ナシ属植物の耐塩性は根から葉へのNaおよびClイオンの転流量と関係がある

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Salt Tolerance in *Pyrus* Species is Linked to Levels of Na and Cl Translocation from Roots to Leaves

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Salt tolerance was tested in five Asian *Pyrus* rootstock species: *Pyrus betulaefolia* Bunge (strains C and N; *P. betulaefolia* C and *P. betulaefolia* N, respectively), *P. calleryana* Dcne. (strain No. 8; *P. calleryana* 8), *P. pyrifolia* Nakai, *P. fauriei* Schneid., and *P. dimorphophylla* Makino (strain No. 6; *P. dimorphophylla* 6). Four-month-old seedlings were subjected to each of 50 mM, 100 mM, 150 mM, and 200 mM NaCl solutions, and leaf injury, shoot growth, leaf water potential, and mineral uptake were evaluated. *P. betulaefolia* C showed the highest salt tolerance with no visible symptoms of injury even in the 200 mM NaCl treatment. *P. betulaefolia* N and *P. dimorphophylla* 6 also exhibited higher salt tolerance. In contrast, *P. calleryana* 8, *P. fauriei*, and *P. pyrifolia* exhibited lower salt tolerance with severe leaf injuries leading to defoliation and death. Leaf water potential decreased via NaCl treatment in all species and there was no difference among species. Sodium and Cl contents in the roots of all species increased within 2 weeks after NaCl treatment, although the differences among species and NaCl treatment was small. On the other hand, Na and Cl contents in leaves were different among species. The salt-sensitive species *P. calleryana* 8 and *P. pyrifolia* accumulated higher concentrations of Na and Cl in the leaves over 150 mM NaCl at 6 weeks after treatment compared to the salt tolerant species *P. betulaefolia* C. These results imply that *P. betulaefolia* C might have a key mechanism such as storage exclusion and/or transport-restriction between the shoot and root to depress the transport of Na and Cl to the upper plant parts, enabling a higher tolerance to NaCl.

Key Words: ion uptake, *Pyrus betulaefolia*, *Pyrus pyrifolia*, rootstock, salinity.

Introduction

Japanese pear (*Pyrus pyrifolia* Nakai) is a major traditional fruit crop in some East Asian countries, such as Japan, Korea, and China (Kajiura, 1994). Recently, the growing area of this species has extended to Brazil (Faoro, 2002), New Zealand, and Australia (White, 2002) and Southwest Asian countries, such as Iran (Arzani, 2002). However, the productivity of pear fruit in these area is frequently restricted by soil salinity, especially in arid and semi-arid areas (Myers et al., 1995). For example, Japanese pear production in Iran is restrained by the supply of fresh water because of high levels of soil salinity (Arzani, 2002).

Fruit trees, including pear (*Pyrus* spp.), are generally sensitive to soil salinity (Bernstein, 1965). They exhibit growth reduction and leaf injury via osmotic and ionic stresses (Hasegawa, 2002). Although the mechanism of salt stress is not fully understood, it is well known that the salt tolerance of some fruit trees would be improved using salt-tolerant rootstocks and/or scion varieties (Storey and Walker, 1999). In *Citrus* and *Persea*, some tolerant rootstocks, especially Cl and Na exclusion rootstocks, were selected for use in cultivation (Bernstein et al., 2001; Storey and Walker, 1999). However, information about the salt tolerance of *Pyrus* species, especially *P. betulaefolia*, which have been used as rootstock in arid conditions is limited (Lombard and Westwood, 1987). In *P. communis*, some experiments on salt tolerance have been conducted under field conditions (Boland et al., 1997; Myers et al., 1995; Oron et al., 1999). In these experiments, the effect of rootstocks and the physiological mechanisms of salt tolerance have not been examined. Okubo and Sakuratani (2000) and Okubo et al. (2000) reported that the salt tolerance of *P. calleryana* (They reported it as *P. betulaefolia* strain Blue) was significantly higher than *P. pyrifolia*. Bell (1991) and Westwood and Lombard (1983) described *Pyrus* species that show large differences in soil adaptation.

