

Aspects of an experimental study on root aerenchyma development and the ecological implications thereof

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ABSTRACT

Anaerobic conditions induced cortical aerenchyma in maize roots cultivated in water culture. Similar results were obtained by growing the plants in nitrate and phosphate deficient solutions but the cavitation was more severe when conditions were anaerobic. Low temperatures delayed the onset of these symptoms. Mineral deficiencies also regulated the formation of root hairs in water culture. In the field, the behaviour of the rooting systems in a group of Restionaceae with aerenchyma was interpreted from anatomical and developmental data.

RÉSUMÉ

ASPECTS D'UNE ÉTUDE EXPÉRIMENTALE SUR LE DÉVELOPPEMENT DE L'AÉRENCHYME RADICULAIRE ET DES IMPLICATIONS ÉCOLOGIQUE QUI EN DÉCOULENT

Les conditions anaérobiques ont induit l'aérenchyme cortical de racines de maïs cultivées en aquiculture. Des résultats similaires ont été obtenus en cultivant des plantes dans des solutions déficientes en nitrate et en phosphate mais la formation de cavités était plus importante quand les conditions étaient anaérobiques. De basses températures retardèrent le déclenchement de ces symptômes. Les déficiences minérales réglèrent aussi la formation des poils radiculaires en aquiculture. En champ, le comportement des systèmes racinaires dans un groupe de Restionaceae avec aérenchyme fut interprété à partir de données de développement et de données anatomiques.

INTRODUCTION

Root aerenchyma is a characteristic feature of many submerged water and marsh plants. These root cavities are classically regarded as reservoirs which facilitate the active diffusion of oxygen into the interior of the root (Williams & Barber, 1961).

One of the fundamental characters of anaerobiosis is the change in the root environment resulting from the marked change in the redox potential of the soil solution. This means that not only is there a decrease in the availability of oxygen in the soil but the availability of nutrients to the plant becomes drastically altered. Such variations in the root environment are reflected in differential growth responses of the root. Growth responses of roots are particularly striking as their lack of determinate structures enables a researcher to observe degrees of phenotypic plasticity in root morphology. This has led to the traditional concept of anaerobic responses of the roots in the field and in the laboratory as the formation of aerenchyma and a thickened, shortened root (Bryant, 1934; McPherson, 1939) with a marked decrease in root hair development (Williams & Barber, 1961).

Recently, interest has been revived in the ontogeny of aerenchyma (Kawase, 1979; Konings & Verschuren, 1980). Our studies of the ontogeny of root aerenchyma show degrees of cavitation; the patterns of cavitation are predictable but more variable than we initially expected. Since this variation appeared to be coupled to environmental conditions, we decided to study it further.

Our initial aim was to investigate the parameters regulating aerenchyma development. It was soon

clear to us, however, that oxygen tension was not the only factor inducing the formation of aerenchyma. As anaerobiosis limits the uptake of nutrients in plants we decided to determine the role of nutrient deficiencies in inducing aerenchyma formation. Initially our research material was *Zea mays*, in which cavitation was readily induced by growing it in water culture solutions lacking essential nutrients such as nitrogen or phosphorus. Efforts were made to prevent aerenchyma formation in plants which normally exhibit it, using the same water culture techniques. Here the plasticity of cavitation was investigated using *Elegia capensis*, one of the Restionaceae.

The ecological significance of aerenchyma formation in a few selected key species of the Fynbos Restionaceae from Pella (the Fynbos Biome Research site 80 km north of Cape Town) was investigated in the field and in the laboratory. As the Restionaceae are a large group of plants about which there is scant physiological data and which are very difficult to manipulate experimentally, our results are preliminary and tentative.

METHODS

Water culture techniques were employed for the cultivation of *Zea mays* and *Elegia capensis* using the Long Ashton solution (Hewitt & Smith, 1975). *Zea mays* plants were cultured 7 days after germination and the roots sampled 10 days later. Plants of *Elegia capensis* were approximately 4 months old when cultured and the material was sampled after 3 months.

