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The role of potassium in alleviating detrimental effects of abiotic stresses in plants§

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Summary—Zusammenfassung

Plants exposed to environmental stress factors, such as drought, chilling, high light intensity, heat, and nutrient limitations, suffer from oxidative damage catalyzed by reactive oxygen species (ROS), *e.g.*, superoxide radical ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2) and hydroxyl radical ($OH^{\bullet}$). Reactive O_2 species are known to be primarily responsible for impairment of cellular function and growth depression under stress conditions. In plants, ROS are predominantly produced during the photosynthetic electron transport and activation of membrane-bound NAD(P)H oxidases. Increasing evidence suggests that improvement of potassium (K)-nutritional status of plants can greatly lower the ROS production by reducing activity of NAD(P)H oxidases and maintaining photosynthetic electron transport. Potassium deficiency causes severe reduction in photosynthetic CO_2 fixation and impairment in partitioning and utilization of photosynthates. Such disturbances result in excess of photosynthetically produced electrons and thus stimulation of ROS production by intensified transfer of electrons to O_2. Recently, it was shown that there is an impressive increase in capacity of bean root cells to oxidize NADPH when exposed to K deficiency. An increase in NADPH oxidation was up to 8-fold higher in plants with low K supply than in K-sufficient plants. Accordingly, K deficiency also caused an increase in NADPH-dependent $O_2^{\bullet-}$ generation in root cells. The results indicate that increases in ROS production during both photosynthetic electron transport and NADPH-oxidizing enzyme reactions may be involved in membrane damage and chlorophyll degradation in K-deficient plants. In good agreement with this suggestion, increases in severity of K deficiency were associated with enhanced activity of enzymes involved in detoxification of H_2O_2 (ascorbate peroxidase) and utilization of H_2O_2 in oxidative processes (guaiacol peroxidase). Moreover, K-deficient plants are highly light-sensitive and very rapidly become chlorotic and necrotic when exposed to high light intensity. In view of the fact that ROS production by photosynthetic electron transport and NADPH oxidases is especially high when plants are exposed to environmental stress conditions, it seems reasonable to suggest that the improvement of K-nutritional status of plants might be of great importance for the survival of crop plants under environmental stress conditions, such as drought, chilling, and high light intensity. Several examples are presented here emphasizing the roles of K in alleviating adverse effects of different abiotic stress factors on crop production.

Key words: abiotic stress / NADPH oxidase / photosynthesis / potassium deficiency / reactive oxygen species / stress tolerance

Die Bedeutung von Kalium für die Verminderung der Schadwirkung abiotischer Stressfaktoren bei Pflanzen

Pflanzen, die in ihrer Umwelt Stressfaktoren wie Trockenheit, Kälte, hoher Lichtintensität, Hitze oder Nährstofflimitierung ausgesetzt sind, leiden unter oxidativer Schädigung durch reaktive Sauerstoff-Spezies (ROS), z. B. Superoxidradikal ($O_2^{\bullet-}$), Wasserstoffperoxid (H_2O_2) und Hydroxyl-Radikal ($OH^{\bullet}$). Es ist bekannt, dass für die Beeinträchtigung zellulärer Funktionen und Wachstumsminderungen unter Stressbedingungen primär ROS verantwortlich sind. In Pflanzen werden ROS hauptsächlich beim photosynthetischen Elektronentransport und der Aktivierung von membrangebundenen NAD(P)H-Oxidasen gebildet. Es gibt zunehmend Hinweise, die vermuten lassen, dass eine Verbesserung des Kalium (K)-Versorgungszustandes der Pflanzen die ROS-Bildung durch eine Verminderung der Aktivitäten der NAD(P)H-Oxidasen und eine Aufrechterhaltung des photosynthetischen Elektronentransportes stark verringert. Kalium-Mangel verursacht eine starke Abnahme der photosynthetischen CO_2-Fixierung und eine Beeinträchtigung der Verteilung und Nutzung von Photosynthaten. Solche Störungen führen zu einem Überschuss von bei der Photosynthese gebildeten Elektronen und dadurch zu einer Erhöhung der ROS-Bildung durch verstärkte Elektronenübertragung auf O_2. Kürzlich wurde gezeigt, dass die Kapazität der Wurzelzellen von Bohne zur Oxidation von NAD(P)H unter K-Mangelbedingungen deutlich erhöht ist. Die NADPH-Oxidation war bei K-Mangel-Pflanzen im Vergleich zu ausreichend mit K versorgten Pflanzen um bis zu einem Faktor 8 erhöht. Entsprechend verursachte K-Mangel auch eine Zunahme der NADPH-abhängigen $O_2^{\bullet-}$-Bildung in Wurzelzellen. Diese Ergebnisse deuten an, dass die Zunahmen der ROS-Bildung bei dem photosynthetischen Elektronentransport und den Reaktionen NADPH-oxidierender Enzyme an der Membranschädigung und dem Chlorophyllabbau von K-Mangel-Pflanzen beteiligt sind. In guter Übereinstimmung mit dieser Vermutung war zunehmender K-Mangel mit erhöhter Aktivität von Enzymen verbunden, die an der Detoxifizierung von H_2O_2 (Ascorbat-Peroxidase) und am Verbrauch von H_2O_2 bei oxidativen Prozessen (Guaiacol-Peroxidase) beteiligt sind. Darüberhinaus sind K-Mangel-Pflanzen sehr lichtempfindlich und werden schnell chlorotisch und nekrotisch, wenn sie hohen Lichtintensitäten ausgesetzt werden. In Anbetracht dessen, dass die ROS-Bildung beim photosynthetischen Elektronentransport und durch NADPH-Oxidasen besonders hoch ist, wenn die Pflanzen Stressbedingungen in ihrer Umwelt ausgesetzt sind, scheint die Vermutung folgerichtig, dass eine Verbesserung des K-Versorgungszustandes von Pflanzen für deren Überleben bei ungünstigen Umweltbedingungen, wie Trockenheit, Kälte und hoher Lichtintensität, von großer Bedeutung ist. Es werden mehrere Beispiele gezeigt, welche die Rolle von K bei der Verminderung ungünstiger Auswirkungen von abiotischen Stressfaktoren auf die Pflanzenproduktion hervorheben.

