BIOLOGIA PLANTARUM (PRAHA)

29 (3) : 221–229, 1987

Diurnal Variations of Potassium Content in Lucerne Plants

F. PLHÁK

Research and Breeding Institute for Fodder Plants, Plant Breeding Station Želešice, 664 43 Želešice (Brno), Czechoslovakia

Abstract. Diurnal changes in K content in leaf blades, petioles, stems and roots of eleven lucerne genotypes were followed. Significant positive correlations between changes in K content in petioles and upper half of stems and significant negative correlations between changes of K content in leaf blades and lower half of stems reflected rapid K movement. The velocity — up to 60 μmol g^{-1}(f.m.)h^{-1} — of changes in K content from leaf blades to lower part of stems and the other way round showed that long distance phloem transport occurred. Only moderate increase of K content contemporarily took place in roots. When total K amount in the whole plant was calculated then K uptake alternatively with K release were noticed during the day. Average K release reached 1.48 μmol g^{-1}(f.m.) h^{-1}. The rate of K movement correlated with irradiance and physiological activity of plants. The time course of K movement was uniform in plants of the same strain and it differed partially in different strains.

Potassium plays an essential role in plant metabolism. It participates in enzyme activation, formation of saccharides and starch, stomatal movement and especially in translocation of important metabolites such as photosynthates (ASHLEY and GOODSON 1972, MENGEL *et al.* 1974), nitrates (BEN ZIONI *et al.* 1971), aminoacids (SECER 1978) *etc.* In legumes, K fertilization increases nodule number and N_2 fixation rate (COLLINS and DUKE 1981) by increasing translocation of photosynthates to roots (MENGEL *et al.* 1974, BARTA 1982).

Due to its role in transport processes, potassium is capable of free movement in the xylem and of unrestricted movement at high concentration in the phloem. It moves efficiently through the roots from the soil and from the downward phloem stream to the ascending xylem stream and through mature leaves again into the phloem so that its recycling in the plant can take place (HALL and BAKER 1972, PATE 1975, MENGEL and KIRKBY 1980).

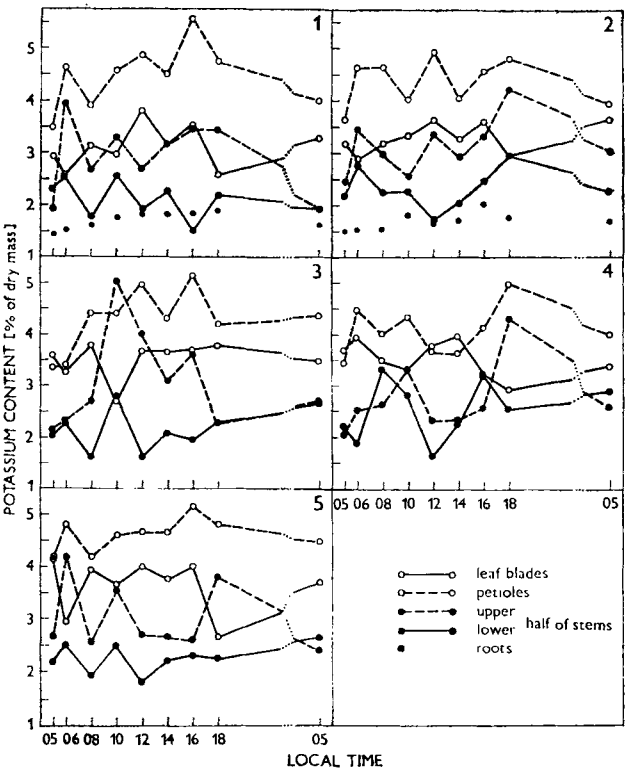
In the preceding study (PLHÁK 1984) contradictory diurnal changes in K content in leaves and stems of lucerne plants were established. These changes reflected possible K movement occurring in plants by time sampling during solar exposure. A more detailed study of K movement in leaf blades, petioles, stems and roots of lucerne plants by sampling at shorter time intervals is involved in the present paper (*cf* also PLHÁK 1987).

