

INFORMATION TO USERS

This reproduction was made from a copy of a document sent to us for microfilming. While the most advanced technology has been used to photograph and reproduce this document, the quality of the reproduction is heavily dependent upon the quality of the material submitted.

The following explanation of techniques is provided to help clarify markings or notations which may appear on this reproduction.

1. The sign or "target" for pages apparently lacking from the document photographed is "Missing Page(s)". If it was possible to obtain the missing page(s) or section, they are spliced into the film along with adjacent pages. This may have necessitated cutting through an image and duplicating adjacent pages to assure complete continuity.
2. When an image on the film is obliterated with a round black mark, it is an indication of either blurred copy because of movement during exposure, duplicate copy, or copyrighted materials that should not have been filmed. For blurred pages, a good image of the page can be found in the adjacent frame. If copyrighted materials were deleted, a target note will appear listing the pages in the adjacent frame.
3. When a map, drawing or chart, etc., is part of the material being photographed, a definite method of "sectioning" the material has been followed. It is customary to begin filming at the upper left hand corner of a large sheet and to continue from left to right in equal sections with small overlaps. If necessary, sectioning is continued again—beginning below the first row and continuing on until complete.
4. For illustrations that cannot be satisfactorily reproduced by xerographic means, photographic prints can be purchased at additional cost and inserted into your xerographic copy. These prints are available upon request from the Dissertations Customer Services Department.
5. Some pages in any document may have indistinct print. In all cases the best available copy has been filmed.

**University
Microfilms
International**

300 N. Zeeb Road
Ann Arbor, MI 48106

1323218

SCHEERENS, GERALDINE ANN

STUDIES ON THE PHYSIOLOGY OF BUFFALO GOURD CUCURBITA
FOETIDISSIMA HBK

THE UNIVERSITY OF ARIZONA

M.S. 1984

**University
Microfilms
International** 300 N. Zeeb Road, Ann Arbor, MI 48106

PLEASE NOTE:

In all cases this material has been filmed in the best possible way from the available copy. Problems encountered with this document have been identified here with a check mark ✓.

1. Glossy photographs or pages ✓
2. Colored illustrations, paper or print ✓
3. Photographs with dark background ✓
4. Illustrations are poor copy _____
5. Pages with black marks, not original copy _____
6. Print shows through as there is text on both sides of page _____
7. Indistinct, broken or small print on several pages ✓
8. Print exceeds margin requirements _____
9. Tightly bound copy with print lost in spine _____
10. Computer printout pages with indistinct print _____
11. Page(s) _____ lacking when material received, and not available from school or author.
12. Page(s) _____ seem to be missing in numbering only as text follows.
13. Two pages numbered _____. Text follows.
14. Curling and wrinkled pages _____
15. Other _____

University
Microfilms
International

STUDIES ON THE PHYSIOLOGY
OF BUFFALO GOURD
CUCURBITA FOETIDISSIMA HBK

by
Geraldine Ann Scheerens

A Thesis Submitted To The Faculty of the
DEPARTMENT OF PLANT SCIENCES
In Partial Fulfillment of the Requirements
For the Degree of
MASTER OF SCIENCE
WITH A MAJOR IN AGRONOMY
AND PLANT GENETICS
In the Graduate College
THE UNIVERSITY OF ARIZONA

1 9 8 4

STATEMENT BY AUTHOR

This thesis has been submitted in partial fulfillment of requirements for an advanced degree at The University of Arizona and is deposited in the University Library to be made available to borrowers under rules of the Library.

Brief quotations from this thesis are allowable without special permission, provided that accurate acknowledgment of source is made. Requests for permission for extended quotation from or reproduction of this manuscript in whole or in part may be granted by the Head of the major department or the Dean of the Graduate College when in his judgment the proposed use of the material is in the interests of scholarship. In all other instances, however, permission must be obtained from the author.

SIGNED: Geraldine Ann Scheeroms

APPROVAL BY THESIS DIRECTOR

This thesis has been approved on the date shows below:

Albert K. Dobrenz
A. K. DOBRENZ
Professor of Plant Sciences

April 26, 1984
Date

ACKNOWLEDGMENTS

The author wishes to acknowledge Dr. A. K. Dobrenz for his encouragement and faith in the author's abilities through the course of the author's graduate program.

The author wishes to acknowledge Dr. W. C. Hofmann and Dr. W. P. Bemis for their assistance in this study.

Special thanks go to Joseph Scheerens who helped the author finish what she had begun.

The author wishes to thank Mr. and Mrs. K. W. Foote (parents) who picked the author up off the ground on more than one occasion.

The author wishes to thank Sam Scheerens for his undying love, devotion and material support (sorry about the lonely nights).

The author wishes to thank her woman friends: Kristie Kreutzfeld, Linda Kloos, Susan Burrows, Helen Scheerens, Morena Seitz, Linda Peterson, and Sandy Ramage, who, like the author, want a better life and more rewards than what history has had to offer.

The author would also like to thank MASTOD for the lighter moments in college life.

TABLE OF CONTENTS

	Page
LIST OF TABLES	vi
LIST OF ILLUSTRATIONS	ix
ABSTRACT	x
1. INTRODUCTION	1
2. LITERATURE REVIEW	4
History	4
Physiology Background	9
3. MATERIALS AND METHODS	21
4. RESULTS AND DISCUSSION	27
Studies of Four Sampling Periods Throughout the Growing Season	27
Apparent Photosynthesis	28
Among Cultivars	28
Among Sampling Periods	28
Transpiration	31
Among Cultivars	31
Among Sampling Periods	33
Dependence/Independence of Transpiration and Photosynthesis	36
Diffusive Resistance	38
Among Cultivars	38
Among Sampling Periods	41
Temperature Differential	42
Among Cultivars	43
Among Sampling Periods	43
Studies of Six Sampling Periods on 3 August 1981	47
Apparent Photosynthesis	48
Among Cultivars	48
Among Sampling Periods	51
Old and Young Leaves Among Sampling Periods and Cultivars	55
Comparison of Old and Young Leaves	58

TABLE OF CONTENTS--Continued

	Page
Transpiration	60
Among Sampling Periods	60
Among Cultivars and Sampling Periods	64
Comparison of Old and Young Leaves	64
Diffusive Resistance	65
Among Sampling Periods	68
Old and Young Leaves Among Sampling Periods and Cultivars	69
Comparison of Old and Young Leaves	74
Temperature Differential	75
Among Cultivars	75
Among Sampling Periods	79
Old and Young Leaves Among Sampling Periods and Cultivars	79
Comparison of Old and Young Leaves	81
5. SUMMARY	85
LITERATURE CITED	90

LIST OF TABLES

Table	Page
1. Average Plot Yields of Buffalo Gourd Hybrid and Pollinator Lines	8
2. Apparent Photosynthetic Rate Means and Coefficients of Variation on Four Sampling Periods Throughout the 1981 Season	29
3. Transpiration Rate Means and Coefficient of Variation on Four Sampling Periods Throughout the 1981 Season	32
4. Mean Values of Diffusive Resistance and Coefficients of Variation on Four Sampling Periods Throughout the 1981 Season	40
5. Temperature Differential Means on Four Sampling Periods Throughout the 1981 Season	44
6. Temperature Differential Means, Standard Deviations, Coded Means and Coded Coefficients of Variation on Four Sampling Periods Throughout the 1981 Season	45
7. Mean Rates of Apparent Photosynthesis on Four Buffalo Gourd Cultivars During Six Periods on 3 August 1981	49
8. Means, Standard Deviations, Coded Means and Coded Coefficients of Variation for Rates of Apparent Photosynthesis During Six Periods on 3 August 1981	52
9. Individual and Mean Rates of Apparent Photosynthesis for Old Leaves During Six Sampling Periods on 3 August 1981	56
10. Individual and Mean Rates of Apparent Photosynthesis in Young Leaves During Six Sampling Periods on 3 August 1981	57

LIST OF TABLES--Continued

Table	Page
11. Means, Standard Deviations, Coded Means and Coded Coefficients of Variation for Rates of Apparent Photosynthesis of Old and Young Leaves During Six Sampling Periods on 3 August 1981	59
12. Mean Rates of Transpiration During Six Periods on 3 August 1981	61
13. Individual and Mean Rates of Transpiration in Old Leaves During Six Sampling Periods on 3 August 1981.	62
14. Individual and Mean Rates of Transpiration in Young Leaves During Six Sampling Periods on 3 August 1981.	63
15. Mean Values of Diffusive Resistance During Six Periods on 3 August 1981	67
16. Individual and Mean Values of Diffusive Resistance in Old Leaves During Six Sampling Periods on 3 August 1981	70
17. Individual and Mean Values of Diffusive Resistance in Young Leaves During Six Sampling Periods on 3 August 1981	72
18. Mean Values of Temperature Differential During Six Periods on 3 August 1981	76
19. Means, Standard Deviations, Coded Means and Coded Coefficients of Variation for Values of Temperature Differential During Six Periods on 3 August 1981	77
20. Individual and Mean Values of Temperature Differential in Old Leaves During Six Sampling Periods on 3 August 1981	79

LIST OF TABLES--Continued

Table	Page
21. Individual and Mean Values of Temperature Differential in Young Leaves During Six Sampling Periods on 3 August 1981	82
22. Means, Standard Deviations, Coded Means and Coded Coefficients of Variation for Values of Temperature Differential of Old and Young Leaves During Six Sampling Periods on 3 August 1981	83
23. Summary of the Means of the Four Physiological Parameters and Their Coefficients of Variations	86

LIST OF ILLUSTRATIONS

Figure	Page
1. Diagrammatic of an Infrared CO ₂ Gas Analyzer	26
2. Temperatures and Relative Humidity for Four Dates Over the 1981 Season	35
3. Scanning Electron Micrographs of Trichomes of Buffalo Gourd. The Area Shown is 4.5×10^{-3} cm ² at a Magnification of 149x	37
4. Scanning Electron Micrographs of Stomates of Buffalo Gourd. The Area Shown is 2.4×10^{-4} cm ² at a Magnification of 619x	39
5. Temperature and Relative Humidity Over the Day on 3 August 1981 as Determined by the National Weather Service, Tucson, Arizona	50
6. CO ₂ Flux Means and Their Standard Deviations for Six Time Periods on 3 August 1981 for Old Leaves	53
7. Photosynthetic and Dark Respiration Means and Their Standard Deviation for Six Time Periods on 3 August 1981 for Young Leaves	54
8. The Transpiration Means and Standard Deviations of Old and Young Leaves for Six Time Periods on 3 August 1981	66
9. The Diffusive Resistance Means of Old and Young Leaves for Six Time Periods on 3 August 1981	73
10. The Temperature Differential Means of Old and Young Leaves for Six Time Periods on 3 August 1981	78

ABSTRACT

Seasonal and daily studies were conducted to establish variation among and within four buffalo gourd (Cucurbita foetidissima HBK) cultivars. Four physiological parameters, photosynthesis, transpiration, diffusive resistance, and temperature differential were used to study the effect of leaf age, environmental factors, and determine the relationship between photosynthetic rate and other physiological parameters.

Among cultivar variation was not found to be significant from either study, due in part to the high levels of variation found within cultivars. The four parameters did vary with time over the season but significant variation over the day was found only for photosynthesis. The effect of leaf age on the four parameters was not significant when observed over the day.

In seasonal studies, correlation coefficients revealed that transpiration, diffusive resistance, and temperature differential all correlated with each other but did not correlate with photosynthesis.

CHAPTER 1

INTRODUCTION

Buffalo gourd (Cucurbita foetidissima HBK) is a feral xerophytic cucurbit that evolved in the semi-arid region of western North America. It can be found growing from central Mexico to the southern border of South Dakota at elevations ranging from 300 to 2100 m (Scheerens et al., 1978).

This perennial species has a large fleshy storage root known to reach fresh weights of over 40 kg in three or four seasons' growth (Bemis, Berry, and Weber, 1979). The species is drought resistant due to an impermeable suberized periderm (Dittmer and Talley, 1964; Dittmer and Roser, 1963) that surrounds the vascular system.

The prodigious vine growth of C. foetidissima was best described by Dittmer and Talley (1964). An individual was found to possess 60 short, perennial stems that produced 360 annual shoots. The average length of each shoot was 6.09 m, and many gave rise to secondary branches. It was estimated that this individual produced a total of 15,720 leaves. Buffalo gourd leaves are gray-green, pubescent, entire, ovate to sagitate in shape, with a base width of 10 to 13 cm and a mid-rib length of 20 to 25 cm.

The buffalo gourd is primarily asexual in reproduction. Large homogeneous colonies of plants have been produced by the development of adventitious roots that originate at the vine nodes, where large.

unisexual flowers are borne singly. The predominant sex expression of this plant is monoecious; however, a dominant mutant has been reported which aborts male flower buds (Dossey et al., 1981).

The use of this species as a potential oilseed crop was first suggested by Curtis (1946). The baseball-sized fruits were found to contain seed rich in protein and vegetable oil. Berry et al. (1976) isolated starch from buffalo gourd roots in potentially commercial quantities. Subsequent to these initial reports, the physical, chemical, and nutritional aspects of buffalo gourd raw products, as well as the genetic and agronomic characteristics of this species, have been studied. These investigations have, in part, determined the species potential as a domesticate.

The high level of variability found in buffalo gourd germplasm should insure improved yield of both oilseed and starch through plant breeding. However, breeding programs are hampered by generation time, large space requirements, and both expensive and time-consuming evaluation of genetic material.

Apparent photosynthetic rate (APS), transpiration rate (TR), diffusive resistance (DR), and temperature differential (TD) were physiological measurements used as tools in a breeding program for adapting sorghum hybrids to severe moisture stress (Hofmann, 1982). A rapid test for identifying high-yielding genotypes for alfalfa was devised by Leavitt, Dobrenz, and Stone (1979). In a physiological evaluation of different sized leaflets, the authors determined that the large leaflet alfalfa genotypes had significantly higher yield and lower specific leaf

weight (SLW) than the small leaflet genotypes. The large leaflet genotypes also had considerably higher rates of total photosynthesis per plant. Pearce et al. (1969) and Carlson et al. (1970) observed positive correlations between SLW and net photosynthesis. Differences in plant populations revealed that SLW was heritable and that net photosynthesis could increase in plants selected for high SLW. Thus, there is increasing interest in the physiological approach to breeding, since selecting and combining desirable physiological characteristics could increase the efficiency of breeding programs.

