



REVIEW ARTICLE

EFFECT OF LIMITED NUTRIENT AVAILABILITY ON THE DEVELOPMENT AND RELEVANCE OF ROOT CORTICAL AERENCHYMA

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Abstract

During the growth of plants, they have to cope up with various stresses which include limited availability of nutrients and also lack or excess of water in the soil. To ensure the survival, plants carry out changes in their above and below ground parts. While the shoot must ensure the capture of light for optimum photosynthesis, the supply of water and nutrients essential for this is to be made by the roots. During these stresses, the external form and internal anatomy of the roots is also changed. One such feature in the root anatomical adaptation is the development of root cortical aerenchyma (RCA). Root cortical aerenchyma develops in plants under different stress conditions which include the limited availability of nutrients like nitrogen, phosphorus, sulphur and flooding or even drought. RCA serves many functions for the plants, which include not only the continued exploration of nutrients in the soil when they are in limited supply, but also to ensure the proper availability of oxygen for the respiration of cells in the roots in the flooded conditions.

Keywords : Root cortical aerenchyma, Nitrogen, Phosphorus, Sulphur

Introduction

Underground parts of the plants such as roots and rhizome fulfill their respiratory oxygen demand from the soil. But in situations when the soil becomes wet, transfer of O₂ from the air to soil gets blocked as large soil pores which usually remain air filled, get filled with water. In such situations, aerenchyma (tissue with large intercellular spaces; Esau, 1977) comprising of gas filled spaces or lacunae, provides the plants with alternative route to O₂. Formation of aerenchyma in plants is a morphological change, taking place (normally) under flooded or hypoxic condition, and enhances the distribution of atmospheric and photosynthetic oxygen from the aerial parts of the plant to the flooded roots. This facilitates aerobic respiration in the roots. Aerenchyma tissues are of two types, one is cortical aerenchyma or primary aerenchyma which forms in the roots of rice, maize, barley and wheat (Nishiuchi *et al.*, 2012), and the other is white and spongy tissue that remains filled with gas spaces and is formed in the stem, hypocotyle, tap roots, adventitious roots and nodes of roots in legumes (Mochizuki *et al.*, 2000; Walker *et al.*, 1983).

Root cortical aerenchyma has numerous lacunae that are interconnected and extend from the root to stem and leaves, and make up an internal aeration system providing the much needed oxygen to the parts of the plant with limited or negligible access to it. The gas filled spaces form within the aerenchymatous organs either by separation of cells at the middle lamella during the development, called shizogeny, or, by the death of cells or dissolution called lysisgeny. In some plants like *Sagittaria lanatifolia*, both of the processes can be observed wherein lysisgenous aerenchyma is formed in the roots and shizogenous aerenchyma in the petiole of leaves (Shussler and Longstreth, 1996). During lysisgenous aerenchyma formation, cell death has been initially detected at some distance (~1cm or less) from the root apical meristem, in the zone of the cells where the process of cell elongation just gets completed (Campbell and Drew, 1983; Kawai *et al.*, 1998). The empty space created by cell death becomes prominent in comparatively older zones behind the tip. Thus, it can be seen that the gas filled lacunae develop

acropetally, and extend into the root towards the tip, concurrent with the extension of roots into the soil.

Development of aerenchyma

Although the formation of aerenchyma is generally attributed to flooding of soil, for example in some varieties of maize (Drew *et al.*, 1989), in *Spartina patens* (Burdick, 1989), and many other wetland plants both monocot and dicots (Justin and Armstrong, 1987). In several other plants like *Tripsacum dactyloides* (eastern gamagrass), *Zea luxurians* (teosinte; Ray *et al.*, 1999), rice (Kawai *et al.*, 1998; Jackson *et al.*, 1985) and *S. lancifolia*, aerenchyma formation is observed constitutively, without any external stimulus requirement. Tolerance to drought and flooding as seen in eastern gamagrass is attributed to its deep rooting and constitutive aerenchyma (Clark *et al.*, 1998). The plant possesses roots extending up to 1.8m in depth, penetrating the resistant clay pan below 0.9m, which happens during the period when the soil remained wet and mechanically least resistant. During this period, aerenchyma probably assists in oxygenation of the tissues. Since soil compaction lowers the oxygen concentration of the soil, therefore, aerenchyma could become beneficial for growth or function of roots in densely packed layers of soil. These facts explain the functional significance of induction of aerenchyma by mechanical impedances observed in maize (He *et al.*, 1996).

