THE MINERAL PROFILE OF WINTER OILSEED RAPE IN CRITICAL GROWTH STAGES – POTASSIUM

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Abstract

Sustainable management of nitrogen in the oilseed rape canopy depends, in the first place, on the supply of potassium during critical yield formation stages. The K status assessment in plants was made in the 2008, 2009, and 2010 seasons. The one-factorial experiment to verify the formulated hypothesis, consisting of six treatments, was as follows: control (C), NP, NPK, NP-K+MgS – $\frac{1}{3}$ rate of the total planned dose applied in spring (NPKMgS1), NPK+1.0 MgS rate in autumn (NPKMgMgS2), NPK+MgS – $\frac{2}{3}$ in autumn + $\frac{1}{3}$ in spring) (NPKMgS3). Plant samples were taken at three stages: full rosette (BBCH 30), the onset of flowering (BBCH 61), maturity (BBCH 89). At each measurement, the harvested sample was partitioned, in accordance with the stage of development, into subsamples of leaves (BBCH 30), stems and leaves (BBCH 61), stems + pericarp (trashed silique) and seeds (BBCH 89). The biomass yield as well as the potassium concentration and content were determined in each part of the plant. The yield forming effect of potassium absorbed by plants during the critical growth stages was decisive for the yield of seeds, as resulted from path and stepwise analyses. The study showed that the N management in oilseed rape canopy was significantly governed by the K management just before and after flowering. An elevated K supply in the first period, leading to the N saturated status of plant parts, resulted in seed density reduction, in turn decreasing the size of the K seed-sink. The seed yield of oilseed rape significantly depended on the net K content increase in vegetative parts of the crop during the seed-filling period. It can be therefore concluded that an adequate supply of K up to the physiological maturity of oilseed rape is a prerequisite of high yield.

Key words: potassium, plant parts, K partitioning, yield structural components, yield.

INTRODUCTION

In agronomic practice, the key concept of sustainable nitrogen management focuses most frequently on nitrogen levels. This simplified approach is acceptable provided an ample supply of other nutrients. Potassium deficien-

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cy is the key cause of an inadequate utilization of the applied nitrogen by plants, resulting in lower and unstable yields, as documented recently for central European countries (Grzebisz et al. 2012a). A sound management of nitrogen based on a balanced supply of nutrients, such as phosphorus, potassium and magnesium, is expected to result in and increased uptake and improved utilization of elements (Grzebisz et al. 2010).

The demand of crop canopy for nitrogen is significantly governed by its stage of growth, and the rate of biomass accumulation. The following three cardinal periods of the crop plant growth are distinguished, based on the rate and trends of dry matter accumulation, i.e. i) the foundation period (FP), ending at the rosette stage, ii) the construction period (CP), ending at the onset of flowering, iii) the yield forming period ending at the plant physiological maturity. Each period exerts a specific impact on the crop plant performance (Sylvester-Bradley et al. 2002). The third stage is of crucial importance for the final yield because of its impact on the number of pods and seeds per pod, termed as seed density (Diepenbrock 2000).

It has been well recognized that an insufficient supply of potassium to a crop leads to the decreased rate of the crop's growth, as documented by Grzebisz et al. (2012b) for sugar beet. The yield forming effect of nitrogen, as documented by Szczepaniak et al. (2014) for maize and Szczepaniak and Potarzycki (2014) for wheat, considerably depends on potassium fertilizing patterns. Despite the well-known physiological background and the recognized dynamics of the accumulation of both nutrients, we still lack information about the potassium impact on the formation of yield components of oilseed rape. The course of potassium accumulation by oilseed rape and its impact on yield are poorly understood. The pot experiment by Rose et al. (2008), based on an optimum supply of nutrients, showed that the potassium accumulation in canola peaked around flowering. The field experiment by Barlóg et al. (2005) showed that potassium accumulates progressively up to the stage of green pods.

The objective of the current study was to define the potassium accumulation pattern and its redistribution among key parts of oilseed rape in cardinal stages of growth. The key aim was to evaluate the effect of the potassium content in the crop parts during the season on i) the development of key structural components of yield, ii) yield of seeds produced by the main raceme and by secondary branches.

