 1,5-diphosphate) and is performed in three different organelles: chloroplasts, mitochondria and peroxisomes (Peltier and Cournac, 2002). This process consists in replacing CO_2 for O_2 during C fixation in photosynthesis, allowing recycling

and transforming the phosphoglycolate (2PG) generated into phosphoglycerate (Maurino and Peterhansel, 2010).

Photorespiration is one of the most important pathways of carbon metabolism in plants, exceeded in its importance at the terrestrial level only by photosynthesis. This is because of the high O_2 concentration in the cells compared to CO_2. Photorespiration can release about 20% of the CO_2 that is absorbed during photosynthesis under normal temperatures. However, it was determined that the amount of CO_2 released could be higher in hot and dry environments (Bauwe et al., 2010; Maurino and Peterhansel, 2010). The interaction between photorespiration and mitochondrial respiration is generated from an allosteric reaction in the TCA cycle using the products of the reaction catalyzed by glycine decarboxylase (GDC) and an interaction between NAD^+ regenerated by the GDC and the electron transport chain (Figure 3B).

The importance of photosynthesis and photorespiration has been observed in tobacco (*Nicotiana tabacum* L.) mutants deficient in complex I expression for mitochondrial OXPHOS, because the proteins of complex I are important for maintaining the redox conditions in the cell that enhance photosynthetic efficiency (Peltier and Cournac, 2002; Plaxton and Podestá, 2006; van Dongen et al., 2011).

Functions of plant respiration

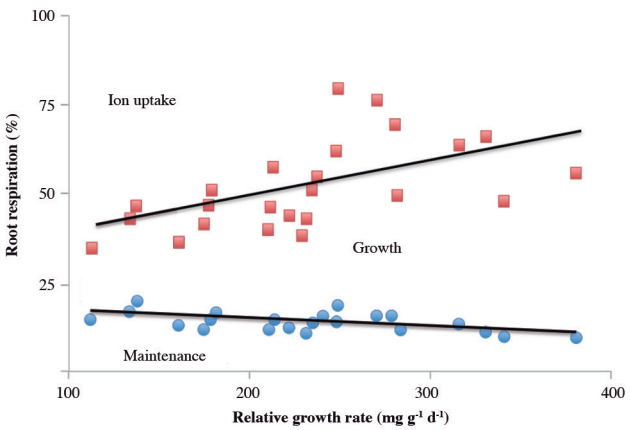
There is a great deal of information available about molecular and physiological aspects of plant respiration and its importance for plant growth and development. However, there is little information about the link between respiration and key processes in the survival of several plant species. Nine processes have been described to take priority from the energetic point of view: growth (Dutilleul et al., 2003), nitrate reduction, symbiotic N fixation, uptake of nitrate and other ions by roots (van Iersel and Seymour, 2000; Thongo M'Bou et al., 2010), protein turnover (Poorter et al., 1991), maintenance of protons gradient (De Visser et al., 1992; Bouma et al., 1994; Scheurwater et al., 2000), waste mechanisms and heat production by alternative pathways (Veen, 1980; Bouma and De Visser, 1993). Generally, these processes are associated with two components of respiration: growth and maintenance respiration (Johnson et al., 1998). Nevertheless, it is possible aggregate a third component when the correlation between relative growth rate (RGR) and net N uptake rate (NNUR) is not tight (Amthor, 2000; Thornley and Cannell, 2000).

Growth respiration is respiration that produces energy and C skeletons for the synthesis of new structures in growing plants (proteins, lipids, organic acids, and structural carbohydrates) (Veen, 1980). Maintenance respiration is respiration that produces energy for all processes related to cellular maintenance such as protein turnover, maintenance of ion gradients and membrane potentials in the cell (Penning de Vries et al., 1974; Penning de Vries, 1975). A mathematical expression of the relationship between these components of respiration is:

$$R_r = R_m + c_g \cdot RGR + c_u \cdot NNUR \qquad [1]$$

where R_r is root respiration rate (µmol O_2 or CO_2 g^{-1} d^{-1}), R_m is respiration rate to produce ATP required for maintenance of biomass, c_g is root respiration to produce ATP for cellular compound synthesis (mmols O_2 or CO_2 g^{-1}), *RGR* is the relative growth rate of roots (mg g^{-1} d^{-1}), c_u is the respiration rate required for maintenance (µmol g^{-1} d^{-1}), and NNUR is the net N uptake rate (Veen, 1980).

