EFFECT OF TEMPERATURE ON ALFALFA GROWTH, CARBOHYDRATE ROOT RESERVES, PHOTOSYNTHESIS, RESPIRATION, AND PHOTOSYNTHATE TRANSLOCATION

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INTRODUCTION

The status of carbohydrate reserves in alfalfa *(Medicago sativa* L.) root is of prime importance to alfalfa management. The carbohydrate root reserves are the only readily available source of energy for regrowth and other metabolic processes. In addition, forage yield and stand persistence have been found to be closely associated with total carbohydrate root reserves. In general, the concentration of total nonstructural carbohydrate (TNC) decreases for a time after forage harvest and then increases as photosynthate is translocated to the root.

In Wisconsin, where temperatures are very cold and snow cover in winter is of long duration, it was reported that 48 percent of available carbohydrate stored in alfalfa roots during the fall were depleted during winter. In contrast, in the southern plains, where snow cover is intermittent and usually of short duration, several assumptions have been made on the effect of winter temperature on status of carbohydrate root reserves, photosynthesis and photosynthate partitioning in alfalfa. Growth of alfalfa in the southern plains is considerably hindered during the months of July and August. High temperatures are commonly blamed for this decrease in growth.

The present study was conducted to obtain information on the influence of selected temperature regimes (12/2, 21/8, and 34/25°C day/night) on alfalfa growth, photosynthesis, photosynthate partitioning, respiration, and TNC in roots. The temperatures were selected on the basis of average daily maximum and daily minimum temperatures during winter, spring, and summer months in central Oklahoma. In addition, a field study was conducted to determine TNC in roots of alfalfa for samples taken throughout the period between the last cut in the fall and the first cut in the spring. Two alfalfa cultivars under different management practices at different locations were used.

Carbohydrate Trends in Alfalfa Roots as Influenced by Fall, Winter, and Spring Temperatures

Safaa Al-Hamdani, and G. W. Todd[1]

ABSTRACT

Determination of total nonstructural carbohydrate (TNC) in roots of alfalfa *(Medicago sativa* L.) was conducted for samples taken throughout the period between the last cut in fall and first cut in spring. Two alfalfa cultivars at different locations under different management practices were used. In general, the TNC root reserves continued to increase until approximately mid-December, followed by a gradual decline. The decline in TNC continued until the end of March when the canopy was re-established allowing the additional photosynthate to be stored in the roots. Root dry matter (DM) was determined as a percentage of saturated weight for the samples used in the TNC determination. The trends of percentage DM showed a pattern similar to that of TNC. Since a high correlation between g TNC and percent DM was obtained at both locations, DM was used to estimate percent TNC. In most cases there were no significant differences between the estimated TNC based on DM and that obtained from chemical analysis.

Additional index words: Total nonstructural carbohydrate (TNC), Percent dry matter (% DM), *Medicago sativa* L.

The status of carbohydrate reserves in alfalfa *(Medicago sativa* L.) roots is of prime importance to alfalfa management. The carbohydrate root reserves are the only readily available source of energy for regrowth and other metabolic processes. In addition, forage yield has been found to be closely associated with total carbohydrate root reserves (3, 4, 5). In general, the concentration of total nonstructural carbohydrates (TNC) decreases initially after forage harvest and then increases as photosynthate is translocated to the root (1, 2, 7, 11).

In Wisconsin, where very cold temperatures are experienced and snow cover in winter is of long duration, Bula and Smith (1) found that 48 percent of available carbohydrates stored in alfalfa roots during the fall were depleted during winter. In contrast, in the southern plains where snow cover is intermittent and usually of short duration, several assumptions have been made on the effect of local winter temperatures on the status of carbohydrate root reserves. Sholar et al. (10) in Oklahoma, Reynolds (9) in Tennessee, and Mays and Evans (6) in Alabama, independently suggested that the mild daily maximum temperature in winter months and the presence of green leaves on alfalfa plants might allow some photosynthetic activity. This could result in adding carbohydrates to the total energy root reserve; however, experimental proof is lacking.

A knowledge of the concentration of TNC in alfalfa roots during the fall, winter, and spring months may provide an answer to the above assumptions. In addition, it may supply clear information on the status of carbohydrate root reserves during each of these periods. A secondary objective of this study was to examine the gravimetric method proposed by Wolf (12) as an alternative procedure for TNC determination in alfalfa roots. The gravimetric method is simple, inexpensive, and less time consuming than the conventional chemical methods, but very little experimental data are available to establish whether the gravimetric procedure is a satisfactory predictor of TNC.

MATERIALS AND METHODS

The carbohydrate trends in alfalfa roots during fall, winter, and spring were followed in two different alfalfa cultivars with different stand ages at two locations separated by approximately 10 miles.

Location 1 (Stillwater, OK)

A 1 1/2-year-old stand of 'Riley' alfalfa grown under irrigated conditions was selected at this location. Elevation of the area is about 795 meters above sea level. The plots are located on a nearly flat area. The soil is fine-silty, mixed, thermic, Cumulic Haplustolls (port silt loam). Soil analysis showed the following: pH 6.7, 2.2 Kg N/ha, 172 kg P/ha and 325 kg K/ha. The alfalfa in this field was harvested in early October which was the last cut for the 1984 growing season.

Location 2 (Perkins, OK)

A 2 1/2-year-old stand of 'Cody' alfalfa grown under dryland conditions was selected at this location. The plots are located on a nearly flat area with a very gentle slope to the east. Elevation of the area is about 822 meters above sea level. The soil is fine-loamy, mixed thermic, Udic Aggiustolls (Teller loam). Soil analysis showed the following: pH 6.0, 3.4 kg N/ha, 22.4 kg P/ha, and 196.1 Kg/ha. Alfalfa has been routinely harvested from this field for hay production. Due to lack of moisture, the last harvest for the 1984 growing season was taken in late August.

Sample Collection and Analysis

Alfalfa root samples from both locations were collected approximately every two weeks for the period between mid-October of 1984 to mid-April of 1985. Five alfalfa root samples were dug at random from each alfalfa field on each sampling date. Each sample consisted of twenty roots, cut off at the crown and sized to a length of 10 cm. Root segments were soaked in ice water for approximately two hours, then washed in tap water, dried with paper towels, and weighed. Root samples were oven-dried for two

hours at 100°C to stop enzymatic activity. Drying was continued at 70°C for approximately 48 hours and then dry weight was recorded.

The root dry matter was determined as percentage of saturated weight as described by Wolf (13). TNC analysis was conducted as follows: the root samples were ground in a Wiley mill to pass through a 2 mm screen. A representative portion of to 0.2 gm from each sample was placed in a 250 ml beaker with 50 ml of 0.2 N HCl and allowed to boil slowly for one hour. The root solution was then filtered into a 100 ml volumetric flask. The beaker and filtrate were washed with 50 ml deionized water, and the solution was then brought to 100 ml volume. Then 0.1 ml of this sample was placed into a 20 ml test tube with 0.9 ml of deionized water. Anthrone reagent, as described by Yemm and Willis (13) was used to determine the TNC content. The anthrone reagent (5.0 ml) was added to the root extract and agitated. The samples were then placed in a hot water bath for 15 minutes, followed by 20 minutes in a cold water bath. Absorbance of the samples was determined with a spectrophotometer (B and L Spectronic 20) at 620 mm.

Significance of treatment effects on % TNC and % DM was determined by conducting analysis of variance (ANOVA) for a completely random design; F and least significant difference (LSD) test for significance used the 0.05 probability level. Comparison between the antheron and the gravimetric method in % TNC determination was obtained by conducting ANOVA for a split-plot design with the main plot as completely random design. Treatments means were subjected to LSD test.

RESULTS AND DISCUSSION

At the Stillwater location, TNC in alfalfa roots continued to increase from two weeks after the last harvest until approximately mid-December. At this time, a decline in TNC root reserves began and continued until the end of March when the canopy was re-established allowing additional photosynthate to be stored in the roots (Table 1). The reduction in TNC during the months of January and February most likely resulted from respiration of the root and utilization in supporting any growth which occurred during that period. On the other hand, the sharp decline in TNC during the month of March was probably due to utilization for the initiation of regrowth of the new growing season.

In general the same result was obtained from the analysis of the root samples taken from the Perkins location except reductions began in mid-November (Table 2). This was most likely due to the management practice used at this location. The last harvest taken at the Perkins location was in late August compared to early October in Stillwater. This allowed the initiation of new growth of the mature plants during late October. In addition to early low temperature injury, the shading of the regrowth at the base of the mature plant could result in reduction in photosynthetic activity causing the regrowth to be more dependent on carbohydrate root reserves.

