CHAPTER IV

ABSORPTION AND TRANSLOCATION IN INTACT SEEDLINGS
INTRODUCTION

Mineral uptake and metabolism in plants are complex phenomena influenced by many factors. The net absorption and transport of elements through the plant involves a number of steps. The elements are actively absorbed into the roots, transported across the root, then moved into the transpiration stream, retranslocated in the phloem, and possibly controlled overall by photosynthesis in the leaves. There appear to be three active transport processes involved. They are located at the outer surface of the cytoplasmic phase (plasmalemma), at the boundary between cytoplasm and vacuole (tonoplast) and between symplast and xylem. From stele, ions are carried to the shoot in the transpiration stream.

Cultivars of many species have genetic variation in properties such as uptake, accumulation, translocation and utilization of nutrients (Feuston and Jefferies, 1964). In many cases the varietal differences in transport are due to differences in the mechanism of selective ion transport (Cacco et al. 1976, Nielsen and Barber 1978, Pettersson 1978). However, genetically-controlled morphological and anatomical differences of the root system between varieties have also been shown to explain observed differences in ion uptake and translocation of nutrients (Lee 1960).

Heterosis in the uptake of nitrogen, phosphorus and potassium was observed by Rabideau et al. (1960), Nössberger (1970),
Rao and Venkateshwarlu (1971). They had expressed results on per plant basis. If the data of Nosberger (1970) and Rao and Venkateshwarlu (1971) were scrutinized on unit weight basis, there was no heterosis in mineral uptake. As early as 1934, Smith observed no heterosis if data were calculated on unit weight basis. In the present study the occurrence of heterosis in the sorghum hybrids in the processes of mineral absorption and transport was examined in detail.

**EXPERIMENTATION**

The following aspects were studied:

1) Absorption and translocation of Rb in CSH-5, CSH-6, CSH-7, CSH-8; a short duration (1-6 hour) experiment.

2) Absorption and translocation of phosphate in CSH-5 and CSH-7; a short duration experiment.

3) Absorption and translocation of chloride in CSH-5 and CSH-7; a short duration experiment.

4) Absorption and translocation of phosphate in maize hybrids Ganga-5 and Ganga-safed; at 2 and 4 hour experiment.

5) Absorption and translocation of Rb in CSH-5; a long duration (15-72 hours) experiment.

6) Absorption and translocation of phosphate in CSH-5 and CSH-7; a long duration experiment.
RESULTS

1) Absorption and translocation of Rb in CSH-5, CSH-6, CSH-7, CSH-8: a short duration (1-6 hours) experiment:

The absorption and translocation of Rb in CSH-5 and CSH-7 is given in Fig. 2 and for CSH-6 and CSH-8 in Fig. 3. The absorption by roots, transport to shoots and the total of absorption and transport, i.e., the uptake by whole plant is expressed on per 5 plant and gram fresh weight basis.

On per plant basis: The absorption was higher in CSH-5 and CSH-7 as compared to their parents, whereas the rate of absorption in CSH-6 and CSH-8 followed the higher parent (Fig. 2 and 3). The rate of transport was significantly higher in all the four hybrids as compared to their parents. For CSH-7 total Rb uptake by whole plant was significantly higher than its parents whereas CSH-5, CSH-6 and CSH-8 followed the higher parent. When heterosis was compared on mid-parent value, all the four hybrids showed heterosis in absorption. This heterosis may be attributed to higher fresh weight of hybrids, or their higher Rb uptake efficiency.

On the basis of per qm. fr. wt.: The hybrids CSH-5 and CSH-6 followed the parent mean and CSH-7 and CSH-8 followed the lower parent in Rb absorption (Figs. 2 and 3). The Rb transport in three hybrids, CSH-5, CSH-7, CSH-8 followed the parent mean, whereas CSH-6 was significantly higher in transport. The total
Fig. 2. Absorption and translocation of Rb from 0.1 mM RbCl, a time course (1-6 hours) short duration experiment. The 14 days-old seedlings of CSH-5, CSH-7 and their parents were used. The values are expressed on per 5 plants and per g. fr. wt. basis.
Fig. 3. Absorption and translocation of Rb from 0.1 mM RbCl; a time course (1-6 hours) short duration experiment. The 14 days-old seedlings of CSH-6, CSH-8 and their parents were used. The values are expressed on per 5 plants and per g. fr. wt. basis.
Rb uptake revealed that three hybrids followed the parent mean and the fourth CSH-8 was lower than its parents. This is because the male parent PD 3-1-11 had comparatively higher rate of transport.