The energy requirements for each process depend on the rates associated with them, which are affected by the species, organ (tissue) and environmental conditions to which the plants are subjected (Lambers, 2008). For example, Figure 4 shows that young plants under high N conditions allocated only 10% to the maintenance component of root respiration (Poorter et al., 1991). On the other hand, the growth component is an important



Source Poorter et al. (1991).

Figure 4. Respiratory costs associated with respiration components of maintenance, growth, and ion uptake.

part of root respiration (20%-45%); however, the majority of the respiration is devoted to the ion uptake process (50%-70%) (Poorter et al., 1991). In a study in *Carex*, maintenance respiration was the most important component associated with respiration because fully grown plants were used, which meant lower RGR and NNUR (van der Werf et al., 1988).

Protein turnover corresponds to the major fraction of the maintenance component of respiration. It is particularly important when rapid changes occur in the environment or during periods of stress. Without this mechanism (protein turnover), the energy requirement would be increased by a high demand from the plant, so protein turnover could keeps the metabolism stable in a wide variety of environments and at all stages of development (van der Werf et al., 1988). It is estimated that between 2% and 5% of all proteins are replaced daily; however, there are reports indicating that protein turnover in leaves could be as much as 20% daily. Some of the processes associated with protein turnover are: biodegradation of proteins, activation and turnover of amino acids, peptide bond formation and posttranslational processes, among others (Bouma et al., 1994).

Some researchers working under different growth conditions, have correlated maintenance respiration rates and protein content of biomass (Poorter et al., 1991); thus, it can be inferred that protein turnover costs are the most important costs of maintenance respiration. In a comparative study on roots of fast-growing (*Dactylis glomerata* L.) and slow-growing (*Festuca ovina* L.), it was shown that the cost associated with protein turnover accounted for between 22% and 33% of daily ATP production, corresponding to 11% to 15% of the total production of ATP by roots (Hachiya et al., 2007). In leaves, protein turnover has been estimated at approximately 200 mmol CO_2 kg^{-1} d^{-1} (Scheurwater et al., 2000). Another portion of the costs associated with maintenance are dedicated to regulating the ionic gradient, also known as the cell's osmotic potential, where the costs of maintaining the ionic gradient are approximately 400 mmol CO_2 kg^{-1} d^{-1} (Amthor, 2000).

Otherwise, the growth component is usually expressed in C units (c_g from Equation [1]), corresponding to new biomass per unit of glucose (Penning de Vries, 1975). Most plant c_g values are between 0.7 and 0.8, equivalent to the cost of constructing the glucose requirement, with values of 1.2 to 1.4 g glucose g^{-1} DM (0.2 to 0.4 g CO_2 g^{-1} DM) (Cannell and Thornley, 2000).

Currently, other studies focus on the contributions that terminal oxidases (COX and AOX) should have on the growth and maintenance components of plant respiration. In *Arabidopsis* plants, Cannell and Thornley (2000) estimated the construction cost of leaf tissues, which corresponded to 5.3 and 0.8 mmol O_2 g^{-1} DM for COX and AOX, respectively, while maintenance respiration via COX and AOX was 14.3 and 9 nmol O_2 g^{-1} s^{-1}. Similar values were found by Florez-Sarasa et al. (2007) in the same species. Respiration through COX consumed 90% and 60% of respired C for growth and maintenance, respectively, while AOX consumed 10% and 40% of available C for growth and maintenance respiration, respectively (Bouma, 2005). These results show an interesting effect, because respiration through COX varies more in response to RGR than AOX (Florez-Sarasa et al., 2007). When RGR is low (decreasing or not the respiration) AOX activity is increased, allowing it to maintain the redox state of the ubiquinone "pool" to inhibit ROS (Florez-Sarasa et al., 2007).