The trends for percent TNC and DM in alfalfa roots were generally similar at both locations (Table 1 and 2). In addition, the correlation between percent TNC and DM were very high, $r^2 = 0.94$ for the Stillwater location, and $r^2 = 0.92$ for the Perkins location. Similar correlations between TNC and DM were obtained in a larger study which involved 11 years of evaluation of a wide range of alfalfa varieties, plant ages, and management practices (12). This correlation was further amplified by Rapoport and Travis (8). They found that root cambium activity was associated with TNC level. An initial decrease in TNC following cutting was accompanied by a reduction in cambial division and root

growth. On the other hand, increased TNC level after re-establishment of the plant canopy was accompanied by an increase in the rate of cell expansion and rapid root growth.

Based on the relationship between g TNC per 100 g saturated weight (formula 1) and percent DM, a regression equation was obtained with intercept –17.10 and slope 0.92 for the Stillwater location, and with intercept –13.00 and slope 0.75 for the Perkins location. As Wolf (12) proposed, the percent DM was used to calculate g TNC (formula 2) and then percent TNC estimated (formula 3).

$$\text{g TNC} = (\%\ \text{TNC} \times \%\ \text{DM}) / 100 \qquad [1]$$

$$\text{g TNC} = \text{Intercept} + \text{Slope} \times \%\ \text{DM} \qquad [2]$$

$$\%\ \text{TNC} = (\text{g TNC} / \%\ \text{DM}) \times 100 \qquad [3]$$

On most of the dates, there was no significant difference between % TNC obtained from the anthrone method to that obtained from the gravimetric method (Table 1 and 2). However, in the few cases where differences were detected, there was no systematic trend.

The data indicate that the gravimetric method can be used as an alternative method for TNC determination. In addition, the results showed that the carbohydrate levels in alfalfa roots continued to decline through winter. We believe that the small regrowth observed on alfalfa plants during winter might contribute to further reduction in TNC root reserves.

REFERENCES

1. Bula, R. J., and D. Smith. 1954. Cold resistance chemical composition in overwintering alfalfa, red clover, and sweet clover. Agron. J. 46:397-401.
2. Cooper, C. S., and C. A. Watson. 1968. Total available carbohydrates in roots of sainfoin *(Onobrycbis viciaefolia* Scop.) and alfalfa *(Medicago sativa* L.) when grown under several management regimes. Crop Sci. 8:83-85.
3. Feltner, K. C., and M. A. Massengale. 1965. Influence of temperature and harvest management on growth, level of carbohydrates in the roots and survival of alfalfa *(Medicago sativa* L.). Crop. Sci. 5:585-588.
4. Graumann, H. O., J. E. Webster, C. L. Canode, and H. F. Murphy. 1954. The effects of harvest practices on the performance of alfalfa. Okla. Agric. Exp. Stn. Bull. 433.
5. Kust, C. A., and D. Smith. 1961. Influence of harvest management on level of carbohydrate reserves, longevity of stands, and yields of hay and protein from Venal alfalfa. Crop. Sci. 1:267-269.
6. Mays, D. A., and E. M. Evans. 1973. Autumn cutting effects on alfalfa yield and persistence in Alabama. Agron. J. 65:390-292.
7. Pearce, R. B., G. Fissel, and G. E. Carlso. 1969. Carbon uptake and distribution before and after defoliation of alfalfa. Crop. Sci. 9:756-759.
8. Rapoport, H. F., and R. L. Travis. 1984. Alfalfa root growth, cambial activity, and carbohydrate cynamics during the regrowth cycle. Crop. Sci. 24:899-903.
9. Reynold, J. H. 1971. Carbohydrate trends in alfalfa *(Medicago sativa* L.) roots under several forage harvest schedules. Crop Sci. 11:103-106.
10. Sholar, J. R., J. L. Caddel, J. F. Stritzek, and R. C. Berberet. 1983. Fall harvest management of alfalfa in southern plains. Agron. J. 75:619-622.
11. Smith, Dale. 1962. Carbohydrate root reserves in alfalfa, red clover, and birdsfoot trefoil under several management schedules. Crop Sci. 2:75-78.

12. Wolf, D. D. 1978. Nonstructural carbohydrate and dry matter relationships in alfalfa tap roots. Crop Sci. 18:690-692.

13. Yemm, E. W., and A. J. Willis. 1954. The estimation of carbohydrates in plant extracts by anthrone. Biochem. J. 57:508-514.

Fig. 1. Average maximum and minimum daily air temperatures for Stillwater and Perkins locations, 1984-1985.

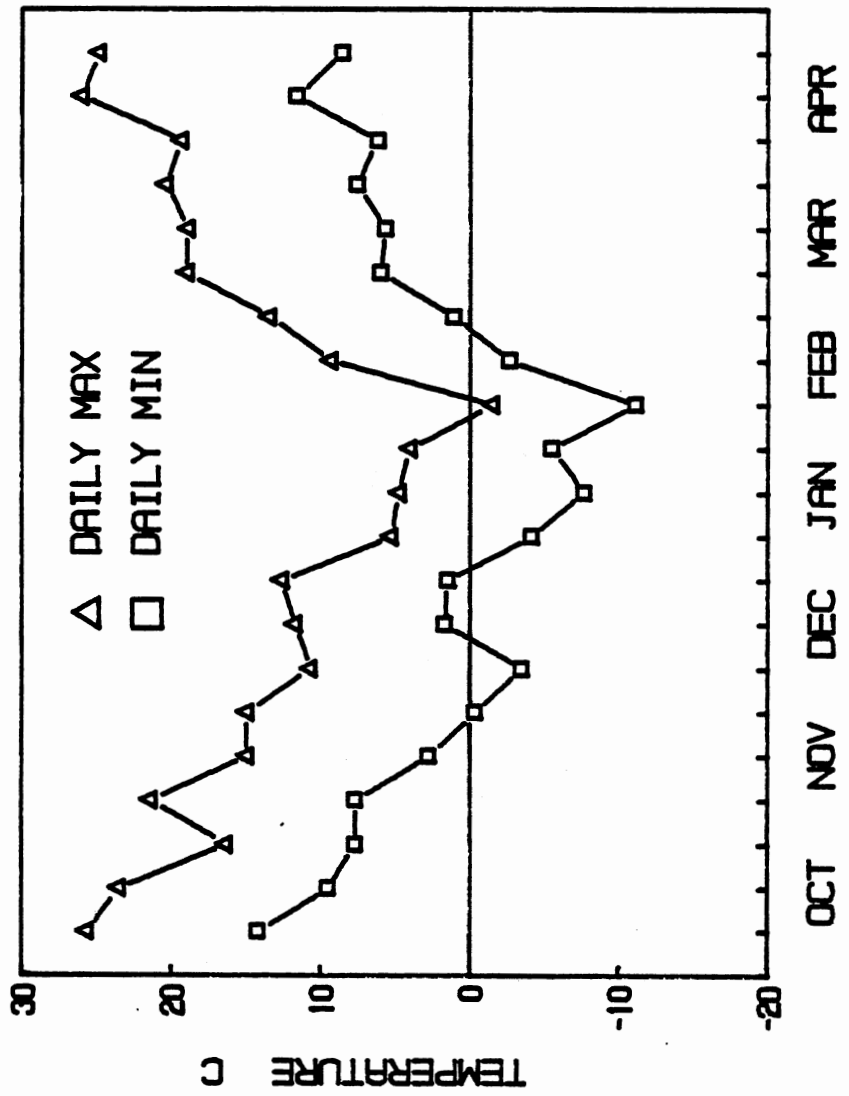
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Table 1. Percent total nonstructural carbohydrate (TNC) and percent dry matter (DM) in alfalfa roots during the period between October and April at Stillwater.

Sampling date	DM	TNC	
		Anthrone method	Gravimetric method
	%		
Oct 15	33.32	38.05**	40.93**
Oct 29	33.95	40.38*	42.09*
Nov 14	34.38	44.38*	42.56*
Nov 30	35.74	46.34*	44.42*
Dec 14	35.56	45.48	44.21
Jan 8	34.84	44.67	43.22
Feb 16	31.74	38.96	38.36
Mar 2	29.58	35.31	34.47
Mar 16	24.94	26.05	24.79
Mar 31	25.15	27.02	26.04
Apr 12	29.80	32.97	34.11
Apr 28	32.44	37.47	38.39
LSD (0.05)†	0.93	2.37	1.57
LSD (0.01)†	1.24	3.16	2.10

*,** Within sampling date, difference between % TNC obtained from anthrone method and that obtained from gravimetric method was statistically significant at the 0.05 and 0.01 levels of probability, respectively, based on LSD test.