As aerenchyma can develop in two ways: either due to stress such as water logging, limited availability of nitrogen, phosphorus, and under limited water availability, or, constitutively. Constitutive aerenchyma formation could be of advantage in certain situations, and for the very reason constitutive aerenchyma formation has been transferred successfully from eastern gamagrass and teosinte to maize by hybridization followed by backcrossing (Ray *et al.*, 1999). During this study a major gene for aerenchyma formation was found in eastern gamagrass. In crops such as soybean (Bacanawo and Purcell, 1999) and *Ranunculus* (He *et al.*, 1999) growing in floodplains, aerenchyma formation is seen to be linked with flooding tolerance.

The important role played by aerenchyma in the root tissues is that it not only provides an internal passage for oxygen transfer, but also brings down the number of cells that consume oxygen.

Lysigenous development of aerenchyma

Under laboratory studies, hypoxia conditions are reported to easily induce the formation of aerenchyma in the roots of maize, similarly hypoxia could be the reason for induction of aerenchyma in flooded soils. It has been proposed that hypoxia condition could be of more common occurrence than otherwise considered, this arises due to the fact that even in well oxygenated environments, the rate of consumption of oxygen during respiration, is more than the rate of oxygen supply in these spiring cells (Ober and Sharp, 1996).

Lysigenous aerenchyma formation requires the initiation of programmed cell death, which is also observed in various other developmental processes in higher plants, for example, development of tracheary elements (Mittler *et al.*, 1995), root cap cells (Wang *et al.*, 1996), degradation of tapetum cells to carry out development of pollen grains (Davies *et al.*, 1992), and formation of sexual organs (Delong *et al.*, 1993). Thus the suicidal capability of individual cells is essential for the development of multicellular organisms.

Ethylene is particularly reported to be a responsible factor for the induction of aerenchyma particularly in maize roots (Drew, 1997), and it has been shown that under well oxygenated condition, even low concentration of ethylene induce cell death. The findings are counter confirmed when inhibitors of ethylene action or ethylene biosynthesis block the formation of aerenchyma in hypoxic roots, while in ethylene treated roots only the inhibitors of ethylene action were found to provide the same results. Hypoxia stimulates ethylene biosynthesis and the activity of 1-aminocyclopropane-1-carboxylic acid (ACC) synthase, and of ACC oxidase increase in extracts from hypoxic roots approximately after 3 hours. Mechanical impedance is also known to increase the activities of these enzymes. When plants are subjected to both hypoxia and mechanical impedance, their effects could be synergistic. Although the formation of aerenchyma in rice is known to be constitutive, in some of the varieties, additional cell death is observed in response to ethylene treatment or hypoxia (Kawai *et al.*, 1998).

In contrary to the requirement of ethylene for initiating the development of aerenchyma in maize, in certain varieties of rice (*Oryza sativa* L.cv. RB3) the formation of aerenchyma was not controlled by ethylene or even a low oxygen level. (Jackson *et al.*, 1985), however, in some other cultivars like BC6, IR8, IR22 and Padma, flooding was found to increase the rate of aerenchyma formation (Das and Jat, 1977).

The process of formation of aerenchyma is reported to differ in maize and rice. In the roots of maize, before the collapse of cells, the tonoplast is reported to lose its integrity (Campbell and Drew, 1983), while in rice, the middle lamella gets degenerated, which is followed by disintegration of the cell wall and then the tonoplast gets disturbed (Webb and Jackson, 1986). In comparison to maize, the aerenchyma of rice is formed rapidly as an integral part of the ordinary root development (Jackson *et al.*, 1985).

The process of lysigenous aerenchyma development is comparatively better explored in case of rice. During the development, death of cells begins at some specific position, and the first cells to crumple are usually located at the center of the cortical tissues. The process of cell death is usually not initiated at the peripheral part (Kawai *et al.*, 1998). As the location of the cells which undergo lysis was found to be very precise, this points to the fact that there exists a targeting mechanism which initiates the first cell death. The characteristic feature of these cells was that they appeared shorter but had large radial diameter than the other surrounding cells. During the development of aerenchyma there is enlargement of cortical cells. In *Sagittaria lancifolia* roots also, it has been shown that cells to undergo lysis had larger diameter (Schussler and Longstreth, 1996). Indirect reasoning for the enlargement of cells has been demonstrated from the study in sunflower stem where the cells treated with cellulase enlarged radially, and some of them disintegrated, leading to the development of intercellular spaces (Kawase, 1974). The expansion of cells was reasoned to be due to the change in cell walls, and the radial cell enlargement was an induction of cellulase acting on the microfibrils which are normally transversely oriented. Since cellulase activity is found to increase upon exposure to ethylene (Horton and Osborne, 1967), it further supports the important role of ethylene in the development of aerenchyma.

