

Studies on the interaction of growth regulators with potassium ions in some physiological processes in the bean (*Phaseolus vulgaris* L.). II. The effect of potassium on growth of bean leaves and on their potassium and hormone levels

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Abstract

The subject of study was the effect of K^+ on the growth of primary and trifoliate leaves of the bean and on their potassium and hormone levels. Bean seedlings were grown in Hoagland's water solution, in which the potassium concentrations ($K^+-NO_3^-$) were 1 and 3 mM. The increase in the amount of potassium in bean leaves, elicited by increased K^+ concentration in the medium or by partial defoliation, was correlated with a stimulation of growth of these organs and an increase in their H_2O content. These effects were connected with an increase in the amount of ABA and bound GA and decrease in the amount of auxins. The effect of potassium on the level of free gibberellins and cytokinins depended on the kind of leaves. In young, i.e. trifoliate leaves, K^+ was found to have a positive effect on the level of free GA, whereas in older, i.e. primary leaves, this effect concerned the level of cytokinins.

Key words: *Phaseolus*, leaf growth, potassium level, hormone level

INTRODUCTION

There is as yet little information in literature on the effect of mineral compounds on the hormone levels in plants. The relevant papers are mostly concerned with microelements (Sójkowski 1971) and nitrogen nutrition (Rajagopal and Rao 1974, Michniewicz et al. 1976, Michniewicz and Stopińska 1980b). Far less research has been done on the effect of other macroelements, e.g. potassium. It has been found so far that deficiency of potassium and phosphorus reduces the auxin content (Michniewicz and

Stopińska 1980b, Anisimov and Bulatova 1982). However, data on this subject are not explicit (Zaniščeva et al. 1977). Also changes in the potassium concentration in the medium have been found to produce quantitative changes in gibberellin-like substances (Wakhloo 1975). The elimination of potassium generally reduces the GA level (Voronina 1970, Stanev et al. 1972, Michniewicz and Stopińska 1980a, b). A deficit of potassium has a similar effect on the level of cytokinins (Jakó 1974, Salama and Wareing 1979, Michniewicz and Stopińska 1980b). Changes in supply of mineral compounds can also modify hormone balance by affecting the ratios of auxins to gibberellins (Jakushkina and Voronina 1968) and cytokinins to growth inhibitors (Jakó 1974). Also there are still no explicit data on the subject of the effect of K^+ on the ABA level in plants. Some of them point out that K^+ deficit causes the ABA content to increase (Mizrahi and Richmond 1972), others indicate the reverse (Zaniščeva et al. 1977, Haeder and Beringer 1981). These changes also depend on the organ (Michniewicz and Stopińska 1980b). So far considerably more research has been done on the plant's response to salinity than to deficiency of elements. It has been pointed out that in tissues exposed to salinity stress, the contents of ABA, phaseic acid and ethylene increase while those of growth stimulators, in particular gibberellins and cytokinins, decrease (Starck 1980). Reports in literature suggest that the effect of K^+ can be related to the activity (Poovaiah and Leopold 1976), biosynthesis (Stanev et al. 1972), or transport of hormones (Anisimov and Bulatova 1975).

The scantiness and divergence of data obtained in experiments on different plant species do not allow any definite conclusions to be drawn on the quantitative or qualitative nature of the effect of potassium on hormonal balance. It was therefore undertaken to determine the effect of normal and lowered K^+ levels, eliciting clearly different growth effects in leaves, on the levels of hormones and potassium in bean leaves.

MATERIAL AND METHODS

The material for study was the bean, *Phaseolus vulgaris* L. var. "Saxa aurea". Five-day-old seedlings from a culture on perlite in a thermostat at 25 C were planted on perforated plates in dishes containing distilled water. On the tenth day after sowing, the plants were stripped of assimilating cotyledones and transferred to Hoagland's medium diluted at a 1:2 ratio, in which KNO_3 occurred in two concentrations, 1 and 3 mM. These concentrations had been selected on the basis of earlier experiments as those producing significant differences in growth of bean leaves. The lower

