A PHYSIOLOGICAL STUDY OF MULTIFOLIOLATE ALFALFA (*MEDICAGO SATIVA* L.)

by

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This work is dedicated to my parents,
Pauline and Ed Retzinger,
whose love and moral support
made this thesis possible.

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ABSTRACT

Populations of trifoliate 'Mesa-Sirsa' and multifoliolate alfalfa (Medicago sativa L.) were evaluated for rates of CO_2 exchange, morphological characteristics, forage yield, total percent protein, and chlorophyll and carotinoid pigments when grown under field conditions. The purpose of this study was to determine if differences in several morphological and physiological characteristics existed between the normal trifoliate (TF) and multifoliate germplasm and if these characteristics were significantly related to yield. Thirty-five percent of the multifoliolate (MF) plants exhibited the MF characteristic.

Apparent photosynthesis and post-illumination CO_2 bursts were significantly higher at each harvest for the multifoliolate population when CO_2 exchange was expressed on a unit leaf area basis. Yield was not significantly different between the two germplasm sources. Yield was significantly and positively correlated to apparent photosynthesis at 2 (r = .58*) and 3 (r = .45*) weeks before harvest when expressed per unit leaf area.

Specific leaf weight was negatively correlated to yield and leaf area index. The protein and chlorophyll content of Mesa-Sirsa and the multifoliolate synthetic were not significantly different. Primary leaflet contents of chlorophyll and carotinoids decreased in a significant linear manner progressing from the bottom to the top of the plant.

INTRODUCTION

Alfalfa is one of the most valuable and widely grown forages. The proper management of this perennial species is of great importance in the maintenance of a vigorous and long-lived stand. To discover the physiological basis of variation in crop yield it is necessary to supplement laboratory studies with direct observations on crops growing in field conditions.

Most of the physiological processes that affect the conversion of CO_2 occur in the leaves. The morphological, physiological, and genetic characteristics of the alfalfa leaf have been scrupulously examined. Positive association of leaf size to yield has been reported by Leavitt (1975). Dobrenz, Cole, and Massengale (1971) reported that dry weight production among alfalfa cultivars was due to an increase in stem and petiole tissue rather than leaf area or total leaf weight. Brick (1975), in a genetic study of the multifoliolate traits in alfalfa, found significantly higher specific leaf weights in multifoliolate plants as compared to trifoliolate 'Mesa-Sirsa.' Brick suggested the multifoliolate characteristic could have an advantage in dry matter production.

The research reported here was designed to determine the morphological and physiological characteristics associated with multifoliolate and 'Mesa-Sirsa' alfalfa grown in the field.

REVIEW OF LITERATURE

Carbon fixation through photosynthesis is the source of nearly all dry matter yield. Carlson et al. (1970) reported that photosynthesis was a fundamental process and that it should be carefully evaluated as a possible selection criterion in a breeding program. These researchers indicated that sufficient genotypic variability exists to justify including it in a breeding program. They warned that if selection for net photosynthesis is to be effective it should be done over a range of environments. Rumbaugh (1963) found that selection indices based upon yield component data obtained in space clonal nurseries may not accurately portray the forage yield potentials of genotypes in solid seeding.

Dry matter production of a crop is the result of the net photosynthesis of individual plants (Alberda 1962). This researcher further suggested that once the photosynthetic efficiency of a green leaf has been estimated it is possible to calculate the upper level of potential crop production. Hanson (1971) and Donald (1962) reported the concept that photosynthetic production gives a reasonable prediction of dry matter yield. Donald further suggested that genetic factors influencing yield such as cell physiology, leaf area, and leaf arrangement do so principally by their effect on photosynthesis. This researcher believed that knowledge of plant stature and leaf concentration, like that of leaf angle was inadequate but clearly of first importance for attaining increased yields. Photosynthetic efficiency has been correlated to leaf size, cell morphology, and water use by Cope and Rawlings (1970), and Parkhurst and Loucks (1972), and Delaney (1972).

Results by Pearce, Brown, and Blazer (1967a) showed that a linear relationship exists between light interception and net photosynthesis at any given angle in barley (Hordeum vulgare L.). They grew barley in flats at various angles to simulate leaf angle and concluded there was no advantage to leaf angle over a diurnal cycle. The most efficient utilization of light on a diurnal basis is associated not only with leaf arrangement but also with leaf morphology.

Carlson et al. (1970) found that net photosynthesis was positively related to yield which depends upon the effect of light interception, photosynthate translocation and utilization. They concluded that the differences in net photosynthesis, which are associated with an easily measured morphological trait, exist in alfalfa.

A significant yield advantage has been shown to exist in large leaflet populations when compared to small leaflet populations (Leavitt 1975). Leavitt concluded the increased yield was due to the total leaf area per plant. This relationship was also found in crownvetch (Coronilla varia L.) Cope and Rawlings (1970) and in barley by Yap and Harvey (1972) and Berdahl, Rasmusson, and Moss (1972). Significantly higher kernel weights were observed in the large leaf lines.

Significant correlations between respiration and leaf area index (LAI = units of leaf area, one side, above units ground area), were reported by Wilfong, Brown, and Blazer (1967). Their investigations indicated that leaf area to leaf weight ratios increased along with LAI in all alfalfa plots. The respiration per unit leaf area at high LAI's suggested to them that more leaves could be added to the stand without proportionately increasing total respiration. Pearce, Brown, and Blazer (1967b) found that as the LAI increased, light penetration decreased exponentially to a value of 1% at an optimum LAI after which it slowly declined. This occurred at all light intensities, but the optimum LAI was less at low light intensities. These scientists concluded that respiration per unit of LAI for natural communities remained constant or was inversely related to LAI. Joy, Poole, and Dobrenz (1972) and Robinson and Massengale (1967) reported that LAI statistically did not appear to have practical application in the prediction of seasonal yields, however, LAI had a positive relationship to forage yield at individual cuttings. A close parallel between the plant dry weights at harvest and leaf areas were reported by Duncan and Hesketh (1968). Leaf area growth was not correlated with the rate of net leaf photosynthesis. These findings suggested that the accumulation of dry matter must be correlated day by day with the product of the leaf area and net photosynthetic rates. Therefore a plant which initiates leaves and produces a canopy faster could utilize sunlight more efficiently with more CO_2 being converted to plant carbohydrates. Smith, Mott, and Bula (1964) have shown that the LAI was an important factor in obtaining dry matter accumulation. They suggested that any factor which increased the photosynthetic capacity of a plant would be useful for increasing yields. Investigations by these scientists revealed that LAI was the most important single independent variable that accounted for variation in dry matter yield.