In this work, we compared the salt tolerance of *Pyrus* rootstock species by measuring the shoot growth, leaf injury, and ion contents of individual organs, and examined the relationship between ion uptake and salt tolerance to reveal the physiological mechanisms of salt tolerance.

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Materials and Methods

Plant materials

Five *Pyrus* rootstock species: *P. betulaefolia* Bunge (strains C and N; *P. betulaefolia* C and *P. betulaefolia* N, respectively), *P. calleryana* Dcne. (strain No. 8; *P. calleryana* 8), *P. pyrifolia* Nakai, *P. fauriei* Schneid., and *P. dimorphophylla* Makino (strain No. 6; *P. dimorphophylla* 6), were used. *P. betulaefolia* originated in northeast China, *P. calleryana,* and *P. pyrifolia* in south China, *P. fauriei* in Korea, and *P. dimorphophylla* in Japan. Seeds were collected from a single tree per species planted in the pear germplasm bank orchard in Tottori University, Tottori, Japan. In the orchard, each species is separately cultivated and two or three lines are adjoined for each species. *P. betulaefolia* C and *P. pyrifolia* were introduced from Oregon State Univ., Corvallis, Ore. USA. *P. betulaefolia* N, *P. fauriei*, and *P. dimorphophylla* 6 were introduced from the Fruit Tree Research Station, Ministry of Agriculture, Forestry and Fisheries, Tukuba, Ibaraki, Japan (At present: National Institute of Fruit Tree Science). *P. calleryana* 8 was introduced from Kyoto Univ., Kyoto, Japan. In January, 2000, more than 2000 seeds per species were germinated in 500 mL plastic pots filled with growing mixture (sand: vermiculite: mold = 1 : 1 : 2 (v/v); TKS-2, Sakata Seed Corp., Yokohama, Japan) in a greenhouse at 20°C. Each pot had single seedlings. To exclude genetic variation, uniform seedlings were selected by the visible characteristics of each species such as plant height, shoot pubescence, and the color, shape, and size of leaves.

Experimental design and NaCl treatments

In early May, 80 pots of four-month-old uniformed seedlings of each species were selected, and each 5 plants were sampled at 0 weeks after treatment. Fifteen plants per species were subjected to 100 mL of 50, 100, 150, or 200 mM NaCl solutions (Electrical conductivity (EC) values were about 5.0, 10.0, 14.0, and 18.0 $dS{\cdot}m^{-1}$, respectively) once a day, and the control plants were irrigated with tap water (EC value was about 0.1 $dS{\cdot}m^{-1}$). Five plants were sampled from each treatment plot at 2, 4, and 6 weeks after treatment.

The experiment was carried out in a greenhouse where the day temperature was 30 ± 5°C and the night temperature was maintained at 20°C. Relative humidity ranged from 60 to 80%. Pots were arranged in a randomized complete block design with three blocks, and 5 plants of each block were harvested at 2, 4, and 6 weeks after treatment, respectively.

Determination of leaf injury rate and leaf water potential

Visible symptoms of leaf injury were recorded and leaf water potential was measured on each sampling date. Leaf injury was expressed as an index of six grades (0–5), from 0, indicating no visible symptoms, to 5, indicating that all leaves were burned or abscised, as described by Motosugi et al. (1987). Leaf water potential was measured according to the method described by McCutchan and Shackel (1992) with some modifications. Briefly, to equilibrate plant water conditions, seedlings were moved into a dark chamber for 12 h before measurement. The youngest fully expanded leaf of each seedling was put into a plastic bag immediately before the leaf was excised, to retain leaf moisture until measurement. Water potential was determined in a pressure chamber (DIK-7000, Daiki Rika Kogyo, Tokyo, Japan).

Measurement of shoot growth

Shoot length from the soil surface to the shoot tip was measured and the growth increment was calculated.