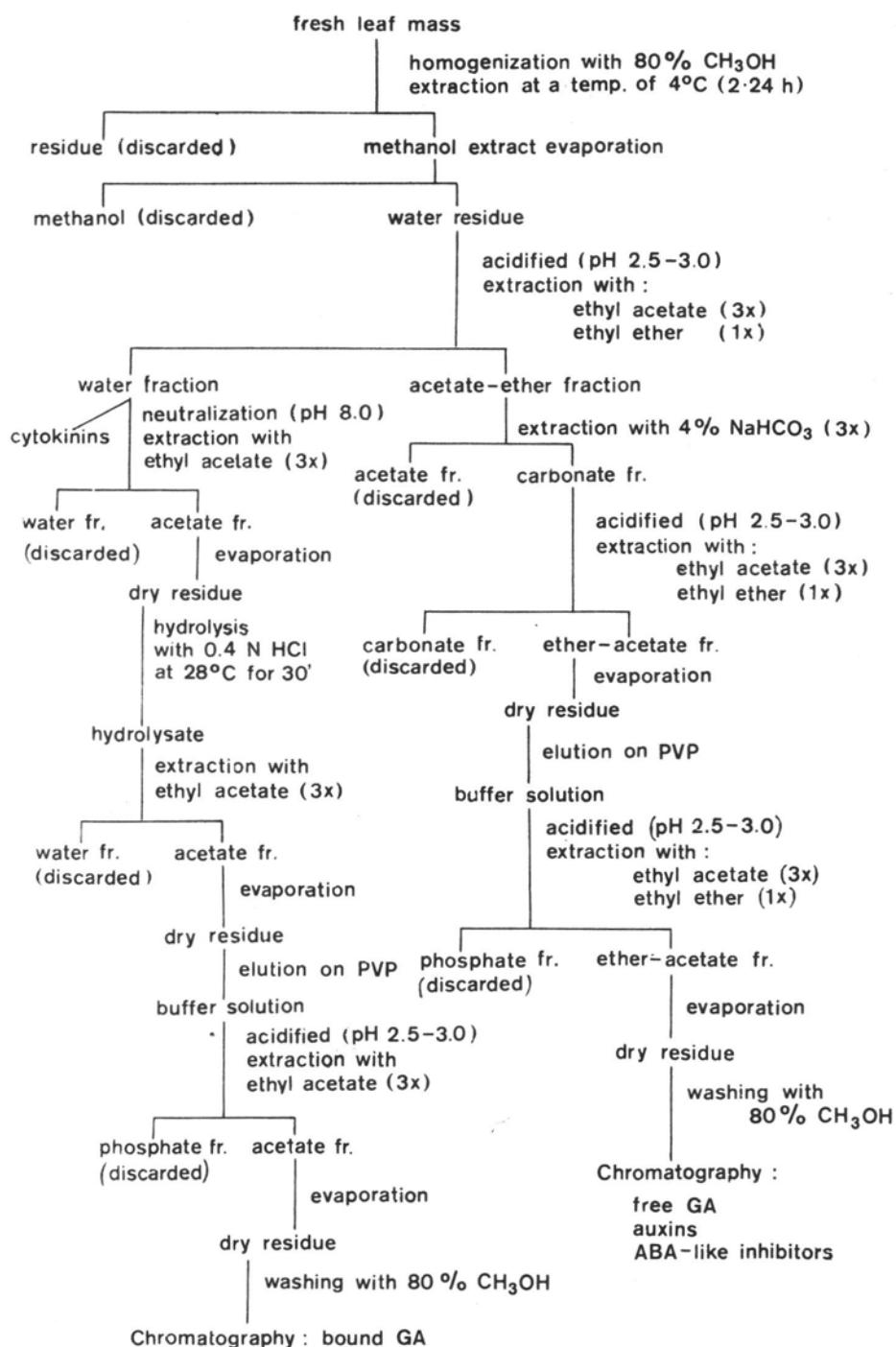


Fig. 1. The scheme of the extraction of auxins, GAs and ABA-like inhibitor

potassium level was supplemented by an equivalent amount of NaNO_3 . The general conditions of further culture were similar to those in Part I (Stopińska 1986a). Nine-day-old plants had one pair of primary leaves and one trifoliate leaf each. Starting from the sixth day of culture on the medium, in part of the plants grown at a reduced potassium level trifoliate leaves were successively removed. This variant made it possible to define the signi-

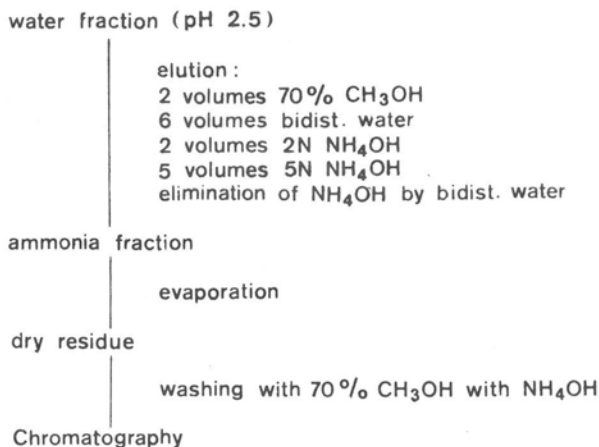


Fig. 2. The scheme of the extraction of cytokinins

ficance of younger leaves for the growth of the older, i.e. primary ones. Studies were made on the effect of the potassium concentration and on the presence of trifoliate leaves on the growth of leaves and on their levels of K^+ and the following hormones: cytokinins, gibberellins, auxins and abscisic acid.

The surface area of the leaves, fresh and dry mass of the leaf blades and potassium level were determined as in Part I (Stopińska 1986a) in the following combinations: in primary and trifoliate leaves grown at 1 and 3 mM K^+ and in primary leaves of defoliated plants grown at a potassium concentration of 1 mM.