MATERIAL AND METHODS

The general characteristics of the experimental field have been described by Szczepaniak (2014). Plants for determinations of dry mater and potassium concentration were sampled from an area of one m^2 in three consecutive stages of oilseed growth, according to the BBCH scale: 30, 61 and 89. At each measurement date, the harvested plant sample was partitioned, in

accordance with the stage of development, into subsamples of leaves (BBCH 30), stems and leaves (BBCH 61), stems + pericarps (trashed siliques) and seeds (BBCH 89), and then dried (65°C). Plant material for mineral element determination was mineralized at 640°C and the ash was next dissolved in 33% HNO_3. The potassium concentration was determined by flame photometry. The results are expressed on a dry matter (DM) basis. The content of the nutrient in each plant part was calculated by multiplying its concentration and the respective biomass of a crop part.

The experimental data were subjected to conventional analysis of variance using the computer program Statistica 7. The differences between treatments were evaluated with the Tukey's test. In tables and figures, results of the F test (***, **, *) indicate significance at the $P < 0.1\%$, 1%, and 5%, respectively. Path analysis was conducted based on correlation coefficients and taking the yield of seed and/or its structural components as effects and the nitrogen accumulation in plant parts as independent variables. A path diagram showing direct and indirect path coefficients was elaborated based on the highest value of the correlation coefficient for a particular set of variables. In the second step of the diagnostic procedure, stepwise regression was applied to define an optimal set of variables for a given crop characteristic. In the computing procedure, a consecutive variable was added to the multiple linear regressions stepwise. The best regression model was chosen based on the highest F-value for the entire model and significance of all independent variables (KONYS, WIŚNIEWSKI 1984).

Acronyms applied in the paper:

MBY – yield of the main branch (inflorescence),

SBY – yield of secondary branches,

TSY – total yield of seeds,

SMB – number of siliques per main branch,

SSB – number of siliques per secondary branch,

SSMB – number of seeds per silique of the main branch,

SSSB – number of seeds per silique of the secondary branch,

K_{RE} – potassium content in oilseed rape at the rosette stage,

K_{LE} – potassium content in leaves of oilseed rape at the onset of flowering,

K_{SH} – potassium content in shoots of oilseed rape at the onset of flowering,

K_{ST} – potassium content in the stem of oilseed rape at maturity,

K_{SE} – potassium content in seeds of oilseed rape at maturity,

K_n – K net uptake by oilseed rape in the period BBCH 61 - BBCH 89,

B_n – oilseed rape biomass net increase in the period BBCH 61 - BBCH 89.

RESULTS AND DISCUSSION

The potassium concentration in oilseed rape throughout the growing season was affected significantly by both factors, years and fertilizing treatments (Table 1). At the rosette stage, the K concentration was much lower in the control plants. In all the years, it showed a significant response

Table 1

Statistical evaluation of potassium concentration in oilseed rape organs during critical growth stages (g kg⁻¹ DM)

Factor	Factor level	BBCH 30	BBCH 61		BBCH 89	
		LE	LE	SH	ST	SE
Fertilization treatments (FT)	AC	34.6^a	26.8^a	30.3^a	16.9^a	8.2^a
	NP	45.0^b	32.5^{bc}	37.8^b	22.1^b	8.6^{ab}
	NPK	47.2^b	34.3^{bcd}	42.4^c	23.7^{bc}	9.2^b
	NPKMgS1	48.1^b	36.6^{cd}	42.8^c	25.8^c	8.8^{ab}
	NPKMgS2	47.7^b	31.5^b	38.9^{bc}	22.7^{bc}	9.0^{ab}
	NPKMgS3	49.4^b	37.1^d	41.2^{bc}	25.3^{bc}	9.2^b
Years (Y)	2008	4.16^a	24.0^a	32.6^a	26.2^c	9.0^b
	2009	46.3^b	43.2^c	44.9^c	24.0^b	8.1^a
	2010	48.1^b	32.1^b	39.3^b	18.0^c	9.5^c
Fertilization treatments (FT)		***	***	***	***	**
Years (Y)		***	***	***	***	***
FT x Y		*	***	**	ns	ns

LE, SH, ST, SE – leaves, shoots, straw, seeds, respectively;
F – probability values: *, **, *** of 0.05, 0.01, 0.001, ns – not significantly different;
[a] the same letters mean the lack of significant differences.