The fresh weight of hybrids and their parents (Table 6) showed that the growth of hybrids was greater as compared to their parents. This revealed that heterosis in Rb absorption on per plant basis was due to greater fresh weight of hybrids and not due to their Rb uptake efficiency. The absorption and total uptake of Rb by the cultivars were rapid for the first 2 hours and then gradually reached a steady state at 6 hours. This biphasic feature denoted the saturation of cytoplasmic compartments, followed by steady filling of vacuole (Hooymans 1971).

The Rb transport index (Fig. 4) for CSH-6 was higher than its parents and this was one of the causes for heterosis in Rb transport to shoot in hybrid CSH-6. Hybrid CSH-8 followed the higher parent, CSH-5 followed the parent mean and CSH-7 followed the lower parent. Based on mid-parent value it can be concluded that hybrids CSH-6 and CSH-8 had higher transport index.

2) Absorption and translocation of phosphate in CSH-5 and CSH-7;

a short duration experiment:

On per plant basis (Fig. 5). CSH-5 showed heterosis in phosphate absorption by roots and its total uptake, whereas it was equal to the better parent in transport. CSH-7 was equal
Fig. 4. Rb transport index of CSH-5, CSH-6, CSH-7, CSH-8 and their parents. The 14 days-old seedlings were allowed to absorb Rb from 0.1 mM RbCl for a period of 6 hours.
Fig. 5. Absorption and translocation of phosphate from 0.1 mM H$_3$PO$_4$; a time course (1-6 hours) short duration experiment. The 14 days-old seedlings of CSH-5, CSH-7 and parents were used. The values are expressed on per 5 plants and per g. fr. wt. basis.
to its better parent in absorption and total uptake and followed the parent mean in transport.

On per g. fr. wt. basis: Both CSH-5 and CSH-7 showed heterosis in absorption, whereas they followed the lower parent in transport. In total uptake CSH-5 showed heterosis while CSH-7 followed the better parent (Fig. 5).

If heterosis is judged on the basis of mid-parent value, both the hybrids would show heterosis on per plant as well as per g. fr. wt. basis for absorption. This revealed that both hybrids were heterotic for efficiency in phosphate absorption. Phosphate transport index (Fig. 6) did not reveal any heterosis. In general, the absorption and transport of phosphate was linear for all cultivars.

3) Absorption and translocation of chloride in CSH-5 and CSH-7; a short duration experiment:

On per plant basis: Absorption, transport and total uptake of chloride were greater for both the hybrids (Fig. 7).

On per g. ft. wt. basis: The absorption and total uptake were greater in hybrid CSH-5, and CSH-7 followed the lower parent.

Using the mid-parent value as the basis, both hybrids showed heterosis for absorption and transport per plant, while on per g. fr. wt. basis, only CSH-5 showed heterosis. Heterosis
Fig. 6. Phosphate transport index of CSH-5, CSH-7 and their parents. The 14 days-old seedlings were allowed to absorb phosphate from 0.1 mM H$_3$PO$_4$ for a period of 6 hours.
Fig. 7. Absorption and translocation of chloride from 0.1 mM KCl; a time course (1-5 hours) short duration experiment. The 14 days-old seedlings of CSH-5, CSH-7 and their parents were used. The values are expressed on per 5 plants and per g. fr. wt. basis.
observed on per plant basis in C3H-5 was predominantly due to
higher Cl uptake and transport efficiency whereas in C3H-7 it
was due to its greater fresh weight (Fig. 7).

