PHOTOSYNTHESIS AND CERTAIN MORPHOLOGICAL CHARACTERISTICS OF ALFALFA AS AFFECTED BY POTASSIUM NUTRITION

by

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INTRODUCTION

Alfalfa (Medicago sativa L.) a perennial forage legume, is used extensively because of high yield potentials and good herbage quality. High yields and longevity of stands are frequently limited by low soil potassium. The importance of potassium fertilization has been realized and practiced in alfalfa culture, but beneficial effects of potassium are not clear.

It appears that potassium is partly responsible for either one or both of the following: (1) an increase in the active photosynthetic surface through increased leaf initiation and development, and (2) an increase in rate of carbon dioxide assimilation per unit leaf area. A study of the relationships between potassium nutrition and these two factors should be of value in more clearly elucidating the causes for yield and stand decline under potassium stress. Other closely related factors should also be investigated to better characterize the function of potassium.

The experiments reported here were designed to study the effects of potassium on certain physiological and morphological characteristics of alfalfa.

REVIEW OF LITERATURE

Potassium (K) is essential for growth and reproduction of higher plants which require it in larger quantities than any other metallic cation (McCollum, et al. 1958). Although many studies have been made on the metabolic role of K in plants, it has been difficult to establish specific functions, perhaps in part because of an inability to isolate it in definite metallo-organic combinations. Potassium, a mobile element, is translocated in the xylem and phloem, and occurs in all plant parts, with considerable accumulations in the leaves and meristematic cells (Thomas, 1956).

Potassium for Alfalfa Growth

The critical K content (per cent of dry weight) required for normal growth of alfalfa varies. MacLean and Langille (1958) found that tissue from K-deficient alfalfa stands contained less than 1.0% K. Chandler, et al. (1946) and Bear and Wallace (1950) arrived at values of 1.25 and 1.4%, respectively, for the critical level. The critical K content reported by Stivers and Ohlrogge (1952) was 0.9 to 1.1%, but there was no consistent relationship between yield and K content. According to Gerwig and Ahlgren (1958), there was a seasonal variation in critical content ranging between 1.42 and 1.84% K, and surviving plants had at least 1.0% K. McNaught (1958) found 0.89 and 2.06% K in K deficient and healthy plants, respectively. Blaser (1962) attained maximum alfalfa yields with K contents between 2.0 and 2.5%.

The first manifestation of K deficiency in alfalfa is usually the presence of small whitish dots along leaf edges with yellowing at the tips and edges of older leaflets. As deficiency continues, the yellowing extends over the entire leaf, and margins turn brown and become necrotic, with lower leaf abscission.

Except for conditions where abundant K was naturally supplied from soils, all workers found increased alfalfa yields with K fertilization; the magnitude of increases varied. With nutrient solution cultures, plants responded to K additions up to 64 ppm (Reid, et al., 1965). Bear and Wallace (1950) reported yield increases in nutrient cultures as K content increased up to 3% in the alfalfa.

Potassium Effects on Plant Morphology

Plant height: Potassium fertilization increased height of alfalfa according to Reid, et al. (1965). McNaught (1958) found heights of 25 and 46 cm for deficient and healthy plants, respectively. Hartt (1929) found increased shoot length of sugar cane (Saccharum officinarum L.) with K additions as did Eaton (1952) with sunflower (Helianthus spp.). An average increase of 15.7 cm in shoot length of apple (Malus malus L.) trees with K fertilization has been reported (Warne, 1937).

The importance of alfalfa plant height in solar radiation interception and growth potential has been pointed out by Stanhill (1962). Crop height accounted for 76% of the variation in the fraction of solar radiation reaching the ground. By extending harvest intervals from 31

to 48 days and cutting at 31 instead of 15 cm, the proportion of light utilized by the alfalfa crop was 46 instead of 33%, and potential yield was increased by 18%.

Leaf size: Thomas (1956) stated that K additions to deficient soils generally increased leaf size and number, while Gregory and Baptiste (1936) concluded that only leaf size was increased when barley (Hordeum vulgare L.) received K in sand culture. Warne (1936, 1937), with beet (Beta vulgaris L.) and apple, noted increases in leaf size of 66 and 71%, respectively, and increases in leaf numbers of 87 and 74% with adequate K. He found an increase in epidermal cell size of beet with adequate K, and this has also been observed with buckwheat (Fagopyrum sagittatum Gilib.) and rape (Brassica napus L.) (Lutman, 1934). Work with sugar cane (Hartt, 1929) and sunflower (Eaton, 1952) showed that K deficiency results in smaller leaves. The authors generally agreed that increased leaf size is associated with cell size, not cell numbers.

Stomatal size and frequency: Desai (1937) found that the number of stomata per unit area was little affected by K level with tobacco (Nicotiana tabacum L.), but stomatal aperture was dependent upon this element. Stomata in K-deficient leaves were irregular in distribution as compared with normal leaves. Lutman (1934) found smaller stomata with low K in rape and buckwheat, but there was no difference in beet with K levels. Warne (1936, 1937) reported increases in stomatal frequency per unit leaf area with K deficiency of beet and apple. The increases were attributed to smaller leaves, not increased numbers per leaf.

Physiological Effects of Potassium

Photosynthesis: Apparent photosynthesis of K-deficient tung (Aleurites fordii) seedings was only 65% of the rate for plants with adequate K (Loustalot, et al. 1950). Murata and Osada (1959) concluded that K limits photosynthetic activity in rice (Oryza sativa L.) only when nitrogen and phosphorus are in ample supply. Briggs (1922) showed that the net rate of photosynthetic O_2 release was reduced in K-deficient bean plants (Phaseolus vulgaris L.). This reduction was evident at both low and high light intensities. Potassium deficiency decreased the photosynthetic rate of barley by 15% and increased respiration by 58% as compared with normal plants (Gregory and Richards, 1929). In other studies with barley, Richards (1932) found a close correlation between net CO_2 uptake and K content of severely deficient leaves. This relationship disappeared when the tissue was only moderately K-deficient.

Rabinowitch (1945) concluded that K has a direct effect on photosynthesis. He stated that K additions to the growing medium caused immediate increases in photosynthesis of many species. He considered the reduced rate of photosynthesis as a result of chlorosis to be an indirect effect of K-deficiency. Chlorella cultures deficient in K showed rapid increases in photosynthesis when K was supplied (Hill and Whittingham, 1955). This response occurred before increases in chlorophyll concentration, indicating that K may have been operative with individual enzymes or enzyme systems. Reid, et al. (1965) grew

alfalfa for 20 days with low K and then supplied a K nutrient solution. Plant recovery was rapid; all differences between deficient and normal plants disappeared in 10 days.

The K effects on photosynthesis have been interrelated with plant or leaf age. Ozbun, et al. (1965, 1965a) found that K effects in bean leaves depended upon the growth stage at which the deficiency was induced. With young, K-deficient leaves, CO_2 fixation decreased within a few days, but with mature K-deficient leaves this did not occur for several weeks. They concluded that K plays a significant role during growth and development of leaf cells and that K requirements diminish with age. They also found that deficient leaves usually respired faster than normal leaves. With corn (Zea mays L.) K concentration in leaves of K-stressed plants and not leaf age controlled assimilation rate (Moss and Peaslee, 1965). Similar results were obtained with rice (Murata, 1961) and wheat (Triticum aestivum L.) (Eckstein, 1939). James (1930) suggested that the loss of K is an important casual factor in leaf aging.

Cell division and development: The association of K in cell division and growth was established by several workers (Ozbun, et al., 1965; Lawton, 1954; Berger, 1954; Cooil, 1952; and Warne, 1936). Lubin and Ennis (1964) found that when mutant cells of Eschericha coli were K depleted, cell division and protein synthesis stopped, but ribonucleic acid synthesis continued. This suggests that low K limits cell growth rates by a specific effect on protein synthesis.

Epidermal tissue from which stomata arise is one of the first to become differentiated. Consequently, most stomata are initiated in young leaf buds. However, differentiation may also occur relatively late in the development of the leaf. Epidermal tissue can be found where relatively undifferentiated stomatal mother cells occur close to mature, functioning stomata (Esau, 1960 and Zucker, 1963).

According to Humbert (1963), K-deficient plants had less control over stomatal movements than K enriched plants. Desai (1937) found that stomatal activity of several species as related to moisture and light conditions, was reduced in K-deficient leaves. Fujiwara and Iida (1955) found widest stomatal openings in K-deficient rice leaves, and Eckstein (1939) observed no difference in stomatal openings in wheat with varying K nutrition.

GREENHOUSE EXPERIMENTS

PROCEDURES

Culture Conditions

Alfalfa cuttings from a single Williamsburg variety clone were treated with "Hormo-Root A" to encourage rooting and placed in a "Weblite"[1] medium in December, 1964. The rooting bed was kept at 26 ± 1C with a heating coil beneath the medium. Tap water was applied daily and excellent root initiation occurred within ten days. In January, 1965, two plants were transplanted into 1-gallon glazed crocks filled with thoroughly washed 8-mesh white quartz sand (size 40-ROK). Distilled water was supplied for two days before imposing the K levels. Supplementary light lengthened the photoperiod to approximately 16 hours to stimulate growth.

A sub-irrigation technique described by Meyer and Anderson (1952) and modified by Henderlong (1964) was used, and the plants were irrigated with the nutrient solutions every four hours during the day.

The nutrient solution was Hoagland and Arnon's (1938) minus K solution, second method of substitution. The solution contained the following nutrients (g/l): $Ca(NO_3)_2 \cdot 4\ H_2O$, 1.181; $MgSO_4 \cdot 7\ H_2O$, 0.493; $Ca(H_2PO_4)_2 \cdot H_2O$, 0.1261; H_3BO_3, 0.0025; $MnCl_2 \cdot 4\ H_2O$, 0.0018;

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[1] An expanded shale material from Weblite Corporation, Roanoke, Virginia.

$ZnCl_2$, 0.001; $CuCl_2 \cdot 2 H_2O$, 0.00005; and MoO_3, 0.00008. Iron was supplied from a solution of 5g $FeCl_3$ plus 5g tartaric acid per liter, 1 ml being used per liter of culture solution. The K variables used are given below:

ppm K	gm KCl/l nutrient solution
0	none
1.95	0.0037
7.80	0.0149
195.00	0.3728

Nutrient solutions were renewed weekly, and the crocks were thoroughly flushed with tap and then with distilled water. The pH of the solutions changed from 6.3 to 7.2 on day 0 and day 7 respectively, regardless of the K level.

A randomized block design with four replications was used. The plants were cut to a 3 cm stubble for yields at 1/10 full bloom, regardless of length of growth period, on four dates.

Laboratory and Greenhouse Determinations

On six dates individual leaves of approximately the same age were excised from plants, one replication at a time. The leaves were floated on water in plastic containers, transported to the laboratory, and placed in an environmental control chamber. P_n measurements were then made by the method of Hesketh and Moss (1963), using the technique described by Pearce, et al. (1965).

Three leaves from each K level were placed in an acrylic plastic chamber so that each received full light from a 500 watt reflector flood lamp. Leaf petioles extended from the chamber into a surrounding water bath to maintain a temperature of 22 ± 1C. Air was pushed through the chamber at 0.85 to 1.25 liters min^{-1}, depending on the rate of CO_2 uptake. The maximum light intensity at the leaf surface was about 5,000 ft-c. Light intensities were reduced by wire screening placed between the leaf chamber and the lamp. Leaf area was determined with a compensating mechanical planimeter.

The K contents of oven-dry excised leaves used in P_n determinations and of leaves from entire plant harvests were determined with a Beckman model DU flame spectrophotometer. The rate of leaf accumulation was measured by cutting and subsequent daily counting of all leaves on both plants of each treatment for several regrowths.