† LSD for difference between means within a column.

Table 2. Percent total nonstructural carbohydrate (TNC) and percent dry matter (DM) in alfalfa roots during the period between October and April at Perkins.

Sampling date	DM	TNC	
		Anthrone method	Gravimetric method
	%		
Oct 19	40.83	41.68*	43.44*
Nov 2	42.51	44.89	44.38
Nov 16	41.00	43.35	43.46
Dec 1	38.15	41.47	40.92
Dec 14	37.38	40.06	40.21
Jan 8	35.10	38.32	37.94
Feb 16	31.96	36.32*	34.32*
Mar 2	28.86	28.76	29.95
Mar 16	25.94	22.19	23.43
Mar 31	26.00	25.07	25.19
Apr 12	28.26	31.38*	28.82*
Apr 28	32.26	36.08	35.90
LSD (0.05)†	1.03	3.14	1.41
LSD (0.01)†	1.38	4.19	1.89

* Within sampling date, difference between % TNC obtained from anthrone method and that obtained from gravimetric method was statistically significant at the 0.05 level of probability, based on LSD test.

† LSD for difference between means within a column.

Effects of Temperature on Photosynthesis, Respiration, and Growth Components of Alfalfa

Safaa Al-Hamdani, and G. W. Todd

ABSTRACT

The influence of three temperature regimes (34/25, 21/8, and 12/2°C day/night) representing conditions during winter, spring and summer in Oklahoma, on alfalfa *(Medicago sativa* L.) growth, photosynthesis, respiration, and total nonstructural carbohydrate (TNC) levels in roots was determined. The plants were grown under greenhouse conditions for approximately 3 months and then clipped back. When regrowth was about 5-8 cm in height, the plants were placed in growth chambers at the selected temperatures, all having a day length of 14 hours. Photosynthetic photon flux density was 520 $\mu Em^{-2}sec^{-1}$.

Greatest plant height, shoot dry weight, and leaf area were obtained from the plants grown at the 21/8°C regime, followed in descending order by those at 34/25 and 12/2°C regimes. Root dry weight was found to be the highest for the plants at the 21/8°C regime followed by those at the 12/2°C regime. The concentration of both chlorophyll a and b in alfalfa leaves increased as growth temperature was increased. Furthermore, percentages of TNC in roots were found to be the highest for the plants grown at the 21/8°C regime followed in descending order by those at the 12/2 and the 34/25°C regimes.

Net photosynthesis of the alfalfa canopy increased from 12.9 $\mu mol\ CO_2m^{-2}s^{-1}$ at 12°C to 18.9 $\mu mol\ CO_2m^{-2}s^{-1}$ at 21°C. However, little increase in net photosynthesis, 0.9 $\mu mol\ CO_2m^{-2}s^{-1}$, was obtained by increasing the growth temperature further to 34°C. Shoot and root respiration were increased continuously in response to an increase in temperature. However, a relatively sharp increase, 1.6 fold for the shoot and 1.9 fold for the root, was obtained as the temperature was increased from 25 to 34°C.

Additional index words: Leaf area, Plant height, Shoot dry weight, Root dry weight, Shoot/Root ratio, Chlorophyll, Total nonstructural carbohydrate (TNC), and *Medicago sativa* L.

Several studies have compared the responses of alfalfa plants grown under diverse temperature conditions using different cultivars starting from seed or from transplants (1, 5, 10, 12, 17, 25). These studies have shown that flowering occurs earlier, and the herbage yield is lower at a specified growth stage, when alfalfa is grown under hot rather than cool temperatures.

Although many photosynthetic studies have been conducted on alfalfa, there is still some controversy on the response to temperature. Murata *et al.* (16) observed a wide range of optimum temperatures, from about 5 to 30°C, for apparent photosynthesis in whole alfalfa seedlings. On the other hand, Brown and Radcliffe (4) found that the optimum temperature for apparent photosynthesis in stem tips was between about 25 to 30°C. Furthermore, Pearson and Hunt (18) measured the effect of temperatures on net carbon dioxide intake of whole alfalfa shoots. The temperatures ranged from 10 to 40°C in 10°C increments. They observed a steep decline in net carbon dioxide intake with increasing temperature (20 mg $dm^{-2}h^{-1}$ at 10°C to 5 mg $dm^{-2}h^{-1}$ at 40°C) for plants grown at 20/15°C day/night temperatures. In contrast, a less rapid decline was recorded by Murata *et al.* (16). The net carbon dioxide intake decreased from 25 mg $dm^{-2}h^{-1}$ at 10°C to 15 mg $dm^{-2}h^{-1}$ at 40°C.

In the southern plains, several assumptions have been made on the effects of winter temperatures on photosynthesis and photosynthate partitioning in alfalfa. Sholar *et al.* (20) in Oklahoma, Reynolds (19) in Tennessee, and Mays and Evans (14) in Alabama, independently suggested that the mild daily maximum temperature in winter months and the presence of green leaves on alfalfa plants might allow some photosynthetic activity, which could result in adding carbohydrate to the total energy root reserve. However, experimental proof is lacking.

The present study was conducted to obtain information on the influence of selected temperature regimes on alfalfa growth, photosynthesis, respiration, and total nonstructural carbohydrate in roots. The temperatures were selected on the basis of average daily

maximum and daily minimum temperatures during winter, spring and summer months in central Oklahoma.

MATERIALS AND METHODS

Alfalfa cultivar 'Cody', which is adapted to the southern plains was selected for this study. Scarified seeds were treated with the fungicide Captan[cis-N-((trichloromethyl)thio)-4-cyclohexene-1,2-dicarboximide] and then planted in plastic pots 11 cm diameter x 14.5 cm deep. Pots were filled with a 2:1:1 mixture of sand-vermiculite-perlite plus complete fertilizer. Seedlings were thinned to 1 plant per pot at 2 weeks after germination. The plants were grown under greenhouse conditions for a period of 3 months. Temperature in the greenhouse varied between 20 and 30°C during the months of establishment. During the last month of establishment, when plants were at the 50% bloom stage, the shoots were clipped back. Six days after shoots removal, when regrowth was 5-8 cm in height, 90 plants were randomly placed in equal numbers within three controlled environment chambers. Growth chambers temperatures were 12/2, 21/8, and 34/25°C day/night with a 14-hour photoperiod. Photosynthetic photon flux density was 520 $\mu Em^{-2}sec^{-1}$. After 30 days of growth, the plants in each chamber were harvested. Seven random plant samples of the harvested plants were used to obtain leaf area readings on an automatic area meter.

At harvest, the height of each plant sample was recorded, then shoots in each pot were severed from the roots at the crown. The roots were washed in tap water and dried with paper towels. Each of the shoot and root samples were dried at 70°C and their weights were recorded. Root samples were ground in a Wiley mill to pass through a 2 mm screen. Total nonstructural carbohydrate (TNC) was determined in root tissues using the anthrone method which is modified by Shroyer *et al.* (21). Results were expressed as percent TNC on a dry weight basis.

To determine the effect of the temperature regimes on chlorophyll content, seven plant samples were randomly selected from each treatment and from each plant sample 0.3 gm sliced leaves were homogenized in 80% acetone. The mixture was then filtered

through Whatman #1 filter paper and the total volume was brought to 50-ml volumes with 80% acetone. Chlorophyll a and b were measured spectrophotometrically according to Arnon (2).

Rates of net photosynthesis at day temperature were measured for the plants growing under each of the temperature regimes. An air-sealed cylindrical glass chamber with a volume of 7 liters was used to enclose the shoots of the intact plant. Air containing approximately 340 ppm of CO_2 was passed through the system with a flow rate of 2 l/min. In addition, day and night shoot respiration were measured for the same plants of the three temperature regimes.

Root respiration was also measured for the same plant samples which were used in net photosynthesis and shoot respiration measurements. The soil surface of each plant sample was covered with a glass disk and sealed with modeling clay. In addition, the base of the pot was sealed, to ensure total enclosure of the root medium. Atmospheric air with a flow rate of 1 l/min. was passed into the root medium from one specifically designed opening in the pot and allowed to exit from the other opening in the opposite side.

Net photosynthesis, shoot respiration, and root respiration were calculated using the difference in CO_2 concentration between the air entering and leaving the system. Carbon dioxide exchange was measured using a Beckman IR gas analyzer. Each data point was obtained as an average of six observations.

The data from this experiment were analyzed as a 3x3 latin square and mean separations were based upon the LSD test.