Delaney and Dobrenz (1974a) demonstrated that apparent photosynthesis was significantly associated with thickness of the palisade tissue. They concluded that leaflet size could serve as a morphological selection tool for photosynthetic rate. Foutz, Wilhelm, and Dobrenz (1976) reported that morphological factors were more reliable indicators of alfalfa production than the physiological factors. These scientists reported CO_2 uptake per unit leaf area was not correlated to yield. However, total apparent photosynthesis expressed on a per plant basis dry matter production was highly and significantly correlated (r = .90*). In both spaced and nonspaced planted studies total apparent photosynthesis per plant was highly correlated to yield. Osman (1971) also reported that gross photosynthetic rates, as determined by sunlight and photosynthetic capacity of the leaves regulate the rate of dry matter production. Gross photosynthesis was 29.3 and 79.6 mg CO_2 dm^{-2} hr^{-1} for the 2nd and 4th leaves respectively in spring wheat (Triticum aestivum L.).

The photochemical and/or diffusion process of leaves was found by Gaastra (1962) to be influenced by a wide range of environmental conditions. Gaastra reported that the daily radiation wasted by leaves exposed to saturating light intensities depended on leaf arrangement, LAI, diurnal course of light intensity, and solar elevation.

Osman (1971) found that the respiration of leaves was of great importance in determining dry weight increases and that variations in sink strength were of minor significance. Hesketh (1968) also found that differences in leaf photosynthetic rates were associated with the apparent photorespiration and variations of stomatal conductance. Decker (1970) concluded that the aspects of photorespiration have obvious significance in the real world and those associated with the breeding of high yielding hybrids should utilize photorespiratory rates as a selection tool.

Specific leaf weight (SLW = units of leaf dry matter per unit leaf area) showed a negative and significant correlation with primary leaflet area (Leavitt 1975). Experiments by Pearce, Brown, and Blazer (1968) showed that SLW appeared to closely interrelate with longevity and the decline of net photosynthesis with age.

For a given species and morphological structure of canopy, SLW and net carbon dioxide exchange (NCE) values decline most rapidly for canopies that grow at the fastest rates (Wolf and Blazer 1972). These researchers reported that if representative samples of all leaves in a canopy are considered, then any factor that encourages large and fast developing canopies reduces the mean values of SLW and NCE. Therefore yield and mean SLW of all leaves in a canopy may have a moderate inverse relationship. High positive correlations between SLW and NCE in these experiments suggested that differential values of SLW might be used in breeding to increase yields. Mutual shading which results in reduced light intensity in dense alfalfa canopies may be a major factor in leaf loss.

Net carbon dioxide exchange curves of Chatterton (1973) showed that SLW of potted alfalfa plants correlated negatively with the diurnal curve for SLW. A close relationship between NCE and SLW was reflected in rapid changes in values of both NCE and SLW. Chatterton suggested that photosynthesis may be reduced by the accumulation of photosynthate or a result of slow translocation that resulted from excessive assimilate accumulation. Increased SLW may be responsible for reduced photosynthesis and therefore reduced plant growth.

Light intensity has a direct effect on both net photosynthesis and SLW. Barnes et al. (1969) reported that the SLW between plant ages at three stages of maturity was significant at the 1% level of probability for nodes 3 to 6, but significant only at the 5% level at nodes 6 to 10 in alfalfa. They concluded that SLW and LAI were under independent genetic control.

Adaptability of alfalfa to changes in light intensity was shown by Pearce and Lee (1969). Net photosynthesis and SLW at any particular age fluctuated to a similar degree. The conclusion was that photosynthesis per unit leaf weight remains fairly constant so that the SLW of the leaf will primarily determine the photosynthetic rate per unit leaf area. Delaney and Dobrenz (1974b) reported a significant correlation (r = .76) between total leaf area and forage yield. Carbon dioxide uptake per unit leaf area was not found to be a limiting factor.

Pearce et al. (1969) reported that variation in net photosynthesis was due to SLW when plants were grown in the greenhouse. In field experiments these researchers reported SLW and net photosynthesis was positively and significantly correlated (r = .79). Net photosynthesis did not increase with increased SLW in high light.

Environmental factors such as light, temperature, water, O_2, and CO_2 concentrations may significantly affect photosynthetic rates and account for variability which has been found within and among cultivars. The effect of the environment on a plant will depend on the previous environmental adaptations of the organism and the annual climatic conditions to which it presently is subjected. Varga et al. (1970) reported the main source of variability in all characteristics studied in alfalfa was the environment, principally irrigation.

Cole, Dobrenz, and Massengale (1972) found significant variation in dry weight production among alfalfa cultivars when gibberillic acid (GA) was applied. The GA application was also significantly associated with water use efficiency. The increase in dry weight with GA application was due to more stem and petiole tissue rather than an increase in leaf area or total leaf area GA plants were also more efficient in water use.

Water management has been found to effect forage quality. Results from Gifford and Jensen (1967) showed yield and quality of alfalfa to be significantly affected by watering schemes and soil bulk density. Crude protein was significantly affected by the percent saturation of the soil. Peterschmidt (1976) concluded that irrigation water in excess of field capacity did not improve yield or quality in alfalfa, feed barley (Hordeum vulgare L.) and malting barley (Hordeum distichum L.), but rather demonstrated a negative effect on these factors. The effects of water on the quality of sudan grass (Sorghum sudanese [Piper Staph]) were insignificant (Koller and Clark 1965). They reported that at the first harvest the moisture percentage decreased as plant density increased.

The effects of temperature on a plant have been studied from single leaves to whole communities. Many researchers have reported the reduction of yield during the summer months (Robinson and Massengale 1967, Bula 1972, and Leavitt 1975). It was hypothesized that the "summer slump" as reported by Robinson and Massengale could be due to both high day and night temperatures and Bula (1972) suggested that temperature could change the anatomy of the leaf. Bula further reported that the effects of temperature appear to be manifested primarily in cell size and therefore smaller leaves. Plants grown under high temperature (35 C) had smaller cells which in turn resulted in smaller leaves and lower leaf areas per plant compared to plants grown at optimum temperatures. Cooper and Qualls (1967) observed more palisade tissue and a thicker cuticle in sun leaves than shade leaves. The leaf are to leaf weight ratios for sun and shade leaves were 194 and 337 cm^2 g^{-1} leaf respectively. Delaney (1972) found in 13 alfalfa clones that leaflet width differed more than 100% throughout the growing season.

Pearson and Hunt (1971) reported the net carbon intake of the cultivar 'Vernal' increased throughout the photoperiod at 20 C day and 15 C night, then declined after 10.5 hours from the start of the photoperiod when temperatures were increased 10 C. Similar results were reported for 'Moapa' when exposed to the same temperature schedule. Supporting evidence was presented by Hesketh, Chase, and Nanda (1969) with maize (Zea maize L.), sorghum (Sorghum vulgare Pers.), and Hungarian millet (Seteria italic L.). These scientists found that both temperature and photoperiod had profound effects on leaf number and associated characteristics. Genotypic differences played a strong role in determining leaf number.

