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Changes in the water-permeability of roots of some trees during drought stress and recovery, as related to problems of growth in urban environment

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Summary In relation to problems encountered in the urban environment a study was made of changes in the root's permeability to water of a number of tree species during a drought period, and of water conductivity during recovery. The results suggest than an important reduction of water conductivity occurs as soon as internal water stress builds up. Recovery appears to proceed irregularly. There appear to be differences in response – both as regards extent and speed – among different species.

Introduction

The public generally being in favour of decorating the city with trees and greenery, parks departments are confronted with the problem of their maintenance. Especially to healthy growth of trees the city environment is adverse. Temperatures fluctuate widely, it is often windy, the atmosphere contains dust and noxious substances, and induces high transpiration rates. Soil conditions usually restrict root development: frequent digging for sewers and cables, soil compaction, paving and use of de-icing salt are unfavourable factors. The overall result is that trees, especially those planted in sidewalks, are under nutrient and water stress for long periods.

Within the parks departments, experience has been gained on the suitability of tree species for this environment. As root permeability to water has been shown to respond to drought in several ways, it was considered worthwhile to investigate and compare root behaviour of a few species.

As soil water becomes insufficient, roots may show the following responses[12, 15]:

(a) root growth slows down and the zone of suberisation comes closer to the tip, thus the main 'absorption' zone decreases in length; recovery can only be achieved through a flush of new root growth.

(b) permeability of roots to water entrance may change in relation to the flux of water, which depends on the gradient in water potential between root and medium. After a preliminary increase this gradient will decrease as the soil dries and also the rate of water supply diminishes. These variations in conductivity for water within short periods can best be explained by changes in the soil membranes[9].

This preliminary research was aimed at investigating whether fluctuations in the permeability of roots to water could be detected during the onset of drought and subsequent recovery. By means of a pressure-bomb technique it was possible to measure transversal water conductivity of intact root systems under standardized conditions. In the choice of trees the experience obtained in maintenance in the city was taken into account. Elm is considered a tolerant species and ash a sensitive one in relation to city environment in The Netherlands.

Materials and methods

The species used in the first experiment were: ash (*Fraxinus excelsior* L.), elm (*Ulmus* X hollandica Mill. 'Groeneveld'), maple (*Acer pseudoplatanus* L. 'Negeria'), oak (*Quercus robur* L.), poplar (*Populus* X canadensis Moench 'Robusta'), willow (*Salix alba* L. 'Belders').

Young 1–2 year old seedlings were obtained from a nursery and planted in 4-l plastic pails, filled with a sandy soil. Of the larger and older batches of plants both stem and root system was pruned before planting. This procedure made it easier to distinguish young and old roots at the end of the experiment. Cultivation was in the open. For the experiment 15 selected plants of one species were placed in the glasshouse and treatments started.

Besides the flow of water forced through the roots, the leaves and roots were weighed and measured, and surface was calculated.

In the second experiment two-year old seedlings of ash were used. After cultivation in the open air, they were brought into a room of constant temperature and artificial light. This was to standardize conditions during the experiment.

The ultimate purpose was to measure the permeability (transversal conductivity) of the root tissue to water under standardized conditions. The best approach to this goal was considered to be the use of external pressure on the roots, attached to a short stump remaining after cutting the stem. That transversal conductivity is indeed the dominating factor is demonstrated by the experience that the flow of water out of the stump is very much larger after the bunch of roots has been partly cut. Thus, it may be accepted that longitudinal resistance in the roots is small in comparison to the transversal entry resistance[10, 13].

In the first trial only 1 bar external pressure was applied. There are, however, objections to this low pressure from a theoretical point of view (confounding effect of osmotic phenomena)[5]. As we could confirm the pressure-versus-flow relationships established by Fiscus and Kramer[5], all further experiments were performed at 4 bar external pressure.

In the plastic pressure bomb used initially, tap-water pressure was reduced to 1 bar by means of a reducing valve. An improved model was made of steel and is depicted in Fig. 1.

