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WATER USE, AND YIELD OF FIVE ALFALFA
(MEDICAGO SATIVA L. 'SONORA') CLONES.

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RELATIONSHIP BETWEEN PHYSIOLOGICAL FACTORS,
WATER USE, AND YIELD OF FIVE ALFALFA
(MEDICAGO SATIVA L. 'SONORA') CLONES

by

Alan Lee Foutz

A Dissertation Submitted to the Faculty of the
DEPARTMENT OF AGRONOMY AND PLANT GENETICS
In Partial Fulfillment of the Requirements
For the Degree of
DOCTOR OF PHILOSOPHY
WITH A MAJOR IN AGRONOMY
In the Graduate College
THE UNIVERSITY OF ARIZONA

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THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

I hereby recommend that this dissertation prepared under my
direction by Alan Lee Foutz
entitled Relationship between physiological factors, water use,
and yield of five alfalfa (Medicago sativa L. 'Sonora')
clones.
be accepted as fulfilling the dissertation requirement of the
degree of Doctor of Philosophy

Albert K. Roberson
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ABSTRACT

Alfalfa (Medicago sativa L.) clones from an experimental synthetic were used to evaluate physiological and morphological variables as possible selection criteria for the isolation of higher-producing genotypes. Five clones were space planted in the field and used to evaluate the relation between CO₂ exchange, morphology and dry matter production.

The physiological factors measured in this study did not account for the variation in yield among the parental clones. Apparent photosynthetic rates (mg CO₂ dm⁻² hr⁻¹) and dark respiration rates (mg CO₂ dm⁻² hr⁻¹) were not correlated with yield. However, when apparent photosynthesis was multiplied by leaf area and expressed as total CO₂ uptake per plant per hour, there was a significant relationship between yield and this calculated variable. The correlation between these two factors was +.59** and +.90** in 1971 and 1972, respectively. The negative relationship between dark respiration rates (mg CO₂ dm⁻² hr⁻¹) and dry matter production suggested that plants should be selected with lower respiration rates.

Regression analysis of more than 30 variables indicated that leaflet area per plant, specific leaflet

weight, and leaflet to stem-petiole ratios accounted for most of the variability in dry matter production among the five alfalfa clones.

INTRODUCTION

Alfalfa breeders are constantly striving to improve the yields of alfalfa. Great advances have been made in yield improvement by selection for plants which exhibit insect and disease resistance. However, scientists have suggested that in order to reach new and higher yield plateaus, selection of plant material will have to be based on physiological criteria.

Ultimately, yield is a function of photosynthesis and photosynthetic products available for growth (40). Researchers have suggested that photosynthesis and respiration may be correlated with yield; however, consistent correlations between photosynthesis, respiration, and yield have never been shown. If physiological factors such as photosynthesis and respiration are to be used as selection criteria for identifying potentially higher-yielding genotypes, relationships between physiological factors and dry matter production need to be evaluated. The objectives of this research were (a) to evaluate genotypic variation of several physiological and morphological factors among selected genotypes of alfalfa; (b) to evaluate seasonal trends of physiological and morphological factors among

selected genotypes of alfalfa; and (c) to evaluate the relationship between the physiological factors, morphological factors, and yield.

REVIEW OF LITERATURE

Advances have been made in recent years in increasing the productivity of our agricultural crops; however, increased yields have become harder to obtain. Recently, scientists have suggested that to obtain increased yield, plants must be selected which are disease and insect resistant, but also have desirable physiological characteristics (26). Yoshida (63) suggested that since physiological processes such as photosynthesis, respiration, and photorespiration by a single leaf are the basis for dry matter production, selection for differences between cultivars with respect to these physiological factors may act as a basis for increased crop yields. Sprague (54) suggested that before physiological traits may be used as possible selection criteria simple and rapid analytical procedures must be used to evaluate the traits, and that a range of variability exists within the plant species being tested.

Photosynthesis

Lawes and Treharne (40) suggested that yield is a function of the quantity of the photosynthetic products available for plant growth. However, little evidence has been found that correlated photosynthetic rates per unit leaf area with yields of crops. Cultivars may have high

potential photosynthetic activity per unit leaf area and yet not produce a high yield because of genetic or environmental factors which would limit the utilization of this potential. Delaney (18) was unable to find any significant relationship between photosynthetic rate and yield in alfalfa. Curtis, Ogren, and Hageman (15) found that differences in seed yield among 36 cultivars of soybeans (Glycine max L.) could not be accounted for by differences in photosynthetic rates among the cultivars. Hanson (29) noted a response between photosynthetic rate and yield in corn (Zea mays L.) similar to that found by Curtis, Ogren and Hageman (15). He observed that net photosynthetic rates were negatively associated with yield, and that the high-yielding selection had lower chlorophyll level, percent dry matter, net photosynthesis, respiration, and Hill reaction rates as compared to the low-yielding selections. These results supported the conclusions of many workers, that variation in net photosynthetic rates did not play a major role in determining yield within an adapted population. Hanson concluded that the primary genetic control for productivity in the maize population appeared to involve genetic processes, such as hormonal control, rather than photosynthesis.

The results of Izhar and Wallace's (36) research with two cultivars of beans (Phaseolus vulgaris L.), Red Kidney and Michelite-62 and their F₁ and F₂ progenies,

indicated that the genetic mechanism which controlled the differences in net CO₂ exchange rate between cultivars was quantitative and that there might be only a few genes involved. They also found some dominance for low photosynthetic efficiencies. Heichel and Musgrave (32) examined the photosynthetic rates of maize and observed differences in mean photosynthetic rates of 100 to 200% among several inbred lines, hybrids, and open pollinated cultivars. Photosynthetic heterosis was observed in single crosses derived from inbreds of divergent ancestry. Sarkissian (52) also found that increased CO₂ fixation was associated with heterotic development in maize seedlings. Carlson et al. (7) suggested that differences in photosynthetic rates in alfalfa were heritable and increased yields could be obtained by selection for increased photosynthetic ability and appropriate changes in morphology and plant geometry. Even though heterosis and heritability may occur with respect to photosynthetic rates, photosynthesis need not be a dominant character. Sprague (54) suggested that cumulative effects of each individual locus which exhibited values above the midparent would lead to heterosis. Lawes and Treharne (40) proposed that a breeding program could transfer such superior attributes to an elite gene pool where further hybridization and selection would allow fuller expression in a different genetic background. Some researchers (2, 45)

have based breeding programs on photosynthetic rates, as suggested by Lawes and Treharne, but results from these programs have not been reported.

Many factors could significantly influence photosynthetic rates and should be considered when measuring rates for selection of superior genotypes. Pearce, Brown and Blaser (47) measured photosynthetic rates of alfalfa leaves of different ages and found that photosynthetic rates based on leaf area declined with increased leaf age after full expansion of leaves. Fuess and Tesar (27) noted a similar response in net photosynthesis versus leaf age in alfalfa. They found that the alfalfa which had been cut three times per season yielded 17% more hay than alfalfa cut two times per season. Two-thirds of the difference in yield was attributed to a reduction in leaf loss in the 3-cut schedule, while the remainder was accounted for by higher rates of net photosynthesis in the younger leaves when compared to the 2-cut schedule. They observed a reduction of one-seventh the photosynthetic rates of 3-week-old leaves as compared to 5-day-old leaves. Feltner and Massengale (24), however, concluded that frequent cutting reduced total available carbohydrates, and therefore dry matter production.

Environmental factors such as light, temperature, O₂ and CO₂ concentration may also significantly affect

photosynthetic rates and account for the variability which may be found between cultivars and among cultivars. Cooper and Wilson (13) found significant variation in photosynthetic rates between genotypes of Lolium at high and low light intensities. Estimates of heritability indicated that effective response to selection for high photosynthetic rates should be possible. Forrester, Krotkov, and Nelson (25) demonstrated that O_2 concentration could affect the rate of apparent photosynthesis in soybeans. They concluded that the inhibition of apparent photosynthesis by O_2 was a result of increased photorespiration and that the response was not a direct affect of O_2 on apparent photosynthesis but an indirect affect through increased respiration. However, Bowes and Ogren (4) showed that O_2 may directly affect the carboxylating enzyme, ribulose, 1,5-diphosphate carboxylase.

Charles-Edwards, Charles-Edwards, and Cooper (10) found that temperature could also account for a certain amount of variability among and within cultivars. They suggested that the optimum temperature for photosynthesis for any one plant was influenced primarily by previous growth environment. Plants which had been grown at low temperatures exhibited low optimum temperatures for high photosynthetic rates. Jolliffe and Tregunna (37) noted similar responses in wheat (Triticum aesativum L.) leaves

in the presence or absence of O_2 . Apparent rates of photosynthesis were inhibited in 21% O_2 as compared to 3% O_2 . Inhibition of apparent photosynthesis increased as temperature increased. A combination of stimulated CO_2 production during photosynthesis, and inhibition of photosynthesis itself accounted for the effect of O_2 and temperature on apparent photosynthesis.

Respiration

Delaney (18) found that dark respiration rates per unit leaf area were not significantly associated with dry matter production in alfalfa. However, a significant decline in dark respiration occurred during July and August with a subsequent increase in September. Trends in dry matter production followed dark respiration. The "slump" observed by Delaney may be accounted for by Robinson and Massengale's (51) observations on the cause of the "summer slump" in yields in alfalfa. They related the slump to high night temperatures which contributed to a decline in vegetative growth and carbohydrate reserves in the roots of alfalfa. Alberta (1) suggested that increased levels of reserve carbohydrates led to increased rates of respiration in plants and concluded that respiration was an important factor which contributed to dry matter production of closed canopies, but that it had received far less attention than photosynthesis.

Ishizuka (35) suggested that a simple way to obtain higher yields would be to lower respiration as much as possible. This would be an extremely important factor in climates where night temperatures are comparatively high and loss of assimilates are high. This scientist questioned whether respiration was always a negative factor in obtaining higher yields and if certain types of respiration were indispensable, how could they be separated to minimize the wasteful portion.

Wolf and Blaser (61) presented data on photosynthesis and respiration of plant parts of alfalfa canopies and suggested that respiration needed to be accounted for in any model expressing yield. Osman (46) suggested that respiration of leaves was of great importance in determining dry weight increases, and that the measurement of this parameter should be made and studied or correlated with dry matter production.

Heichel (30) examined the increased dry weight of two maize inbreds known to differ in photosynthetic capacity. The faster-growing inbred exhibited slower respiration rates in the leaves and roots than the slower-growing inbred, but had only an insignificant advantage in photosynthesis. The slow respiration of the faster-growing hybrid was well correlated with its rapid accumulation of dry matter. Sarkissian and McDaniel (53) have reported

that polymorphism does exist with plant mitochondria and that heterosis and complementation also occurred with respect to mitochondria. They demonstrated these phenomena in studies of a maize hybrid and its parents. Heterosis and complementation were associated to NAD-linked enzymes which may control energy flow through the electron transport pathway. Later, McDaniel (43) reported a strong positive association between mitochondrial activity and grain yield of a large number of barley (Hordeum vulgare L.) hybrids.

Whether respiration of chlorophyll containing cells is increased, inhibited, or unaffected during illumination was a basic question which intrigued investigators since the days of the first quantum yield determinations (42). March, Galinecke, and Gibbs (42) observed that light had little effect on the Krebs's cycle and that respiration occurred in green leaves in the light as well as in the dark in Scenedesmus obliquus, (Trup.) Kruger. However, considerable research exists which indicates that relatively low light inhibits the dark respiratory processes (28, 49, 50, 56, 65).

Ludwig and Canvin (41) studied the rate of photorespiration during photosynthesis in sunflower (Helianthus annuus L.) and concluded that the total CO₂ evolution in the light was composed of two processes, dark respiration and light respiration. Light respiration was a process that

occurred only in the light, persisted for some time on darkening, and metabolized substrates that were quite different from those of dark respiration.

Recent research has strongly supported the concept that respirational losses are important factors which contribute to net photosynthesis. This was especially true due to the large amount of CO_2 lost by many species during light respiration. Zelitch (65) concluded that information about light respiration could be obtained only by indirect methods, and therefore, questions as to its magnitude in relation to dark respiration have been raised by researchers for many years.

Decker (16) first demonstrated light respiration, or photorespiration, in 1955 as a post-illuminational outburst of CO_2 . Zelitch (64) postulated that the loss of fixed carbon caused an increased internal concentration of CO_2 and resulted in lower CO_2 gradients and therefore, lower net photosynthetic rates. He found that the use of an inhibitor of the oxidation of glycolate, the substrate for photorespiration, resulted in increased CO_2 uptake by (Nicotianna tabacum L.) and behaved photosynthetically like an efficient plant. High rates of photorespiration could limit net CO_2 uptake in many plant species. In a later paper by Zelitch and Day (66) the hypothesis that net photosynthesis was decreased in many plant species because of high rates of

light respiration was tested. Low photorespiratory CO_2 evolution was correlated with higher photosynthetic efficiency. They concluded that increased CO_2 uptake could be achieved by selection for plants with low photorespiratory rates.

Carlson et al. (8) studied photosynthesis and photorespiration in two clones of orchardgrass (Dactylis glomerata L.). Clone A7 exceeded clone P3 by 50% in photosynthesis and 40% in photorespiration. Clone P3 exhibited the lowest photosynthetic rate and the highest amount of apparent photorespiratory substrate. Photorespiration was inversely related to photorespiratory substrate concentration. Volk and Jackson (57) concluded that a finite photorespiratory process occurred in maize and the CO_2 generated was efficiently recycled.

Steward et al. (55) suggested that leaf age and prior environment influenced photorespiratory rates. Evidence was presented which indicated that photorespiration could be affected prior to analysis of the tissue, and that standardization in the laboratory was not enough. Charles-Edwards (9) observed that the response of net photosynthesis to changing light-flux density by leaves of Lolium multiflorum L. and Lolium perenne L. were more adequately described by models when a term which allowed for photorespiration was included.

Zelitch (64) had found considerable variation in photorespiratory rates among species. Wilson (58) noted that significant differences in rates of photorespiration occurred among plants within a Lolium population. These differences appeared to be independent of the environment under which the plants had been grown. Wilson suggested that increased yields could be obtained by selection for genotypes with low photorespiratory rates, and that even small reductions in the respiratory component could significantly increase yield since it would be integrated over an entire growth period.

Carbon Dioxide Compensation Point

Carbon dioxide compensation point is a function of photorespiration (65). Zelitch (64) found that an application of an inhibitor of photorespiration to tobacco tissue in the light diminished the CO_2 compensation point. Decker (17) suggested that net photosynthetic rate and photorespiratory rate measured by the CO_2 compensation point was probably the most useful index of photosynthetic efficiency available to plant breeders. He indicated that the aspects of photorespiration of obvious significance were those associated with breeding high-yielding hybrids. Plants with low CO_2 compensation points would have high photosynthetic capacity and low photorespiratory ability. Heichel (31), on the other hand, suggested that the CO_2 compensation

point may not reflect respiratory activity since significant differences in CO_2 compensation points have never been found among tobacco cultivars that differed greatly in photorespiration. He concluded that CO_2 compensation points, therefore, would be of little value for screening inefficient species for individual lines low in photorespiration.