Determination of mineral content

The mineral content was measured in three species: *P. betulaefolia* C, *P. pyrifolia*, and *P. calleryana* 8. Plants were removed from pots and divided into leaves, shoots, and roots. After washing with distilled water, the fresh weight of individual organs was recorded and then they were oven dried at 78°C for 72 h to measure dry weight. Finally, they were ground into powder for mineral analysis. To determine the Na, K, Ca, and Mg contents, 200 mg of powder of each sample was dry-ashed at 250°C for 2 h and 480°C for 3 h, then soaked with 0.5 N HCl. The Na, K, Ca, and Mg concentrations were determined with an atomic absorption spectrophotometer (170–30, Hitachi, Tokyo, Japan). The Cl content was determined by the mercury (II) nitrate titration method, with diphenylcarbazone added as an indicator. Two hundred mg of each powdered sample, 300 mg of activated carbon, and 25 mL of 0.1 N acetic acid were added into a plastic tube, and it was shaken for 1 h. The solutions were then filtered with filter paper (No. 4A, Toyo Roshi, Tokyo, Japan) and 2 mL of each sample solution was mixed with the indicator (diphenylcarbazone, bromophenol blue, and xylene cyanol FF) and titrated with 0.0141 N mercury (II) nitrate.

Statistical analysis

Statistical analysis was conducted using a one-way ANOVA with a Tukey-Kramer HSD test for all pairs with an alpha-level of 0.05 using JMP IN (SAS Institute Inc., NC) software.

Results

Leaf injury

The degree of leaf injury caused by NaCl treatment was different among the species (Fig. 1). *P. betulaefolia* C showed no visible symptoms of leaf injury during the whole experimental period with any NaCl treatment. For *P. betulaefolia* N with 200 mM NaCl, the margin of a few basal leaves showed burning symptoms from 4 weeks after treatment. However, there was no injury in other NaCl treatments. *P. dimorpho-*

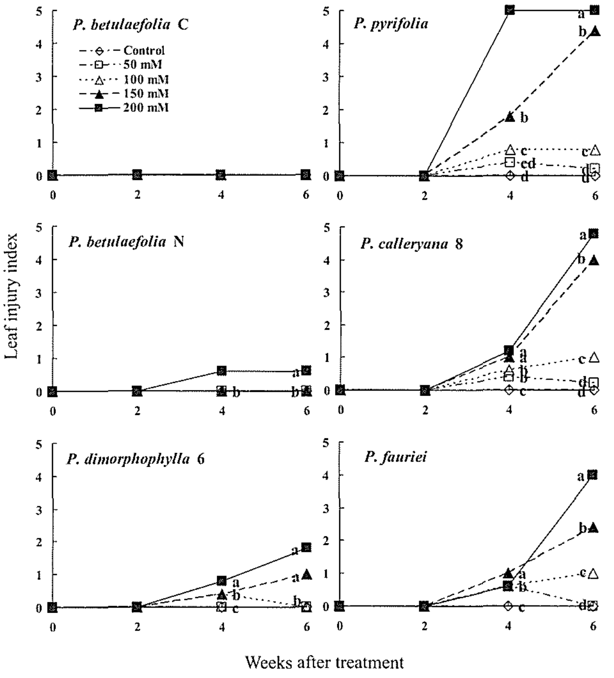

Fig. 1. Occurrence of leaf injury in *Pyrus* species treated with different concentrations of NaCl. Values are the means of five replications. Leaf injury index: 0 = no visual symptoms to 5 = all leaves burned or abscised. Different letters indicate significantly different ($P > 0.05$) according to Tukey-Kramer's HSD tests.

phylla 6 also showed leaf injury, although the extent of the injury was extremely limited compared with *P. pyrifolia*, *P. calleryana* 8, and *P. fauriei*. *P. pyrifolia* showed the most severe leaf injury at 4 weeks after treatment with 200 mM NaCl, and some plants became defoliated and died. At the end of the experiment, *P. fauriei* and *P. calleryana* 8 treated with 200 mM NaCl also showed necrosis on most of the leaves, ultimately leading to defoliation and plant death (Fig. 1).