For plant hormone analysis taken were 80 g fresh mass of leaf blades, which were first frozen then extracted. In order to protect the hormones from oxidation, extraction was carried out in the presence of 0.001% sodium diethyl-dithiocarbamate in 80% methanol. The extracts were purified from phenol compounds in PVP (Polyvinylpyrrolidone) filled columns, 9 cm long 1 cm in diameter. Before applying to the PVP, the dry residue was washed with 0.5 M phosphate buffer at pH 8.0. For elution 0.1 M phosphate buffer, pH 8.0 was used in the columns. Fractioning was carried out at a temperature of ca. 22°C in diffuse light according to the following scheme (Fig. 1).

Extraction of cytokinins was made from the water fraction evaporated

to 20 cm³. Cytokinins were isolated on columns filled with the cationite, Dowex 50 H⁺, X8, 50-100 mesh, 21 cm in length 2 cm in diameter, by Hewett and Wareing's (1973) method (Fig. 2).

All solvents used in fractioning were evaporated in a vacuum evaporator at a temp. of 40°C, in an N₂ atmosphere.

Cytokinins were separated by paper chromatography on Whatman 3 MM paper. The amounts of extracts applied to the chromatograms were equivalent to 0.5 g dry mass. The chromatograms were developed in the solvent system: isopropanol: ammonia: water (10:1:1, v/v). In order to determine the cytokinin level, the soya callus test after Miller (1968) was used. The results are presented in the form of histograms as the increase in the callus mass in g per flask. For a relative estimate of the results, diagrams have been drawn also showing the increase in callus mass caused by kinetin at a concentration of 10 µg·dm⁻³.

Separation of both free and bound gibberellins was performed by thin-layer chromatography on silica gel G (Merck). The extracts were applied in amounts equivalent to 0.250 g dry mass. The chromatograms were developed in the solvent system: chloroform:ethyl acetate:acetic acid (9:10:5, v/v). For quantitative determination of gibberellin-like substances, the lettuce hypocotyl (var. Böttner) test after Frankland and Wareing (1960) was used. The gibberellin level was estimated accepting as significant a 12% growth stimulation in the lettuce hypocotyl relative to control at P = 0.05. Basing on the standard curve for GA₃, the significant stimulations were normalized to the total amount of gibberellin-like substances in a given organ.

Separation of auxins was done by column chromatography after Steen and Eliasson (1969) on Sephadex LH-20 gel, on columns 30 cm long and 2.5 cm in diameter. Using a fraction collector and applying 70% ethanol with 1 mM HCl as the developing system, 28 10 cm³-fractions were collected. Following a Gordon-Weber (1951) reaction and an oat coleoptile, var. „Zwycięzca”, test after Bönner (Audus 1959) it was established that synthetic IAA was located in fraction 23. The individual fractions from 19 to 28 in amounts corresponding to 0.200 g dry mass of the leaf samples under study were analysed for auxin level by the oat coleoptile test. After evaporating the solvent, growth of the coleoptiles was studied in a medium containing 2% sucrose in 1 mM phosphate buffer, pH 6.3. The auxin level was established, accepting growth stimulation of oat coleoptile segments by at least 5% compared with control at P = 0.05 as significant. The significant growth stimulations found to fall in fractions 22-24 were normalized to the total amount of auxins in the given organ using the standard curve for IAA.

Separation of growth inhibitors of the abscisic acid-like substances was done by column chromatography in the same way as the separation of

auxins. The coleoptile test of wheat, var. „Kolibri”, after Rudnicki (1969) revealed the location of synthetic (mixed isomers) ABA in fractions 14 and 15. Individual fractions from 9 to 18 in amounts corresponding to 0.200 g dry mass were analysed for the level of ABA-like inhibitors in a wheat coleoptile test. Growth of wheat coleoptiles was studied in a medium consisting of 2% sucrose in 1 mM citrate buffer, pH 5.0. The ABA level was estimated, accepting as significant inhibition of wheat coleoptile growth by at least 20% compared with control at $P = 0.05$. Significant inhibition values falling on fractions 13-16 were normalized to total amount of ABA in the given organ using the standard curve for ABA.

All biological tests were done three times in triplicate.

For precise identification of the inhibitors, fractions 13-16 were mixed together and evaporated to dry residue. The residue was washed with 1% CH_3COOH in methanol and rechromatographed on plates with silica gel H (Merck) in the solvent system: isopropanol-butanol-ammonia:water (6:2:1:2, v/v). The zones from 0.4 to 0.8 R_f corresponding to the location of synthetic ABA were eluted with 20 cm^3 of 1% CH_3COOH in methanol. After evaporation the dry residue was washed with 80% methanol. The ultimate identification of ABA was done by gas chromatography on a GCHF 18.3-4 chromatograph (“Chromatron”), using glass columns sized 1.5 m \times 3 mm filled with Gas Chrom Q-100/120 mesh with the 3% SE-30 liquid phase. The samples were esterified by silylation using BSA (N,O-bis(trimethylsilyl)acetamid). The identifications were made under the following conditions: flow of carrier gas (N_2) — 40 $\text{cm}^3 \cdot \text{min}^{-1}$, column temperature 210°C, feeder temp. 250°C, detector (FID) temp. 310°C.