Received April 2, 1986; accepted September 16, 1986

MATERIAL AND METHODS

Five lucerne *Medicago sativa* L. strains — progenies of open pollinated clones 9 — cv. Hodonínka, 45 — cv. Košice, 60 — cv. Přerovská, 81 — cv. Flandria and 82 — cv. Isis, four cultivars Pálava, Bobrava, Verko and Euvere, and 2 new breedings PŠ and PP/B were used in experiments. Experimental plants were grown in a greenhouse in containers with soil or in the field. Plants were sampled every time in early bud stage. The sampling began at 05.00 CET, followed at 06.00 and then at 2-h intervals up to 18.00 and at 05.00 next day. In two experiments the sampling occurred at 2—3 h intervals also during the night. Irradiance was measured simultaneously and average day's irradiance calculated (PLHÁK 1981). Each sample of plant material consisted of 10—12 shoots.

The analyses of K and total nonstructural saccharide (TNS) content were made in triplicate by flame photometry and colorimetry (PLHÁK 1981, 1983) in leaf blades, petioles, the upper and lower halves of stems and in the roots. The values of K content were expressed in % dry mass after TNS subtraction. Changes in TNS content occurring especially in leaves during



Figs. 1—5. Diurnal changes of K content in overground organs and roots of different lucerne strains. K content is expressed in % d.m. (in overground organs after TNS subtraction). — Progenies of open pollinated clone 9 derived from cv. Hodonínka (Fig. 1); 45 from cv. Košice (Fig. 2); 60 from cv. Přerovská (Fig. 3); 81 from cv. Flandria (Fig. 4); 82 from cv. Isis (Fig. 5).

TABLE 1

Statistical evaluation of variability in K content in different plant organs during 24 h time sampling of two lucerne progenies (clone 9 derived from cv. Hodonínka and 45 from cv. Košice) by means of analysis of variance (a), and *t*-test (b)

(a)

Plant organ	F values for variability caused by			
	time sampling		replication	
	Clone 9	Clone 45	Clone 9	Clone 45
Leaf blades	146^{++}	97^{++}	21.3^{++}	0.59
Petioles	76^{++}	18^{++}	0.34	2.46
Stems — upper half	694^{++}	63^{++}	1.19	4.0^{+}
Stems — lower half	500^{++}	145^{++}	9.6^{++}	5.0^{+}
Roots	12.2^{++}	8.3^{++}	2.4	2.67

(b)

Differences between time of sampling	t_3 values for clone 9				
	Leaf blades	Petioles	Stems — upper half	Stems — lower half	Roots (n = 7)
0500—0600	5.8^{++}	6.6^{++}	10.0^{++}	7.6^{++}	2.7^{+}
0600—0800	6.2^{++}	4.1^{+}	12.9^{++}	18.0^{++}	0.8
0800—1000	2.1	6.8^{++}	6.5^{+}	12.3^{++}	1.2
1000—1200	10.0^{++}	3.3^{+}	18.2^{++}	19.4^{++}	0.9
1200—1400	9.7^{++}	3.9^{+}	9.3^{++}	8.8^{++}	1.4
1400—1600	5.7^{++}	12.8^{++}	5.6^{+}	22.0^{++}	0.2
1600—1800	10.0^{++}	13.8^{++}	0.9	10.0^{++}	0.6
1800—0500	6.0^{++}	8.9^{++}	65.7^{++}	23.9^{++}	3.2^{++}

$^{+}$ significant at 0.05 level; $^{++}$ significant at 0.01 level.

light exposure changed the K content in single plant organs (PLHÁK 1981, 1984).

Statistical evaluation of the results obtained was made by means of linear correlations, analysis of variance, variation coefficients and by the *t*-test.