Heichel and Musgrave (33) found that increased CO_2 compensation points were significantly associated with decreased photosynthetic rates. Wilson (58) also reported significant positive correlations between photorespiration and CO_2 compensation points in the genus Lolium. Dvork and Natr (23) reported differences in CO_2 compensation points in Triticum and Aegilops species. They concluded that the investigation of the genera for CO_2 compensation points would be valuable. Criswell and Schibles (14) observed that CO_2 compensation points were the least variable of the physiological factors they examined. Cannell, Brun, and Moss (6) screened 2458 genotypes of soybeans for survival at low CO_2 concentrations near the CO_2 compensation point of corn. They suggested that survival in such an atmosphere would have required a low CO_2 compensation point and would have indicated a high maximum net photosynthetic rate. However, they were unable to make any selections, as none of the genotypes survived the selection process.

Morphology

Yoshida (63) suggested that dry matter production of a single plant must be correlated with the product of leaf area and photosynthetic rate. Delaney (18) found that dry forage yield of a single plant was significantly correlated with the product of apparent photosynthesis and leaf area per plant. He indicated that the correlation was a result of differences in total leaf area per plant rather than differences in photosynthetic rates. Khan and Tsunoda (39) also noted that low relative growth rates of semi-dwarf wheat 'Mexi Pak' were due to low leaf area of the plants rather than low photosynthetic rates. Duncan and Hesketh (22) compared the growth rates of 22 races of corn grown as single plants, and found that dry matter production was dependent on leaf area development rather than on leaf photosynthetic rate. Hanson (29) also observed, among juvenile maize plants, that the principal correlated response to selection for differential productivity was leaf area.

Photosynthesis by leaves accounts for most of the carbon dioxide incorporated into a plant. Many workers have, therefore, looked at leaf characteristics for a basis of selection of plants with high photosynthetic rates. Pearce et al. (48) found positive correlations ($r = +.79$) between specific leaf weight and net photosynthesis of

13 alfalfa clones. Net photosynthesis increased from 20 ± 7 to 50 ± 8 mg CO₂ dm⁻² of leaf area hr⁻¹ as specific leaf weight increased from 1.9 to 5.3 mg cm⁻². Carlson et al. (7) also observed that net photosynthesis of individual leaves from selected plants of alfalfa, birdsfoot trefoil (Lotus corniculatus L.), and orchardgrass were positively correlated with specific leaf weight and certain anatomical traits.

Barnes et al. (3) found significant variation in specific leaf weight within and among alfalfa cultivars. This factor appeared to be under genetic control. Carlson et al. (7) concluded that differences in specific leaf weights in alfalfa populations indicated that specific leaf weight was heritable. Pearce et al. (48) found that the relationship between specific leaf weight and photosynthesis remained constant whether it was influenced by genetics or environment. They concluded that there was a possibility of increased net photosynthesis in plants selected for high specific leaf weight.

Cooper and Wilson (13) found that photosynthesis was negatively associated with mesophyll cell size, but positively associated with mesophyll cell number. Delaney (18) observed that apparent photosynthesis was significantly related to palisade thickness in alfalfa leaflets. A positive correlation between specific leaf weight and leaf

thickness was noted. Delaney concluded that palisade tissue thickness of alfalfa leaflets could be used as selection criteria for photosynthetic potential. Wilson and Cooper (59) found that heritabilities were high for mesophyll size ($r = 0.79$) and mesophyll thickness ($r = 0.34$). Wilson and Cooper (60) also studied the effect of selection for mesophyll cell size on the growth and assimilation of perennial ryegrass. Selection for small mesophyll cells resulted in smaller mesophyll cells, heavier seed, and greater yield of shoot dry matter than selection for large cells. Mesophyll cell size appeared to be a useful criterion for selection for genotypes having high photosynthetic capacity.

Water Use

Briggs and Shantz (5) defined the term water requirement as the ratio of the weight of water absorbed by a plant during its growth to the weight of dry matter produced. Cole (11) examined the water-use efficiency of seven cultivars of alfalfa and reported that significant variation in water-use efficiency occurred among and within cultivars. Sufficient variation within cultivars was found to warrant further investigations of water-use efficiency among genotypes within a cultivar rather than among cultivars. Dobrenz, Cole, and Massengale (20) reported that stem and petiole weight, leaflet weight, yield, and leaf area were

all significantly associated with the water requirement of alfalfa. However, leaf thickness and palisade cell density were not associated with either the water requirement or total transpired water of the alfalfa cultivars examined. Joy (38) found that alfalfa cultivars with the highest forage production were the most efficient in water use under field conditions. Cole et al. (12) also found a significant relationship between forage production and water requirement of alfalfa and concluded that water use by alfalfa could be decreased by selection for high-yielding genotypes.

MATERIALS AND METHODS

Alfalfa clones used in this study were selected from the 38 parental components of an experimental alfalfa, Reselect Sonora, developed by Dr. M. H. Schonhorst at The University of Arizona. Selection was based on dry matter production. Yields of the five clones, compared to the check cultivar 'Moapa,' were 125, 125, 112, 101, and 103% for clones 22, 29, 39, 1, and 3, respectively. One cutting from each of the five clones was space planted August 12, 1970 on 91.4 cm centers in a randomized complete block design with twenty replications. The plot was located at the Tucson Plant Materials Center, Tucson, Arizona.

Apparent photosynthetic rates and dark respiration rates were measured at seven harvest dates in 1971 and four harvest dates in 1972, using an air-sealed chamber. A 30-cm stem cut from each of the five clones from four replications was placed in a 125-ml bottle in the evening. Stems were allowed to equilibrate in the dark until the following morning, when the measurements were made. An air-sealed chamber, similar to that described by Wolf et al. (62) was used. Air containing 340 ppm CO₂ was passed over the plant at a flow rate of 3 liters min⁻¹. A 1.5 x 20 cm tube filled with 6 to 16 mesh, moisture-indicating silica gel was used to

remove water vapor before air entered the analyzer. Carbon dioxide exchange was then monitored by a Beckman 215 Infrared Gas Analyzer. The light source was seven Sylvania 500-watt flood lamps submerged in 15 cm of water for temperature control.

In addition to the air-sealed chamber used in 1972, apparent photosynthesis (AP), dark respiration (DR), post-illumination CO₂ burst (PIB), substrate level (SL), and CO₂ compensation point (CCP) were also measured using a closed chamber (Figure 1). Six 30-cm stems were cut from each of the five clones in four replications and placed in a 65-ml vial of water in the evening. The stems were allowed to equilibrate in the dark until the following morning when the measurements were made. Five stems were used to determine CO₂ compensation points. The remaining stem was used to measure photosynthesis and respiration.

The volume of the closed system was 1.1 liter. Air was circulated through the system at a rate of 6.9 liters min⁻¹. The system, Figure 1, was flushed with gas at ambient levels of CO₂ at approximately 360 ppm, after the plant had been placed in the chamber. The chamber was then sealed and the resulting response was recorded. Measurements were made in a range of CO₂ concentrations of 360 ppm to 280 ppm CO₂. Photosynthetic measurements were made with a range in light intensity of 107.6 Klux at the top of the stem to 43.0 Klux

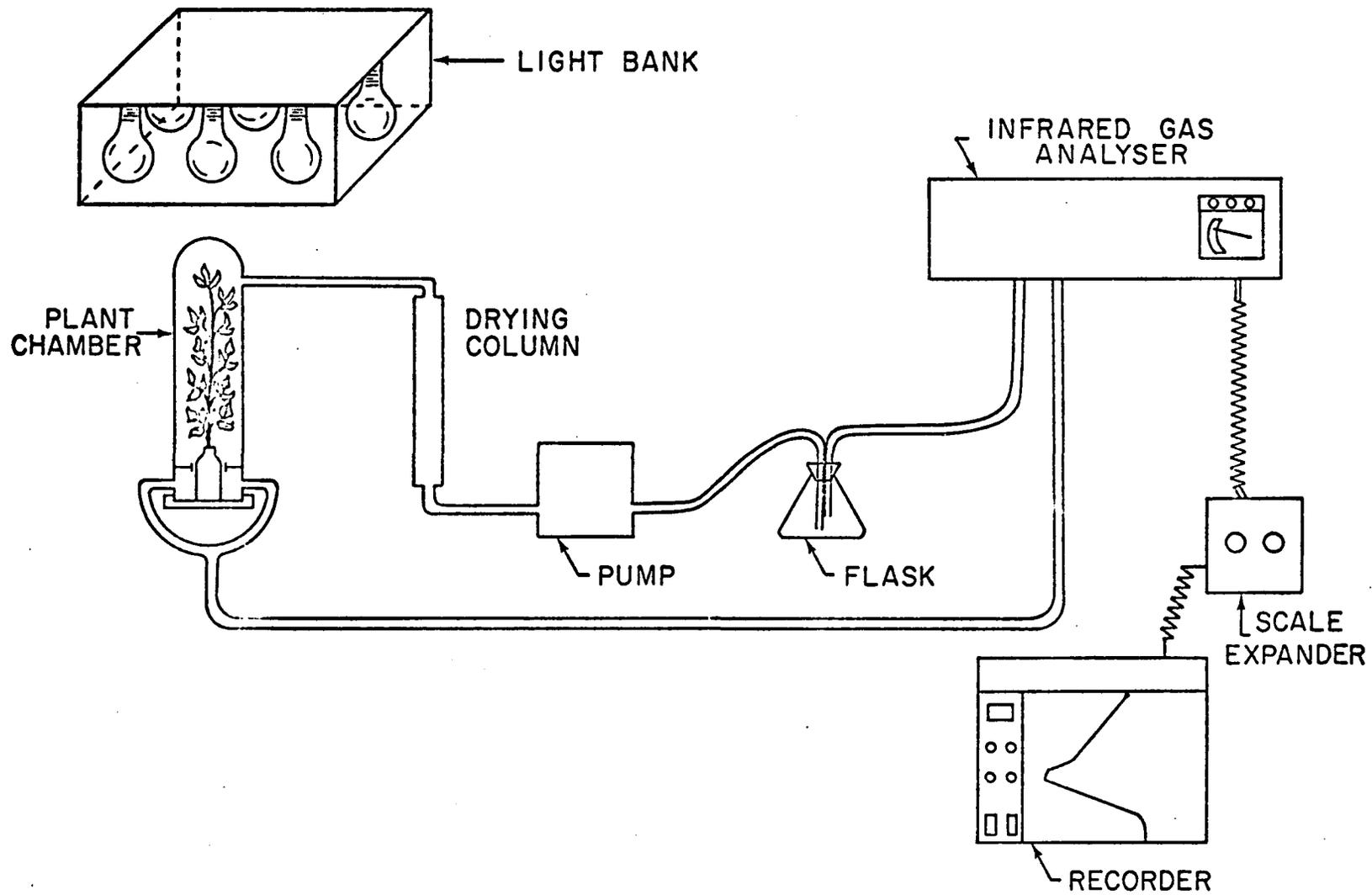


Figure 1. Diagram of the closed system used for physiological measurements in 1972.

at the base of the stem, and at a temperature of 30 ± 2 C in both systems. Dark respiration was measured at 25 ± 2 C. A typical recorder tracing for a plant in the closed system is shown in Figure 2. Apparent photosynthetic rates, dark respiration rates, and post-illumination CO_2 burst rates were evaluated from the tracing as the change in ppm $\text{CO}_2 \text{ min}^{-1}$. Substrate level was measured at the height of the CO_2 burst in mm.

Carbon dioxide exchange rates in both 1971 and 1972 were calculated on a leaf area basis as $\text{mg CO}_2 \text{ dm}^{-2}$ of leaf area hr^{-1} . These techniques were similar to those described by Carlson et al. (8). Calculations for the air-sealed system were made according to Hesketh and Moss (34). Calculations of CO_2 exchange rates in the closed system were made from the following equation:

$$\frac{\Delta \text{ ppm CO}_2 \text{ min}^{-1} \times 44,000 \text{ mg CO}_2 \text{ mole}^{-1}}{22.4 \text{ liters/mole} \times \text{leaf area}} \times \frac{1.1 \text{ liters} \times 692/760 \text{ mm Hg} \times 270/300 \text{ K}^\circ}{22.4 \text{ liters/mole} \times \text{leaf area}}$$

From the measured variables several other variables were generated (Tables 1 and 2) and evaluated as possible selection criteria.

Leaf area was determined with an air flow planimeter. Leaflets were dried at 80 C for 24 hours and leaflet dry weight was used to calculate specific leaflet weight (48).

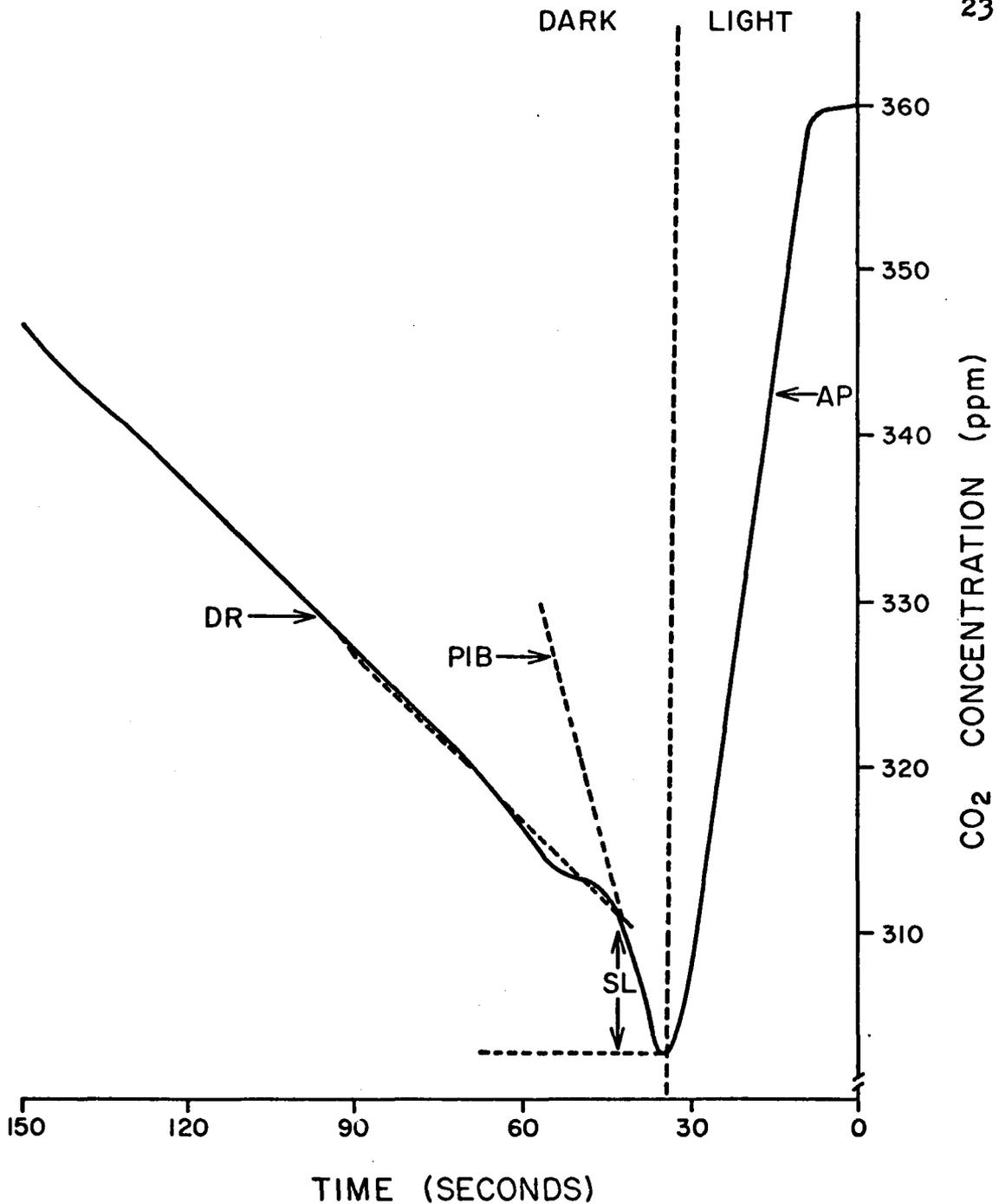


Figure 2. A recorder tracing showing CO₂ exchange of an alfalfa plant in the light and dark in a closed system (AP, apparent photosynthesis; DR, dark respiration; PIB, post-illumination CO₂ burst; and SL, substrate level).