After Experiment I, it appeared desirable to study an additional K level, therefore a second experiment was begun.

Williamsburg alfalfa cuttings from one field plant were rooted as in Experiment I. Two-gallon crocks were used to avoid root restriction. The design was as for Experiment I except for adding an additional K treatment (4.88 ppm K; 0.0093 g KCl/l). After approximately four months the same experiment was repeated with newly rooted plants and fresh sand.

P_n and K content were determined in the same manner as previously described. Additional data were obtained on stomatal and epidermal cells. Leaf surface replicas were made on two dates using Sampson's

(1961) silicone rubber technique with modifications by Zelitch (1961). Stomatal and epidermal cell size and number were determined from attached leaves at the various K levels. Varying light conditions were not confounding factors since four replications of each treatment could be obtained within five minutes.

The level to which leaves reduced the carbon dioxide concentration in a closed system (CO_2 compensation point) was determined on two dates at all K levels. The system was essentially the same as that used for studying P_n in Experiment I. After the leaves in the plastic chamber reached maximum photosynthesis at the atmospheric CO_2 concentration and 5000 ft-c, a closed system was used. The same air stream repeatedly passed over the leaf and through the analyzer, giving the rate of CO_2 reduction and the final equilibration level to which it was reduced.

RESULTS

Yield and Potassium Content

Yields of plants grown at 195 ppm K were higher than for other treatments for eight of eleven harvests, Table 1. Differences in yield with zero and 1.95 ppm K were small, while 7.80 ppm gave higher yields than zero K in nine of eleven harvests.

It appears that yields in both experiments increased with K content of leaves up to some value between 1.35 and 3.74% K, Table 1 and 2. Yields were positively correlated with K content in all but

Table 1. Effect of potassium nutrition on yield (gm/pot) of alfalfa.

K Applied (ppm)	Experiment I Harvest Date					Experiment II Harvest Date							
	1-15	2-13	3-17	4-9	Average	8-14	9-14	10-23	11-17	12-17	1-14[2]	2-22	Average
0	0.99a[1]	1.23	3.91a	3.49a	2.41	3.12a	1.64a	2.17a	1.61a	1.69a	0.95a	0.34a	1.65
1.95	1.67a	1.38	6.84b	5.18ab	3.77	6.37ab	2.71ab	3.53ab	2.33ab	3.09ab	1.28a	1.91b	3.03
4.88	--	--	--	--	--	9.05b	4.63bc	5.38bc	2.67ab	2.41ab	1.05a	1.96b	3.88
7.80	2.61b	1.56	7.65bc	6.85b	4.67	9.29b	6.11c	7.19c	3.63b	3.63b	1.15a	1.75b	4.68
195.00	4.88c	1.06	8.96c	12.00c	6.73	15.34c	11.11d	13.68d	6.69c	6.37c	1.41b	2.25b	8.12

[1] Means in each column followed by the same letter are not significantly different at the .05 level.

[2] New plants and culture sand installed on December 19, 1965.

Table 2. Effect of potassium nutrition on potassium content (%K) of alfalfa leaves.

K Applied	Experiment I Harvest Date					Experiment II Harvest Date							
(ppm)	1-15	2-13	3-17	4-9	Average	8-14	9-14	10-23	11-17	12-17	1-14[1]	2-22	Average
0	0.76	1.67	0.70	0.85	1.00	0.68	0.81	0.61	0.89	1.08	0.79	0.68	0.79
1.95	0.93	2.12	0.65	0.81	1.13	0.66	1.06	0.74	0.96	1.57	1.02	0.84	0.95
4.88	--	--	--	--	--	0.78	0.97	0.80	1.09	1.54	1.14	1.02	1.05
7.80	1.23	2.39	0.93	1.13	1.43	0.89	1.05	0.79	1.21	1.84	1.48	1.60	1.27
195.00	4.74	4.97	3.58	3.95	4.31	2.64	3.45	3.16	3.29	3.68	3.61	3.05	3.27

[1] New plants and culture sand installed on December 19, 1965.

one harvest, Table 3. Variations in yield due to regrowth periods make comparisons among harvests within each experiment difficult. Also, light intensity and duration during the course of each experiment changed markedly.

Net Photosynthesis

There were significant increases in P_n of individual leaves with added K on four of six dates (Experiment I, Table 4). On the first two dates, K in leaves from the no K treatment was relatively high, and this probably accounted for the lack of differences. On dates when differences existed, P_n reductions occurred when the plants received 1.95 or less and 4.88 ppm or less K in the first and second experiments, respectively. The high K treatment did not cause large increases in P_n as compared with lower rates of 4.88 and 7.80 ppm. Generally, in four of the six determinations (Experiment I), P_n increased with added K, as indicated by the correlation coefficients in Table 5.

In Experiment II there was a significant difference in P_n with K nutrition in four of five trials, Table 4. A comparison of zero and 195 ppm K treatments on four dates when relationships were significant reveals that P_n was reduced by an average of 9.23 mg CO_2 dm^{-2} hr^{-1} with low K. P_n rates at the other three K levels were generally intermediate between the two extremes. A critical value for K content is not evident since % K fluctuated for treatments, Table 6. Correlation

Table 3. Linear correlation coefficients (r values)[1] and standard errors of estimate (Se) for relationships between yield and potassium content (%K) of alfalfa.

	Experiment I				Experiment II						
	Harvest Date				Harvest Date						
	1-15	2-13	3-17	4-9	8-14	9-14	10-23	11-17	12-17	1-14[2]	2-22
r value	.88	.33NS[3]	.67	.90	.53	.73	.86	.69	.66	.54	.31NS
Se	.79	.38	1.57	1.58	4.60	2.71	2.36	1.64	1.78	3.16	.88

[1] Correlation coefficients for quadratic relationships (not listed) were not significantly higher, .05 level, than for linear.

[2] New plants and culture sand installed on December 19, 1965.

[3] NS indicates correlation not significant. All other correlations significant at .01 level.

Table 4. Effect of potassium nutrition on P_n (mg CO_2 dm^{-2} hr^{-1}) of alfalfa.

K Applied (ppm)	Experiment I						Experiment II				
	Determination Date						Determination Date				
	2-6	2-26	3-16	3-29	4-6	4-22	8-3	9-4	9-13	2-18	2-21
0	23.50	25.19	22.29a[1]	30.97a	26.25a	27.54a[2]	9.08a	27.92a	25.95a	28.92b	11.42
1.95	26.71	21.50	23.62a	34.28a	27.05a	25.66a	14.74b	31.47a	28.19a	24.09a	12.75
4.88	--	--	--	--	--	--	15.73b	35.94b	33.28b	37.72d	16.46
7.88	29.95	25.69	24.65ab	39.43b	35.97b	29.68ab	16.42b	31.48a	32.06b	33.33c	17.61
195.00	24.96	22.15	26.85b	35.18ab	33.19b	31.87b	17.61b	36.73b	37.30c	37.16cd	16.54

[1] Means in each column followed by the same letter are not significantly different at the .05 level.

[2] Means in column followed by the same letter are not significantly different at the .10 level.

Table 5. Correlation coefficients (r values) and standard errors of estimate (Se) for relationships between P_n (mg CO_2 dm^{-2} hr^{-1}) and potassium content (% K) of alfalfa.

	Experiment I						Experiment II				
	Determination Date						Determination Date				
	2-6	2-26	3-16	3-29	4-6	4-22	8-3	9-4	9-13	2-18	2-21
Linear r value	.07NS[1]	.22NS	.68[3]	.01NS	.29NS	.49NS	.52[2]	.39NS	.65[3]	.51[2]	.25NS
Se	5.09	4.13	1.75	5.17	6.21	3.72	3.14	4.51	4.05	4.12	4.25
Quadratic r value	.50[2]	.39NS	.69[3]	.01NS	.55[2]	.50[2]	.61[3]	.41NS	.71[3]	.59[3]	.33NS
Se	4.59	4.04	1.78	5.37	5.65	3.83	3.00	4.62	3.88	3.97	4.28

[1] NS indicates correlation not significant.

[2] Correlation significant at .05 level.

[3] Correlation significant at .01 level.

Table 6. Effect of potassium nutrition on potassium content (%K) of individual leaves used for P_n determinations.

K Applied (ppm)	Experiment I Determination Date						Experiment II Determination Date				
	2-6	2-26	3-16	3-29	4-6	4-22	8-3	9-4	9-13	2-18	2-21
0	1.49	1.22	0.56	0.76	0.52	0.85	0.67	0.96	0.45	0.45	0.46
1.95	1.91	1.34	0.50	0.62	0.70	0.80	0.98	1.27	0.65	0.66	0.55
4.88	--	--	--	--	--	--	1.16	1.05	0.62	0.82	0.67
7.80	2.71	1.52	0.80	0.76	0.96	0.95	1.21	1.09	0.80	0.83	0.83
195.00	4.44	4.12	3.50	3.62	3.53	4.69	3.28	3.24	3.11	3.02	2.39

coefficients show a positive relationship between K content and P_n on three of the five dates, Table 5.

On most dates where differences existed, the correlation coefficients between K content and P_n were higher for quadratic than linear analysis, indicating that a straight-line relationship did not exist. This is exemplified in Figure 1 where linear r = .52 (significant at .05 level) and quadratic r = .61 (significant at .01 level). Per cent K in leaves is plotted against P_n, irrespective of K treatments. There was a rather sharp increase in P_n with increased K up to about 2 to 2.5%, with little increase as K increased to about 4%. P_n was relatively low on this as compared with other dates, probably because of advanced plant age.

Light response curves for various K contents on one date are presented in Figure 2. Potassium at 195 ppm gave an increase of approximately 11 mg CO_2 dm^{-2} hr^{-1} compared with no K, and the other treatments gave P_n rates intermediate between the two extremes. Light saturation apparently occurred at lower light intensities with low as compared with high K. The K rates tend to converge between 500 and 1000 ft-c and all have a similar light compensation point of 100 ft-c. The quadratic correlation coefficient, .71, for the relationship between P_n and K content on this date is significant at the .01 level.

P_n and yield relationships for data collected on similar dates are shown in Figure 3. It is apparent that higher P_n rates increased dry matter accumulation, the correlation coefficient being .67.

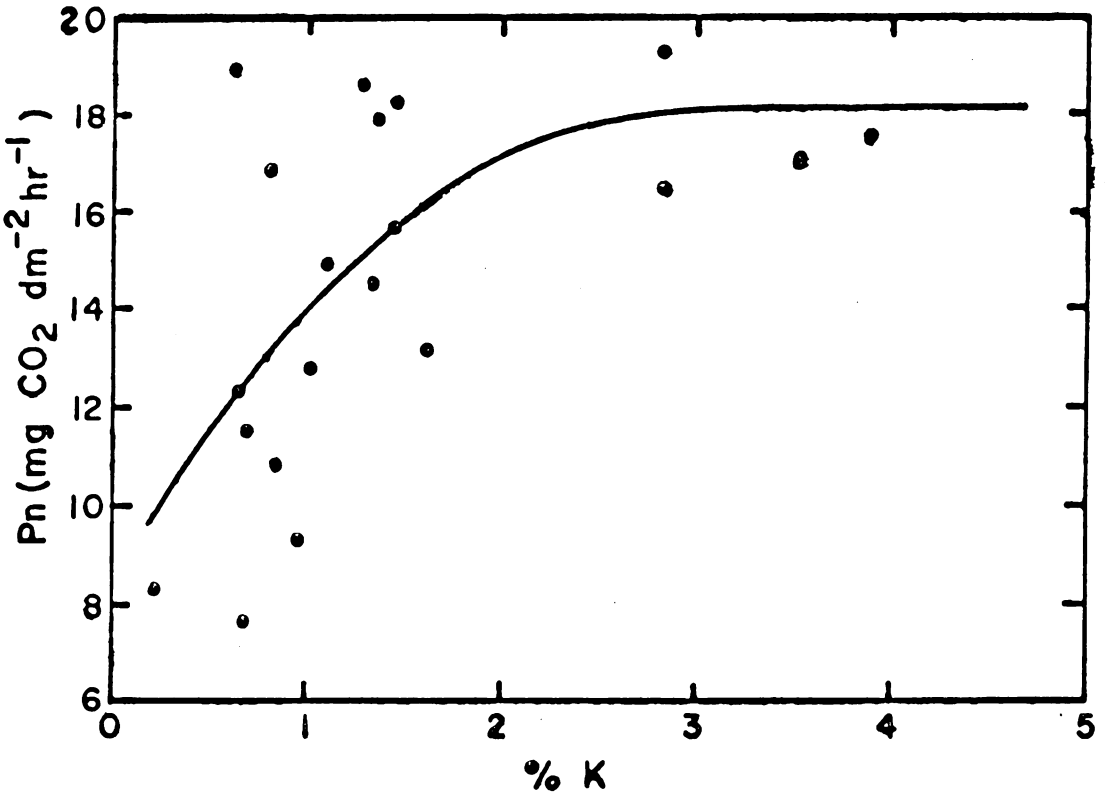

Figure 1. Effect of potassium content in leaves on P_n, correlation coefficient = 0.61 (determinations on August 3, 1965).

