Phosphorus and potassium accumulation by *Brassica napus* L., and effects of phosphorus and potassium deficiency late in the season

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Abstract

In many arid environments, topsoil containing the bulk of soil immobile nutrients may dry out (rendering the nutrients unavailable for plant uptake) whilst water remains available in the low-nutrient subsoil. In Australian conditions, topsoil drying frequently occurs in spring during the reproductive growth phases of crops. The impact of topsoil drying (and low external P and K supply) on yields depends on the magnitude of the crop demand for these nutrients late in the season; however, the phosphorus and potassium accumulation patterns of canola (rapeseed) are currently not known. In a series of glasshouse experiments, we examined the uptake and distribution of P and K in canola cultivars compared to wheat and the impact of limited external P and K supply post-flowering on canola seed yields and oil content. Maximum P accumulation by all canola cultivars occurred during late flowering (84 days after sowing), whereas P accumulation in wheat plants had peaked just prior to anthesis (73 days after sowing). Maximum accumulation of K in two canola cultivars (Tribune and Trigold) peaked during mid-flowering (73 days after sowing) but peaked earlier (61 days after sowing) in Boomer canola and Nyabing wheat. The seed (grain) was a strong sink for P but contained less than 10 % of total plant K in both species. The majority of seed P was redistributed from stems and silique walls of canola and from the stems and leaves of wheat, rather than from the soil. The bulk of K in mature canola plants remained in the stem (23-35 %) and silique walls (27-32 %), or was lost in senesced leaves (25-30 %). The impact of reduced P and K supply late in the growing season are discussed in relation to distribution and redistribution of these nutrients within the plant.

Key words: Canola, Phosphorus, Potassium, Uptake

Introduction

In many arid environments, topsoil containing the bulk of soil immobile nutrients may dry out (rendering the nutrients unavailable for plant uptake) whilst water remains available in the low-nutrient subsoil. In Australian conditions, topsoil drying frequently occurs in spring during the reproductive growth phases of crops. The impact of topsoil drying (and correspondingly low availability of P and K) on yields depends on the magnitude of the crop demand for these nutrients late in the season; however, the post-flowering phosphorus and potassium requirements of canola (rapeseed) are currently not known.

Our earlier glasshouse studies found that P and K accumulation by canola cultivars continued until later in the season than wheat grown under the same conditions. In the same study, canola cultivars reached maximum P accumulation during early silique filling (GS 5,5) (Sylvester-Bradley and Makepeace 1984) and maximum K accumulation at full bloom (GS 4,8). In the field, accumulation of both nutrients may continue until the later stages of silique filling (Barraclough 1989), suggesting that environmental conditions and nutrient availability effect accumulation patterns.

Continued uptake of P or K post-anthesis is often unnecessary in annual grain crops, as redistribution of these nutrients from vegetative organs to the developing grain can meet plant demands. For example, wheat crops generally only require P until heading for maximum grain yields (Boatwright and Haas 1961; Batten et al. 1986). Wheat plants can continue to accumulate P post-anthesis when P is available; however, this tends to result in increased grain P concentrations rather than increased yields (Batten et al. 1986). Thus, accumulation of nutrients post-flowering may reflect soil availability rather than plant demand alone.

This study aimed to determine the growth stage by which canola plants had accumulated sufficient P and K at adequate and high levels of nutrient for maximum seed yields. The effect of nutrient level and time of nutrient removal on redistribution of P and K from vegetative organs to the seed was also investigated.

Methods and materials

Design

Two sand culture experiments were established under glasshouse conditions. Both experiments were 2 x 2 x 4 factorial designs with nutrient treatments [P (exp. 1) or K (exp. 2) supplied at ‘adequate’ or ‘high’ concentrations], two harvests (immediately before imposition of nutrient removal treatment and maturity) and four nutrient (P or K) removal treatments (nutrient removed at mid flowering (GS 4,7), late flowering (GS 4,9-5,5), mid silique-filling (GS 6,2) or maturity). Each experiment had three replicates and was laid out in a completely randomised design.

Growth conditions

We conducted a series of preliminary experiments to evaluate canola growth in nutrient solutions containing a range of P and K concentrations to determine adequate and high nutrient levels. Adequate P and adequate K treatments were developed, using the lowest levels of P or K possible to sustain maximum canola dry matter growth until flowering. High P and high K treatments were developed to produce plants with the same dry matter accumulation (biomass) at flowering and phenological characteristics (time of first flower) to 'adequate' plants, but higher in nutrient status. The two P supply regimes required to produce 'adequate' and 'high' P plants (exp. 1) were:

1. plants grown for 10 days at 500 µM, then 200 µM for duration of experiment (adequate)
2. plants grown at 500 µM for duration of experiment (high)

The K concentrations in nutrient solution required to produce plants of 'adequate' and 'high' K status (exp. 2) were 400 and 1000 µM respectively. The basal solutions contained (µM): NH_4NO_3 2000, $MgSO_4$ 1000, FeNaEDTA 20, H_3BO_3 9.8, $MnSO_4.H_2O$ 2, $ZnSO_4.7H_2O$ 2, $CuSO_4.5H_2O$ 0.5, and $Na_2MoO_4.2H_2O$ 0.08. The basal nutrient solution was supplemented in each experiment as follows (µM):

Experiment 1 - KNO_3 2000, $Ca(NO_3)_2$ 1600, KH_2PO_4 (200 or 500), KCl (300 or 0, respectively, to compensate for different additions of K in the different P treatments).