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1 Introduction

The world population is expanding rapidly and is expected to be around 8 billion by the year 2025 (*Pinstrup-Andersen* et al., 1999). This represents an addition of nearly 80 million people to the present population (6 billion) every year. It is forecast that the increases in world population will occur almost exclusively in developing countries, where serious nutritional problems exist at present, and population pressure on the agricultural soils is already very high.

To feed the increasing world population and sustain well-being of humankind, food production must be increased by up to 100% over the next 25 years (*Borlaug* and *Dowswell*, 1993; *Dyson*, 1999). The projected increases in food production must be achieved on the already cultivated land, because the potential for expanding the area of agricultural soils is very limited. However, recent trends indicate that productivity and fertility of soils are globally declining due to degradation and intensive use of soils without consideration of proper soil-management practices (*Gruhn* et al., 2000; *Cakmak*, 2002). Inadequate and unbalanced supply of mineral nutrients and impaired soil fertility are particular problems, causing decreases in global food production, especially in the developing countries. It is estimated that around 60% of cultivated soils have growth-limiting problems associated with mineral-nutrient deficiencies and toxicities (*Cakmak*, 2002). According to *Byrnes* and *Bumb* (1998), in the next 20 years fertilizer consumption has to increase by around 2-fold to achieve the needed increases in food production. It seems that in the coming decades plant-nutrition-related research will be a high-priority research area contributing to crop production and sustaining soil fertility.

Environmental problems (*e.g.*, water deficiency, extreme temperatures, salinity, flooding, soil acidity, and pathogenic infections) are increasing as a result of increasing world population and intensive use of natural resources. These environmental stresses contribute significantly to reducing crop yields well below the potential maximum yields. According to *Bray* et al. (2000), the relative decreases in potential maximum crop yields (*i.e.*, yields under ideal conditions) associated with abiotic stress factors vary between 54% and 82% (Tab. 1). Most of yield decreases caused by abiotic stresses result from drought, salinity, high or low temperatures, excess light, inadequate mineral nutrient supply, and soil acidity. Therefore, for sustaining food security, a high priority should be given to minimizing the detrimental effects of environmental stresses on crop production by (1) applying modern breeding techniques and biotechnological tools and (2) increasing physical and chemical fertility as well as maintaining productivity of cultivated soils by adequate and balanced supply of mineral nutrients.

Plants have developed a wide range of adaptive/resistance mechanisms to maintain productivity and ensure survival under a variety of environmental stress conditions. Increasing evidence suggests that mineral-nutrient status of plants plays a critical role in increasing plant resistance to environmental stress factors (*Marschner*, 1995). Of the mineral nutrients, K plays a particular role in contributing to the survival of crop plants under environmental stress conditions. Potassium is essential for many physiological processes, such as photosynthesis, translocation of photosynthates into sink organs, maintenance of turgescence, activation of enzymes, and reducing excess uptake of ions such as Na and Fe in saline and flooded soils (*Marschner*, 1995; *Mengel* and *Kirkby*, 2001).

This review deals with the roles of K in minimizing adverse effects of environmental stress conditions on crop production, with particular emphasis on abiotic stress factors.

2 Protective role of K against light-induced cell damage

Chloroplasts are the major organelles producing ROS, such as the superoxide radical ($O_2^{\bullet -}$), hydrogen peroxide (H_2O_2), and singlet oxygen ($^1O_2$) during photosynthesis (*Asada*, 2000). Production of ROS in chloroplasts can be particularly high when plants are exposed to environmental stresses such as drought, chilling, nutrient deficiency, and salinity (*Foyer* et al., 1994; *Marschner* et al., 1996; *Asada*, 2000; *Vranova* et al., 2002). Reactive O_2 species are highly toxic, causing membrane damage and chlorophyll degradation, and are thus responsible for development of leaf chlorosis and necrosis. Under normal conditions, up to 20% of the total photosynthetic electron flux is transferred to molecular O_2, forming $O_2^{\bullet -}$ and other $O_2^{\bullet -}$-driven reactive O_2 species (*Robinson*, 1988; *Biehler* and *Fock*, 1996; *Cakmak*, 2000). When utiliza-

Table 1: Average yields and record yields of corn, wheat, soybean, and potato and the losses in record yield caused by abiotic stresses. Record yield is assumed to represent crop production under ideal conditions. Abiotic stress factors include drought, salinity, extreme temperatures, flooding, and nutrient deficiencies (*Bray* et al., 2000).

Tabelle 1: Durchschnittliche Erträge und Spitzenerträge von Mais, Weizen, Sojabohnen und Kartoffeln und durch abiotische Stressfaktoren bewirkte Verminderung der Spitzenerträge. Der Spitzenertrag stellt den unter idealen Bedingungen erreichbaren Ertrag dar. Abiotische Stressfaktoren umfassen Trockenheit, Salinität, extreme Temperaturen, Wasserüberstau und Nährstoffmangel (*Bray* et al., 2000).