RESULTS AND DISCUSSION

The data in Fig. 3 indicate that a reduction in K^+ concentration in the medium from 3 to 1 mM significantly reduced the dynamics of growth of both kinds of leaves. The removal of trifoliolate leaves in plants grown at the reduced K^+ level enhanced the dynamics of growth of primary leaves; it exceeded the growth rate not only of non-defoliated plants growing on the same medium but even on plants grown on the full medium (Fig. 3).

The data presented below (Figs. 4, 5 and 6) indicate that a decrease in K^+ concentration from 3 to 1 mM significantly reduced the surface areas (Fig. 4) and the fresh and dry matter (Fig. 5) of both kinds of leaves as well as their water (Fig. 5) and K^+ contents (Fig. 6). The potassium concentration did not change in either kinds of leaves. This

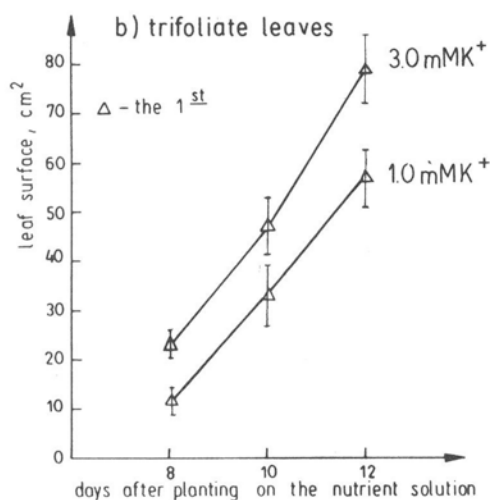
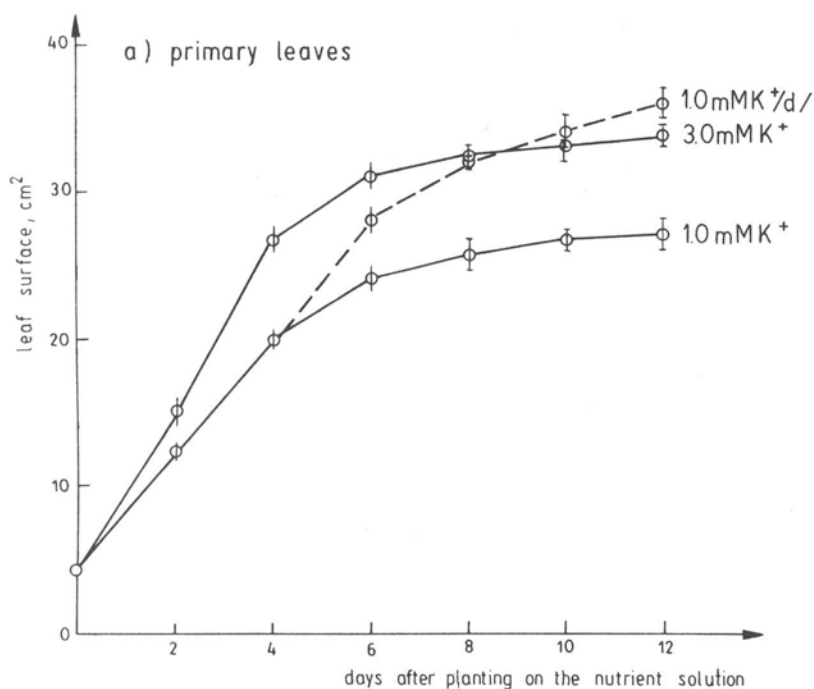


Fig. 3. The effect of potassium on the growth dynamics in bean leaves (mean of 20 plants). d — defoliated plants, vertical lines — standard errors

fact indicates that the potassium level in leaves was not deficient. In defoliated plants growing at the lowered K⁺ level in the medium, growth stimulation and elevated K⁺ content and amount were found in the primary

leaves, while their water content did not differ significantly from that in the leaves of non-defoliated plants. It has been known for a long time that under reduced potassium conditions the growth and development of plants becomes inhibited as a result of a reduction in the assimilating surface

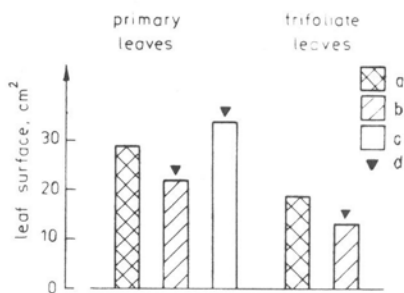


Fig. 4. Growth of bean leaves depending on potassium concentration in the medium and the presence of trifoliate leaves. a — 3 mM K⁺, b — 1 mM K⁺, c — 1 mM K⁺ (defoliated plants). d — significant differences relative to control (3 mM K⁺) at P = 0.05

area, in the intensity of photosynthesis, in the increase in respiration processes and in the transport of assimilates (see Moorby and Besford 1983). The lowered K⁺ concentration in the medium reduced the amount of potassium and the percentage water content in both kinds of leaves.