The purpose of this study is to identify varietal variation in photosynthetic rates among and within varieties; study the effects of leaf age on photosynthetic rate, and the environmental effects on photosynthetic rate; and determine the relationship between photosynthetic rate and the physiological parameters of transpiration, diffusive resistance, and temperature differential.

CHAPTER TWO

LITERATURE REVIEW

History

Buffalo gourd was considered a weed until the second world war. At that time a disruption of vegetable oil supplies occurred, which created interest in developing oil supplies at home from plants that were readily available. Soybeans, which originated in China, grew well in the United States and were incorporated into American agriculture. Wild plants which produced oil were under consideration at the time and buffalo gourd was in this category.

Curtis (1946), was the first researcher to look at the buffalo gourd as a potential agronomic crop. He made four points in its favor as a potential crop: (a) the plants are perennial; (b) they grow on wastelands in regions of low rainfall; (c) they can produce an abundant crop of fruit which contain seed rich in oil and protein; and (d) the fruit lends itself to mechanical harvesting. Many reports (Bolley, McCormick, and Curtis, 1950; Shanani et al., 1951, and Paur, 1952) on the use and composition of the seed and on the agronomic properties of the plant were published at this time. The properties of the root starch in buffalo gourd were not considered until much later (Berry et al., 1975).

The primary goals of research on buffalo gourd were to increase yield and domesticate the plant. The first effort to improve germplasm of C. foetidissima and to domesticate the plant was in Lebanon under the direction of Dr. Lawrence Curtis (Curtis and Rebeiz, 1974). Curtis received germplasm from a single collection site in Texas, but still discovered substantial variation in a number of traits including fruit yield. Only 230 out of 730 seedlings produced fruit the first year. Fruit bearing plants yielded from 1 to 283 pepos per individual plant. The yield of progeny from a single open-pollinated parent ranged from 1 to 160 gourds per plant. Vine habit and sex expression were highly variable. Crude fat ranged from 25.6% to 42.8% and protein ranged from 25.9% to 35.0% in the seed on a dry weight basis.

In 1974, an interdisciplinary approach to buffalo gourd domestication was organized at the University of Arizona which emphasized three major disciplines: (1) genetics and plant breeding; (2) biochemistry; and (3) nutrition and toxicology (Bemis et al., 1979). An initial objective of the program was to survey variation inherent within the species through collection and evaluation of diverse germplasm. To establish a germplasm nursery, 145 accessions were obtained from 10 U.S. states and Mexico over a three-year period.

Prior to establishment of germplasm nurseries, a preliminary investigation of fruit and seed characteristics of 85 accessions was undertaken (Scheerens et al, 1978). Sufficient variation was found in the traits of seed weight per fruit (C.V. = 36.9%), seed number per fruit (C.V. = 28.3%) and seed weight per 100 seeds (C.V. = 20.0%) to suggest the feasibility of yield improvement through breeding. Possible

improvements through selection for the traits of percent embryo in the seed and percent crude fat of whole seeds were also indicated. Higher percent crude fat values were associated with a higher percent embryo in the seed ($r = 0.74$).

Three germplasm nurseries were planted successively in 1976, 1977, and 1978. The full extent of inherent genetic diversity was not expressed by growing the germplasm nursery in a single location. (Bemis, personal communication).

The progeny of superior accessions were identified and seed was obtained for crude protein and fat analysis. Open-pollinated seed was collected from high yielding plants which descended from accessions 142, 158, and 300 whereas agronomically suited plants from accessions 140, 162, 185, and 250 were sib-crossed prior to seed collection. Seed was also obtained from a cross between superior progeny of accessions 140 and 156. All seed parents were gynoecious except for 300. These seed sources were employed to create population hybrids for use in yield trials.

Hybrid production plots were established in 1977 and 1978 which yielded the following seven population hybrids: 158 x 142, 142 x 158, 140 x 142, 162 x 142, 185 x 142, 250 x 300, (140 x 156) x 300. Controlled pollination was accomplished by roguing monoecious plants from seed parent lines segregating for sex-expression.

A replicated yield trail was initiated in 1979 at the Marana Agricultural Center, Marana, Arizona, to evaluate the aforementioned

hybrids and their pollinators 142, 158 and 300. Each replicate (four per hybrid or pollinator) contained approximately 120 plants. Data from the first season yield did not reflect the ultimate potential of buffalo gourd yields because many of the wild collections failed to flower and therefore produced little or no fruit in the first season's growth. Bemis (personal communication) noted that the seven experimental hybrids were superior in the first season for seed yield compared with the selected open-pollinated parental lines 142, 158 and 300, indicating the possible effects of heterosis.

Data for first and second year seed and root yield are summarized in Table 1. Variability among plots within lines was high due in part to inherent variability of individual plants. More importantly, a residual herbicide present in the sub-surface layer of some plots severely reduced seed yield. The effects of the herbicide were most dramatic in the third season of growth, rendering plot yields highly variable and for the most part meaningless (Bemis, personal communication).

Seed harvested from hybrid plants of the yield trial were bulked and designated as SYN-1 (Synthetic Number 1). SYN-1 and hybrid seed stocks were utilized in cultural experiments to determine consumptive water use, root yields of close-spaced annual plantings for starch production (Nelson et al., 1983) and similar agronomic parameters.

Concurrent with genetic and cultural experimentation, the utilization of buffalo gourd raw and processed products has been extensively studied (Bemis et al., 1967; Bemis et al., 1979; Berry et al., 1975; Berry et al., 1976; Berry, Scheerens, and Bemis, 1978; Cossack et al.,

Table 1. Average plot yields of buffalo gourd hybrid and pollinator lines. ^{1/}

Line	\bar{X} Seed		\bar{X} Root	
	Yield (kg/HA)		Yield (kg/HA)	
	1979	1980	1979	1980
158 x 142	350.4	385.7	7,077	12,730
142 x 158	283.2	176.2	9,215	14,772
140 x 142	400.8	560.7	8,835	14,202
162 x 142	908.4	1088.1	8,270	12,825
185 x 142	319.2	564.3	10,117	14,107
250 x 300	512.4	488.1	10,402	17,147
(140 x 156) x 300	580.8	726.2	10,459	17,622
142	140.4	238.1	9,357	16,387
158	20.4	150.0	8,265	14,962
300	229.2	244.0	11,162	14,915

^{1/} Bemis, personal communication.

1979; Dreher et al., 1983; Thompson et al., 1978; Vasconcellos, Berry, and Weber, 1980; Vasconcellos et al., 1981).

Investigations of buffalo gourd continue. A major emphasis will be placed on improving yield and quality of buffalo gourd products through plant breeding. According to Gathman and Bemis (in press)

"future breeding work on the buffalo gourd should center on mass selection to produce superior inbred lines and hybrids, and on determination of modes of inheritance of the important product quality parameters. It should be determined if maximum starch products precludes maximum oil yield, and if so, specialized lines for each of these purposes should be developed. Field observations suggest that inbreeding depression, although rare in Cucurbita, may occur in C. foetidissima. This should also be studied further."

Physiology Background

The goal of plant breeding traditionally has been the production of higher yielding and more standardized crops. But the cost of breeding in terms of fuel, machinery and lack of variability within the species has been high. Good and Bell (1980) state,

"It is here that studies of the controls and limitations of photosynthesis can make their greatest contributions. Breeding for the end result of interactions of a multiplicity of unknown gene-controlled processes is inevitably a matter of unsystematic and very time consuming trial and error."

Good and Bell go on to say that identifying components of yield in terms of specific physiological processes should take much of the randomness out of breeding, and might ultimately lead to the identification of the genes involved. Good and Bell conclude their statement with, ". . . only to the extent that we can describe productivity in terms of the

mechanisms that control photosynthesis and growth can we bring productivity improvement out of the dark ages of pure empiricism."

Carlson et al. (1970) concur that breeders have taken little interest in the selection of plants which show a greater efficiency of conversion of light and nutrients into yield. Carlson et al. (1970) state,

" . . . that physiological traits, as well as morphological traits which can be closely associated with physiological traits, may be used as selection criterion for yield and quality increase. However, heritable differences in these traits must exist within a crop. The physiological or morphological trait must be easily measured and these traits must be closely related to yield."

Barrs (1968), found a correspondence between photosynthesis and transpiration in leaves of cotton, pepper, and sunflower. It is true that carbon dioxide and water vapor compete for the same physical pathway through the stomata. This correlation could be useful for those wishing to estimate the photosynthetic capability of crops indirectly from measurement of transpiration or from the diffusive resistance of the stomata. In another study of barley lines (Miskin, Rasmusson and Moss, 1972) stomatal diffusive resistance and transpiration rates differed statistically whereas photosynthetic rates did not. Lines with low stomatal frequency had higher stomatal resistances, and transpired less than lines with more stomata. Stomatal frequency didn't influence the rate of photosynthesis. The possibility exists of altering transpiration rates without altering photosynthetic levels by selecting variety with fewer stomata (Miskin et al., 1972).

Donald (1962) claims that yield is the direct outcome of the extent and duration of photosynthesis. Therefore plant breeders should be concerned with the effectiveness of this process as it relates to yield. Conversely, Kueneman et al. (1979) found no correlation of photosynthesis with seed yield in field-grown dry beans. They concluded that measurements of photosynthetic rates at one period of crop growth, on a small portion of the total canopy would not be a useful selection criterion in a breeding program. Ojima (1972) found rates of photosynthesis per unit leaf area to be quantitatively inherited when studying soybean. He obtained his highest yielding lines from parental lines with high photosynthetic rates. Conversely, Heichel and Musgrave (1969) reported that improvement in maize through breeding was not associated with marked improvement in net photosynthetic rates. Evans and Dunstone (1970) reported that certain ancestral lines of wheat (*Triticum*, sp), had average rates for C₃ plants, and only modern single cross hybrids ranked consistently high. In the evolution of wheat, photosynthetic rates decreased as leaf size and grain yield increased. No evidence for inheritance of photosynthetic rates has been adduced for sugarcane (*Saccharum officinarum* (L.)) cultivars, although some of the older cultivars have lower rates than modern interspecific hybrids forming the bulk of the world's sugarcane crop (Irvine, 1975). Commercial hybrid cultivars of sugarcane have higher photosynthetic rates than the cultivated forms, but the rates of both are less than those of the wild, ancestral clones.

Thorne (1966) believes that selection for high photosynthetic rates per se has not been a productive approach to increasing yields. However, Thorne states, ". . . when stress is involved, ability of the plants to continue a relatively high rate of photosynthetic activity may very well contribute to yield."

Photosynthesis may be defined as the absorption of light energy and its conversion into stable chemical potential by the synthesis of organic chemicals (Bidwell, 1979). Therefore, plant productivity is really a measure of the total photosynthesis of the plant less any photorespiration or dark respiration that occurs during growth (Good and Bell, 1980). Nevertheless, supporting evidence for photosynthesis as a major yield limiting factor is inconclusive. There are reports of genotypic differences in single leaf photosynthesis, but little correlation between leaf-apparent photosynthesis and seed yield has been evidenced (Bhagsari et al., 1977; Curtis, Ogren, and Hageman, 1969; Dornhoff and Shibles, 1970; Dreger, Brum, and Cooper, 1969). Other reports found no correlation between photosynthetic rates and grain yield or dry matter accumulation (Heichel and Musgrave, 1969, Nelson, Asay, and Horst, 1975; and Irvine, 1975). Generally, no correlation has been found with respect to photosynthesis per unit leaf area and yield in alfalfa or cassava under non-stressed conditions (Mahon, Lowe, and Huni, 1975; Delaney and Dobrenz, 1974).

It was noted, however, that during periods of stress, e.g., close spacing of plants during podfilling, there was a significant correlation in field grown dry beans, between photosynthesis per unit leaf area, and seed and biological yield (Kueneman et al., 1979). A study by Sullivan and Ross (1979) showed that when water stress was involved, the plants' ability to continue relatively high rates of photosynthesis may well contribute to yield. The response of photosynthesis to water stress has been reviewed (Dastur, 1925; Slavik, 1963, 1965; El Sharkawy and Hesketh, 1964; Jones, 1973; Turner et al., 1978; Berry and Bjorkman, 1980; Boyer, 1970, 1976). These studies confirm that photosynthesis is sensitive to lowered leaf water potential. The buffalo gourd has long been known to survive well under water stress conditions (Bemis et al., 1979; Curtis and Rebeiz, 1974; Bemis, personal communication) but no studies have been done to determine its photosynthetic capacities and the possible correlation with drought tolerance.

Tatum (1954) reported on breeding for drought and heat tolerance in corn (Zea mays L.). He surmized that the major effect of heat was in increasing evaporation from the surface of the leaf and subsequent transpiration rather than its direct effect on the plant. Consequently Alexandrov (1964) concluded that the photosynthetic process is most sensitive to high ambient temperatures. There are many reports that detail the effects of water deficits and high temperatures on the activity of isolated chloroplasts (Plaut, 1971; Huffaker et al., 1970; Santarius and Heber, 1967; Santarius and Earnst, 1967; Santarius, 1967; Boyer and Bowen, 1970; Fry, 1970; Sullivan, Norica and Eastin, 1977).

During periods of water stress, closure or partial closure of the stomata retards transpiration losses. A subsequent decrease in temperature differential usually occurs.

Basically, the stomatal response acts to impede vapor diffusion from the leaf, but many also alter substantially the temperature of the leaf as a result of latent heat exchange. Absorbed solar irradiance can cause leaf temperatures to rise many degrees above air temperature and, thus, may also have a substantial effect on the water vapor gradient. Therefore, the interactive effects of all of these parameters may either increase or decrease leaf transpiration, depending upon individual leaf properties and environmental conditions. (Smith and Geller, 1980).

Cucurbits have been evaluated in relation to their response to CO₂ levels and light, as measured through specific weight (SLW) and apparent photosynthesis (APS). Frydrych (1976), in his study of Cucumis sativus (cucumber), noted that the highest rate of photosynthesis (18.96 mg CO₂ dm⁻²hr⁻¹) was found in conjunction with the highest atmospheric CO₂ levels and highest irradiation. However, APS was inversely related to SLW if low CO₂ levels were present. Turgeon (1973) measured rates of 11 mg CO₂ dm⁻²hr⁻¹ with Cucurbita pepo (pumpkin) under growth chamber conditions with a mean surface area of the leaf of 1.30 dm² at 70% expansion. According to Sisson (1981), the APS highest rate for pumpkin (22.5 mg CO₂ dm⁻²hr⁻¹) was achieved on the fourth day after emergence with a total leaf area of .23 dm². After that, the APS per unit leaf area declined slowly although the leaf was still expanding.