Crop	Record yield	Average yield	Average losses by abiotic stress	Losses by abiotic stress
	t ha^{-1}			(%)
Corn	19.3	4.6	12.7	65.8
Wheat	14.5	1.9	11.9	82.1
Soybean	7.4	1.6	5.1	69.3
Potato	94.1	28.3	50.9	54.1

tion of absorbed light energy in CO_2 fixation is limited by biotic or abiotic stresses, the electron flux to O_2 is intensified, resulting in a large accumulation of ROS in chloroplasts. Under these conditions, excitation energy is also transferred to O_2 to form highly toxic $^1O_2$. Production of ROS in chloroplasts becomes more pronounced when plants grown under an environmental stress are exposed to high light intensity, resulting in the occurrence of photooxidative damage to chloroplasts. There are several examples showing that combination of high light intensity and an environmental stress causes very rapid development of leaf chlorosis and necrosis (*Cakmak* and *Marschner*, 1992; *Foyer* et al., 1994; *Wise*, 1995; *Huner* et al., 1998; *Cakmak*, 2000; *Choi* et al., 2002).

Plants suffering from K deficiency are extremely sensitive to increased light intensity. At the same low supply of K, leaf chlorosis and necrosis occurred in plants growing under high light intensity, but not in plants under low light intensity (*Marschner* and *Cakmak*, 1989; *Marschner* et al., 1996). Partial shading of the K-deficient leaves also prevented development of leaf chlorosis and necrosis. Such marked effects of high light intensity on the occurrence of chlorosis were not related to K concentrations in leaf tissues: shaded and nonshaded parts of K-deficient leaves had similar K concentration (*Marschner* and *Cakmak*, 1989). These observations support the idea that photooxidative damage to chloroplasts catalyzed by ROS plays a critical role in occurrence of leaf symptoms characteristic of K deficiency.

There are several reasons for the high sensitivity of K-deficient plants to increasing light intensity. Potassium plays a central role in maintenance of photosynthesis and related processes. As shown in different plant species, K deficiency results in severe decreases in net photosynthesis (Fig. 1). The decreases in photosynthesis by K deficiency become more distinct when plants are exposed to elevated atmospheric concentrations of CO_2 and O_3 (*Barnes* et al., 1995), indicating an enhanced K requirement of plants growing under CO_2-enriched atmosphere. This effect of K is important and needs further investigation in view of the fact that the global atmospheric CO_2 concentration is increased and will be possibly doubled at the end of the 21st century (*Bolin*, 1986). The decrease in photosynthesis by K deficiency appears to be related to reduced stomatal conductance, increased mesophyll resistance and lowered ribulose bisphosphate carboxylase activity (*Peoples* and *Koch*, 1979; *Cakmak* and *Engels*, 1999; *Zhao* et al., 2001a; and references therein). Maintenance of photosynthesis at high rate is also dependent on export and utilization of photoassimilates within plants. It is well-documented that when compared to plants supplied adequately with K, there is a several-fold increase in sucrose concentration in source leaves and a marked reduction in roots under K deficiency (*Cakmak* et al., 1994a, b; *Huber*, 1984; *Marschner* et al., 1996; *Bednarz* and *Oosterhuis*, 1999; Zhao et al., 2001a). These findings are consistent with results showing that K deficiency causes a

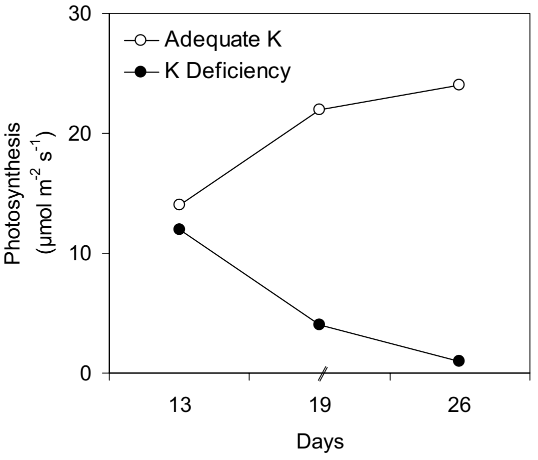

Figure 1: Photosynthesis rate in leaves of cotton plants grown in pots over 26 d with adequate and deficient supply of K (redrawn from *Bednarz* and *Oosterhuis*, 1999).

Abbildung 1: Photosyntheserate der Blätter von Baumwollpflanzen, die in Gefäßen für 26 Tage mit ausreichendem oder zu geringem K-Angebot wuchsen (nach *Bednarz* und *Oosterhuis*, 1999).