Symptoms of leaf injury were also different among species. In *P. calleryana* 8 and *P. fauriei*, black spot-like necrosis was initially observed on young leaves. The necrosis subsequently developed at the lower leaf margin, and then reached the leaves of upper nodes. In contrast, *P. pyrifolia* did not show black spot-like necrosis on young leaves. However, the rate of necrosis on the leaves of lower nodes was higher than that of *P. calleryana* 8, and *P. fauriei*, and then the necrosis spread to the leaves of upper nodes.

Shoot growth

Shoot growth in all species was inhibited by each NaCl treatment (Fig. 2). With 100 mM NaCl treatment, the growth reduction exhibited by *P. betulaefolia* C was less than the other species and 67% of the control. In contrast, the growth of the other species was 18–26% of the control. On 150 mM NaCl treatment, the growth of *P. betulaefolia* C and *P. betulaefolia* N was 47% and 33% of the control, respectively. On the other hand, the growth of the other species was 16–21% of the control. The growth increment of *P. betulaefolia* C, *P. betulaefolia* N, and *P. dimorphophylla* 6 was smaller than *P. pyrifolia*, *P. calleryana* 8, and *P. fauriei*, without NaCl treatment.

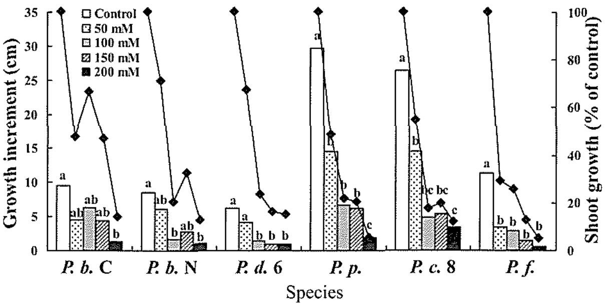

Fig. 2. Effect of NaCl treatments on the growth of shoots for 6 weeks in *Pyrus* species. The bar chart indicates the absolute growth increment. The line chart indicates relative shoot growth compared to the control. *P. b.*: *P. betulaefolia*, *P. d.*: *P. dimorphophylla*, *P. p.*: *P. pyrifolia*, *P. c.*: *P. calleryana*, *P. f.*: *P. fauriei*. Values are the means of five replications. Different letters in each kind of rootstock indicate significantly different ($P > 0.05$) growth increments according to Tukey-Kramer's HSD tests.

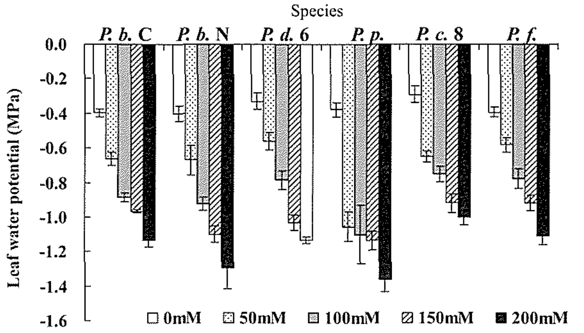

Fig. 3. Effect of NaCl treatments on the leaf water potential at 2 weeks in *Pyrus* species. *P. b.*: *P. betulaefolia*, *P. d.*: *P. dimorphophylla*, *P. p.*: *P. pyrifolia*, *P. c.*: *P. calleryana*, and *P. f.*: *P. fauriei*. Vertical bars represent SE (n = 5).

Leaf water potential

The leaf water potential of all species decreased along with the increase of NaCl concentrations within 2 weeks after treatment. No remarkable difference among species was observed in water potential (Fig. 3).

Na ion concentration

At 2 weeks after treatment, the NaCl treatment caused a significant increase in the Na of roots (Fig. 4). However, there was no further increase in the root Na content among each species at 6 weeks after treatment, even in the 100 mM or 200 mM NaCl treatment (Fig. 4).