Photosynthetic rates of Cucurbita fall into the same range as do many crop species. Dreger (1967) tested nine varieties of soybeans and reported mean varietal net photosynthetic rates ranging from 18.7 to 23.0 mg CO₂dm⁻²hr⁻¹. Curtis et al., (1969) tested 36 varieties of

soybean and reported varietal rates varying from 12 to 24 mg CO₂dm⁻²hr⁻¹. Bhagsari et al. (1977), analyzing three separate sets of measurements of apparent photosynthetic rates in soybeans, found that they ranged from 23 to 37 mg CO₂dm⁻²hr⁻¹. Differences among cultivars were observed in all three studies. Kueneman et al., (1979) measured field-grown dry beans (Phaseolus vulgaris) and found photosynthetic rates ranging from 18.66 to 30.80 mg CO₂dm⁻²hr⁻¹. In cotton (Gossypium hirsutum L.), El-Sharkawy and Hesketh (1964) found ranges of 35 to 45 mg CO₂dm⁻²hr⁻¹. The effects of CO₂ concentration, light, temperature and transpiration are all interrelated with photosynthesis and are dependent on a number of physiological and anatomical characteristics of the plant.

Under field conditions, temperature does not greatly influence the rates of photosynthesis over the range of 16 to 29 C unless the light intensity is so high that the dark reactions are limiting, (Bidwell, 1979). When temperatures continually exceeded 30 C over the summer months, apparent photosynthesis and dark respiration were reduced by 38% and 19% respectively which resulted in forage yield reduction in alfalfa (Delaney, Dobrenz and Poole, 1974). Differences between leaf temperature and ambient temperature were reported for leaves of native plants of Mauretania and Costa Brava when fully exposed to sunlight (Lange, 1959; Lange and Lange, 1963). Temperatures of the leaves were measured under conditions of high radiation, low wind speed and low diffusive resistance (< 2 cm⁻¹). At air temperatures of 48 C the leaves displayed a corresponding temperature of 38 C (temperature difference = 10 C).

Gates et al. (1964) reported observations of Minulus wherein leaf temperatures were distinctly below air temperatures in intense sunlight and nearly still air conditions. When the air temperature was 18 to 20 C, the temperature of sunlit Minulus leaves were 25 to 30 C. When the air temperature was 37 C, the sunlit leaves were from 30 to 35 C. Linacre (1964) reported that leaf temperatures were equal to air temperatures at about 33 C for many plant species. Leaf temperatures equalled air temperatures at 30 C under low humidity (20%). Below this temperature, leaves are warmer than the air. When leaf temperatures increase, there is a tendency for stomatal resistance to drop, therefore at high air temperatures, lower leaf temperatures would result.

Schulze et al. (1974) conducted experiments under constant evaporative conditions and varying temperature and showed that stomata opened with an increase in leaf temperature if water stress was low. The counter-balancing effect of leaf temperature is of importance for the regulation of the heat balance of the leaf which in turn also determines the magnitude of the water vapor concentration between the leaf and the air. "As the leaf temperature is raised, the metabolic activity within the guard cells and the leaf as a whole will increase, reach an optimum, and then decrease as more and more cell damage occurs. The effect of the increased metabolic activity within guard cells initially will be to stimulate stomatal opening." (Willmer, 1983). There are also indirect effects of temperature on stomatal behavior. It is possible that the temperature increases will affect internal CO₂ concentrations which, in turn, will affect stomatal movements. If respiration outpaces

possible that the temperature increases will affect internal CO_2 concentrations, which, in turn, will affect stomatal movements. If respiration outpaces photosynthesis as the temperature increases, CO_2 levels will increase within the leaf, which will eventually cause stomate closure (Willmer, 1983).

Gases must enter and leave a leaf via diffusion through stomata, lenticels, or cuticle. "The forces motivating the outward diffusion of H_2O vapor are higher than those moving CO_2 into the leaf. Yet plants absorb CO_2 at a maximum rate, while at the same time the rate of H_2O loss is reduced to a minimum." (Bidwell, 1979). Plants achieve this by creating a diffusion shell of CO_2 on the surface of the leaf and the number, distance, and circumference of the stomata play a key role in its effectiveness.

The ability of sorghum stomata to stay open under stressed conditions of lower leaf H_2O potential may help explain its superiority to other less drought-tolerant cultivars (Shimshi and Ephrat, 1975). Conversely, when studying relationships obtained between leaf area index and water use in the field, Johns and Lazenby (1973) concluded that stomatal closure had been ineffective in reducing the water use per unit leaf area of four temperate herbage species under dry hot conditions. Such a conclusion is contrary to the commonly accepted viewpoint that stomatal closure is the main cause for transpiration decrease as water stress insues (Hsiao, 1973; Milthorpe and Moorby, 1974).

"Transpiration is essentially the evaporation of water from cell surface and its loss through the anatomical structures of the plant." (Bidwell, 1979). The process of transpiration cools the leaf and mobilizes minerals from the soil. Temperature reduction from transpiration is normally about 2 to 3 C.

Statistically significant variation has been found among indeterminate soybean cultivars for transpiration. Bhagsari et al. (1977) evaluated 16 cultivars and found a significant deviation among them with rates ranging from 7.2 to 11.88 $\mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$. Significant differences in transpiration rates were also found among lines pretreated to assure open stomata within five populations of barley (Hordeum vulgare L.) (Miskin et al., 1972). Transpiration rates among barley lines varied between 7.90 and 12.31 $\mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$. Transpiration rates of sorghum, grown with adequate moisture, ranged from 10.6 to 45.0 $\mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$ and under stressed moisture conditions, from 1.1 to 32.2 $\mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$ (Dobrenz, personal communication).

Variation also has been noted for stomatal resistance. Blum (1974) was able to find several different response patterns in sorghum with respect to drought tolerance. The range of stomatal resistance of 14 genotypes tested were 3.1 to 20.2 s cm^{-1} . There has been a wide range of data recorded on over 200 sorghum germplasm sources that were grown on an irrigation gradient system at Yuma, Arizona (Dobrenz, personal communication). In addition to yield and growth differences, leaf diffusive resistances with adequate soil moisture went from 0.7 to 4.2 s cm^{-1} and

showed a range of 2.3 to 44.4 s cm⁻¹ in the stressed plants.

Shimshi and Ephrat (1975) tested several wheat cultivars and found diffusive resistance rates ranging from 2.6 to 4.2 s cm⁻¹. Brun, Kanemasu and Mason (1978) reported that over a growing season, diffusive resistance in sorghum ranged from 1.25 to 5.60 s cm⁻¹. Teare and Kanemasu (1972) found a range for sorghum leaf diffusive resistance to be between 1.0 and 7.0 s cm⁻¹. Hofmann, (1982) working with the same species, reported a similar range of 1.6 to 4.81 s cm⁻¹.

Stomatal movements are directly affected by light quantity and quality, water availability (plant-soil water status), water vapor pressure deficit (atmospheric humidity, CO₂ concentration and temperature). Some of these factors, combined with wind movement, may also effect stomata in an indirect manner. All of these environmental factors tend to interact, making studies of the effects of one factor on stomatal movements difficult, e.g., increasing leaf irradiance will tend to increase the leaf temperature which, in turn will lower the leaf water potential, the increased temperature may also change intercellular CO₂ concentrations by changing rates of photosynthesis, respiration, and photorespiration. Thus, all factors may be in play at one time so that stomatal aperture is a resultant of all these factors. (Smith and Geller, 1980).

Various anatomical features of a leaf help prevent leaf senescence during periods of stress and thus help improve yield. Transpiration can be decreased by concurrent reductions of leaf size and stomata density, sunken stomates, a reduction of surface area per unit mass, stomatal size reduction, and presence of epidermal hairs (trichomes). Sunken stomata and trichomes are effective when the plant is subjected to high winds, since they prevent disturbance of the boundary layer and consequent shortening of the water vapor diffusion path.

Investigations involving desert plants have evaluated the importance of leaf morphology in the temperature, water and photosynthetic relations of the plants. The work of Parkhurst and Loucks (1970) predicted that the size of a leaf could be increased, if the leaf had a low absorption to solar irradiance while exposed to high air temperatures and low relative humidity. Under these conditions, increasing leaf size would lead to increases in the plant's ability to conserve water. Gates and Papian (1971) produced a comprehensive evaluation of the influence of air temperature, humidity, wind speed, leaf size, stomatal resistance, and absorption of solar radiation on transpiration. According to their results, for higher air temperatures, leaves with highly reflective surfaces, leaves in the shade, or leaves oriented away from direct sunlight, would have a high critical stomatal resistance to water vapor diffusion, i.e., the maximum stomatal resistance at which transpiration would initially decrease with increasing leaf size would be relatively high. Thus, transpiration for a highly pubescent, sunlit leaf, under hot desert conditions, would decrease significantly with increasing leaf size for stomatal resistance lower than about 2 to 5 s cm^{-1} , (Smith, 1978). Smith also found that for several desert broadleafed plants, leaf temperature was up to 17°C below air temperature, due to rapid transpirational fluxes, a large leaf size (6 to 8 cm in length, and low solar radiation due to more pubescence.

CHAPTER 3

MATERIALS AND METHODS

Field research concerning physiological responses of the buffalo gourd hybrids and their parents was conducted during the 1981 growing season. The experiments were conducted on a Brazito loam at the University of Arizona Campus Agricultural Center.

Seed was obtained through Dr. W. P. Bemis at the University of Arizona. Two hybrids (140 x 156) x 300, and 250 x 300, and two open-pollinated, 300 and Synthetic #1, varieties were chosen as germplasm sources for this experiment.

For field experiments, beds were shaped 101.6 cm apart and pre-irrigated. Treatment of nitrogen fertilizer (type and rate unknown) Bensulide, 0,0-diisopropyl phosphorodithioate S-ester with N-(2-mercaptoethyl) benzenesulfonamide (5.63 kg ha^{-1}), a pre-emergent herbicide, were incorporated into the soil with the first irrigation. The seed was planted 5 to 10 seeds per hill and hills were planted 9 to 10 m apart within the row. Four rows were planted with a fallow row between each row planted. Ten hills were planted per row.

The seeds were planted by hand on 20 May 1981, using a randomized complete block design. The plot plan consisted of ten blocks, four hills per block. Each hill within a block was planted at random with one of the four varieties. The plants were thinned to one plant per hill after emergence.

After the five leaf stage, physiological measurements were begun. Two field studies were undertaken: one depicting fluctuations in four physiological measurements throughout the season using all plants, the other delineating fluctuations of the same measurements over the course of one day. One leaf from each plant was analyzed during the seasonal study. Two leaves from each plant were analyzed during the daily study. The most mature healthy leaf closest to the crown was labeled the old leaf, and the most fully expanded leaf closest to the apical meristem was called the young leaf.

Measurements for the seasonal study were performed between the hours of 1000 MST and 1200 MST on the individual days measured. On the one-day study (3 August 1981), six hourly measurements were conducted throughout the day, starting at 800 MST and ending at 1430 MST.

Apparent photosynthesis rates ($\text{mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$) (APS) in the field were determined using the syringe method developed by Clegg and Sullivan (1975); and Sullivan, Clegg, and Bennett (1976). An airtight, clear, plexiglass 2.2ℓ box shaped chamber (CO_2 chamber) was sealed around the apex portion of the leaf. A fan, located under a central grid that the leaf rested on, insured adequate circulation. Two rubber septa, located on the side of the CO_2 chamber, allowed gas samples to be taken with 6 ml syringes. After the leaf was sealed in the CO_2 chamber, and the gases were allowed to circulate for several seconds, a labeled syringe full of the gas was taken from the first septum. A person holding a stop watch would begin a 30-second count down at this time.

Another person would mark the leaf along the outer edge of the box. The second labeled syringe was pulled 30 seconds later from the second septum. The leaf was then cut along the lines that were marked, and the portion of the leaf that was encased in the CO₂ chamber was placed on ice and taken to the laboratory for leaf area determination. The two labeled syringes from each plant tested were then returned to the laboratory for analysis in the Beckman Model 865 CO₂ infrared gas analyzer (Fig. 1).

The CO₂ concentration differences between the two gas samples taken from each plant analyzed were measured using the method described by Clegg, Sullivan and Eastin (1978). The flow rate of the carrier gas (N₂) was adjusted to approximately 1 ml min⁻¹. Only the measurement of peak heights was necessary to obtain the CO₂ concentration of the injected gas sample. The peak heights were measured with a Heath-Schlumberger Model SR-205 strip chart recorder. The system was calibrated with standard gases of known CO₂ concentration. CO₂ concentrations were then converted to apparent photosynthesis on a leaf area basis using the calculations described by Musgrave and Moss (1961).

Leaf sections used in CO₂ flux measurements were then placed on a light-sensitive automatic area meter from the Hayashi Denko Co., Ltd., Tokyo, Japan. Each leaf section was cycled through the machine three times and an average was taken in order to get an accurate estimate of the leaf area.

Concurrent field measurements were taken on transpiration ($\mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$), diffusive resistance (s cm^{-1}), leaf temperature (C), and cuvette temperature (C) using a LiCor model LI-1600 steady state porometer. This apparatus was described in detail by Beardsell, Jarvis and Davidson (1972).

Stomate densities of leaves from plants grown in the field were determined in 1981 from images obtained with a scanning electron microscope magnification. Stomate images were obtained from the midrib of the leaf as well as the interveinal portion of the leaf. One leaf from each variety was used to determine an average stomatal density of the abaxial and adaxial surfaces of the leaf.

The statistical analysis of the data for photosynthesis, transpiration, diffusive resistance and temperature differential (ambient-leaf temperature) was calculated using the Statistical Packages for Social Sciences (SPSS) (Nie, 1975).

A split plot design for repeated measures in a randomized complete block design was employed for the statistical analysis in this study. Coefficients of Variation, (C.V.'s) which utilize the standard deviation and the mean to attain a percent variation within a population, were used to show the variation within a population over the season for one variable (e.g., photosynthesis). Coefficients of variation were also used to show variation within a population over one day for one variable. The seasonal and diurnal coefficients of variation were compared, but only in reference to one variable. Coefficients of variation were not

used to compare variation within a population for more than one variable. due to other factors (such as coding of some means, and variation within a population due to method utilization problems, humidity, soil moisture, temperature differences, and position in the field) that may confuse results. Data coding was incorporated for the means when negative values were encountered in order to calculate coefficients of variation for the variables with negative values.