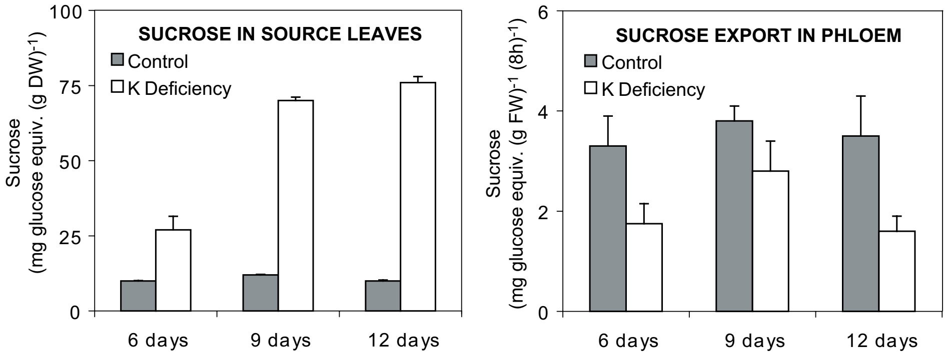

Figure 2: Sucrose concentrations in source leaves and phloem exudates collected from source leaves of bean (*Phaseolus vulgaris*) plants over 12 d of growth in nutrient solution with adequate (2000 µM) and deficient (50 µM) K supply. Phloem exudates were collected from detached primary leaves using the EDTA-promoted exudation technique (redrawn from *Cakmak* et al., 1994b).

Abbildung 2: Saccharosekonzentrationen in Source-Blättern und im Phloemexsudat, das von Sourceblättern von Bohnen (*Phaseolus vulgaris*) während einer 12-tägigen Wachstumsdauer bei ausreichendem (2000 µM) und zu geringem (50 µM) K-Angebot gesammelt wurde. Phloemexsudat wurde mit der EDTA-geförderten Exsudationstechnik von abgeschnittenen Primärblättern gesammelt (nach *Cakmak* et al., 1994b).

severe decrease in phloem export of sucrose from source leaves (Fig. 2; *Mengel* and *Viro*, 1974; *Mengel,* 1980; *Cakmak* et al., 1994b).

Due to such a distinct impairment of photosynthetic CO_2 fixation as well as reduced utilization of photoassimilates in K-deficient leaves, enhanced production of ROS is unavoidable, which in turn leads to photooxidative damage (Fig. 3). Increases in severity of leaf chlorosis by K deficiency were associated with enhanced activities of enzymes involved in detoxification of H_2O_2 (ascorbate peroxidase) and utilization of H_2O_2 in oxidative processes (guaiacol peroxidase) (*Cakmak*, 1994; Fig. 4). The rise in H_2O_2 detoxification capacity of K-deficient leaves supports the suggestion that production of ROS is intensified in K-deficient leaves at the expense of CO_2 fixation. It can be concluded that plants exposed to high light intensity or grown under long-term sunlight conditions as occurs like in southern countries of the northern hemisphere may have larger K requirements at physiological levels than plants grown under low light intensity. Increased requirement for K by high light intensity is needed for an efficient utilization of absorbed light energy in photosynthetic CO_2 fixation and transport of photosynthates into sink organs.

3 Potassium-induced plant resistance to drought

There is increasing evidence that plants suffering from environmental stresses like drought have a larger internal requirement for K (*Cakmak* and *Engels,* 1999). Environmental stress factors that enhance the requirement for K also cause oxidative damage to cells by inducing formation of ROS, especially during photosynthesis (*Bowler* et al., 1992; *Elstner* and *Osswald*, 1994; *Foyer* et al., 1994). The reason for the enhanced need for K by plants suffering from environmental stresses appears to be related to the fact that K is required for maintenance of photosynthetic CO_2 fixation. For example, drought stress is associated with stomatal closure and thereby with decreased CO_2 fixation. Based on the model given in Fig. 3, formation of ROS is intensified because of inhibited CO_2 reduction by drought stress. Obviously, formation of ROS under drought stress would be dramatic in plants exposed to high light intensity, with concomitant severe oxidative damage to chloroplasts. Increases in ROS production in drought-stressed plants are well known and related to impairment in photosynthesis and associated disturbances in carbohydrate metabolism (*Seel* et al., 1991; *Quartacci* et al.,

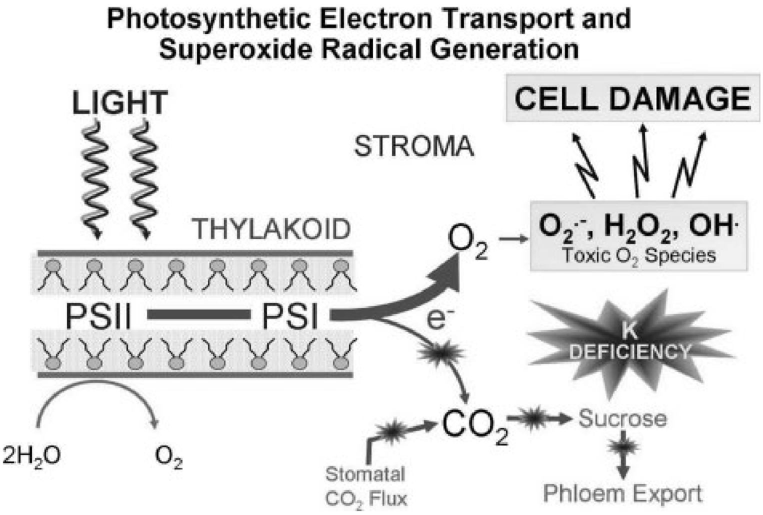

Figure 3: Schematic representation of superoxide radical production in chloroplasts of K-deficient leaves (✸ refers to the inhibition of the corresponding reaction by K deficiency).

Abbildung 3: Schematische Darstellung der Bildung von Superoxid-Radikalen in Chloroplasten von K-Mangel-Blättern (✸ bedeutet Inhibierung des entsprechenden Prozesses durch K-Mangel).