In contrast, increases in the leaf Na content at increasing concentrations of NaCl treatment were relatively small, and a significant increase was observed in only *P. calleryana* 8 with 200 mM NaCl at 2 weeks

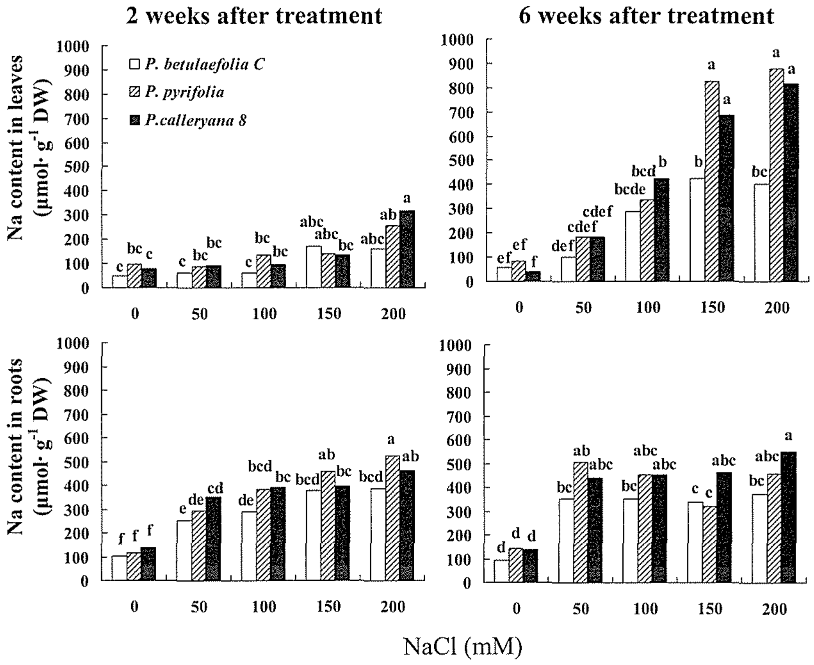

Fig. 4. Effect of NaCl treatment on the Na content in leaves and roots among 3 *Pyrus* species. Different letters indicate significantly different ($P<0.05$) according to Tukey-Kramer's HSD tests.

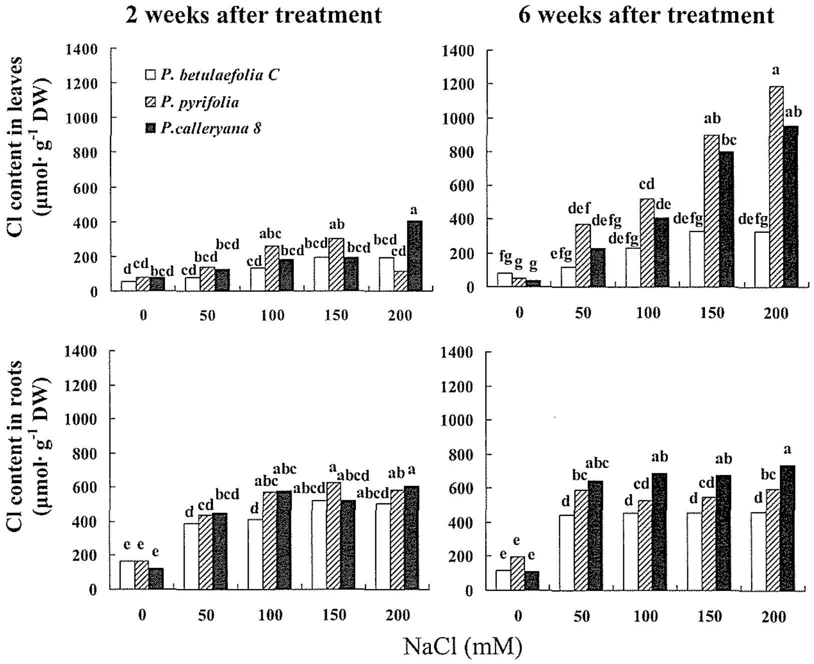

Fig. 5. Effect of NaCl treatment on the Cl content in leaves and roots among 3 *Pyrus* species. Different letters indicate significantly different ($P<0.05$) according to Tukey-Kramer's HSD tests.

after treatment (Fig. 4). However, the Na content of leaves increased via NaCl treatment at 6 weeks after treatment (Fig. 4). The Na content in the leaves of all species increased by elevating NaCl concentration. The Na content in the leaves of *P. pyrifolia* and *P. calleryana* 8 was significantly higher than that of *P. betulaefolia* C on 150 mM and 200 mM NaCl treatments. The Na content in the leaves of *P. betulaefolia* C on 200 mM NaCl was less than half of *P. pyrifolia* and *P. calleryana* 8, and the content of *P. betulaefolia* C on 200 mM NaCl was almost the same as *P. pyrifolia* and *P. calleryana* 8 on 100 mM NaCl (Fig. 4).