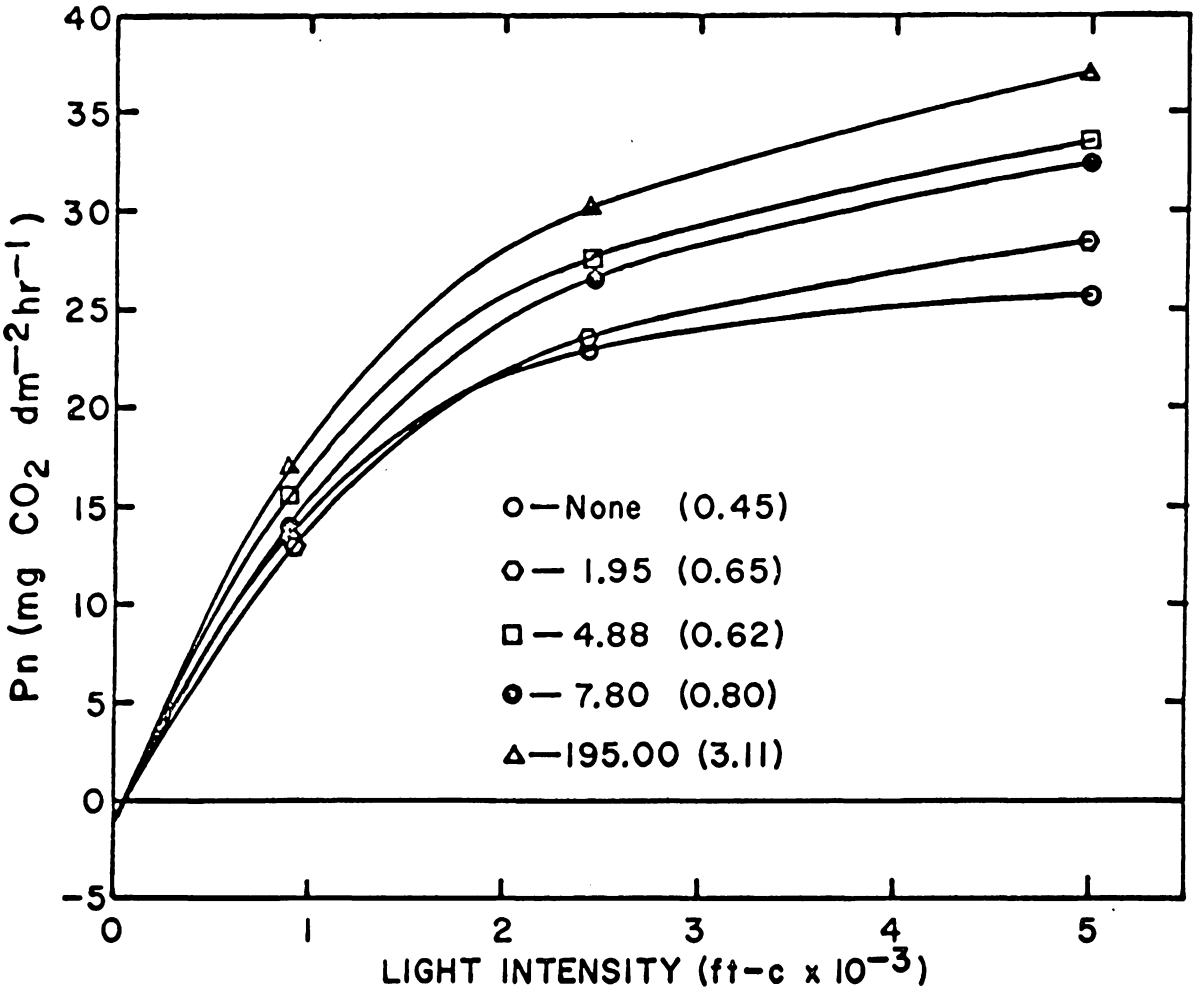

Figure 2. Effect of potassium supply (ppm) on P_n of leaves. Numbers in parenthesis are % potassium in leaves (average of 4 replications on Sept. 13, 1965).

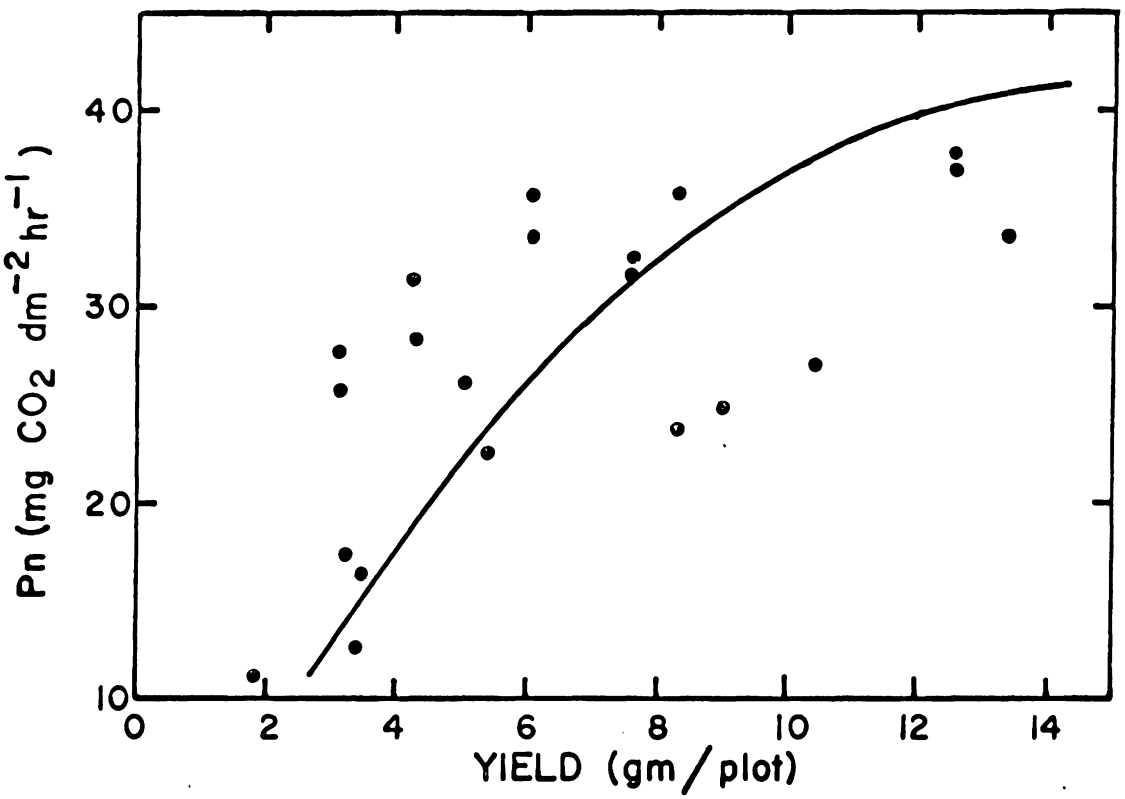

Figure 3. Relationship between P_n and yield, correlation coefficient = 0.67.

Preliminary work with leaves of different ages indicates that extreme care should be taken in selecting leaves for CO_2 uptake to avoid leaf age by K interactions. It appears that excised leaves were representative of the leaf population for each K treatment within $\pm$ 0.1% K, ($r = .92$).

Carbon Dioxide Compensation Point

Leaves from K plants reduced the CO_2 concentration of air to approximately 95 ppm as compared with 138 ppm for leaves from no K plants on February 21, Figure 4. Differences among K treatments were small. On March 8, all leaves had a much lower CO_2 compensation point, but the differences between minus K and the other treatments were small, Figure 5. Potassium concentrations in all leaves were much higher on this than the previous date.

Plant Morphology

The rate of leaf accumulation increased with K levels, Figure 6 (Experiment I). After several days of slow leaf formation, leaves at the highest K level began accumulating very rapidly. Maximum accumulation rates occurred at similar periods for the treatments. During 4-13 to 4-14, 10 leaves were initiated on the two zero K plants, while approximately 24 appeared with 195 ppm K. Values for the other two K levels were intermediate.

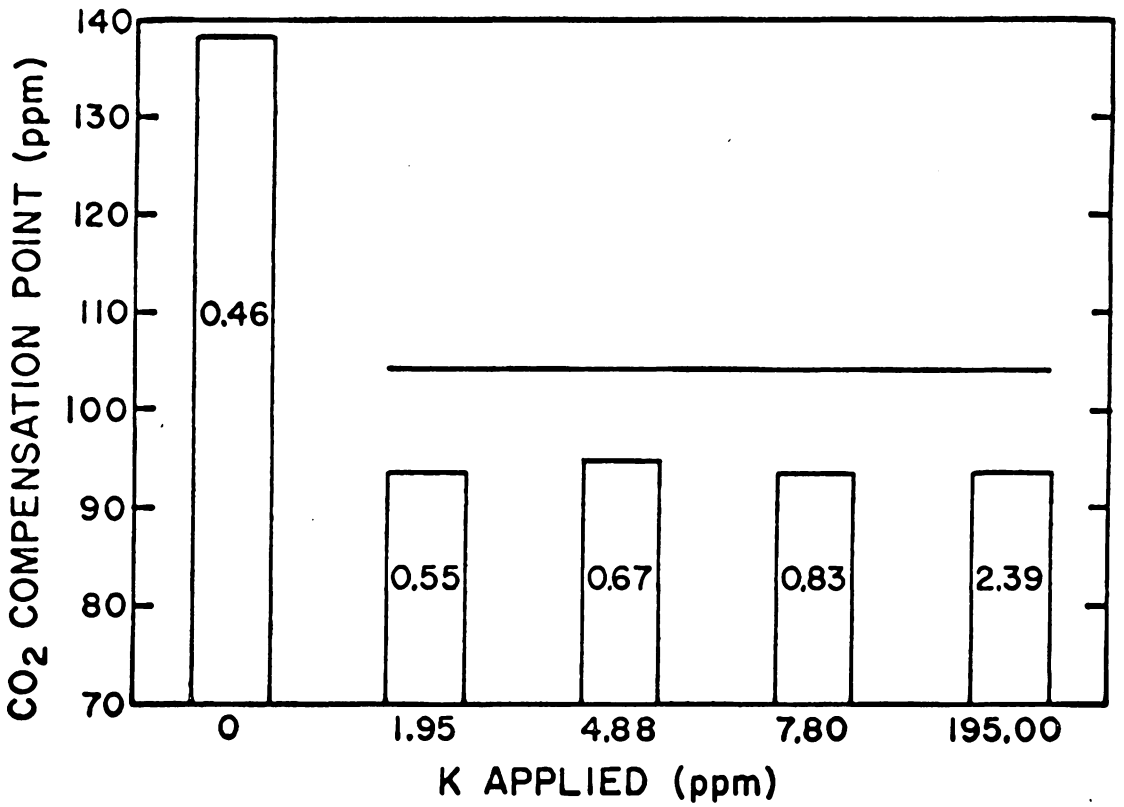

Figure 4. Effect of potassium nutrition on CO_2 compensation points of alfalfa leaves. Numbers within bars are % potassium in leaves. Bars covered by the line are not significantly different at the .05 level (determinations on Feb. 21, 1966).