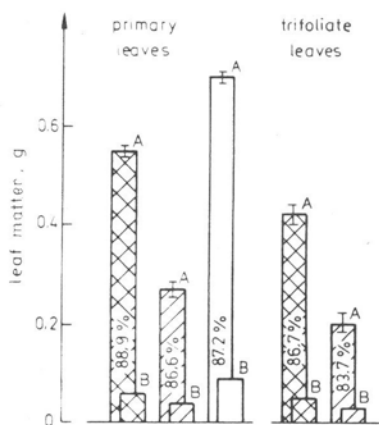


Fig. 5. Fresh and dry matter content in bean leaves depending on potassium concentration in the medium and the presence of trifoliate leaves (numbers in columns show H₂O%). A — fresh matter, B — dry matter, vertical lines — standard errors. Abbreviations as in Fig. 4

This effect was probably due to the enhancement of transpiration, which is confirmed by a later investigation (Stopińska 1986b), as well as other authors' reports (Peaslee and Moss 1968), since adequate potassium supply is necessary for economical utilization of water by a plant. The numbers

above the columns in Fig. 6 indicate that the trifoliolate, i.e. younger leaves contain much more K^+ than do the primary leaves, which is in accordance with general view on this subject.

In the study on the mechanism of action of environmental factors, among them also of mineral nutrition conditions, on the growth and develop-

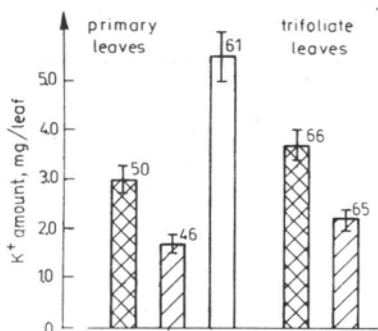


Fig. 6. Total amount of potassium in bean leaves (the numbers over the columns denote K^+ content in $mg \cdot g^{-1}$ dry matter). Vertical lines — standard errors. Abbreviations as in Fig. 4

ment of plants, attention was directed towards plant hormones. The data obtained in the present work indicate that the levels of cytokinins, gibberellins, auxins and ABA in bean leaves change depending on potassium concentration in the medium (Figs. 7-9, 11). The lowered K^+ concentration in the medium produced a decrease in the cytokinin level in the primary leaves (Fig. 7). No such effect was observed in trifoliolate leaves, which were characterized by a similar and a relatively high potassium content in dry mass at both potassium concentrations in the medium (Fig. 6). In defoliated plants, a considerable rise in the cytokinin level in the intensively growing primary leaves was found. The fact that certain cytokinins may moderate the negative effects of K^+ lack in bean leaves suggests that K^+ takes part in the metabolism of cytokinins (Stanev et al. 1972). A decrease in the cytokinin level following a reduction of K^+ concentration in the medium was also found in experiments concerning pine roots (Michniewicz and Stopińska 1980b) and sunflower leaves, buds, roots and root exudations (Salama and Wareing 1979). It is suggested that under conditions of potassium deficiency, the synthesis of cytokinins is inhibited and the growth rate of organs is modified, as Jakó (1974) suggests, by the change in the ratio of cytokinins to inhibitors in the roots. It was also demonstrated that the younger leaves contained more cytokinins than older ones in both medium variants (Fig. 7) which is in line with the results of other authors (Mayak and Halevy 1970, Hewett and Wareing 1973). The role of