Cl ion concentration

The NaCl treatment caused a significant increase in

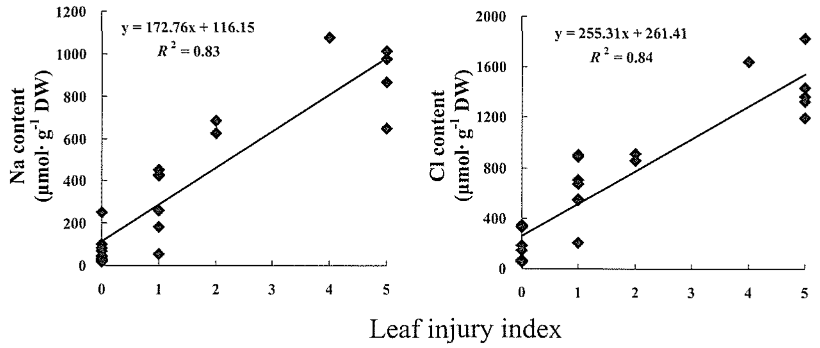

Fig. 6. Relationship between the leaf injury index and Na or Cl content in leaves of *Pyrus pyrifolia* exposed to 4 weeks NaCl treatment.

the Cl content of roots at 2 weeks after treatment (Fig. 5). However, there was little increase in the Cl content at 6 weeks after treatment (Fig. 5).

At 2 weeks after treatment, the change in the leaf Cl content caused by NaCl treatment was small (Fig. 5). However, the Cl content in the leaves of *P. pyrifolia* and *P. calleryana* 8 increased by elevating NaCl concentration, but the increase of *P. betulaefolia* C was not significant at 6 weeks after treatment. Therefore, the Cl content in the leaves of *P. pyrifolia* and *P. calleryana* 8 was significantly higher than that of *P. betulaefolia* C on 150 mM and 200 mM NaCl treatment. The Cl content in the leaves of *P. betulaefolia* C on 150 mM and 200 mM NaCl was less than half of *P. pyrifolia* and *P. calleryana* 8 (Fig. 5).

K, Ca, and Mg concentrations

There were no significant differences in K, Ca, and Mg contents among all species, with or without NaCl treatments (data not shown).

Relationship between leaf injury and leaf Na and Cl concentrations

A significant correlation was observed between the degree of leaf injury and Na and Cl contents in the leaves of *P. pyrifolia* with NaCl for 4 weeks ($R^2 = 0.83$ and 0.84 respectively, n = 25, $P < 0.01$; Fig. 6).

Discussion

Pear is one of the most salt-sensitive fruit trees and its tolerance is lower than other fruit trees, eg., fig, grape, and orange (Bernstein, 1965). Although many studies have been conducted on salt tolerance in fruit trees, knowledge of the salt tolerance of *Pyrus* species is limited (Boland et al., 1997; Myers et al., 1995; Okubo et al., 2000; Oron et al., 1999). Recently, the cultivation of Japanese pear has been spreading to out of East Asian countries. Therefore, the selection of salt tolerance *Pyrus* rootstock is necessary for stable fruit production. In this experiment, we have obtained some fundamental information about the salt tolerance of *Pyrus* species.

