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Differences in responses of various radish roots to salinity

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Abstract

Extension growth of tap-roots, initiation of lateral roots and extension growth of first lateral roots were investigated with young radish plants (*Raphanus sativus* cv. Rex) in aeroponic growth cabinets.

Growth was not affected by 50 m*M* NaCl. At higher NaCl concentrations the three growth processes were adversely affected, but not at the same magnitude: Initiation of new laterals was found to be the most salt-tolerant process, whereas growth of laterals was the most sensitive one. Thus, it seems that even within one root sytem, different root-types respond independently to environmental stresses. Such individual responses may alter the appearance of the root system and, thus, be of ecological significance.

Introduction

It is commonly accepted that roots are among the first organs to be affected by salt stresses: their growth and cytokinin production are immediately reduced (Böttger, 1978) and under severe stresses are stopped altogether.

Roots are also among the most sensitive organs to salinity (Levitt, 1980; Okusanya and Ungar, 1984; Waisel, 1972) and inhibition of their performance affects the survival capability of the entire plant. In most plant species, individuals with extensive and highly active roots are much more resistant to salinity and temperature stresses than those plants with poorly developed roots (Waisel, 1972).

As plant root-systems are not comprised of identical roots, the questions arise whether all the roots of a single plant respond to an environmental stress in a similar way? and consequently, if it is correct to talk about a general 'response of the root system' to salinity stress? These questions were the subject of the following investigation.

Materials and methods

Three-days-old, healthy and uniform seedlings of radish (*Raphanus sativus* c.v. Rex) were grown in four specially designed Rhizotron cabinets (Waisel and Breckle, unpublished). The seedlings were grown aeroponically on diluted half-strength Johnson's solution (Johnson *et al.*, 1957, containing 3 m*M* NaCl. Whenever needed, higher concentrations of NaCl or of abscisic acid were added. The root-chambers were pulse-sprayed with a fine mist of the solution, at a frequency of 10 seconds every minute.

At pre-designed times (1 or 2 hours) the shutters of the Rhizotrons were opened and the roots were illuminated and photographed. Exposure of the roots to light did not last longer than 30 seconds each time. Preliminary experiments have shown that such pulse-illumination did not affect the growth of these roots. The developed films were then projected on a large sheet of paper and the size of the individual roots was recorded.

Relative Growth Rates $\left(R = \frac{\log_e L_1 - \log_e L_0}{T_1 - T_0}\right)$

were then calculated, based on the extension of root length (L) between time 0 and time 1.

Whenever needed, the solutions in the Rhizotron chambers were exchanged. Changing of the solutions, including a rinse of the chambers, did not take more than 2 minutes.

The Rhizotrons were kept inside a growth chamber under controlled conditions: continuous light ($1.1 \times 10^3\,W.cm^{-2}$), constant temperature (25°C ± 2°C) and a relatively constant air humidity (R.H. 70% ± 20%).

Experiments and results

Rates of initiation of lateral roots, as well as the rates of extension-growth of the tap roots and of the laterals were followed for 53 hours, with periodic photographs and subsequent measurements. The plants were grown either on a half-strength Johnson's nutrient solution + 3 m*M* NaCl ($175.5\,mg.l^{-1}$ NaCl; $1.4\,ds.m^{-1}$) or on NaCl concentrations of 50 m*M* and 200 m*M* ($2925\,mg.l^{-1}$ NaCl or $5.9\,dS.m^{-1}$ and $11700\,mg.l^{-1}$ NaCl or $19.8\,dS.m^{-1}$ respectively).

Root growth showed a similar pattern in the non-saline control solution as well as in the 50 m*M* NaCl treatment. The average growth rate was $2.6\,mm.h^{-1}$ in the control and $2.4\,mm.h^{-1}$ in the 50 m*M* NaCl treatment (Table 1).

Growth of the tap roots was apparently linear with time (Fig. 1). The rate of lateral root initiation in the control and in the 50 m*M* NaCl treatments also followed an approximately linear pattern, with an average rate of 0.67 new lateral roots.h^{-1}.tap root^{-1} in the control treatment and 0.69 roots h^{-1}.tap root^{-1} in the 50 m*M* NaCl treatment.