Aerenchyma under flooded conditions

The adaptive significance of aerenchyma in flooded soil arises due to the fact that aerenchyma improves the oxygenation of root tissues due to flow of oxygen from shoots to roots through diffusion (Grosse *et al.*, 1991). The additional advantage in case of C₃ plants is concentration of CO₂ from root respiration and channeling it to the leaf intercellular spaces, enabling better photosynthetic output (Constable and Longstreth, 1994).

Aerenchyma under limited nutrient availability

Most of the research on aerenchyma has concentrated on its significance during hypoxia, but this development can also be an adaptive strategy of plants under limited availability of various nutrients in the soil. For example, aerenchyma development has been reported in adventitious roots of maize under limited availability of nitrogen and phosphorus (Konings and Verchuren, 1980), similar observations were also reported in case of common bean (Eshel *et al.*, 1995) and rice also (Lu *et al.*, 1999).

The argument that aerenchyma facilitates gas movement within the plant in flooded condition seems well justified; however, its relevance under limited supply of soil nutrients needs further exploration.

(I) Aerenchyma under N limited condition

Production of maize worldwide is principally limited by the availability of nitrogen (Ladha *et al.*, 2005). While contamination of surface and groundwater with nitrates poses health risks, like methemoglobinemia and N-Nitroso-induced cancers (UNEP and WHRC, 2007), nitrous oxides when emitted due to agricultural activities become responsible for the damage to ozone layer, and also a factor for global warming (Sutton *et al.*, 2011).

Production of nitrogenous fertilizers is a costly affair, and therefore proper application of these fertilizers and utilization is need of the hour. Although the quantities of N

fertilizer applied in the field could be very high in some regions, less than half of the applied N is actually required and properly utilized by the crop plants, and the remaining N becomes a source of environmental pollution (Tilman *et al.*, 2002). It has been reported that N and P effluents into the marine systems from agriculture cause eutrophication and hypoxic zones (Robertson and Vitousek, 2009). While the excess application of fertilizers to the soil have unavoidable environmental burden, the production of these fertilizers requires considerable energy from fossil fuels, and with increasing cost of energy with time, farmers in almost every part of the world face severe economic pressure from increasing N fertilizer costs, which are ultimately linked to higher food prices. There have been assessments that even 1% increase in the crop N use efficiency could save more than \$1 billion annually worldwide (Kant *et al.*, 2011).

Nitrogen in soil is distributed heterogeneously and dynamically, its availability to the plants depends on the balance between mineralization, nitrification and denitrification rates in the soil. Each of this process is determined by several factors which include besides several others, soil composition, activity of microbes, temperature of soil and the status of water in the soil (Miller and Cramer, 2004). Since the form of N available to plants in agricultural systems is nitrate, which is quite soluble in water and therefore mobile in the soil (Marschner, 1995), when N fertilizers are applied at the beginning of the growing season, and the fields experience precipitation or are provided irrigation, this creates a pulse of nitrate, that could exceed the capacity of seedling to acquire N. The result is leaching of N below the root zone. Keeping these facts in mind, it has been argued that fast root exploration of deep soil for N could benefit N acquisition capacity of the plants (Lynch, 2013). The arguments sound good, but at the same time it need not be overlooked that there are structural investments and metabolic expenditures in the root systems which are substantial, and at times can exceed half of the daily photosynthetic output (Lambers *et al.*, 2002). Therefore, the situation needs to be analyzed holistically, taking due note of the cost and benefit of root systems that are crucial for identification of root traits, which can help in improving crop production in water and nutrient limited conditions.

It has been previously positively shown that RCA could substantially reduce root respiration and tissue N content. Similarly, a 20% RCA has been responsible for 50% reduction in respiration in seminal root segments of maize, and 30% RCA was found to be essential for similar reduction of root respiration in crown root segments (Saengwilai *et al.*, 2014). Although crown and seminal root anatomy are fundamentally similar, there are differences in size and number of cells in these root classes. Of the two types of roots, crown roots have greater diameter, more cortical cell layers and larger cortical area (Burton *et al.*, 2013). Since root respiration is substantially influenced by living portions of the root segments (Jaramillo *et al.*, 2013), and crown roots have a larger proportion of living tissues than seminal roots, it is expected that more RCA is needed to significantly affect the root respiration in crown roots.]

Increase in RCA content in the roots is associated with reduction in the N content of the roots. It has been found that N from lysed root tissues of plants with high RCA could be used to support growth of plants, which is supported by the findings that high RCA plants had greater root and shoot

growth in comparison to plants with low RCA, in soils with low N content. When N content is low, RCA provides additional benefit to plants as part of the metabolically costly root phenes, such as larger number of crown roots. Since a higher number of crown roots allows more soil volume to be explored, provision of RCA subsists in the expense of root growth and maintenance (York *et al.*, 2013).