P. betulaefolia C did not show any leaf injury symptoms during the 6 weeks experimental period even with 200 mM NaCl treatment (Fig. 1). Leaf injury of *P. betulaefolia* N and *P. dimorphophylla* 6 did not reach a critical degree when cultivated with 200 mM NaCl for 6 weeks. Therefore, *P. betulaefolia* C, *P. betulaefolia* N, and *P. dimorphophylla* 6 can be regarded as salt-tolerant rootstocks. In contrast, *P. calleryana* 8, *P. fauriei*, and *P. pyrifolia* can be graded as salt-sensitive species, because of the occurrence of leaf injuries (Fig. 1). Among the *P. betulaefolia* lines, strain C presented a much higher salt tolerance compared with the N line. This difference might have been due to the fact that *P. betulaefolia* C was selected at Oregon State Univ., which is located in an arid climate (Banno, 1992).

Leaf injury is a typical symptom of salt stress (Ruiz et al., 1997), and the salt tolerance level among species and cultivars can be estimated by the extent of this damage. In this study, leaf injury developed in *P. calleryana* 8 and *P. pyrifolia*, which showed higher Na and Cl contents in the leaves compared to *P. betulaefolia* C, which showed no leaf injury (Figs. 1, 4, and 5). Moreover, the degree of leaf injury was correlated with the Na and Cl content of the leaves of *P. pyrifolia* with NaCl for 4 weeks (Fig. 6). However, leaf water potential was decreased by NaCl treatment in all examined species (Fig. 3). Therefore, it was suggested that leaf injury was caused by an overaccumulation of Na and Cl in plant parts above the ground, especially leaves (Munns, 2002). Bernstein (1965) also suggested that leaf injury in some fruit trees develops when the leaf ion content is more than 0.2% DW for Na and/or 0.5% DW for Cl. Moreover, Okubo and Sakuratani (2000) reported that leaf injury begins at 0.4%–0.6% DW for Na and 1.4% DW for Cl in the leaves of *P. calleryana* and *P. pyrifolia*. In this study, leaf injury of *P. pyrifolia* was observed when Na and Cl in leaves exceeded 0.66% DW (289 µmol·g^{-1} DW) and 1.83% DW (517 µmol·g^{-1} DW), respectively (Fig. 6). The Na and Cl contents of leaves in *P. betulaefolia* C were significantly lower than *P. calleryana* and *P. pyrifolia* when treated with 150 mM and 200 mM NaCl (Figs. 4 and 5). The Cl content of *P. betulaefolia* C without any leaf injury was lower than this threshold value during the experimental period, and the Na content was almost the same as the threshold value even when grown with 150 mM and 200 mM NaCl (Figs. 4 and 5).

In spite of the differences in salt tolerance, little difference was detected in root Na and Cl contents among *Pyrus* species (Figs. 4 and 5). Moreover, root weight was decreased by NaCl treatments in both salt-tolerant and salt-sensitive species (data not shown). However, large differences were detected in the Na and Cl contents of leaves at 6 weeks after treatment (Figs. 4 and 5). These results suggest that the efficiency of Na and/or Cl transport differed among species (Boland et al., 1997; McKersie and Leshem, 1994; Ruiz et al., 1997; Storey and Walker, 1999) and that the salt tolerance ability of *Pyrus* rootstocks is closely related to the level of salt translocation from the roots to upper plant parts.

Several studies suggested that non-vigorous growth restricted Na and Cl transport to the leaves (Massai et al., 2004). Certainly, the growth increment of the control plant *P. betulaefolia* C was lower than *P. calleryana* 8 and *P. pyrifolia* (Fig. 2). Therefore, the non-vigorous growth of *P. betulaefolia* C might contribute to the restriction of Na and Cl transport to above ground organs. However, on higher than 100 mM NaCl, the growth increment of these three species were almost the same. Moreover, non-vigorous *P. fauriei* developed a higher level of leaf injury compared with *P. betulaefolia* C. In addition, *P. betulaefolia* C also restricted Na and Cl transport to above ground organs compared to *P. calleryana* 8 and *P. pyrifolia* when a same kind of scion was grafted (Matsumoto, 2003). These results suggest that another factor rather than plant vigour affects the efficiency of Na and Cl transport to above ground organs.

