DIURNAL CHANGES IN THE SPECIFIC LEAF WEIGHT OF NON-DORMANT ALFALFA CULTIVARS

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Abstract: Specific Leaf Weight (SLW) is one of the few morphological characteristics that exhibits diurnal fluctuation. This field study was conducted to monitor the diurnal variation in SLW of non-dormant alfalfa (Medicago sativa L.) and to compare the SLW fluctuation of highly divergent alfalfa populations. The SLW of a single cultivar (cv. 'Mesa-sirsa') was assessed every 2 hours for 32 hours to determine the time of day of minimum and maximum SLW and 12 alfalfa cultivars, with significantly different yield capabilities, were evaluated for their change in SLW at 0600 and 1600 hours. Highest SLW occurred late in the afternoon before sunset and lowest values in the morning just following daybreak. The average change in SLW during the course of single day was greater than 21%. Cultivars varied more in their degree of diurnal change in SLW than in their average SLW. Higher yielding cultivars appeared to have a lower early morning SLW and a greater increase in SLW during the daylight hours than less adapted populations. The diurnal effect on leaf weight determination in alfalfa is significant and should be considered when interpreting SLW data. Time-course SLW studies provide an effective way of evaluating the accumulation and translocation of photosynthate in leaves.

Keywords: Alfalfa, specific leaf weight.

INTRODUCTION

Extensive studies have been conducted on the leaf morphology and physiology of alfalfa (Medicago sativa L.) due to the important contribution of the foliage to nutritional quality and yield (Fick et al., 1988). During the 1970s a foliage characteristic that received particular research attention was Specific Leaf Weight (SLW) which is the ration of leaf dry weight to its surface area. Researchers have reported significant positive correlations between photosynthetic rate and leaf thickness (Delaney and Dobrenz, 1974) and SLW (Pearce et al., 1969) but there is no consistent relationship between photosynthetic rate and alfalfa yield (Heichel et al., 1988). Porter and Reynolds (1973) and Song and Walton (1975) reported a lack of significant relationship between SLW and yield in alfalfa.

The high degree of environmental, phenological, and morphological (leaf position) variability that exists may explain the lack of correlation between SLW and yield. Delaney et al., (1974) reported significant seasonal and plant-spacing effects on SLW and Barnes et al. (1969) demonstrated significant variation in SLW attributable to alfalfa cultivar and plant age. Chilcothe et al. (1981) suggested that due to this variability, large numbers of SLW measurements are required to elucidate actual SLW:yield relationships.

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There are also reports of significant differences in Specific Leaf Weight of alfalfa related to time of day that SLW was measured (Chatterton et al., 1972). The SLW of field-grown alfalfa changes during the day primarily due to the interplay of photosynthate accumulation and translocation. This diurnal effect is characterized by an increase in SLW during the daylight hours, primarily as a result of photosynthate accumulation in the leaves, and a decrease in SLW at night, due to respiration and translocation of carbohydrates out of the leaves (Lechtenburg et al., 1971). Due to a negative relationship between photosynthetic rate and SLW (Chatterton, 1973), leaf carbohydrate build-up may play a role in the feedback inhibition of photosynthesis in leaves (Travis and Prendergast, 1987). Results of CO_2-enrichment and defoliation studies of alfalfa at the seedling and mature plant stages have shown that while size of the photosynthetic source may limit CO_2 fixation in the former the size of the photosynthate sink limits CO_2 fixation in the latter stage (Baysdorfer and Bassham, 1985).

Specific Leaf Weight is unique for its ease of measurement and dynamic response to the environment and could provide a practical way for plant breeders to evaluate photosynthate sink:source relationships in alfalfa germplasm. The objectives of this research were to: 1) document the complete diurnal pattern in SLW in plants of a single alfalfa cultivar grown in the field, 2) compare the diurnal patterns in SLW of 12 highly divergent alfalfa populations, and 3) test whether hourly changes in SLW might be a reliable indicator of forage yield potential in alfalfa.

MATERIALS AND METHODS

Diurnal Study: This study was conducted at Tucson, AZ (760-m elevation). Ten plants of the non-winter-dormant alfalfa cultivar 'Mesa-Sirsa' that had been space planted as seedlings in a 1-m grid in November, 1984 were used. Soil was a Comoro loamy sand (coarse-loamy, mixed, calcareous, thermic Typic Torrifluvent). Specific Leaf Weight determination was made when plants were in their third regrowth period of the 1985 growing season. Plants were in the bud stage and had approximately 60 stems when evaluated.

Specific Leaf Weight measurements were made at 1200 h and were continued at 2 hour intervals for the next 32 hours. Ten leaflets were randomly removed from each of the 10 plants for each measurement. Individual leaflets were fully expanded and selected from the top five nodes of the plants below the growing point and thus exposed to full sunlight. Leaflet areas were determined using an electronic area meter LI-COR, Inc., Lincoln, NB), dried for 24 hours at 80°C and weighted.