Table 1. Physiological variables measured in 1971 and 1972 with an open system.

Variables	Units of Measurement	Abbreviation
<u>Measured</u>		
Apparent photosynthesis	mg CO ₂ dm ⁻² hr ⁻¹	AP
Dark respiration	mg CO ₂ dm ⁻² hr ⁻¹	DR
Apparent photosynthesis per plant	mg CO ₂ per plant	TAP
Dark respiration per plant	mg CO ₂ per plant	TDR
<u>Calculated</u>		
AP/DR		
TAP/TDR		
AP + DR		
TAP + TDR		
(AP + DR)/DR		
(TAP + TDR)/TDR		

Table 2. Physiological variables measured in 1972 with a closed system.

Variables	Units of Measurement	Abbreviation
<u>Measured</u>		
Apparent photosynthesis	mg CO ₂ dm ⁻² hr ⁻¹	AP
Dark respiration	mg CO ₂ dm ⁻² hr ⁻¹	DR
Post-illumination CO ₂ burst	mg CO ₂ dm ⁻² hr ⁻¹	PIB
Apparent photosynthesis per plant	mg CO ₂ per plant	TAP
Dark respiration per plant	mg CO ₂ per plant	TDR
Post-illumination CO ₂ burst per plant	mg CO ₂ per plant	TPIB
Substrate level	mm	SL
Substrate level per unit leaf area	mm dm ⁻²	SLA
Substrate level per plant	mm per plant	TSL
CO ₂ compensation point	ppm CO ₂	CCP
<u>Calculated</u>		
AP/DR		
TAP/TDR		
AP + DR		
TAP + TDR		
(AP + DR)/DR		
(TAP + TDR)/TDR		
AP + PIB		
PIB - DR		
TAP + TPIB		
TPIB - TDR		
(AP + PIB) - DR		
(TAP + TPIB) - TDR		
AP + PIB + DR		
TAP + TPIB + TDR		
(AP + PIB)/DR		
(TAP + TPIB)/DR		
AP/(DR + PIB)		
TAP/(TDR + TPIB)		
AP/(PIB - DR)		
TAP/(TPIB - TDR)		

Five stems were selected from each plant at each harvest in 1971 and 1972 and leaflets were separated from the petioles and stems. These components were dried at 80 C for 24 hr, weighed, and used to determine leaflet to stem-petiole ratios. Yields on a per plant basis were determined on the same plants, and on the same dates that the physiological variables were evaluated. Leaflet area per plant was determined from specific leaflet weight, percentage leaflet weight, and dry matter production by the following equation:

$$LA/Plant = \frac{\% \text{ leaflet weight}}{\text{specific leaflet weight}} \times \frac{\text{dry matter production per plant}}{\text{specific leaflet weight}}$$

Analysis of variance, correlations, and multiple regression analyses were made on all measured and calculated variables by the Agriculture Experiment Station statistician in cooperation with personnel at the University of Arizona Computer Center. Mean separations were made according to Duncan's New Multiple Range Test (21).

Water-use efficiency was determined on the five clones under greenhouse environment at the Tucson Plant Materials Center. Light intensity in the greenhouse was 53.8 Klux with a temperature range of 29 C during the day to 18 C during the night. The experimental design was a randomized complete block with six replications. One cutting from

each of the five clones was placed in a 4.2-liter pot filled with soil as described by Cole et al. (12). Styrofoam (11 g) was added to each pot to reduce evaporation of water from the soil as described by Dobrenz, Cole, and Joy (19). Pots were watered to bring the soil to field capacity at the beginning of each trial. Each pot was weighed daily and rewatered to field capacity when 50 - 55% of the available soil moisture had been depleted. Water requirement values were calculated by dividing the amount of water transpired (g) during the growth period by the amount of dry forage produced (g).

RESULTS AND DISCUSSION

Several physiological and morphological factors were significantly different among the five clones in 1971 and 1972 when measured with both open and closed systems as shown in Tables 3, 4, and 5.

Dry Matter Production

Significant differences in dry matter production among the five alfalfa clones were noted during both the 1971 and 1972 harvest seasons (Tables 3 and 4). Yields of the clones were different at all harvest dates except April and June, 1971 (Table 6), and all harvest dates in 1972 (Table 7). Clones 22 and 29 produced more dry forage than clones 1 and 3, in both 1971 and 1972 harvest seasons. These data on dry matter production coincided with the data (personal communication, M. H. Schonhorst, Department of Agronomy, University of Arizona, 1970) on polycross progeny dry matter production used to select the five genotypes.

Average dry matter production per harvest of clone 3 was 82 g per plant in 1971 and 42 g per plant in 1972. Clones 22 and 29 each produced an average of 146 g of dry forage per harvest in 1971. However, clone 22 produced more dry forage than clone 29 in 1972. Forage production of clone

Table 3. A statistical summary of significance of several characteristics on five alfalfa clones measured at seven harvest dates in 1971.

Factors	Harvest Date in 1971							Combined
	4/21	5/19	6/10	7/1	7/26	8/24	9/28	
<u>Physiological</u> [†]								
AP	NS	NS	NS	*	NS	*	*	NS
DR	NS	*	*	*	*	NS	NS	*
TAP	NS	NS	NS	*	NS	*	*	*
TDR	NS	*	NS	NS	*	NS	*	NS
DM	NS	*	NS	*	*	*	*	*
AP/DR	NS	*	NS	NS	*	NS	*	*
TAP/TDR	NS	*	NS	NS	*	NS	*	*
AP + DR	*	NS	NS	*	NS	NS	*	NS
TAP + TDR	NS	NS	NS	*	NS	*	*	*
(AP + DR)/DR	NS	*	NS	NS	*	NS	*	*
(TAP + TDR)/TDR	NS	*	NS	NS	NS	NS	*	*
<u>Morphological</u>								
LA	*	*	*	*	*	*	*	*
SLW	*	NS	*	*	NS	NS	*	*
L/S	*	*	NS	*	*	*	*	*

[†]CO₂ exchange measured in an open system.

*Significant at the .05 level according to Duncan's New Multiple Range Test.

Table 4. A statistical summary of significance of several characteristics on five alfalfa clones measured at four harvest dates in 1972.

Factors	Harvest Date in 1972				Combined
	6/13	7/15	7/27	8/15	
<u>Physiological⁺</u>					
AP	*	NS	NS	*	*
DR	*	*	*	NS	*
TAP	*	*	*	*	*
TDR	*	*	*	*	*
DM	*	*	*	*	*
AP/DR	NS	*	NS	NS	*
AP + DR	*	NS	*	*	*
TAP + TDR	*	*	*	*	*
(AP + DR)/DR	NS	*	NS	NS	*
(TAP + TDR)/TDR	NS	*	NS	NS	*
<u>Morphological</u>					
LA	*	*	*	*	*
SLW	NS	NS	NS	NS	*
L/S	NS	*	*	*	*

⁺CO₂ exchange measured in an open system.

* Significant at the .05 level according to Duncan's New Multiple Range Test.

Table 5. A statistical summary of significance of several characteristics on five alfalfa clones measured at three harvest dates in 1972.

Physiological Factors [†]	Harvest Date in 1972			Combined
	7/16	7/27	8/15	
AP	*	*	NS	*
DR	*	NS	NS	*
TAP	*	*	*	*
TDR	NS	*	*	*
PIB	*	NS	NS	*
TPIB	*	*	*	*
SL	NS	NS	NS	NS
SL/A	NS	NS	NS	*
TSL	NS	*	*	NS
CCP	NS	NS	*	*
AP/DR	NS	NS	NS	NS
TAP/TDR	NS	NS	NS	NS
AP + DR	*	*	NS	*
TAP + TDR	*	*	*	*
(AP + DR)/DR	NS	NS	NS	NS
(TAP + TDR)/TDR	NS	*	NS	NS
AP + PIB	*	*	NS	*
PIB - DR	*	*	NS	*
TAP + TPIB	*	*	*	*
TPIB - TDR	*	*	*	*
(AP + PIB) - DR	*	*	NS	*
(TAP + TPIB) - TDR	*	*	*	*
AP + PIB + DR	*	*	*	*
TAP + TPIB + TDR	*	*	*	*
(AP + PIB)/DR	NS	*	NS	NS
(TAP + TPIB)/TDR	NS	*	NS	NS
AP/(DR + PIB)	NS	*	NS	*
TAP/(TDR + TPIB)	NS	*	NS	NS
AP/(PIB - DR)	NS	*	NS	NS
TAP/(TPIB - TDR)	NS	*	NS	NS

[†]CO₂ exchange measured in a closed system.

*Significant at the .05 level according to Duncan's New Multiple Range Test.

Table 6. Average dry matter production of five alfalfa clones at seven harvest dates in 1971.

Clone	Dry Matter Production [†] (g per plant)							Means
	Harvest Date in 1971							
	4/21	5/19	6/10	7/1	7/26	8/24	9/28	
1	132 a	224 b	130 a	104 ab	88 ab	97 ab	53 a	118 vw
3	75 a	117 a	122 a	75 a	55 a	72 a	60 ab	82 v
22	156 a	147 a	138 a	152 b	144 c	172 c	110 c	146 w
29	175 a	211 b	150 a	127 b	114 bc	148 bc	97 bc	146 w
39	109 a	130 a	109 a	138 b	124 c	135 abc	101 bc	121 vw
Means	129 x	170 y	130 x	119 wx	105 w	125 wx	84 v	
CV	51	22	25	24	21	33	31	

[†]Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

Table 7. Average dry matter production of five alfalfa clones at four harvest dates in 1972.

Clone	Dry Matter Production [†] (g per plant)				Mean
	Harvest Date in 1972				
	6/13	7/16	7/27	8/15	
1	118 b	124 b	44 ab	20 a	76 w
3	68 a	59 a	18 a	22 a	42 v
22	180 c	194 c	120 d	68 b	141 x
29	112 ab	113 ab	66 bc	30 a	80 w
39	144 bc	156 bc	77 c	51 b	107 wx
Mean	124 x	129 x	65 w	38 v	
CV	25	27	29	33	

[†]Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

22 was more consistent from harvest to harvest in both years than any of the other four clones.

Significant differences in dry matter were noted among harvests in both 1971 and 1972 seasons (Tables 6 and 7). A 35% reduction in forage production occurred from May 19 to September 28 during the 1971 harvest season, while a 60% reduction occurred from the June 13 to August 15 harvest in 1972. The reductions may have been due to decreased stem initiation during the warmer periods of the growing season. The decreased stem initiation and subsequent decreased dry forage production may have been a result of reduced carbohydrate levels in the roots as suggested by Feltner and Massengale (24), and Robinson and Massengale (51).

Physiological Factors

Apparent Photosynthesis

The rate of apparent photosynthesis was significantly different among the five clones only at the September 28 harvest date in 1971 (Table 8), and the June 13 harvest date in 1972 (Table 9). However, significant differences in photosynthetic rates among the five clones were detected when comparisons were made over the harvest season in 1972 (Table 9). Clone 3 had the highest photosynthetic rate of

Table 8. Average apparent photosynthesis of five alfalfa clones measured with an open system at seven harvest dates in 1971.

Clone	Apparent Photosynthesis ⁺ (mg CO ₂ dm ⁻² hr ⁻¹)							Means
	Harvest Date in 1971							
	4/21	5/19	6/10	7/1	7/26	8/24	9/28	
1	17.7 a	32.2 a	32.4 a	37.0 ab	35.7 a	29.2 ab	12.7 a	28.2 v
3	25.0 a	35.3 a	38.2 a	41.3 b	36.9 a	16.4 a	6.4 a	27.1 v
22	16.4 a	28.4 a	24.9 a	29.1 a	28.7 a	26.1 a	27.1 b	25.8 v
29	20.5 a	33.1 a	26.0 a	34.6 ab	34.5 a	21.0 ab	15.7 a	26.5 v
39	22.4 a	26.4 a	29.4 a	33.0 ab	30.0 a	34.8 b	10.2 a	26.6 v
Means	20.4 w	31.1 yz	28.2 xy	35.0 z	33.1 z	25.5 x	14.4 v	
CV	26	22	28	17	19	36	48	

⁺Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

Table 9. Average apparent photosynthesis of five alfalfa clones measured with an open system at four harvest dates in 1972.

Clone	Apparent Photosynthesis [†] (mg CO ₂ dm ⁻² hr ⁻¹)				
	Harvest Date in 1972				Mean
	6/13	7/16	7/27	8/15	
1	30.4 a	29.9 a	37.2 a	25.1 a	30.1 wx
3	36.9 a	23.8 a	36.3 a	29.8 b	31.7 x
22	27.0 a	23.9 a	33.7 a	25.7 a	27.6 vwx
29	27.6 a	25.9 a	29.8 a	25.1 a	27.1 wx
39	26.8 a	27.0 a	28.5 a	17.5 a	24.9 v
Mean	29.7 w	26.1 v	32.7 w	24.7 v	
CV	9	24	21	23	

[†]Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

31.7 mg CO₂ dm⁻² hr⁻¹ while clone 39 had the lowest rate of 24.9 mg CO₂ dm⁻² hr⁻¹. No differences in rates of CO₂ uptake were found among the five clones in 1971 when photosynthetic rates were averaged over all harvest dates.