A Student Newman Keul test was used to classify the varietal means from the seasonal study into separate populations. A second Student Newman Keul test was used to classify the sampling period means from the seasonal study into separate populations. Correlation coefficients were used to determine the correlation of the four variables (apparent photosynthesis, diffusive resistance, temperature differential and transpiration) to each other in the seasonal study.

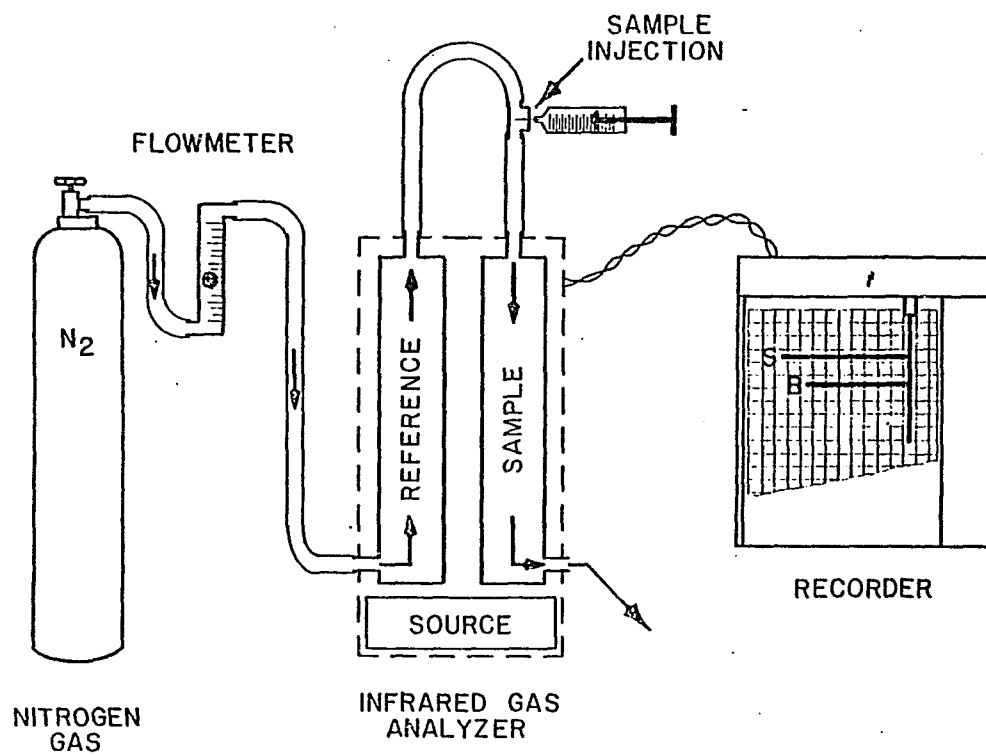


Figure 1. An open system used with an infrared CO₂ gas analyzer used for the determination of CO₂ concentrations taken in the field.

CHAPTER 4

RESULTS AND DISCUSSION

Studies of Four Sampling Periods Throughout the Growing Season

Four physiological measurements (apparent photosynthesis (APS), transpiration (TR), diffusive resistance (DR), and temperature differential (cuvette temperature-leaf temperature) (TD) were studied on four dates over the growing season to determine variability within and among buffalo gourd cultivars. Differences among seedstocks were not statistically significant due in part to the high level of variability found within cultivars.

Because crop environment during the growing season is dynamic, one might expect physiological measurements associated with individual plants to vary within a day, within a canopy, within a season, and over years. Different cultivars may vary at different stages of physiological development at any one sampling period in the season. Environmental conditions are also known to interact differently among cultivars (Kueneman et al., 1979).

All interactions of physiological measurements among sampling periods were significant at the .01 level. Significant differences in sampling period means were determined by the Student Newman Keul test. Due to die back from root rot (causal agent - Erwinia fusarium), analysis of variance was performed to accommodate missing plots.

Apparent Photosynthesis

"Environmental factors which influence total yield - water, light, nutrients, oxygen, carbon dioxide, and temperature either directly or indirectly influence the rate and/or duration of photosynthesis."
(Donald, 1962).

Among Cultivars

The apparent photosynthetic rates (APS) for buffalo gourd have a wide range, varying mostly within cultivars (Table 2). When cultivars were compared, synthetic #1 showed the highest mean rate during the season ($24.18 \text{ mg CO}_2\text{dm}^{-2}\text{hr}^{-1}$). The lowest mean rate over the season, observed in 300 was $21.45 \text{ mg CO}_2\text{dm}^{-2}\text{hr}^{-1}$. The population average for all dates measured was $22.34 \text{ mg CO}_2\text{dm}^{-2}\text{hr}^{-1}$.

The highest APS rate of the season ($67.69 \text{ mg CO}_2\text{dm}^{-2}\text{hr}^{-1}$) was exhibited by an individual plant within variety (140 x 156) x 300 whereas the lowest rate ($6.44 \text{ mg CO}_2\text{dm}^{-2}\text{hr}^{-1}$) was found within variety 250 x 300. Extreme values were recorded on 3 August 1981. Variability among individuals was greatest in synthetic #1 (C.V. 53.8%) and least in 300 (C.V. 38.0%)(Table 2). Buffalo gourd APS rates fall in the same range as some conventional crops (Dreger, 1967; Curtis et al., 1969; Bhagsari et al., 1977; Keuneman et al., 1979; El-Sharkawy and Hesketh, 1964).

Among Sampling Periods

If the photosynthetic capacity were the limiting factor at a critical developmental stage (e.g., at flowering or during seed maturation), then this might be the best stage for measuring photosynthesis to

Table 2. Apparent photosynthetic rate means and coefficients of variation on four sampling periods throughout the 1981 season.

Varieties	Mean Apparent Photosynthesis (mg CO ₂ dm ⁻² hr ⁻¹)				Varietal Means ²	C.V.% ¹
	Sampling Periods					
	7 July	3 August	14 August	8 September		
300	17.01	29.09	28.20	17.64	21.45 ^a	38.0
(140 x 156) x 300	15.46	23.04	35.37	19.17	21.75 ^a	46.8
Synthetic #1	17.12	21.23	40.83	24.65	24.18 ^a	53.8
250 x 300	16.54	23.56	30.90	20.66	21.80 ^a	45.2
Sampling Period Means ³	16.52 ^c	23.90 ^b	33.97 ^a	20.57 ^b		
C.V.%	14.0	50.6	35.3	32.3		
Grand Mean					22.34	47.0

1. C.V. = Coefficient of variation where the standard deviation is expressed as a percentage of the mean.
2. Varietal means with the same superscripts are not significantly different from each other at the .05 level. The Student Newman Keul (SNK) (mean separation technique) was used.
3. Sampling Period means with the same superscripts are not significantly different from each other at the .05 level. The Student Newman Keul (SNK) (mean separation technique) was used.

predict yield (Kueneman et al., 1979). Among sampling periods, the highest average rate measured ($33.97 \text{ mg CO}_2 \text{ dm}^{-2}\text{hr}^{-1}$ on 14 August 1981) corresponded with a physiological period of flowering and seed filling (Table 2). The lowest average APS rate, among sampling periods was $16.52 \text{ mg CO}_2 \text{ dm}^{-2}\text{hr}^{-1}$ on 17 July 1981. During this sampling period, plants were vegetative. The APS rate of buffalo gourd was most stable on 17 July 1981 (C.V. 14.0%) and most variable on 3 August 1981 (C.V. 50.6%)(Table 2). The lowest and least-variable APS rates in buffalo gourd occurred most during initial growth stages (vegetative growth) (Table 2). In contrast, Sisson (1981) found the highest rate for squash ($22.5 \text{ mg CO}_2 \text{ dm}^{-2}\text{hr}^{-1}$) on the fourth day after emergence, with total leaf area of $.23 \text{ dm}^2$. The APS rate then declined slowly although the leaf was still expanding. Data of Murata (1961) and Saeki (1959) on rice suggest that young and fully expanded leaves tend to have maximum photosynthetic rates.

Net photosynthetic rates (NPS) for soybean began to increase around 4 August approximately when seed filling began (Dornhoff and Shibles, 1970). Dornhoff and Shibles postulated that the increase in NPS rate was a result of: (a) decreased CO_2 diffusive resistance within the leaf, and/or increased demand for photosynthates during seed formation. Peet et al. (1977) found a highly significant correlation between photosynthesis during the pod-filling period and both seed yield ($r = 0.75^{**}$) and biological yield ($r = 0.92^{**}$) for eight dry bean cultivars grown for a single season.

As previously discussed, the 3 August sampling period displayed the highest variability among individuals (C.V. 50.6%) and corresponded to a stage of fruit set and seed development. Extremes of apparent photosynthetic activity were also recorded on this date.

Selection for high photosynthesizing genotypes would most easily be accomplished during this period due to the higher range in apparent photosynthesis observed on this date. This finding agreed well with Osment (1978), who found high variation among 30 clones of alfalfa early in the season. Osment concluded that this period would be optimal for selecting rapidly photosynthesizing genotypes. Substantial variation in APS rates among genotypes during this period, coupled with evidence for a strong relationship between photosynthetic rate and yield in field grown dry bean during a similar growth phase (Peet et al., 1977), might suggest the advantage of selecting for maximum photosynthetic activity at this time. More tests might verify the above trends and determine the relationship between APS rates and yield potential in buffalo gourd.

Transpiration

Among Cultivars

As demonstrated by coefficients of variation (Table 3), transpiration rates (TR) varied more among cultivars. Mean TR rates decreased due to natural and environmental fluctuations throughout the season. Cultivar 300 demonstrated the highest mean TR rate over all sampling periods ($26.51 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$), variety 250 x 300 showed an average rate throughout the season of $25.08 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$ representing

Table 3. Transpiration rate means and coefficient of variation on four sampling periods throughout the 1981 season.

Varieties	Mean Transpiration Rate ($\mu\text{g H}_2\text{Ocm}^{-2}\text{hr}^{-1}$)				Varietal Means ²	C.V.% ¹
	Sampling Periods					
	17 July	3 August	14 August	8 September		
300	34.64	28.33	19.00	16.33	26.51 ^a	32.5
(140 x 156) x 300	32.13	27.94	17.63	15.13	25.03 ^a	34.4
Synthetic #1	31.67	27.09	19.01	16.88	25.43 ^a	28.9
250 x 300	33.43	30.04	17.07	16.82	26.08 ^a	32.2
Sampling Period Means ³	32.91 ^a	28.27 ^b	18.16 ^c	16.27 ^c		
C.V. %	9.9	17.5	15.1	30.9		
Grand Mean					25.75	31.8

1. C.V. = Coefficient of variation where the standard deviation is expressed as a percentage of the sampling period mean and varietal mean.
2. Varietal means with similar superscripts are not significantly different from each other at the .05 level. The Student Newman Keul mean separation technique was used (SNK).
3. Sampling period means with similar superscripts are not significantly different from each other at the .05 level. The Student Newman Keul mean separation technique was used (SNK).

the lowest value. The population average for all dates measured was $25.75 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$.

The highest individual TR rate for buffalo gourd was $37.71 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$, measured on 17 July 1981 in cultivar 300. The lowest value observed, $6.29 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$, measured on 8 September 1981 from an individual plant also from cultivar 300. Coefficients of variation among cultivars were similar, with the highest (34.4%) and the lowest (28.9%) being displayed by (140 x 156) x 300 and synthetic #1, respectively (Table 3). This suggests little variation in TR rate among cultivars.

The transpiration rates resemble rates found in conventional crop plants. Shimshi and Ephrat (1975) measured transpiration in 10 cultivars of wheat and found differences ranging from 13.9 to $20.1 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$. Beadle et al. (1973) measured TR rates of drought tolerant sorghum (Sorghum bicolor) and found them to be as high as $25.5 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$. Hofmann (1982) reported a similar result for sorghum of $26.00 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$.

Among Sampling Periods

In contrast to the many studies of APS rate at different physiological ages, seasonal fluctuations in TR rate have been measured for few crop species. In this study, mean TR rates decreased from $32.91 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$ 17 July 1981 to $16.27 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$ 8 September 1981 as the season progressed (Table 3). Variation among individuals was greatest during the final sampling period (C.V. 30.9%).

The developmental stage of plants was thought to influence the expression of this physiological trait (Lott, 1970). Older plants transpire less while younger plants undergo more metabolic reactions requiring higher TR rates. Transpiration rates are also affected by seasonal fluctuations in ambient temperature, light intensity, relative humidity, wind velocity and water availability (Gates, 1971). Environmental factors interact with the stage of growth and morphological characteristics of leaves, such as leaf size and shape, stomatal size, density, placement, and density of trichomes if present, to influence transpiration rates.

The environmental impact on transpiration in buffalo gourd over the season was very clear. Temperatures of 36 and 37 C with corresponding low relative humidity (35%) at the beginning of the experiment were concurrent with TR rates at their highest observed levels for the young leaves (Fig. 2). Toward the end of the season, temperatures fell to 32 C and the relative humidity rose to 41%. Transpiration rates at this time decreased in response to the combined effect of growth stage and environmental conditions.

Transpiration is an important process needed to cool leaves during high ambient temperatures, and to help incorporate mineral nutrients to the plant through the transpiration gradient. Parkhurst and Loucks (1970) found that when leaf temperature was high (35 to 45 C) and humidity low (20%), a leaf could be cooled appreciably by transpiration if its stomatal resistance remained low. Stomatal resistance did remain low under conditions similar to the above for buffalo gourd over the season.