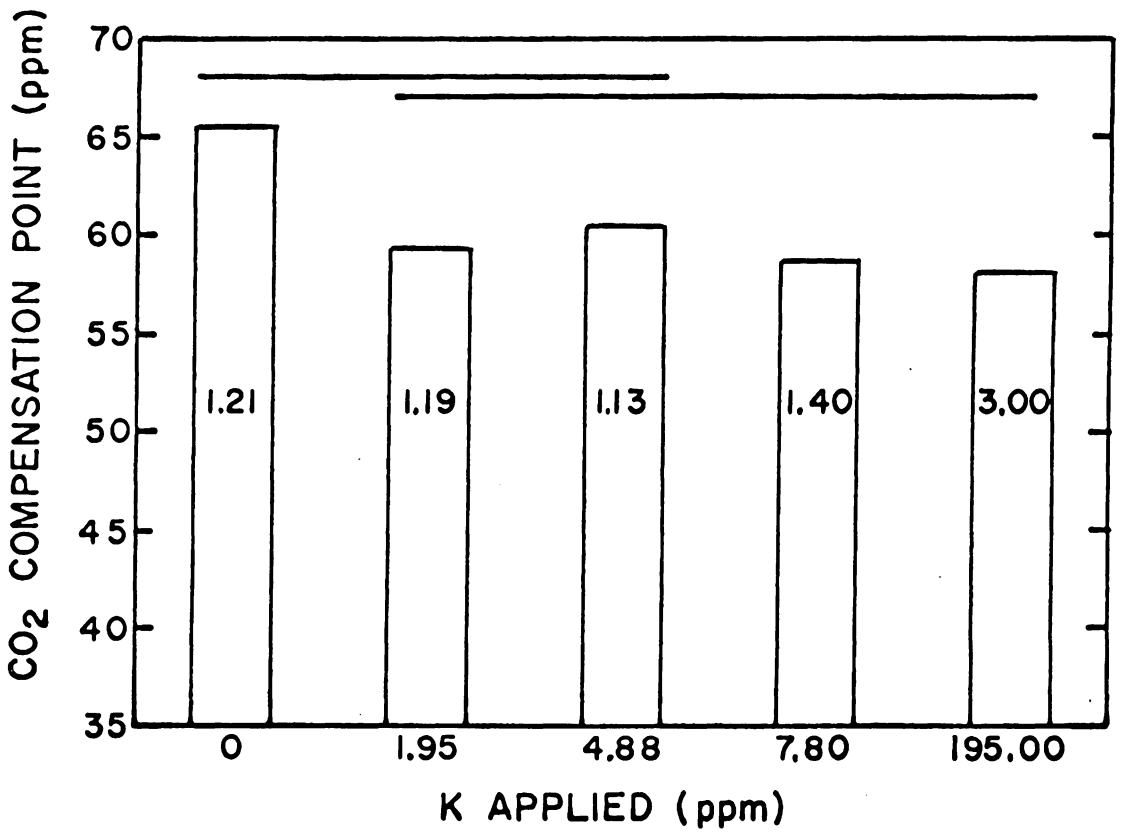

Figure 5. Effect of potassium nutrition on CO_2 compensation points of alfalfa leaves. Numbers within bars are % potassium in leaves. Bars covered by the same line are not significantly different at the .05 level (determinations on March 8, 1966).

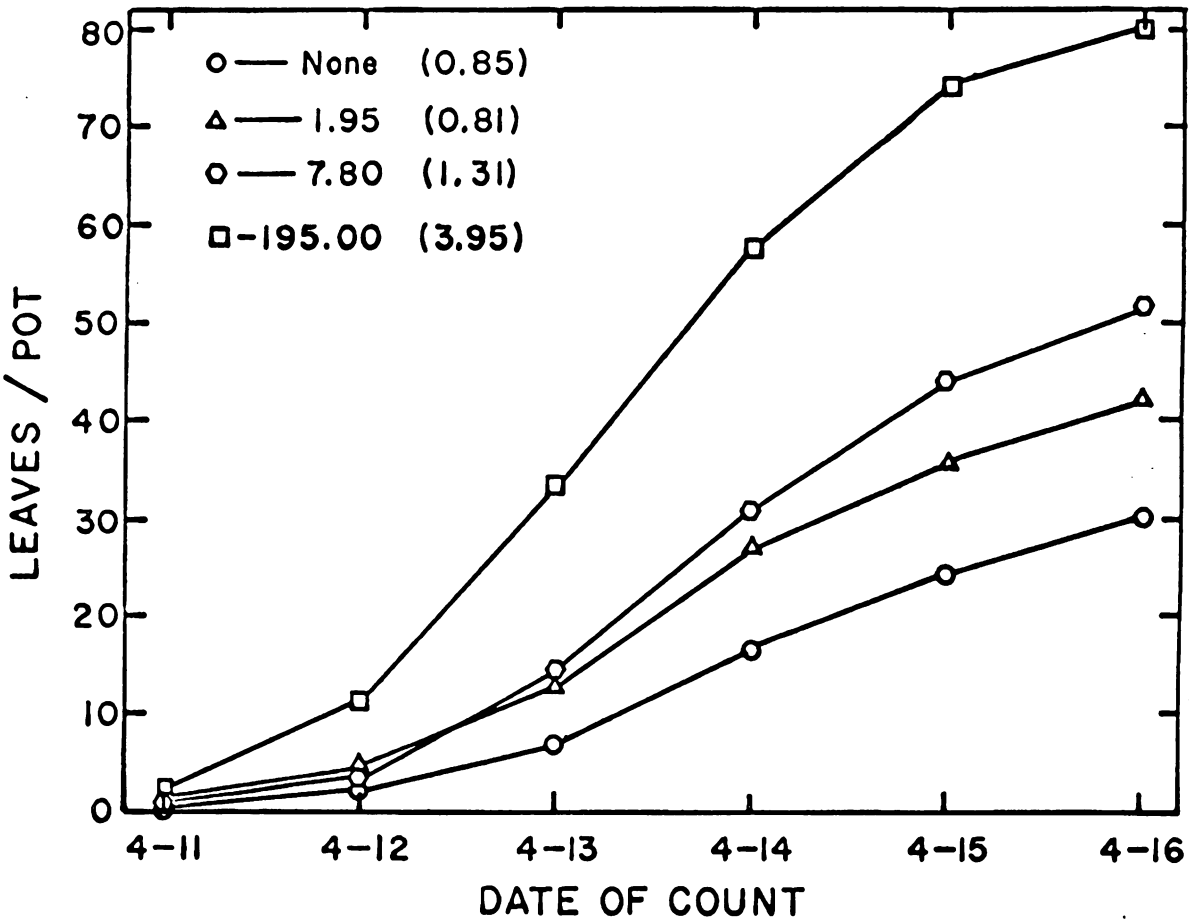

Figure 6. Leaf accumulation rates at various potassium levels after complete removal of leaves on April 9, 1965. Numbers in parenthesis are % potassium in leaves.

In Experiment II, the higher K levels caused significant increases in leaf number (Table 7); the accumulation rates were similar to those for Experiment I (Figure 6). The average number of leaves after 17 days regrowth was 42.5 for no K and 90.2 for 195 ppm K; other K levels were between these two extremes.

Leaf size and plant height increased with added K. Height increases were attributed primarily to internode elongation, not increased number of internodes. Calculations of average leaf area to leaf weight ratio reveal that leaves grown with adequate K were heavier per unit area than those with low K. No K leaves averaged 4.18 and 195 ppm K leaves 3.28, on a dm^2 gm^{-1} basis.

Stomata per unit leaf area increased significantly ($r = .54$) as K content increased up to about 2% K in the leaves, Figure 7. Potassium in nutrient solutions of 4.88 ppm and above gave more stomata per unit area than the two lowest K levels, Table 8.

Stomatal apertures increased significantly as % K in the leaves increased ($r = .77$), Figure 8. Stomatal apertures for leaves receiving 195 ppm K were higher than for all other K treatments, and those with 4.88 and 7.80 ppm were higher than for no K. High K caused an average stomatal aperture increase of 23.5 u^2 over no K. High K gave more and larger cells per leaf than no K, Table 8. The increase in number of stomata with increasing epidermal cell size is shown in Figure 9, indicating that greater stomatal differentiation and development occurred at the higher K levels. Relative sizes of stomata and epidermal cells can be seen in Figures 10 and 11.

Table 7. Effect of potassium nutrition on number of leaves per pot following complete defoliation.

K Applied (ppm)	Experiment I Days After Cutting 13	Experiment II Days After Cutting 17	17	17	17	Average
0	30.5a[1]	46.8a	56.0a	36.4a	30.6a	42.5a
1.95	42.8ab	63.8ab	84.6b	80.6b	38.6a	66.6b
4.88	--	74.3ab	64.5ab	100.0b	101.0b	84.0bc
7.80	52.0b	71.0ab	80.0b	97.8b	82.0b	82.7bc
195.00	80.5c	88.5b	84.0b	96.2b	91.6b	90.2c

[1] Means in each column followed by the same letter are not significantly different at the .05 level.

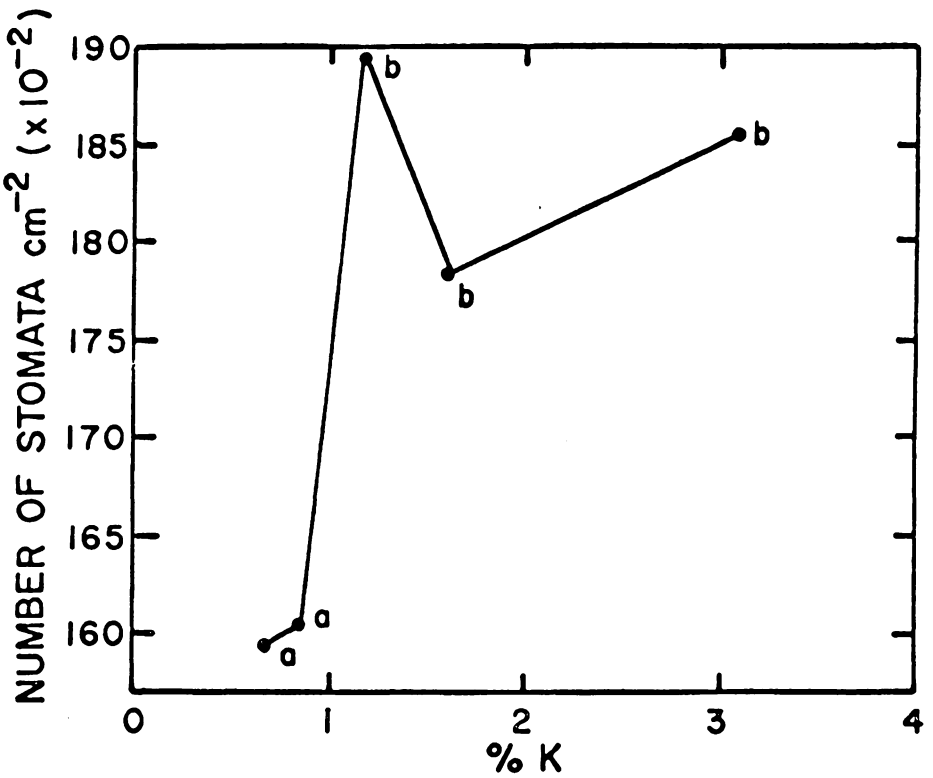

Figure 7. Effect of potassium content of leaves on number of stomata. Points with the same letter are not significantly different at the .05 level.