RESULTS AND DISCUSSION

The largest plant height, shoot dry weight, and leaf area were obtained from the plants at the 21/8°C regime, followed in descending order by those at the 34/25 and 12/2°C regimes (Table 1). Root dry weight was also found to be greatest in plants held at 21/8°C, but was followed by those at the 12/2°C regime. Plants at the 34/25°C regime had the highest shoot/root ratio, and the ratios were found to decline in order by the 21/8°C and 12/2°C regimes. Although the temperature regimes were not identical, the present trend differs from the report by Ueno and Smith (24). They found that Cody alfalfa grown at 32/27°C (day/night) showed greater height, and shoot and root dry weight than plants grown at 21/15°C. The current study is in general agreement with Gist and Matt (9), Chatterton and Carlson (6), and Bula (5) in the finding that alfalfa growth response to temperature regimes around 20°C was greater than at temperatures around 30°C.

Smith and Young (22) were the first to report that a threshold temperature exists for chlorophyll formation. Furthermore, the rate of chlorophyll production increased with increasing temperature. The present study clearly showed that the concentration of both chlorophyll a and chlorophyll b in alfalfa leaves increased with increasing temperatures (Table 2). However, no significant difference in the chlorophyll a/chlorophyll b ratio was observed among the three temperature regimes. Millerad and McWilliam (15) obtained similar results in corn *(Zea mays* L.) seedlings over the temperature range of 12 to 27°C.

The percentage of total nonstructural carbohydrate (TNC) of the roots was found to be significantly different among the three temperature regimes (Table 3). Plants in the 21/8°C regime showed the highest percentage of TNC followed in descending order by those in the 12/2°C and 34/25°C regimes. These results were in agreement with findings of Feltner and Massengale (8). They attributed much of the depletion in TNC in alfalfa roots to high temperatures. Higher TNC reduction was found during warm summer months compared to cool temperature periods. In addition, Cooper and Watson (7)

reported a more rapid depletion in TNC of alfalfa root following cutting during summer. Furthermore, Chatterton and Carlson (6) found that the concentration of TNC tended to be higher in herbage of alfalfa plants growing under 20/15°C than those in the 29/24°C regime. However, Ueno and Smith (24) found that the percentages of TNC were higher in alfalfa roots grown at 32/27°C (day/night) than in the 21/15°C regime.

Net photosynthetic rates of the alfalfa canopies increased from 12.9 μmol CO_2 $m^{-2}s^{-1}$ at 12°C to 18.9 μmol CO_2 $m^{-2}s^{-1}$ at 21°C (Fig. 1). However, little increase in net photosynthesis was observed by increasing the growth temperature further to 34°C.

Increasing temperature was found to increase photorespiration at the expense of net photosynthesis, consequently increasing the CO_2 compensation point in several studies (11, 13, 23). In addition, Badger and Andrews (3) reported a greater increase in ribulose diphosphate oxygenase activity than in ribulose diphosphate carboxylase activity in response to an increase in temperature.

Murata *et al.* (16) observed that shoot respiration of alfalfa plants was linearly related to temperature from about 0 to 50°C. Similar results were obtained by Brown and Radcliffe (4). The current study also showed a continuous increase in CO_2 efflux in both shoots and roots (Fig. 2 and 3, respectively) as the growth temperature increased from 2 to 34°C. However, the relationship was not linear, exhibiting a relatively sharp increase in shoot and root respiration as the temperature increased from 25 to 34°C.

These data provide a partial explanation for the generally low alfalfa yields when the crop is grown under hot temperatures. Plants grown at warm temperatures exhibited higher shoot and root respiration, lower leaf area, and lower TNC root reserves compared with plants growing under cooler temperatures. In addition, the results indicated that plants grown under cool temperature conditions such as 12/2°C, maintain relatively high TNC in roots. This most likely is due to low respiration in both shoots and roots and to the slow growth rate which is observed under low temperature conditions.

REFERENCES

1. Arbi, N., D. Smith, and E. T. Bingham. 1979. Dry matter and morphological responses to temperatures of alfalfa strains with differing ploidy levels. Agron. J. 71: 573-577.
2. Arnon, D. I. 1949. Copper enzymes in isolated chloroplasts. Polyphenoloxidase in *Beta vulgaris*. Plant Physiol. 24: 1-15.
3. Badger, M. R., and T. J. Andrews. 1973. Effects of CO_2, O_2 and temperature on a high-affinity form of ribulose diphosphate carboxylase-oxygenase from spinach. Biochem. Biophys. Res. Comm. 80: 204-210.
4. Brown, R. H., and D. E. Radcliffe. 1986. A comparison of apparent photosynthesis in sericea lespedeza and alfalfa. Crop Sci. 26: 1208-1211.
5. Bula, R. J. 1972. Morphological characteristics of alfalfa plants grown at several temperatures. Crop Sci. 12: 683-686.
6. Chatterton, N. J. and G. E. Carlson. 1981. Growth and photosynthate partitioning in alfalfa under eight temperature-photosynthetic period combinations. Agron. J. 73: 392-394.
7. Cooper, C. S., and C. A. Watson. 1968. Total available carbohydrates in roots of sainfoin *(Onobrycbis viciaefolia* Scop.) and alfalfa *(Medicago sativa* L.) when grown under several management regimes. Crop Sci. 8: 83-85.
8. Feltner, K. C., and M. A. Massengale. 1965. Influence of temperature and harvest management on growth, level of carbohydrates in roots, and survival of alfalfa *(Medicago sativa* L.). Crop Sci. 5: 585-588.
9. Gist, G. R., and G. O. Mott. 1957. Some effects of light intensity, temperature, and soil moisture on the growth of alfalfa, red clover and birdsfoot trefoil seedlings. Agron. J. 49: 33-36.
10. Greenfield, P. L., and D. Smith. 1973. Influence of temperature change at bud on composition of alfalfa at first flower. Agron. J. 65: 871-874.

11. Jackson, W. A., and R. J. Volk. 1970. Photorespiration. Ann. Rev. Plant Physiol. 21: 385-432.

12. Jensen, E. H., M. A. Massengale, and D. O. Chilcote. 1967. Environmental effects on growth and quality of alfalfa. Nevada Agric. Exp. Stn. Bull. T9.

13. Jolliffe, P. A., and E. B. Tregunna. 1973. Environmental regulation of the oxygen effect on apparent photosynthesis in wheat. Can. J. Bot. 51: 841-853.

14. Mays, D. A., and E. M. Evans. 1973. Autumn cutting effect on alfalfa yield and persistence in Alabama. Agron. J. 65: 390-392.

15. Millerd, A., and J. R. McWilliam. 1968. Studies on a maize mutant sensitive to low temperature. I. Influence of temperature and light on the production of chloroplast pigments. Plant Physiol. 43: 1967-1972.

16. Murata, V., J. Iyama, and T. Honma. 1965. Studies on the photosynthesis of forage crops. IV. Influence of air-temperature upon the photosynthesis and respiration of alfalfa and several southern type forage crops. Proc. Crop Sci. Jpn. 34: 154-158.

17. Pearson, C. J., and L. A. Hunt. 1972. Effect of temperature on primary growth of alfalfa. Can J. Plant Sci. 52: 1007-1015.

18. Pearson, C. J., and L. A. Hunt. 1972. Effects of pretreatment temperature on carbon dioxide exchange in alfalfa. Can. J. Bot. 50: 1925-1930.

19. Reynolds, J. H. 1971. Carbohydrate trends in alfalfa *(Medicago sativa* L.) roots under several forage harvest schedules. Crop Sci. 11: 103-106.

20. Sholar, J. R., J. L. Caddel, J. F. Stritzke, and R. C. Berberet. 1983. Fall harvest management of alfalfa in Southern plains. Agron. J. 75: 619-622.

21. Shroyer, J. P., J. F. Stritzke, and L. I. Croy. 1979. Carbohydrate levels and control of blackjack oak and winged elm treated with tebuthiuron and 2,4,5-T. Range Manage. 32: 60-62.

22. Smith, J. H. C., and V. M. K. Young. 1956. Chlorophyll formation and accumulation in plants. In: Radiation Biology. A. Hollaender, ed. McGraw-Hill, New York. p. 393-442.

23. Todd, G. W. 1982. Photosynthesis and respiration of vegetative and reproductive parts of wheat and barley plants in response to increasing temperature. Proc. Okla. Acad. Sci. 62: 57-62.