Although photosynthetic rates were approximately 24% less in the closed system (Table 10) than in the open system, clones maintained their respective rank regardless of the system used to evaluate photosynthetic rates. Differences in photosynthetic rates between the two systems were probably due to greater reduction of CO₂ in the environment around the plant in the closed system. In contrast, air at 340 ppm CO₂ was continually passed across the plant in the open system throughout the measurement.

Apparent photosynthesis was not correlated with yield either in 1971 or 1972. These data are in agreement with Delaney (18) who found that apparent photosynthesis expressed as mg CO₂ dm⁻² hr⁻¹ was not related to yield of 13 'Mesa Sirsa' clones. Since an association between apparent photosynthesis and yield was not found, this physiological factor does not appear to have potential use for isolating genotypes with high yielding potential.

Dark Respiration

Dark respiration was different among the five clones at six of 11 harvest dates in 1971 and 1972 (Tables 11 and 12). The five alfalfa clones maintained the same rank

Table 10. Average apparent photosynthesis of five alfalfa clones measured with a closed system at three harvest dates in 1972.

Clone	Apparent Photosynthesis [†] (mg CO ₂ dm ⁻² hr ⁻¹)			
	Harvest Date in 1972			Mean
	7/16	7/27	8/15	
1	20.0 ab	23.3 b	26.6 a	23.3 w
3	25.7 b	30.6 c	28.4 a	28.6 x
22	16.6 a	23.1 b	23.7 a	21.2 vw
29	13.1 a	21.1 b	20.0 a	18.1 v
39	18.0 a	12.2 a	20.9 a	17.0 v
Mean	18.7 v	22.1 v	23.9 v	
CV	24	14	39	

[†]Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

Table 11. Average dark respiration of five alfalfa clones measured with an open system at seven harvest dates in 1971.

Clone	Dark Respiration [†] (mg CO ₂ dm ⁻² hr ⁻¹)							Means
	Harvest Date in 1971							
	4/21	5/19	6/10	7/1	7/26	8/24	9/28	
1	5.4 a	4.6 ab	6.2 bc	6.1 ab	4.8 a	5.7 a	2.0 a	5.0 v
3	6.7 a	6.4 b	7.4 c	7.7 b	6.4 b	14.6 a	3.5 a	7.5 w
22	6.2 a	4.1 ab	4.1 a	3.7 a	4.9 ab	6.5 a	2.3 a	4.4 v
29	5.3 a	6.0 ab	4.2 a	4.7 a	5.3 ab	4.4 a	2.7 a	4.7 v
39	6.4 a	3.5 a	4.8 ab	4.2 a	5.6 ab	6.4 a	2.4 a	4.8 v
Mean	5.8 w	4.9 w	5.3 w	5.3 w	5.4 w	7.5 x	2.6 v	
CV	27	35	19	36	16	83	43	

[†]Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

Table 12. Average dark respiration of five alfalfa clones measured with an open system at four harvest dates in 1972.

Clone	Dark Respiration [†] (mg CO ₂ dm ⁻² hr ⁻¹)				Mean
	Harvest Date in 1972				
	6/13	7/16	7/27	8/15	
1	3.2 ab	5.4 b	6.6 a	5.9 a	5.3 w
3	3.8 b	5.0 ab	9.1 b	6.0 a	6.0 w
22	2.3 a	2.6 a	5.3 a	4.2 a	3.7 v
29	3.4 ab	2.4 a	5.8 a	4.6 a	4.1 v
39	2.4 a	4.2 ab	5.6 a	3.8 a	4.1 v
Mean	3.0 v	3.9 vw	6.6 x	4.9 w	
CV	23	40	25	40	

[†]Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

regardless of the system used for evaluation in 1972 (Tables 12 and 13). Dark respiration rates were different among the five clones only at the July 16 harvest date when CO₂ exchange was measured with the closed system (Table 13). However, dark respiration rates among the five clones were significantly different in both years when averaged over all harvest dates. Differences were also noted regardless of the system used for evaluation of dark respiration rates. Clone 3 had the highest respiration rate for all harvests in 1971 and 1972 with seasonal means of 7.5 and 6.0 mg CO₂ dm⁻² hr⁻¹, respectively, when plants were evaluated with the open system (Table 11 and 12). Clone 22 had the lowest respiration rates in 1971 and 1972 with seasonal means of 4.4 and 3.7 mg CO₂ dm⁻² hr⁻¹.

Dark respiration rates were highest during the warmer months of July and August (Figure 3). These data are in contrast to the "slump" reported by Delaney (18). The increased dark respiration rates in 1971 and 1972 were immediately followed by significant decreases in both years when plants were measured with the open system. However, respiration of plants measured with the closed system did not vary among harvest dates (Table 13). These findings appear to be in contrast to the hypothesis proposed by Delaney (18) that substrate levels may be reduced due to the deterioration in the structure of photosynthetic tissue and a decrease in metabolism.

Table 13. Average dark respiration of five alfalfa clones measured with a closed system at three harvest dates in 1972.

Clone	Dark Respiration [†] (mg CO ₂ dm ⁻² hr ⁻¹)			
	Harvest Date in 1972			Mean
	7/16	7/27	8/15	
1	3.4 a	4.1 a	3.4 a	3.6 v
3	6.0 b	3.4 a	6.3 a	5.3 w
22	2.3 a	3.3 a	4.1 a	3.3 v
29	2.7 a	4.8 a	2.9 a	3.4 v
39	3.8 ab	3.0 a	4.2 a	3.7 v
Mean	3.6 v	3.7 v	4.2 v	
CV	41	41	53	

[†]Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

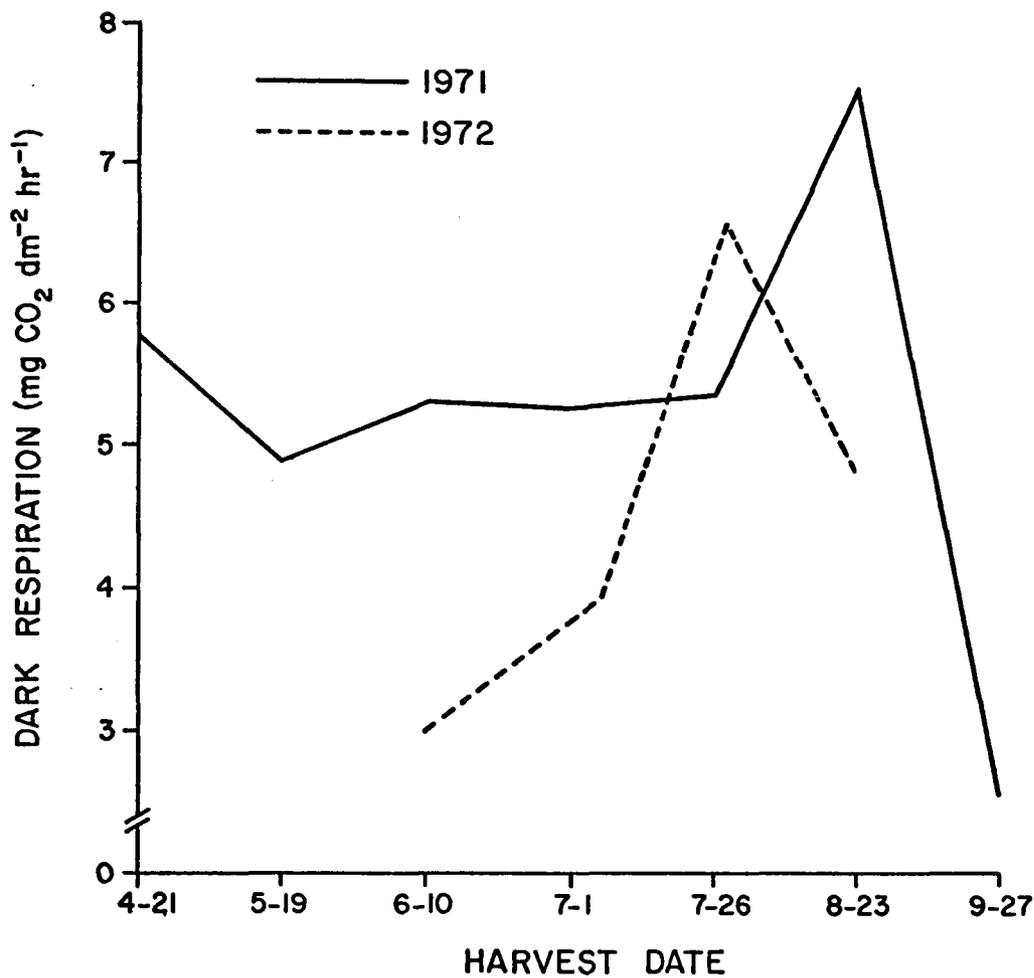


Figure 3. Average dark respiration of five alfalfa clones measured with an open system at seven harvest dates in 1971 and four harvest dates in 1972.

The relationship between dark respiration and yield was significant in 1972 ($r = -.42^*$) but was not significant in 1971 ($r = -.11$). The negative relationship found in both years suggested that plants should be selected which have low dark respiration rates.

An attempt was made to isolate mitochondria from vegetative tissue of the five alfalfa clones to obtain a biochemical estimate of respiratory efficiency. Isolation procedures used were modified techniques of McDaniel and Sarkissian (44). Consistent results were not obtained with the isolated organelles; therefore, estimates of respiratory efficiency could not be made at the biochemical level.

Post-illumination CO₂ Burst Rates and Substrate Levels

The slope of the recorder tracing per unit time immediately following the light period was termed post-illumination CO₂ burst (photorespiration). The burst was always noted with the five alfalfa clones when they were measured in an atmosphere containing 21% O₂. However, when the plants were measured in an atmosphere of 0% O₂, the burst was absent.

Post-illumination CO₂ burst rates were significantly different only at the July 16 harvest date in 1972 (Table 14). Clone 3 had the highest post-illumination CO₂ burst rates, with an average of 25.7 mg CO₂ dm⁻² hr⁻¹. Clone 3

Table 14. Average post-illumination CO₂ burst rates of five alfalfa clones measured with a closed system at three harvest dates in 1972.

Clone	Post-illumination CO ₂ Burst [†] (mg CO ₂ dm ⁻² hr ⁻¹)			
	Harvest Date in 1972			
	7/16	7/27	8/15	Mean
1	16.3 ab	19.0 a	13.8 a	16.4 v
3	25.7 c	29.8 a	25.8 a	27.1 w
22	13.1 ab	27.0 a	20.2 a	20.1 v
29	11.0 a	18.8 a	14.2 a	14.7 v
39	20.7 b	13.2 a	17.2 a	17.1 v
Mean	17.4 v	21.6 v	18.2 v	
CV	30	46	48	

[†]Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

also had the highest seasonal mean of $27.1 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$. The sharp increase in the coefficient of variability noted on the July 27 and August 15 harvest dates probably accounted for the lack of significance in post-illumination CO_2 burst rates at the two harvest dates.

The relationship between post-illumination CO_2 burst and yield was not significant ($r = -.15$). However, a significant relationship existed between apparent photosynthetic rates and post-illumination CO_2 burst rates. Correlation coefficients of $+.68^*$, $+.53^*$, and $+.49^*$ were found for the July 16, July 27, and August 15 harvest dates, respectively. Post-illumination CO_2 burst rate and apparent photosynthesis were significantly correlated ($r = +.52^*$) when analyzed over the growth period for 1972. These data are in contrast to the data presented by Zelitch (64) which indicated a negative relationship between apparent photosynthesis and photorespiration. Post-illumination CO_2 burst (photorespiration) was not related to yield of the five clones used in this study and therefore should not be used as a selection criterion for high-producing southwestern alfalfa genotypes.

Substrate levels, height of the post-illumination CO_2 burst peak (Figure 2), substrate levels per unit leaf area, and substrate levels per plant were not different among the five genotypes. Substrate levels appeared to vary

independently of the genotype, as no significant relationships between apparent photosynthesis, dark respiration or post-illumination CO_2 burst were found. Undoubtedly, the technique used for these was not acceptable for measuring substrate levels. The height of the peak may have represented the length of time required for stomatal closure.

CO_2 Compensation Point

Carbon dioxide compensation points were significantly different among clones only at the August 15 harvest date in 1972 (Table 15). However, significant differences were noted on seasonal means which suggested that genotypic variation could be detected over the entire growing period. Clone 29 had the highest compensation point with a seasonal mean of 75.9 ppm CO_2 . Clone 22 had the lowest compensation point with a seasonal mean of 59.6 ppm CO_2 . Even though differences were not significant at each harvest date, clone 29 generally had the highest compensation point while clone 22 had the lowest.

Carbon dioxide compensation points varied significantly among harvest dates (Figure 4). The lowest CO_2 compensation point occurred at the July 16 harvest date. The CO_2 compensation point increased at the July 27 harvest and remained relatively high for the remainder of the growing season.

Table 15. Average CO₂ compensation points of five alfalfa clones measured with a closed system at four harvest dates in 1972.