to the applied nitrogen and phosphorus (NP). The resultant increase was year-specific. In 2008, the highest increase appeared in plants grown in the treatment with split dose of magnesium sulfate (NPKMgS3), while in 2009, the maximum K concentration was revealed in plants fertilized with NPK. In 2010, the highest K concentration was noted for the NP treatment. Addition of other nutrients such as K and MgS did not affected K concentration increase. At the beginning of flowering, the K concentration in leaves was year-to-year different. In 2009, the K concentration fluctuated around 2.4%. In 2009, it was much higher, rising up in response to fertilizer K, more strongly owing to the split application of magnesium sulfate. The same trend, but on a much higher level, was noted in shoots. However, in 2008, the maximum K concentration was characteristic of the treatment with magnesium applied in autumn, and in 2009 the highest K concentration was induced by the NPK treatment. The main cause of the year-to-year variability of K concentrations

was the course of weather. The amount of precipitation in the three spring months (April, May and June) was about 100 mm in 2008, 190 mm in 2009 and 138 mm in 2010. The long-term average is 136 mm (SZCZEPANIAK 2014). The analyzed relationship between the K concentration in leaves and N accumulation in leaves showed a curvilinear course:

$$N_{LE} = -0.692K_{LE}^2 + 8.594K_{LE} - 8.412 \text{ for } n = 18, R^2 = 0.68 \text{ and } p < 0.000.$$

Quite a different regression model was achieved for the relationship between the K concentration in shoots and the nitrogen content in oilseed rape vegetative parts at the onset of flowering:

$$N_{LE} = 5.349K_{SH} - 8.952 \qquad \text{for } n = 18, R^2 = 0.84 \text{ and } p < 0.000,$$
$$N_{SH} = 4.034K_{SH} - 5.81 \qquad \text{for } n = 18, R^2 = 0.52 \text{ and } p < 0.000.$$

The above regression models inform us that the K concentration in leaves obtained a saturation-like status, raising up the N content in leaves to the K optimum of 6.2%. The linear model indicates the unsaturated status of nitrogen. This discrepancy probably results from the limited size of leaves for nitrogen accumulation and, at the same time, the continuous growth of branches during the flowering phase, resulting in an increasing nitrogen accumulation capacity.

The amount of potassium accumulated in parts of oilseed rape during the cardinal growth stages was significantly affected by years and fertilizing treatments (Table 2). Interaction, however, was noted only at the beginning

Table 2

Statistical evaluation of potassium accumulation and distribution in oilseed rape plant organs during critical growth stages (g m^{-2})

Factor	Factor level	BBCH 30	BBCH 61		BBCH 89	
		LE	LE	SH	ST	SE
Fertilization treatments (FT)	AC	7.71^a	3.26^a	12.00^a	17.36^a	2.35^a
	NP	14.05^b	6.52^b	20.23^b	28.42^b	3.25^b
	NPK	14.38^b	7.64^b	22.94^b	36.37^{bc}	3.93^c
	NPKMgS1	14.61^b	7.93^b	20.78^b	33.45^{bc}	4.12^c
	NPKMgS2	14.16^b	6.41^b	20.95^b	36.16^{bc}	3.61^{bc}
	NPKMgS3	13.02^b	8.05^b	22.91^b	36.87^{bc}	3.98^c
Years (Y)	2008	11.39^b	3.49^a	14.21^a	42.52^c	4.28^c
	2009	13.72^b	11.89^b	30.52^b	29.73^b	3.44^b
	2010	13.84^b	4.53^a	17.19^a	22.07^a	2.91^a
Fertilization treatments (FT)		***	***	***	***	***
Years (Y)		*	***	****	***	***
FT x Y		ns	**	***	**	ns