Oxygen availability for plant respiration

A major factor that affects plant respiration is O_2 depletion, in the rhizosphere or directly in tissues. The O_2 availability in tissues and cells depends on the plant's age and especially on the O_2 supply from the environment, tissue O_2 having a great influence on the central pathways of carbohydrate synthesis (Millar et al., 1998). In plants, the major external factors affecting O_2 availability are flooding and waterlogging of soil (Liao and Lin, 2001). Under these conditions we can distinguish three broad categories of oxygen status induced by water: normoxia, hypoxia, and anoxia (Table 1). Excess water in soil decreases the O_2 diffusion rate, because the diffusion of O_2 is 10^4 times slower in water than in air (Liao and Lin, 2001; Jackson and Colmer, 2005). The reason for this is the high level of interaction between O_2 and H_2O through hydrogen bonds (Mommer et al., 2004). In flooded soils not only is the diffusion of O_2 reduced, but also the diffusion of several other gases such as CO_2 and ethylene (Wegner, 2010). It is important to consider that low O_2 availability in cells can even occur in some situations under normoxia, due mainly to a high resistance

Table 1. Description of three states of O_2 deficiency due to excess water.

	Normoxia	Hypoxia	Anoxia
Metabolism[1]	Aerobic	Enhanced anaerobic	Anaerobic
NAD+ regeneration[1]	Oxidative phosphorylation (OXPHOS) pathway	Alcoholic and lactic fermentation pathways	Alcoholic and lactic fermentation pathways
ATP production[1]	≈ 30-36 mol ATP mol^{-1} glucose consumed	Dependent on species	≈ 4 mol ATP mol^{-1} of glucose consumed
ATP and/or ADP cellular content[1]	Normal	Low ATP	Low ATP and high ADP
Oxygen content[2]	8.0-8.5 mg O_2 L^{-1}	1.5-6.0 mg O_2 L^{-1}	0 mg O_2 L^{-1}

8.5 mg O_2 L^{-1} = 21% O_2 = 270 µM O_2 = 100% O_2 saturation. The oxygen content defined for each condition is not the same for all species.
[1]Moore et al. (2002); Sweetlove et al. (2010).
[2]Moore et al. (2002); Arnholdt-Schmitt et al. (2006).

to O_2 diffusion between different plant tissues (Gibbs and Greenway, 2003) such as roots and stems (van Dongen et al., 2011).

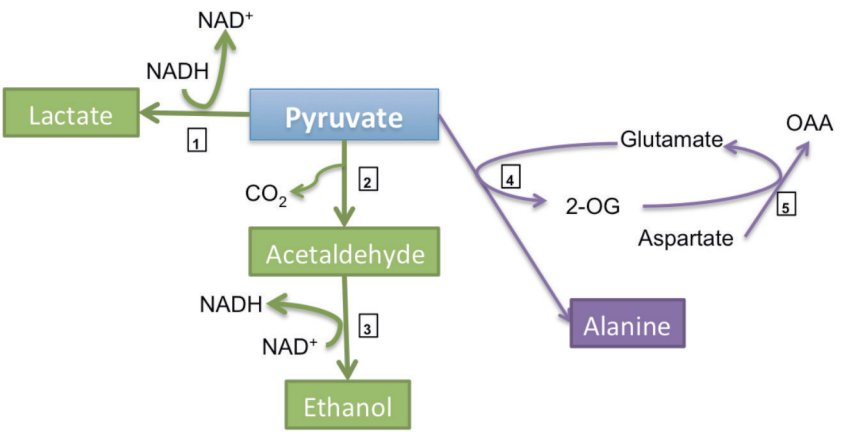
Sometimes, to reduce the anaerobic state in shoots, roots regulate frequency of absorption (Armstrong et al., 1994; Zabalza et al., 2009) and oxygen consumption (Mancuso and Marras, 2006). Morphological adaptations also play a key supporting role in promoting the O_2 flux from the roots through the rest of the plant, e.g. aerenchyma formation due to induction by ethylene (Greenway and Gibbs, 2003). One of the main effects of anaerobiosis on metabolism is a decreased adenylate energy charge (AEC), which also reduces the ATP:ADP ratio (Drew et al., 2000).

