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### Retranslocation of nitrogen and potassium from leaves to grains in wheat

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#### Abstract

In spring wheat (cv. Kolibri) the relationship between leaves as source, and grains as sink was investigated for nitrogen and potassium. To eliminate a further delivery of nutrients from the root to the shoot during long-term experiments commencing 19 or 20 days after anthesis, culms with 3 leaves were detached and placed in water. Nitrogen was readily mobilized in all plant parts and translocated to the grains. Potassium also decreased considerably in the leaf blade, however, influx to the grains was limited and part of the potassium accumulated in the non-grain parts of the ear. This suggests that, in contrast to the bulk of sucrose, potassium is partly unloaded during the movement from source to sink. In this way potassium which usually is present in high concentrations in the phloem sap, may provide an osmotic gradient for solute transport in addition to that caused by the grains. The reabsorption of potassium from the phloem may also be an essential factor for the regulation of the amounts of potassium entering the grains. No evidence was found for a possible circulation of potassium through the ear. Experiments with culms, whose stems were steam girdled between the flag leaf and the ear, showed that a phloem discontinuity at the stem did not change the amounts of nitrogen retranslocated and transported to the ear. Translocation of potassium, however, was almost completely inhibited by the phloem discontinuity.

#### Introduction

It is well-known that the amount of nitrogen deposited in the grains of cereals varies widely depending on nitrogen nutrition. In contrast, the amount of potassium deposited is largely independent of the potassium nutrition of the plant. The limitation in potassium concentration in the grains appears to be in contrast to the high concentration of potassium usually found in phloem sap (*e.g. Hall and Baker, 1972*). In view of the differing ability of the grain to accumulate nitrogen and potassium, the pattern of retranslocation of these nutrients from leaves was investigated in spring wheat.

## Results

### *Effect of sink reduction on grain nitrogen and potassium*

When part of the ear is removed shortly after anthesis, the source to sink ratio is changed at the beginning of the phase of development in which retranslocation from vegetative plant parts plays an increasing role in supplying nutrients for grain growth. Therefore the response of the grains to a higher nutrient supply can be investigated without changing the fertilization of the plant. The result of an experiment with such a treatment confirmed general findings from experiments with varied nitrogen or potassium nutrition: In grains of halved ears (upper half removed) nitrogen increased strongly, while potassium was not influenced in spite of a significant increase in single grain weight.

### *Retranslocation in detached culms*

To eliminate the influence of the root in supplying nutrients in the xylem stream to the shoot, isolated culms were used for some of the investigations on retranslocation of nitrogen and potassium. Culms with 3 leaves were detached 19 days after anthesis and placed in deionized water in a growth chamber. The culms developed normally except that the grain yield was somewhat lower at maturity (for details see *Martin, 1982*). Between 20 days after anthesis and maturity nitrogen decreased strongly in all plant parts except the grains, while potassium decreased only in some vegetative parts, most notably in the leaf blade of the flag leaf (table 1). In the rachis and the glumes the amount of potassium increased, suggesting a transport to the ear in excess of that needed for grain development.

*Table 1* Changes of nitrogen and potassium in various plant parts of detached culms (with 3 leaves attached) developing in deionized water from day 20 after anthesis until maturity. Data are given in milligrams per culm, and at maturity also as a percentage increase or decrease

	20 days after anthesis			Maturity		
	Dry weight	N	K	Dry weight	N	K
Grains	620	9.82	5.22	1470	24.90	6.92
				+137	+154	+33
Glumes*	380	5.36	3.11	347	1.72	4.76
				-9	-68	+53
Rachis	105	1.16	0.85	97	0.40	1.05
				-8	-66	+24
Flag leaf						
blade	113	2.74	1.73	69	0.33	0.75
				-39	-88	-57
sheath	150	1.58	1.70	124	0.47	1.68
				-17	-70	-1
2nd and 3rd leaf	311	3.33	5.31	235	0.93	4.27
				-24	-72	-20
Stem	1630	4.86	10.50	989	1.46	8.04
				-39	-70	-23

\* Including paleas and lemmas.