Clone	CO ₂ Compensation Point at 30 C [†] (ppm CO ₂)				Mean
	Harvest Date in 1972				
	6/13	7/16	7/27	8/15	
1	66.2 a	55.8 a	68.8 a	81.6 b	68.1 w
3	68.5 a	47.4 a	72.0 a	75.0 b	65.8 w
22	55.7 a	48.4 a	70.6 a	63.6 a	59.6 v
29	79.7 b	64.4 a	75.4 a	84.3 b	75.9 x
39	67.0 a	51.6 a	71.8 a	77.4 b	67.0 w
Mean	67.4 w	53.5 v	71.7 wx	76.4 x	
CV	12	14	12	8	

[†]Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

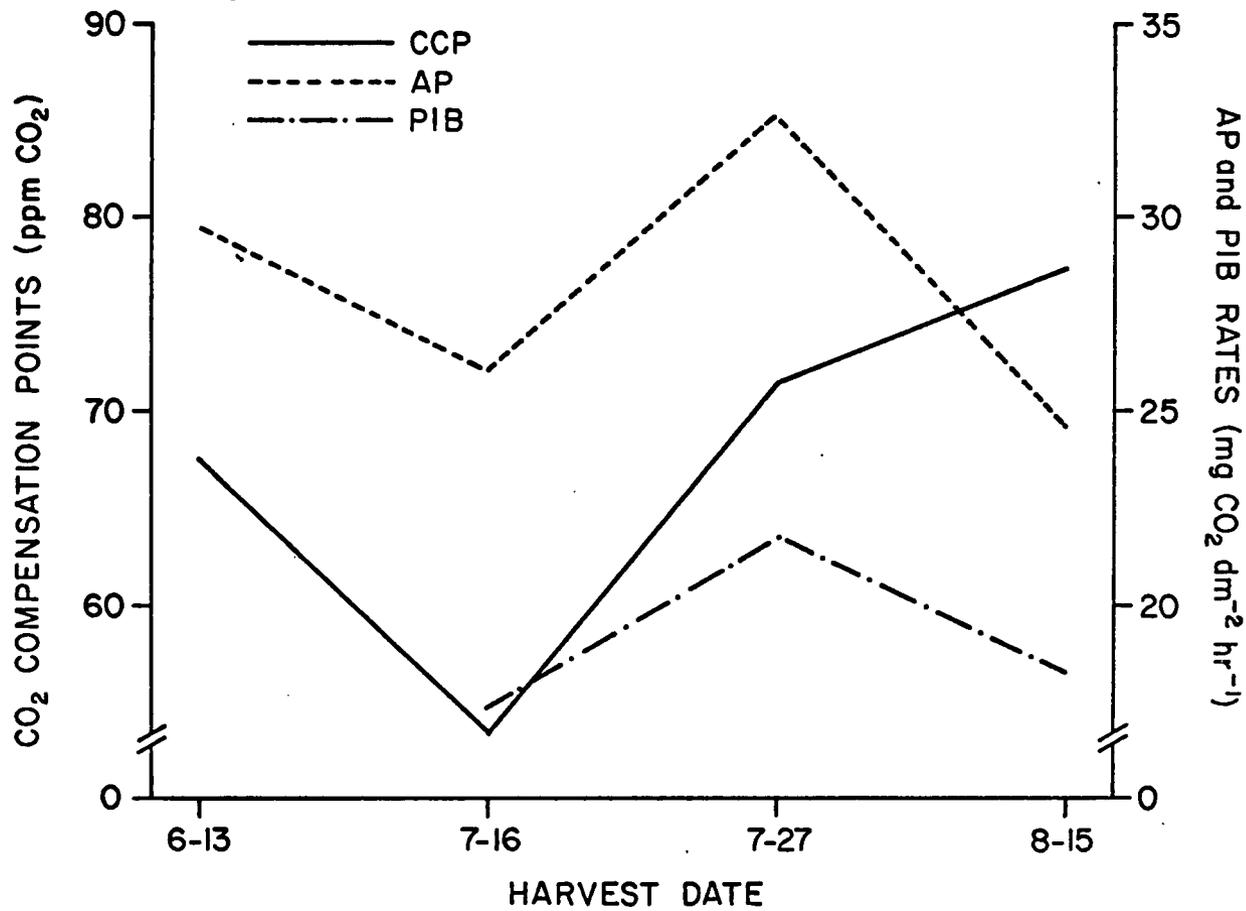


Figure 4. Average CO₂ compensation points, apparent photosynthesis, and post-illumination CO₂ burst of five alfalfa clones in 1972.

Carbon dioxide compensation point was not related to post-illumination CO_2 burst, dark respiration, or apparent photosynthesis. These data are in contrast to Zelitch's (65) hypothesis that CO_2 compensation point is a function of photorespiration. His data showed that an increase in post-illumination CO_2 burst rate, or photorespiration, was accompanied by lower photosynthetic rates and higher CO_2 compensation points. Decker (17) suggested that the relationship of apparent photosynthesis to photorespiration as measured by the CO_2 compensation point could be a useful index of photosynthetic efficiency. The present data suggested, contrary to Decker's hypothesis, that CO_2 compensation points were not a good measure of photosynthetic efficiency for the five clones used in this study. Carbon dioxide compensation point was not significantly associated with dry matter production of the material studied.

Apparent Photosynthesis Per Plant

Significant differences in apparent photosynthesis per plant were noted only at the July 1 harvest date in 1971 (Table 16). However, differences were found among all harvest dates in 1972 regardless of the system used for evaluation (Tables 17 and 18). The highest-yielding plants (clone 22) incorporated 52% more CO_2 per plant than the lowest-yielding plants (clone 3) in 1971, and 78% more in 1972 when averaged over all harvest dates.

Table 16. Average apparent photosynthesis per plant of five alfalfa clones measured with an open system at seven harvest dates in 1971.

Clone	Apparent Photosynthesis Per Plant ⁺ (mg CO ₂ per plant)							Means
	Harvest Date in 1971							
	4/21	5/19	6/10	7/1	7/26	8/24	9/28	
1	2407 a	4613 a	3166 a	3711 ab	2570 a	2391 a	512 a	2767 vw
3	1264 a	2925 a	3372 a	1777 a	2243 a	1706 a	264 a	1936 v
22	1951 a	4815 a	4144 a	5254 b	3293 a	6773 b	2332 b	4080 w
29	2334 a	3904 a	4807 a	5232 b	4330 a	4385 ab	1064 a	3594 w
39	1649 a	5253 a	3017 a	4190 b	2913 a	6865 b	1069 a	3566
Means	1921 v	4302 x	3701 wx	4033 x	2891 w	4424 x	1048 v	
CV	64	35	45	35	38	57	55	

⁺Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

Table 17. Average apparent photosynthesis per plant of five alfalfa clones measured with an open system at four harvest dates in 1972.

Clone	Apparent Photosynthesis Per Plant [†] (mg CO ₂ per plant)				Mean
	Harvest Date in 1972				
	6/13	7/16	7/27	8/15	
1	3112 ab	1990 ab	1402 ab	580 a	1771 vw
3	1823 a	965 a	510 a	687 a	997 v
22	6016 c	2844 bc	3903 c	2558 b	4188 z
29	3673 ab	3466 bc	2049 b	1153 a	2430 wx
39	4114 ab	4277 c	2493 b	1192 a	2816 x
Mean	3748 y	2708 x	2071 w	1234 v	
CV	32	36	37	43	

[†]Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

Table 18. Average apparent photosynthesis per plant of five alfalfa clones measured with a closed system at three harvest dates in 1972.

Clone	Apparent Photosynthesis Per Plant [†] (mg CO ₂ per plant)			
	Harvest Date in 1972			Mean
	7/16	7/27	8/15	
1	1049 ab	918 ab	645 a	990 v
3	1077 a	427 a	1564 ab	1022 v
22	2963 c	2647 c	2408 b	2673 w
29	1382 ab	1459 b	759 ab	1200 v
39	2310 bc	1084 ab	1448 ab	1614 vw
Mean	1828 w	1307 v	1365 v	
CV	36	33	67	

[†]Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

The association between total CO₂ incorporation per plant and leaflet area per plant was significant when averaged over the harvest periods in both 1971 and 1972 (Table 19).

Apparent photosynthesis per plant was significantly related to yield in both 1971 and 1972 (Table 19). These data support the hypothesis of Yoshida (63) that dry matter production of a single plant must be correlated with the product of leaf area and photosynthetic rate. These findings suggested that apparent photosynthesis per plant may be used as a criterion for selecting high-yielding alfalfa genotypes. However, the time involved to obtain leaflet area and photosynthetic rates, limits the use of this physiological factor as a screening method.

Dark Respiration Per Plant

Differences in dark respiration per plant among the five alfalfa clones were found at the May and September harvest dates in 1971 when the plants were measured with the open system (Table 20). However, dark respiration per plant was not significantly different among clones when averaged over all harvest dates in 1971. Significant differences were found with both the open and closed systems in 1972 (Tables 21 and 22). Dark respiration rates per plant ranged from 528 mg CO₂ dm⁻² hr⁻¹ for clone 22, to 166 mg CO₂ dm⁻² hr⁻¹ for clone 3, when the plants were evaluated in the

Table 19. Correlation coefficients between apparent photosynthesis per plant and leaflet area per plant and dry matter production.

Year	Apparent Photosynthesis Per Plant Versus:	
	LA	DM
	(r)	(r)
1971	.87**	.59**
1972	.96**	.90**

**Significant at the .01 level.

Table 20. Average dark respiration per plant of five alfalfa clones measured with an open system at seven harvest dates in 1971.

Clone	Dark Respiration Per Plant [†] (mg CO ₂ per plant)							Means
	Harvest Date in 1971							
	4/21	5/19	6/10	7/1	7/26	8/24	9/28	
1	620 a	772 abc	582 a	657 a	338 a	536 a	84 a	513 v
3	321 a	522 ab	865 a	339 a	354 ab	1065 a	153 ab	517 v
22	622 a	560 abc	718 a	672 a	533 ab	1230 a	213 ab	650 v
29	574 a	911 c	781 a	698 a	518 ab	995 a	197 ab	668 v
39	465 a	491 a	486 a	534 a	559 b	1294 a	280 b	587 v
Means	520 wx	651 x	686 x	580 wx	460 w	1024 y	185 v	
CV	44	35	42	43	28	49	45	

[†]Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

Table 21. Average dark respiration per plant of five alfalfa clones measured with an open system at four harvest dates in 1972.

Clone	Dark Respiration Per Plant [†] (mg CO ₂ per plant)				Mean
	Harvest Date in 1972				
	6/13	7/16	7/27	8/15	
1	321 ab	326 a	257 ab	125 a	257 vw
3	188 a	210 a	114 a	151 a	166 v
22	530 b	473 a	690 c	418 b	528 x
29	446 b	233 a	454 bc	177 a	328 vw
39	313 ab	546 b	482 bc	252 ab	399 wx
Mean	360 w	358 w	400 w	225 v	
CV	40	49	44	57	

[†]Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

Table 22. Average dark respiration per plant of five alfalfa clones measured with a closed system at three harvest dates in 1972.

Clone	Dark Respiration Per Plant [†] (mg CO ₂ per plant)			Mean
	Harvest Date in 1972			
	7/16	7/27	8/15	
1	236 a	166 ab	81 a	161 v
3	263 a	48 a	119 a	143 v
22	406 a	399 b	420 b	408 w
29	292 a	362 b	128 a	261 vw
39	492 a	269 ab	289 ab	349 w
Mean	338 w	249 vw	208 v	
CV	53	55	64	

[†]Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

open system in 1972. However, dark respiration per plant ranged from 408 mg CO₂ dm⁻² hr⁻¹ for clone 22, to 143 mg, CO₂ dm⁻² hr⁻¹ for clone 3, with the closed system.

A significant relationship between CO₂ respired per plant in the dark and yield was found in both 1971 and 1972 ($r = +.47^*$ and $r = +.64^*$, respectively). Even though total dark respiration and yield are highly correlated, the lack of differences in dark respiration per plant among the five clones in 1971 limits the use of this factor as a criterion for separating high-yielding genotypes. Total CO₂ respired per plant was directly related to total leaf area per plant when averaged over all individual observations in both 1971 and 1972 ($r = +.77^*$ and $r = +.64^*$, respectively).

Post-illumination CO₂ Burst Per Plant

Significant differences in the amount of CO₂ respired per plant in the light among the five clones were found at all harvests in the closed system in 1972 (Table 23). Clone 22 had the highest light respiration rates for all harvests with an average of 2442 mg CO₂ per plant per hour. Clone 3 had the lowest light respiration rates with a mean of 716 mg CO₂ per plant per hour when averaged over all harvest dates.

A 47% reduction in the amount of CO₂ respired per plant in light occurred over the harvest season in 1972. The reduction in light respiration per plant could be

Table 23. Average post-illumination CO₂ burst per plant of five alfalfa clones measured with a closed system at three harvest dates in 1972.

Clone	Post-illumination Burst Per Plant at 30 C [†] (mg CO ₂ per plant)			
	Harvest Date in 1972			Mean
	7/16	7/27	8/15	
1	1097 a	773 a	302 a	723 v
3	1124 a	445 a	579 a	7716 v
22	2272 ab	3038 b	2017 b	2442 x
29	1250 a	1367 ab	506 a	1041 vw
39	2696 b	1218 ab	1208 ab	1708 w
Mean	1688 w	1368 vw	922 w	
CV	48	72	72	

[†]Clone, harvest date, and clone within harvest date means followed by the same letter are significantly different at the .05 level according to Duncan's New Multiple Range Test.

accounted for by the concurrent reduction in leaflet area which occurred during the 1972 growing season.

A significant relationship between post-illumination CO₂ burst per plant and yield was found ($r = +.65^*$). This relationship could be explained by the involvement of leaflet area per plant in the calculation of post-illumination CO₂ burst per plant. Post-illumination CO₂ burst per plant appeared to be of some value as a selection method for the isolation of superior-yielding genotypes.

Morphological Factors

Leaflet Area Per Plant

Leaflet area per plant was significantly different among the five clones during the 1971 and 1972 harvest seasons (Tables 24 and 25). Clone 22 had the highest average leaflet area in both 1971 and 1972 with means of 154 and 154 dm², respectively. Clone 3 had the lowest average leaflet area in both years with means of 66 and 32 dm², respectively.

Differences in leaflet area per plant were found among harvest dates in both 1971 and 1972 (Tables 24 and 25). In general, leaflet area decreased with advancing harvest dates in 1971, except for the increase at the August 23 harvest date. Decreases in leaflet area were noted at each harvest date in 1972 (Figure 5). A 60% reduction in leaflet area per plant occurred over the harvest season.

Table 24. Average leaflet area per plant of five alfalfa clones at seven harvest dates in 1971.

Clones	Leaflet Area Per Plant [†] (dm ²)							Means
	Harvest Date in 1971							
	4/21	5/19	6/10	7/1	7/26	8/24	9/28	
1	114 b	175 b	96 ab	98 a	73 a	106 a	56 ab	102 vw
3	50 a	81 a	115 a	42 a	57 a	75 a	44 a	66 v
22	120 b	137 b	186 a	184 c	112 b	246 b	89 ab	154 x
29	113 ab	152 b	183 a	155 b	102 a	223 b	70 ab	143 wx
39	72 ab	139 b	101 a	127 b	100 a	200 b	95 b	119 wx
Means	94 v	137 w	136 w	121 w	89 v	170 x	71 v	
CV	38	24	40	32	31	33	34	

[†]Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

Table 25. Average leaflet area per plant of five alfalfa clones at four harvest dates in 1972.