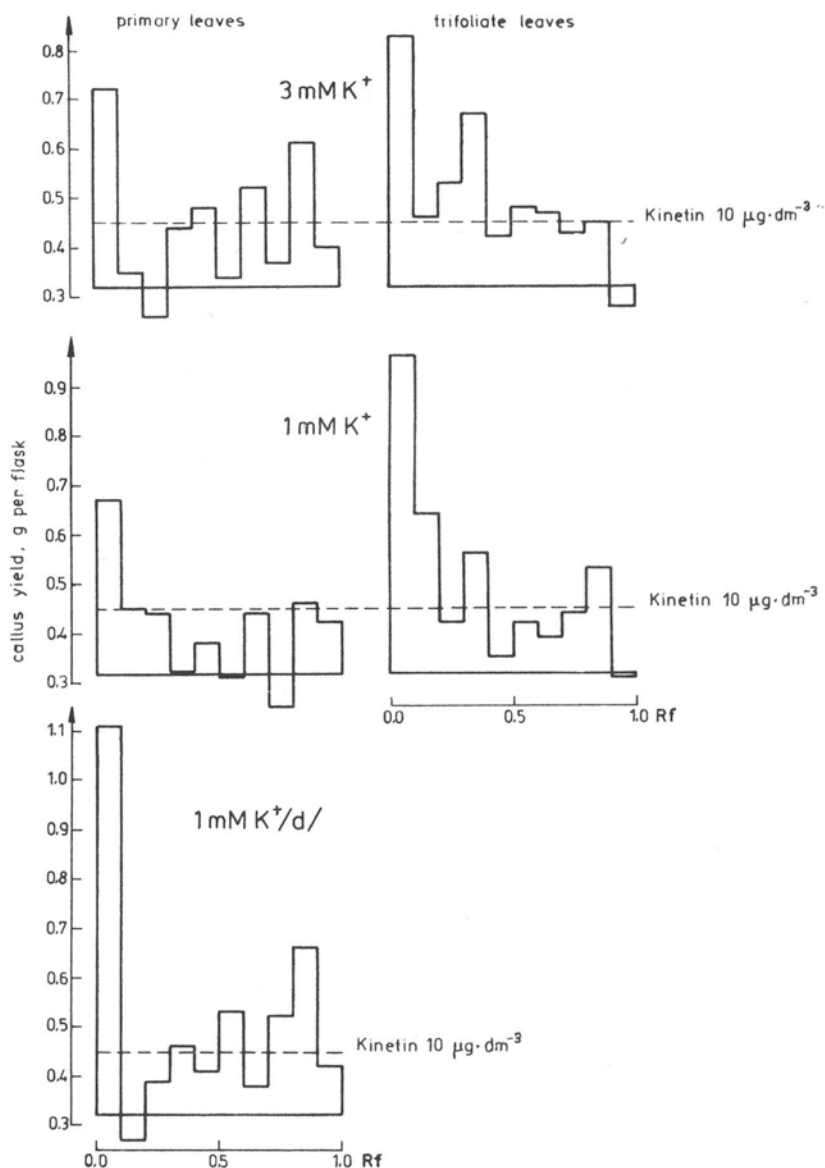


Fig. 7. Chromatographic analysis of cytokinins in bean leaves depending on the potassium concentration in the medium and the presence of trifoliate leaves. d — defoliated plants

cytokinins in the growth of bean leaves has been also demonstrated by experiments in which treating bean with kinetin stimulated growth of both kinds of leaves and raised the amount of K⁺ in them (Stopińska 1986a).

The data in Fig. 8 indicate that a reduction of the K⁺ level in the medium decreased the amount of free and bound gibberellins in trifoliate

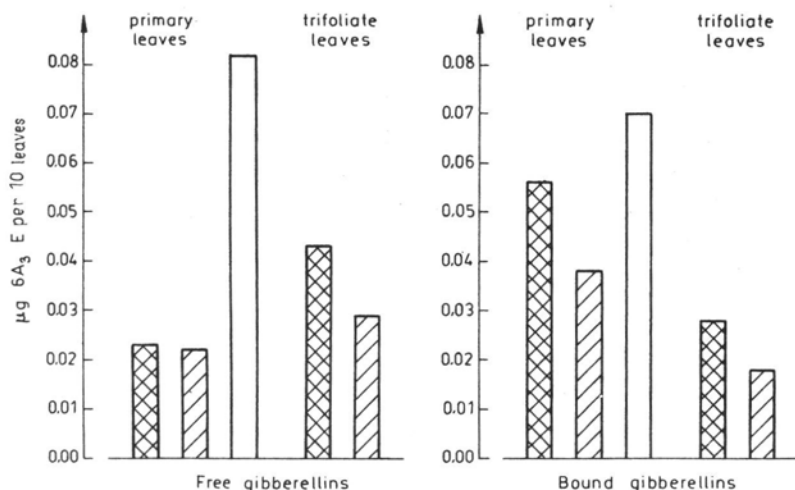


Fig. 8. Total amount of gibberellins in bean leaves depending on the potassium concentration in the medium and the presence of trifoliolate leaves. Abbreviations as in Fig. 4

leaves as well as of the bound gibberellins in primary leaves. A drop in free GAs was observed only in young and intensively growing leaves. The removal of young leaves from plants grown at the lowered level of potassium in the medium caused a rise in both kinds of GA in older leaves. Reports in literature indicate that quantitative and qualitative changes in