The Cl absorption rate increased in the first hour,
then slowed down and again rose in the 5th hour. A similar sharp
increase in Cl uptake after 3 hours of absorption was noted by
Hooymans (1971). The transport was biphasic in C3H-5 and parents
whereas it was linear in C3H-7 and parents. This revealed that
cultivars differed in their absorption and transport patterns for
chloride. In Cl transport index (Fig. 8) hybrid followed the
better parent. This throws light on the C3H-7 behaviour that
less absorption of Cl was the main characteristic whereby its
total uptake was lowered as compared to its parents.

4) Absorption and translocation of phosphate in maize hybrids

Ganga-5 and Ganga-safed for 2 and 4 hours:

The absorption and transport of phosphate was examined
in 14-day old seedlings of two maize hybrids namely Ganga-5 and
Ganga-safed along with their parents for 4 hours. There was no
heterosis in fresh weight (Table 8), or in the absorption and
translocation based either on per plant (Table 13) or per gram
fresh weight basis (Table 14). This indicated that though there
was heterosis for phosphate uptake (Fig. 5) in sorghum it was
not observed in maize.
Fig. 8. Chloride transport index of CSH-5, CSH-7 and their parents. The 14 days-old seedlings were allowed to absorb chloride from 0.1 mM KCl for a period of 5 hours.
Table 13

ABSORPTION AND TRANSPORT OF PHOSPHATE IN MAIZE HYBRIDS AND THEIR PARENTS AT 2 AND 4 HOURS OF ABSORPTION

The concentration of experimental solution H₃PO₄ was 0.1 mM. The maize seedlings were grown in 0.1 mM Ca₃(PO₄)₂ solution for 14 days.

<table>
<thead>
<tr>
<th>Hours</th>
<th>Cultivars</th>
<th>Absorption (millimoles/plant)</th>
<th>Transport (millimoles/plant)</th>
<th>Total uptake (millimoles/plant)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ganna-5</td>
<td>0.283 ± 0.018</td>
<td>0.005 ± 0.001</td>
<td>0.288 ± 0.018</td>
</tr>
<tr>
<td></td>
<td>CM 102</td>
<td>0.301 ± 0.090</td>
<td>0.006 ± 0.002</td>
<td>0.337 ± 0.091</td>
</tr>
<tr>
<td></td>
<td>CM 111</td>
<td>0.284 ± 0.027</td>
<td>0.003 ± 0.001</td>
<td>0.316 ± 0.091</td>
</tr>
<tr>
<td></td>
<td>CM 500</td>
<td>0.670 ± 0.103</td>
<td>0.018 ± 0.004</td>
<td>0.688 ± 0.106</td>
</tr>
<tr>
<td></td>
<td>Ganna-</td>
<td>0.843 ± 0.108</td>
<td>0.024 ± 0.004</td>
<td>0.868 ± 0.106</td>
</tr>
<tr>
<td></td>
<td>safad</td>
<td>0.307 ± 0.028</td>
<td>0.009 ± 0.003</td>
<td>0.316 ± 0.031</td>
</tr>
<tr>
<td></td>
<td>CM 300</td>
<td>1.261 ± 0.150</td>
<td>0.082 ± 0.005</td>
<td>1.343 ± 0.070</td>
</tr>
<tr>
<td></td>
<td>CM 400</td>
<td>1.181 ± 0.040</td>
<td>0.095 ± 0.003</td>
<td>1.275 ± 0.060</td>
</tr>
<tr>
<td></td>
<td>CM 600</td>
<td>0.625 ± 0.009</td>
<td>0.038 ± 0.003</td>
<td>0.656 ± 0.060</td>
</tr>
<tr>
<td></td>
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<td></td>
</tr>
</tbody>
</table>
Table 14

ABSORPTION AND TRANSPORT OF PHOSPHATE IN MAIZE HYBRIDS AND THEIR PARENTS AT 2 AND 4 HOURS OF ABSORPTION

The concentration of experimental solution H\textsubscript{3}PO\textsubscript{4} was 0.1 mM.
The maize seedlings were grown on 0.1 mM Ca\textsubscript{3}PO\textsubscript{4} solution for 14 days.