RESULTS

Five lucerne strains of the clones 9, 45, 60, 81, and 82 grown in containers were used in the first experiment (August 19, 1982). K content changed expressively in leaf blades, petioles and stems during the day in all five strains (Figs. 1—5). The changes were mostly highly significant (Table 1). K content estimated in the roots of strains of clones 9 and 45 increased moderately during time sampling similarly in both cases (r = 0.70^{+}). Significant positive correlations were established between K changes in petioles and upper half of stems and significant negative correlations between K changes

TABLE 2

Correlations between diurnal changes in K content of different overground organs of lucerne strains of the clone 9 — derived from cv. Hodonínka, 45 — from cv. Košice, 60 — cv. Přerovská, 81 — cv. Flandria and 82 — cv. Isis

Correlation between plant organs	Correlation coefficients (r) of strains examined					
	9	45	60	81	82	Average of all strains
Leaf blades *vs.* petioles	0.32	−0.05	0.19	−0.65	−0.39	−0.08
Leaf blades *vs.* stems — upper half	−0.33	−0.26	0.20	−0.79^{+}	−0.85^{++}	−0.54
Leaf blades *vs.* stems — lower half	−0.70^{+}	−0.63	−0.71^{+}	−0.61	−0.37	−0.73^{+}
Petioles *vs.* stems — upper half	0.72^{+}	0.76^{+}	0.62	0.35	0.35	0.77^{+}
Petioles *vs.* stems — lower half	−0.28	0.20	0.34	−0.16	0.29	−0.04
Stems — upper half *vs.* lower half	0.24	0.57	0.12	0.24	0.35	0.21

$^{+}$ significant at 0.05 level; $^{++}$ significant at 0.01 level.

in leaf blades and the upper and especially the lower half of stems. These correlations showed the same tendency in all five strains. No important correlations were established in other cases (Table 2). Established K movement reached values up to 1.2 % d.m. h^{-1} that is up to 60 μmol g^{-1} (f.m.) h^{-1} at 40 cm distance — length of experimental plants.

Mostly positive correlations — in 7 cases significant or highly significant — were established between changes in K content in identical organs of five lucerne strains. The most uniform changes in K content were established in petioles. Very similar changes in K content in all three overground organs were established in the strain of the clones 9 and 82 (Table 3).

The mass of the first sampled plants and their organs of the strains of clones 9 and 45 were used for K amount calculation (Table 4). This K amount changed in single plant organs during the day in correspondence with the changes in K content. Total K amount calculated for the whole plant changed during the day as well. The lowest K amount per plant was determined at first sampling, then it increased and decreased alternately during the day as a result of rapid changes of K content occurring in aboveground organs. The differences in K amount between succeeding samplings were calculated and expressed as K uptake (+) or K release (−) by the plant. K uptake prevailed over K release during 24 h by 6.7 % in the strain of clone 9 and by 13.3 % in the strain of clone 45. It was conditioned by plant growth during 24 h sampling.

TABLE 3
Correlations between changes of K content in overground organs of lucerne strains of the clone 9 derived from cv. Hodonínka, 45 — from cv. Košice, 60 — cv. Přerovská, 81 — cv. Flandria and 82 — cv. Isis, during 24 h sampling time

Plant organs	Correlation coefficients (r) of compared strains										
	9 *vs.* 45	9 *vs.* 60	9 *vs.* 81	9 *vs.* 82	45 *vs.* 60	45 *vs.* 81	45 *vs.* 82	60 *vs.* 81	60 *vs.* 82	81 *vs.* 82	Average
Leaf blades	0.90^{++}	0.25	0.17	0.72^{++}	−0.01	−0.04	0.67^{+}	−0.05	0.11	0.31	0.30
Petioles	0.62	0.64	0.39	0.95^{++}	0.45	0.73	0.52	0.08	0.48	0.50	0.54
Stems — upper half	0.48	0.20	0.41	0.73^{+}	−0.30	0.61	0.43	0.05	−0.06	0.55	0.31
Stems — lower half	0.20	0.57	−0.50	0.36	0.40	0.23	0.51	0.11	0.91^{++}	0.20	0.30
Average	0.55	0.42	0.12	0.69^{+}	0.14	0.38	0.53	0.05	0.36	0.39	—
Roots	0.70^{+}	—	—	—	—	—	—	—	—	—	—

$^{+}$ significant at 0.05 level; $^{++}$ significant at 0.01 level.