Ueno and Smith (1970) suggested that temperature influences the conversion of nonstructural and structural carbon. They reported that carbohydrates are utilized by growing plants for respiration and for synthesizing constituents and that any surplus was accumulated in storage tissue. Ku and Hunt (1973) indicated that leaf carbon exchange characteristics are most affected by the temperature at which the plants are grown. Patterns of change throughout regrowth differed among various physiological and physical characteristics.

Plants grown at higher temperatures matured more rapidly than those grown under cool ambient temperatures (Jensen, Massengale, and Chilcote, 1967). It was noted that soil temperatures had less effect on growth and quality than air temperatures. These results are contrary to those of Parks and Fisher (1958) and Gifford and Jensen (1967). Parks and Fisher suggested that higher yields resulted from cooler soil temperatures because of greater amounts of stored carbohydrates.

Leaf carbon-exchange characteristics are most affected by the growth temperature. The best time to select plants that would overcome this seasonal change is controversial. Delaney, Dobrenz, and Poole (1974) showed similarities in photosynthesis and yield distribution over the growing season and suggested that plants selected under high temperatures would reduce the magnitude of the summer yield slump. Respiration was found to vary inversely with the average daily minimum air temperature. Individual observations of dark respiration were significantly correlated to photosynthetic measurements at both low and high light intensity over the growing season. Leavitt (1975) evaluated large leaflet alfalfa genotypes and suggested selection should be made early in the spring when leaflet size was optimal.

Dvorak and Natr (1971) demonstrated that CO_2 compensation points were affected by age and previous water status. Similar correlations between plant water status and CO_2 compensation points were found by other researchers. Parkhurst and Loucks (1972) concluded that every environment selects for leaf sizes that increase the efficiency of water utilization. They developed a water-use-efficiency model that demonstrated differences in both size and shape between sun and shade leaves. This model provided evidence that the leaf size does have adaptive significance.

Many statistical and computer models have been brought forth to predict both plant growth and yield. Kuehl, Buxton, and Briggs (1976) found significant correlations between a time series analysis and environmental factors affecting cotton (Gossypium hirsutum L.) Time series techniques were effectively used for certain agronomic problems relating environmental factors to flowering and boll retention, based on historical time series records. Foutz (1973) verified with multiple regression analysis that the morphological factors would probably be more effective as predictive criteria for the isolation of higher producing alfalfa clones than physiological factors. He suggested that selection of plants on a morphological basis with desirable physiological traits would be advantageous to an alfalfa breeding program. Using the multiple regression analysis Foutz et al. (1976) revealed that percent leaves, leaf weight, and leaflet to stem-petiole ratios accounted for more than 98% of the variation in yield.

Genotypic differences of alfalfa were studied by Schneiter et al. (1976) in an experiment designed to correlate ADP:O ratios to forage yields. Significant positive correlations were found between the genotypic ADP:O ratios and forage yield at each harvest and average forage yield over all harvests. They concluded that laboratory analysis of ADP:O ratios could be used as a screening tool for selection of individual plants having high yield potential prior to field evaluation.

Jensen et al. (1967) reported that the quality of alfalfa was affected by genotype, number of days between harvests, air and soil temperatures, soil moisture, and geographic location of production. Geographic location will determine the quality, quantity, and duration of light, precipitation, annual and diurnal temperature fluctuations, and thus the frequency of harvest for crops such as alfalfa. Smith (1962) recommended that alfalfa should be harvested three times in the northern states. Cutting schedules for the southwest are once every 30 days beginning in April and lasting until October. Fuess and

Tesar (1968) reported a sharp decline in photosynthetic activity of leaves after they were 3 weeks old. This poses the question of whether an alfalfa leaf has fulfilled its function of food manufacture by 30 days after emergence.

Jensen et al. (1967) suggested that leafiness of forages is often considered a major factor in determining quality. As the plant matures the percentage of leaves in the hay decreases. Reid et al. (1959) reported that the nutritive qualities of the leafy portions are known to be superior to the stems of plants. They showed that the leaf content of first growth forage was an excellent index of energy value. They noted that this factor lacked predictive values for subsequent forage harvests.

Alfalfa genotypes exhibiting the multifoliolate characteristic have been investigated since 1928 by plant breeders. The quest for an increased, more efficient, photosynthetic area has not been fruitless. The multifoliolate characteristic has been reported in several plants of the Leguminosae family. Bingham (1964, 1966) has been a leading scientist in the research associated with the multifoliolate characteristic in alfalfa. He found a significant difference between trifoliate and multifoliolate alfalfa in the total size of the vascular bundles in petioles of multifoliolate leaves. The double vascular area of multifoliolate petioles was adequate to carry the greater volume of photosynthate. This finding would suggest greater photosynthetic capacity due to an elimination or delay in feedback inhibition as suggested by Neales and Incoll (1968). Bingham (1966) demonstrated that the increase in translocation was due to the median bundle which increased in size as the number of leaflets increased. Bingham also reported that the size of the lateral bundles did not increase significantly.

In conjunction with the studies of the multileaflet trait there has been a comprehensive evaluation of internode length. Ferguson and Murphy (1973) observed positive associations between plant weight to plant height and plant weight to average internode length. It was suggested that stem production past a certain plant height exceeded leaf production resulting in further increases in biological yield. The negative correlation of leaves to stems suggested that there was no easy way to improve leafiness.

There has been some disagreement as to the length of internodes in multifoliolate alfalfa compared to trifoliate. Bingham and Murphy (1965) reported internodes were significantly longer in multifoliolate when planted on 0.91 m (3 ft) centers and the field overseeded with timothy. Brick (1975) found no significant internode length in multifoliolate progeny. These plants were spaced on 0.30 m (1 ft) centers with no overseeding of a companion crop. The competitive environments could explain the differences reported. Brick further suggested that the multifoliolate character appeared to have an advantage for increased leaf percentage. Therefore the development of a multifoliolate cultivar could improve the quality of alfalfa forage.

MATERIALS AND METHODS

Certified 'Mesa-Sirsa' alfalfa seed for this experiment was obtained from Dr. M. H. Schonhorst, at The University of Arizona. The Syn_2 multifoliolate seed was produced from clones described by Brick (1975). Plots were sown at the rate of 20.2 kg/ha on October 13, 1975, in a single border. The plots were arranged in a randomized block design with three replications. A 1 meter buffer strip separated each plot and each of the replications. The border was located at Tucson Plant Materials Center, Tucson, Arizona.