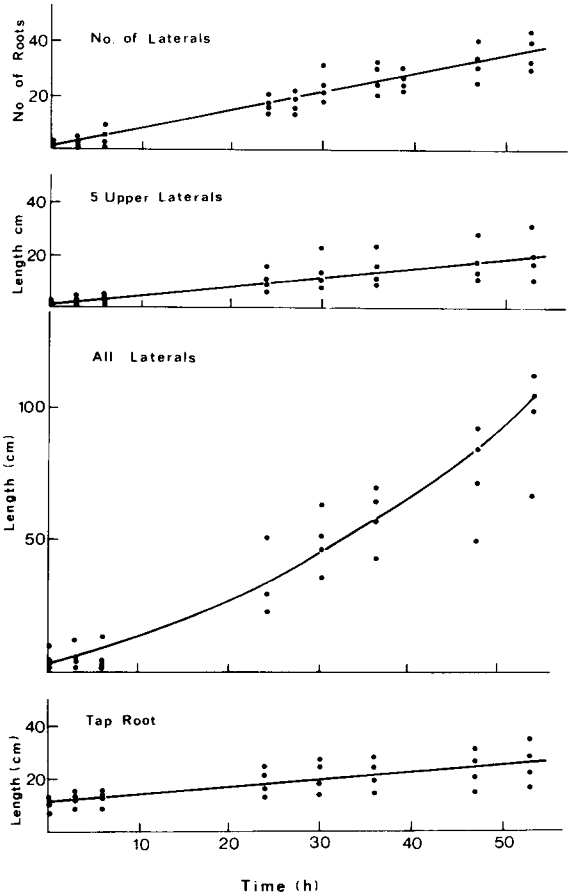

Fig. 1. Time course of initiation of new laterals and of extension growth of the lateral roots and of the tap-roots of radish plants grown under non-saline conditions.

The pattern of extension growth of all the lateral roots together was exponential in the control (Fig. 1), as well as in the 50 m*M* NaCl treatments. The

Table 1. Extension growth rates and rates of root initiation in radish plants subjected to various treatments of NaCl and of ABA. (Means ± standard deviation, and percent of control in parentheses)

Growth parameter / Treatment	Growth of tap root ($mm.h^{-1}$)	Average growth of the five oldest laterals ($mm.h^{-1}.root^{-1}$)	Average growth rates of all laterals for the 53 hours period ($mm.h^{-1}$)	Average growth rate of lateral roots ($mm.h^{-1}.root^{-1}$)	Average increase in number of lateral roots ($roots.h^{-1}$)
Control	2.6 ± 0.2 (100)	0.73 ± 0.02 (100)	16.1 ± 0.51 (100	0.44 (100)	0.67 ± 0.07 (100)
50 m*M* NaCl	2.4 ± 0.2 (93.3)	0.76 ± 0.06 (109.1)	18.3 ± 0.48 (113.7)	0.43 (97.7)	0.69 ± 0.06 (103.0)
200 m*M* NaCl	0.9 ± 0.1 (34.6)	0.11 ± 0.03 (15.1)	1.4 ± 0.03 (8.7)	0.08 (18.2)	0.24 ± 0.02 (35.8)
50 m*M* NaCl + ABA	0.7 ± 0.1 (26.9)	0.06 ± 0.01 (8.2)	1.1 ± 0.02 (6.8)	0.06 (13.6)	0.35 ± 0.06 (52.1)

Relative Growth Rates of these roots were low: 0.03 for the control plants and 0.02 for the 50 m*M* NaCl treatment plants. The values of R were approximately constant throughout the experiment, proving that growth actually increased exponentially (*cf.* Hunt, 1981).

Growth of the 5 oldest laterals yielded values of 0.73 mm.h^{-1}.$root^{-1}$ in the control treatment and 0.76 mm.h^{-1}.$root^{-1}$ in the 50 m*M* NaCl treatment (Table 1).

Root growth was strongly inhibited by the 200 m*M* NaCl treatment. The rate of growth of the tap roots was 0.9 mm.h^{-1} only, whereas that of the 5 upper lateral roots was 0.11 mm.h^{-1} only. This is approximately 15% of the growth rate of the lateral roots in the control plants. The growth rate of all the laterals, in the 200 m*M* NaCl treatment, was only 8% of the growth rates of the laterals of the control plants (Table 1). Those roots showed linear relationships with time. The rate of root initiation and the growth rates of the different root types in the 200 m*M* NaCl were similar to those which were grown in the 50 m*M* NaCl + ABA treatment.