TABLE 4
Changes in K amount in single plant organs and in whole plant of two lucerne strains of the clone 9 — derived from cv. Hodonínka and 45 — from cv. Košice in the course of 24 h sampling time. The mass of plant organs of the first sample (12 plants) was taken for calculation

Plant organ	K amount in single plant organs and in whole plant [mg per organ/plant]										Dry mass of first sample [g]
	August 19							August 20			
	0500	0600	0800	1000	1200	1400	1600	1800	0500		
Clone 9											
Leaf blades	262	229	271	240	300	242	271	203	295		9.69
Petioles	62	82	69	80	80	77	94	81	72		2.00
Stems — upper half	69	138	93	115	92	108	119	119	70		3.95
Stems — lower half	141	155	109	155	117	137	93	132	120		6.73
Roots	140	148	156	170	174	177	176	182	162		9.58
Whole plants	674	752	698	760	763	741	753	717	719		31.95
Change in K amount	—	+78	−54	+62	+3	−22	+12	−36	+2	Total +157 −112	Difference +45 6.7 %
Clone 45											
Leaf blades	297	273	295	297	313	303	303	245	348		10.18
Petioles	46	58	59	51	61	50	56	58	51		1.38
Stems — upper half	75	106	92	78	101	88	100	129	96		3.46
Stems — lower half	150	183	144	146	108	133	157	190	150		7.21
Roots	147	148	149	175	160	174	198	172	165		9.72
Whole plants	715	768	739	747	743	748	814	794	810		31.95
Change in K amount	—	+53	−29	+8	−4	+5	+66	−20	+16	Total +148 − 53	Difference +95 13.3 %

TABLE 5

Changes of K content during 24 h sampling time expressed as average variation coefficients and average irradiances during experimental days in four experiments performed with 5, 2, 4 and 1 lucerne cultivars. Dark sampling occurred in 2—3 h intervals in two experiments. Insecticide spray was applied 3 days before the day of sampling in the experiment on June 1, 1983

Date of experiment	Number of cultivars	Average PhAR irradiance [W m^{-2}]	Average variation coefficient [%] day	night
August 19, 1982	5	206	15.2	—
June 21, 1984	2	128	12.7	11.6
Sept. 2, 1982	4	112	11.7	—
June 1, 1983 insecticide application	1	209	8.8	8.9

Other three experiments were made with cultivars Pálava, Bobrava and new breeding PŠ and PP/B growing in field conditions (September 2, 1982), with cv. Pálava cultivated in containers (June 1, 1983), with cv. Verco and cv. Euvere growing in field conditions (June 21, 1984). Average irradiance was measured and compared with changes in K content during sampling in overground organs expressed as average variation coefficients (Table 5). The values of variation coefficients of changes in K content decreased together with irradiances. Exception was on the 1st June 1983 when irradiance was high but K changes were low as a result of preceding insecticide application. Similar values of K changes expressed as average variation coefficients were determined by sampling during day and the following night (Table 5).

DISCUSSION

Different methods such as aphid styled technique (PEEL 1975), incision exudation technique (VAN DIE and TAMMES 1975), isolated phloem strands technique (FENSON 1975) also in connection with radioactive traced compounds technique, were used for the study of phloem solute movements in plants. K movement upward through xylem and downward through phloem and its recirculation in connection with transport of important metabolites was proved (BEN ZIONI *et al.* 1971, HALL and BAKER 1972, MENGEL and KIRKBY 1980, PETTERSSON 1984). Phloem transports downward, upward and simultaneously bidirectional are also established in plants (ESCHRICH 1975, PATE 1975).