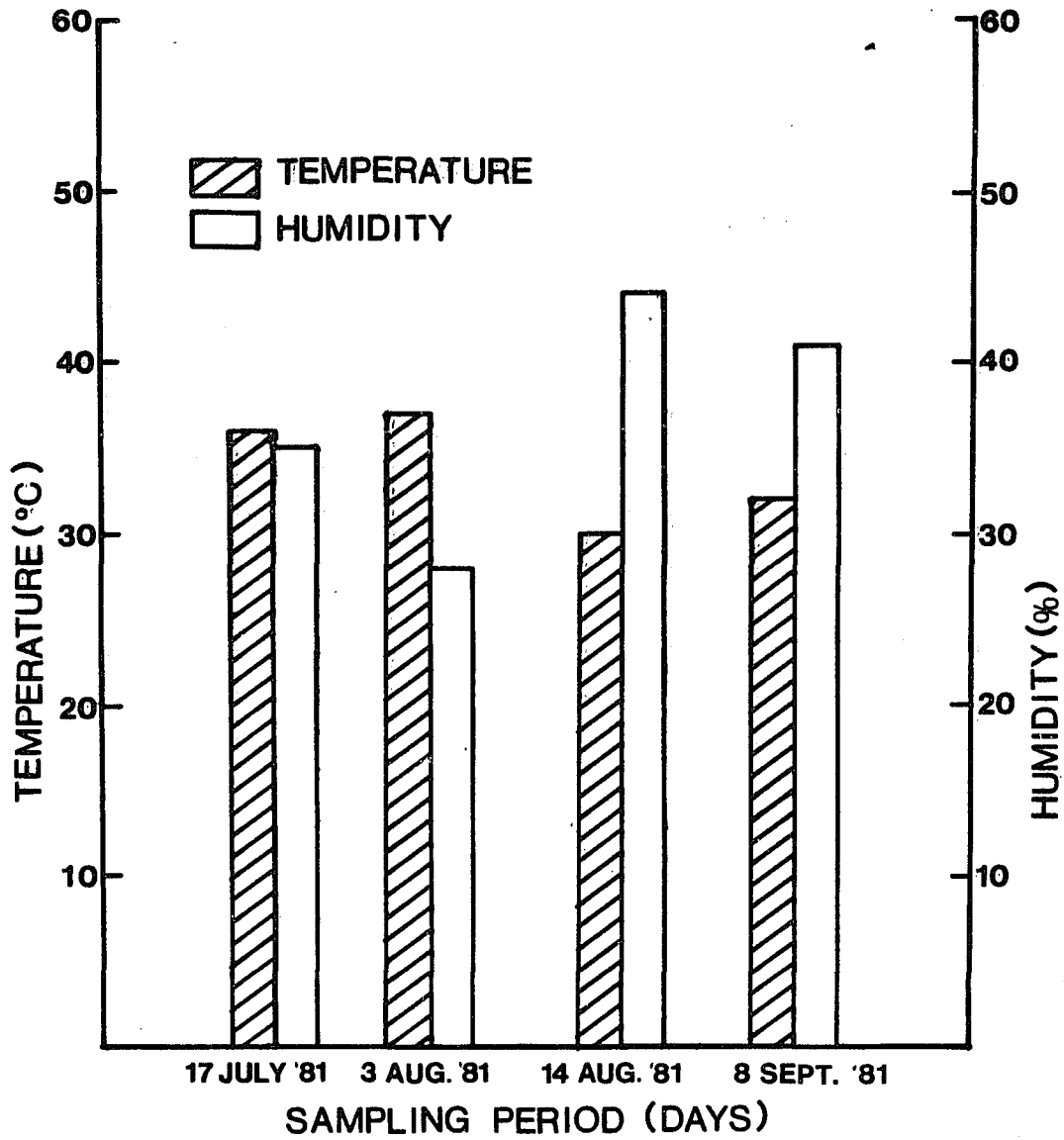


Figure 2. Temperatures and Relative Humidity For Four Dates Over The 1981 Season.

Because wind velocities were not measured during sampling periods, effects of boundary layer disturbance upon recorded transpiration rates were not discernible. However, boundary layers of buffalo gourd leaves might have been protected by a preponderance of trichomes or epidermal hairs. Trichomes, together with lower stomatal frequency, prevent disturbance of the boundary layer and shorten the water-vapor diffusion path (Bidwell, 1979). A preponderance of trichomes may also cause light to be reflected, thus decreasing the temperature of the leaf.

Buffalo gourd trichomes were variable in both form and structure (Fig. 3). They appear to be either unicellular or multicellular. Certain buffalo gourd varieties have more pubescence than others. Further studies are necessary to determine whether or not these highly pubescent plants also have the lowest transpiration rates.

Dependence/Independence of Transpiration and Photosynthesis

Stomata are involved in control of the two important plant processes of transpiration and apparent photosynthesis. Although both are related to stomatal function, they appeared unrelated to one another in buffalo gourd as shown by mean values among sampling periods (Tables 2 and 3) and their correlation ($r = .191$). Environmental factors such as above optimum temperature and humidity may play a larger role than in the photosynthetic process of buffalo gourd. These results resemble those of Miskin et al. (1972), who suggested a possible control of transpiration, through limitation of stomatal number independent of effects upon photosynthesis.

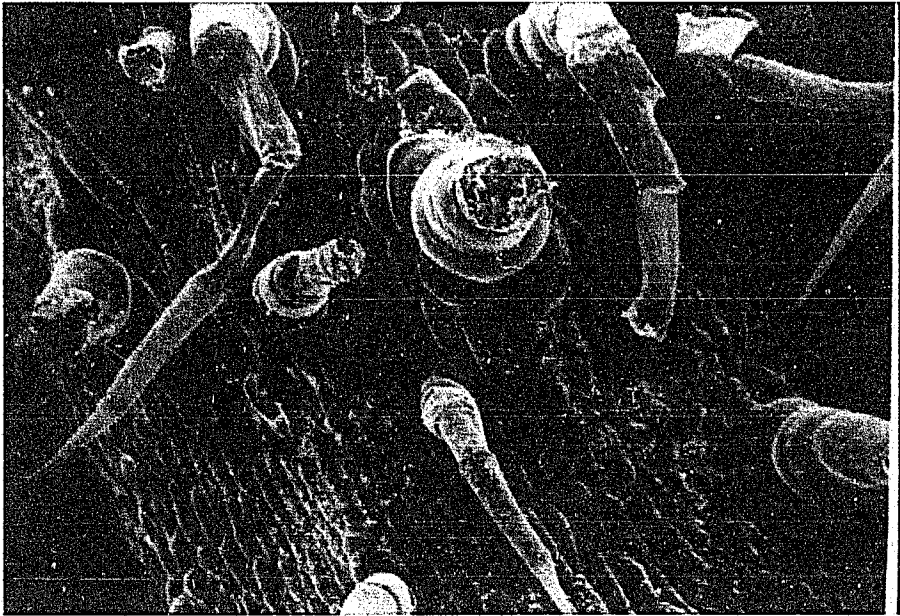


Figure 3. Scanning Electron Micrographs of Trichomes of Buffalo Gourd. The area shown is $4.5 \times 10^{-3} \text{ cm}^2$ at a magnification of 149x.

Buffalo gourd stomata are depicted by scanning electron micrograph in Fig. 4. Buffalo gourd are unique in that they possess roughly equal numbers of stomata on both surfaces of the leaf. The stomata are elliptical and possess kidney shaped guard cells. An analysis of all four varieties found an average of 4,470 stomata cm^{-2} adaxial surface and 5,240 on the abaxial surface.

Diffusive Resistance

Because of its role in the regulation of transpiration and photosynthesis, stomatal behavior is a trait that can be used as a criterion in evaluating crop performance. Information to date cannot ascertain to what extent stomatal diffusive resistance controls these two processes, but empirically it is seen that stomatal resistance is a dominant factor for the diffusion of gases into and out of the plant.

Among Cultivars

Diffusive resistance values (DR) for buffalo gourd exhibited a small range and were generally lower than those reported for other crop species (Table 4). Cultivar (140 x 156) x 300 demonstrated the highest mean value of 0.82 s cm^{-1} over the season. The season's lowest mean value was 0.73 s cm^{-1} displayed by cultivar 300. Variation among cultivars was not significant. The population average for all dates measured was 0.77 s cm^{-1} .

The highest individual value (6.77 s cm^{-1}) on 8 September 1981 was within cultivar synthetic #1. The individual displaying the lowest

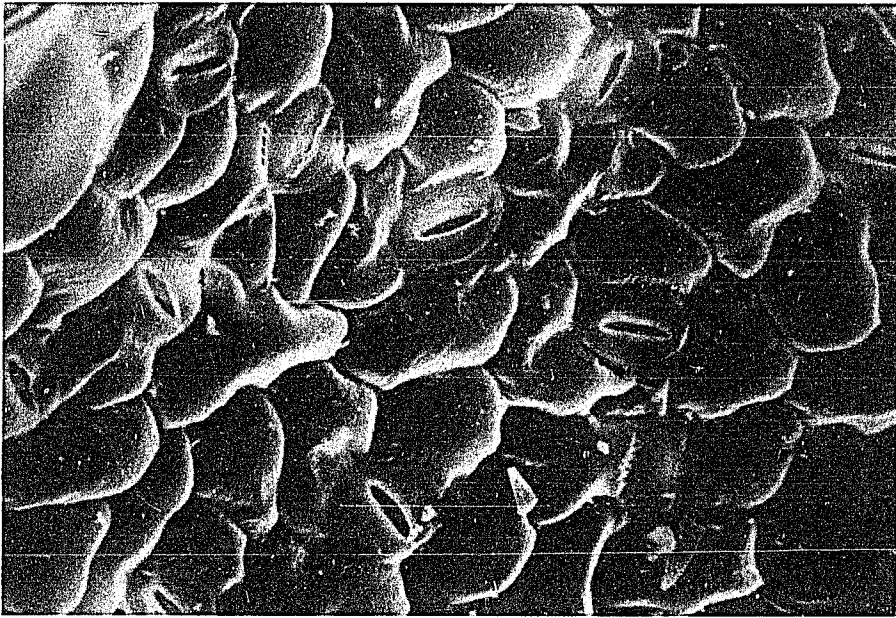


Figure 4. Scanning Electron Micrographs of Buffalo Gourd. The area shown is $2.4 \times 10^{-4} \text{ cm}^2$ at a magnification of 619x.

Table 4. Mean values of diffusive resistance and coefficients of variation on four sampling periods throughout the 1981 season.

Cultivars	Mean Diffusive Resistance ($s\ cm^{-1}$)				Cultivar Means ²	C.V.% ¹
	Sampling Period					
	17 July	3 August	14 August	8 September		
300	0.50	0.90	0.63	1.17	0.73 ^a	64.4
(140 x 156) x 300	0.57	1.04	0.70	1.30	0.82 ^a	61.0
Synthetic #1	0.55	0.97	0.65	1.22	0.78 ^a	61.5
250 x 300	0.49	0.80	0.80	1.17	0.74 ^a	62.2
Sampling Period Means ³	0.53 ^a	0.93 ^c	0.70 ^b	1.22 ^d		
C.V.	22.6	38.7	27.1	66.4		
Grand Mean					0.77	62.3

1. C.V. = Coefficient of variation where the standard deviation is expressed as a percentage of the sampling period mean and varietal mean.

2. Varietal means with similar superscripts are not significantly different from each other at the .05 level. The Student Newman Keul mean separation technique was used (SNK).

3. Sampling period means with similar superscripts are not significantly different from each other at the .05 level. The Student Newman Keul mean separation technique was used (SNK).

rate of DR (0.41 s cm^{-1}) on 17 July 1981 was within cultivar (140 x 156) x 300.

Genetic variation exists for stomatal behavior in other crops. When looking at stomata behavior, Shimshi and Ephrat (1975) demonstrated the presence of consistent, wide ranging differences in diffusive resistance of different cultivars of the same botanical species of (Triticum sativum L.) Soybean cultivars differ significantly in their components of leaf diffusive resistance to gaseous exchange, according to several researchers (Curtis, Ogren and Hageman, 1969; Dornhoff and Shibles, 1970; Dornhoff and Shibles, 1976; Throen and Koller, 1974; Bhagsare et al., 1977).

Among Sampling Periods

Mean DR appeared to increase dramatically on the final sampling date (1.22 s cm^{-1}) (Table 4). Variation and range among individuals within and among cultivars was also greatest 8 September 1981 due in part perhaps to senescence in some individuals (Table 4). Gases were exchanged most freely during the earliest sampling period (mean DR = 0.53 s cm^{-1}) and plants were most similar on this date.

High average values of DR (measured on 8 September 1981) corresponded to low average TR rates (Table 3). Conversely, low mean DR values measured on 17 July 1981 parallel high rates of TR on the same date. As these two measurements are mathematically dependent, (they are both measured using the LiCor porometer) a high correlation was expected. The correlation coefficient between TR and DR over the

season was significant ($r = -.462^{***}$). The correlation coefficient between TD and DR was even higher ($r = -.560^{***}$). Apparent photosynthetic rates during these periods (17 July 1981 and 8 September 1981)(Table 2) were similar. This again suggested possible control of TR through lower stomatal number without modification of APS rates.

As the season progressed, stomatal resistance tended to increase but stomata remained open during these measurements, as can be inferred from the continued photosynthetic activity. For stomatal control to have an effect on both TR and APS, APS must be limited at least partially by the rate of CO_2 diffusion through the stomata. Partial closure of the stomata would effect a decrease in the APS rate.

No correlation between DR and APS in buffalo gourd over the season was observed ($r = -.087$). In contrast, Dornhoff and Shibles (1970) found a trend toward an inverse relationship between leaf net photosynthesis and DR in soybean. This indicated that leaf DR was largely responsible for the cultivar differences in leaf net photosynthesis. Dornhoff and Shibles also found that DR declined linearly during the testing period; stomatal resistance, in particular, declined by about one-half.

Temperature Differential

Temperature differential (TD), the difference between the cuvette temperature and the leaf surface temperature, is known to exert a strong influence on both the TR and photosynthetic apparatus of plants through its effect on the stomata (Willmer, 1983).

Among Cultivars

Differences in TD were greater in variety 250 x 300 (2.98 C) and least in (140 x 156) x 300 (2.54 C)(Table 5) for the season average. The population average for all dates measured was 2.70 C. All varieties displayed high levels of variation (Table 6).

The highest individual TD value was found within cultivar synthetic #1 on 3 August 1981. The leaf surface of this plant was 7 C cooler than the surrounding air. The lowest TD value exhibited by an individual, -3.3 C, was recorded on 8 September 1981 within cultivar 250 x 300. This leaf was actually 3.3 C hotter than the ambient air on the date measured.

The buffalo gourd leaf is characteristically large (20 to 25 cm in midrib length) and has dense pubescence in most varieties. Smith (1978) found that TR rates for a highly pubescent sunlit leaf under hot desert conditions would decrease significantly with increasing leaf size for stomatal resistances lower than 2 to 5 s cm⁻¹. He also observed that leaves of several desert broadleaved plants were well below air temperature due to rapid transpirational fluxes, large leaf size, and low solar absorbance created by dense leaf pubescence.

Among Sampling Periods

The highest average TD value per sampling period (3.74 C) was found on 17 July 1981 (Table 5). This corresponds to the highest average TR rate, which can explain the leaf's coolness at this time (Tables 3 and 5). Temperature differential decreased with decreasing transpiration over the

Table 5. Temperature differential means on four sampling periods throughout the 1981 season.