Prior to planting the border was fertilized with 120 kg/ha P_2O_5. Benefin (N-butyl-N-ethyl-a-a-a-trifluro-2,6-dinitro-p-toluidine) was preplant incorporated at the rate of 1.5 kg/ha. Trifluralin (a,a,a-trifluoro-2,6-dinitro-N,N-diprophyl-p-toluidine) was irrigated in 173 days after seeding at the rate of 3.2 kg/ha. The border was hand weeded to eliminate London Rocket (Sisymbrium irio L.) on two occasions. Irrigations were scheduled when 50% of the available moisture was utilized.

Apparent photosynthesis (AP), post-illumination bursts (PIB), and dark respiration (DR) were measured in a closed system on a Beckman 215 infrared gas analizer described by Foutz (1973). The plant material collected for CO_2 exchange was cut prior to sunset, labeled, and placed in distilled water to equilibrate overnight. The next morning three stems per plot were taken out of the dark for measurements. The stems were pre-illuminated 10 to 20 minutes to activate the stomates for maximum gaseous exchange. Measurements were taken at harvest and 2 and 3 weeks post-harvest.

Carbon-dioxide fluxes were calculated by incorporating the volume of the system, atmospheric temperature, pressure, and the moles per liter of CO_2 according to the formula reported by Foutz (1973).

Leaf area was determined with a light sensitive photometric Hayashi Denko automatic area machine. The leaflets were dried at 80 C for 24 hours. Specific leaf weight per plant was calculated from 100 stems selected at random at each harvest. From the same source of material 15 stems were selected and the leaflets removed to calculate leaflet to stem-petiole ratios. Both stems and leaves were dried as previously described, in order to express the ratio on a dry weight basis.

Total dry matter yield was estimated from a harvest strip 0.76 meters by 6.1 meters. Subsamples from the harvest strip were taken to determine moisture percentages. The samples were weighed and dried at the Tucson Plant Materials Center for 48 hours at 60 C.

Percentage N was measured by the micro-Kjeldahl method described by the Association of Official Agriculture Chemists (1955) and multiplied by 6.25 to estimate crude protein percentage.

Pigments were extracted from 3-week-old plants selected at random from each plot. Three sources of plant material were used; multifoliolate (MFf), multifoliolate germplasm trifoliates (MFt), and trifoliate (TF). The first fully expanded primary leaflets from three positions, top three nodes, next three nodes, and lower three nodes, were freeze dried and extracted by the methods described by Wolf (1959).

Analyses of variance, correlations, and multiple regression were used to statistically evaluate the factors listed in Table 1 over the growing season.

Table 1. Characteristics evaluated throughout the 1976 growing season.

	Variables	Units
AP	Apparent photosynthetic rate	mg CO_2 dm^{-2} hr^{-1}
DR	Dark respiration rate	mg CO_2 dm^{-2} hr^{-1}
PIB	Post-illumination CO_2 burst	mg CO_2 dm^{-2} hr^{-1}
Yield	Total dry matter	kg/ha
SLW	Specific leaf weight	mg leaf weight/cm^2 leaf area
L/S	Leaflet to stem-petiole ratio	
LAI	Leaflet area per plant per unit ground area	dm^2/dm^2
Protein	% crude protein	
Chl a	Chlorophyll a	ug/gm
Chl b	Chlorophyll b	ug/gm
C	Carotinoids	ug/gm

RESULTS AND DISCUSSION

The Syn_2 population of multifoliolate alfalfa (MF) showed significant differences in apparent photosynthesis (AP), post-illumination CO_2 bursts (PIB), specific leaf weight (SLW), and leaflet to stem-petiole ratios (L/S), even though only 35% of the population expressing the multifoliolate characteristic.

Apparent photosynthesis (AP) expressed as mg CO_2 dm^{-2} hr^{-1} was significantly higher in the multifoliolate population for the entire 1976 season. The seasonal averages were 15 and 12 mg CO_2 cm^{-2} hr^{-1} for MF and Mesa-Sirsa (MS) respectively (Table 2). The second week in June the highest CO_2 exchange values of 19 and 21 mg CO_2 dm^{-2} hr^{-1} were recorded for MF and MS respectively. After the August harvest, the apparent photosynthetic rates in the MF population declined steadily from 13 to 10 mg CO_2 dm^{-2} hr^{-1} at the final harvest in September. Mesa-Sirsa also followed a similar pattern of decreasing CO_2 incorporation beginning at the August harvest until the final September harvest.

Post-illumination CO_2 burst (PIB) was a short 10 to 15 second measure of dark and light respiration release of CO_2 that was obtained immediately after light energy is eliminated. The range of measurements showed less deviation from the mean than was evidenced by CO_2 incorporation. The range of PIB for the MF population during the entire growing season was 7 to 14 mg CO_2 dm^{-2} hr^{-1}. Similar seasonal trends were exhibited by MS where the release of CO_2 ranged from 6 to

Table 2. Average apparent photosynthesis (AP), post-illumination CO_2 burst (PIB), and dark respiration (DR) mg CO_2 dm^{-2} hr^{-1} of multifoliolate (MF) and Mesa-Sirsa (MS) alfalfa measured at harvest (H) and 2 and 3 weeks post-harvest (2PH, 3PH).

		Sampling Date													
		May			June			July			Aug.			Sept.	
		3PH	H	2PH	3PH	H	2PH	3PH	H	2PH	3PH	H	2PH	3PH	H
Apparent Photosynthesis	MF	13b*	16	14	12	14a	19	17	19a	14	13	17	13	12	10
(mg CO_2 dm^{-2} hr^{-1})	MS	16a	14	12	14	9b	21	17	12b	13	12	16	12	12	10
Post-Illumination Burst	MF	8	12a	9	13	14	13	10	9	12	10	13	9	7	7
(mg CO_2 dm^{-2} hr^{-1})	MS	8	8b	7	13	12	13	8	7	10	9	12	8	7	6
Dark Respiration	MF	4	5	4	5	4	4	4	3	5	5	4	4	3	3
(mg CO_2 dm^{-2} hr^{-1})	MS	3	3	4	6	5	4	4	4	5	4	4	4	3	3

* Significant difference indicated where applicable in table at .05 level.

13 with a mean of 9 mg CO_2 dm^{-2} hr^{-1} (Table 2). The MF population had significantly higher PIB values.

Dark respiration (DR) displayed the least variability of all the CO_2 exchange rates measured throughout the season. There was no statistical significant difference between the two populations (Table 3). The seasonal mean DR rates were 4 mg CO_2 dm^{-2} hr^{-1} for MF and MS plants, respectively (Table 2).

