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Root adaptations of Mediterranean species to hypoxia and anoxia

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ABSTRACT

Mediterranean species are popular ornamentals in the UK. Originating from climatic zones of hot dry summers and mild wet winters they exhibit features of drought adaptation, and are therefore suited to the predicted climate change scenarios of hotter drier summers. This work investigates how these species will respond to the predicted wetter winters and increased frequency of spring and summer flooding. Initial work on flooding of four Mediterranean species in a pot experiment, showed that the detrimental effects of waterlogging were only severe when the temperature was high and flooding prolonged. To examine the response of roots to oxygen deprivation over a range of conditions from total absence of oxygen (anoxia), low oxygen (hypoxia) and full aeration, small plants of *Salvia officinalis* were grown in a hydroponics-based system and mixtures of oxygen and nitrogen gases bubbled through the media. When the plants were subjected to a period of 5 days of hypoxia they responded by increasing the production of lateral roots in the upper part of the root system. This enabled them to acclimate and survive a subsequent period of 5 days anoxia. A rapid onset of 5 days of anoxia from full aeration caused serious loss of root and inhibited further lateral root production. There was no evidence that these species increased their root porosity, during periods of hypoxia as hydrophytes readily do, so it is concluded that a rapidly developing flexible root system is their strategy for surviving periods of waterlogging.
KEYWORDS: waterlogging, flooding, lateral roots, root porosity

1. INTRODUCTION

Mediterranean shrubs are drought adapted and generally exhibit the typical morphological characteristics associated with reducing evapotranspiration. These adaptations can include reduced size, upright orientation, grey colouration and hairiness of leaves or the production of sclerophyllic leaves which are thick leathery leaves with a waxy cuticle and reduced stomatal size (Dallman 1998). Two water seeking strategies are developed in root systems; either the development of tap roots to access deep water resources or the development of a shallow, wide, spreading surface mat designed to intercept infrequent showers or coastal fogs. These roots although confined to the top 20cm consist of many fine roots and spread far beyond the upper parts of the plant crown. (Kumerow 1981).

Mediterranean plants are popular garden and landscape plants in the UK. Climate change models predict the UK climate moving towards temperatures experienced in Mediterranean Climate Zones today. However average annual precipitation although predicted to decrease by about 10 per cent will be redistributed through the year, with a decrease in summer precipitation and an increase in winter precipitation (Hulme et al. 2002). In addition the frequency of damaging storms (summer and winter) has increased over recent years and soil sealing within urban areas intensifies storm run-off and increases flood risk.

Mediterranean species will be well suited to the predicted hotter drier summers but may be at greater risk of injury and death in warmer and wetter winters or periods of summer flooding, especially in the context of the UK where many of our soils are heavy textured and slowly permeable compared to the free-draining soils of the Mediterranean scrublands (Bisgrove and Hadley 2002).

Preliminary work on flooding of four Mediterranean species (*Lavandula angustifolia* ’Munstead’*, Salvia officinalis, Stachys byzantina and Cistus x hybridus (syn. C. x corbariensis*) in a pot experiment, showed that the effects of waterlogging were only severe when the temperature was high (22 – 39 ^{o}C) and flooding prolonged (17 days). All plants survived the flooding in winter, but during the summer a 17-day flood resulted in the death of about one third of *Salvia officinalis* and *Cistus x hybridus (syn. C. x corbariensis*). In view of the evident ability of these species to survive some degree of waterlogging, this work sought to understand the effects of oxygen depletion on the structure and anatomy of the root system using *Salvia officinalis* as the indicator species. As hydrophytes acclimate to anoxia through a preceding period of hypoxia, a range of oxygen concentrations were studied from the total absence of oxygen (anoxia), low oxygen (hypoxia) to full aeration, to ascertain if Mediterranean plants showed any ability to acclimate.

2. METHOD

Young plants were grown in a sealed hydroponic system and gases were circulated through the root zone to regulate oxygen status. Full aeration was achieved by circulating atmospheric air, anoxia by circulating oxygen-free nitrogen gas, and hypoxia by circulating a mixture of 3% oxygen in nitrogen, through the root zone. The treatments compared an aerated control with different combinations of hypoxia and anoxia, shown in Table1. After 10 days all treatments were re-aerated for a 7-day recovery period. Each plot consisted of four plants inserted into a 4 L sealed plastic container and the five treatments were replicated 8 times in a randomised block design and the experiment repeated 3 times. Plants were assessed for maximum root length, development of young lateral roots and shoot borne roots, and root porosity.