The vessel containing soil, roots and the remaining stump was placed into the large bomb. Water was led in and the lid screwed on. The stump protruded through a hole in the lid. Closure around the stump was achieved with a greased perforated rubber stopper, which was slipped over the stump and then compressed. Additional water was led in until it flowed out and then the lid was screwed on tight. In this manner hardly any air remained in the bomb.

The whole system was then connected to a suction pump aspirator to evacuate air in the bomb and in the soil. After that, pressure was applied to the whole water-filled system by means of compressed N_2, which pressure was reduced to 4 bar.

The expressed fluid was collected in a vessel connected to the stump with short pieces of tubing. In the case of very young seedlings the exudate was drained off into a graduated pipette by means of a bunch of glass fibres.

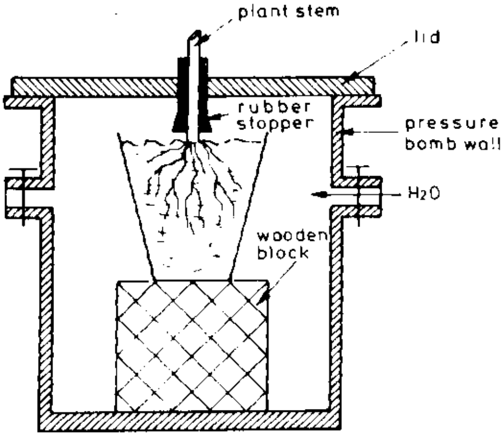

Fig. 1. Schematic drawing of pressure bomb.

As the outflow of water usually fluctuated more or less within a period of 2–3 hours observation, the recorded data are those occurring during a period of about one hour's steady flow.

The reason for evacuating air from the soil in the pots is to achieve complete filling of all pores of the soil with water. If shrinkage of roots occurs during drought, normal rewetting of the soil may result in pockets of air remaining between root and soil. This would result in exclusion of part of the root system from water supply and thus lead to incorrect conclusions[11].

From an ecological point of view, however, the possible occurrence of air gaps upon rewetting of the soil must be considered. The extent to which this occurs could be a measure of root shrinkage occurring in dry soil and could indicate how closely soil/root contact during normal rewetting is again established.

Results

Comparison of six species at 1 bar pressure

Treatment consisted of withholding water for 2–3, 5–7, or 11–14 days and renewed water supply for 2–3, 3–5, 6–8, or 9–10 days.

The differences in response of root conductivity to drought are shown in Table 1. Ash and oak were slow in their response, while elm and maple showed a fast and larger decline in permeability. As regards the recovery after rewatering, oak and elm showed the quickest response, while poplar and ash only responded slowly. For the two contrasting species elm and ash more details of the total behaviour are given in Fig. 2.

Although the technique had not yet been improved, the results clearly suggest differences in response among the species tested.

Table 1. Root permeability (μl water per 30 min. per g root) changes during drought and recovery (percent of control)

	2–3 days dry		5–8 days dry		Average	
Species	decrease to	recovery to	decrease to	recovery to	decrease to	recovery *with*
Oak	78%	145%	29%	66%	53%	*52%*
Elm	28	58	5	75	17	*50*
Willow	37	67	14	50	25	*37*
Maple	11	38	4	38	7	*30*
Poplar	52	63	19	54	36	*23*
Ash	74	62	37	49	55	*0*

Results with ash at 4 bar pressure

In these experiments two-year old seedlings of ash were used, and water flux was measured with 4 bar pressure after evacuation of air. Treatment consisted of a drought period of 8 days, at the end of which a decline in daily transpiration was evident. Rewatering was started on the ninth day. Results are shown in Fig. 3.

No clear reduction in 'root permeability' occurred before the rate of transpiration showed a decrease, which occurred after a loss in weight of the potted plants of about 600 g. This took about 6 days. The transfer capacity of the root system for water then fell from an average of about 0.50 ml to less than 0.10 ml per g fresh roots per hour. After rewatering recovery was slow and showed fluctuations (Fig. 3). This confirms the slow recovery rates obtained in the experiments at 1 bar overpressure for ash.