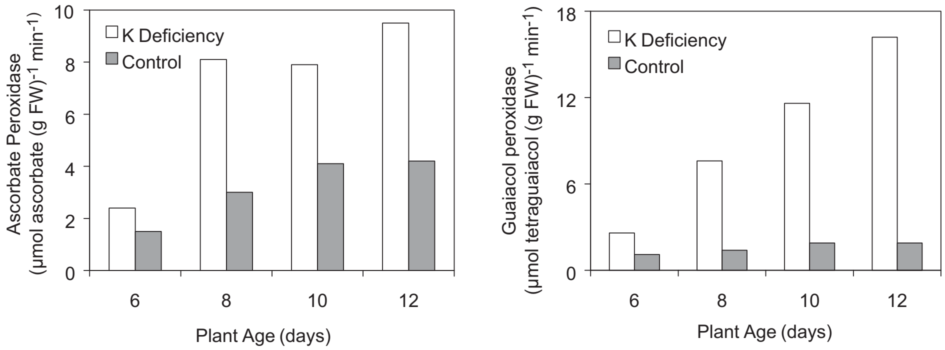

Figure 4: Activities of ascorbate peroxidase and guaiacol peroxidase in leaves of bean (*Phaseolus vulgaris*) plants over 12 d of growth in nutrient solution with adequate (2000 µM) and deficient (50 µM) K supply (redrawn from *Cakmak*, 1994).

Abbildung 4: Aktivitäten der Ascorbat-Peroxidase und Guaiacol-Perooxidase in Blättern von Bohnenpflanzen (*Phaseolus vulgaris*), die für 12 Tage in Nährlösung bei ausreichendem (2000 µM) oder zu geringem (50 µM) K-Angebot wuchsen (nach *Cakmak*, 1994).

1994; *Jiang* and *Zhang*, 2002). These results indicate that when plants are grown under low supply of K, drought-stress-induced ROS production can be additionally enhanced, at least due to K-deficiency-induced disturbances in stomatal opening, water relations, and photosynthesis (*Marschner,* 1995; *Mengel* and *Kirkby*, 2001). In addition, most importantly, under drought conditions chloroplasts lose high amounts of K to further depress photosynthesis (*Sen Gupta* and *Berkowitz,* 1987) and induce further ROS formation. These results strongly support the idea that increases in severity of drought stress result in corresponding increases in K demand to maintain photosynthesis and protect chloroplasts from oxidative damage. The results presented in Fig. 5 for wheat are in accordance with this suggestion, and show that decreases in photosynthesis caused by drought stress are particularly high in plants supplied with low K, and are minimal when K is sufficient (*Sen Gupta* et al., 1989). Alleviation of detrimental effects of drought stress, especially on photosynthesis, by sufficient K supply has also been shown in legumes (*Sangakkara* et al., 2000). In field experiments conducted in Egypt, it was found that decreases in grain yield resulting from restricted irrigation could be greatly eliminated by increasing K supply (*Abd El-Hadi* et al., 1997). In view of these results, it can be concluded that improvement of K-nutritional status of plants seems to be of great importance for sustaining high yields under rain-fed conditions.

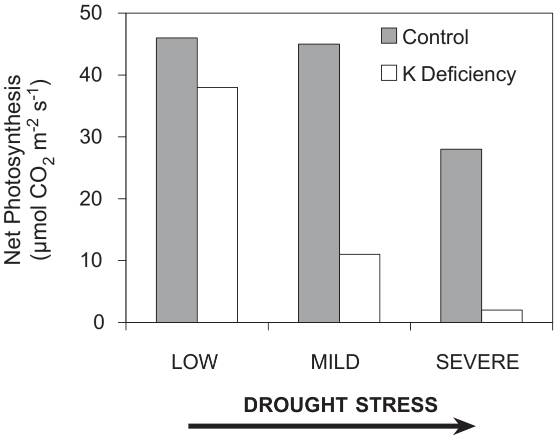

Figure 5: Net photosynthesis of wheat leaves subjected to varied drought stress and K supply. Data calculated from *Sen Gupta* et al. (1989).

Abbildung 5: Nettophotosynthese von Weizenblättern bei unterschiedlichem Trockenstress und K-Angebot. Daten errechnet nach *Sen Gupta* et al. (1989).

4 Enhanced resistance of plants to low-temperature stress by K supply

Like drought stress, both chilling and frost stresses are also responsible for photooxidative damage to chloroplasts due to the impairments in photosynthetic C metabolism. Generally, low-temperature stress affects the fluidity of membrane lipids and thus alters membrane structure (*Marschner*, 1995). Under low-temperature stress, absorbed light energy exceeds the capacity of chloroplasts to use it in CO_2 fixation, and the excess energy is alternatively used for activation of O_2 to ROS (*Huner* et al., 1998; *Foyer* et al., 2002). Increases in activity of enzymes scavenging for H_2O_2 and $O_2^{\bullet -}$ in plants upon exposure to chilling or freezing temperatures indicate participation of ROS in chilling-induced cell damage (*Foyer* et al., 1994; *Lee* and *Lee*, 2000; *Allen* and *Ort*, 2001). Photosynthetic electron transport, stomatal conductance, rubisco activity, and CO_2 fixation are the major targets impaired by low-temperature stress in plants (*Allen* and *Ort*, 2001). These cellular targets are also major targets adversely affected by K deficiency. Therefore, under low supply of K, chilling- or frost-induced photooxidative damage can be exacerbated causing more decreases in plant growth and yield. It seems highly possible that supply of K in high amounts can provide protection against oxidative damage caused by chilling or frost. In accordance with this suggestion, it has been shown that increasing K concentration in irrigation water provided important protection against stem damage from low night temperatures in carnation plants (*Kafkafi,* 1990). Similarly, decreases in yield and increases in leaf damage induced by frost in potato plants under field conditions could be alleviated by high application of K fertilizer (Tab. 2). Improving low-temperature-stress tolerance of plants by increasing K supply was also shown in tomato, pepper, and eggplant seedlings growing outside, with temperatures ranging from 4°C to 16°C. Depending on the source of K fertilizers, K supply enhanced total plant yield by 2.4-fold, 1.9-fold, and 1.7-fold in tomato, pepper, and eggplant, respectively (*Hakerlerler* et al., 1997). Although the effect was not significant, K supply also reduced the rate of seedlings death due to low temperature.