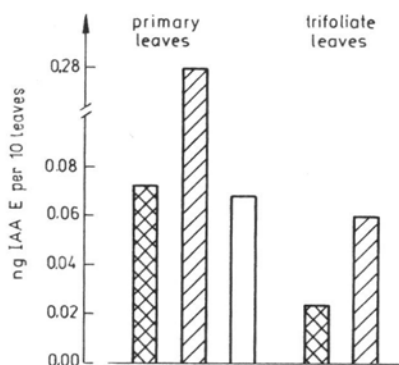


Fig. 9. Total amount of auxins in bean leaves depending on the potassium concentration in the medium and the presence of trifoliolate leaves. Abbreviations as in Fig. 4

gibberellin-like substances depend on the potassium content (Wakhloo 1975). It has also been pointed out that GA can eliminate the negative effects of K^+ deficiency (Wakhloo 1976), and that a reduction in GA level is associated with the elimination of K^+ from the medium in many plant species, such as maize and broad bean (Voronina 1970), pine (Michnie-

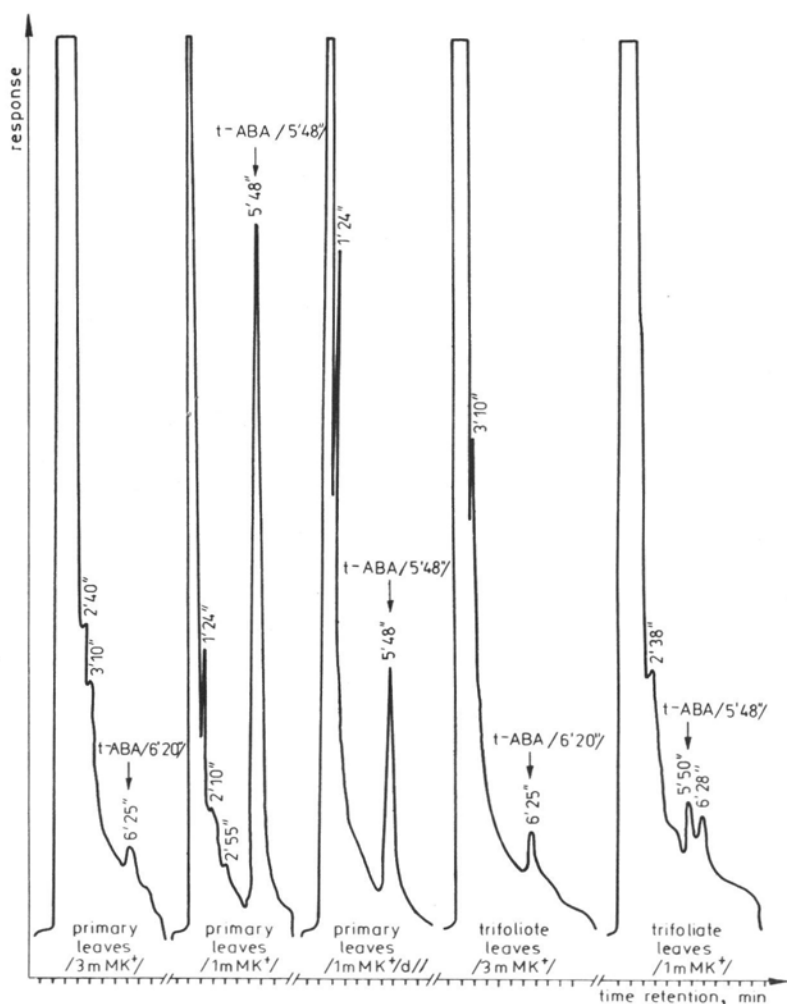


Fig. 10. Gas chromatography analysis of ABA-like inhibitor in bean leaves depending on the potassium concentration in the medium and the presence of trifoliolate leaves. d — defoliated leaves

wicz and Stopińska 1980b) and bean (Stanev et al. 1972). In comparing trifoliolate leaves, characterized by high growth intensity, with primary leaves, showing lower growth intensity, it is seen that the younger leaves contained much more free GA and much less bound GA than the older ones. This is in agreement with the general opinion on this subject (see Goodwin 1978). The primary leaves of defoliated plants also showed much more free than bound GAs demonstrating, in this respect, characteristics of young leaves. Drastic reduction of active gibberellins in young, intensively growing leaves testifies to the specific role of these regulators in metabolically active tissues. This is also confirmed by the results of the experiments on the

effect of exogenous GA on the growth and K^+ amount in bean leaves (Stopińska 1986a), where this effect proved stronger in younger leaves.

The reduction in the K^+ level in the medium from 3 to 1 mM raised the auxin amount in both kinds of leaves (Fig. 9). The removal of trifoliate leaves in plants grown at a lowered potassium level, on the other hand,