Table 8. Effect of potassium nutrition on certain leaf characteristics of alfalfa (Leaves 33 days old).

K Supplied (ppm)	No. Stomata $cm^{-2} \times 10^{-3}$	Stomatal Aperture (μ^2)	No. Epidermal Cells cm^{-2} ($X 10^{-3}$)	No. Epidermal Cells $Leaf^{-1}$ ($X 10^{-3}$)
0	15.83a[1]	42.0a	98a	138a[2]
1.95	16.17a	47.0ab	---	---
4.88	19.00b	51.0b	---	---
7.80	18.00b	52.0b	---	---
195.00	18.50b	65.5c	82b	173b

[1] Means in each column followed by the same letter are not significantly different at the .05 level.

[2] The two means are significantly different at the .10 level.

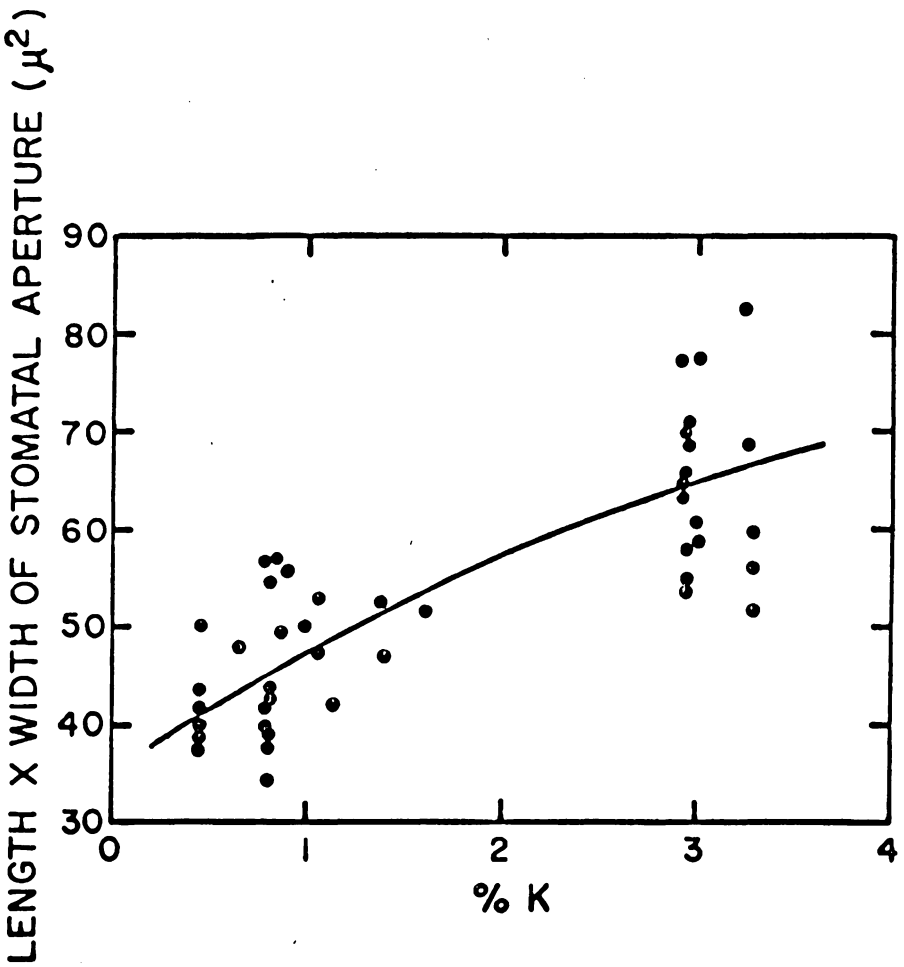

Figure 8. Effect of potassium content of leaves on stomatal aperture, correlation coefficient = 0.77.

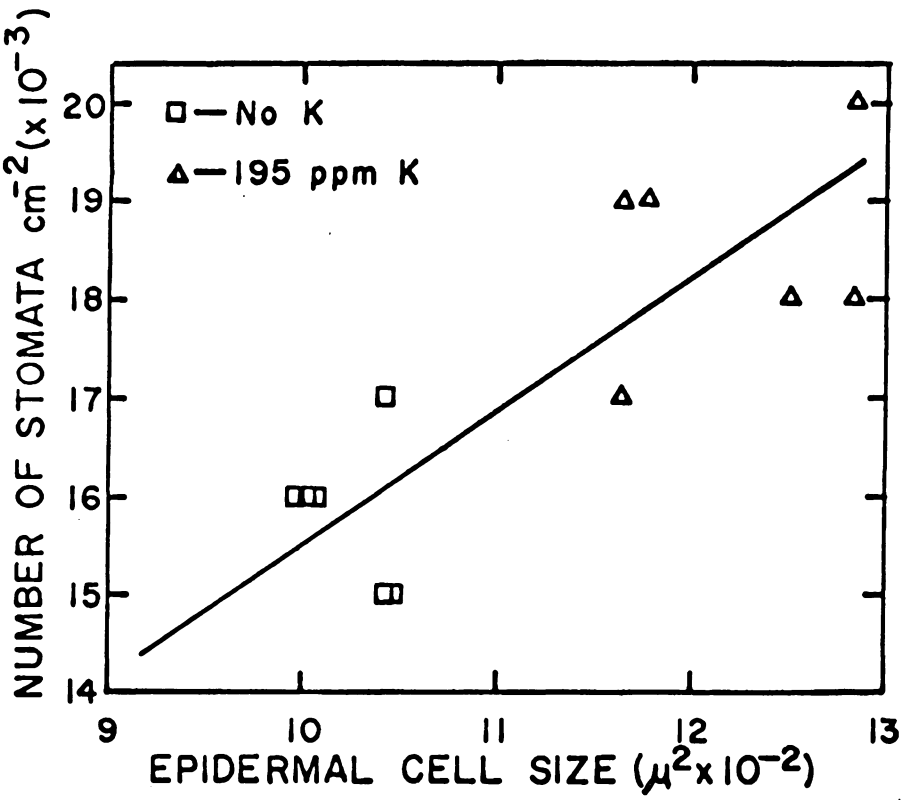

Figure 9. Number of stomata as related to epidermal cell size in alfalfa leaves.

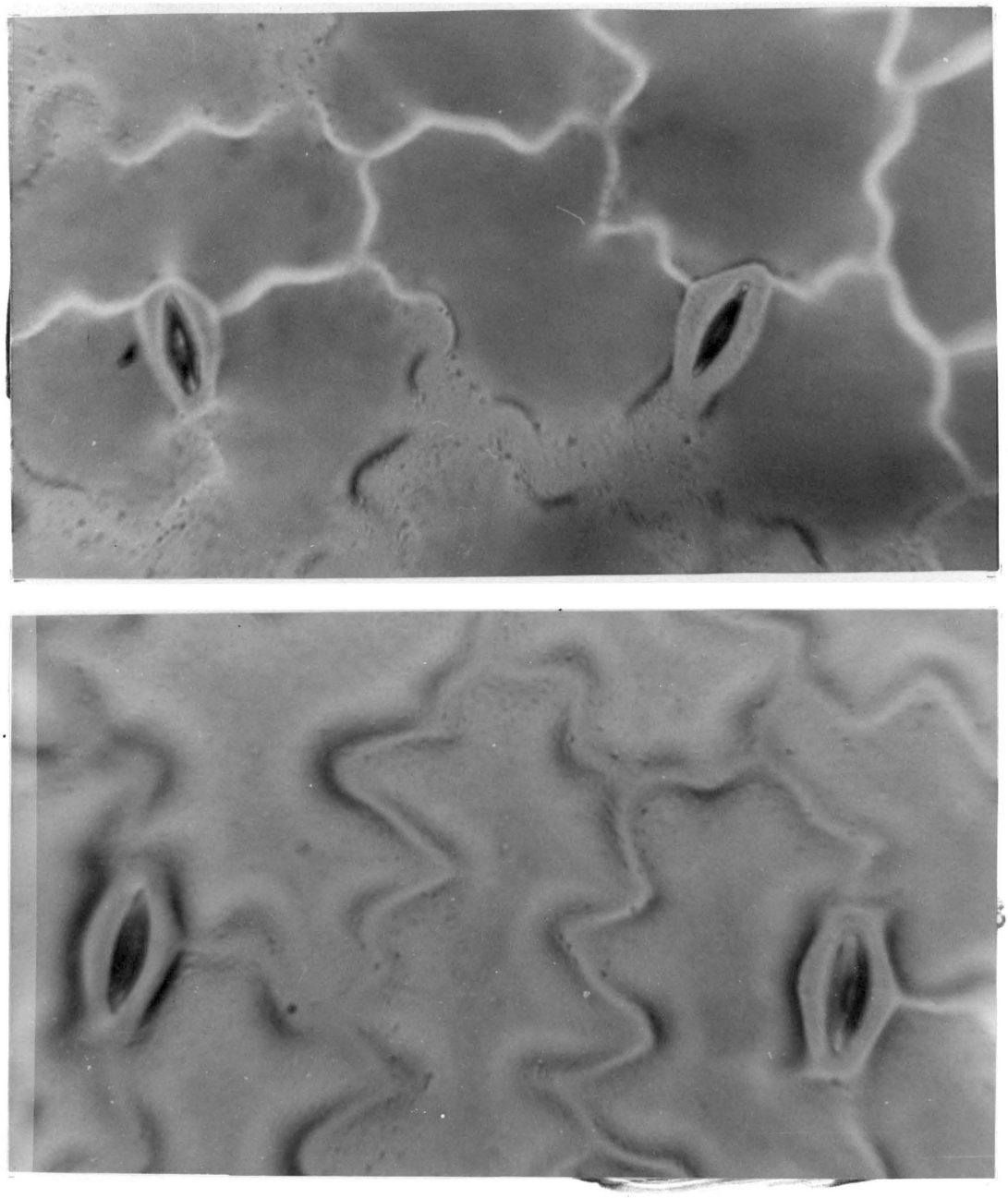

Figure 10. Photomicrographs of epidermis replicas for leaves deficient in K (upper view) and leaves from plants receiving 195 ppm K (X 900).