RESULTS

Induction of cavitation in Zea mays

Variations in cavitation patterns developed under different regimes are shown in Fig. 1. In this study it

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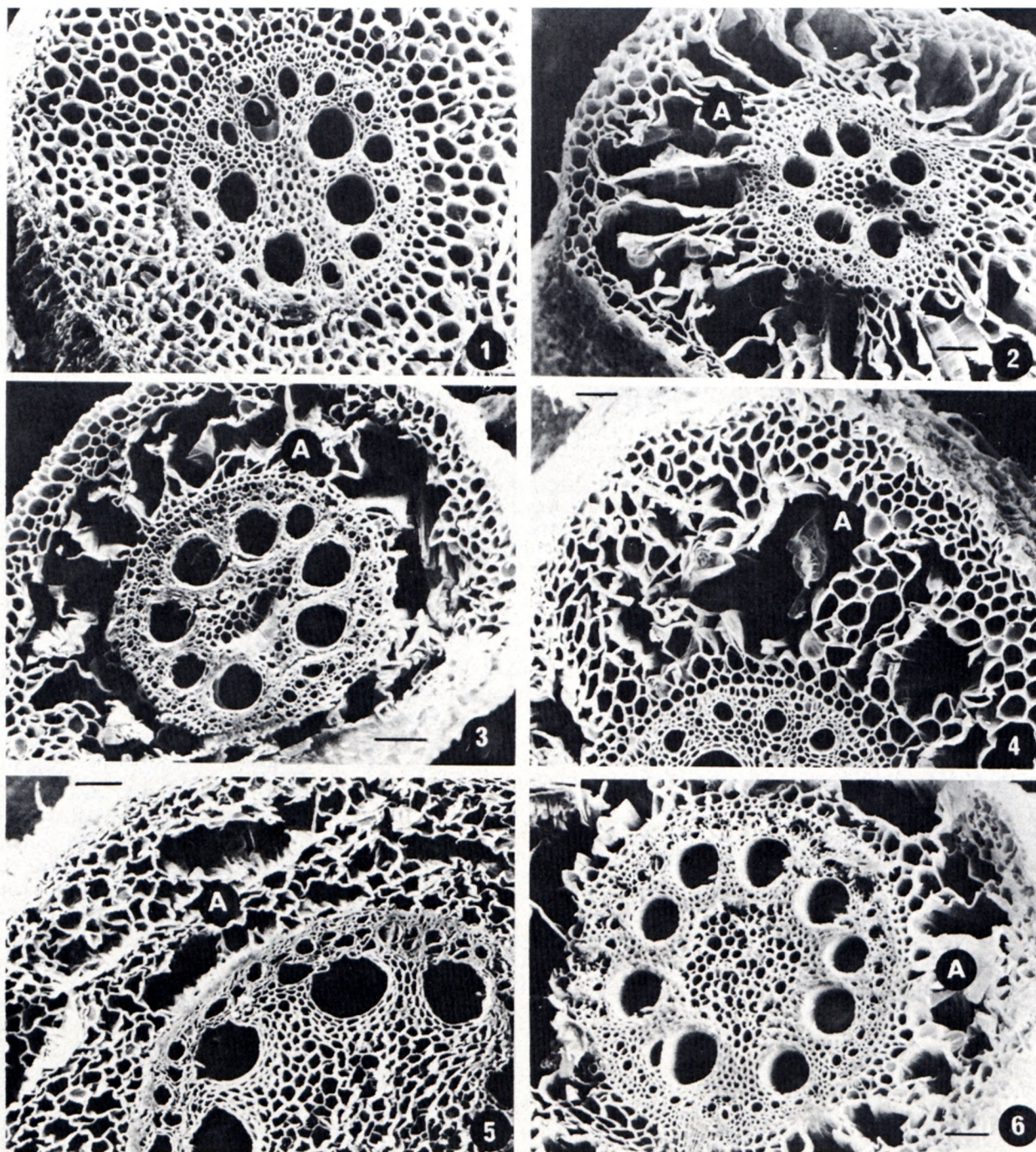


FIG. 1.—Comparison of root cortical development in *Zea mays* under varying experimental regimes. Bar = 100 μ m. 1, Control, full nutrient solution, aerobic conditions; 2, Control, distilled water only, aerobic conditions; 3, Nitrate deficient medium, anaerobic conditions; 4, Nitrate deficient medium, aerobic conditions; 5, Phosphate deficient medium, anaerobic conditions; 6, Phosphate deficient medium, aerobic conditions. A = Aerenchyma.

was noted that the occurrence of aerenchyma, in relation to the root tip, varied markedly depending on the nutrient deficiency and ambient temperatures. These results are shown in Table 1.