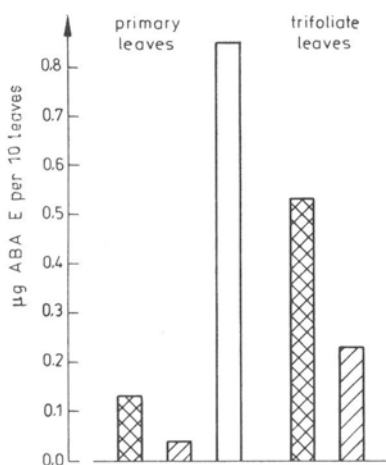


Fig. 11. Total amount of ABA-like inhibitor in bean leaves depending on the potassium concentration in the medium and the presence of trifoliate leaves. Abbreviations as in Fig. 4

caused a decrease in the amount of auxins in primary leaves. There have been very divergent opinions on the effect of K^+ on the level of these hormones. Some authors say that K^+ deficiency reduces the level of auxins in many different plants (Wakhloo 1965, Jakushkina and Voronina 1968, Michniewicz and Stopińska 1980b, Anisimov and Bulatova 1982). Other reports, however, testify to the contrary (Zanišćeva et al. 1977). Younger, i.e. trifoliate, leaves also contained less auxins than older, i.e. primary, ones. According to Wheeler (1968), the activity of auxins in the leaves of *Phaseolus vulgaris* is at its highest when their growth rate is at its highest, and falls to lower level when the leaf matures. The above results can be partly due to the fact, that only auxins in blades without petioles were determined.

Variation in K^+ concentration in the medium caused changes in the level of plant growth inhibitors. The results of gas chromatography have shown that in fractions 13-16 an inhibitor occurred which corresponded to abscisic acid in trans form (Fig. 10). The data concerning ABA, presented in Fig. 11, indicate that a reduction of K^+ level in the medium reduced the amount of this hormone in both kinds of leaves, while the removal of trifoliate leaves in plants growing on the lowered K^+ medium elicited an increase in the amount of ABA in the primary leaves. Only a few papers have been devoted to this problem, and the data reported in them are often

controversial, as in the case of auxins. Some of these reports point to an increase in the level of this inhibitor under various stresses, e.g. under mineral stress due to nutritional deficiency (Mizrahi and Richmond 1972, Michniewicz and Stopińska 1980b). Other authors, on the other hand, have demonstrated a definite increase in ABA content in plant tissues, associated with an increase in K^+ concentration (Zanišćeva et al. 1977, Haeder and Beringer 1981). Younger leaves contained more ABA-like inhibitors than the older ones. This fact seems to contradict the generally accepted opinion that the highest ABA level is found in mature and ageing tissues, where it is synthesized. However, high levels of inhibitors in the growing parts of plants have been found repeatedly by a large number of writers (Kamieńska 1966, Powell 1976, Raschke and Zeevaart 1976). In an experiment on bean, mature and ageing leaves were found to contain considerably more bound than free ABA in contrast to young leaves (Weiler 1980). This fact suggests that bound ABA accumulates in ageing leaves. Considering the data indicating that ABA reduced both growth in bean leaves and the K^+ amount in them (Stopińska 1986a), the interpretation of the present results is rather difficult. However, it must be taken into account that growth and development depend on equilibrium between stimulators and inhibitors.

Very often the senescence of one plant part is influenced or controlled by another. Leaf senescence for example may be promoted by actively growing regions and removal of these regions may delay senescence of nearby leaves. It is clear, that senescence of a particular organ is marked by an exodus of nutrients. Among them potassium ions as well as hormones, such as cytokinins and gibberellins, play an important role in senescence of leaves (see Nooden and Leopold 1978). Thus the removal of young leaves probably reduced the nutrient and hormonal competition between trifoliate and primary leaves with the later becoming physiologically similar to younger.

To sum up, changes in K^+ concentration in the medium resulting in changes in the amount of K^+ in bean leaves affected the growth regulator levels in these organs. It seems highly probable that potassium, or the changes associated with its uptake, directly affect the activity of hormones, their synthesis, releasing and transport. It is, however, also possible that the effect of K^+ ions on the activity and the level of regulators is of an indirect nature; they may involve the plant's growth and general metabolism, in particular the changes in water content in the tissues, accompanying the cell's growth process.

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Studia nad współdziałaniem regulatorów wzrostu z jonami potasowymi w niektórych procesach fizjologicznych u fasoli (Phaseolus vulgaris L.). II. Wpływ potasu na wzrost liści fasoli i na poziom w nich potasu i hormonów

Streszczenie

Badano wpływ K^+ na wzrost młodocianych i trójdzielných liści fasoli i na poziom w nich potasu i hormonów. Siewki fasoli rosły na wodnej pożywce Hoaglanda, w której stężenie potasu ($K^+-NO_3^-$) wynosiło 1 i 3 mM. Zwiększenie ilości potasu w liściach fasoli, wywołane wzrostem stężenia K^+ w pożywce, bądź częściową defoliacją, wiązało się ze stymulacją intensywności wzrostu tych organów i ze zwiększeniem w nich zawartości wody. Efekty te związane były ze zwiększeniem ilości ABA i GA w formie związanej oraz ze zmniejszeniem ilości auksyn. Wpływ potasu na poziom wolnych giberelin i cytokinin zależał od rodzaju liści. Dodatni efekt K^+ na poziom wolnych GA ujawnił się w młodych liściach, tj. trójdzielných, natomiast na poziom cytokinin w liściach starszych, tj. młodocianých.