K transport mediated by recirculation through the xylem — phloem system can pass fluently without irregularities of K distribution in plants. The great differences in K content occurring in lucerne plants in our experiments were probably conditioned by one-way K movement upward and downward in the plant. Such differences cannot be and were not registered by the method mentioned above. Time sampling as well as plant integrity are necessary for that. The time course of changes in K content in different lucerne organs reflects rapid K movement with all features of long distance phloem transport

(PEEL 1975, PLHÁK 1987). This K pulsation was correlated with irradiance. It also occurred in the following dark period but more slowly. Its frequency was 1 to 2 h during light and 3 h during the dark period. CONTI and GEIGER (1982) established that photosynthate transport occurred more intensively during the day than during the night. A number of studies provide evidence that K promotes the translocation of photosynthates, predominantly sucrose (HARTT 1970, MENGEL and HAEDER 1977, DOMAN and GEIGER 1979). HARTT (1970) established that translocation of photosynthates was more dependent on K deficiency than net photosynthetic rate. Similarly transport of photosynthates was more dependent on irradiance than photosynthetic TNS formation (PLHÁK 1983). High ATP/ADP ratio and turnover, Pi incorporation in ATP and ATP-ase activity are detectable in sieve tubes (GARDNER and PEEL 1972, GILDNER and CRONSHAW 1973). It may therefore be assumed that long distance photosynthate transport occurring in sieve tubes is connected in some way with K movement and that the K movement is highly dependent on energy supply.

Rapid changes in K content occurring in overground lucerne organs did not appear in roots. Only moderate increase in K content was observed in the roots during light exposure. When comparing the total K amount in the whole plant, it changed during sampling time. It showed that some part of K content migrated out and into the plant (Table 4). K efflux from barley roots into nutrient solution was established by MENGEL and HAEDER (1971). PETTERSSON (1984) reported the values of K efflux from sunflower roots 1 to 1.49 μmol g^{-1} (f.m.) h^{-1}. In our case an average value of K release during 13 h solar exposure in two lucerne strains reached 1.48 μmol g^{-1} (f.m.) h^{-1}. Our results show that this K efflux can be a result of rapid K movement up and down the plant.

Each sample consists of 10—12 plants and the K content changes reflected an average K movement in all these individual plants. The results show that very similar K movements up and down had to occur at the same time in plants of the same lucerne strain. Time similarities were also established in K movement between some lucerne strains. In other cases similarities as well as differences occurred between lucerne strains and cultivars as in the previous study (PLHÁK 1984). This indicates that K movements in lucerne plants are probably conditioned by external factors such as irradiance and others which cause the time uniformity in K movement. Alternation in time course can be evoked by internal metabolic processes of lucerne genotypes.

REFERENCES

ASHLEY, D. A., GOODSON, R. D.: Effect of time and plant K status on ^{14}C labeled photosynthate movement in cotton. — Crop Sci. **12** : 686—690, 1972.

BARTA, A. L.: Response of symbiotic N_2 fixation and assimilate partitioning to K supply in alfalfa. — Crop Sci. **22** : 89—92, 1982.

BEN ZIONI, A., VAADIA, Y., LIPS, S. H.: Nitrate uptake by roots as regulated by nitrate products of the shoots. — Physiol. Plant. **24** : 288—290, 1971.

DOMAN, D., GEIGER, D. R.: Effect of exogenously supplied foliar potassium on phloem loading in *Beta vulgaris* L. — Plant Physiol. **64** : 528—533, 1979.

COLLINS, M., DUKE, S. H.: Influence of potassium-fertilization rate and form on photosynthesis and N_2 fixation of alfalfa. — Crop Sci. **21** : 481—485, 1981.

CONTI, T. R., GEIGER, D. R.: Potassium nutrition and translocation in sugar beet. — Plant Physiol. **70** : 168—172, 1982.