Table 2: Influence of potassium supply on tuber yield, potassium concentration of leaves, and leaf damage caused by frost in potato (*Grewal* and *Singh*, 1980).

Tabelle 2: Einfluss des K-Angebotes auf den Knollenertrag, die Blatt-K-Konzentration und die durch Frost bewirkte Blattschädigung bei Kartoffel (*Grewal* and *Singh*, 1980).

Potassium supply	**Tuber yield**	**Potassium concentration**	**Leaf damage**
(kg ha^{-1})	(t ha^{-1})	(mg (g dry wt)$^{-1}$)	(%)
0	2.39	24.4	30
42	2.72	27.6	16
84	2.87	30.0	7

5 NADPH-dependent $O_2^{\bullet -}$ formation

Beside the photosynthetic electron transport, NADPH-dependent oxidases represent another major source for production of ROS in plant cells (*Cakmak*, 2000; *Jones* et al., 2000; *Vranova* et al., 2002). Superoxide-generating NADPH-oxidases are generally localized in plasma membranes, and are activated by a number of biotic and abiotic stress factors, such as chilling (*Shen* et al., 2000), ozone treatment (*Pellinen* et al., 1999), wounding (*Orozco-Cardenas* and *Ryan*, 1999), Zn deficiency (*Cakmak* and *Marschner*, 1988), drought (*Zhao* et al., 2001b; *Jiang* and *Zhang*, 2002), pathogenic attacks (*Lamb* and *Dixon*, 1997; *Bolwell* and *Wojtaszek*, 1997), and salt treatment

(*Kawano* et al., 2002). As shown schematically in Fig. 6, NADPH-oxidizing enzymes catalyze one-electron reduction of O_2 to $O_2^{\bullet -}$ by using NADPH as an electron donor. Reactive O_2 species produced by NADPH oxidases are involved in peroxidation of vital cell constituents and programmed cell death (*Jones* et al., 2000; *Neill* et al., 2002). It is generally accepted that $O_2^{\bullet -}$-generating NADPH oxidases play a major role in cell damage and associated decreases in growth by abiotic stresses. For example, preventing NADPH oxidation or NADPH-dependent $O_2^{\bullet -}$ generation in cucumber plants under chilling stress reduced chilling-induced leaf necrosis and lipid peroxidation (*Shen* et al., 2000).

Very recently, we found that the activity of NADPH oxidase increased in cytosolic fractions of bean roots with increasing severity of K deficiency (Tab. 3). The increases in NADPH oxidation by K deficiency were up to 8-fold. Such marked increases were not reported in literature, for example neither in the case of chilling (*Shen* et al., 2000) and water stress (*Zhao* et al., 2001b; *Jiang* and *Zhang*, 2002) nor in Zn-deficient plants (*Cakmak* and *Marschner,* 1988). Potassium deficiency also resulted in an increase in NADPH-dependent $O_2^{\bullet -}$ generation; however, the extent of $O_2^{\bullet -}$ generation was much lower and inconsistent as compared with the level of NADPH oxidase activity (Tab. 3). It seems possible that K deficiency can aggravate $O_2^{\bullet -}$-generating NADPH oxidase in plants suffering from biotic and abiotic stresses. As mentioned above, $O_2^{\bullet -}$-generating NADPH-oxidase is activated by different stress factors such as drought (*Jiang* and *Zhang,* 2002; *Zhao* et al., 2001b) and chilling (*Shen* et al., 2000). The well-described protective roles of K against drought and chilling stresses might also be explained by the inhibiting effect of increasing K concentration on the activity of NADPH oxidase. Moreover, $O_2^{\bullet -}$-generating NADPH-oxidases could also be involved in K-deficiency-induced blackspot-browning formation in potato tubers. The reason for the blackspot pigmentation in K-deficient tubers is not well understood and has been attributed to the enhanced activity of polyphenoloxidase by K deficiency (*McNabnay* et al., 1999).

The reason for the increases in NADPH oxidase by K deficiency is not known; and needs to be investigated in future studies. It might be related to abscisic acid (ABA), because ABA accumulates in plants suffering from K deficiency. For example, in *Ricinus communis* low supply of K strongly enhanced biosynthesis of ABA in roots and resulted in 4.6-fold increase in ABA transport from roots to shoots (*Peuke* et al., 2002). Abscisic acid is known to induce activity of NADPH oxidase and NADPH-dependent formation of ROS (*Zhao* et al., 2001b; *Jiang* and *Zhang,* 2002; *Neill* et al., 2002). Irrespective of NADPH oxidase, ABA has also been shown to be effective in increasing H_2O_2 and $O_2^{\bullet -}$ accumulation in roots or leaves (*Jiang* and *Zhang*, 2001; *Lin and Kao*, 2001). Large increases in peroxidase activity in K-deficient plants (*Cakmak*, 1994) can also be explained by high ABA accumulation, because increasing concentration of ABA induces activity of peroxidase in rice roots (*Lin* and *Kao*, 2001). Based on these results, one may speculate that K-deficiency-induced NADPH oxidase activity is possibly related to enhanced accumulation of ABA. This point needs to be clarified in future studies.