Specific Leaf Weight (SLW)

The multifoliolate populations had a significantly higher SLW than the trifoliate Mesa-Sirsa for the 1976 season (Figure 1). These differences were significant at harvest (H), 2 weeks (2PH), and 3 weeks post-harvest (3PH). The average SLW increased in both populations as the plants matured from 2PH to harvest (Figure 1). At harvest the average value for the MF population was 4.1 mg cm^{-2}. Similar but significantly lower values were obtained by MS at each of the respective sampling dates, 3.1, 3.2, and 3.8 mg cm^{-2} for 2PH, 3PH, and harvest, respectively. Specific leaf weight was significantly different at the 99% confidence level in relation to harvest date (Table 3). The variations exhibited followed the seasonal temperatures. Measurements of SLW by Pearce and Lee (1969) and Brick (1975) showed higher values in space planted studies. The discrepancy is probably due to greater light infiltration into the plant canopy. Cooper and Qualls (1967) reported that the ratio leaflet area to leaflet weight (inverse of SLW) increased with increased shading. Individual genotypes displayed significant differences in SLW within a population (Table 3).

Table 3. Summary of analysis of variance between multifoliolate and Mesa-Sirsa for specific leaf weight and CO_2 flux at three sampling dates for the 1976 season.

Variable	Sampling Date		
	Harvest	2 weeks post-harvest	3 weeks post-harvest
SLW	*	*	**
AP	**	NS	NS
PIB	**	NS	NS
DR	NS+	NS	NS

* Significant at the 5% level.

** Significant at the 1% level.

\+ Non-significant at the 5% level.

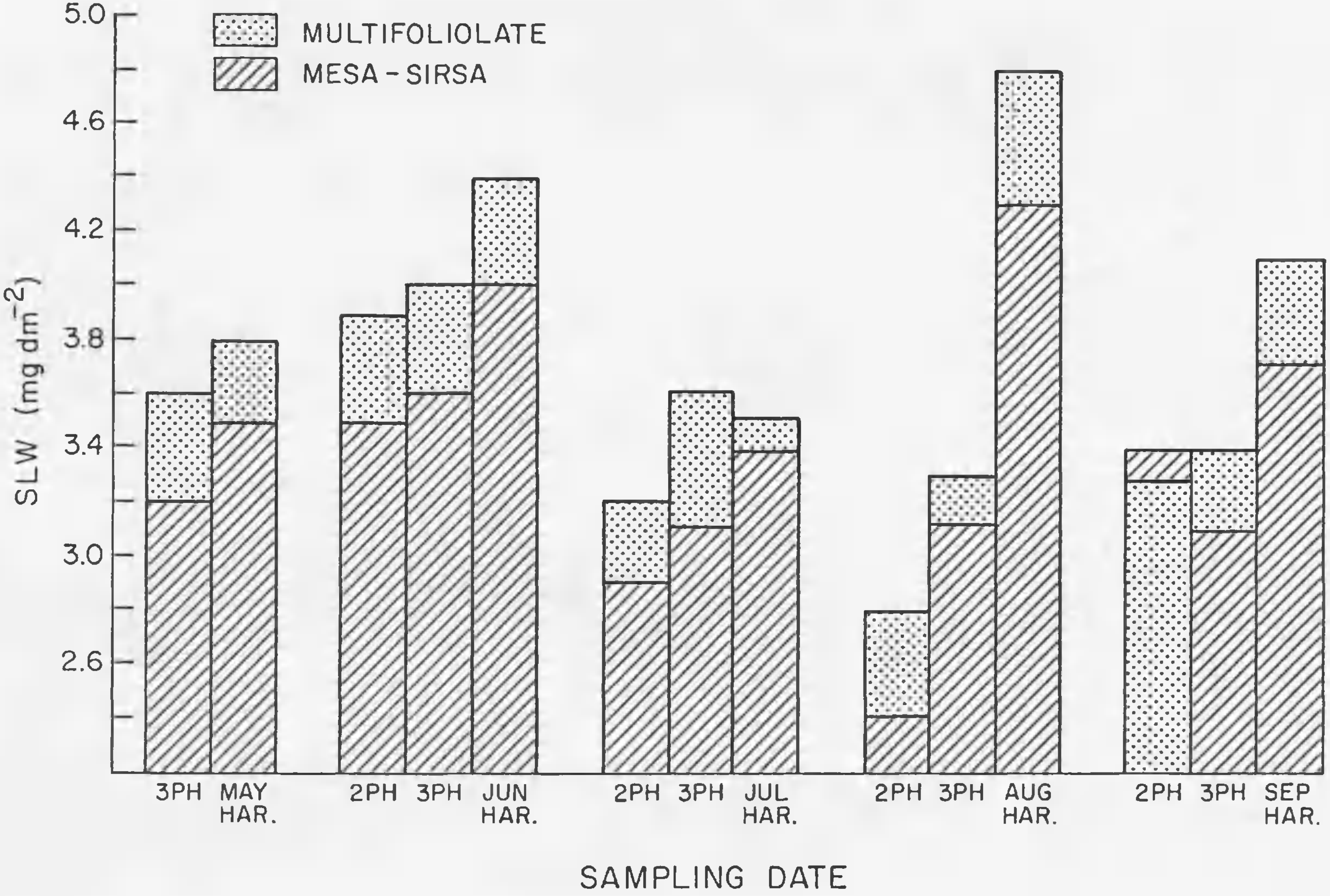

Figure 1. Average specific leaf weight of multifoliolate and Mesa-Sirsa alfalfa at five harvest dates, 2 and 3 weeks post-harvest (2PH, 3PH) for 1976.

Leaflet:Stem-Petiole (L/S)

The mean leaflet:stem-petiole ratios for the six harvest dates were .7:1 and .67:1 for the multifoliolate and trifoliolate 'Mesa-Sirsa' populations, respectively (Figure 2). This difference was significant at the 10% confidence level for the 1976 growing season. The seasonal trend was similar to specific leaf weight. Values reported here are higher than those of a nonspace planted study of alfalfa reported by Delaney (1972), but lower than those from a planted study of multifoliolate alfalfa (.8:1) reported by Brick (1975). Brick also reported that leaflet percentage on the parent clones ranged from 41.2 to 51.4%. These percentages were also higher than the 35.2 to 47.6% range in MF observed in this study. Leaflet percentage of Mesa-Sirsa ranged from 36.4 to 46.5. The differences in L/S between spaced and nonspaced experiments would probably be due to greater gibberillic acid breakdown in the nonspaced studies where light penetration would be greater.