key under Table 1

of flowering and for the stem at the physiological maturity. In the period of stem elongation, the content of potassium underwent a significant change versus the beginning of flowering (Figure 1). The key reason of the observed variation was the course of weather, only slightly modified by the fertilizing treatments. In 2009, the content of potassium in leaves was around 3 times
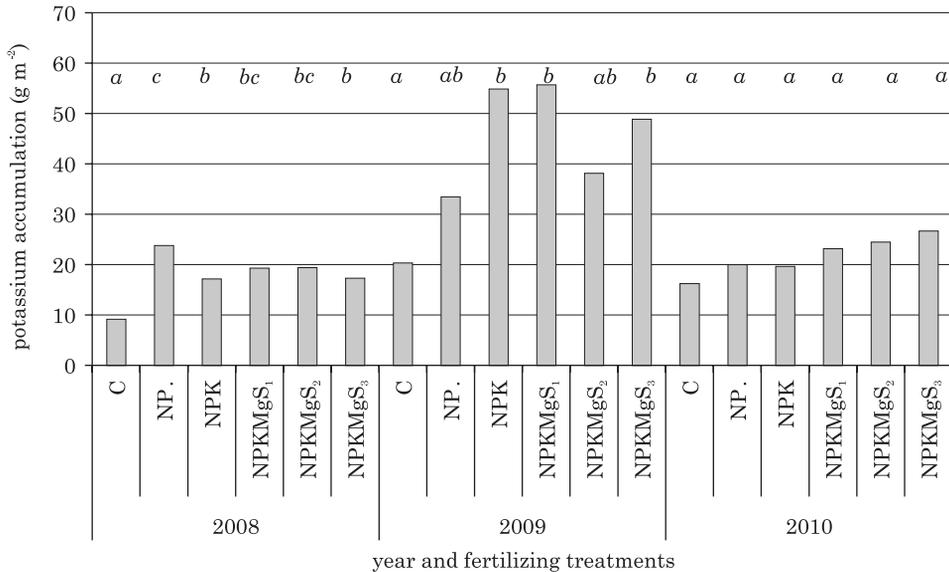
Fig. 1. Effect of fertilizing treatments on potassium accumulation in oilseed rape canopy at the beginning of flowering; [a] the same letters mean the lack of significant differences

higher than in the other years. Its content in the control plant was on the same level as noted for the best treatments in the other years. The application of fertilizers resulted in its increase: 2-forld for NP, 2.-7-fold for NPK and 3-fold for NPKMgS1. The N content in leaves and in shoots showed a curvilinear response to the K content in leaves:

$$N_{LE} = -0.095K_{LE}^2 + 2.495K_{LE} + 1.307 \quad \text{for } n = 18, R^2 = 0.85 \text{ and } p < 0.000,$$
$$N_{SH} = -0.071K_{LE}^2 + 2.194K_{LE} + 2.237 \quad \text{for } n = 18, R^2 = 0.88 \text{ and } p < 0.000.$$

The same pattern of K accumulation was observed in shoots, with the maximum values recorded in the NPK treatment. The analysis of the impact of the K_{SH} content on the nitrogen accumulation course in leaves and in stems showed an identical trend as for K_{LE}:

$$N_{LE} = -0.017K_{SH}^2 + 1.256K_{SH} - 5.49 \quad \text{for } n = 18, R^2 = 0.93 \text{ and } p < 0.000,$$
$$N_{SH} = -0.01K_{SH}^2 + 0.933K_{SK} - 6.445 \quad \text{for } n = 18, R^2 = 0.84 \text{ and } p < 0.000.$$

The regression models show a saturation-like status of nitrogen in response to the increased K supply to oilseed plants at the onset of flowering.

This implicates that excess of available potassium leads to an elevated accumulation of nitrogen, in turn boosting the growth of the vegetative biomass of oilseed rape at the expense of seed setting (Szczepaniak 2014).

The amount of potassium accumulated in the stem at physiological maturity was significantly affected by the weather and slightly modified by the fertilizing treatments (Figure 2). In 2008, the content of K in this plant organ showed a considerable response to the increasing input of nutrients, re-
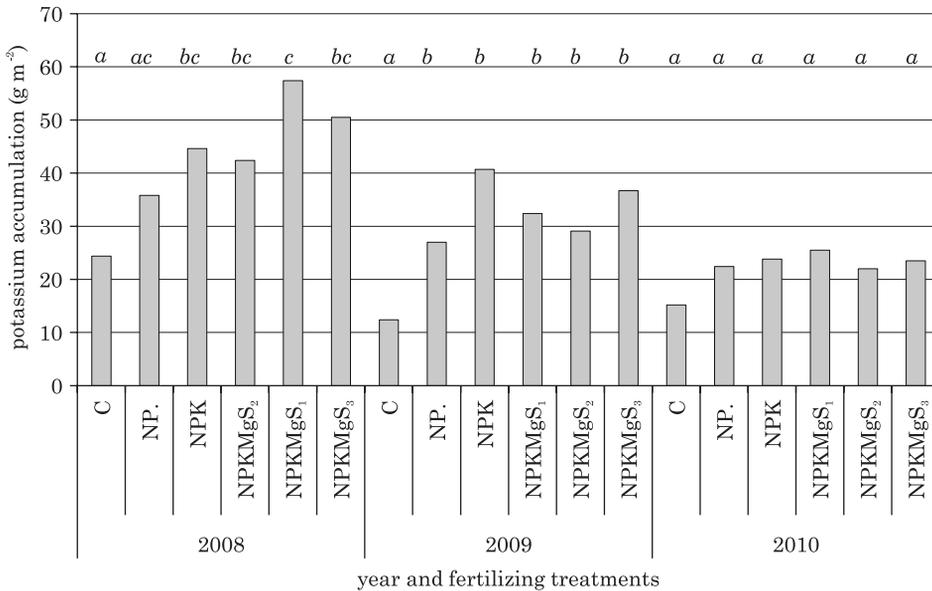
Fig. 2. Effect of fertilizng treatments on potassium accumulation in oilseed rape postharvest residues; [a] the same letters mean the lack of significant differences