Table 3: Effect of increasing K supply on NADPH oxidase and NADPH-dependent $O_2^{\bullet -}$ production in cytosolic fraction of roots of bean plants grown 8 d in nutrient solution. Values in parentheses show the percentage of those in K-sufficient (2000 µM) plants. Each value represents the means ± SD of three independent replications (S. Eker, unpublished results).

Tabelle 3: Wirkung von steigendem K-Angebot auf die NADPH-Oxidase und die NADPH-abhängige $O_2^{\bullet -}$-Bildung in der cytosolischen Fraktion der Wurzeln von Bohnen, die für 8 Tage in Nährlösung wuchsen. Die Zahlen in Klammern geben den Prozentsatz von bei ausreichendem K-Angebot (2000 µM) wachsenden Pflanzen an. Jede Zahl stellt den Mittelwert ± SD von drei unabhängigen Wiederholungen dar (S. Eker, unveröffentlichte Ergebnisse).

K supply	**NADPH oxidase**	**$O_2^{\bullet -}$ Production**
(µM)	(µmol NADPH (g FW)$^{-1}$ min^{-1})	(nmol $O_2^{\bullet -}$ (g FW)$^{-1}$ min^{-1})
10	191±7 (817)	138±9 (124)
25	170±11 (723)	130±14 (117)
50	61±3 (254)	154±14 (139)
100	53±9 (225)	151±6 (136)
200	30±1 (128)	133±11 (120)
2000	24±4 (100)	111±11 (100)

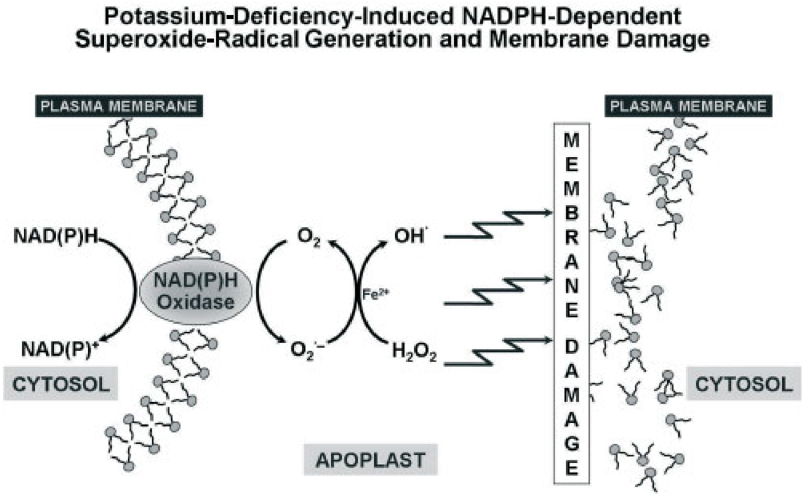

Figure 6: Model of the K-deficiency-induced NADPH oxidase, superoxide-radical production, and membrane damage in root cells.

Abbildung 6: Modell für die K-Mangel-induzierte Superoxid-Radikal-Bildung durch NADPH-Oxidase und die dadurch bewirkte Membranschädigung in Wurzelzellen.

6 Role of K in alleviating detrimental effects of salt stress

Soil salinity is an increasing constraint threatening crop production globally. Around 30% of cultivated soils are affected by accumulation of salts (*Epstein* et al., 1980; *Zhu* et al., 1997). Soil salinity generally results from excess accumulation of NaCl and exerts detrimental effects on crop production by causing ion toxicity and inducing osmotic stress (water deficiency) in root environment and in plants (*Zhu* et al., 1997; *Zhu*, 2001).

Like most of other environmental stresses, salt stress also strongly affects photosynthesis and causes oxidative stress by inducing water deficiency (stomatal closure), ion toxicity, and K deficiency. Consistent with this result, most of salt-tolerant genotypes respond to salinity by increasing antioxidative defense systems for detoxification of ROS (*Rodriquez-Rosales* et al., 1999; *Sudhakar* et al., 2001; *Zhu,* 2001). The critical role of antioxidative defence in expression of high salt tolerance was demonstrated in the *Arapidopsis* mutant line (*pst 1*). This mutant line has an impressive tolerance to NaCl (up to 400 mM) and also to excess light intensity. High salt tolerance of this *Arabidopsis* mutant line was associated with enhanced activities of enzymes scavenging for $O_2^{\bullet -}$ and H_2O_2 (*Tsugane* et al., 1999). The *pst* seedlings were also highly tolerant to the treatment by $O_2^{\bullet -}$-producing herbicides. These results support the idea that salt stress reflects an oxidative stress and induction of antioxidant defence system is critical for development of salt tolerance. Similar conclusions were also reached by *Hernandez* et al. (2000) and *Sudhakar* et al. (2001) in the studies with sensitive cultivars of pea and mulberry, respectively.