Leaf transpiration rates were measured with a LI-COR 1600 steady state porometer (LI-COR, Inc., Lincoln, NB) at each sampling time. The porometer was also used to measure air temperature, relative humidity and photon flux density (PFD).

Total above ground dry matter production was determined 10 days after SLW was measured, when plants were at 50% bloom. Plants were harvested by hand leaving 0.1-m stubble.

Cultivar Study: Plants of 12 alfalfa cultivars grown in the field were compared for diurnal changes in SLW. These cultivars represent the entire spectrum of non-winter-dormant alfalfa germplasm from early plant introductions to modern-day cultivars popular in the southwestern U.S. The cultivars used in this study, and their approximate year of introduction to Arizona, were: 'Chilean' (1910), 'Hairy Peruvian' (1923), 'African' (1924), 'Indian' (1943), 'Moapa' (1957), 'Zia' (1958), 'El Unico' (1964), Mesa-Sirsa (1966), 'Moapa-69' (1971), 'UC Cargo' (1975), 'Lew' (1976) and 'CUF-101' (1980) (Melton et al., 1988). Plots consisted of 2-m-long single rows, spaced 0.5m apart with four replications arranged in a randomized complete block design. Lew was planted on the perimeter to remove border effects. The test had been planted in October 1987.

Based upon results of the diurnal study determinations of SLW were made at 1600 h and at 0600 and 1600 h the following day. Single leaflets from ten different plants in each of the 48 plots were removed each sampling time. Plants were in the pre-bud stage of growth. SLW was measured as previously described. The test was harvested 15 d after SLW measurements were made. Immediately before harvest plots were ranked for vigor (1=least vigorous, 5=most vigorous) and percent stand. Yield data is expressed on a dry matter basis.

RESULTS AND DISCUSSION

Diurnal Study: Changes in temperature, relative humidity and light radiation (PFD) in the field over the course of this study are shown in Figure 1. There was no measurable PFD between 2000 and 0400 h and PFD increased most rapidly between 0800 and 1000 h reaching its maximum (2100 μmol m^{-2}s^{-1}) between 1200 and 1400 h. The most rapid decrease in PFD occurred between 1600 and 2000. Air temperatures were highest from 1200 to 1600 h and lowest at 0600. The maximum temperature on the first afternoon was 20°C higher than during the second afternoon. Relative humidity in the field was highly variable but tended to be greater in the late morning and lower in the early evening.

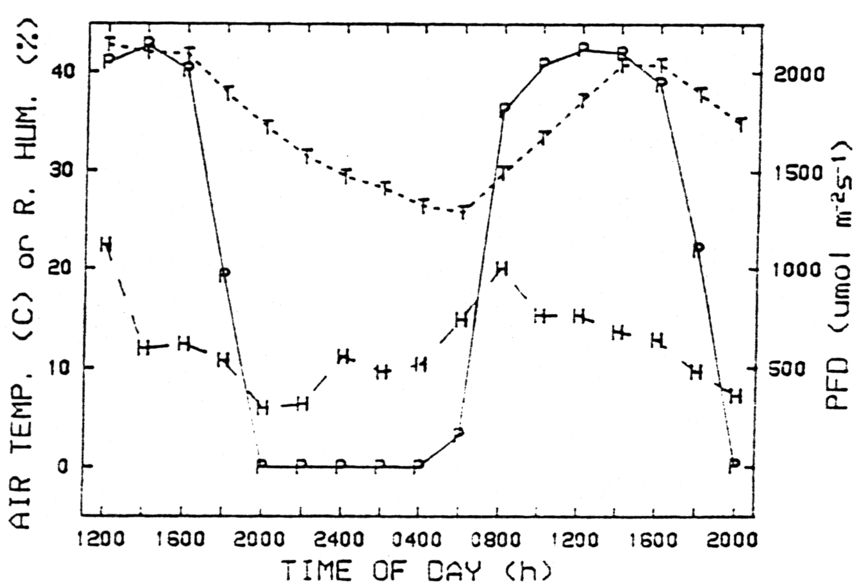

Fig. Fluctuations in air temperature (T), Relative Humidity (H), and Photon Flux Density during SLW measurements.

Specific Leaf Weight exhibited a sigmoid-shaped response throughout the day, increasing during the daylight hours and decreasing at night. Specific Leaf Weight was lowest at 0600 h and steadily increased soon after sunrise presumably due to photosynthate accumulation (Fig. 2).