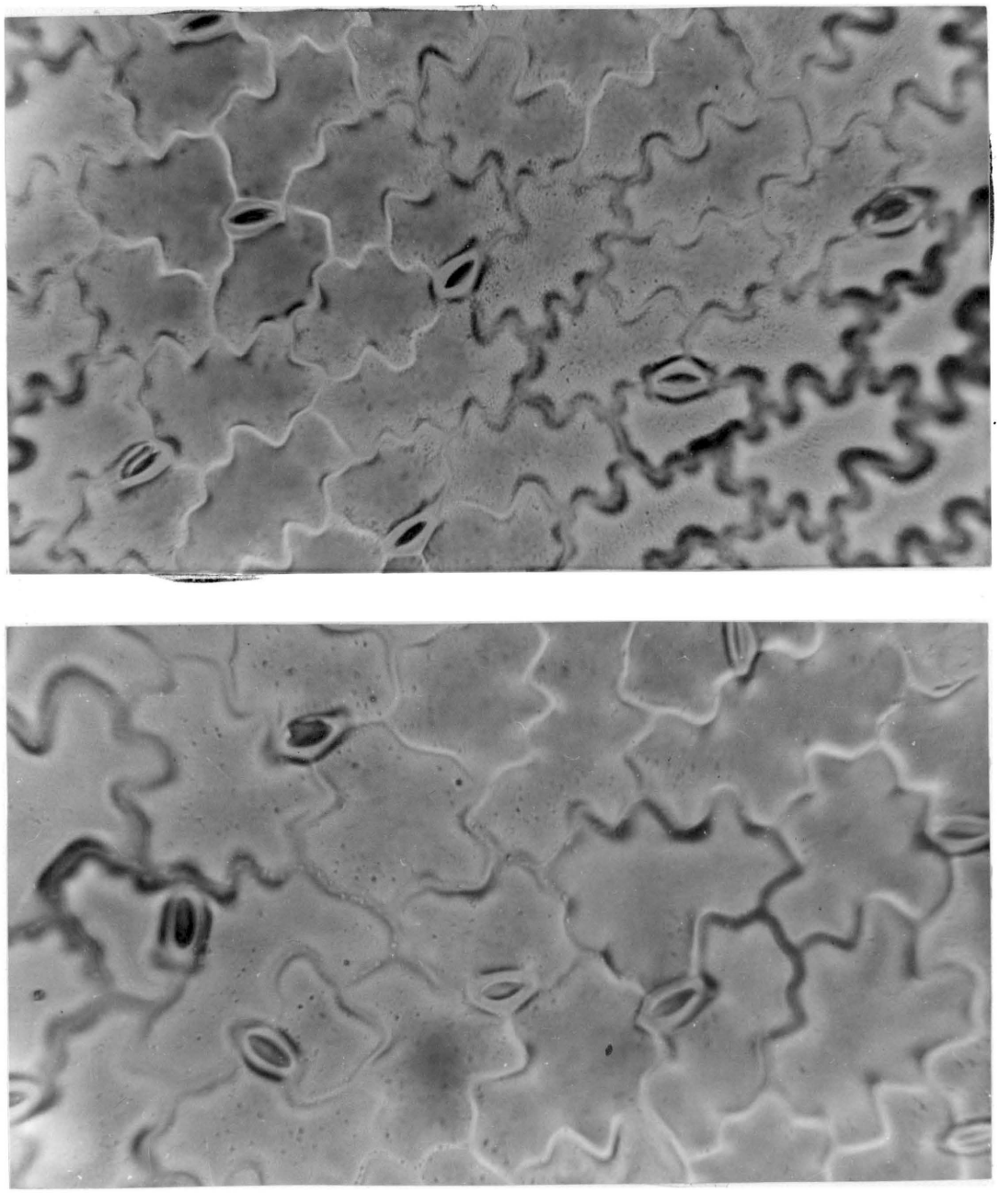

Figure 11. Photomicrographs of epidermis replicas for leaves deficient in K (upper view) and leaves from plants receiving 195 ppm K (X 430).

FIELD EXPERIMENT

Procedures

Plots were formed by cylinders (46 cm long X 61 cm diameter) cut from 55 gallon drums. The cylinders were placed in the ground with a 10 cm rim above the surface and were sealed from underlying soil with heavy plastic sheets. A "C" horizon colluvial Hiwassee soil material low in K (35 lb. K_2O per acre) was mixed with equal proportions of industrial grade sand and placed in the cylinders. One ton of lime and 200 lb. of P_2O_5 per acre were incorporated into the top 10 cm of soil. The plots were seeded with Williamsburg alfalfa in April, 1965. After establishment plants were thinned to 125 per plot.

In July, after cutting to four cm, four K levels, 0, 25, 75, and 300 lb. K_2O per acre, were applied. The 300 lb. rate was split into two equal applications. Three plots of each K level were cut at 1/10 full bloom stage (old foliage) and three were cut when 1/2 as old (young foliage). The treatments were arranged in a completely randomized design with three replications. Potassium was applied as murate of potash and was thoroughly watered into the soil. A minor element concentrate containing 6.0% Fe, 9.0% Mn, 3.0% Cu, 2.0% B, 3.0% Zn, 0.5% Mo, and 0.4% Mg was applied (1 oz. in 6½ gal. H_2O per 250 $ft.^2$).

P_n was measured with the open system technique described by Pearce, et al. (1965) and the differential CO_2 method of Hesketh and Moss (1963). Two clear plexiglass chambers, 24 inches high for mature

stands and 12 inches high for immature stands, were used. These chambers were equipped with a fan and cooling coil to control temperature and circulate air and were fastened to the barrel rims by a rubber band. Air was drawn from a 500 gallon mixing tank through plastic tubing and pushed through the chamber at a rate of 150 l min^{-1} by an air pump. Temperature was controlled at 25 $\pm$ 1C.

To determine leaf area, several stems were taken at random from each plot and the area of random leaves from each stem was measured with a photoplanimeter described by Wilfong (1966). Leaf area within each plot was calculated from average leaf size and leaf number.

The K content of oven-dry leaf samples was determined with a Beckman model DU flame spectrophotometer. P_n of excised leaves was determined on two dates for each stage of maturity in the manner described for greenhouse Experiment I.

RESULTS

Initial yields (July 17) indicated fairly uniform plots prior to K applications, Table 9. Higher yields were obtained in three of five harvests with 300 lb. of K_2O than with other rates. Yields for the first three rates did not differ. Leaf K content was 1.2% or higher, even on control plots, and the first three K rates affected content only slightly (Table 10). Potassium content at the high K rate was significantly higher than at the others in four harvests, and there was a significant positive correlation between K content and yield in all harvests after applying K (Table 11).

Table 9. Effect of potassium fertilization on dry matter yield (gm m^{-2}).

K_2O Applied (lb/A)	Young Foliage Date				Old Foliage Date		
	7-17[1]	8-6	9-6	10-3	7-17[1]	8-30	9-29
0	213	111a[2]	119a[2]	66	236	335	174a[3]
25	225	123a	152a	77	229	283	202a
75	199	139a	138a	86	211	303	210a
300	230	158b	182b	92	247	383	250b

[1]Initial harvest at 1/10 full bloom before K application.

[2 & 3]Means in each column followed by the same letter are not significantly different at the .10 and .05 levels, respectively.

Table 10. Effect of potassium fertilization on potassium content (% K) of leaves.

K_2O Applied (lb/A)	Young Foliage Date			Old Foliage Date	
	8-6	9-6	10-3	8-30	9-29
0	1.69a[1]	1.63a[1]	2.13a[1]	1.20a[2]	1.63a[1]
25	1.95a	1.84ab	2.15a	1.51ab	1.72a
75	1.90a	1.97b	2.47b	1.45ab	1.82a
300	2.49b	2.72c	3.27c	1.79b	2.97b
Plant age (days)	20	31	28	44	30

[1 & 2]Means in each column followed by the same letter are not significantly different at the .01 and .05 levels, respectively.

Table 11. Quadratic correlation coefficients (r values) and standard errors of estimate (Se) for relationships between potassium content and yield, respiration, P_n, and height.

Factor Studied		Young Foliage Date 8-6	Young Foliage Date 9-6	Young Foliage Date 10-3	Old Foliage Date 8-30	Old Foliage Date 9-29
Yield (gm m^{-2})	r	.56[2]	.73	.77	.76	.87
	Se	10.53	7.04	3.39	11.45	5.31
Respiration (mg CO_2 m^{-2} land area hr^{-1})	r	--	.91	.58	--	.84
	Se	--	1.86	3.09	--	2.15
Height (cm)	r	.74	.66	.74	.85	.41[2]
	Se	3.20	6.04	3.20	5.09	8.04
P_n[3] (excised leaves mg CO_2 dm^{-2} hr^{-1})	r	.80	.58[2]	--	.59[2]	.26NS[1]
	Se	2.31	4.07	--	5.34	6.87

[1] NS indicates correlation not significant.

[2] Correlation significant at the .05 level, other coefficients significant at the .01 level.

[3] P_n measurements for stands cut on 8-6, 9-6, 8-30, and 9-29 were made on 8-4, 9-3, 8-15, and 9-17, respectively.

A trend for leaf area index (LAI) to increase with K application was significant at two harvests for young foliage, Table 12. Plant height increased with added K, Table 13, and the height differences increased with plant age. Relationships between leaf K content and plant height were highly significant on all dates, Table 11. Total number of leaves per m^2 (ground area) increased with K fertilization at the last harvest for both stages of maturity, Table 14. Leaf size increased from approximately 3 cm^2 at 1.15% K to 4.5 cm^2 at 3.0% K, figure 12.

Significant increases in P_n (mg CO_2 m^{-2} land area hr^{-1}) with K application were obtained on one date only, Table 15. Figure 13 shows the relationship between P_n and LAI with values for K levels averaged. It is evident that smaller leaf areas in young foliage gave P_n rates comparable to those of higher leaf areas with old foliage. Respiration (mg CO_2 m^{-2} land area hr^{-1}) was correlated positively with leaf K content, Table 11.

There was a linear decrease in NAR (mg CO_2 dm^{-2} leaf area hr^{-1}) with increasing LAI, Figure 14 ($r = -.75$). P_n determinations of individual leaves taken from young foliage differed with K level, Table 16. Increases of 5.75 and 6.89 mg CO_2 dm^{-2} hr^{-1} were obtained with 300 lb. K_2O over no K on two dates. Correlation coefficients for relationships between P_n and leaf K were significant on three dates. Representative light response curves for individual leaves are shown in Figure 15. The correlation coefficient for relationships between

Table 12. Effect of potassium fertilization on LAI.

K_2O Applied (lb/A)	Young Foliage			Old Foliage	
	Date			Date	
	8-6	9-6	10-3	8-30	9-29
0	2.51	2.07a*	1.16a	4.49	2.80
25	2.62	2.68ab	1.44ab	4.11	3.55
75	3.03	2.65ab	1.72bc	4.07	3.24
300	3.27	3.17b	1.95c	5.93	4.03

*Means in each column followed by the same letter are not significantly different at the .05 level.

Table 13. Effect of potassium fertilization on plant height (cm).

K_2O Applied (lb/A)	Date		
	9-6	9-29	10-3
0	25.4a*	32.2a	13.1a
25	30.9b	35.6ab	18.6b
75	30.5b	37.3bc	18.6b
300	36.4c	40.2c	20.7b

*Means in each column followed by the same letter are not significantly different at the .05 level.

Table 14. Effect of potassium fertilization on leaf number per m^2.

K_2O Applied	Young Foliage			Old Foliage	
	Date			Date	
(lb/A)	8-6	9-6	10-3	8-30	9-29
0	5396	5245	3087a*	16702	6557a
25	5362	6650	3618ab	14924	7136a
75	6908	6424	4228bc	13197	8017ab
300	7417	7177	4468c	16106	9315b

*Means in each column followed by the same letter are not significantly different at the .05 level.

Table 15. Effect of potassium fertilization on P_n (mg CO_2 m^{-2} land area hr^{-1}) of alfalfa.

K_2O Applied	Young Foliage			Old Foliage	
	Date			Date	
(lb/A)	8-6	9-6	10-3	8-30	9-29
0	4431a*	5391	2611	5096	4842
25	4345a	6134	2920	5514	5154
75	5106ab	5003	3060	4369	5062
300	5802b	5415	3396	3941	5658

*Means in each column followed by the same letter are not significantly different at the .10 level.