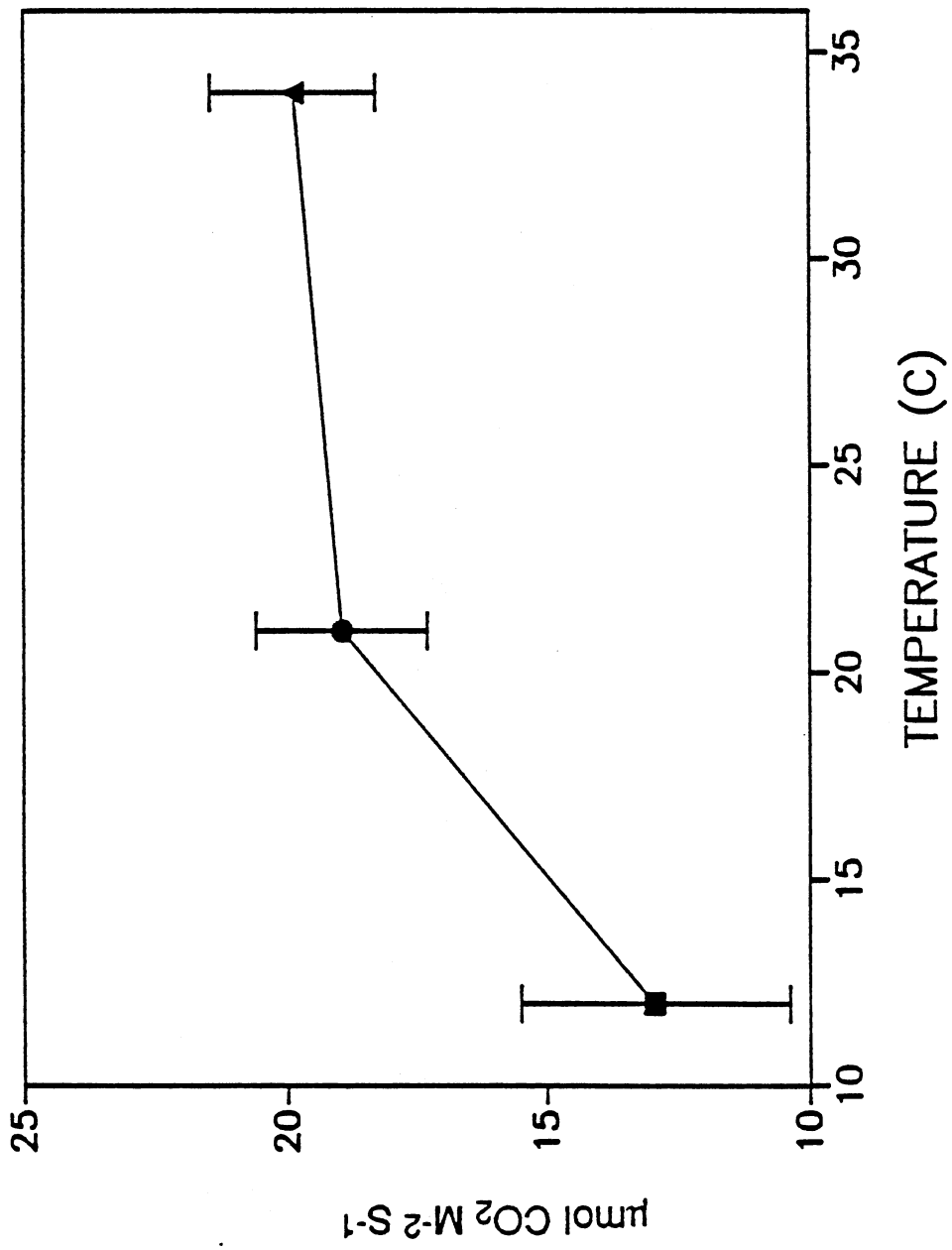
24. Ueno, M., and D. Smith. 1970. Influence of temperature on seedling growth and carbohydrate composition of three alfalfa cultivars. Agron. J. 62: 764-767.

25. Vough, L. R., and G. C. Marten. 1971. Influence of soil moisture and ambient temperature on yield and quality of alfalfa forage. Agron. J. 63: 40-42.

Fig. 1. Net photosynthetic rate of alfalfa shoots grown under day/night temperature regime of 12/2, 21/8 or 34/25.

Fig. 2. Respiration rate of alfalfa shoots grown under day/night temperature regime of 12/2, 21/8 or 34/25.

Fig. 3. Respiration rate of alfalfa root grown under day/night temperature regime of 12/2, 21/8 or 34/25.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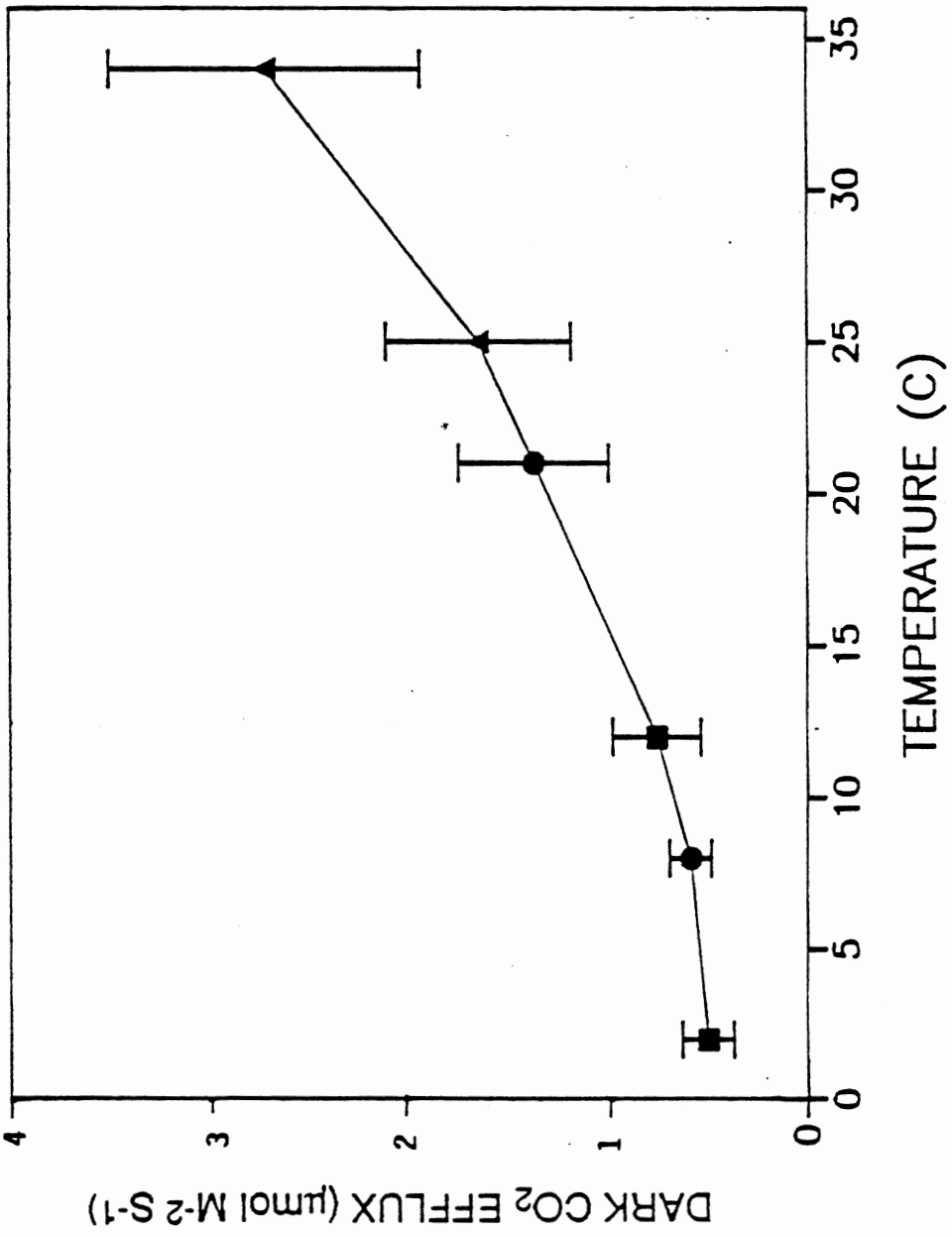
TEMPERATURE (C)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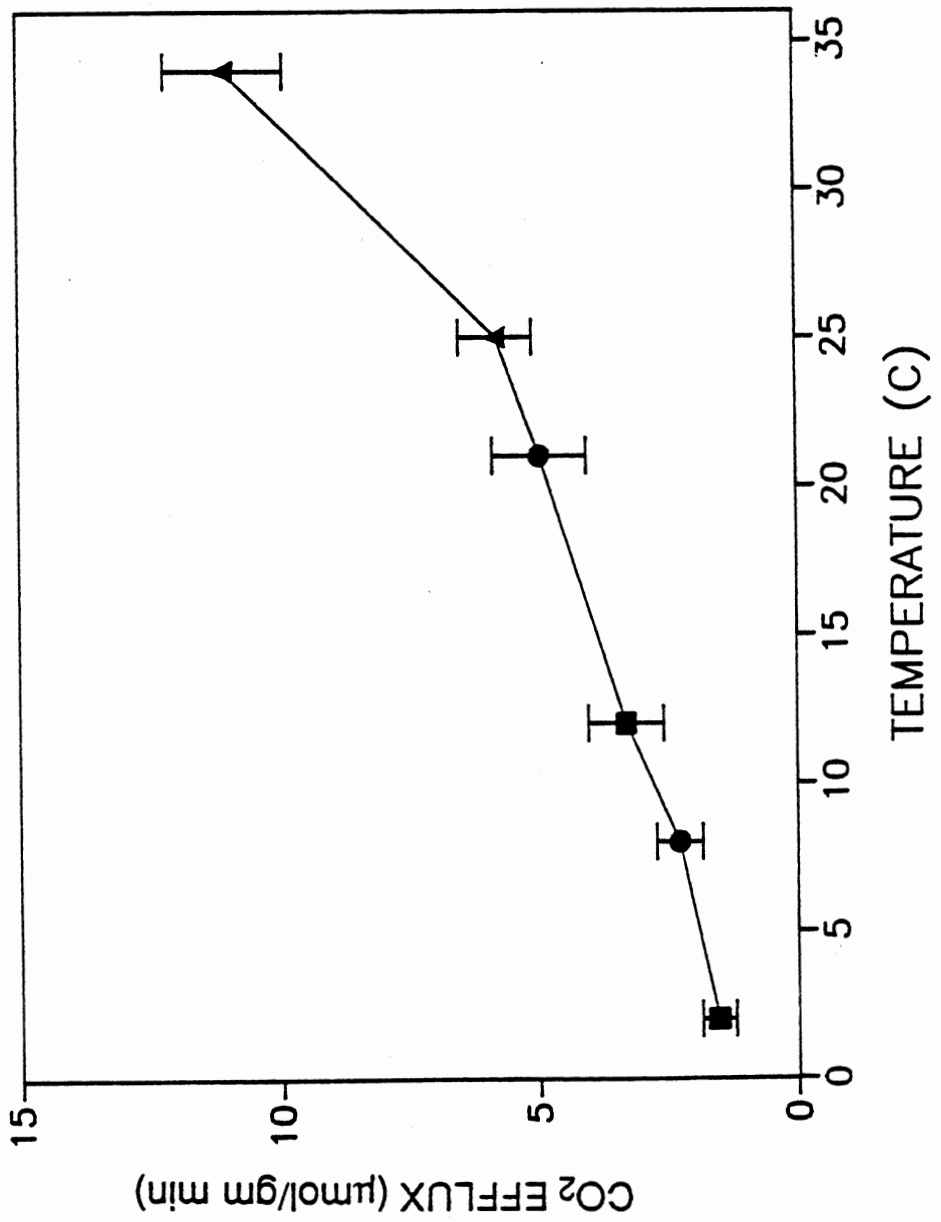
CO2 EFFLUX (µmol/gm min)
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TEMPERATURE (C)