Clones	Leaflet Area Per Plant [†] (dm ²)				Mean
	Harvest Date in 1972				
	6/13	7/16	7/27	8/15	
1	104 ab	64 ab	40 a	26 a	59 vw
3	48 a	42 a	13 a	23 a	32 v
22	277 c	179 c	117 c	100 c	154 y
29	132 b	104 bc	70 ab	42 ab	87 wx
39	154 b	128 c	88 bc	67 b	110 x
Mean	132 y	104 x	66 w	52 v	
CV	31	29	35	39	

[†]Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

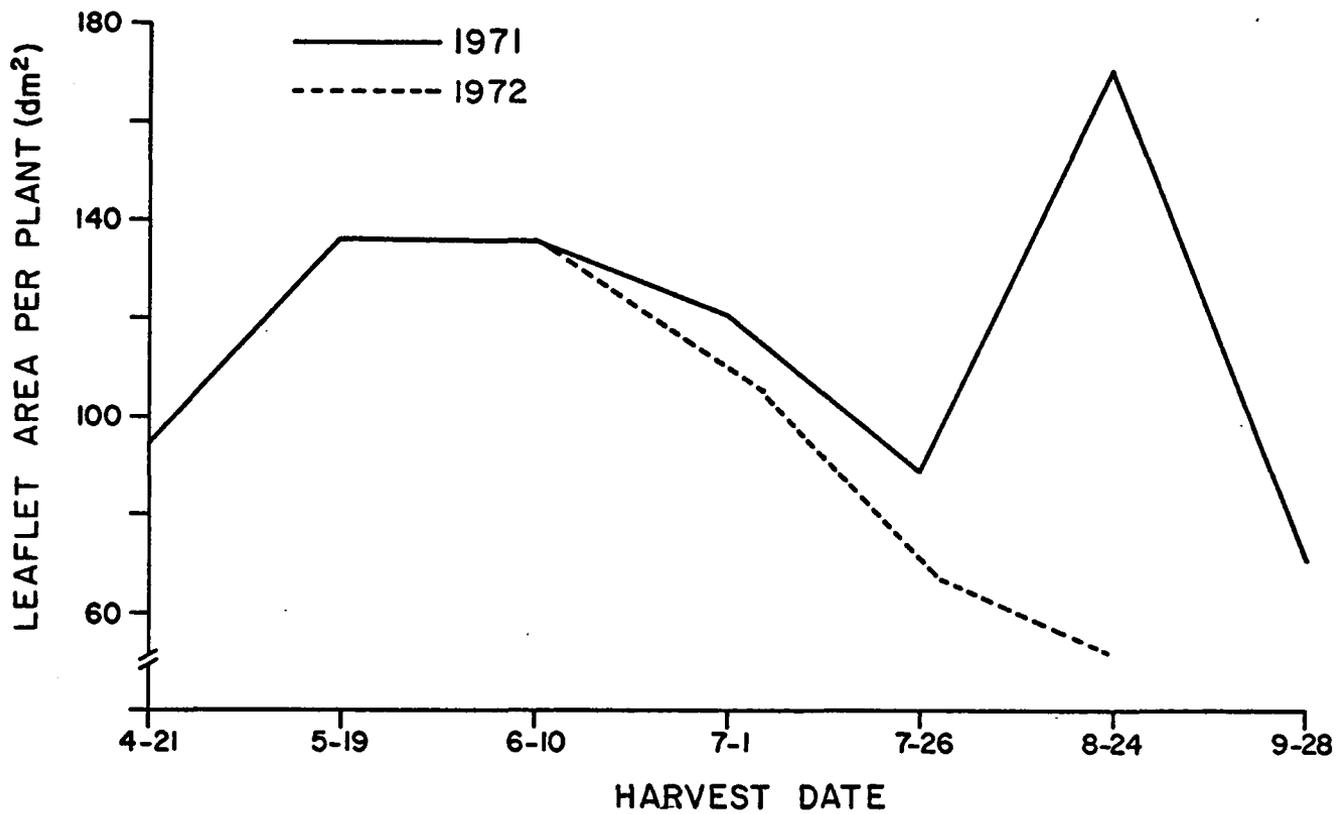


Figure 5. Average leaflet area per plant of five alfalfa clones at seven harvest dates in 1971 and four harvest dates in 1972.

The association between leaflet area and yield was significant (Table 26). This relationship was $r = +.75^{**}$ and $r = +.90^{**}$ for 1971 and 1972, respectively. These data suggested that due to genotypic variation and correlations with yield, leaflet area would be a useful criterion for selection of superior-producing genotypes.

Leaflet area per plant was negatively associated with specific leaflet weight in both 1971 and 1972. This relationship has been noted by previous researchers (18, 20). Plants which display high specific leaf weight also have less total leaf area, smaller leaflets, and lower yields. The decreased leaflet area per plant may also have been a result of a decreased number of stems per plant along with decreased numbers of nodes per stem and subsequently decreased numbers of leaves per plant.

Specific Leaflet Weight

The weight of leaves per unit area (SLW) among the five clones was significantly different when averaged over the seven harvest dates in 1971 (Table 27). There were no differences in specific leaflet weight among the five clones at the four harvest dates in 1972 (Table 28). Means ranged from .409 to .448 g dm^{-2} in 1971 and from .332 to .397 g dm^{-2} in 1972. These data suggested that specific leaflet weight would not be a useful criterion for the selection of high-producing genotypes.

Table 26. Correlation coefficients between leaflet area per plant and physiological and morphological variables in 1971 and 1972.

Leaflet Area Per Plant Versus:	Year	
	1971	1972
	(r)	(r)
AP	.13	-.16
DR	-.12	-.57
TAP	.87**	.96**
TDR	.77**	.64**
SLW	-.47*	-.45*
L/S	.09	-.07
DM	.75**	.90**

*Significant at the .05 level.

**Significant at the .01 level.

Table 27. Average specific leaflet weight of five alfalfa clones at seven harvest dates in 1971.

Clone	Specific Leaflet Weight [†] (g dm ⁻²)							Means
	Harvest Date in 1971							
	4/21	5/19	6/10	7/1	7/26	8/24	9/28	
1	.573 a	.438 a	.447 a	.375 b	.442 a	.317 a	.406 a	.428 vw
3	.589 a	.473 a	.376 a	.430 c	.460 a	.298 a	.370 a	.428 vw
22	.617 a	.442 a	.338 a	.312 a	.460 a	.251 a	.443 a	.409 v
29	.646 a	.534 a	.343 a	.337 a	.485 a	.253 a	.420 a	.431 vw
39	.802 b	.434 a	.387 ab	.323 a	.459 a	.255 a	.477 b	.448 w
Means	.646 z	.464 y	.379 wx	.355 w	.461 y	.275 v	.423 xw	
CV	18	24	20	7	14	14	14	

[†]Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

Table 28. Average specific leaflet weight of five alfalfa clones at four harvest dates in 1972.

Clone	Specific Leaflet Weight [†] (g dm ⁻²)				Mean
	Harvest Date in 1972				
	6/13	7/16	7/27	8/15	
1	.364 a	.442 a	.394 a	.387 a	.397 w
3	.374 a	.363 a	.371 a	.391 a	.375 vw
22	.316 a	.343 a	.340 a	.327 a	.332 v
29	.313 a	.343 a	.370 a	.427 a	.363 v
39	.309 a	.399 a	.326 a	.343 a	.344 v
Mean	.335 v	.378 v	.360 v	.375 v	
CV	14	16	16	21	

[†]Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

Average SLW varied considerably among harvest dates in 1971 (Table 27). Specific leaflet weights ranged from $.646 \text{ g dm}^{-2}$ at the April 21 harvest date to $.275 \text{ g dm}^{-2}$ at the August 24 harvest date in 1971. Significant differences were not found among harvest dates in 1972. Highest specific leaflet weights were found in April in 1971, and since no harvests were made early in the growing season the second year, this could account for uniformity in specific leaflet weight among harvest dates in 1972 (Figure 6).

Specific leaflet weight was not correlated with yield (Table 29). Due to the lack of genotypic variation and lack of correlation with dry matter production, specific leaflet weight could not be recommended as a measure of yield potential.

The negative association between specific leaflet weight and total apparent photosynthesis may have been related to the number of mesophyll cells and the thickness of the mesophyll layer in a leaflet. Delaney (18) reported a significant relationship between apparent photosynthesis and palisade thickness. Specific leaflet weight was also related to palisade thickness. Due to this relationship he concluded that selection for palisade thickness and density could lead to increased apparent photosynthesis.

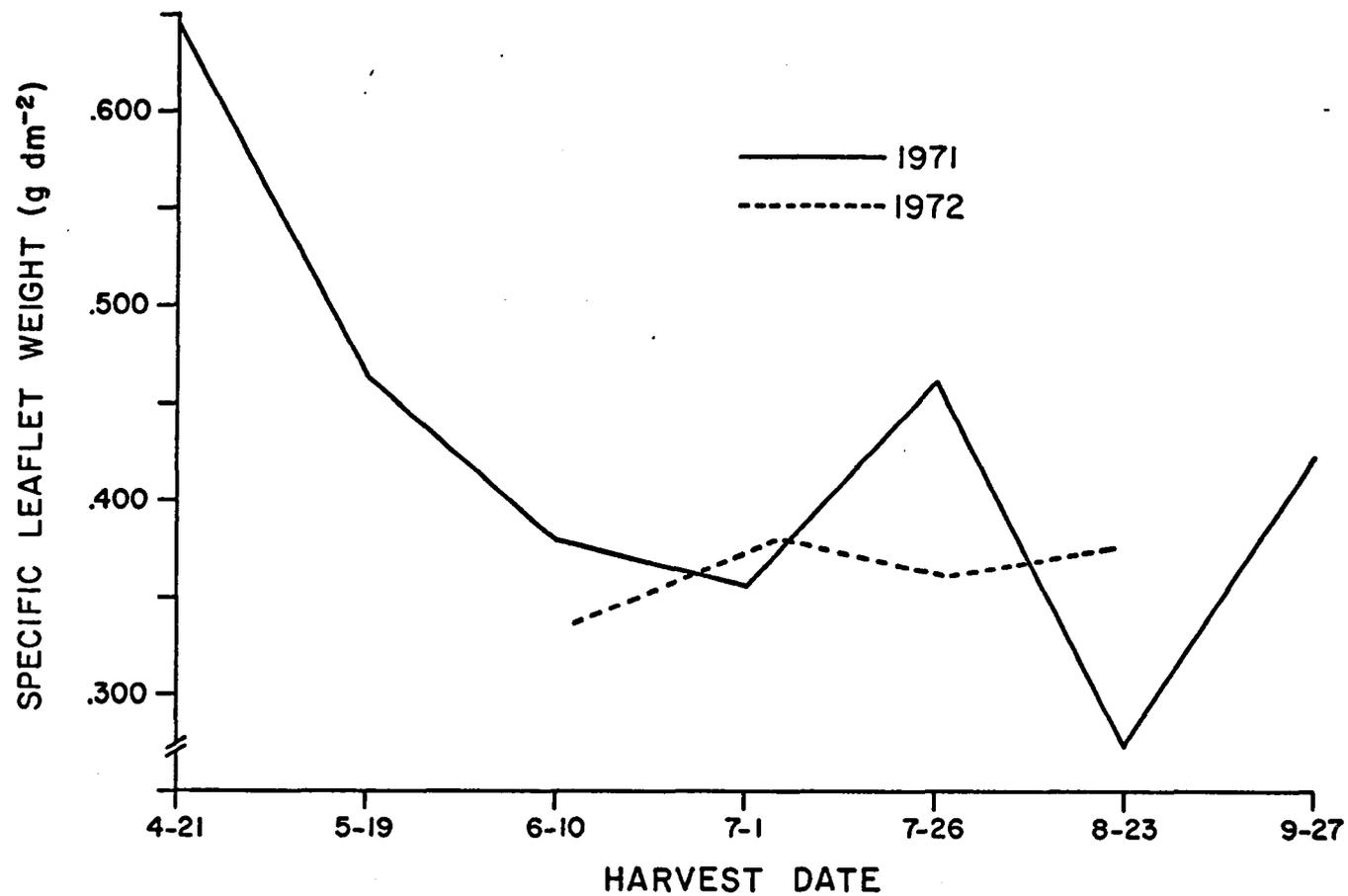


Figure 6. Average specific leaflet weight of five alfalfa clones at seven harvest dates in 1971 and four harvest dates in 1972.

Table 29. Correlation coefficients between specific leaflet weights and physiological and morphological variables measured in 1971 and 1972.

Specific Leaflet Weight Versus:	Year	
	1971	1972
	(r)	(r)
AP	.04	.29
DR	.06	.50
TAP	-.36**	-.36**
TDR	-.30**	-.12
L/S	.43**	-.02
DM	.01	-.22

**Significant at the .01 level.

Leaflet to Stem-Petiole Ratio

The ratio of the dry weight of the leaves and the dry weight of stems and petioles was significantly different among the five clones in both 1971 and 1972 when averaged over the growing season (Tables 30 and 31). Clones 1 and 3 had leaflet to stem-petiole ratios of .56 and .47, respectively, while clones 22 and 29 had leaflet to stem-petiole ratios of .64 and .60, respectively, in 1971. The clones maintained their same rank in leaflet to stem-petiole ratios in 1972. The 12% difference in leaflet to stem-petiole ratio among the clones was apparently a reflection of the larger amount of leaflet area on the higher-producing plants.

Leaflet to stem-petiole ratios varied among harvest dates in both 1971 and 1972 (Tables 30 and 31). The highest leaflet to stem-petiole ratios occurred at the April 21 harvest date and the lowest at the July 1 harvest date in 1971 (Figure 7). These data are in agreement with those of Joy (38) who reported the seasonal trends of leaf-stem ratios for broadcast alfalfa. Although alfalfa produces less forage in July, there is a smaller percentage of leaves compared to stems in the warmer part of the growing season. The low leaflet to stem-petiole ratios in July may have been a result of fewer stems and nodes during this part of the growing season and subsequently less proliferation of leaf tissue. A significant positive correlation ($r = +.88^*$) was noted

Table 30. Average leaflet to stem-petiole ratios of five alfalfa clones at seven harvest dates in 1971.

Clone	Leaflet to Stem-Petiole Ratio [†]							Means
	Harvest Date in 1971							
	4/21	5/19	6/10	7/1	7/26	8/24	9/28	
1	.78 ab	.52 ab	.49 a	.43 b	.50 a	.45 a	.74 c	.56 w
3	.64 a	.45 a	.50 a	.34 a	.47 a	.50 ab	.36 a	.47 v
22	.94	.70 bc	.61 c	.51 c	.55 a	.56 ab	.65 bc	.64 x
29	.72 a	.59 ab	.58 bc	.48 bc	.74 b	.62 b	.46 ab	.60 wx
39	.95 b	.86 c	.58 bc	.46 bc	.58 a	.61 b	.80 c	.69 x
Means	.81 y	.62 x	.55 w	.44 v	.57 wx	.55 w	.60 wx	
CV	17	19	18	8	13	15	22	

[†]Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

Table 31. Average leaflet to stem-petiole ratios of five alfalfa clones at four harvest dates in 1972.

Clone	Leaflet to Stem-Petiole Ratio [†]				Means
	Harvest Date in 1972				
	6/13	7/16	7/27	8/15	
1	.47 a	.30 a	.55 ab	.82 ab	.54 vw
3	.48 a	.35 ab	.40 a	.68 a	.48 v
22	.63 a	.47 bc	.49 ab	.91 b	.62 x
29	.63 a	.43 abc	.57 ab	1.18 c	.70 y
39	.49 a	.49 c	.60 b	.86 ab	.61 wx
Means	.54 w	.41 v	.52 w	.89 x	
CV	23	19	29	17	

[†]Clone, harvest date, and clone within harvest date means followed by the same letter are not significantly different at the .05 level according to Duncan's New Multiple Range Test.