<table>
<thead>
<tr>
<th>Hours</th>
<th>Ganga-5</th>
<th>CM 202 X</th>
<th>CM 500</th>
<th>Ganga-</th>
<th>CM 400 X</th>
<th>CM 600</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>safed</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>0.829</td>
<td>1.008</td>
<td>1.066</td>
<td>1.130</td>
<td>1.499</td>
<td>0.883</td>
</tr>
<tr>
<td></td>
<td>± 0.127</td>
<td>± 0.102</td>
<td>± 0.112</td>
<td>± 0.115</td>
<td>± 0.112</td>
<td>± 0.126</td>
</tr>
<tr>
<td>4</td>
<td>2.367</td>
<td>2.405</td>
<td>2.170</td>
<td>2.289</td>
<td>2.674</td>
<td>1.375</td>
</tr>
<tr>
<td></td>
<td>± 0.042</td>
<td>± 0.283</td>
<td>± 0.501</td>
<td>± 0.110</td>
<td>± 0.326</td>
<td>± 0.049</td>
</tr>
</tbody>
</table>

Absorption (m moles/g. fr. wt.)

<table>
<thead>
<tr>
<th>Hours</th>
<th>Ganga-5</th>
<th>CM 202 X</th>
<th>CM 500</th>
<th>Ganga-</th>
<th>CM 400 X</th>
<th>CM 600</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>safed</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>0.010</td>
<td>0.014</td>
<td>0.006</td>
<td>0.017</td>
<td>0.030</td>
<td>0.013</td>
</tr>
<tr>
<td></td>
<td>± 0.001</td>
<td>± 0.002</td>
<td>± 0.001</td>
<td>± 0.004</td>
<td>± 0.006</td>
<td>± 0.003</td>
</tr>
<tr>
<td>4</td>
<td>0.039</td>
<td>0.079</td>
<td>0.066</td>
<td>0.084</td>
<td>0.159</td>
<td>0.034</td>
</tr>
<tr>
<td></td>
<td>± 0.009</td>
<td>± 0.007</td>
<td>± 0.001</td>
<td>± 0.003</td>
<td>± 0.024</td>
<td>± 0.002</td>
</tr>
</tbody>
</table>

Transport (m moles/g. fr. wt.)

<table>
<thead>
<tr>
<th>Hours</th>
<th>Ganga-5</th>
<th>CM 202 X</th>
<th>CM 500</th>
<th>Ganga-</th>
<th>CM 400 X</th>
<th>CM 600</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>safed</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>0.280</td>
<td>0.437</td>
<td>0.340</td>
<td>0.402</td>
<td>0.628</td>
<td>0.277</td>
</tr>
<tr>
<td></td>
<td>± 0.024</td>
<td>± 0.048</td>
<td>± 0.025</td>
<td>± 0.053</td>
<td>± 0.065</td>
<td>± 0.031</td>
</tr>
<tr>
<td>4</td>
<td>0.729</td>
<td>0.951</td>
<td>0.669</td>
<td>0.881</td>
<td>0.921</td>
<td>0.483</td>
</tr>
<tr>
<td></td>
<td>± 0.056</td>
<td>± 0.112</td>
<td>± 0.072</td>
<td>± 0.137</td>
<td>± 0.035</td>
<td></td>
</tr>
</tbody>
</table>
5) Absorption and translocation of Rb in CSH-5; a long duration, 15 to 72 hours experiment:

Absorption pattern was also examined over a period of 72 hours. In Rb absorption per plant (Fig. 9), CSH-5 followed the higher parent, whereas it was heterotic for transport and total uptake. On per g. fr. wt. basis, hybrid CSH-5 followed the lower parent in absorption, while there was no significant difference between hybrid and parents for transport and total uptake. These findings reveal that the heterotic pattern observed in short duration experiments on per plant basis is maintained in long duration experiments also.

The absorption reached maximum at 15 hours and then decreased. The reason for decrease is not known. It is possible that there was no further absorption and what has been absorbed till then was lost in transport to shoot. The transport, and the total uptake were steady throughout. The transport index (Figure 10) revealed that there was continuous increase in Rb transport for 72 hours. The hybrid followed the parent mean for transport index. The same trend was observed in short duration experiment.