### *Influence of a local phloem interruption in the stem ('girdling')*

The accumulation of potassium in the glumes (and rachis) described in the preceding section may have been caused by a movement in the xylem in spite of the absence of the root. Therefore, again using detached culms, the stem was steam girdled between the flag leaf and the ear interrupting the phloem stream in the sieve tubes but leaving the water stream in the xylem largely unaffected. The

treatment resulted in an almost complete inhibition of potassium translocation to the plant parts above the girdle suggesting that the accumulation in the non grain parts of the ear was not due to a xylem transport (table 2). Nitrogen retranslocation was, however, not significantly influenced by the phloem block. Obviously, nitrogen can be transferred from the phloem to the xylem and bypass the phloem interruption with the transpiration stream.

*Table 2* Effect of phloem interruption of the stem on changes in nitrogen and potassium in various plant parts from girdling until maturity. Culms were steam girdled between the flag leaf and the ear (120 mm below the ear) 19 days after anthesis and placed in water. Data are given in milligrams per culm and at maturity also as percentage increase of decrease. The weight of a single grain at the start of the experiment was 16 mg and at maturity for the control 34 mg and for the girdled culms 28 mg. Significance for differences between control and steam girdled culms:  $P=0,01$

	Day 19		Maturity			
	Nitrogen	Potassium	Nitrogen		Potassium	
			Control	girdled	Control	girdled
Plant parts above point of girdling						
Grains	10.15	5.30	25.87	24.46	6.85	6.35
			+155	+141	+29	+20
Others	7.24	4.42	2.36	2.88	6.40	3.88*
			-67	-60	+45	-12
Plant parts below point of girdling						
Leaves and stem	12.28	18.67	3.13	4.05	14.48	18.14*
			-75	-68	-22	-3

*Table 3* Influence of steam girdling the stem between flag leaf and ear and of darkening the plant parts above the point of girdling on retranslocation of nitrogen.  $^{15}\text{N}$  ( $^{15}\text{NH}_4^{15}\text{NO}_3$ ) was sprayed onto the leaves 1-3 (from above) 20 days after anthesis. Culms were detached immediately before  $^{15}\text{N}$  application and placed in water. Duration of the experiment was 24 hours. Data are given in  $\mu\text{g}$   $^{15}\text{N}$  per culm

	Culms without girdle		Culms girdled	
	Light	Dark	Light	Dark
Plant parts above point of girdling				
Grains	290.7	279.7	137.3	19.6
Glumes*	7.5	5.7	10.8	3.4
Rachis	6.8	4.3	10.1	0.8
Stem	8.0	5.8	13.8	3.3
% of total $^{15}\text{N}$	55.4	54.8	29.4	4.8
Plant parts below point of girdling				
Leaves	176.2	169.7	246.2	324.1
Stem	75.7	73.4	171.1	211.8
% of total $^{15}\text{N}$	44.6	45.2	70.6	95.2

\* Including paleas and lemmas.

The result that nitrogen in girdled culms can be translocated in the xylem during the course of retranslocation from the leaves to the ear gave rise to the question of whether the xylem also plays a role as pathway for nitrogen during

retranslocation in intact culms. A short-term experiment in which  $^{15}\text{N}$  was applied to the leaves suggests that only small amounts of nitrogen reach the ear via the xylem (table 3). The amount of  $^{15}\text{N}$  in the glumes, the most actively transpiring organs of the ear, remained low and reduction of the transpiration by darkening the ear had only little effect on the pattern of  $^{15}\text{N}$  in the ear. The distribution of  $^{15}\text{N}$  between grains and non-grain parts in girdled culms (in light) suggests a rapid return of nitrogen to the phloem from the xylem above the girdle. In contrast to the long-term experiment described earlier, in this short-term experiment the transport of nitrogen ( $^{15}\text{N}$ ) through the girdled section was reduced to about one half of that of the non-girdled culms: This may reflect a dilution of  $^{15}\text{N}$  by  $^{14}\text{N}$  during translocation in leaves and stem.