Table 1. Influence of temperature regime on several growth parameters of alfalfa.

Temperature (day/night)	Plant height	Shoot dry wt	Root dry wt	Shoot/root ratio	Leaf area
°C	cm	g	g		cm^2
12/2	32.33 a**	3.50 a*	4.20 a*	0.84 a**	369.05 a*
21/8	68.77 b	6.37 b	5.60 b	1.14 b	812.04 b
34/25	58.50 c	4.83 c	3.06 c	1.57 c	583.80 c

* Means followed by the same letter in each column are not significantly different at .05 level of probability, based on LSD test.
** Means followed by the same letter in each column are not significantly different at .01 level of probability, based on LSD test.

Table 2. The effect of growth temperature on chlorophyll content in alfalfa leaves.

Temperature (day/night)	Chlorophyll a	Chlorophyll b	Chlorophyll a/Chlorophyll b
°C	-----mg Chlorophyll / gm. fresh weight-----		
12/2	2.63 a*	0.58 a*	4.53 a*
21/8	3.36 ab	0.80 b	4.20 a
34/25	4.05 b	0.99 c	4.09 a

* Means followed by the same letter in each column are not significantly different at the 0.05 level of probability, based on LSD test.

Table 3. The effect of growth temperature on total nonstructural carbohydrate (TNC) in alfalfa roots.

Temperature (day/night)	TNC
°C	%
12/2	28.04 a*
21/8	32.27 b
34/25	18.77 c

*Means followed by the same letter in each column are not significantly different at the 0.05 level of probability, based on LSD test.

Effect of Temperature on Photosynthate Partitioning

in Alfalfa

Safaa Al-Hamdani, and G. W. Todd

ABSTRACT

Translocation and circulation of photosynthate in alfalfa *(Medicago sativa* L.) plants was measured under three temperature regimes (12/2, 21/8, and 34/25°C day/night) representing conditions during winter, spring and summer in Oklahoma. Plants were grown under greenhouse conditions for approximately 3 months and then clipped back. When regrowth was at the bud stage, the plants were placed in growth chambers at the three temperatures, all having a day length of 14 h. Two hours after the onset of the photoperiod of the second day, foliar application of ^{14}C-labelled urea was used to provide a source of $^{14}CO_2$ for tracing the movement of photosynthate from the source leaf to other parts of the alfalfa plant. Plants were harvested 24 h later and each plant subdivided into six portions. The plant parts included the source leaf, treated upper shoot, treated lower shootd, untreated shoot, crown, and roots.

The percent of ^{14}C exported of the total recovered radioactivity by the source leaf was significantly influenced by the temperature regimes. The plants in the 34/25°C regime showed the highest percent of ^{14}C export followed in descending order by those in 21/8 and 12/2°C. Radioactivity recovery was increased in treated upper shoot, untreated shoots, and roots as temperature increased. The highest recovery of ^{14}C from the crown was obtained from the plants which were treated with 21/8°C followed by those in 12/2 and 34/25°C. Total ^{14}C recovered from the treated lower shoot was decreased as temperature increased. The results also showed that at the bud stage of growth, the roots were the major sink of photosynthate from the source leaf.

Additional index words: Source-sink relation, ^{14}C export, total radioactivity recovery, and *Medicago sativa* L.

Photosynthate translocation in phloem is considered to be a physical process driven by an osmotically induced pressure gradient from source to sink (8). The rate of photosynthate transport is an important physiological parameter because alteration in translocation rate can influence plant productivity. Chatterton (2) studied the relationship between net carbon dioxide exchange rate and specific leaf weight of alfalfa *(Medicago sativa* L.). He concluded that a reduction in rate of photosynthate translocation from the leaf resulted in increasing the specific leaf weight which may be responsible for reduced photosynthesis and subsequently reduced plant growth. In addition, evidence was provided in several studies (7, 9, 15, 19) that sink demand for photosynthate influenced leaf photosynthesis, carbohydrate formation, and export. On the other hand, sink demand for photosynthate was found to be highly influenced by its temperature (12, 21).

Hewitt and Curtis (10) reported that carbohydrate export from the source leaf of milkweed *(Asclepias syriaca* L.), tomato *(Lycopersicum esculentum* Mill.), and bean *(Phaseolus vulgaris* L.) was significantly greater when the plants were held in darkness for 13 h at 30°C compared with 10 and 4°C. Swanson and Whitney (18) studied the influence of petiole temperature of bean plants on the rate of distribution of foliar-applied ^{32}P, ^{42}K, ^{45}Ca and ^{137}Cs. After 4 h at 5°C, translocation was inhibited by 85 percent or more when compared with the 30°C optimum. However, translocation dropped to between 25 to 60 percent of the optimal rate when temperature rose to above 40°C.

Most partitioning studies in alfalfa were conducted at day temperatures between 20 and 25°C (4, 5, 6). However, data representing the effect of high or low temperature on photosynthate partitioning in alfalfa are lacking. The present study was conducted to obtain information on the influence of selected temperature regimes on translocation and circulation of photosynthate within the alfalfa plant. The temperatures were selected on the basis of average daily maximum and minimum temperatures during winter, spring and summer months in central Oklahoma.