Under hypoxic conditions the TCA cycle pathway gives more flexibility to the overall metabolism (Table 1). For instance, in *Lotus japonicus*, it was shown that alanine aminotransferase (AlaAT) generates a link between glycolysis and the TCA cycle through the conversion of 2-oxoglutarate to succinate. This generates NADH that is used in the transformation of OAA into malate; together with succinate CoA ligase, both contribute to the generation of ATP under conditions of oxygen deficit (Geigenberger, 2003; Bailey-Serres and Voesenek, 2008).

Moreover, glycolysis is affected when O_2 concentration falls below 1.5-2.0 mg O_2 L^{-1} in the bulk solution (hypoxia). This decreases glycolysis and increases the activities of enzymes involved in fermentation (Li et al., 2010). In maize subjected to hypoxia, PDC activity increases 5-to-9-fold compared to that under normal conditions (Gupta et al., 2009). It is known that there are two major control points for electron transfer under oxygen deficit, corresponding to AOX and COX. Some studies suggest that the response to oxygen deficiency in roots is driven by the terminal oxidation of respiration (Kennedy et al., 1992). Under some conditions, when the availability of O_2 in roots is decreased, adaptation to stress may occur through two strategies; the first is a decrease in ATP consumption which leads to a metabolic crisis at the cellular level (Igamberdiev et al., 2010), and the second is an increase in the glycolytic flux (Mancuso and Marras, 2006). The latter is called the "Pasteur effect" (Gibbs et al., 2000), consisting of a progressive acceleration in carbohydrate metabolism that allows the plants to maintain their energy level, especially during the early phase of acclimation to oxygen deficiency (Turner, 1951; Greenway and Gibbs, 2003; Camacho-Pereira et al., 2009; Wegner, 2010).

Although many authors emphasize the importance of the "Pasteur effect" in acclimatization processes to compensate for the energy inefficiency caused by OXPHOS inhibition (Gibbs and Greenway, 2003; Huang et al., 2008), this can only generate ATP at about 37.5% of the rate produced in tissues under optimal oxygen conditions (Geigenberger, 2003).

The O_2 is a molecule that participates as a final electron acceptor in the transport chain complexes (Gibbs and Greenway, 2003); therefore, when oxygen availability decreases dramatically in the rhizosphere (anoxia, Table 1), OXPHOS is inactivated (Moller, 2001) and terminal oxidase (COX) is inhibited (Liao and Lin, 2001; Greenway and Gibbs, 2003; Mancuso and Marras, 2006; Mailloux et al., 2007). Under these conditions, plants have developed alternative pathways to aerobic respiration in order to maintain glycolysis through the regeneration of NAD^+ (Gupta et al., 2009) and thus obtain the energy needed to maintain key processes of metabolism such as membrane integrity and thus ion selectivity (Tadege et al., 1999), protein synthesis and turnover and regulation of cytosolic pH, among others (Blokhina et al., 2003). These alternative pathways are known as fermentations.



Source: Author based on Gupta et al. (2009).

OAA: Oxaloacetate.

Figure 5. Representation of anaerobic respiration. Green boxes and arrows show the lactic acid and alcoholic fermentation. Purple boxes and arrows show the cycle that involves alanine.

Three fermentative pathways are known (Greenway and Gibbs, 2003) that are active under conditions of oxygen deficiency (Figure 5): alcoholic fermentation, lactic fermentation (Sousa and Sodek, 2002) and the alanine pathway; the last one is specific to plants and its final product is alanine from glutamate and the pyruvate reaction (Tadege et al., 1999). There are also other final products of fermentation such as succinate, malate, and γ-aminobutyric acid (Dennis et al., 2000).

From the energy point of view, fermentative pathways can produce between 5% and 10% of the ATP per mole of glucose oxidized in aerobic respiration (Drew, 1997; Sousa and Sodek, 2002). In the roots of grapevines, for example, under normal conditions about 22.5 nmol ATP g^{-1} fresh weight are obtained, but in anoxia only 2 nmol ATP g^{-1} fresh weight are produced (Geigenberger, 2003).