Leaf Area Index (LAI)

Leaf area index was calculated by the following equation:

$$\frac{\text{percent leaves x dry weight of harvest strip } (g^{-2})}{\text{specific leaf weight } (g\ cm^{-2})}$$

There were no significant differences in either percent leaves or dry weight of the harvest strip, therefore the numerator for both MF and MS was essentially the same. The season trends for LAI are presented in Table 4. The MF synthetic had a significantly higher SLW at each harvest. The higher SLW value lowered the LAI in MF populations. The

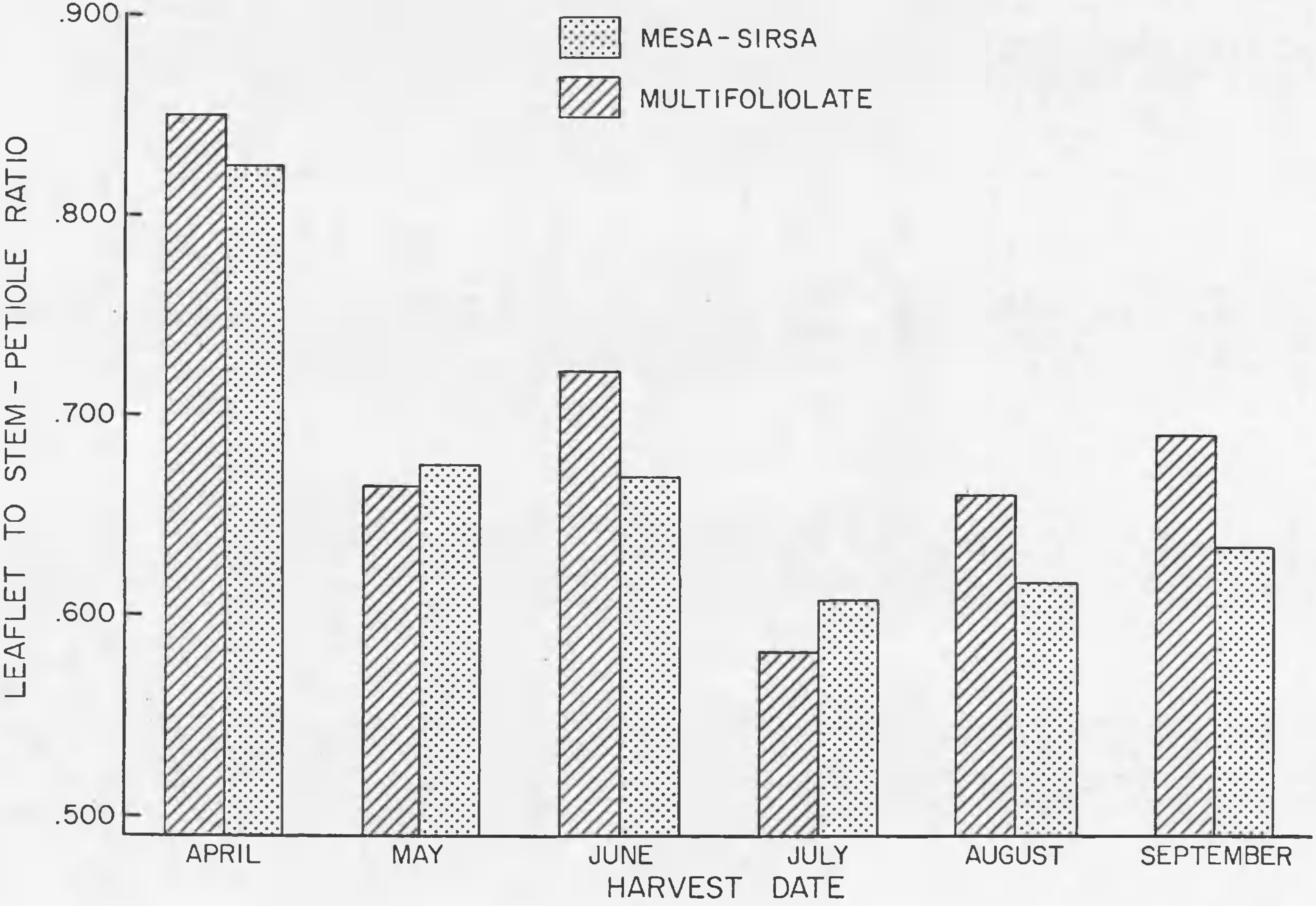

Figure 2. Average leaflet to stem-petiole ratios for multifoliolate and Mesa-Sirsa alfalfa measured at six harvest dates in 1976.

Table 4. Mean leaf area index for multifoliolate and Mesa-Sirsa alfalfa at six harvest dates in 1976.

Germplasm Source	Harvest Date						
	April	May	June	July	Aug.	Sept.	Mean
	Leaf area index						
Multifoliolate	4.6a+	4.1a	3.7a	4.6a	2.9a	3.4a	3.4a
Mesa-Sirsa	4.9a	4.2a	3.7a	4.4a	2.9a	3.8a	4.0a

+ Means followed by the same letter are not significantly different at the 5% level according to Student-Newman-Kuel's multiple range test.

range in LAI was from 3.39 to 4.00 for MS during the growing season. These LAI values correspond well with those of Wilfong et al. (1967) who reported LAI values in alfalfa between 2 and 6. Joy et al. (1972) also reported LAI values of 2.5 to 6 from a 2-year-old stand of alfalfa.

Protein

Average crude protein measured at harvest did not differ significantly between the two germplasm sources (Table 5). Multi-foliolate synthetic population maintained a trend of slightly higher protein percentage than the Mesa-Sirsa over the season (Table 5). The seasonal mean values were 21.7 and 20.6% for the MF synthetic and MS, respectively. These values are higher than those reported by Smith (1962) who found 15 to 18% protein at 0.10 to full bloom. Regional and varietal differences could be major causes of this variation. Protein, leaflet:stem-petiole ratios, specific leaf weights, and leaf area index are all parameters that are used to measure quality. Dobrenz, Schonhorst, and Thompson (1969) analyzed the highest yielding alfalfa cultivars in Arizona and found protein of leaves ranged from 27.5 to 26.5% while protein of stems ranged from 11.6 to 10.5%. The cultivar with the higher percentage of leaves and higher leaflet:stem-petiole ratios would be the variety with the greatest potential of producing a higher quality crop.

Yield

There was no significant difference between the two germplasm sources over the 1976 growing season in total dry matter produced

Table 5. Average crude protein percentages for multifoliolate and Mesa-Sirsa alfalfa at six harvest dates in 1976.

Germplasm Source	Harvest Date						
	April	May	June	July	Aug.	Sept.	Mean
				Protein (%)			
Multifoliolate	21.7a[+]	24.1a	21.0a	21.1a	21.7a	20.9a	21.7a
Mesa-Sirsa	21.6a	22.8a	19.8a	20.8a	19.4a	19.2a	20.6a

[+] Means followed by the same letter are not significantly different at the 5% level according to Student-Newman-Keul's multiple range test.