METHODS AND MATERIALS

Alfalfa cultivar 'Cody', which is adapted to the southern plains was selected for this study. Scarified seed was treated with the fungicide Captan [*cis*-N-((trichloro-methyl)thio)-4-cyclohexene-1,2-dicarboximide] and then planted in plastic pots 11 cm diameter x 14.5 cm deep. Pots were filled with a 2:1:1 mixture of sand-vermiculite-perlite. Seedlings were thinned to 1 plant per pot at 2 weeks after germination. The plants were grown under greenhouse conditions for 3 months. Temperature in the greenhouse was between 20 and 30°C during the months of establishment. The shoots were harvested when plants were at 50% bloom. Twenty-five days after shoots removal, when regrowth was at the bud stage, the plants were randomly placed in equal numbers within 3 controlled environment chambers. The temperatures in the growth chambers were 12/2, 21/8, and 34/25°C day/night with a 14 h photoperiod. Photosynthetic photon flux density was 520 $\mu Em^{-2}sec^{-1}$. Two hours after the onset of the photoperiod of the second day, foliar application of ^{14}C-labelled urea was used to provide a source of $^{14}CO_2$ for tracing the movement of photosynthate from the source leaf to elsewhere in the alfalfa plant. The selection of the source leaf was based on full maturation and a position at the midpoint of the selected stem. The use of ^{14}C-urea as a source of ^{14}C was based on the premise that ^{14}C in urea is photosynthetically fixed after urea is absorbed by the leaf and hydrolysed by urease to give $^{14}CO_2$ and NH_3. This was shown to occur in several plants including bean (22), and lupin *(Lupinus angustifolius* cv.) (16).

Prior to labelling the plant with ^{14}C-urea, the surface of the source leaf was treated with droplets of 0.01% surfactant (Triton X-100) and allowed to dry. The ^{14}C-urea was then applied directly as a 2 µl droplet (containing 0.01% surfactant) to each of the three leaflet. Total ^{14}C-urea droplets gave a dose rate of 2.8 µCi/plant.

Plants were harvested 24 hours later and each plant subdivided into six parts. As shown in Fig. 1, the plant parts included the source leaf, treated upper shoot, treated lower shoot, untreated shoots, crown, and roots. All of the plant parts were freeze-dried and

subsequently ground in a Wiley mill. Subsamples of 0.08 g were taken from each plant sample and homogenized in 95% ethanol with a high speed homogenizer. Samples of 0.5 ml from the homogenate were assayed for radioactivity by liquid scintillation counting.

The radioactivity in the various parts of the plant was expressed as relative specific activity (RSA) and as percent of total plant radioactivity (%TPR) (4, 6) according to the following equations:

$$RSA = \frac{\text{dpm/g dry weight of a given part}}{\text{dpm/g dry weight of the whole plant (excluding the source leaf)}}$$

$$\%TPR = \frac{\text{dpm of plant part}}{\text{dpm of the whole plant (including the source leaf)}} \times 100$$

where dpm is disintegrations per minute.

In addition, the radioactivity of plant parts and the percent of ^{14}C exported by the source leaf (% Exp) was calculated from the formula:

$$\text{dpm of the plant part} = \text{dpm (subsample)} \times \frac{\text{mass of whole sample}}{\text{mass of subsample}}$$

$$\%\ Exp = \frac{\text{dpm of the whole plant (excluding the source leaf)}}{\text{dpm of the whole plant}} \times 100$$

This experiment was statistically analyzed as a 3x3 latin square and mean separations were based upon the LSD test.

RESULTS AND DISCUSSION

The percent of ^{14}C exported by the source leaf was significantly different among the three temperature regimes (Table 1). The plants in the 34/25°C regime showed the highest percentage of ^{14}C exported followed in descending order by those in 21/8 and 12/2°C. Marowitch et al. (13) observed similar temperature dependence curves for photosynthate translocation in bean and soybean *(Glycine max* L.). Measuring translocation as the accumulation of ^{14}C in the sink leaf, they found that the translocation rate showed a continuous increase with increasing growth temperature from 5 to 40°C. In addition, Hilliard and West (11) noted that starch grains disappeared from the chloroplast of pangola grass *(Digitaria decumbens)* after 12 h of darkness at 30°C. In contrast, the starch grains remained in the chloroplast after the same period of darkness at 10°C.

The reduction in photosynthate translocation from the source leaf with decreasing temperature is probably due, in part, to a direct effect of low temperature on transport. In addition, a low respiration rate of alfalfa was reported at low temperatures (1, 14) and this probably influenced sink demand.

There were no significant statistical differences in total plant recovered radioactivity among the three temperature regimes (Table 1). However, a decreasing trend in total plant recovered radioactivity was obtained with an increase in temperature. This may be the result of an increased hydrolysis rate of urea in the source leaf resulting in a greater level of $^{14}CO_2$ being released from the plant.

Trends in photosynthate partitioning among the three temperature regimes were similar regardless whether the measurement was RSA or %TPR (Tables 2 and 3). The radioactivity recovery increased in the treated upper shoot, untreated shoots, and roots as temperature increased. The highest recovery of ^{14}C of the crown was obtained from the plants which were treated with 21/8°C followed in descending order by those in 12/2 and 34/25°C. Total ^{14}C recovered from the treated lower shoot decreased as temperature increased. This was probably as a direct effect of high temperature in enhancing

photosynthate translocation to sink areas, causing most of ^{14}C to be transported out of this region to other plant parts.

The highest percent of total radioactivity recovery among the plant parts under the three temperature regimes was obtained from the roots followed by untreated shoots (Table 2). This was a result of the largest proportions of the plant's mass being from the root and untreated shoot, respectively. However, a relatively small concentration of ^{14}C was recovered from roots and untreated shoots as shown when photosynthate partitioning was measured as RSA (Table 2).

Among all the plant parts measured for photosynthate partitioning, the treated upper and lower shoot had the highest RSA in all three temperature regimes (Table 3). This result could have been caused by the short distance which separated the source leaf from the selected sinks. Cook and Evans (3) reported that ^{14}C partitioning among competing sinks of wheat *(Triticum aestivum* L.) was highly influenced by the distance between the ^{14}C source and sinks. The highest radioactivity was recovered from the sink closest to the source leaf. Thrower (20) obtained similar results with soybean. He found that the concentration of labelled photosynthate in the root and the shoot apex was inversely proportional to its distance from the source leaf.

The values of RSA and %TPR indicated that photosynthate partitioning to the root from the source leaf exceeded that obtained from the untreated shoots and crown in all three temperature regimes (Table 2 and 3). This result is in agreement with the findings of Pearce et al. (17). They measured the partitioning of photosynthate in alfalfa at a late stage of growth and found that 30% of the ^{14}C in the plant was recovered from crown and roots. Of this, nearly 75% was obtained from the large roots.

These data clearly showed that photosynthate export from source to sinks was increased by increasing the temperature. In addition, the highest RSA among the plant organs was obtained from the treated upper shoot and treated lower shoot which were the closest sinks to the source leaf. This supports the concept that photosynthate partitioning

is influenced in part by the distance separating the source from the sink. Furthermore, the root was shown as the major sink in alfalfa, at the bud stage, in relation to the total photosynthate export from the source leaf.

REFERENCES

1. Brown, R. H. and Radcliffe, D. F. 1986. A comparison on apparent photosynthesis in sericea lespedeza and alfalfa. Crop Sci. 26: 1208-1211.
2. Chatterton, M. H. 1973. Product inhibition of photosynthesis in alfalfa leaves as related to specific leaf weight. Crop Sci. 13: 284-285.
3. Cook, M. G. and Evans, L. T. 1978. Effect of relative size and distance of competing sink on the distribution of photosynthetic assimilates in wheat. Aust. J. Plant Physiol. 5: 495-509.
4. Cralle, H. T. and Heichel, G. H. 1985 . Interorgan photosynthate partitioning in alfalfa. Plant Physiol. 79: 381-385.
5. Cralle, H. T. and Heichel, G. H. 1986. Photosynthate and dry matter partitioning in effectively and ineffectively nodulated alfalfa. Crop Sci. 26: 117-121.
6. Cralle, H. T., Heichel, G. H. and Barnes, D. K. 1987. Photosynthate partitioning in plants of alfalfa populations selected for high and low nodule mass. Crop Sci. 27: 96-99.
7. Geiger, D. R. 1976. Effect of translocation and assimilate demand on photosynthesis. Can. J. Bot. 54: 2337-2345.
8. Giaquinta, R. 1983. Phloem loading of sucrose. Annu. Rev. Plant Physiol. 34: 347-387.
9. Hall, A. J. and Milthrope, F. L. 1978. Assimilate source-sink relationships in *Capsicum annuum* L. III. The effect of fruit excision on photosynthesis and leaf and stem carbohydrates. Aust. J. Plant Physiol. 5: 1-13.
10. Hewitt, S. D. and Curtis, O. F. 1948. The effect of temperature on loss of dry matter and carbohydrate from leaves by respiration and translocation. Am. J. Botany 35: 746-755.
11. Hilliard, J. H. and West 1970. Starch accumulation associated with growth reduction at low temperatures in a tropical plant. Science 168: 494-496.