(II) Aerenchyma under P limited condition

According to the Rhizo-economic theory (Lynch, 2006), phosphorus deficient plants need to invest more carbon in the nutrient acquisition strategies, e.g., P deficient bean plants (*Phaseolus vulgaris*) need to devote up to 40% of their daily photosynthesis on root respiration, wherein up to 89% of the root respiration is devoted for the maintenance of the existing tissues. On the other hand maize and bean roots with RCA experience reduction in root respiration. Formation of RCA can help in economic utilization of less available phosphorus depends on the fact that air spaces in the RCA do not contain phosphorus and hence, save valuable quantities of the nutrient. Although it has been argued that the phosphorus saved by RCA is small quantitatively, it can have significant effect in due course of time because even a small improvement in the phosphorus status of the plant supports greater growth rates, which in turn enables greater soil exploration and further acquisition of phosphorus (Wissuwa, 2003). It has been proposed that induction of aerenchyma under low availability of phosphorus could be an adaptive strategy by reducing the respiratory requirement and phosphorus concentration of the root tissues, which simultaneously reduces the metabolic burden of exploration of soil (Lynch and Brown, 1998). Plants with RCA are reported to be less stressed and grew faster when phosphorus was suboptimally available. In terms of growth over time, plants with RCA (maize) grew up to 70% larger than plants without RCA (Postma and Lynch, 2011).

Although aerenchyma helps to save valuable P in the root tissue, its presence is reported to interfere with the radial transport of some nutrients also. For example, aerenchyma formation is reported to reduce the uptake of phosphates in 14 to 16 day old plants (Hu *et al.*, 2014). The radial transport of the nutrient involves both the apoplast and the symplast, and it has been observed that for nutrient ions to enter via the symplastic pathway, they can use all the cell types that are outside the endodermis (Tester and Leigh, 2001). Formation of aerenchyma was found to interfere with the transport of phosphates through the symplast (and similarly to sulphates, because of similar size and charge), by bringing down the number and surface area of living cells that occupy the space between the epidermis and the stele. The transport of nutrients via the apoplastic radial pathway involving the cortex is also very difficult due to few intercellular routes possible. It has been argued therefore that if part of aerenchyma is lined or filled with aqueous solution (Van der Weele *et al.*, 1996), it is possible for the ions to diffuse along the inside of the lacunae and then to be taken up by the cortical cells.

(III) Aerenchyma under sulphate starvation

Development of aerenchyma under flooding of soil, and also limited availability of nitrogen and phosphorus is well documented. Along with these observations, research is being extended to study its relevance and utility under limited availability of sulfur also (Bouranis *et al.*, 2003). When plants are deprived of sulphates, aerenchyma is

reported to start developing in the roots and gets fully developed by 12 days (Bouranis *et al.*, 2003). The development of aerenchyma was lysigenous and the process of lysis started from the middle cells of the cortex, where the cells were comparatively larger in comparison to other cells. Gradually there remain only chains of cells bridging the hypodermis to the endodermis and stele of the roots in the experimental plant maize. Most of the aerenchyma development was observed in S deprived plants and to a much lesser extent in S supplied plants. It was also reported that the cell walls of the hypodermal cells of the S deprived plants, were comparatively more suberised in comparison to plants with optimum supply of S. Similar to the utility of aerenchyma under N and P limited conditions, cell death and lysis during aerenchyma formation under S limitation is advantageous in providing essential inorganic nutrients and metabolites which maintain the activity of meristematic cells. During the formation of aerenchyma in the root cortex, nuclei of cells undergoing programmed cell death contain fragmented DNA (Mittler and Lam, 1995). This indicates the activation of DNA degradation mechanism prior to the final disruption of the nucleolus that occurs during the autolysis in the cell group. During the development of aerenchyma in S deprived plant roots, there was higher Ca^{2+} concentration in the endodermal and epidermal cell walls after 12 days of treatment (Bouranis *et al.*, 2003), which is attributed to elevated hydrogen peroxide.

Conclusion

Although the development of aerenchyma was primarily considered to be the result of hypoxic condition (flooding) in the soil, its significance under various other stressful conditions is being recently understood. Under the flooding, aerenchyma facilitates the easy diffusion of oxygen essential for respiration, from the aboveground parts of the plants to root cells. The same anatomical feature, which is extensive formation of lacunae in the root cells, reduces the metabolic burden on plants. With the development of lacunae in the cortical tissues, valuable nutrients like nitrogen, phosphorus, sulphur etc. are mobilized from these tissues, as they are not required in the empty spaces formed in the cortical tissues, and utilized elsewhere, either for root growth for exploration of nutrients and water in the soil, or mobilized to above ground parts of the plants for growth of new leaves, which in turn carry out photosynthesis and provide the carbohydrates to the entire plant.

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