6) Absorption and translocation of phosphate in CSH-5 and CSH-7; a long duration experiment:

Absorption, transport and total uptake of phosphate by CSH-5 on per plant and per g. fr. wt. basis followed the higher parent whereas CSH-7 was heterotic in transport and total uptake.
Fig. 9. Absorption and translocation of Rb from 0.1 mM RbCl; a time course (15-72 hours) long duration experiment. The 14 days-old seedlings of CSH-5 and parents were used. The values are expressed on per 5 plants and per g. fr. wt. basis.
Fig. 10. Rb transport index of CSH-5 and parents. The 14 days-old seedlings were allowed to absorb Rb from 0.1 mM RbCl for a period of 72 hours.
(Fig. 11). CSH-7 was heterotic for absorption on per plant basis and had no difference from parents on per g. fr. wt. basis. Both hybrids were non-heterotic for phosphate transport in short duration experiment, whereas they were heterotic in long duration experiment.

A saturation in absorption was reached at 24 hours in CSH-5 triplet (male, female and their hybrid), whereas in CSH-7 it took 48 hours. This showed the genotypic differences in absorption capacity. The transport pattern was bihasic and reached steady state after 72 hours. CSH-5 followed the lower parent whereas CSH-7 was heterotic in transport index (Fig. 12).

DISCUSSION

Rao and Khanna (1975) in their review article on heterosis concluded that "since root growth in hybrids is increased because of increase in shoot growth and photosynthetic availability, it is obvious that heterosis in nutrient uptake will be observed even if the absorption per unit weight remains unchanged. Once the results are analyzed to the component level there is really no heterosis". Most of the work on heterosis from the view point of nutrient uptake showed that the mineral uptake was expressed as mineral content in the plant part. However, the present study is directed to examine heterosis on the level of absorption and translocation of a few nutrients by hybrids and parents.
Fig. 11. Absorption and translocation of phosphate from 0.1 mM $\text{H}_3\text{PO}_4$; a time course (15-72 hours) long duration experiment. The 14 days-old seedlings of CSH-5, CSH-7 and parents were used. The values are expressed on per 5 plants and per g. fr. wt. basis.
Fig. 12. Phosphate transport index of CSH-5, CSH-7 and parents.

The 14 days-old seedlings were allowed to absorb phosphate from 0.1 mM H$_3$PO$_4$ for a period of 72 hours.
The results of the experiments (Fig. 2, 5, 7) revealed that on per plant basis, hybrids showed heterosis in Rb, phosphate and chloride absorption. This heterosis in absorption can be due to increase in fresh weight or due to increase in absorption per unit weight of nutrient uptake. Table 6 shows that hybrids had greater fresh weight as compared to their parents. There was heterosis for phosphate absorption but not for Rb absorption. However, chloride absorption showed heterosis in one hybrid. Similar heterosis was observed by Frick and Bauman (1978) for K uptake expressed on unit wt. basis. Beauchamp et al. (1976) observed greater N accumulation rate in one of the three corn hybrids than its inbreds. Rao and Venkateshwarlu (1971) measured N, P, K content in leaf and stem of sorghum hybrids and their parents. Then mineral content was expressed on per plant basis, there was heterosis, but not so when it was expressed on percent plant tissue. These findings support our results on Rb uptake. Jensen and Jonsson (1981) observed that the heterotic effect on growth of rye wheat was mainly localized in the shoots, and not on ion flux or transport to shoot. Whiteaker et al. (1976) observed that in the F1 generation of bean, several matings gave evidence of over-dominance for phosphate efficiency; in other families, the F1 progenies were about the same as the more efficient parents and the performance in one hybrid F1 was near the parent's mean.