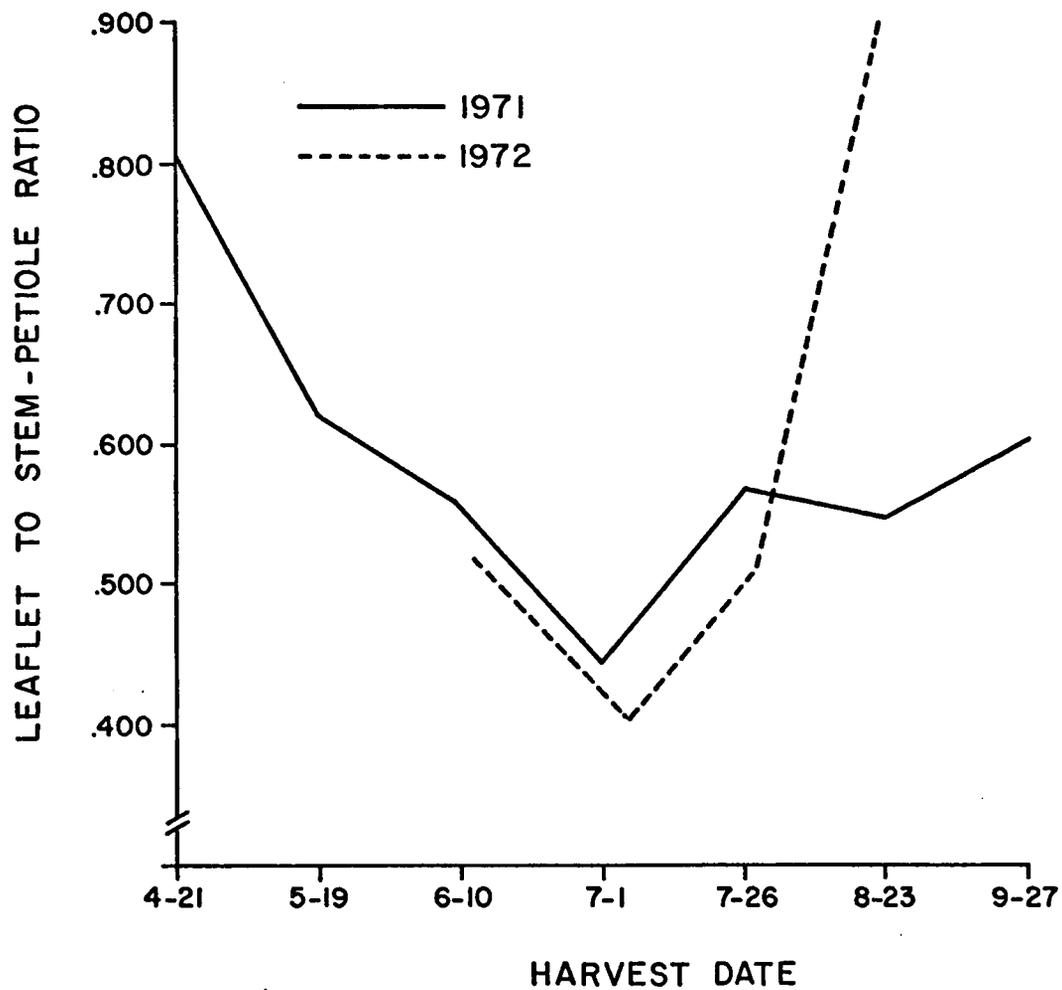


Figure 7. Average leaflet to stem-petiole ratios of five alfalfa clones at seven harvest dates in 1971 and four harvest dates in 1972.

between leaflet to stem-petiole ratios and yield in 1971. However, a negative correlation ($r = -.35^*$) was noted in 1972. Leaflet to stem-petiole ratios do not appear to be useful for isolating higher-producing genotypes of alfalfa.

Multiple Regression Analyses

Multiple regression analyses were made on the physiological and morphological variables to determine which combinations of variables gave the best estimate of dry matter production. Only those variables which were significantly related to yield at the .05 level were entered into the regression analyses. The variables which accounted for the greatest amount of variability in dry matter production with the open system in 1971, and with open and closed systems in 1972 are shown in Tables 32, 33, and 34.

Physiological factors such as apparent photosynthesis per plant plus dark respiration per plant along with morphological variables such as leaflet area per plant, specific leaflet weight, and leaflet to stem-petiole ratios could be used together as selection criteria for higher-producing genotypes. However, as the season progressed, the morphological factors appeared to become better criteria for the prediction of high-producing genotypes. In the overall analysis, leaflet area per plant plus specific leaflet weight plus leaflet to stem-petiole ratios accounted for 70 and 94% of the variability associated with yield when plants

Table 32. Multiple regression analyses between yield and physiological and morphological factors of five alfalfa clones measured with an open system at seven harvest dates in 1971.

Harvest Date	Factor	R ²
4/1	(TAP + TDR)	.69
	(TAP + TDR) + SLW	.76
	(TSP + TDR) + SLW + LA	.83
5/19	TAP	.51
	TAP + LA	.62
	TAP + LA + SLW	.81
6/10	(TAP + TDR)	.57
	(TAP + TDR) + SLW	.61
	(TAP + TDR) + SLW + LA	.73
7/1	LA	.70
7/26	LA	.53
	LA + SLW	.71
	LA + SLW + (AP + DR)	.87
8/24	LA	.89
	LA + L/S	.92
	LA + L/S + SLW	.94
9/28	LA	.66
	LA + L/S	.76
	LA + L/S + SLW	.93
Combined	LA	.51
	LA + SLW	.65
	LA + SLW + L/S	.70

Table 33. Multiple regression analyses between yield and physiological and morphological factors of five alfalfa clones measured with an open system at four harvest dates in 1972.

Harvest Date	Factor	R ²
6/13	TAP	.87
	TAP + L/S	.94
	TAP + L/S + SLW	.95
7/16	(TAP + TDR)	.89
	(TAP + TDR) + L/S	.91
	(TAP + TDR) + L/S + LA	.93
7/27	LA	.93
	LA + L/S	.96
	LA + L/S + SLW	.98
8/15	LA	.92
	LA + TDR	.94
	LA + TDR + L/S	.95
Combined	LA	.81
	LA + L/S	.89
	LA + L/S + SLW	.94

Table 34. Multiple regression analyses between yield and physiological and morphological factors of five alfalfa clones measured with a closed system at three harvest dates.

Harvest Date	Factor	R ²
7/16	LA	.83
	LA + SLW	.91
	LA + SLW + L/S	.98
7/27	LA	.83
	LA + L/S	.96
	LA + L/S + SLW	.98
8/15	LA	.92
	LA + TSL	.94
Combined	LA	.83
	LA + L/S	.91
	LA + L/S + SLW	.96

were measured with the open system in 1971 and 1972, respectively. These same variables accounted for 96% of the variability when plants were measured with the closed system in 1972.

Regression analysis showed that morphological factors were more useful in the selection of high-yielding genotypes of alfalfa than physiological factors. However, since many of the physiological factors are heritable, germplasm pools containing material with desirable physiological traits, such as high apparent photosynthetic rates and low dark respiration rates, should be maintained. These germplasm pools with desirable physiological factors could be used in the development of superior cultivars. Selection of plants on a morphological basis combined with germplasm, which contains highly desirable physiological characteristics, would be advantageous to a breeding program as a mechanism for increasing the yield potential of alfalfa.

Water Requirement

Total water transpired, forage yield, and water requirement were not different among the five clones during the first growth period following the establishment of the cuttings (Figure 8). Dry forage yields ranged from 1.48 to 1.88 g per plant for clones 22 and 29, respectively, while water requirements ranged from 576 to 639 for clones 3 and

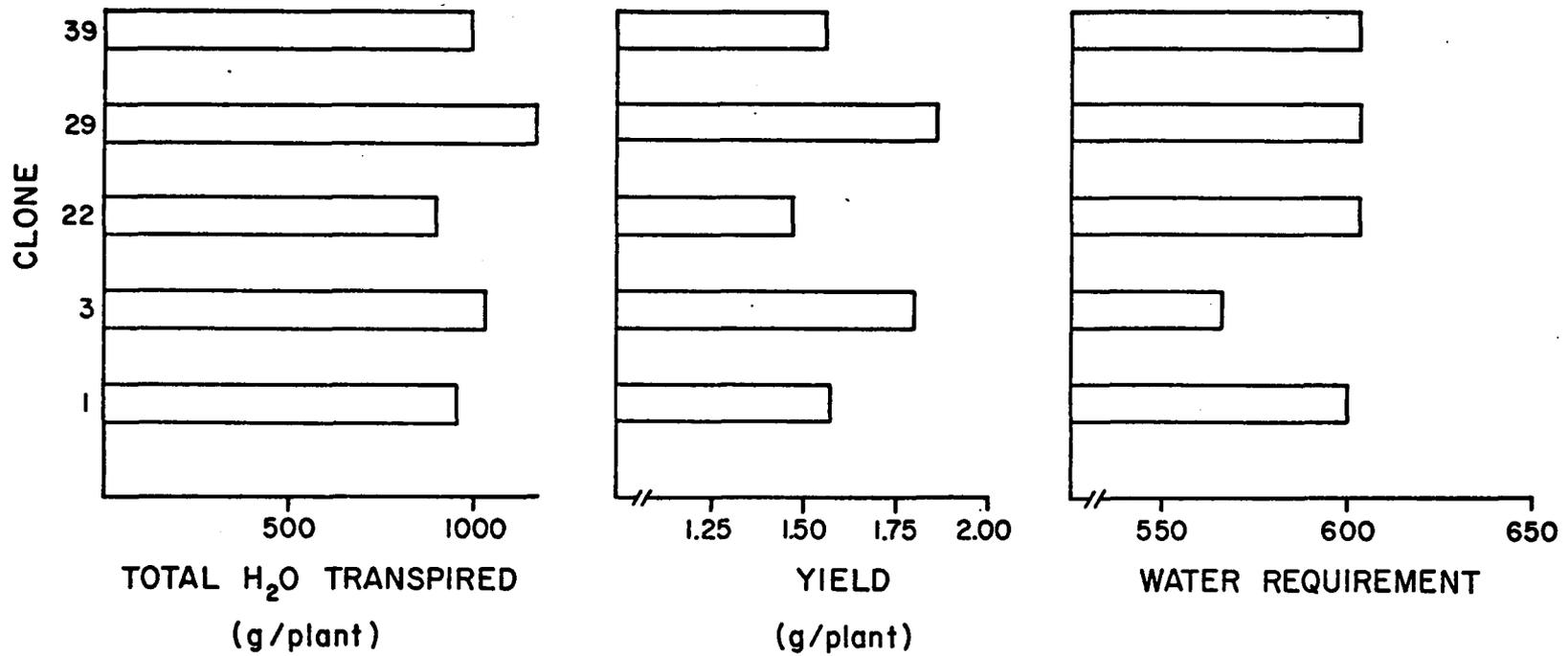


Figure 8. Average amount of water transpired per plant, dry forage production per plant, and water requirement of five alfalfa clones for the first growth period.

29, respectively. The lack of significant differences in transpired water, yield, and water requirement may have been due to plant to plant variation found in cuttings of alfalfa.

Significant differences, however, were found during the course of the second growth period in total water transpired and dry forage yield per plant (Figure 9). Clone 29 transpired 29.9% more water during the growth period than clone 1. Clone 29 also produced 36.9% more dry forage than clone 3. Since the differences in yield between the clones were accompanied by comparable linear increases in total water transpired, water requirements were similar for the clones. Five alfalfa clones may have represented too narrow a germplasm for determining significant differences in water requirements.

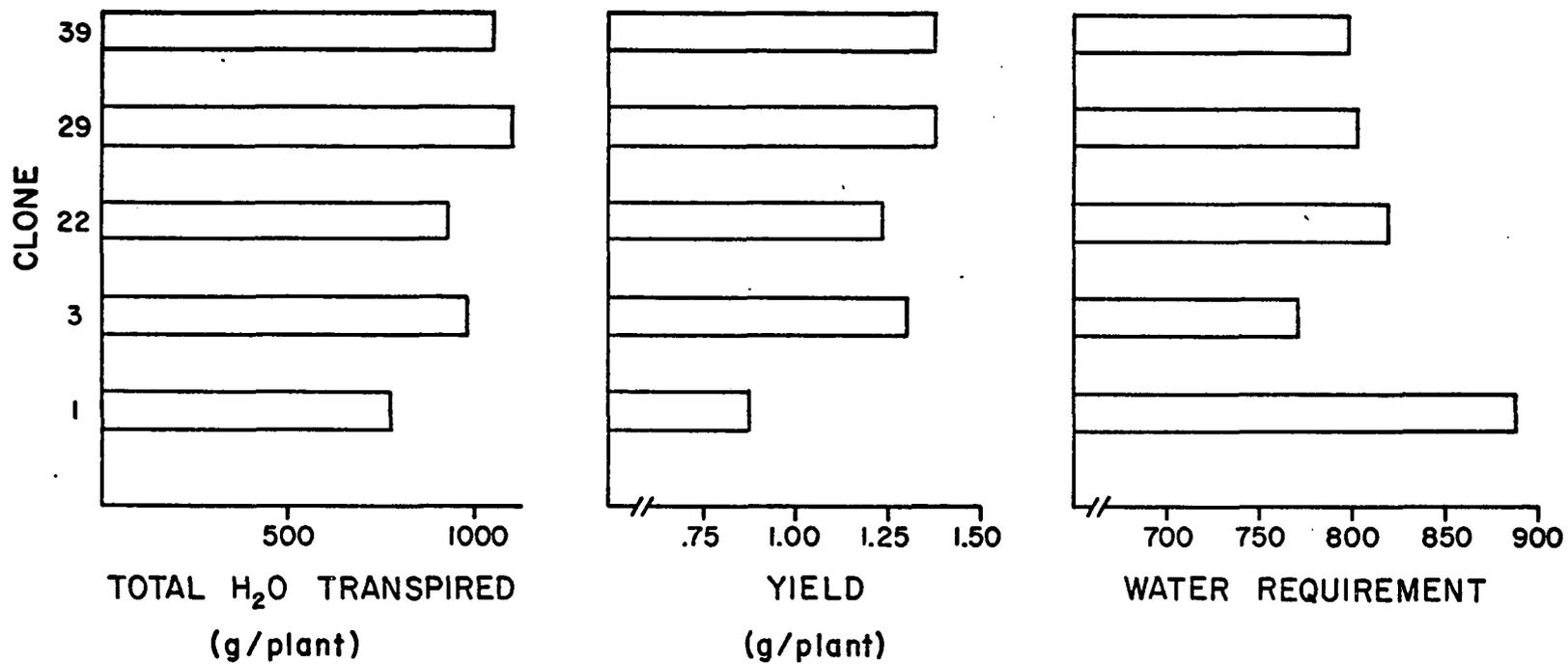


Figure 9. Average amount of water transpired per plant, dry forage production per plant, and water requirement for five alfalfa clones for the second growth period.

SUMMARY AND CONCLUSIONS

Clones of alfalfa, which were chosen from an experimental synthetic (Reselect Sonora), were used to evaluate the relationship between forage yield and physiological, morphological, and calculated variables. The clones were selected for their differences in yield potential. Twenty replications of the five alfalfa clones were grown under space-planted conditions in the field.

Differences in apparent photosynthesis ($\text{mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$) were noted among the five alfalfa clones at only two harvest dates in 1971 and 1972. Apparent photosynthesis did not account for a significant portion of the variability in dry matter production. Apparent photosynthetic rates could not be used as a criterion for the isolation of superior-producing genotypes.