Experiment 2 - $Ca(NO_3)_2$ 2600, KH_2PO_4 400, KCl (0 or 900).

Plants were grown in 30-cm-diameter, free-draining plastic pots in a glasshouse at the University of Western Australia, Perth (31.58 S, 115.49 E). Pots were filled with approximately 12 kg of dried, washed river sand. On 20th June 2006, six seeds of canola cv. Boomer were sown 5mm deep in each pot, and thinned to three evenly spaced seedlings 10 days after emergence. Pots were irrigated daily with 1.5 L of nutrient solution, to flush out any nutrients that may have accumulated.

Measurements and statistical analyses

At each harvest, shoots were dried in an air-forced oven at 70 °C for 72 h, weighed and ground. A sample of approximately 0.5 g was digested with a mixture of 10 mL of concentrated nitric acid and 1 mL of concentrated perchloric acid (see Valizadeh et al. 2003). Phosphorus concentration of the samples from experiments 1 and 3 were then measured using the molybdo-vanadophosphate method (Kuo 1996). Potassium concentration of the samples from experiments 2 and 4 were measured by atomic absorption spectrometry (AAnalyst 300, Perkin Elmer, Norwalk, CT, USA).

Data were analysed in Genstsat release 8.2 (Rothamsted, UK). At final harvest, yield parameters (total seed weight, seed weight on raceme/secondary branches, total pods per pot, pods per pot on raceme/secondary branches, total seeds per pod, seeds per pod on raceme/secondary branches, individual seed weight from raceme/secondary branches) were subjected to a general ANOVA with P removal (T1-T4) and nutrient level (adequate or high) as the treatment effects. Total P and K accumulation were subjected to a general ANOVA with harvest date as the treatment effect.

Results

Dry matter, P and K accumulation

Dry matter accumulation peaked at maturity (harvest 4) in both experiments at both nutrient levels (adequate and high) and all nutrient removal treatments (data not shown). Accumulation of K continued until early/mid silique-filling (GS 6,2) under both high and adequate K supply (Fig. 1c,d). Under high P supply, P uptake continued until GS 6,2 (Fig. 1a), whereas in the adequate P supply treatment, uptake continued until maturity (Fig. 1b).

Seed yields

There was no difference in total seed yields, siliques per pot or seeds per silique between any treatments at either adequate or high K supply or at high P supply (data not shown). Under adequate P supply, total seed yields were significantly reduced in T1 (P removal at GS 4,7) and T2 (P removal at GS 4,9-5,5) (Table 1). Reduced total seed weight in T1 was due to significantly less pods on secondary branches per pot, and fewer seeds per pod on secondary branches compared to the control (T4) (Table 1). The reduction in total seed weight in T2 was due to reduced number of seeds per pod on the secondary branches (Table 1).