The difference in ion absorption among plant species may depend on the ability to exclude ions (Blom-Zanstra et al., 1998; Lacan and Durand, 1996; Matsushita and Matoh, 1991). It has been reported that Citrus species have some Na and/or Cl excluder rootstocks and the exclusion efficiencies are different according to the species or salt concentrations (Storey and Walker, 1999). Our results suggest that *Pyrus* species also have a range of exclusion mechanisms as the range of the Cl and Na content in leaves between species was wide (Figs. 4 and 5). Several studies have been conducted on ion-exclusion mechanisms of roots or lower parts of shoots. Boland et al. (1997) reported that apricot and pear accumulate Na ions to the heartwood at the initial stages of salt absorption. Subsequently, when the absorption capacity of the heartwood is exceeded, Na is translocated to the sapwood and upper part of the plants causing injuries. The buffer role of heartwood has also been reported in sweet pepper (Blom-Zandstra et al., 1998). Moreover, Myers et al. (1995) reported that the Na and Cl contents in leaves of 40-year-old 'Bartlett' pear trees, which were given long-term saline irrigation, increased just before plant death. In this study, the Na and Cl contents of roots increased significantly by NaCl treatment within 2 weeks after treatment (Figs. 4 and 5). On the other hand, there was little increase in the Na and Cl contents of leaves at 2 weeks after treatment (Figs. 4 and 5). Thus, in *Pyrus* rootstock species, both roots and the lower parts of shoots appear to be used as storage organs of Na and Cl. Additionally, *P. betulaefolia* C showed lower concentrations of Na and Cl in leaves compared with *P. calleryana* 8 and *P. pyrifolia* at 6 weeks after treatment (Figs. 4 and 5). Therefore, *P. betulaefolia* C may have a high salt tolerance when grown on saline substrates through the effective compartmentation of Na and Cl in both roots and the lower parts of shoots, and the restriction of Na and Cl transport from roots to shoots (Marschner, 1995).

Consequently, we confirmed that the salt tolerant *Pyrus* rootstock species *P. betulaefolia* C restricted the translocation of Na and Cl from roots to upper plant parts under high saline conditions. This mechanism prevented the development of leaf injury in *P. betulaefolia* C and it survived during the 6 weeks experimental duration with up to 200 mM NaCl treatment. Moreover, differences in this exclusion and/or transport-restriction mechanism may determine differences in the salt tolerance of *Pyrus* rootstock species under saline soil conditions.

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ナシ属植物の耐塩性は根から葉へのNaおよびClイオンの転流量と関係がある

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5種のアジアナシ台木種：*Pyrus betulaefolia* C，*P. betulaefolia* N，*P. calleryana* 8，*P. pyrifolia*，*P. fauriei*，*P. dimorphophylla* 6を用いて，耐塩性の評価を行った．播種後4か月の実生ポット苗に0，50，100，150および200 mMのNaCl溶液を処理し，葉の障害程度，茎の伸長量，葉の水ポテンシャルおよび各組織の無機成分含量を調査した．*P. betulaefolia* Cは最も強い耐塩性を示し，6週間の実験期間中200 mMのNaCl処理下でも，葉に全く障害を発生しなかった．*P. betulaefolia* Nおよび*P. dimorphophylla* 6は比較的強い耐塩性を示した．一方，*P. calleryana* 8，*P. fauriei*および*P. pyrifolia*の耐塩性は弱く，NaCl処理により葉に障害が発生し，著しいものは落葉，枯死した．葉の水ポテンシャルはNaCl処理により低下したが，種間に大きな差異はみられなかった．根のNaおよびCl含量は，NaCl処理後2週間以内に全ての種で増加し，処理間および種間の差異はわずかであった．一方，葉のNaおよびCl含量は，150 mMおよび200 mMのNaCl処理区において，処理6週間後，耐塩性の強い*P. betulaefolia* Cに比べ，耐塩性の弱い*P. calleryana* 8および*P. pyrifolia*で多かった．これらの結果より，*P. betulaefolia* Cの強い耐塩性は，NaおよびClの根から葉への輸送や蓄積を阻害する何らかの機構により，地上部のNa，Cl濃度の上昇を抑制することによるものと考えられた．