aching the maximum in the NPKMgS1 treatment. In turn, in 2009, the total K amount in straw was 30% lower on average than 2008, reaching the maximum in the NPK treatment. In the third year, 2010, the same trend was observed as in 2008, but the amount of K in straw was 50% lower. The effect of the fertilizing treatments on the K content in seeds increased stepwise in accordance to the number of applied nutrients.

The K content in stems at the onset of flowering exerted the highest direct effect on the yield of the main inflorescence. However, it was significantly depressed by the indirect impact of the other variables. On the other hand, a moderate direct effect of the potassium content in seeds, through the impact of the other variables, became the key factor defining the yield produced by the principal branch (Table 3). Its effect was modified the most by the K content in straw (Figure 3a). The optimum sets of variables, as results from the stepwise analysis, except K_{SE}, were slightly different:

$$MBY = 0.234K_{SE} + 0.45 \qquad \text{for } n = 18, R^2 = 0.39 \text{ and } p < 0.0053,$$
$$MBY = 0.037K_{SH} + 0.211K_{SE} + 0.28 \quad \text{for } n = 18, R^2 = 0.65 \text{ and } p < 0.0035,$$
$$MBY = -0.048K_{RE} + 0.055K_{SH} + 0.247K_{SE} + 0.665$$
$$\text{for } n = 18, R^2 = 0.79 \text{ and } p < 0.00006.$$

This set of equations clearly indicates that the straw K content is an important factor influencing seed yields. The yield of seeds produced by secondary branches was most strongly affected by the K content in straw, due to the indirect effect of K in seeds (Figure 3*b*, Table 3). Thus, it can be concluded that the degree of K-seed sink saturation depended on the K supply from vegetative plant parts during the seed filling:

a

$$MBY = \begin{cases} K_{RE} = -0.388 \\ K_{LE} = -0.375 \\ K_{SH} = +1.094 \\ K_{ST} = +0.302 \\ K_{SE} = +0.366 \end{cases}$$

$+0.291 \quad +0.131 \quad -0.053 \quad -0.108$

$R^2 = 0.80$

b

$$SBY = \begin{cases} K_{RE} = -0.027 \\ K_{LE} = +0.329 \\ K_{SH} = -0.230 \\ K_{ST} = +0.595 \\ K_{SE} = +0.380 \end{cases}$$

$+0.365 \quad -0.021 \quad +0.041 \quad -0.006$

$R^2 = 0.97$

c

$$TSY = \begin{cases} K_{RE} = -0.150 \\ K_{LE} = +0.120 \\ K_{SH} = +0.195 \\ K_{ST} = +0.552 \\ K_{SE} = +0.408 \end{cases}$$