Cultivars	Mean Temperature Differential (degrees C)				Cultivar Means ^{1/}
	Sampling Periods				
	17 July	3 August	14 August	8 September	
300	3.47	2.19	1.54	2.50	2.67 ^a
(140 x 156) x 300	3.39	2.28	1.39	2.18	2.54 ^a
Synthetic #1	3.57	2.47	1.35	2.17	2.64 ^a
250 x 300	4.56	2.90	1.14	1.83	2.98 ^a
Sampling Period Means ²	3.74 ^a	2.47 ^b	1.35 ^c	2.18 ^b	
Grand Mean					2.70

1. Varietal means with similar superscripts are not significantly different from each other at the .05 level. The Student Newman Keul mean separation technique was used (SNK).
2. Sampling period means with similar superscripts are not significantly different from each other at the .05 level. The Student Newman Keul mean separation technique was used (SNK).

Table 6. Temperature differential means, standard deviations, coded means and coded coefficients of variation on four sampling periods throughout the 1981 season.

	Temperature Differential (Degrees C)		
	Mean and S.D.	Coded Mean ¹	Coded C.V. ²
<u>Cultivar Means</u>			
300	2.67 \pm 1.32	7.67	17.2
(140 x 156) x 300	2.67 \pm 1.84	7.54	24.4
Synthetic #1	2.64 \pm 1.50	7.64	19.6
250 x 300	2.98 \pm 2.53	7.98	31.7
<u>Sampling Period</u>			
<u>Means</u>			
17 July	3.74 \pm 1.59	8.74	18.2
3 August	2.47 \pm 1.79	7.47	24.0
14 August	1.35 \pm 0.69	6.35	10.9
8 September	2.18 \pm 2.04	7.18	28.4
<u>Grand Mean</u>	2.70 \pm 1.84	7.70	23.9

1: Coded mean = Mean + 5

2. Coded C.V. = Standard deviation expressed as percentage of the coded mean.

season ($r = .376^{***}$). The lowest average TD value among sampling periods was 1.35 C on 14 August 1981, during flowering and fruit fill. The temperature was 30 C on that day and the humidity was at its peak (44%). The environmental conditions coupled with the lower levels of TR suggested a closing of stomata to control its internal environment (Tables 3 and 5). The average APS rates were highest during the third sampling period (Table 2) suggesting that the photosynthetic machinery is not as affected by summer ambient temperatures of between 35 and 30 C. Other factors, such as time of day and humidity play a role in photosynthetic efficiency. Rogers, Powell and Sharpe (1979) found stomatal apertures to be at a maximum in this temperature range in pea (*Vicia faba* L.) APS rates are found to be more adversely affected by dry and hot conditions (Fig. 2). Apparent photosynthetic rates were not correlated to temperature differential over the season ($r = -.087$).

Over all cultivars, TD of buffalo gourd was the most variable on 8 September 1981 (Table 6). This date corresponds to the last day of measurements when the buffalo gourd appeared to be in senescence. This was also the same date exhibiting the highest variability in TR and DR (Tables 3 and 4).

If ambient temperatures were deleteriously high during a critical developmental stage, this can adversely affect the processes of APS and TR and may affect yield. Sorghum genotypes have been selected that maintain the ability to photosynthesize at higher temperatures than their progenitors (Sullivan and Ross, 1979). Measurements of leaf temperatures or temperature differential may have promise as a screening technique.

Temperatures were highest during the sampling period on 3 August 1981. The ability of these plants to maintain lower than ambient leaf temperatures on this date (Table 6) suggests the possibility of breeding for this trait. The plant's ability to cool itself during periods of high temperature stress would prevent the destruction of heat labile enzymes involved in the process of photosynthesis. The plant would therefore be able to continue photosynthesizing which may allow for more production and yield.

Studies of Six Sampling Periods on 3 August, 1981

Plants from blocks three and five containing all four cultivars were randomly chosen and then examined at six consecutive intervals throughout the day on 3 August 1981. All four parameters of apparent photosynthesis (APS), transpiration (TR), diffusive resistance (DR) and temperature differential (TD) were measured on old and young leaves of each plant analyzed. The first fully expanded leaf on a stem was chosen as the young leaf and a healthy leaf closest to the crown was chosen as the old leaf. The same leaves were evaluated throughout the day. As the day progressed, all plants in the field became visibly wilted.

As in the four-day study, differences among seed stocks were not statistically significant due in part to the high level of variation found within varieties. Statistical significance among time intervals over the day was only found for photosynthesis (.05% confidence level).

Apparent Photosynthesis.

Among Cultivars. The wide range in APS rates observed for sampling periods throughout the season was also evident in the study of daily fluctuations (Table 6). The range among cultivars for mean APS over the whole day was observed to be between $18.46 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ (300) and $1.48 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ (140 x 156) x 300 (Table 7). Within cultivars variability was high. Individual plant values recorded on both old and young leaves varied from net dark respiration of 63.63 to the APS $84.17 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$. The net respiration rates are a representation of the amount of CO_2 lost from the leaf rather than gained as in APS.

Among cultivar APS means, only the highest fell into the range of cultivar averages displayed during the seasonal study. Low rates of APS between the hours of 1130 MST and 1430 MST may have contributed greatly to this effect.

As in most growth processes, temperature strongly affects photosynthesis. In most plants, temperature related decreases in APS rate are reversible over a considerable range (commonly 10 to 35 C), but exposure to temperatures above and below this range may permanently injure the photosynthetic mechanisms. The day-long ambient temperatures in this study ranged from 32 C to 40 C (Fig. 5), while the population average was $9.13 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$, well below the population average for the seasonal mean rate of $22.34 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$. Variation among individuals was greater here than in the seasonal study (coded C.V. = 8.6% and 23.0% for seasonal and daily studies, respectively) (Table 8).

Table 7. Mean rates of apparent photosynthesis in four buffalo gourd cultivars during six periods on 3 August 1981. ¹

Cultivars	Apparent Photosynthesis (mg CO ₂ dm ⁻² hr ⁻¹)						Cultivar Means
	Sampling Periods						
	0800 MST	0900 MST	1000 MST	1100 MST	1330 MST	1430 MST	
300	37.61	31.57	18.54	26.63	-13.16	9.60	18.46
(140 x 156) x 300	30.24	20.85	0.57	- 3.50	-32.38	- 6.01	1.48
Synthetic #1	22.74	8.18	20.97	22.51	-19.17	- 5.81	8.24
250 x 300	31.09	16.46	20.78	20.77	-30.92	-17.50	6.98
Sampling Period Means	30.42	19.04	16.19	16.63	-23.34	- 4.12	
Grand Mean							9.13

1. Negative units express dark respiration.

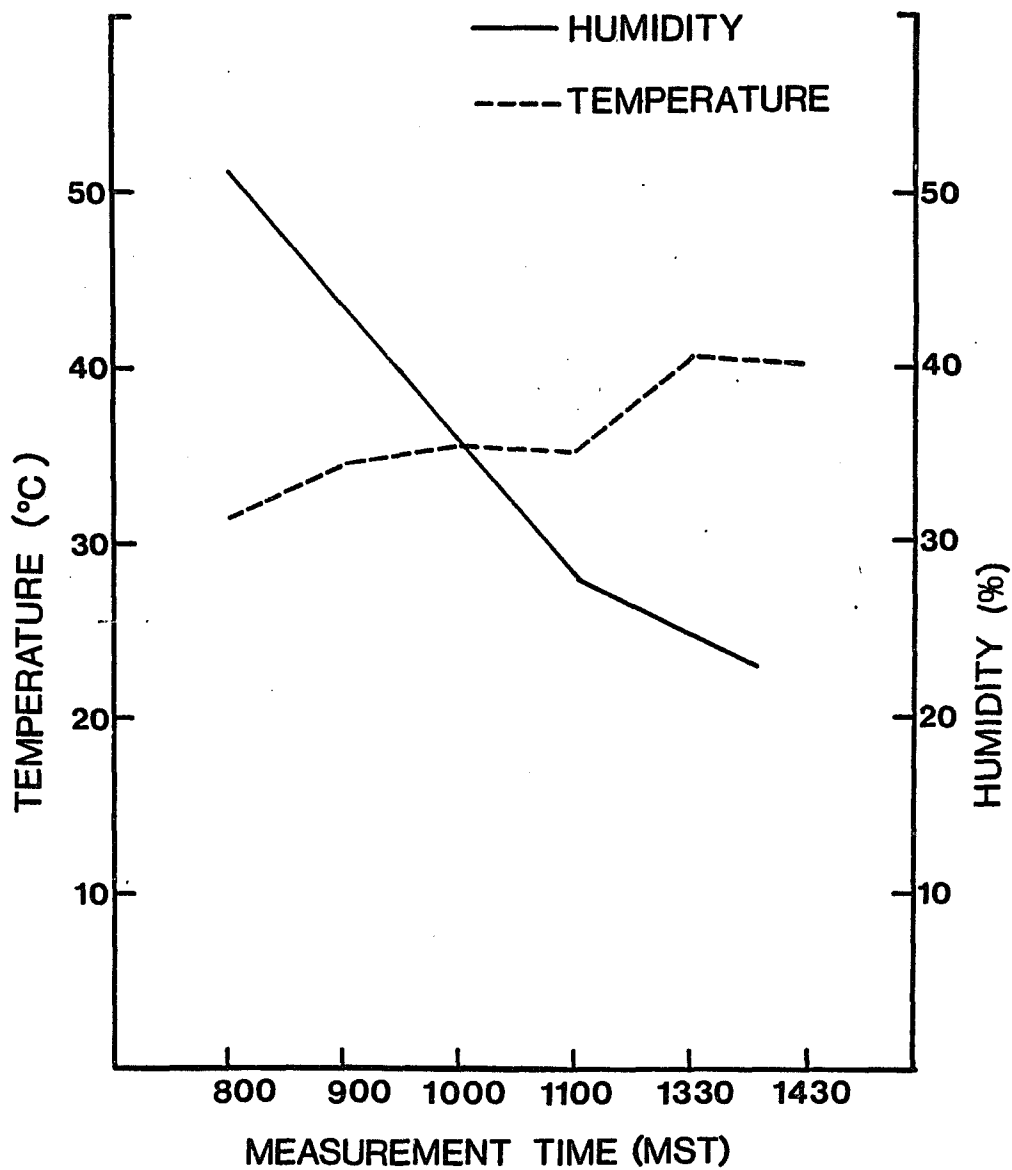


Figure 5. Temperature and relative humidity over the day on 3 August 1981 as determined by the National Weather Service, Tucson, Arizona

Among Sampling Periods. If photosynthesis is curtailed at some critical point in the day (due to environmental changes) the ultimate yield of the plant over the day may be affected (Barrs, 1968; Schulze, et al, 1974). The APS rates among cultivars of buffalo gourd were highest and least variable at 800 MST (Fig. 6 and 7). This time period corresponds to the coolest time of day (32 C) and the highest relative humidity (51%) (Fig. 5). The highest respiration rate among sampling periods was $23.34 \text{ mg CO}_2 \text{ dm}^{-2}\text{hr}^{-1}$ at 1330 MST. The lowest APS rates occurred mainly the afternoon during high-stress periods caused by high temperatures (40 C) and low humidity (23%).

Experiments done by Delaney and Dobrenz (1974), suggest that decreased forage yields during high stress may be caused by increased temperatures. They concluded that enhanced respiration resulting from high temperatures best explains this phenomenon. Results reported herein compare with data on maize obtained by Verduin and Loomis (1944). Their data determined that air temperatures of 25 to 30 C gave the highest APS rate with decreased photosynthetic efficiency at both higher and lower temperature. An average drop in photosynthetic rates was noted at the higher and lower temperature. An average drop in photosynthetic rates was noted at the higher air temperatures during the one day measurements (Fig. 5, 6, and 7). Murata, Iyama and Honma (1966) showed that alfalfa maintained optimum photosynthetic rates over a wide range in temperature (10 to 25C), and only a small rate reduction at 30 C. Respiration was found to increase steadily with increasing temperature.

Table 8. Means, standard deviations, coded means and coded coefficients of variation for rates of apparent photosynthesis during six periods on 3 August 1981.

Apparent Photosynthesis ($\text{mg CO}_2 \text{dm}^{-2} \text{hr}^{-1}$)				
	Mean and S.D.		Coded Mean ¹	Coded C.V. ²
<u>Cultivar Means</u>				
300	18.45	+ 27.00	118.46	22.9
(140 x 156) x 300	1.48	+ 23.90	101.48	23.6
Synthetic #1	8.24	+ 18.33	108.24	16.9
250 x 300	6.98	- 28.49	106.98	26.6
<u>Sampling Period Means</u>				
800 MST	30.42	+ 10.34	130.42	7.9
900 MST	19.04	+ 16.68	119.04	14.0
1000 MST	16.19	+ 12.12	116.19	10.4
1100 MST	16.63	+ 17.71	116.63	15.2
1330 MST	-23.34	+ 16.13	76.66	21.0
1430 MST	- 5.41	- 29.06	94.59	30.7
Grand Mean	9.13	+ 25.10	109.13	23.0

1. Coded mean = mean + 100

2. Coded C.V. = Standard deviation expressed as percentage of the coded mean. Coefficient of variation cannot be measured with negative numbers in the means, therefore a coding of the mean has been performed to alleviate that problem.