Discussion

The observed results, i.e. the decrease in transverse conductivity for water across the roots during drought is in agreement with other observations[7, 8, 14].

The recovery on rewatering is often too fast to be attributable to a rapid development of new young roots. Thus real conductivity variations must be involved, such as described by Aston and Lawlor[1], Brouwer[3] and Weatherley[16]. The response seems to be such that when the gradient across the root is large (wet soil and high transpiration), permeability is high; it decreases when the gradient is low (dry soil)[4]. These fast fluctuations in permeability may be due to changes in the fatty-acids in the plasmalemma under stress[9].

The observation that the water flux (transpiration) out of the leaves is in the same range as the flux into the roots at 4 bar overpressure indicates that the established gradient is comparable to that occurring

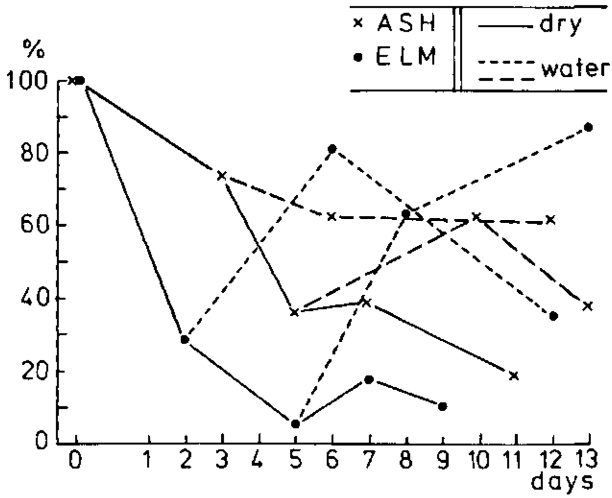

Fig. 2. Water conductivity at 1 bar overpressure for elm and ash during drought and recovery.

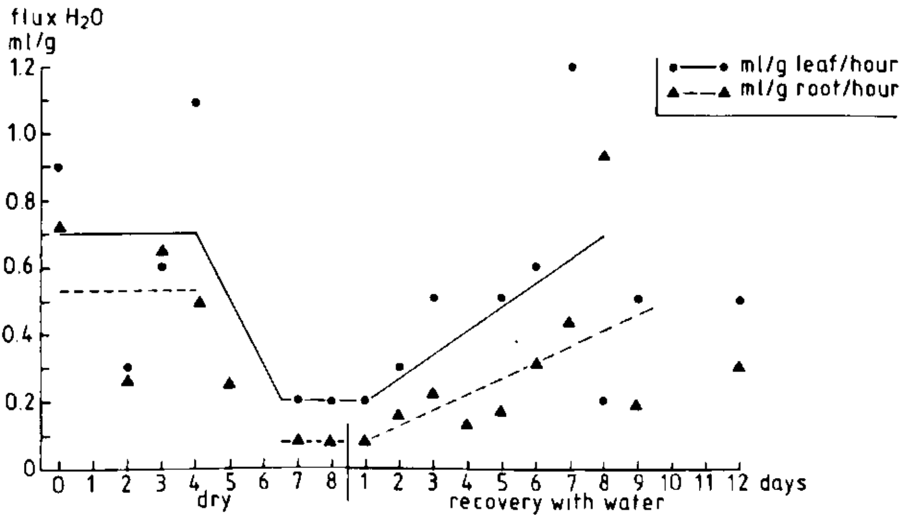

Fig. 3. Water flux of ash at 4 bar overpressure during drought and recovery.

naturally. Thus the results can be considered ecologically valid. The finding that leaf and root surface area are in the same range is in agreement with observations of Fiscus and Markhart[6].

It has to be further investigated whether the observed differences in response to and recovery from water stress between elm and ash can be linked to their tolerance of adverse city conditions. Ash and elm have also been reported to differ in sensitivity to tolerance of flooding[2].

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