$+0.393 \quad -0.018 \quad +0.015 \quad -0.035$

$R^2 = 0.96$
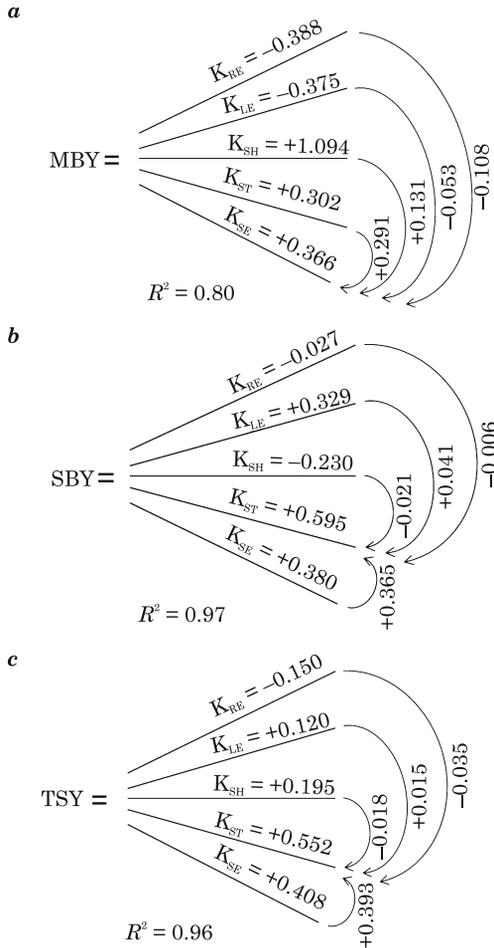
Fig. 3. Path diagrams: The arrangement of potassium concentrations affecting directly and indirectly the yield of oilseed rape produced by: *a* – the main inflorescence, *b* – secondary branches, *c* – whole plant

Components of the path analysis of the impact of K concentrations on oilseed rape yield, $n = 18$

Yield type/ K variable	MBY		SBY		TSY	
	DI[*]	IDs[**]	DI	IDs	DI	IDs
K_{RE}	-0.388	0.546	-0.027	0.331	-0.150	0.433
K_{LE}	-0.375	0.896	0.329	-0.112	0.120	0.218
K_{SH}	1.094	-0.511	-0.230	0.404	0.195	0.131
K_{ST}	0.302	0.313	0.595	0.379	0.552	0.390
K_{SE}	0.366	0.260	0.380	0.584	0.408	0.530

[*] direct effect, [**] sum of indirect effects

$$SBY = 0.059K_{ST} + 0.885 \quad \text{for } n = 18, R^2 = 0.95 \text{ and } p < 0.00000.$$

The above regression model implicitly indicates the importance of the K post-flowering management in the oilseed rape canopy on the yield produced by secondary branches. The dominant effect of this plant part was corroborated by the analysis of the varied K impact on the total yield of seeds (Figure 3c). It depended on the K content in straw, as revealed by the stepwise analysis, which highlighted the decisive effect of K in straw on yield:

$$TYS = 0.076K_{ST} + 1.638 \quad \text{for } n = 18, R^2 = 0.89 \text{ and } p < 0.00000,$$
$$TYS = 0.053K_{SH} + 0.074K_{ST} + 1.134 \text{ for } n = 18, R^2 = 0.97 \text{ and } p < 0.00000.$$

In order to explain the dominant effect of K_{SH} on oilseed rape yield, the potassium content in plant parts throughout the season was related to the size of its structural components. The number of siliques on the main stem was affected directly by the K content in straw (Figure 4a). However, it was significantly modified by indirect effects of the other variables, most markedly by K accumulated in seeds (Table 4). The negative signs of K in seeds can be explained by the insufficient K-sink seed capacity, which in fact depended on the limited K supply from stems. The stepwise analysis revealed a significant but negative effect of the K content in oilseed rape at the rosette stage on the number of siliques on the main inflorescence. To attain high accuracy of the developed model, an additional set of variables is required, including K in both the rosette and the stems:

$$SMB = 0.463K_{ST} + 31.81 \quad \text{for } n = 18, R^2 = 0.55 \text{ and } p < 0.00044,$$
$$SMB = -0.865K_{RE} + 0.515K_{ST} + 41.42 \text{ for } n = 18, R^2 = 0.67 \text{ and } p < 0.00027,$$
$$SMB = -1.386K_{RE} + 0.621K_{SH} + 0.525K_{ST} + 43.72$$
$$\text{for } n = 18, R^2 = 0.76 \text{ and } p < 0.00013.$$

The seed density was taken as the principal variable, affecting the plant's K requirement during the seed-filling period. The highest effect on the number of seeds per silique on the main branch, as indicated by the cor-

relation coefficient, was exerted by the K content in shoots. Its impact was negative, although it was modified the most by the K content in leaves (Figure 4*b*, Table 4). The final seed density on the main branch resulted from the balance between the K content in leaves and shoots at the onset of flowering. At the same time, the stepwise analysis revealed a significant effect of the K content in leaves at the rosette stage:

$$\text{SSMB} = 0.675K_{RE} - 0.55K_{SH} + 9.286 \text{ for } n = 0.18,\ R^2 = 0.39 \text{ and } p < 0.0234.$$