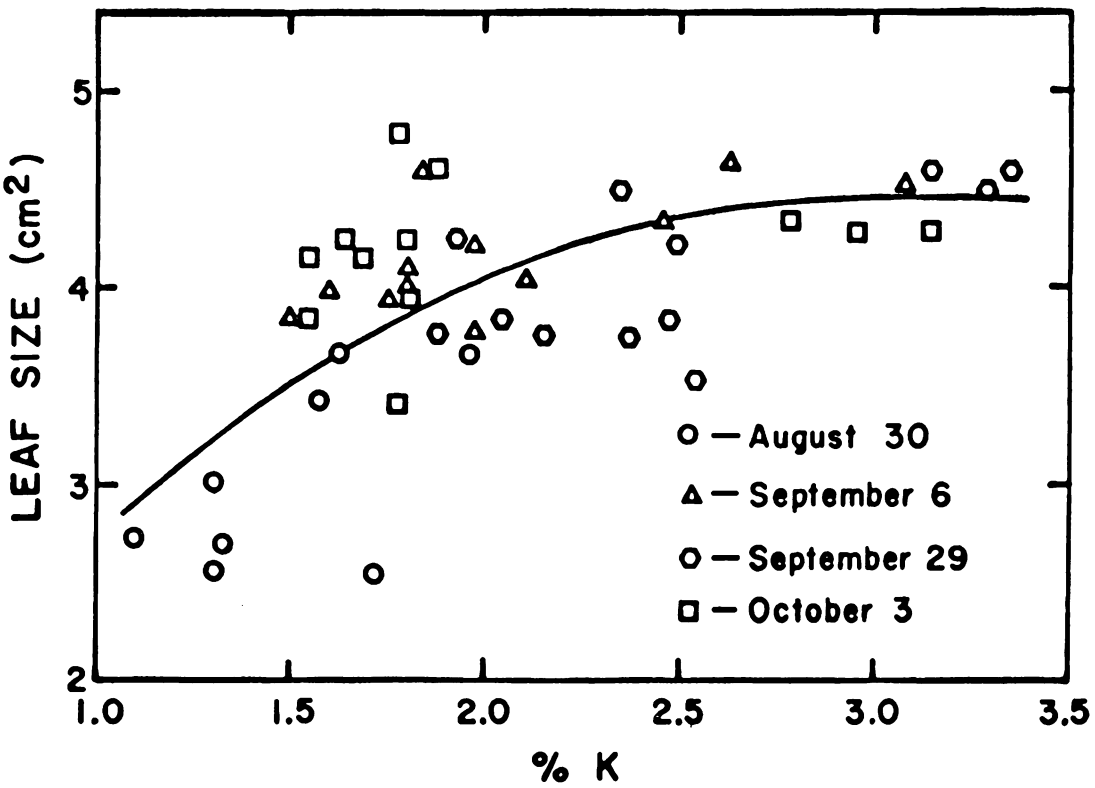

Figure 12. Effect of potassium content on leaf size. Correlation coefficient = 0.65, significant at .01 level.

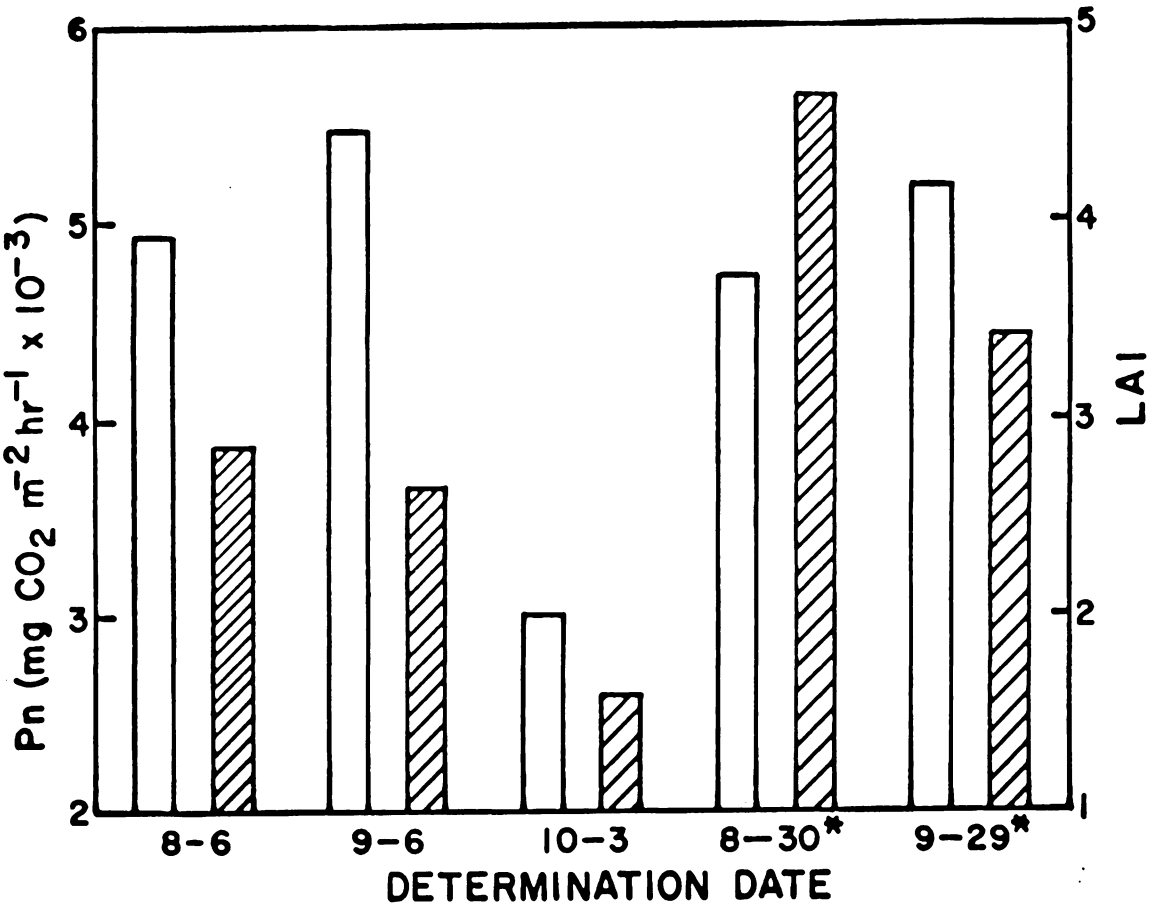

Figure 13. Net photosynthesis (open bars) and LAI (shaded bars) of alfalfa on five dates. *Old foliage.

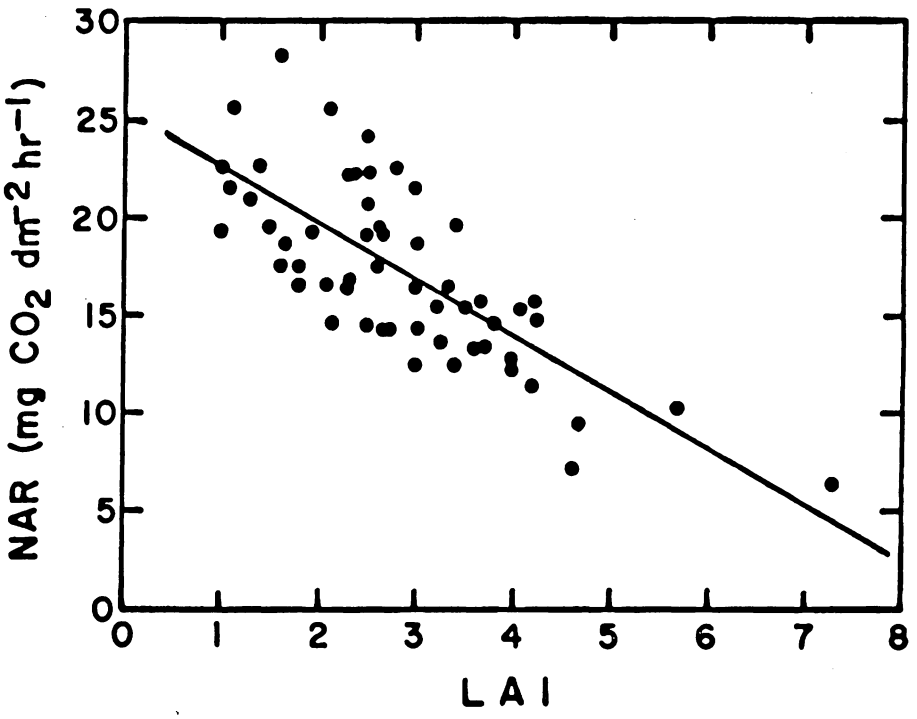

Figure 14. Effect of LAI on NAR on five dates. Correlation coefficient = 0.75, significant at .01 level.

Table 16. Effect of potassium fertilization on P_n (mg CO_2 dm^{-2} hr^{-1}) of individual leaves.

K_2O Applied (lb/A)	Young Foliage		Old Foliage	
	Date		Date	
	8-4	9-3	8-15	9-17
0	13.02a[1]	27.05a[2]	20.81	28.90
25	16.23b	31.74b	23.36	32.26
75	16.45bc	32.81b	28.46	33.50
300	18.77c	33.94b	29.35	39.41

1 & 2 Means followed by the same letter are not significantly different at the .05 and .10 levels, respectively.

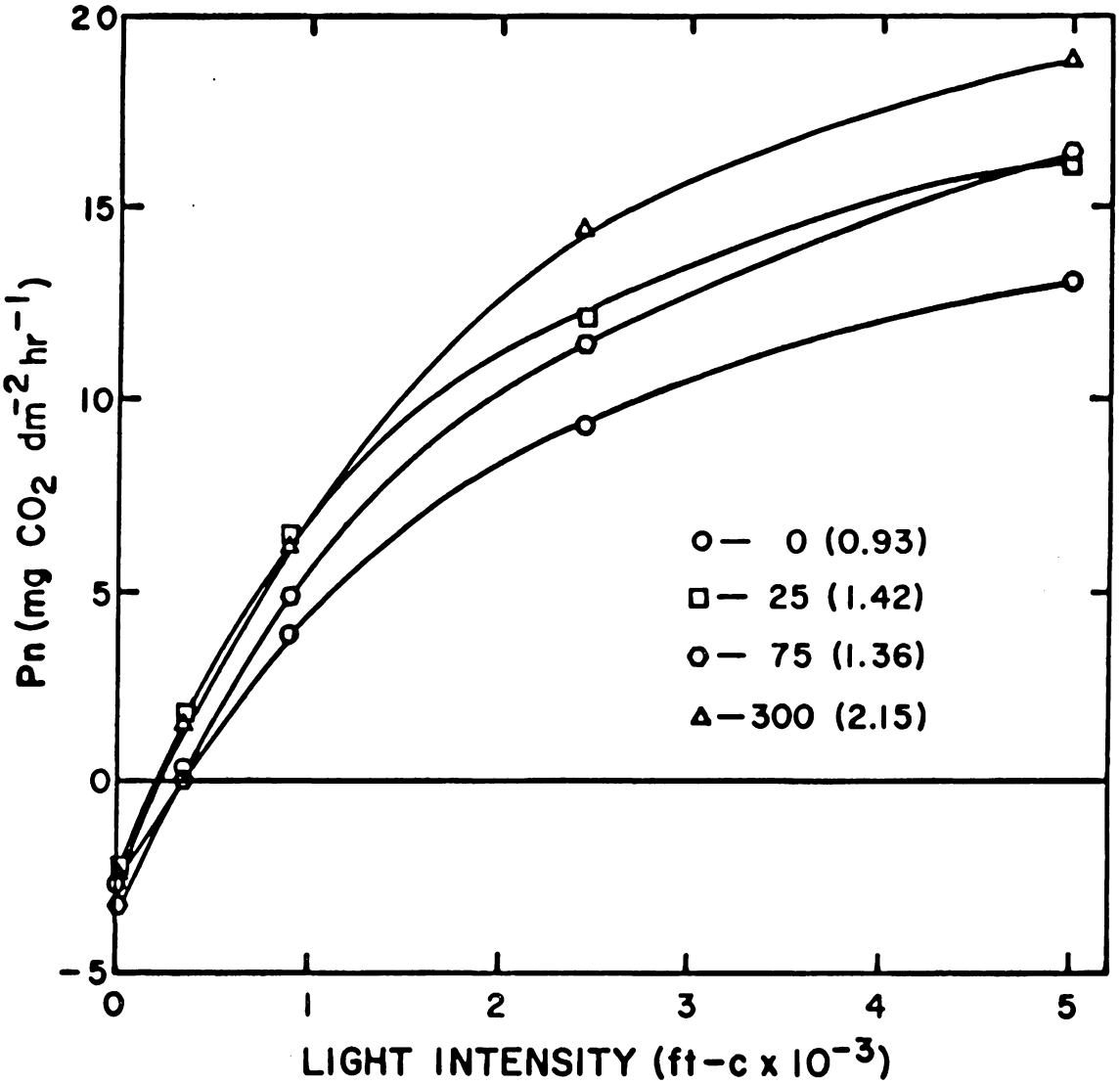

Figure 15. Light response curves of individual leaves from alfalfa stands fertilized with different potassium rates. Numbers in parenthesis are % potassium in leaves (averages of 3 replications on August 4, 1965).