12. Hurewitz, J. and Janes, H. W. 1983. Effect of altering the root-zone temperature on growth, translocation, carbon exchange rate, and leaf starch. Plant Physiol. 73: 46-50.

13. Marowitch, J., Richter, C. and Hoddinott, J. 1986. The influence of plant temperature on photosynthesis and translocation rates in bean and soybean. Can. J. Bot. 64: 2337-2342.

14. Murata, V., Lyama, J. and Honma, T. 1965. Studies on the photosynthesis of forage crops. IV Influence of air-temperature upon the photosynthesis and respiration of alfalfa and several southern type forage crops. Proc. Crop Sci. Jpn. 34: 154-158.

15. Neales, T. F. and Incoll, L. D. 1968. The control of leaf photosynthesis rate by the level of assimilate concentration in the leaf: A review of the hypothesis. Bot. Rev. 34: 107-125.

16. Pate, J. S. and Farrington, P. 1981. Fruit set in *Lupinus angustifolius* cv. Unicrop. II. Assimilate flow during flowering and early fruiting. Aust. J. Plant Physiol. 8: 307-318.

17. Pearce, R. B., Fissel, G. and Carlson, G. E. 1969. Carbon uptake and distribution before and after defoliation of alfalfa. Crop Sci. 9: 756-759.

18. Swanson, C. A. and Whitney, J. B. Jr. 1953. Studies on the translocation of foliar-applied ^{32}P and other radioisotopes in bean plants. Am. J. Bot. 40: 816-823.

19. Thorne, J. H. and Koller, H. R. 1974. Influence of assimilate demand on photosynthesis, diffusive resistance, translocation and carbohydrate levels of soybean leaves. Plant Physiol. 54: 201-207.

20. Thrower, S. L. 1962. Translocaton of labelled assimilates in the soybean II. The pattern of translocation in intact and defoliated plants. Aust. J. Biol. Sci. 15: 629-649.

21. Walker, A. J. and Ho, L. C. 1977. Carbon translocation in the tomato: effects of fruit temperature on carbon metabolism and the rate of translocation. Ann. Bot. 41: 825-832.

22. Webster, G. C., Varner, J. E. and Gansa, A. N. 1955. Conversion of carbon-14-labelled urea into amino acid in leaves. Plant Physiol. 30: 372-374.

Fig. 1. Schematic Drawing of an Alfalfa Plant Illustrating the Plant Organs Used in ^{14}C Determination.

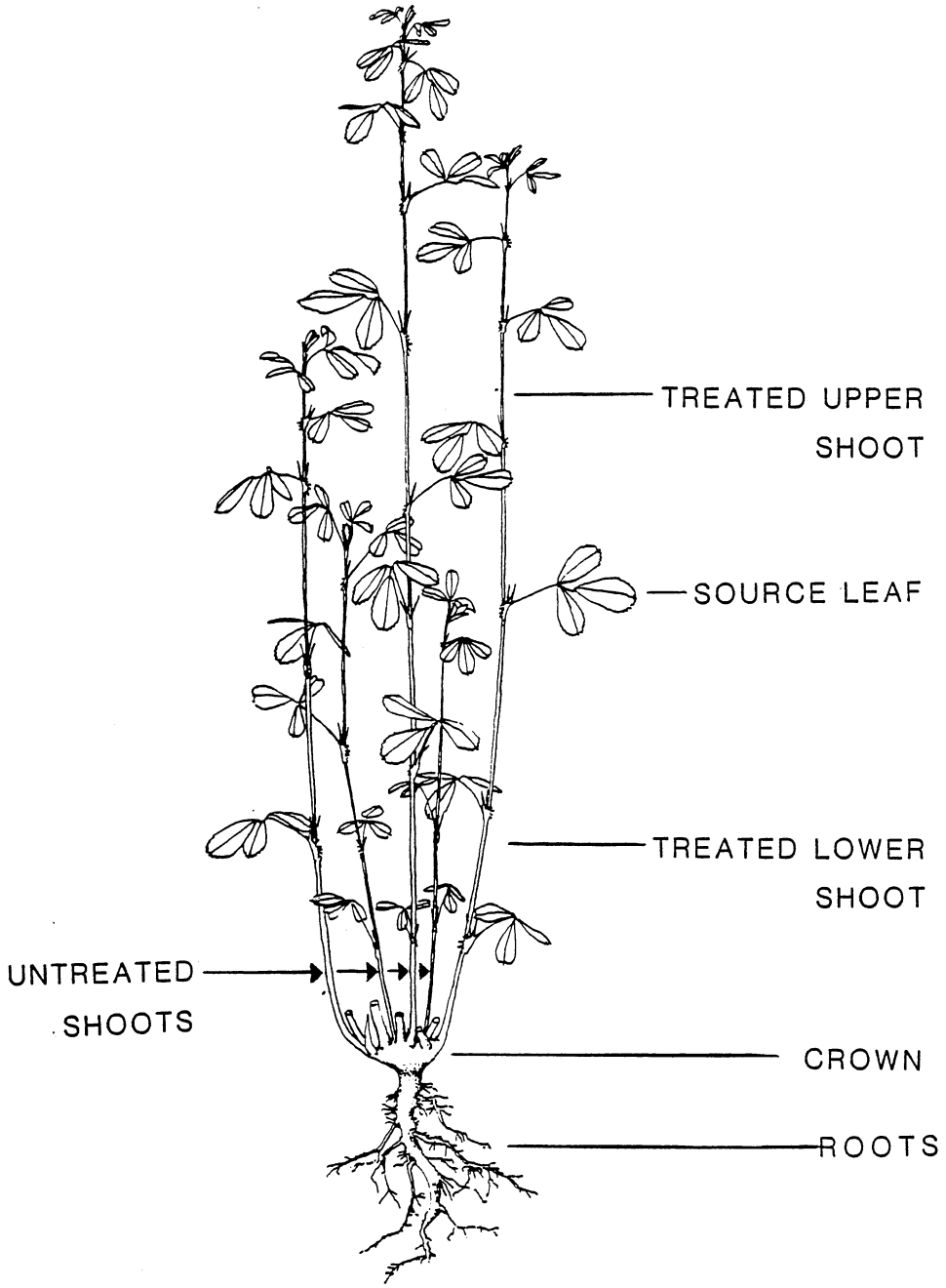
TREATED UPPER SHOOT
SOURCE LEAF
TREATED LOWER SHOOT
UNTREATED SHOOTS
CROWN
ROOTS

Table 1. Effect of temperature regimes on percent of ^{14}C exported (EXP) by the source leaf and on the total plant recovered radioactivity (TPR).

Temperature (day/night)	EXP	TPR
°C	%	DPM†
12/2	75.2a*	413402.1a
21/8	81.8b	330304.4a
34/25	89.4c	273782.4a

*Means within a column followed by the same letter are not significantly different at the 0.05 level of probability, based on LSD test.

†DPM (disintegrations per minute).

Table 2. Effect of temperature regime on photosynthate partitioning, expressed as % TPR (percent of total plant recovered radioactivity), among various plant organs of alfalfa 24 h after urea ^{14}C application to source leaf.

Temperature (day/night)	Treated upper shoot	Treated lower shoot	Untreated shoot	Crown	Root
°C	----------%TPR----------				
12/2	5.4a*	9.9a	19.4a	8.5a	31.9a
21/8	7.1a	8.3a	24.1a	9.7b	32.5a
34/25	9.8b	6.3a	30.4b	7.5a	35.4b

*Means within a column followed by the same letter are not significantly different at the 0.05 level of probability, based on LSD test.

Table 3. Effect of temperature regimes on photosynthate partitioning, expressed as RSA (relative specific activity) among various plant organs of alfalfa 24 h following urea ^{14}C application to source leaf.

Temperature (day/night)	Treated upper shoot	Treated lower shoot	Untreated shoot	Crown	Root
°C	----------%TPR----------				
12/2	1.3a*	2.6a	0.6a	0.9ab	1.1a
21/8	1.7ab	1.8b	0.7a	1.1a	1.2a
34/25	2.1b	1.7b	0.8b	0.8b	1.3a

*Means within a column followed by the same letter are not significantly different at the 0.05 level of probability, based on LSD test.

VITA

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Doctor of Philosophy

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