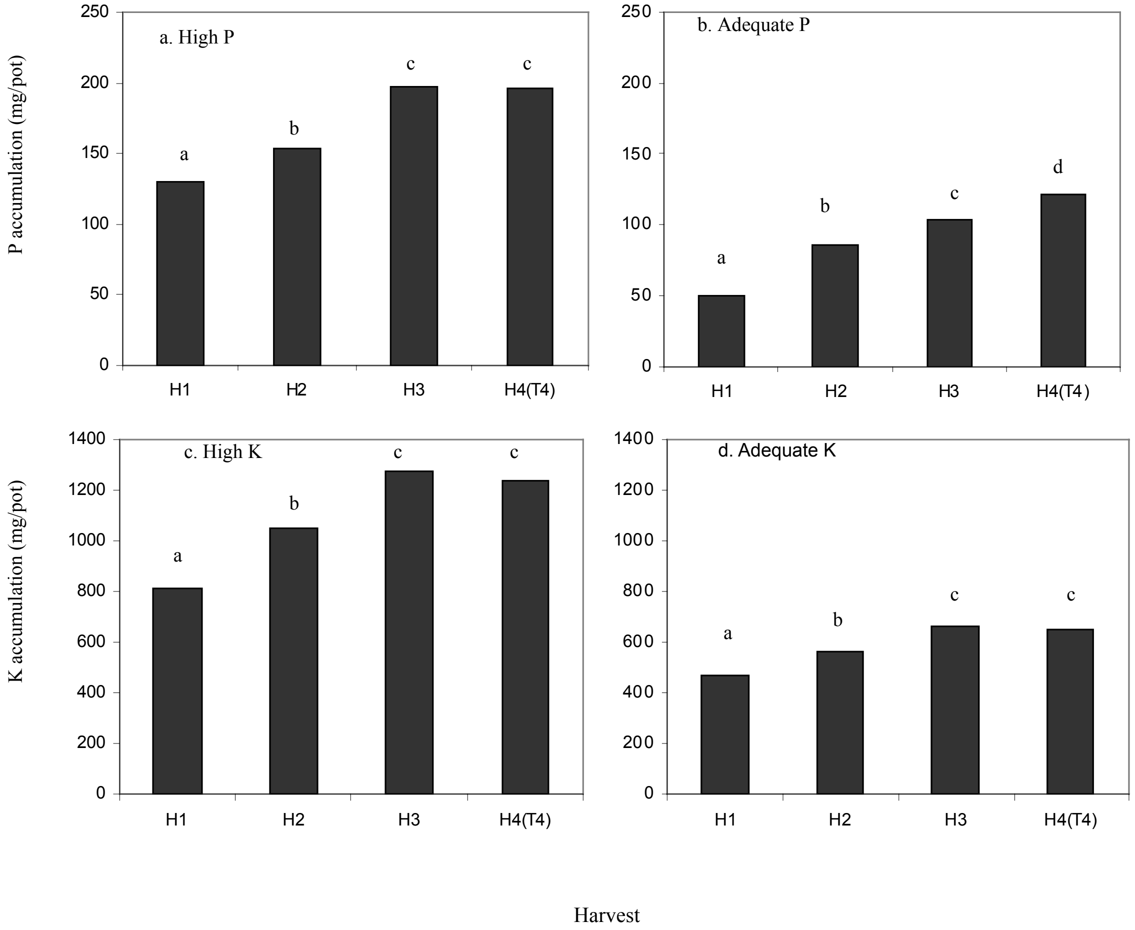

Fig. 1 – accumulation of P and K by Boomer canola from mid-flowering (H1-GS 4,7) to maturity (H4). Columns not labeled with the same letter are significantly different ($P < 0.05$).

Table 1 - Effect of cessation of external P supply on seed yield in Adequate P treatment. Values followed by the same letter in each row are not significantly different (at $p \leqslant 0.05$)

Treatment (Growth stage of P removal)	Seed weight (yield) per pot			Siliques per pot		Seeds per silique	
	total	raceme	secondary	raceme	secondary	raceme	secondary
1 (GS 4,7)	16.0 a	7.7 b	8.3 a	164 a	245 a	10.5 a	10.9 a
2 (GS 4,9-5,5)	22.2 b	9.8 b	12.4 b	182 a	350 b	13.6 a	9.1 a
3 (GS 6,2)	27.0 c	9.2 b	17.8 c	173 a	359 b	12.6 a	11.6 b
4 control	27.8 c	9.6 b	18.2 c	183 a	392 b	13.0 a	11.6 b

Discussion and conclusions

Silique formation and growth is dependent on continuous assimilate supply (Diepenbrock 2000) and any stresses that reduce the assimilate supply lead to losses through silique or seed abortion (Tayo and Morgan 1979). Because plant biomass accumulation continued until maturity in all treatments (data not shown), P was required for its normal role in photosynthesis, assimilate transfer to the grain, oil synthesis and to meet the minimum seed P requirement. Under an adequate P supply, canola plants require an external P supply until early silique-filling (GS 6,2) for maximum seed yields (Table 1). Removal of P prior to this stage led to decreased seed yield (weight) due to reduced seed number per silique (T2) or a combination of silique abortion and reduced seed number per silique (T1) (Table 1). It appears that in T1 and T2, competition for P between physiological processes led to reduced assimilate supply and hence, silique and/or seed abortion. Although some reports suggest that seed and silique number are determined by the completion of flowering (Habekotte 1993, Diepenbrock 2000), our results suggest that stress at the end of flowering (T2, GS 4,9-5,5) leads to further reductions in seed number during silique-filling.

Keiller and Morgan (1988) found that limited supply of assimilates tended to affect higher order branches or siliques initiated later, rather than main stem pods, possibly due to higher sink strength of the main stem siliques. The results from our study concurred with this theory, as yield reductions due to seed or silique abortion occurred primarily on the secondary branches (Table 1).

In contrast to plants supplied with only adequate P, plants supplied with above adequate P (High P treatment) during vegetative growth had accumulated sufficient P by mid-flowering (GS 4,7) to attain maximum seed yields. These results confirm that plant P status plays a decisive role in determining the plant growth stage at which sufficient P has been accumulated for maximum seed yields.

Although K plays a role in assimilate transport to seeds, canola has high K uptake during vegetative growth and minimal K concentration required in the seed. Hence, it appears that sufficient K has been obtained by mid-flowering (GS 4,7) to fulfill plant requirements for maximum seed yields when supplied with adequate or above adequate K prior to flowering.

In field situations, it is unlikely that low P supply would coincide with an excessive supply of all other plant nutrients (particularly N and S), or that external P supply would be completely cut off while all other nutrients remain available for uptake. In conclusion, when P and K are not the limiting growth factors, canola plants have generally accumulated sufficient P and K for maximum seed yields by mid-flowering. If P supply is limiting, continued accumulation of P until mid-silique filling (GS 6,2) may be required for maximum seed yields.

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