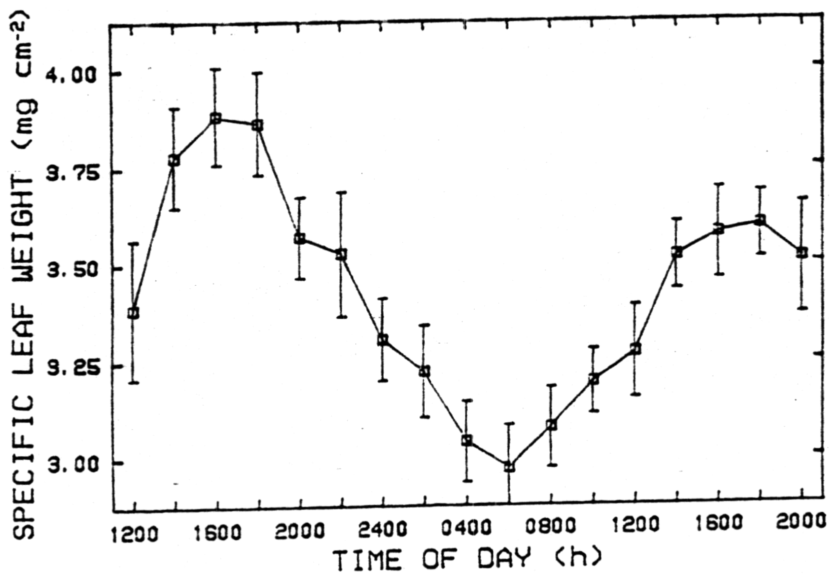

Fig. 2. Changes in Specific Leaf Weight during the course of the diurnal study. Plants were in the bud stage. Each data point represents the mean of ten plants ± SE.

About 0.62 mg cm^{-2} of dry matter was added to the leaves during the daylight hours of the second day causing SLW to reach its maximum at 1800 h. This is equivalent to an increase in mean SLW of 21% over the 12-hour daylight period. Peak SLW values during the first afternoon were significantly higher ($P \leq 0.02$) than during the second afternoon, possibly due to unmeasured change in plot environment or alteration of the plants due to repeated leaf sampling. On the first day, SLW began decreasing at 1600 hours and continued to decrease linearly until sunrise. The mean decline in SLW was 0.91 mg cm^{-2}, representing a 23% decline over the 14-hour evening period.

The average SLW for the ten plants used in this study, across the 32-hour period was 3.43 mg cm^{-2}. Specific Leaf Weight values for individual plants varied from 2.99 to 3.97 mg cm^{-2}. The average coefficient of variation for the ten plants during the course of this study was a constant 11%. Forage yield for the plants averaged 189 g per plant with a coefficient of variation of 23%. No significant correlations were observed between plant dry matter production and rate of SLW increase ($r=0.09$) or SLW decline ($r=0.18$).

Cultivar Study: The cultivar study was conducted to determine if there was a genetic effect on the diurnal changes in SLW in nondormant alfalfa. There were significant differences in forage yield between the 12 varieties, ranging from 283 to 571 g plot^{-1} (Table 1).

Table 1. Year of release, Specific Leaf Weight and forage yield of 12 alfalfa cultivars, from the cultivar study, at 1600 h and at 0600 and 1600 h the next day.

	Year of	Yield *	SLW (mg cm^{-2})		
Cultivar	Release	(g plot-1)	1600*	0600$	1600$
Chilean	1910	375 cde	3.96 a	3.20	4.10
Hairy Peruvian	1923	413 bcd	3.93 a	3.21	3.94
African	1924	283 e	3.94 a	3.38	4.02
Indian	1943	352 de	3.77 ab	3.28	4.01
Moapa	1957	410 bcd	3.89 a	3.18	4.14
Zia	1958	524 ab	3.42 b	2.96	3.86
El Unico	1964	491 abc	3.60 ab	3.12	4.10
Mesa-Sirsa	1966	571 a	3.76 ab	2.94	4.04
Moapa-69	1971	388 cde	3.89 a	3.12	3.99
UC Cargo	1975	374 cde	3.84 a	3.16	3.91
Lew	1976	485 abc	3.63 ab	3.01	4.02
CUF-101	1980	457 abcd	3.68 ab	3.08	4.01

Means with the same letter are not significantly different by the LSD test at the 0.05 level of significance.

$ No differences at the 0.05 level of significance.

Contemporary cultivars tended to outyield older cultivars. There was greater variability in SLW among the 12 cultivars during the initial sampling in the late-afternoon of the first day than during the next day's readings. There was no significant interaction between genotypes for SLW and time of day. Cultivars differed significantly in mean SLW and at the first SLW reading at 1600 h on the first day but not for the other two sampling times. Generally, ancestral cultivars appeared to have a higher mean SLW than did the more modern cultivars.