The number of siliques per secondary branch was most distinctly affected by the K content in leaves at the onset of flowering (Figure 3*c*). The trait was significantly modified by the K content in shoots, which affected it indirectly albeit negatively, as indicated by path coefficients (Table 4). The stepwise analysis corroborated the dominating but relatively weak impact of the K content in leaves on the number of siliques:

$$\text{SSB} = 2.349K_{LE} + 109.4 \qquad \text{for } n = 18,\ R^2 = 0.42 \text{ and } p < 0.0034.$$

Secondary branches showed the same seed density pattern in response to the K content as the main inflorescence. The key factor, only slightly affected by the other variables, was the K content in shoots at the beginning of flowering and in straw (Figure 4*d*, Table 4). This model was fully corroborated by the stepwise analysis:
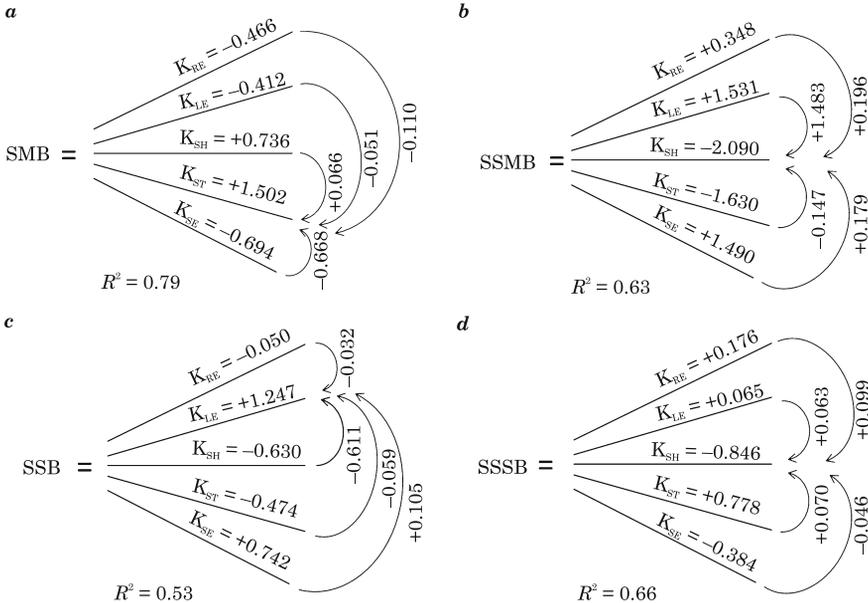
Fig. 4. Path diagrams: The arrangement of potassium concentrations affecting yield structural components:
a – number of siliques per main inflorescence, *b* – number of seeds per silique in the main inflorescence, *c* – number of siliques on the secondary branch, *d* – number of seeds per silique on the secondary branch

Table 4

Components of path analysis of the impact of K concentrations on oilseed rape yield structural components, $n = 18$

Yield component /K variable	SMB		SSMB		SSB		SSSB	
	DI*	IDs**	DI	IDs	DI	IDs	DI	IDs
K_{RE}	-0.466	0.306	-0.050	0.553	0.348	-0.148	0.176	-0.359
K_{LE}	-0.412	0.497	1.247	-0.598	1.531	-1.787	0.065	-0.664
K_{SH}	0.736	-0.609	-0.630	1.226	-2.090	1.709	-0.846	0.186
K_{ST}	1.502	-0.762	-0.474	0.799	-1.630	1.516	0.778	-0.397
K_{SE}	-0.694	1.345	0.742	-0.368	1.490	-1.504	-0.384	0.705

* direct effect, ** sum of indirect effects

$SSSB = -0.6K_{SH} + 14.38$ for $n = 18$, $R^2 = 0.44$ and $p < 0.0029$,

$SSSB = -0.636K_{SH} + 0.15K_{ST} + 9.9$ for $n = 18$, $R^2 = 0.63$ and $p < 0.00057$.