On per plant basis (Fig. 2, 5, 7) for transport, both hybrids GSH-5 and GSH-7 were heterotic for Rb and chloride absorption.
and were not heterotic for phosphate. The heterotic behaviour can be due to greater shoot weight of hybrids and due to their greater mineral transport per unit shoot weight. The shoot weight of hybrids was greater, as compared to their parents. Transport per q. fr. wt. basis indicated that all hybrids except CSH-6, were non-heterotic. Hybrid CSH-6 which was heterotic in Rb transport index (Fig. 4) was also heterotic for transport on per q. fr. wt. basis and on per plant basis. This further illustrates the genotype difference for transport parameter in CSH-6. Similar difference (Foy and Barber 1968) in Mg transport to the stem rather than difference in rate of absorption was noted in inbred lines of corn. Ramani (1983) observed that the Zn transport to shoot in CSH-7 and CSH-8 was much higher than in their parents, which indicated a clear evidence for heterosis in Zn transport.

The heterosis in P absorption and not in Rb, revealed that genotypes differed in their ion uptake capacity. Schenk and Barber (1980) also have noted that uptake parameters varied several folds among genotypes and there was no linkage between the uptake of two like K and P. Thus, a genotype having greater ability to absorb K need not be so, for P uptake.

All the four hybrids were nonheterotic in Rb absorption per q. fr. wt. (Fig. 2, 3). CSH-5, CSH-7, CSH-8 were nonheterotic and CSH-6 was heterotic for Rb transport and this is reflected
in the transport index (Fig. 4). Chevalier and Schrader (1977) observed that in dry wt. and NO₃ content heterosis was noticed in all plant parts.

Hooymans (1968) obtained a biphasic uptake pattern of Rb against time in excised and intact barley roots. On the basis of this he suggested that fast phase I and steady phase II represented cytoplasmic and vacuolar accumulation. In general, the absorption pattern on per g. fr. wt. basis was biphasic for Rb, linear for phosphate, and exponential for chloride. Among genotypes there are variations in the absorption patterns. The average amounts absorbed during 5 hours were 11.16 μmoles Rb, 5.00 μmoles of P and 1.37 μmoles of Cl (Figs. 2, 5, 7). The transport pattern was linear for Rb, phosphate and chloride and the amount transported were 2.62, 0.51 and about 0.25 μmoles respectively. The amount transported comes to nearly 1/5 of that absorbed and hence the total uptake pattern was similar to absorption patterns. The values of total uptake for Rb, phosphate, chloride were 6.68, 2.19, 0.72/μmoles at 5 hour uptake period (Fig. 2, 5, 7).

The study with maize indicates that there is no heterosis in growth or phosphate uptake and transport. Similar results were observed by Ramani (1983). She observed that maize hybrid Ganga-5 was not heterotic in absorption and transport for Zn. As those hybrids are released for cultivation in India, it is presumed that they are heterotic in
grain yield. The possible explanation is that these hybrids are not heterotic in phosphate uptake, or, the growth stage of 14 days is too early to show the difference. Nosberger (1970) observed that in early stage the differences between maize hybrids and inbreds were very small, but increased with time.

A 72-hour (Fig. 9 and 11) Rb and phosphate uptake and translocation study confirms the heterotic pattern observed during short duration experiments. Phosphate transport in both sorghum hybrids was not heterotic during 1-6 hours, but was heterotic at 72 hours. This feature indicates that hybrids were comparatively slow for phosphate uptake in the short periods of absorption.

A comparative study of these cultivars (CSH-5, CSH-7 and parents) in Rb and phosphate absorption over a long duration revealed that the absorption reached saturation at 15 hours for Rb, whereas, it took 24 hours for CSH-5 and parents and 48 hours for CSH-7 and parents. This again revealed the genotypic difference in Rb and phosphate uptake. The response of hybrids and its inbreds, was very much similar i.e., they behave as a unit.

Studies on per g. fr. wt. basis revealed that in Rb absorption hybrid CSH-5 and CSH-7 followed the female parent, whereas in transport both hybrids resembled the male parent. The absorption pattern in hybrids for phosphate was not clear, whereas in transport CSH-5 resembled male parent and CSH-7 resembled female parent. For chloride absorption CSH-5 resembled
male parent, and CSH-7 the female and in case of transport CSH-5 resembled the male, and there was no difference in CSH-7 and parents for transport. In general, it can be concluded that in absorption, hybrids resembled female parent whereas in transport they resembled male parent.