Our experimental results show that the rate at which aerenchyma appears is related to the availability of nutrients and that this availability is modified by aeration of the substrate. Low temperatures slow down the plant metabolism of the plant and the distance, from the root apex at which cavitation is first noted, is far greater than that determined at higher temperatures. Aerenchyma develops earlier in roots under anaerobic treatments

regardless of the nutrient deficiency in the culture medium.

Induction of non cavitation in ELEGIA capensis

Elegia occurs in swamps with exceptionally low nutrient levels. We were unable to cultivate it in standard nutrient media (water culture methods). It does, however, thrive in water culture with only micronutrients added. Aerenchyma formation is repressed in aerated solutions.

These simple experiments show that the rooting systems can be manipulated to induce or repress cavitation and that certain factors such as oxygen

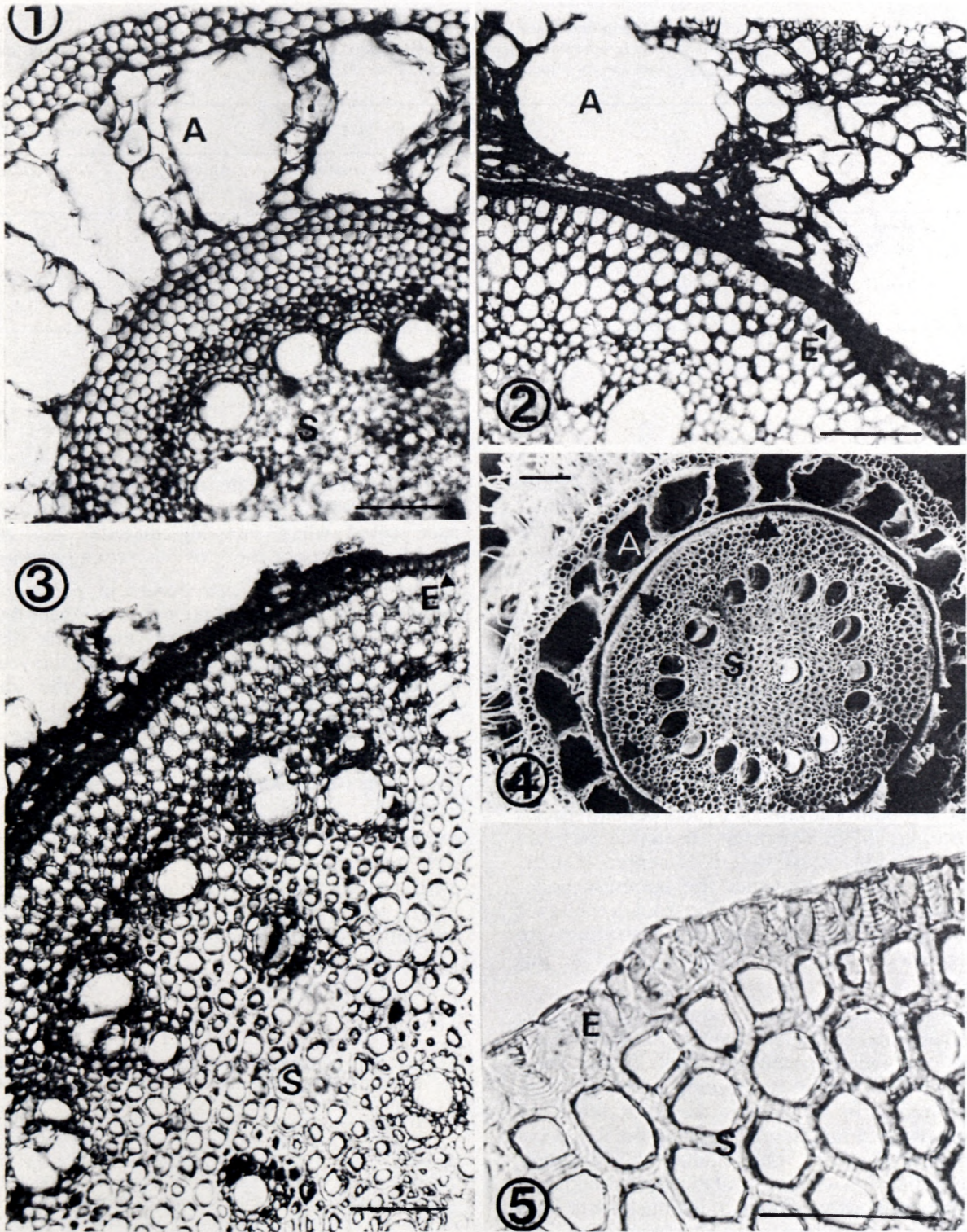


FIG. 2.—Root development in *Cannamois* showing possible relationship between thick and thin roots. Bar = 100 μ m. 1, Transverse section of thick root showing initial aerenchyma development; 2, Transverse section of thick root showing thickened cells of the endodermis and cortical region; 3, SEM micrograph showing initial stage (see arrows) in the 'sloughing off' of the cortical region. Note dense roothairs; 4, Transverse section of thin root showing remnants of the cortex adjacent to the endodermis; 5, Transverse section of thin root showing thickened endodermal cells. A = aerenchyma; E = endodermis; S = stele.

TABLE 1.—A comparison of the effects of nutrient deficiencies on aerenchyma formation in *Zea mays* grown in aerobic or anaerobic water culture for 10 days at two different temperature regimes. The formation of aerenchyma was related to the distance in mm, from the root apex at which cavitation was first noted

		Temperature 28° C		Temperature 12° C	
		Aerated solution	Non-aerated solution	Aerated solution	Non-aerated solution
Nutrient deficiency	Nitrate	25	15	60	44
	phosphate	28	20	152	130
Control	Distilled water	20	10	40	27

Sample size 20 plants per treatment. SD = 1,23

tension, nutrient status and temperature are clearly implicated. Armstrong (1971) came to similar conclusions and his studies on rice showed that 'the extensive gas-space development in the roots is an obvious response to conditions associated with soil anoxia and may be delayed, reduced or even prevented if the soil is made aerobic.'

ECOLOGICAL IMPLICATIONS