The activation of a fermentation pathway is usually initiated when an anaerobic event occurs (Tadege et al., 1999; Bailey-Serres and Voesenek, 2008); later, the pyruvate is reduced to lactic acid by lactate dehydrogenase (LDH) in the cell's cytoplasm (Tadege et al., 1999). LDH acts at a pH near 7.4 (Kato-Noguchi and Morokuma, 2007) and is responsible for maintaining the redox balance without the loss of C associated with alcoholic fermentation. However, the accumulation of this enzyme leads to a decrease in cytosolic pH to levels between 6.4 and 6.8 (Tadege et al., 1999). Acidification of the cytoplasm inactivates LDH and activates pyruvate decarboxylase (PDC) (Roberts et al., 1984), which decarboxylates pyruvate and forms acetaldehyde, which in turn is finally reduced to ethanol by alcohol dehydrogenase (ADH) (Felle, 2005). In *Vitis riparia* Michx. and *V. rupestri* Scheele plants subjected to anoxia during 24 h, both species showed high levels of ethanol as the principal component of fermentation, yielding 225 and 175 μmol g^{-1} fresh weight (*V. riparia* and *V. rupestri*, respectively) at 20 h of treatment. Under normal conditions the level was 40 μmol g^{-1} fresh weight (Tadege et al., 1999; Kato-Noguchi and Morokuma, 2007). The importance of alcoholic fermentation in tolerance to oxygen deficiency has also been shown in rice, where the response of different cultivars to 48 h of anoxia has been demonstrated. This study showed that at the end of the treatment LDH activity was insignificant. In contrast, PCD and ADH activities were, on average, were induced 9-fold compared with their status in the same coleoptiles under normal conditions (Mancuso and Marras, 2006).

Evaluation in *Arabidopsis* mutants has indicated that overexpression of PCD and ADH promotes stress tolerance during oxygen deficiency, because the carbon flux is controlled through alcoholic fermentation and through the lactate and alanine pathways (Kato-Noguchi and Morokuma, 2007). Nevertheless, additional information about the special features associated with fermentative pathways, and specifically alcoholic fermentation, where the absence of oxygen would not be responsible for inducing enzymes such as PCD and ADH, is highly desirable (Kennedy et al., 1992; Rahman et al., 2001; Ismond et al., 2003; Kursteiner et al., 2003).

CONCLUSIONS

Plant respiration is a highly dynamic process, because the pathways involved present a high capacity to adapt to different environmental conditions. Glycolysis is one of these pathways; controlling several reactions in which exist two key enzymes participating as control points: hexokinase and pyruvate kinase. Both enzymes can control glycolysis not only in mitochondria but also at a posttranslational level.

The tricarboxylic acid (TCA) cycle has a strong influence on respiration metabolism through enzymatic control. The TCA cycle is not only involved in regulating the respiration rate, but also participates in the synthesis of intermediates of the same cycle such as isocitrate, malate, and succinate. In turn, the TCA cycle regulates some key processes in photosynthetic metabolism such as CO_2 assimilation. The existence of alternative pathways such as GABA and the glyoxylate cycle gives the TCA cycle further plasticity in adapting to environmental changes.

There is little information with respect to the link between energy for respiration and processes important for a plant metabolism. Components of respiration associated with growth and ion uptake are highly dependent on factors such as the species, plant organ and environmental conditions affecting the relative growth rate and net N uptake rate coefficients. The maintenance component also responds favorably to rapid changes in the environment, due to its high capacity to modify protein turnover in the cells.

A plant's capacity to tolerate anaerobic conditions not only relates to biochemical properties of the roots, but also the plant's capacity to transport O_2 transport from oxygenated organs to anoxic organs. Both glycolysis and fermentation are principal mechanisms of energy maintenance in the cells and their function is important in a plant's tolerance to O_2 deficiency.

Plant respiration is considered a principal mechanism of ecosystem maintain on the planet. Therefore, it is important that new research should focus on predicting the impact that climate change will have on respiratory metabolism, especially at the functional and genomic levels.

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