No significant relationship was observed between leaflet area and yield or SLW in these materials (Table 2).

Table 2. Correlation coefficients of yield, yield components and Specific Leaf Weight of 12 alfalfa cultivars, from the cultivar study. SLWpm1 represents Specific Leaf Weight measured at 1600 h while SLWam1 and SLWpm^{2} were measured at 0600 and 1600 h, the next day.

	Yield	Rank	Stand	LA	SLWpm1	SLWam1	SLWpm2	xSLW	SLW Dc.	SLW In.
Vigor Rank	0.81**	----	----	----						
Stand (%)	0.84**	0.90**	----	----						
Leaflet Area (cm^{2})	0.47	0.34**	0.32	----						
SLWpm1 (mg cm^{-2})	-0.70*	-0.32	-0.49	-0.27	----					
SLWam2 (mg cm^{-2})	-0.93**	-0.80**	-0.78**	-0.36	0.68*	----	----			
SLWpm2 (mg cm^{-2})	-0.06	-0.13	-0.07	0.43	0.33	-0.20	----			
Mean SLW (mg cm^{-2})	-0.79**	-0.55	-0.61*	-0.19	0.92**	0.85**	0.52			
SLW Decrease (%)	0.16	0.49	0.26	0.02	0.53	-0.26	0.18	0.23		
SLW Increase (%)	0.86**	0.69*	0.69*	0.50	-0.47	-0.87**	0.30	-0.55	0.38	----
SLW Activity (%)	0.70*	0.75**	0.64*	0.41	-0.08	-0.75**	0.30	-0.29	0.75**	0.89**

* Significant at the 0.05 level.
** Significant at the 0.01 level.

Specific Leaf Weights from the readings on first the afternoon were negatively correlated with yield whereas the readings from the second afternoon were not. negative correlations were also observed between forage yield and early morning SLW. The morning SLW was significantly negatively correlated with vigor rank and percent stand. Hart et al. (1978) also reported a negative relationship between yield and SLW of spaceplanted alfalfa.

Change in SLW during the day differed significantly among cultivars. Those cultivars that exhibited the greatest percent increase in SLW during the daylight hours also tended to produce higher forage yields (Fig. 3),

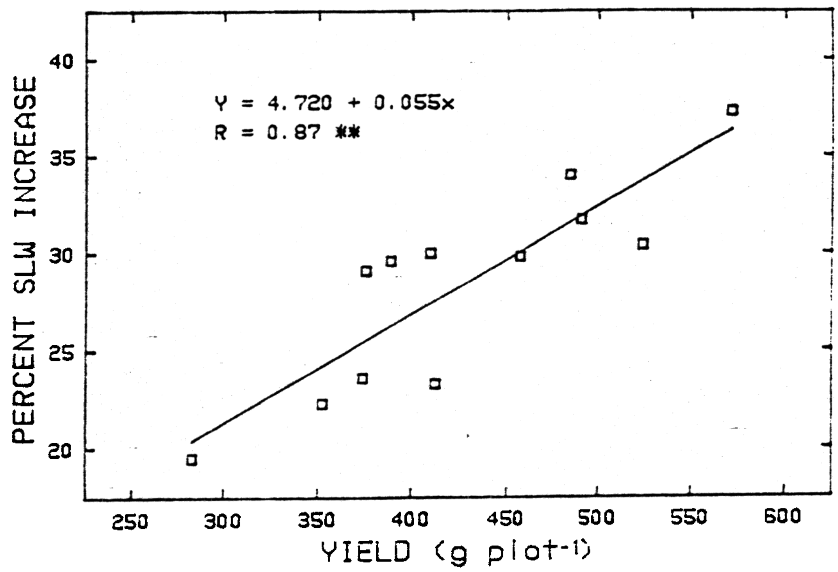

Fig. 3. Relationship between forage yield and percent increase in Specific Leaf Weight from 0600 to 1600 h for 12 cultivars.

higher vigor rankings and better stands (Table 2). There was no relationship between the various yield components and percent decline in SLW at night. When the total change in SLW was determined and expressed as percent of the mean SLW those cultivars showing the greatest diurnal SLW fluctuation also showed greater yield, stand and rank. The higher yielding cultivars, therefore, may have the ability to continue fixing CO_2 during the afternoon in spite of product-feedback inhibition mechanisms.

Specific Leaf Weight is an easily determined characteristic in leguminous forages, like alfalfa, and responds in a dynamic fashion to both the environmental and physiological changes that occur diurnally. There appears to be a closer relationship between plant vigor and SLW measured in the early morning hours or the relative increase in SLW during the daylight period than for single SLW measurements taken in the afternoon. Future studies involving Specific Leaf Weight determination need to take diurnal variability into account.

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