The specific adaptations of plants to cope with conditions of nutrient imbalance is still speculative (Epstein, 1972). Aerenchyma formation is an obvious adaptation to the wetland condition and it is at best only poorly developed in non-wetland species (Armstrong, 1979). The occurrence of aerenchyma in the Restionaceae is well documented (Cutler, 1969) and rooting strategies are currently under investigation (Stock, 1981). The root systems of *Elegia*, *Wildenowia*, *Cannamois* and *Hypodiscus* are among those that are being investigated in this study.

The group comprising *Wildenowia*, *Cannamois* and *Hypodiscus* exhibit two types of roots during the spring and winter months, thick fleshy roots commonly referred to as 'feeding roots' and thin fibrous roots. In *Cannamois* the thick roots are approximately 5 mm in diameter and the thin roots 1.5 mm in diameter. Our studies of *Cannamois* during spring and winter reveal the rapid production of new foliage, active growth of the thick roots, with concomitant aerenchyma development (Fig. 2.1) and a high transpiration rate of $4\text{g}/\text{dm}^2/\text{h}$. [cf. *Citrus*, $7\text{g}/\text{dm}^2/\text{hr}$ (Salim & Todd, 1965)]. It would appear that these thick aerenchymatous roots are produced in response to lower soil temperatures (Stock, 1981), low nutrient status (Stock, 1981) and an anaerobic root environment as a result of persistent winter rain. As seasonal temperatures rise, the soil dries out thereby improving aeration of the substrate, the aerenchymatous cortex is characterized by marked suberization and lignification of the cells (Fig. 2.2). Finally, the cortex disintegrates and is 'sloughed off' (Fig. 2.3) resulting in the thin fibrous type of root (Fig. 2.4). In this root the endodermis is markedly thickened (Fig. 2.5) and appears to be 'water-proofed' as a result of lignin and suberin deposits

thereby sealing off the central stele during the summer months. This then forms the thin fibrous root noted when sampling material and could therefore represent the previous year's growth.

By comparison, *Elegia* occurs in permanently moist soils in swamp-like areas and has been noted to have a predominance of the thick fleshy aerenchymatous type of root throughout the year in marked contrast to that noted in the above mentioned species. As *Elegia* is not subjected to the periodic gradual drying out of the root environment, the aerenchymatous cortex remains intact. These thick roots were manipulated during initial studies.

At this stage the whole phenomenon of root aerenchyma development appears to be associated with the water relations and nutrient supply of the plant. Aerenchyma development demonstrates a rapid, plastic response to the environment with fascinating ecological and physiological implications.

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