(kg/ha). There was, however, significant differences between populations among harvest dates (Figure 3). Moisture percentages ranged from 80 to 85% at harvest throughout the season and did not differ between germplasm sources. A midsummer yield slump was observed in August which was 1 month later than normal. The delay was a result of unseasonably rainy, cool weather in July. For the year, multifoliolate plots produced an estimated 22605 kg/ha which was 567 kg/ha more than the 'Mesa-Sirsa' (MS) which yielded 22038 kg/ha. Multifoliolate alfalfa (MF) was a cross between a northern 'Ladak 65' and southern Mesa-Sirsa (MS) and the influence of the northern genome was expressed in the MF growing pattern. In the early months of the growing season MF yielded higher. In August and September, MS produced more forage than MF. This shift in seasonal productivity could be used to achieve a more uniform distribution of dry matter over a growing season.

Correlations

Pearson correlations at sampling times of harvest, 2 weeks post-harvest (2PH), and 3 weeks post-harvest (3PH) (Table 6) revealed that as the plant matured the correlation between yield and apparent photosynthesis (AP) diminished to a nonsignificant level. At 2PH a significant correlation ($r = .58^*$) existed between AP (mg CO_2 dm^{-2} hr^{-1}) and yield (kg/ha). This relation diminished to $r = .45^*$ a week later, and at harvest the relation was no longer significant. Wilhelm (1973), Delaney (1972), and Foutz (1973) measured gas exchange rates at harvest and found no significant correlation to yield when

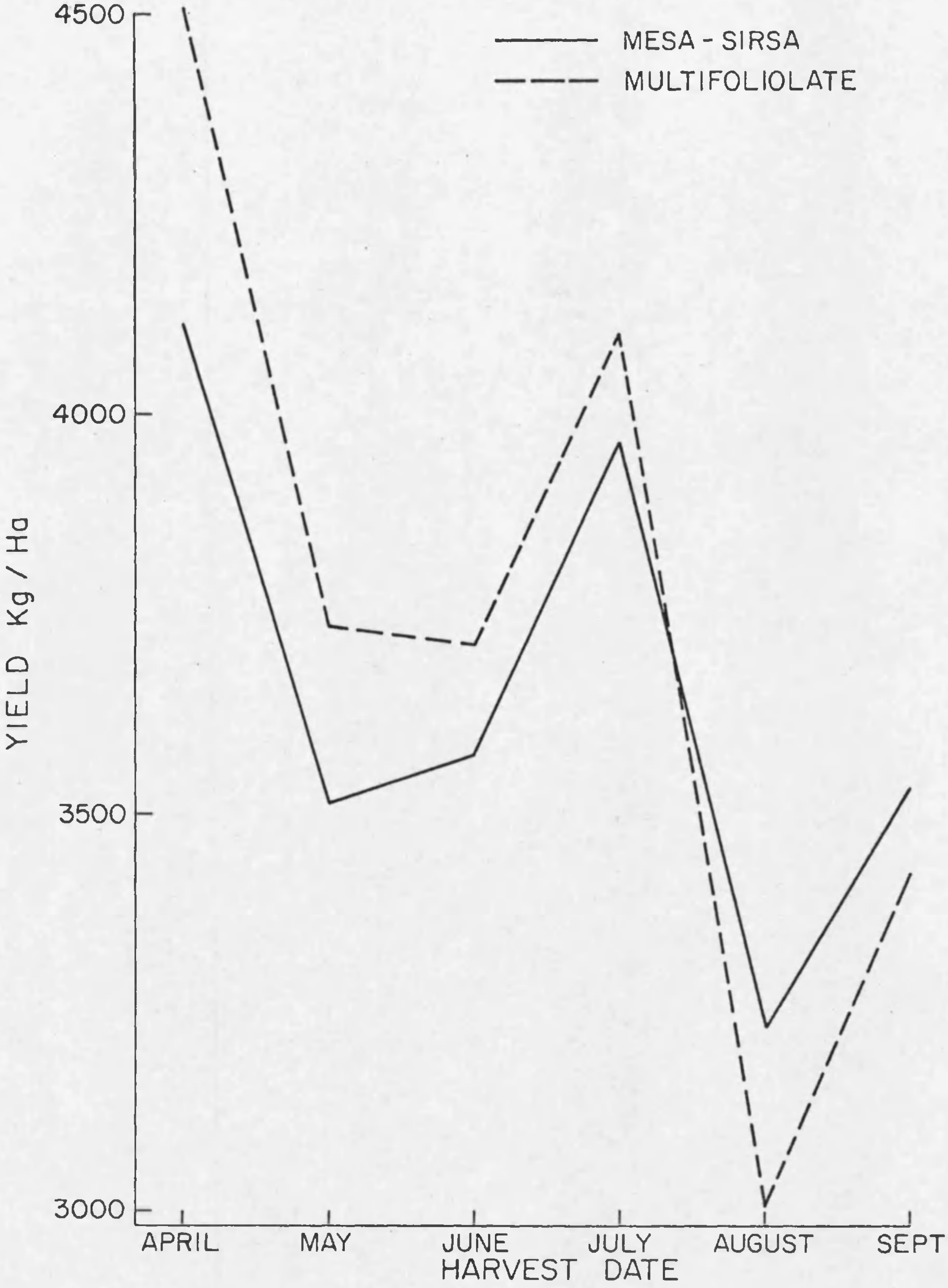

Figure 3. Yield of multifoliolate and Mesa-Sirsa alfalfa measured at six harvests in 1976.

Table 6. Correlation coefficients among yield, protein, leaf area index, and mean values of specific leaf weight, apparent photosynthesis, post-illumination CO_2 bursts, and dark respiration at harvest (H) and 2 and 3 weeks post-harvest (2PH, 3PH) in 1976.

	Specific Leaf Weight			Apparent Photo-synthesis			Post-illumination** CO_2 Bursts			Dark Respiration		
	H	2PH	3PH	H	2PH	3PH	H	2PH	3PH	H	2PH	3PH
					Correlation coefficients							
Yield***	-.39*	-32	.01	.04	.58*	.45*	-.10	.30	.15	-.12	-.32	.10
Protein+	-.21	.03	.04	.40*	.22	.14	.12	.19	-.19	.12	.10	-.12
Leaf Area Index	-.82*	.27	.05	-.01	.47*	.47*	-.34	.44*	.05	-.39*	.19	.03

* Significant at .05 level.

** mg CO_2 dm^{-2} hr^{-1}.

*** kg/ha.

\+ Percent crude protein.

measurements were based on leaf area basis. The analysis of variance (ANOVA) (Table 3) indicated a significant difference between genotypes in apparent photosynthesis (AP) rates only at harvest. Pearson correlation coefficients indicated that at 2 weeks post-harvest the strongest correlations occurred between CO_2 incorporation, apparent photosynthesis, and dry matter accumulation. However, the analysis of variance indicated that there were no observable differences between AP rates for the two germplasm sources. Therefore, selection of high yielding plants by apparent photosynthetic rates would not be feasible based on mg CO_2 dm^{-2} hr^{-1}.