#### *Influence of darkening the flag leaf*

It is known that potassium plays an essential role in sucrose loading into the phloem (Doman and Geiger, 1979). Information is lacking, however, on the relationship between potassium and sugar movement during phloem transport. To get some information on this question the flag leaf of wheat culms was darkened to eliminate photosynthetic assimilation and to reduce sugar transport drastically. It was found, that potassium retranslocation from the leaf blade is much more influenced than nitrogen retranslocation (table 4).

**Table 4** Influence of darkening the flag leaf (blade and sheath) of detached wheat culms placed in water on retranslocation of nitrogen and potassium. Data at the start of the experiment (18 days after anthesis) are given in milligrams per culm and at maturity as percentage increase or decrease. Significance for differences between control and darkened leaves: \*  $P=0,05$ ; \*\*  $P=0,01$

Nutrient	Leaf blade			Leaf sheath		
	Day 18	Maturity		Day 18	Maturity	
		Control	darkened		Control	darkened
Nitrogen	3,19	-88	-77*	1,69	-84	-79
Potassium	1,49	-63	-33**	2,18	0	+ 6

#### *Does potassium cycle through the ear?*

The increase in potassium in the non-grain parts of the ear during grain development gave rise to the question of whether part of the potassium is retranslocated from the ear back down the stem. In an experiment using  $^{86}\text{Rb}$  as a marker for K, no indication was found for a cycling of potassium through the ear (table 5). Downward transport of  $^{86}\text{Rb}$  was induced however by removing the grains. This suggests that, under these conditions, some sugar was moving downward from the ear which was accompanied by potassium.

**Table 5** Translocation of  $^{86}\text{Rb}$  from a 30 mm stem section immediately below the ear to which  $^{86}\text{Rb}$  was applied 22 days after anthesis (intact plants) 5 replicates were taken per sample. Data are given as  $\text{cpm} \times 10^4$

	Hours after application					
	2	8	24	48	72	24
Ear	Intact ear					Grains removed
	20	31	44	41	53	0,5
Stem below section of application	0	0	0	0	0	10

## Discussion

The results of experiments with girdled culms show that a continuous connection by the sieve elements between leaves as source and grains as sink in wheat is not a prerequisite for the retranslocation of nitrogen. However, in non-girdled plants 20 days after anthesis, xylem seemed not to have played a significant role for retranslocation. It has still to be investigated whether the contribution of xylem transport increases in later stages of development when senescence reaches the internodal part of the stem.

From the data in tables 1 and 4 it is obvious that a relatively high proportion of potassium is retranslocated from the leaf blade. On the other hand potassium accumulates partly in the non-grain parts of the ear. This suggests that potassium accompanies sucrose in the phloem en route to the grain in amounts in excess of that required for grain development. The need for potassium in the grain appears mainly confined to the normal functions of cell growth and metabolism, since a sink, in the sense of the removal of a compound from the solute by conversion to an insoluble storage-form, does not exist for potassium in the grain.

It is known that potassium promotes sucrose loading into the phloem (Mengel and Haeder, 1977; Doman and Geiger, 1979). Possibly mediating the sucrose loading process, potassium itself is loaded into the phloem where it is usually present in relatively high concentrations (Hall and Baker, 1972). From the present data it may be concluded that potassium unloading takes place all along the transport path. This is in contrast to sucrose unloading which mainly occurs in the grain. Evidence for a more rapid movement of sucrose than potassium was found by Fensom and Davidson (1970) when these compounds were injected into a single sieve element in *Heracleum*. Wardlaw (1974) reported on a pronounced pattern of accumulation in the stem of wheat after application of  $^{86}\text{Rb}$  to the flag leaf which was in contrast to the translocation pattern of  $^{32}\text{P}$ . A partial reabsorption of potassium from the phloem during movement from leaves as source to grains as sink in wheat may affect this source-sink relationship in two ways. Firstly, it regulates the amount of potassium entering the grain and secondly, potassium creates an osmotic gradient in addition to the solute gradient induced by unloading in the grain, thereby accelerating the sugar movement to the grain.

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