K content of excised leaves and that of leaves on plants for entire plots is highly significant, r = .87 (slope = -1.15 x). This indicates that excised leaves used for P_n determinations were similar to those in the stand.

Soil, placed in the cylinders in April, contained 35 lb. available K_2O per acre by the quick-test method. This value had increased to 73 lb. on plots where no K was applied by July 21. However, similar soil stored in drums still contained 35 lb. in July, indicating that additional K release from some source had occurred under field conditions.

DISCUSSION

Rate of growth of alfalfa plants may be accounted for by two general factors: (1) potential assimilation rate per unit leaf area and (2) area of assimilating leaves. Stems fix some CO_2, but this amount is small. Differential growth rates due to K nutrition may be explained by the above factors.

Assimilation by leaves with different K contents in these experiments shows that K-deficient leaves were less efficient than those with high K. The differential photosynthetic responses of alfalfa leaves to varying levels of K nutrition probably cannot be explained by effects on any one process. Rather, it is probably the result of indirect effects of K on several factors that affect photosynthesis.

Greater stomatal numbers with larger apertures could cause higher P_n rates under differential K supply. According to Kuiper (1961), the diffusion rate of CO_2 from the air to substomatal cavities depends on the stomatal resistance to diffusion, i.e. the stomatal aperture. Several workers have found that partially closed stomata may limit CO_2 fixation (El-Sharkaway and Hesketh, 1964; Howe, 1962; and Maskell, 1928). Stomatal development is reduced by inadequate moisture (Penfound, 1931 and Schuermann, 1959), and since K functions in the maintenance of cell turgor (Nason and McElroy, 1963; Lawton, 1954; Humbert, 1963; and Warne, 1937), low K could limit stomatal development.

Under bright light conditions, CO_2 compensation points of K-deficient leaves were approximately 22% higher than for leaves high in

K. When the supply of CO_2 is limiting, photosynthesis should be proportional to the CO_2 gradient from the outside air to the cell surface in substomatal cavities. If the CO_2 compensation point is characteristic of the concentration of CO_2 inside the leaf, then a larger gradient exists for leaves with adequate K than for K-deficient leaves. Moss (1962) stated that the different ability of plants to remove CO_2 to low levels would effect the production of plants in environments where CO_2 was limiting photosynthesis.

Lower concentrations of flavin mononucleotide, a compound necessary for the activation of glycolic acid oxidase, in leaves with high K content might account for differing CO_2 compensation points. Tregunna (1966) concluded that glycolic acid oxidase is probably responsible for the production of CO_2 during photosynthesis. He found flavin mononucleotide absent in corn leaves and considered this to be the reason that corn had a CO_2 compensation point near zero.

Potassium may be operative with individual enzymes or enzyme systems, since immediate increases in CO_2 uptake occurred when deficient Chlorella cells were supplied K (Hill and Whittingham, 1955). Jones (1961) found leaf symptoms of K deficiency in tomato (Lycopersicon lycopersicon L.) below 0.5 meq liter^{-1} of K in the nutrient solution, and these symptoms increased in severity as the K level was reduced. He concluded that K functioned as an essential micronutrient in a vital phase of metabolism, that this requirement was satisfied at 0.5 meq liter^{-1}, and that above this level it stimulates

less essential reactions. The decrease in CO_2 compensation point in alfalfa from control leaves to the lowest level of added K indicates an effect similar to a cofactor in an enzyme system.

Responses of detached leaves used in these experiments were apparently representative of differences between K levels that existed among plants. P_n rates for excised leaves from the field and greenhouse were similar to the NAR for field plants at low LAI values. Turner and Bidwell (1965) found little difference in photosynthesis rates of attached and detached bean leaves up to two days after detachment.

Significant effects of K on P_n did not occur until plants grew for several weeks in the nutrient cultures. This may have been due to K carry-over from the Weblite rooting medium. Total K content of this material was 1.93% (Spasoff, 1965).

Data from the greenhouse experiments probably could have been improved with greater increments among lower K treatments. This likely would have given leaves with graduations in K contents, thus allowing more critical evaluation of K effects.

The effect of K on leaf area expansion is more difficult to assess than its effect on P_n. Larger leaves with adequate K nutrition indicate a definite function of K in the process of leaf expansion in these experiments. Increased leaf size can apparently be attributed to both increased cell size and number. Therefore, increased leaf expansion may be due to more available energy and material from more efficient leaves.

Rapid leaf area development at high K levels, apparent in these experiments, is important in the establishment of a photosynthetic base.

Yields increased with K content of leaves up to between 1.35 and 3.74% K. Bear and Wallace (1950) reported alfalfa yield increases up to 3% K in the plants. Increases in yield were consistently associated with increases in leaf number per plant and per plot.

Comparisons of yields among harvests should not be made because of variable regrowth periods and light conditions. However, if it is assumed that lengthened regrowth periods would have increased yields, the differential in yield between extreme K levels would have increased. The more extensive root development at the high K level (unreported greenhouse data), probably stimulated nutrient absorption, and contributed to yield differences. Plants with liberal K also had more basal shoots from which to initiate new leaves after harvesting, thereby permitting more rapid leaf accumulation, i.e. establishment of a photosynthetic base.

It is likely that carbohydrate levels in the roots contributed to the relationships between leaf initiation, yield and K uptake in these experiments. Reid, et al. (1965) found that K uptake by alfalfa was rapidly reflected in the level of carbohydrate stored in the roots. They concluded that increased growth after cutting resulted from increased levels of stored carbohydrate which accumulated as an indirect result of increased K content of the plant.

Assuming that growth is a process limited by energy availability rather than hormonal control, differences in P_n among different K levels could account for growth rate differences in these experiments. Differences in CO_2 assimilation between leaves well supplied with K and those receiving inadequate quantities were of a magnitude that marked differences in growth (leaf expansion) would be expected. Brown, et al. (1966) concluded that differences in capacity for CO_2 uptake among species are likely to be translated into growth rate differences in the field, since higher CO_2 uptake rates provide more energy for leaf expansion. Higher levels of stored carbohydrate in alfalfa with increased K application (Reid et al., 1965) indicate that reduced P_n under a K deficiency is limiting carbohydrate production and thereby limiting leaf initiation and expansion.

Plants receiving 195 ppm K in greenhouse Experiment II had approximately 490% higher average yields than K-deficient plants. However, P_n of individual leaves was increased only 30% by high K. This discrepency between CO_2 fixation and yield may be explained by large differences in productive leaf areas. Percentage differences of the products of P_n x leaf area at each K level show that plants receiving 195 ppm K were actually 400% higher in potential photosynthesis per pot than for low K when mutual shading is not considered. This is an oversimplified estimate of yield differences since factors such as night respiration of leaves and stems, fluctuations in light intensity and progressive changes in leaf area account for the final yield.

The relationship between P_n and leaf area was also evident in the field experiment. Excised leaves had P_n (mg CO_2 dm^{-2} hr^{-1}) rates that reflected the K level applied, but significant differences in P_n (mg CO_2 m^{-2} land area hr^{-1}) among K levels were small and inconsistent. Different light conditions and some fluctuation in stands when P_n determinations were made resulted in variability among replications and made K differences less detectable.

In the field, young foliage had higher P_n rates (per unit land area) at comparable LAI's than did old foliage. This reflects the influences of leaf shading with high leaf areas and leaf age on CO_2 uptake. The combined effect of age and stem position on P_n of leaves in an alfalfa stand was determined in a preliminary study. It was found that CO_2 assimilation approached 35 mg dm^{-2} hr^{-1} in upper leaves, lower leaves were almost half as efficient, and the values for middle leaves were intermediate.

SUMMARY AND CONCLUSIONS

Two greenhouse experiments and one field experiment were conducted to study the influence of K on CO_2 assimilation, growth and morphological characteristics of alfalfa. The consistent yield increases obtained with high K applications were associated with taller plants with more leaves per plant and per plot. Leaf size, weight per unit area, and stomatal number and aperture increased with added increments of K. This is attributed to larger epidermal cells and greater numbers per leaf.

P_n rates of excised leaves from greenhouse plants were generally higher as K increased, and maximum rates usually occurred with leaves from the 195 ppm K treatment. High K gave increases of 9.23 and 6.17 mg CO_2 dm^{-2} hr^{-1} in greenhouse (Experiment II) and field grown leaves, respectively. Light saturation occurred at lower levels with no K, but leaves from all K treatments had similar light compensation points. Increases in P_n of alfalfa stands with added K were usually not apparent under field conditions, perhaps because of variability in light intensity and penetration. Leaves from high K plants had low CO_2 compensation points, indicating higher efficiency at low CO_2 levels. Yield and P_n of individual leaves were positively correlated in most of the experiments.

Based on these results and the work of others, it appears that K functions both to increase the active photosynthetic surface through

greater leaf initiation and development and to increase the rate of CO_2 utilization per unit leaf area. These two factors are interrelated, leaf growth probably being dependent upon CO_2 assimilation rates.

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ABSTRACT

Photosynthesis and Certain Morphological Characteristics of Alfalfa as Affected by Potassium Nutrition

by

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The enhancing effect of K on alfalfa (Medicago sativa L.) yield has frequently been reported, but the nature of this influence has not been clearly shown. It was assumed that K contributed either to increased leaf expansion, thereby resulting in a larger photosynthetic surface, or to higher CO_2 assimilation rates per unit leaf area. Sand culture technique for growing plants was used in two greenhouse experiments, while field plants were grown in plots with soil differing in available K.

Yield increases were consistently obtained with high K. Added K increased plant height and leaves per plant and per plot. The rate of leaf accumulation was higher as K increased. Leaf size and weight per unit area also increased, as did stomatal number and aperture. Larger epidermal cells and greater numbers per leaf were observed with high K nutrition. Per cent K in plants was associated with rate of K application.

Net photosynthesis rates of excised leaves increased with potassium application, but all K levels had similar light compensation points. Leaves from plants with added K had lower CO_2 compensation points, indicating higher efficiency of CO_2 assimilation.

Based on these data, K appears to function both to increase the effective photosynthetic surface through greater leaf initiation and development and to increase the rate of CO_2 utilization per unit leaf area. The latter increase probably results from greater CO_2 diffusion into substomatal cavities.