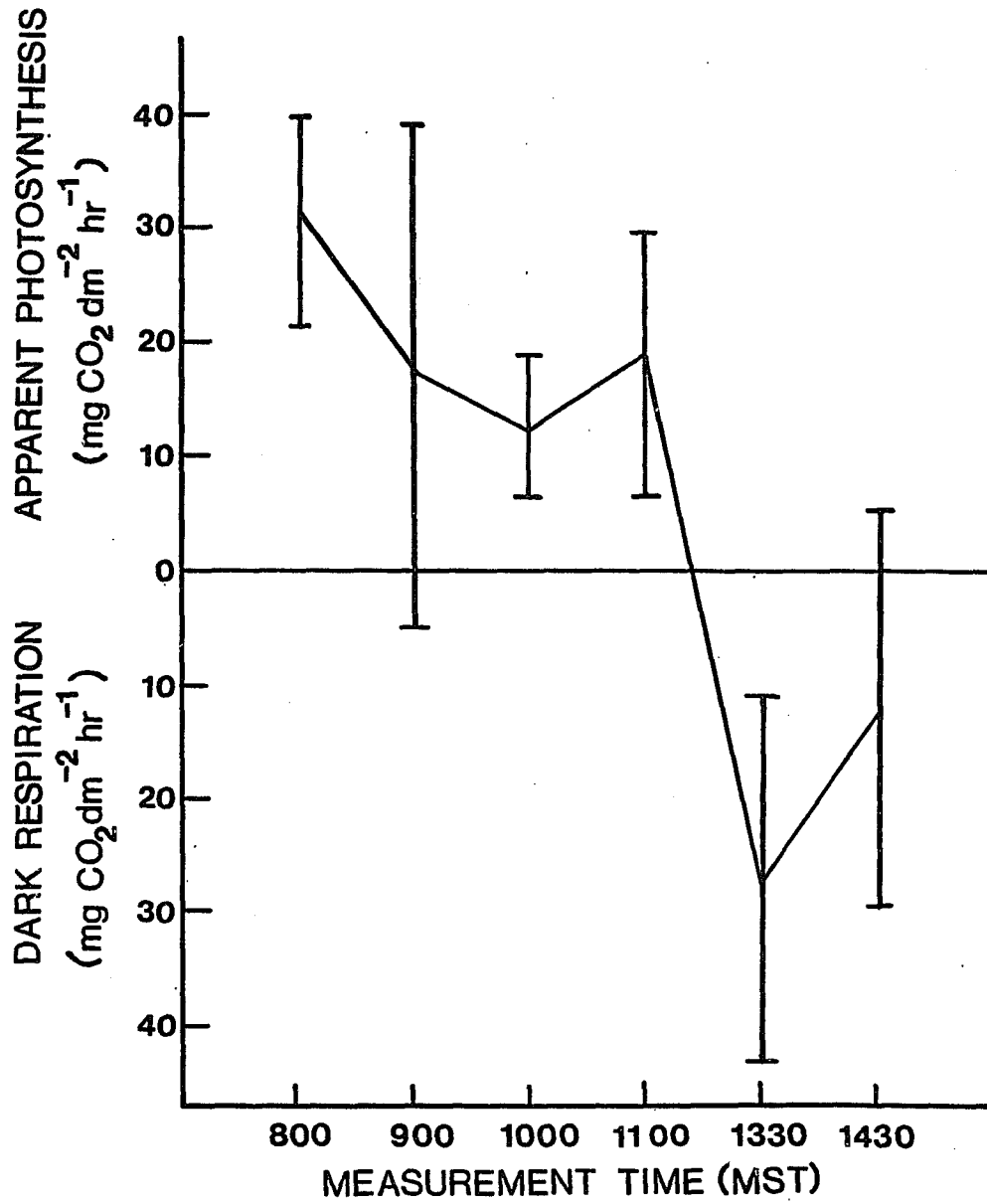


Figure 6. CO_2 Flux Means and Their Standard Deviations for Six Time Periods on 3 August 1981 for Old Leaves.

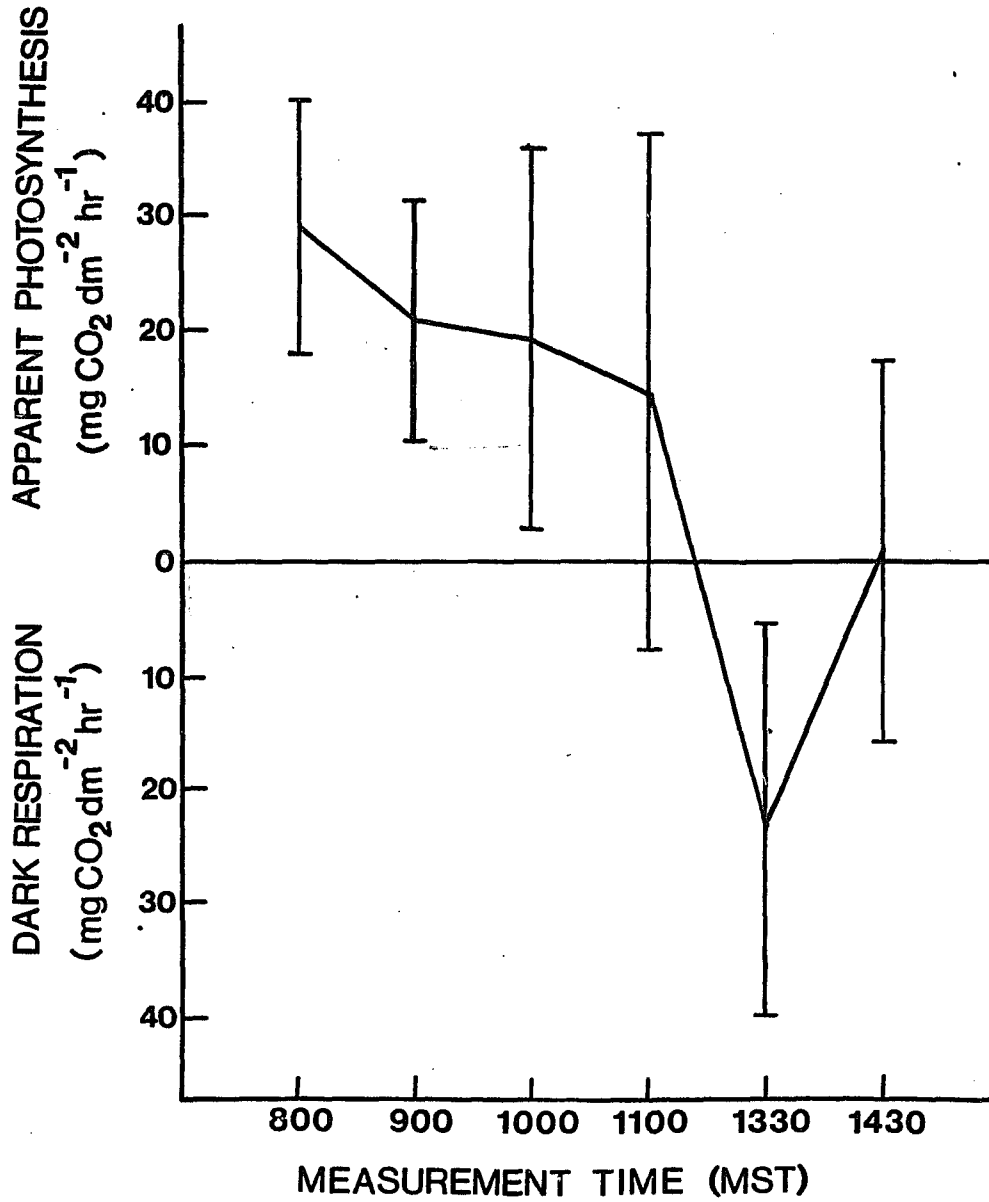


Figure 7. Photosynthetic and Dark Respiration Means and Their Standard Deviation for Six Time Periods on 3 August 1981 for Young Leaves.

Old and Young Leaves Among Sampling Periods and Cultivars. Old

and young leaves at different stages of development may have different physiological reactions to environmental changes. For example, the highest APS rate ($48.96 \text{ mg CO}_2\text{dm}^{-2}\text{hr}^{-1}$) expressed by an old leaf was recorded at 900 MST in an individual of cultivar 300 (Table 9). The lowest rate recorded for an old leaf of the same age was a net dark respiration rate of $63.63 \text{ mg CO}_2\text{dm}^{-2}\text{hr}^{-1}$ at 1330 MST in an individual of cultivar 250 x 300. Daily average APS rates of old leaves ranged from a net dark respiration rate of $7.40 \text{ mg CO}_2\text{dm}^{-2}\text{hr}^{-1}$ (individual from 250 x 300) to an APS of $16.26 \text{ mg CO}_2\text{dm}^{-2}\text{hr}^{-1}$ (individual from 300).

When old leaves of individuals among sampling periods were averaged, the highest mean rate ($31.37 \text{ mg CO}_2\text{dm}^{-2}\text{hr}^{-1}$) was at 800 MST (Table 9). The highest dark respiration rate for the older leaves was $27.14 \text{ mg CO}_2\text{dm}^{-2}\text{hr}^{-1}$, as measured at 1330 MST.

The highest APS rate found for a young leaf was $84.17 \text{ mg CO}_2\text{dm}^{-2}\text{hr}^{-1}$ exhibited by a leaf from cultivar 300 at 1430 MST (Table 10). This unusual rate may be attributed to improper clearing of CO_2 from the CO_2 chamber. The next highest APS rate found for a young leaf over the day was $41.07 \text{ mg CO}_2\text{dm}^{-2}\text{hr}^{-1}$ at 800 MST by cultivar (140 x 156) x 300. An individual of this cultivar also displayed the lowest leaf rate seen at this age bracket, a net dark respiration rate of $48.56 \text{ mg CO}_2\text{dm}^{-2}\text{hr}^{-1}$ at 1330 MST. Daily average APS rates of young leaves of individual plants ranged from $34.36 \text{ mg CO}_2\text{dm}^{-2}\text{hr}^{-1}$ (140 x 156) x 300 (Table 10). Among sampling periods, the highest mean APS rate for the younger leaves was $29.47 \text{ mg CO}_2\text{dm}^{-2}\text{hr}^{-1}$ at 800 MST (Table 10). The highest net dark

Table 9. Individual and mean rates of apparent photosynthesis for old leaves during six sampling periods on 3 August 1981.

		Apparent Photosynthesis (mg CO ₂ dm ⁻² hr ⁻¹)						
		Sampling Periods						Replicate
Cultivars	Blocks ¹	800 MST	900 MST	1000 MST	1100 MST	1330 MST	1430 MST	Means
300	3	+43.37 ²	+48.96	+ 8.99	+ 6.92	-13.69	+ 3.01	+16.26
	5	+29.49	+12.42	+16.11	+46.04	-13.66	-13.66	+12.76
(140 x 156)	3	+23.23	---	+12.09	+ 9.82	-16.44	2.99	+ 6.34
	5	+38.50	+13.99	---	+14.92	-32.14	- 2.74	+ 6.51
Synthetic #1	3	+32.81	+ 5.32	+ 7.02	+23.15	-13.01	-24.28	+ 5.17
	5	+29.46	+ 5.05	+16.32	+20.81	-28.81	- 3.29	+ 6.59
250 x 300	3	+38.71	+47.05	+ 5.80	+20.22	-35.72	-45.70	+ 5.06
	5	+15.41	- 6.85	+20.32	+ 6.44	-63.63	-15.07	- 7.40
Sampling Period ² Means		+31.37	+17.99	+12.38	+18.54	-27.14	-12.34	
Grand Mean								+ 6.44

1. Single individual of each cultivar measured in each block.
2. Positive and negative units expressed, apparent photosynthetic rate and net dark respiration.

Table 10. Individual and mean rates of apparent photosynthesis in young leaves during six sampling periods on 3 August 1981.

Varieties	Blocks ¹	Apparent Photosynthesis (mg CO ₂ dm ⁻² hr ⁻¹)						Replicate
		800 MST	900 MST	1000 MST	1100 MST	1330 MST	1430 MST	Means
300	3	+35.32	+35.32	+22.92	+30.56	- 2.16	+84.17	+34.36
	5	+42.27	+29.59	+26.12	+22.99	+23.14	-35.13	-10.45
(140 x 156) x 300	3	+18.15	---	- 2.83	-31.73	-48.56	+ 0.93	-12.81
	5	+41.06	+27.70	- 7.56	- 6.61	- 5.60	-25.21	+ 4.00
Synthetic #1	3	+10.74	+ 2.15	+29.07	+28.46	-19.69	+ 6.60	+ 9.55
	5	+17.96	+20.18	+31.46	+17.68	-15.17	- 2.28	+11.97
250 x 300	3	+35.91	+12.99	+30.22	+28.71	-11.95	+ 2.24	+32.65
	5	+34.31	+12.64	+26.79	+27.68	-12.36	-11.48	+12.93
Sampling Period ²								
Means		+29.41	+20.08	+19.52	+14.71	-19.00	+ 2.51	+11.88
Grand Mean								

1. Single individual of each cultivar measured in each block.
2. Positive and negative units, express apparent photosynthesis and net respiration.

respiration rate for the younger leaves was at 1330 MST and observed to be $19.00 \text{ mg CO}_2 \text{ dm}^{-2}\text{hr}^{-1}$.

Comparison of Old and Young Leaves. The extremes in mean apparent photosynthetic activity (800 MST and 1330 MST respectively) occurred during identical sampling periods in both old and young leaves (Table 9). Old leaves seemed to have a wider range in rate of APS, (Table 9) but the extent of variability was similar within populations (as depicted by coded coefficients of variation, (Table 11). Combined rates of APS over all sampling periods were also similar (grand means of old and young leaf populations are 6.44 and $11.88 \text{ mg CO}_2\text{dm}^{-2}\text{hr}^{-1}$, respectively).

Over the whole day both old and young aged leaves began to decrease their APS rates (Fig. 6 and 7). Near midday they were near or at zero photosynthetic rate and began to increase only after 1330 MST. By 1430 MST, only the young leaves resumed photosynthetic activity. It is generally assumed that the CO_2 content of midday air is too low by several times for maximum rates of APS (Verduin and Loomis, 1944). If the CO_2 concentration is normally low, then the observed midday field level of 20 to 40% below normal shown by their analyses might be an important factor limiting rates of APS. This analysis found most leaves in the field visibly wilted by noon.

In cassava (Manihot exculenta L.) grown under controlled environment, Mahon et al. (1975) found that young leaves had similar rates of CO_2 uptake over a wide range in temperature. However, in the high temperature regime, the APS rate of old leaves was greatly reduced in

Table 11. Means, standard deviations, coded means and coded coefficients of variation for rates of apparent photosynthesis of old and young leaves during six sampling periods on 3 August 1981.

Leaf Age	Sampling Period	Apparent Photosynthetic Rate ($\text{mg CO}_2\text{dm}^{-2}\text{hr}^{-1}$)			
		Mean and S.D. ³	Coded Mean ¹	Coded C.V. ²	
Old	800 MST	31.37 \pm 9.09	131.37	6.9	
	900 MST	17.99 \pm 21.59	117.99	18.3	
	1000 MST	12.38 \pm 5.42	112.38	4.8	
	1100 MST	18.54 \pm 12.85	118.54	10.8	
	1330 MST	-27.14 \pm 17.36	72.86	23.8	
	1430 MST	-12.34 \pm 16.52	87.66	18.8	
	Grand Mean	6.44 \pm 24.90	106.44	23.4	
Young	800 MST	29.47 \pm 12.01	129.47	16.2	
	900 MST	20.08 \pm 11.60	120.08	9.6	
	1000 MST	19.52 \pm 15.53	119.52	13.0	
	1100 MST	14.71 \pm 22.33	114.71	19.5	
	1330 MST	-19.00 \pm 14.63	81.00	18.1	
	1430 MST	2.51 \pm 38.93	102.51	38.0	
	Grand Mean	11.88 \pm 29.29	111.88	26.2	

1. Coded mean = mean + 100
2. Coded C.V. = standard deviation expressed as percentage of the coded mean.
3. Negative rates than apparent photosynthesis.

contrast to the relatively uniform rates measured for old leaves at lower temperatures.