The growth process which was least inhibited by the high salt treatment was root initiation (Table 1). The average numbers of laterals which have developed after 53 h in the control, in the 50 m*M* NaCl and in the 200 m*M* NaCl treated plants were 35.5 ± 6.3, 36.6 ± 5.9 and 12.7 ± 2.3, respectively.

Roots of plants which had been subjected to a NaCl solution for 33 h and then transferred to a control solution, or vice versa showed a change in their growth pattern; from exponential in the non-saline treatments to linear in the saline ones.

Addition of $1 \times 10^{-5} M$ ABA to the 50 m*M* NaCl treatment, caused a reduction of all growth parameters (Table 1). Roots which had been exposed to such a treatment behaved similarly to roots which had been exposed to 200 m*M* NaCl. ABA had a moderate effect on lateral root initiation (48% inhibition), but a strong effect on the extension growth of the tap roots (73% inhibition) and of the laterals (92% inhibition).

Discussion

It is well known that root-systems are comprised of a variety of different roots (Böhm, 1979; Feldman, 1984; Wilcox, 1968) and variations in growth of various types of roots could have been expected following exposure to stresses. Indeed, each of the growth processes which were measured in the present investigation, *i.e.* root initiation, tap-root and lateral root-extension growth, responded differently to the high NaCl treatments: the least affected process was the process of root initiation whereas the other growth processes were affected much more.

Initiation of lateral roots in young radish plants seems to be spontaneous and their location follows a typical series (Charlton, 1983). Two types of laterals can be distinguished on young roots of this species: laterals which initiated in acropetal series beyond the growing root-tip and laterals which initiated subsequently. Initiation of the first ones is practically unaffected by external growth regulators, whereas the initiation of the subsequent laterals is affected (Blakely *et al.*, 1982). We do not know which of the initials are more tolerant to salinity or to ABA. However, according to the literature, the laterals which had been initiated in our experiments were of the first type.

Growth of the lateral roots was not simply inhibited by salinity, but showed a dual response:

(a) A decrease in the growth rates of the roots.

(b) A change in the apparent growth patterns from an exponential pattern in the controls and in the 50 m*M* NaCl plants to a linear one in the highly saline or in the ABA treatments.

Salinity had an apparent effect on the growth of the tap roots as well. Tap-root growth in the 200 m*M* NaCl treatment was approximately one third of that of the control plants, whereas inhibition of the lateral roots under such salinity treatments was higher than 80%. A similar behaviour was exhibited by the ABA treated roots. The ecological implication of such a behaviour is that a horizontally spread root system would develope under non-saline conditions whereas a predominantly vertical system would develop under highly saline ones.

The information presented herein indicates that the various types of roots enjoy a certain level of autonomy and some independence in their response to environmental signals (*cf.* Waisel, 1985). Initiation of new roots is the process which is least affected by salt stresses, in spite of the fact that their consequent growth would be highly inhibited under the very same conditions. What might be the logic in producing new roots under environmental conditions which prevent their subsequent growth? Three answers can be offered: Effects of time, of surface area and of root-tip functions. The presence of differentiated root-tips, which await the chances for better growth conditions may give plants an earlier start when conditions improve. Such a phenomenon was also shown in other plants: Plants of *Sinapis alba* produced short roots under drought conditions. Following rehydration, those roots elongated rapidly and produced laterals with abundant root-hairs (Vartanian, 1981). A similar behaviour can be expected by salt stressed plants: upon reduction in salinity, growth of the pre-existing root-tips would be fast, support the plant at an early stage of development and give it an advantage over its neighbours. The second explanation would be based on a possible contribution of such new primordia to the absorbing surface area of the root system of salt affected plants. However, in most cases, the contribution of the undeveloped root-tips to the surface area of the system is insignificant. The third explanation is based on the fact that an increase in the number of root-tips multiplies the number of sites for cytokinin production (Weiss and Vaadia, 1965). Thus, it is tempting to assume that the large number of new primordia enables the plants to endure the deleterious effects of high concentrations of NaCl and of a high content of ABA (*cf.* Böttger, 1978; Rivier and Savgy, 1986) which otherwise might have caused serious physiological damage.

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