Average dark respiration rates among the five clones differed in both years when averaged over all harvest dates. Although the negative relationship between dark respiration rates and dry matter production was not significant in 1972, the data suggested that plants should probably be selected which have low respiration rates. There appears to be a minimum amount of respiration needed for ATP and energy

production, and any CO₂ lost above the amount required for growth results in an overall loss to the plant.

Post-illumination CO₂ burst rates and substrate levels were not different among the five alfalfa clones and were not related to yield. Post-illumination CO₂ burst rates were positively correlated ($r = +.52^*$) with apparent photosynthesis. These data suggested that alfalfa plants with high apparent photosynthetic rates could be chosen by selecting plants with high light respiration rates.

Carbon dioxide compensation points among the five clones were significantly different when averaged over all harvest dates. However, no relationship was found between CO₂ compensation points and dry matter production.

Apparent photosynthesis, dark respiration, and post-illumination CO₂ burst rates expressed on a plant basis rather than a leaf area basis were significantly related to dry matter production. These data suggested that physiological factors should be considered on a total plant basis rather than on a unit leaf area basis. Plants which have low apparent photosynthetic rates may produce more dry matter due to a larger amount of photosynthetic tissue.

Differences were noted in leaflet area per plant among the five alfalfa clones during the 1971 and 1972 harvest seasons. Leaflet area per plant was also related to dry matter production, with correlation coefficients of $+0.75^{**}$ for 1971 and $+0.90^{**}$ for 1972.

Specific leaflet weight was not different among five clones used in this study. This factor appeared to be of little value for use as a selection criterion to isolate high forage-producing clones.

Average leaflet to stem-petiole ratios were different among the five alfalfa clones. Leaflet to stem-petiole ratios were positively correlated ($r = +.88^*$) with dry matter production in 1971, and negatively correlated ($r = -.35^*$) with dry matter production in 1972. The change from a positive correlation to a negative correlation for this characteristic reduces its potential use in a breeders program aimed at isolating higher-producing germplasm.

The results from the multiple regression analysis indicated that the morphological factors would probably be more effective as predictive criteria for the isolation of higher-producing alfalfa clones than physiological factors. Due to the heritability of many of the physiological variables, selection of plants on a morphological basis with desirable physiological traits would be advantageous to an alfalfa breeding program. However, the use of physiological and morphological variables may be questionable due to the amount of time and labor required in their measurement.

LITERATURE CITED

1. Alberta, T. 1970. The influence of carbohydrate reserves on respiration, photosynthesis, and dry matter production of intact plants. Int. Grassland Congr., Proc. 11th (Queensland, Aust.). pp. 517-522.
2. Asay, K. H., and C. J. Nelson. 1972. The potential role of photosynthetic efficiency in the improvement of forage grasses. Agron. Abstr. Amer. Soc. Agron. pp. 51.
3. Barnes, D. K., R. B. Pearce, G. E. Carlson, R. H. Hart, and C. H. Hanson. 1969. Specific leaf weight differences in alfalfa associated with variety and plant age. Crop Sci. 9:421-423.
4. Bowes, G., and William Ogren. 1972. Oxygen inhibition and other properties of soybean ribulose 1,5-diphosphate carboxylase. J. Biol. Chem. 247:2171-2176.
5. Briggs, L. J., and H. L. Shantz. 1913. The water requirements of plants. I. Investigations in the Great Plains in 1910 and 1911. USDA Bur. Plant Ind. Bull. 284.
6. Cannell, R. Q., W. A. Brun, and D. M. Moss. 1969. Search for high net photosynthetic rate among soybean genotypes. Crop Sci. 9:840-841.
7. Carlson, G. E., R. H. Hart, C. H. Hanson, and R. B. Pearce. 1970. Overcoming barriers to higher forage yields through breeding for physiological and morphological characteristics. Int. Grassland Congr. Proc. 11th (Queensland, Aust.). pp. 248-251.
8. Carlson, G. E., R. B. Pearce, D. R. Lee, and R. H. Hart. 1971. Photosynthesis and photorespiration in two clones of orchardgrass. Crop Sci. 11:35-37.
9. Charles-Edwards, D. A. 1971. Photosynthesis and photorespiration in Lolium multiflorum and Lolium perenne. J. Exp. Bot. 22:663-669.

10. Charles-Edwards, D. A., J. Charles-Edwards, and J. P. Cooper. 1971. Influence of temperature on photosynthesis and transpiration in ten temperate grass varieties grown in four different environments. *J. Exp. Bot.* 22:650-662.
11. Cole, D. F. 1969. Water-use efficiency of seven cultivars of alfalfa (Medicago sativa L.). M.S. Thesis, Agronomy Department, Univ. Arizona.
12. Cole, D. F., A. K. Dobrenz, M. A. Massengale, and L. Neal Wright. 1970. Water requirement and its association with growth components and protein content of alfalfa (Medicago sativa L.). *Crop Sci.* 10:237-240.
13. Cooper, J. P., and D. Wilson. 1970. Variation in photosynthetic rate in *Lolium*. *Int. Grassland Congr. Proc.* 11th (Queensland, Aust.). pp. 522-527.
14. Criswell, J. G., and R. M. Schibles. 1971. Physiological basis for genotypic variation in net photosynthesis of oat leaves. *Crop Sci.* 10:550-553.
15. Curtis, P. E., W. L. Ogren, and R. H. Hageman. 1969. Varietal effects in soybean photosynthesis and photorespiration. *Crop Sci.* 9:323-327.
16. Decker, J. P. 1955. A rapid, post-illumination deceleration of respiration in green leaves. *Plant Physiol.* 30:82-84.
17. Decker, J. P. 1970. Photosynthetic efficiency, photorespiration and heterosis. *Arizona State Univ. Bioeng. Bull.* 12.
18. Delaney, R. H. 1972. Morphological features of alfalfa (Medicago sativa L.) clones and their relation to photosynthesis and respiration. Ph.D. Diss. Agronomy Department, Univ. Arizona. (Diss. Abstr. 33:2241B).
19. Dobrenz, A. K., D. F. Cole, and R. J. Joy. 1968. Comparison of materials for reducing evaporation of soil moisture in water efficiency studies. *Agron. J.* 60:446.

20. Dobrenz, A. K., D. F. Cole, and M. A. Massengale. 1971. Yield components and leaf characteristics associated with the water requirement of alfalfa. *Crop Sci.* 11:124-125.
21. Duncan, D. B. 1955. Multiple range and multiple F test. *Biometrics.* 11:1-42.
22. Duncan, W. G., and J. D. Hesketh. 1968. Net photosynthetic rates, relative leaf growth rates, and leaf number of 22 races of maize grown at eight temperatures. *Crop Sci.* 8:670-674.
23. Dvork, J., and L. Natr. 1971. Carbon dioxide compensation points of Triticum and Aegilops species. *Photosynthetica.* 5:1-5.
24. 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.
25. Forrester, M. L., G. Krotkov, and C. D. Nelson. 1966. Effect of oxygen on photorespiration and respiration in detached leaves. I. Soybean. *Plant Physiol.* 41:422-427.
26. Frey, K. J. 1971. Improving crop yields through plant breeding, p. 15-58. In J. D. Eastin, R. D. Munson (ed.) *Moving off the yield plateau.* Amer. Soc. Agron., Crop Sci. Soc. Amer., and Soil Sci. Soc. Amer. Madison, Wis.
27. Fuess, F. W., and M. B. Tesar. 1968. Photosynthetic efficiency, yields, and leaf loss in alfalfa. *Crop Sci.* 8:159-163.
28. Graham, D., and D. A. Walker. 1962. Some effects of light on the interconversion of metabolites in green leaves. *Biochem. J.* 82:554-560.
29. Hanson, W. D. 1971. Selection for differential productivity among juvenile maize plants; associated net photosynthetic rate and leaf area changes. *Crop Sci.* 11:334-338.
30. Heichel, G. H. 1971. Confirming measurements of respiration and photosynthesis with dry matter accumulation. *Photosynthetica.* 5:93-98.

31. Heichel, G. H. 1971. Response of respiration of tobacco leaves in light and darkness and the CO₂ compensation concentration to prior illumination and oxygen. *Plant Physiol.* 48:178-182.
32. Heichel, G. H., and R. B. Musgrave. 1969. Varietal differences in net photosynthesis of Zea mays L. *Crop Sci.* 9:483-486.
33. Heichel, G. H., and R. B. Musgrave. 1969. Relation of CO₂ compensation concentration to apparent photosynthesis in maize. *Plant Physiol.* 44:1724-1728.
34. Hesketh, J. D., and D. Moss. 1963. Variation in the response of photosynthesis to light. *Crop Sci.* 3:107-110.
35. Ishizuka, Y. 1969. Engineering for higher yields. In J. D. Eastin, F. A. Haskins, C. Y. Sullivan, C. van Bavel, and R. C. Dinauer (ed.) *Physiological aspects of crop yield.* Amer. Soc. Agron. and Crop Sci. Soc. Aner. Madison, Wis.
36. Izhar, S., and D. H. Wallace. 1967. Studies on the physiological basis for yield differences. III. Genetic variation in photosynthetic efficiency of Phaseolus vulgaris L. *Crop Sci.* 7:457-460.
37. Jolliffe, P. A., and E. B. Tregunna. 1968. Effect of temperature, CO₂ concentration, and light intensity on oxygen inhibition of photosynthesis in wheat leaves. *Plant Physiol.* 43:902-906.
38. Joy, R. J. 1970. Consumptive water-use efficiency of alfalfa (Medicago sativa L.) grown under three irrigation regimes. M.S. Thesis, Agronomy Department, Univ. Arizona.
39. Khan, M. A., and S. Tsunoda. 1970. Differences in leaf photosynthesis and leaf transpiration rates among six commercial wheat varieties of West Pakistan. *Jap. J. Breeding.* 20:344-350.
40. Lawes, D. A., and K. J. Treharne. 1971. Variation in photosynthetic activity in cereals and its implications in a plant breeding programme. I. Variation in seedling leaves and flag leaves. *Euphytica.* 20:86-92.

41. Ludwig, L. J., and D. T. Canvin. 1971. Rate of photorespiration during photosynthesis and the relationship of the substrate of light respiration to the products of photosynthesis in sunflower leaves. *Plant Physiol.* 48:712-719.
42. March, J. V., Jr., J. M. Galinecke, and M. Gibbs. 1964. Respiration during photosynthesis. *Rec. Chem. Progr.* 25:259-271.
43. McDaniel, R. G. 1972. Mitochondrial heterosis and complementation as biochemical measures of yield. *Nature (London)*. 236:190-191.
44. McDaniel, R. G., and I. V. Sarkissian. 1966. Enhancement of oxidation and phosphorylation of maize scutellum mitochondria by physiological concentration of indoleacetic acid. *Physiol. Plant.* 19:187-193.
45. Menz, K. M., D. M. Moss, R. Cantrell, and W. A. Brun. 1969. Screening of photosynthetic efficiency. *Crop Sci.* 9:692-694.
46. Osman, A. N. 1971. Dry-matter production of a wheat crop in relation to light interception and photosynthetic capacity of leaves. *Ann. Bot.* 35:1017-1035.
47. Pearce, R. B., R. H. Brown, and R. E. Blaser. 1968. Photosynthesis of alfalfa leaves as influenced by age and environment. *Crop Sci.* 8:667-680.
48. Pearce, R. B., G. E. Carlson, D. K. Barnes, R. H. Hart, and C. H. Hanson. 1969. Specific leaf weight and photosynthesis in alfalfa. *Crop Sci.* 9:423-426.
49. Postuka, J. 1968. Photosynthesis, photorespiration and respiration of detached spruce twigs as influenced by oxygen concentration and light intensity. *Physiol. Plant.* 21:1129-2236.
50. Postuka, J., C. D. Nelson, and G. Krotkov. 1967. Effects of metabolic inhibitors on the rates of CO₂ evolution in light and in darkness by detached spruce twigs, wheat, and soybean leaves. *Plant Physiol.* 42:1187-1190.

51. Robinson, G. D., and M. A. Massengale. 1969. Effect of night temperature on growth and development of alfalfa (Medicago sativa L.). J. Ariz. Acad. Sci. 5:227-231.
52. Sarkissian, I. V. 1963. The hybrid plant--a superior photosynthetic system. Barley Newsletter. 6:57-58.
53. Sarkissian, I. V., and R. G. McDaniel. 1967. Mitochondrial polymorphism in maize. I. Putative evidence for de novo origin of hybrid-specific mitochondria. Proc. Nat. Acad. Sci. 57:1262-1266.
54. Sprague, G. F. 1969. Germplasm manipulation of the future. In J. D. Eastin, F. A. Haskins, C. Y. Sullivan, D. van Bavel, and R. C. Dinauer (ed.) Physiological aspects of crop yield. Amer. Soc. Agron. and Crop Sci. Soc. Amer. Madison, Wis.
55. Steward, F. C., G. H. Craven, S. P. R. Weerasinghe, and R. G. S. Bidwell. 1971. Effects of prior environmental conditions on the subsequent uptake and release of carbon dioxide in the light. Can. J. Bot. 49:1999-2007.
56. Tregunna, E., G. Kroktov, and C. D. Nelson. 1964. Further evidence on the effect of light on respiration during photosynthesis. Can. J. Bot. 42:989-997.
57. Volk, R. J., and W. A. Jackson. 1972. Photorespiratory phenomena in maize: Oxygen uptake, isotope discrimination and carbon dioxide efflux. Plant Physiol. 49:218-223.
58. Wilson, D. 1972. Variation on photorespiration in Lolium. J. Exp. Bot. 23:517-624.
59. Wilson, D., and J. P. Cooper. 1969. Diallel analysis of photosynthetic rate and related leaf characters among contrasting genotypes of Lolium perenne L. Heredity. 248:633-649.
60. Wilson, D., and J. P. Cooper. 1970. Effect of selection for mesophyll cell size on growth and assimilation in Lolium perenne L. New Phytol. 69:233-245.

61. Wolf, D. D., and R. E. Blaser. 1971. Photosynthesis of plant parts of alfalfa canopies. *Crop Sci.* 11:55-58.
62. Wolf, D. D., R. B. Pearce, G. E. Carlson, and D. R. Lee. 1969. Measuring photosynthesis of attached leaves with air sealed chambers. *Crop Sci.* 9:24-27.
63. Yoshida, S. 1972. Physiological aspects of grain yield. *Ann. Rev. Plant Physiol.* 23:437-464.
64. Zelitch, I. 1966. Increased rate of net photosynthetic carbon dioxide uptake caused by inhibition of glycolate oxidase. *Plant Physiol.* 41:1623-1631.
65. Zelitch, I. 1971. Photosynthesis, photorespiration, and plant productivity. Academic Press, Inc. New York.
66. Zelitch, I., and P. R. Day. 1968. Variation in photorespiration. The effect of genetic differences in photorespiration on net photosynthesis in tobacco. *Plant Physiol.* 43:1838-1844.