ESCHRICH, W.: Bidirectional transport. — In: ZIMMERMANN, M. H., MILBURN, J. A. (ed.): Transport in Plants I. Phloem Transport. Pp. 245—255. Springer-Verlag, Berlin—Heidelberg—New York 1975.

FENSON, D. S.: Work with isolated phloem strands. — In: ZIMMERMANN, M. H., MILBURN, J. A. (ed.): Transport in Plants I. Phloem Transport. Pp. 223—244. Springer-Verlag, Berlin—Heidelberg—New York 1975.

GARDNER, D. C. J., PEEL, A. J.: Some observations on the role of ATP in sieve tube translocation. — Planta **107** : 217—226, 1972.

GILDNER, J., CRONSHAW, J.: Adenosine triphosphatase in the phloem of *Cucurbita*. — Planta **110** : 189—204, 1973.

HALL, S. M., BAKER, D. A.: The chemical composition of *Ricinus* phloem exudate. — Planta **106** : 131—140, 1972.

HARTT, C. E.: Effect of potassium deficiency upon translocation of ^{14}C in detached blades of sugarcane. — Plant Physiol. **45** : 183—187, 1970.

MENGEL, K., HAEDER, H. E.: The effect of nitrogen nutritional status of intact barley plants on the retention of potassium. — Z. Pflanzenernähr. Bodenk. **128** : 105—115, 1971.

MENGEL, K., HAEDER, H. E.: Effect of potassium supply on the rate of phloem sap exudation and the composition of phloem sap of *Ricinus communis*. — Plant Physiol. **59** : 282—284, 1977.

MENGEL, K., HAGHPAROST, M. R., KOCH, K.: The effect of potassium on the fixation of molecular nitrogen by root nodules of *Vicia faba*. — Plant Physiol. **54** : 535—538, 1974.

MENGEL, K., KIRKBY, E. A.: Potassium in crop production. — Adv. Agron. **33** : 59—110, 1980.

PATE, J. S.: Exchange of solutes between phloem and xylem and circulation in the whole plant. — — In: ZIMMERMANN, M. H., MILBURN, J. A. (ed.): Transport in Plants I. Phloem Transport. Pp. 451—473. Springer-Verlag, Berlin—Heidelberg—New York 1975.

PEEL, A. J.: Investigations with aphid stylets into the physiology of the sieve tube. — In: ZIMMERMANN, M. H., MILBURN, J. A. (ed.): Transport in Plants I. Phloem Transport. Pp. 171—195. Springer-Verlag, Berlin—Heidelberg—New York 1975.

PETTERSSON, S.: Effects of nitrate on influx, efflux and translocation of potassium in young sunflower plants. — Physiol. Plant. **61** : 663—669, 1984.

PLHÁK, F.: Changes in total nonstructural saccharides content of alfalfa plants during light and dark periods. — Photosynthetica **15** : 122—128, 1981.

PLHÁK, F.: Photosynthetic production, consumption and transport of total nostructural saccharides in alfalfa shoots. — Photosynthetica **17** : 491—498, 1983.

PLHÁK, F.: Diurnal variations of photosynthates, proteins and mineral substances in alfalfa leaves. — Photosynthetica **18** : 338—343, 1984.

PLHÁK, F.: Relation between potassium content and vascular bands volume in overground organs of lucerne. — Acta Univ. Carol. Ser. biol., 1987.

SECER, M.: Der Einfluss des Kaliums auf die Stickstoffmetabolisierung und die Kornproteinbildung bei Sommerweizen. — Kali-Briefe (Büntehof) **14** : 393—402, 1978.

VAN DIE, J., TAMMES, P. M. L.: Phloem exudation from monocotyledonous axes. — In: ZIMMERMANN, M. H., MILBURN, J. A. (ed.): Transport in Plants I. Phloem Transport. Pp. 196 to 222. Springer-Verlag, Berlin—Heidelberg—New York 1975.