In view of the fact that high NaCl treatments impair K nutrition of plants, it is suggested that K deficiency at the cellular level might be a contributory factor to salt-induced oxidative stress and related cell damage. Therefore, improving K nutrition of plants under salt stress could be essential to minimizing oxidative cell damage, at least in part by reducing ROS formation during photosynthesis (Fig. 3) and inhibiting activation of $O_2^{\bullet -}$-generating NADPH oxidase (*Shen* et al., 2000; see also Fig. 6). Consistent with these suggestions, *Kaya* et al. (2001) showed that salinity-induced increase in chlorophyll and membrane damage and decrease in biomass production in tomato could be significantly reduced by foliar application of K fertilizer in the form of KH_2PO_4. In this work, salinity caused not only K deficiency but also P deficiency, and foliar supply of KH_2PO_4 was effective in correcting both nutrient deficiencies.

Accumulation of Na and impairment of K nutrition is a major characteristic of salt-stressed plants. Therefore, K : Na ratio in plants is considered a useful guide to assessing salt tolerance. Selection or breeding genotypes with high K : Na ratios is an important strategy to minimize growth decreases in saline soils (*Deal* et al., 1999; *Santa-Maria* and *Epstein*, 2001; and references therein). *Rascio* et al. (2001) identified a wheat mutant with a high ability to accumulate K in the shoot and showed that this mutant compared to other wheat genotypes greatly improved tissue hydration, seed germination, and seedling growth under increasing concentrations of NaCl. The importance of K nutrition in salt tolerance was also shown in studies with *Arabidopsis* mutant lines. Mutant lines showing hypersensitivity to NaCl were also hypersensitive to low K supply. High salt sensitivity of *Arabidopsis* mutant line was found to be associated with extremely poor capacity to take up K from a growth medium (*Liu* and *Zhu*, 1997; *Zhu* et al., 1998). Similarly, in tomato the salt-hypersensitive mutants were defective in K uptake and had an impaired K nutrition (*Borsani* et al., 2001). These results again highlight the critical importance of adequate K nutrition in alleviation of detrimental effects of salinity in plants.

7 Alleviation of iron toxicity by potassium

Potassium interacts not only with uptake of Na, but also of iron (Fe), especially in rice. Iron toxicity is a common nutritional problem in wetland rice, resulting in severe losses in growth and yield (*Neue* et al., 1998). Toxicity of Fe is ascribed to formation of ROS, especially hydroxyl radical ($OH^{\bullet}$), which is the most toxic ROS to aerobic cells (*Becana* et al., 1998). There are some Fe species which are also very toxic, and produced by the reaction of Fe^{2+} with molecular O_2, forming ferryl ($Fe^{2+}O$) and perferryl ($Fe^{2+}O_2$) species (*Girotti,* 1985; *Cakmak*, 2000).

Iron toxicity in rice generally occurs in soils containing low levels of K, Zn, and P (*Benckiser* et al., 1984; *Neue* et al., 1998). Accumulation of Fe in rice plants and development of Fe toxicity symptoms in shoots is particularly aggravated by K deficiency (*Li* et al., 2001). In rice, increasing supply of K reduced Fe concentration in leaves by at least 2-fold and improved plant growth (*Li* et al., 2001). The reason for the ameliorating effect of adequate K supply on Fe toxicity is not well understood. It was proposed that adequate supply of K enhances root-oxidizing capacity for Fe, thereby preventing its uptake (*Neue* et al., 1998). Alternatively, K deficiency can result in exudation of organic compounds that facilitate reduction and uptake of Fe. Regardless of the reason, however, sufficient K supply appears to be beneficial in alleviation of Fe toxicity in wetland rice, and therefore improvement of the K nutritional status of rice plants is of great importance in soils containing excess levels of soluble Fe.

8 Conclusions

Potassium deficiency is an important nutritional problem affecting crop production and quality. Potassium-deficient plants are very sensitive to high light intensity, rapidly becoming chlorotic and necrotic. Partial shading of leaves prevents development of chlorosis and necrosis, indicating that photooxidative damage to chloroplasts is a major contributory factor in the development of K-deficiency symptoms. Shaded (green) and nonshaded (chlorotic and necrotic) parts of the same leaf had the same K concentration or the necrotic parts even tended to contain more K. These results suggest that crop plants grown under conditions of high light intensity over a long period have a higher internal requirement for K than the plants exposed to lower light intensities during growth.

The susceptibility of K-deficient plants to high light intensity can be ascribed to the generation of ROS during photosynthesis. In K-deficient plants, due to impairment in (1) stomata regulation, (2) conversion of light energy into chemical energy, and (3) phloem export of photosynhates from source leaves into sink organs, photosynthetic CO_2 fixation is substantially limited. At the expense of such disturbances in photosynthetic CO_2 fixation, molecular O_2 is activated leading to extensive generation of ROS, and thereby oxidative degradation of chlorophyll and membranes. Enhanced production of ROS by K deficiency is not confined only to impaired photosynthetic electron transport. It also appears likely that an NADPH-dependent oxidase is another important source of ROS in K-deficient plants. Potassium-deficient plants show a substantial increase in capacity to oxidize NADPH. Consistent with enhanced activity of NADPH oxidase, NADPH-dependent $O_2^{\bullet -}$ generation was increased by K deficiency. Reactive O_2 species produced by NADPH oxidase or during photosynthesis are a major mediator of cell damage by different environmental stresses such as chilling, drought, ozone treatment, wounding, and salinity. When K supply is low, plants can, therefore, become very sensitive to environmental stresses. Several examples have been presented here showing that improving K-nutritional status of plants greatly minimizes detrimental effects of drought, salinity, and low termperatures on plant growth. The larger K requirement of plants under different abiotic stresses appears to be related to the inhibitory role of K against ROS production during photosynthesis and NADPH oxidase.

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