Table1. Experimental treatments

Treatment	Duration
Control	Fully aerated for 10 days
Short hypoxia	5 days air , 5 days hypoxia
Long hypoxia	10 days hypoxia
Anoxia	5 days air, 5 days anoxia
Hypoxia followed by anoxia	5 days hypoxia, 5 days anoxia

3. RESULTS AND DISCUSSION

All treatments showed significant reduction in the longest living root compared to the control ($p = <0.001$). Anoxia caused a serious reduction in root growth both where it was preceded with either full aeration or hypoxia resulting in a reduction in root length of more than 50%. Hypoxia alone also significantly reduced root length, with greater effect the longer the duration of hypoxia This reduction in root growth appeared to be the result of slowed root growth and root dieback. Dieback was particularly evident when anoxia was preceded by full aeration and a proportion of the plants subsequently died; 27% compared to 5 % death where plants experienced 10 days of hypoxia or 5 days of hypoxia followed by 5 days of anoxia. There were no deaths where the plants experienced 5 days of hypoxia or full aeration.

The actual numbers of young lateral roots produced and their distribution with depth after the treatment period are given in Fig 1. Fully aerated plants produced most of their lateral roots at the lower parts of the root system, maintaining only about 10% above 40 mm depth. Plants that experienced hypoxia for 10 days or hypoxia followed by anoxia, maintained at least the same total number of lateral roots per plant as the control plants. However they redistributed them and proliferated significantly more lateral roots in the upper part of the root system close to the stem base ($p = <0.001$); plants receiving 5 days of hypoxia followed by 5 days of anoxia produced 58 of their lateral roots above 40 mm and plants receiving 10 days of hypoxia produced 42% of their lateral roots above 40 mm. In a natural soil system this has the advantage of developing roots close to the soil surface where there is a greater chance of finding oxygen when waterlogging occurs. In contrast, the sudden onset of a period of 5 days of anoxia had devastating effects on the root system resulting in an almost total loss of lateral roots. This confirms the ability of *Salvia officinalis* to acclimate to anoxia through a preceding period of hypoxia.

Shoot borne roots also have a role to play in maintaining the survival of root systems experiencing hypoxia and anoxia. Anoxia following hypoxia, and the longer hypoxic treatment had small but significant increases in shoot borne roots compared to the control. In some of the plants that had received 5 days of anoxia following full aeration the whole seminal root system had died and the survival of the plant was dependent on the growth of a new root system emanating from shoot borne roots.

True hydrophytes and some mesophytes show a number of root adaptations to waterlogging. These are principally the production of aerenchyma to maintain an oxygen pathway through leaves and stems to the root tips (Evans 2004; Vartepetian 1997) and/or the increased production of shoot borne (adventitious) roots which penetrate the surface layers and thus are able to maintain their oxygen supply (e.g., Malik et al. 2001; 1990; Vartepetian 1997); . A few workers also mention the ability of some species to produce surface laterals as a direct response to hypoxia (Gibberd et al. 2001; Shibata et al. 1995). Indeed, the proliferation of lateral roots is also a response to other environmental stresses.

Although *Salvia officinalis* does not exhibit the formation of aerenchyma as a response to hypoxia it does show the more generalized response of increased production of lateral roots in the surface layers, which allowed survival through 5 days of subsequent anoxia. This indicates that the flexible and fibrous rooting system provides some protection against waterlogging stress, and if relatively common in Mediterranean species, is encouraging, as it suggests that they will have at least some tolerance of waterlogged soils within UK conditions.

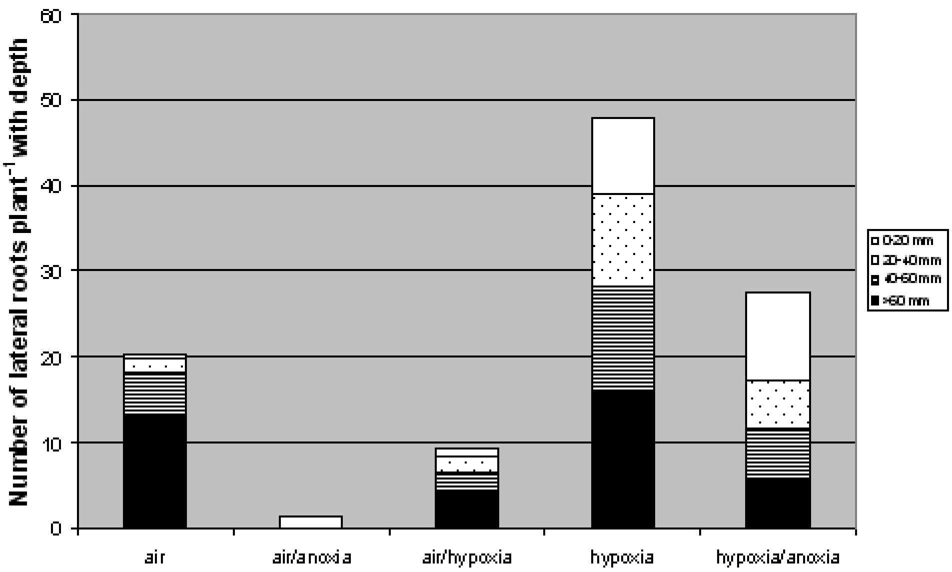

Fig 1. Numbers of young lateral roots and their distribution with depth after treatment

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