It can be concluded, based on the above equations, that the seed density as a prerequisite of final yields depends on the K management pattern in oilseed rape canopy before and just after flowering. It was observed that an increase in the net K accumulation affected significantly the net biomass production, most distinctly in 2008 (Figure 5). This finding implicates the K oilseed rape economy as the key cause of positive correlation between the dry

$Bn = 19.54Kn + 566.3$
for $n = 18$, $R^2 = 0.83$ and $p < 0.000$
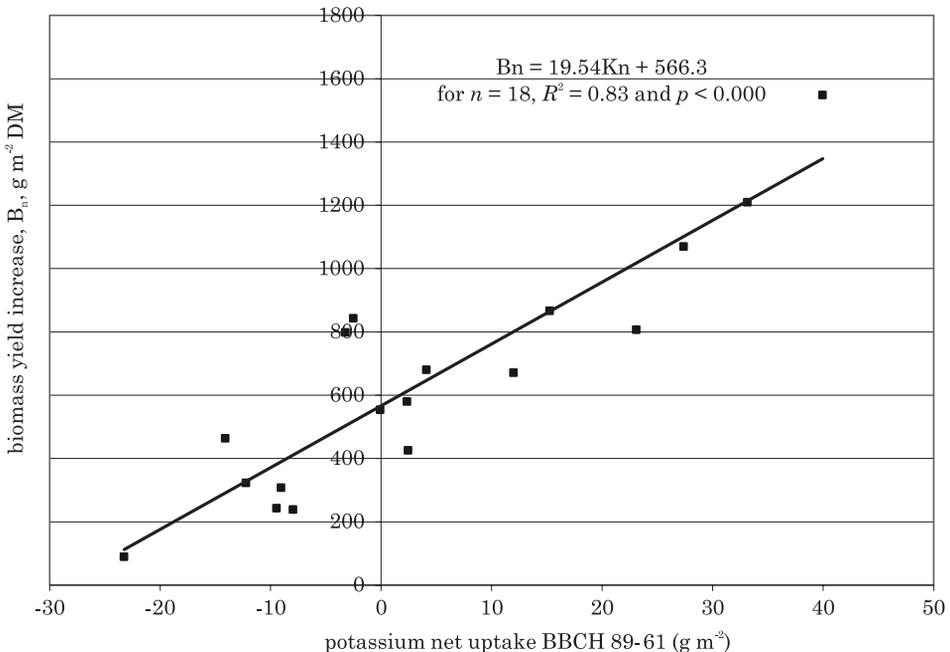
Fig. 5. A net vegetative biomass increase during the seed-filling period as a function of the net potassium accumulation in straw

matter increase during oilseed rape flowering and seed density. In 2009 and, in few instances, in 2010. there was a negative K_n balance. Consequently, the number of seeds per silique on the secondary branch considerably depended on this trait of oilseed rape plants:

$$SSSB = 0.184K_n + 9.61 \quad \text{for } n = 18 \text{ and } R^2 = 0.62 \text{ for } p < 0.00000.$$

This study showed that the yield forming effect of potassium is intrinsic to the seed density on secondary branches. Therefore, the suggestion expressed by Rose et al. (2008), that potassium has a yield effect until the flowering stage was confirmed only under an ample water supply, which occurred in 2009. In general, oilseed production is conducted under rainfed conditions. Oilseed rape, as shown in Figures 1 and 2, requires a huge amount of potassium. The most important factor which determined the K uptake by plants is the soil resources. As reported by Škarpa and Hlušek (2012), the actual content of soluble and exchangeable potassium depends on the weather course during the growing season. However, the negative impact of the weather on this K form can be ameliorated by K fertilizer application. In addition, non-exchangeable K resources should also be considered in making fertilization plans (Grzebisz, Oertli 1993).

CONCLUSION

The study proved that potassium is a major nutritient, which affects the N economy in oilseed rape, formation of yield components and, consequently, oilseed rape yield. Despite fluctuations of the K content during the growing season, the key predictor of yield is the potassium content in stems. This relationship can be explained by the requirements of growing seeds during plant maturation. Therefore, sucessful control of the seed density, which defines the size of K physiological sink, is the challenging task for farmers. The study showed that the pattern of potassium uptake by the crop since the onset of flowering significantly affected the development of structural yield components. Any excess of potassium taken up by oilseed rape before flowering, resulting in the saturation-like model of nitrogen uptake, leads to a significant reduction in the seed density on the main branch and, especially, on secondary branches. The oilseed rape yield, in the light of the above study, depends on the net K content increase in vegetative parts of the crop during the seed-filling period.

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