Apparent photosynthesis (AP), post-illumination CO_2 bursts (PIB), and dark respiration (DR) were all more closely associated to each other at harvest than at the two dates before harvest (Table 7). These significant correlations among: AP with PIB, AP with RS, and PIB with RS were also observed by Delaney (1972), and Leavitt (1975).

The strongest correlation observed of all the parameters measured was between leaf area index (LAI) and specific leaf weight (SLW) ($r = -.82^{**}$) (Table 6). This relationship would be expected due to the manner in which LAI was estimated. Leavitt (1975) reported a significantly negative relationship between leaflet area and SLW. Leaf area index was significantly correlated to apparent photosynthesis ($r = .47^{*}$) at both 2PH and 3PH. Post-illumination CO_2 burst was significantly associated with LAI only at 2PH.

Correlation coefficients between SLW and AP per unit leaflet area were positive and nonsignificant at 2PH and 3PH but negative and

Table 7. Correlation coefficients between apparent photosynthesis (AP), post-illumination CO_2 bursts (PIB), dark respiration (DR), and specific leaf weight (SLW) in multifoliolate and Mesa-Sirsa alfalfa at harvest (H) and 2 and 3 weeks post-harvest (2PH, 3PH) in 1976.

	AP^+			PIB^+			DR^+		
	H	2PH	3PH	H	2PH	3PH	H	2PH	3PH
	(r)	(r)	(r)	(r)	(r)	(r)	(r)	(r)	(r)
SLW^{++}	-.11	.06	.10	-.09	.30*	.21*	.28*	.33*	.31*
AP				.39*	.26*	.19	.28*	.07	.18
PIB							.54*	.38*	.25*

+ mg CO_2 dm^{-2} hr^{-1}.

++ mg dm^{-2}.

* Significant at .05 level.

nonsignificant at harvest (Table 7). The negative and nonsignificant correlation at harvest are in contrast to Pearce et al.(1969). The negative association is in contrast to Wilhelm (1973) and Delaney (1972).

A significant and positive association was obtained between protein and mean apparent photosynthesis (r = .72*) at harvest. The correlation coefficient between yield and protein was nonsignificant but negative. This would support the work of Dobrenz et al. (1969) who showed that increased yields were due to a greater increase in stems rather than leaves. They further showed that the stem had only half the protein of the leaf. Leaf:stem-petiole ratios were not significantly related to any of the parameters measured.

Chlorophyll and Carotinoids (μg/gm)

Chlorophyll content among the three plant sources examined, multifoliolate multifoliolate (MFm), multifoliolate trifoliolate (MFt), and trifoliate (TF), showed no significant differences in total pigment content among the plant sources (Table 8). There was, however, a strong linear trend (r = .99**) for chlorophyll a (chl a) and carotinoid pigments which increased from the top to lower stem nodes. Chlorophyll b (chl b) did not demonstrate this trend. A highly significant correlation (r = .99**) for the linear relationship between leaf position and pigment content. Cooper and Qualls (1967) found a similar relationship between sun and shade leaf pigments when chlorophyll content was expressed as μg/gm leaf tissue. The sun leaves had less total pigment

Table 8. Average concentrations (μg/g dry weight) of chlorophyll a, chlorophyll b, carotinoids from multifoliolate multifoliolate (MFm), multifoliolate trifoliolate (MFt) and trifoliate Mesa-Sirsa (TF) at 3 leaf positions.

	Germplasm Source								
	MFm			MFt			TF		
	Leaf position			Leaf position			Leaf position		
Pigment	Top	Mid.	Bot.	Top	Mid.	Bot.	Top	Mid.	Bot.
Chlorophyll a (μg/g)	3.4	4.1	4.2	3.3	3.6	3.6	3.4	3.4	3.9
Chlorophyll b (μg/g)	1.4	1.2	1.5	0.9	1.1	1.1	1.1	0.9	1.1
Carotinoids (μg/g)	1.0	1.2	1.2	1.0	1.0	1.7	0.9	1.1	1.1

than the shade leaves. When chlorophyll content was expressed as mg/dm^2 the sun plants contained higher concentrations of chlorophyll. These researchers also measured transverse sections of the leaves and found that the sun leaf had a more clearly differentiated palisade layer than the shade leaf.

The darker leaf color observed in the MF populations could be a result of higher chlorophyll content, if expressed as $mg\ dm^{-2}$ or a result of a greater amount of light reflected due to the thicker leaves, as measured by specific leaf weight.

Pearson correlation coefficients revealed that chlorophyll a content could be used to predict chl b and carotinoid contents. However, chl b content alone could not be used to predict carotinoid content.

SUMMARY AND CONCLUSIONS

Multifoliolate and 'Mesa-Sirsa' alfalfa populations were evaluated for rates of CO_2 exchange, morphological characteristics, yield, and chlorophyll content. In the multifoliolate populations, 35% of the plants exhibited the multileaflet trait.

Multifoliolate alfalfa maintained significantly higher apparent photosynthetic and post-illumination burst rates at each of six harvests. Average yield for each population over the entire season followed a trend similar to that of ambient temperature and CO_2 flux. Highest yields and CO_2 exchange occurred when ambient temperatures were cool. The unseasonal summer rains and cool temperatures in July would explain the delayed mid-summer yield slump which is a generally accepted characteristic of alfalfa production in lower Arizona.

Leaf area index and specific leaf weight were negatively ($r = -.82^*$) associated with CO_2 exchange at harvest. Yield was negatively associated with specific leaf weight. Specific leaf weight was significantly higher in multifoliolate plants.

Protein content did not differ between the multifoliolate and 'Mesa-Sirsa' populations, but the multifoliolate synthetic tended to be slightly higher in protein content at each harvest. Protein percentage was significantly correlated with apparent photosynthesis at harvest time ($r = .40^*$).

Leaflet to stem petiole ratios were significantly higher in the multifoliolate populations for the season. The multifoliolate Syn_2 alfalfa produced higher leaflet to stem-petiole ratios at four of the six harvests. No correlations existed between leaflet to stem-petiole ratios and the other parameters measured.

Chlorophyll a and carotinoid contents (μg/g) differed significantly at the three positions of the plants tested. Highest total pigment contents were found in the lower fully expanded leaves and decreased linearly to the top leaflets. The linear trend accounted for 99% of the variation for chlorophyll a and carotinoids. Significant correlations existed among chlorophyll a and chlorophyll b, chlorophyll a and carotinoids, but not between chlorophyll b and carotinoids. There was no significant difference between total pigment content in multifoliolate multifoliolate, multifoliolate trifoliate, and trifoliate Mesa-Sirsa plants. The color difference observed between these germplasm sources could have been due to the amount of light reflected or by the higher specific leaf weight of the multifoliolate populations.

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