Transpiration

Trends in seasonal transpiration rates (TR) appeared more variable among individuals than among cultivars. Over the day means among cultivars fell between $27.53 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$ (300) and $17.15 (140 \times 156) \times 300$ (Table 12). Variability within cultivars was moderately high (Table 13 and 14). Individual plant values recorded on both old and young leaves varied from 5.98 to $40.40 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$ (Tables 13 and 14).

Daily cultivars means were in the same range as cultivar averages during the seasonal study. The population average for the whole day, $22.97 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$, resembled the seasonal mean rate of 25.75 (Table 3). Variation among individuals was slightly greater than that in the seasonal study (coded C.V. = 31.80% and 34.52% for seasonal and daily studies, respectively) (Table 12).

Among Sampling Periods. Environmental factors can strongly affect the rate of TR throughout the day. TR rates among buffalo gourd cultivars were most stable at 1000 MST but the lowest average rate occurred at 800 MST ($17.04 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$) (Table 12). These data correspond to cooler temperatures and higher humidity found early in the day (Fig. 5). TR rates varied most at 1330 MST and the highest average TR rate ($25.93 \text{ g H}_2\text{O cm}^{-2}\text{s}^{-1}$) was noted at 1430 MST. (Table 12).

Table 12. Mean rates of transpiration during six periods on 3 August 1981.

Cultivars	Transpiration ($\mu\text{g H}_2\text{Ocm}^{-2}\text{s}^{-1}$)						Cultivar Means	C.V.%
	Sampling Periods							
	0800 MST	0900 MST	1000 MST	1100 MST	1330 MST	1430 MST		
300	18.47	25.11	27.40	31.86	32.74	29.63	27.53	19.7
(140 x 156) x 300	10.61	21.66	19.54	17.58	13.61	20.14	17.15	41.0
Synthetic #1	18.35	18.63	21.35	24.47	28.68	28.46	23.17	35.4
250 x 300	20.72	25.03	27.94	23.43	19.34	25.33	23.56	32.1
Sampling Period								
Means	17.04	22.42	24.11	24.33	24.26	25.93		
C.V. %	34.6	29.1	24.6	24.6	43.0	31.7		
Grand Mean							22.97	34.5

Table 13. Individual and mean rates of transpiration in old leaves during six sampling periods on 3 August 1981.

Cultivars	Blocks ¹	Transpiration ($\mu\text{g H}_2\text{Ocm}^{-2}\text{s}^{-1}$)						Replicate Means	C.V.%
		Sampling Periods							
		0800 MST	0900 MST	1000 MST	1100 MST	1330 MST	1430 MST		
300	3	18.01	26.09	27.11	34.58	30.13	26.89	27.14	19.73
	5	17.56	23.98	28.60	31.97	30.64	32.86	27.61	
(140 x 156) x 300	3	5.98	15.68	12.32	12.08	14.99	16.04	12.85	31.10
	5	14.92	23.54	22.83	12.62	15.40	19.57	18.15	
Synthetic #1	3	23.46	29.44	30.60	31.55	18.59	19.63	25.55	32.13
	5	11.08	10.84	19.15	18.14	27.40	27.16	18.96	
250 x 300	3	20.01	23.51	23.04	13.42	9.43	10.28	16.62	28.84
	5	20.64	26.22	30.52	29.34	13.97	35.09	25.96	
Sampling Period Means		16.46	22.41	24.27	22.96	20.07	23.44		
C.V. %		34.3	27.3	26.0	42.6	40.7	36.3		
Grand Mean								21.60	35.4

1. Two individuals of each cultivar measured in each block

Table 14. Individual and mean rates of transpiration in young leaves during six sampling periods on 3 August 1981.

Cultivars	Blocks	Transpiration ($\mu\text{g H}_2\text{Ocm}^{-2}\text{s}^{-1}$)						Replicate Means	C.V.%
		Sampling Periods							
		0800 MST	0900 MST	1000 MST	1100 MST	1330 MST	1430 MST		
300	3	16.66	22.76	23.10	29.18	36.56	31.22	26.58	20.58
	5	21.63	27.60	30.79	31.69	33.62	27.55	28.81	
(140 x 156) x 300	3	2.33	8.40	17.16	15.44	10.44	15.31	11.51	46.42
	5	19.20	25.77	25.84	30.16	27.41	29.61	26.33	
Synthetic #1	3	19.48	30.02	22.01	25.69	38.48	40.40	29.35	38.73
	5	19.39	14.44	14.43	22.49	30.26	26.65	21.28	
250 x 300	3	19.29	23.52	30.32	21.17	16.29	14.41	30.83	23.47
	5	22.94	26.85	27.88	29.78	37.67	36.62	29.29	
Sampling Period Means		17.62	22.42	23.94	25.70	29.05	28.77		
C. V.%		36.6	32.7	24.9	21.8	28.5	25.9		
Grand Mean								24.39	33.0

1. Two individuals of each cultivar measured in each block.

Among Cultivars and Sampling Periods. The highest TR rate expressed by an old leaf ($35.09 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$) was measured at 1430 MST in an individual in cultivar 250 x 300. The corresponding low TR rate for an individual old leaf over the day was $5.98 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$ by cultivar (140 x 156) x 300 at 800 MST (Table 13). Individual daily rates of old leaves ranged from $35.09 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$ (250 x 300) to $5.98 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$ (140 x 156) x 300.

When averaging old leaves of individuals among sampling periods, the highest mean TR rate was measured at 1000 MST and was calculated to be $24.27 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$ (Table 13). The lowest average TR rate for the older leaves was $16.46 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$ as measured at 800 MST.

The highest TR rate found for a young leaf was $40.40 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$ exhibited by an individual within synthetic #1 at 1430 MST. The lowest individual TR rate, $2.33 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$, was recorded at 800 MST in cultivar (140 x 146) x 300. Daily average TR rates of young leaves of individual plants ranged from $40.40 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$ (synthetic #1) to $11.51 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$ (140 x 156) x 300 (Table 14).

Among sampling periods, the highest mean TR rate for the younger leaves was $29.05 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$ at 1330 MST (Table 13), while the lowest average TR rate was $17.62 \mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$ at 800 MST.

Comparison of Old and Young Leaves. Extremes for the lowest TR rate occurred during identical sampling periods in old and young leaves (Table 13 and 14). However, the highest TR rates occurred at 1000 MST for old leaves but not until 1330 MST in young leaves.

Although young leaves generally displayed a higher range in TR rates over the day (Table 14), variability within leaves of the same age (depicted by coefficients of variation) (Tables 13 and 14) was similar for old and young leaves. Combined average TR rates over the day, as depicted in the grand means of old and young leaf populations, were also similar (21.60 and 24.39 g H₂O cm⁻²s⁻¹, respectively). On a given plant the younger leaf nearly always produced higher TR rates than the older leaf (Tables 13 and 14).

On the average over the day, the old and young leaves followed a similar TR rate pattern until 1000 MST, after which they differed. The old leaves maintained lower values of transpiration at the hottest time of day (Fig. 8).

Diffusive Resistance

The range in values of diffusive resistance (DR) throughout the season was not substantially greater than that found over the day (Table 4). Among cultivars the mean DR over the day ranged between 2.02 s cm⁻¹ (140 x 156) x 300 and 0.79 s cm⁻¹ (300) (Table 15). This compares with the diffusive resistance of between 15 to 70 s cm⁻¹ (in darkness) and 1 s cm⁻¹ during the full sunlight (approximately 1000 μE) of eight plant species under study by Ehrlner and Bavel (1968).

Within buffalo gourd cultivars variability was high. Individual plant values recorded on both old and young leaves varied from 7.69 to 0.46 s cm⁻¹ over the day (Fig. 8). Variations in stomatal resistance on the same leaf and between different leaves have physiological advantages. This sensitive regulatory system can be of great importance for

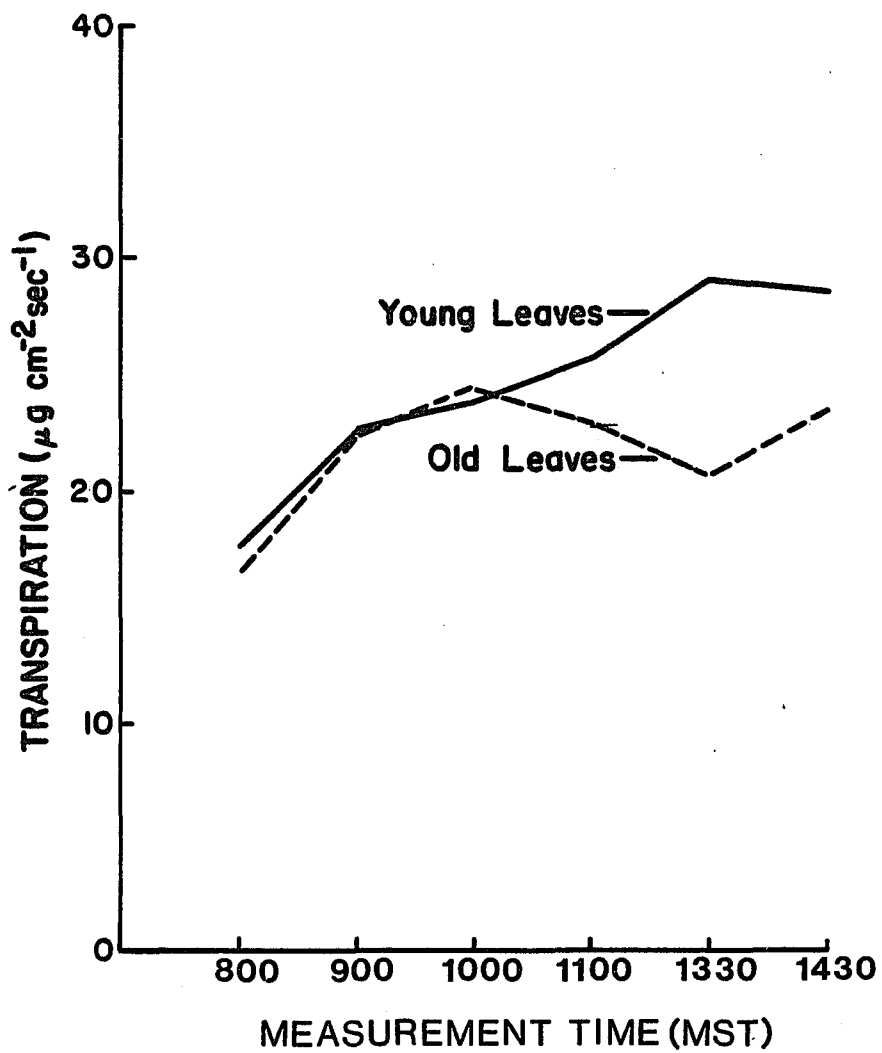


Figure 8. The Transpiration Means and Standard Deviations of Old and Young Leaves for Six Time Periods on 3 August 1981.

Table 15. Mean Values of Diffusive Resistance During Six Periods on 3 August 1981.

Cultivars	Diffusive Resistance ($s\ cm^{-1}$)						Cultivar	
	Sampling Periods						Means	C.V.%
	0800 MST	0900 MST	1000 MST	1100 MST	1330 MST	1430 MST		
300	.66	.66	.85	.76	.81	1.01	0.79	20.3
(140 x 156) x 300	2.95	.88	1.33	2.13	2.76	1.95	2.02	74.8
Synthetic #1	.82	1.33	1.23	1.12	1.11	1.13	1.13	47.8
250 x 300	.60	.58	.74	1.27	2.02	1.67	1.12	74.1
Sampling Period								
Means	1.26	.89	1.04	1.32	1.60	1.42		
C.V.%	42.1	64.4	42.3	56.1	58.8	51.4		
Grand Mean							1.25	78.4

adaptation of broad-leaved species in xerophytic habitats. The existence of a plant species in a desert climate is dependent on a balanced regulation of water loss and production in response to ambient climate. (Schulze et al., 1974).

Among cultivars DR means, only the lowest daily measurements were in the range of cultivar averages displayed during the seasonal study (Tables 4 and 15). High temperatures and low humidity during the afternoon hours of 3 August 1981 may have contributed to this effect.

The population average for the whole day was 1.25 s cm^{-1} , well above that of the seasonal mean rate of $.77 \text{ s cm}^{-1}$. Variation among individuals was greater than that observed in the seasonal study (C.V. = 62.34% and 78.40% for seasonal and daily studies, respectively.) Diffusive resistance was comparatively high for the 1100 MST measurement on 3 August 1981 in the four-day study, but due to higher diffusive resistance values in the afternoon, the overall average DR was higher for the all-day study.

Among Sampling Periods. The diffusive resistance values among cultivars of buffalo gourd were highest at 1330 MST and most variable at 900 MST. (Table 15). Among sampling periods the average lowest rate was at 900 MST ($.89 \text{ s cm}^{-1}$) while the mean DR varied least at 800 MST. The highest DR average value corresponds to the highest temperature (40 C) and lowest humidity (22%) found over the day; the lowest DR corresponds to the lowest temperature (35 C) and highest humidity (50%) (Table 8).

Results similar to those found here have been found for Prunus armeniaca (L.) (apricot). Schulze et al. (1974) reported that stomata respond to changes in relative humidity. At high humidity, stomata were found to be open and low humidity resulted in stomatal closure. According to Schulze et al. (1974), a change in relative humidity affecting stomatal closure is important because it is a "readily responding mechanism to avoid any unreasonable water loss." This ability for stomata to close before a high water loss takes place inside mesophyll is a very effective reaction of the plant to prevent irreversible damage. In buffalo gourd, by 1200 MST respiration outpaced photosynthesis and the diffusive resistance increased correspondingly.

Schulze et al. (1974) concluded that humidity and temperature played an interrelated role and were the dominating factors in controlling the daily course of diffusive resistance, which in turn affects both photosynthesis and transpiration in apricot. Buffalo gourd and apricot both react to high temperature and low humidity, when observed over the day, in a similar fashion.

Old and Young Leaves Among Sampling Periods and Cultivars. The highest value of diffusive resistance found in an old leaf was 3.24 s cm^{-1} in an individual from cultivar 250 x 300 at 1430 MST (Table 16). The lowest DR recorded for an individual leaf of the same age was $.49 \text{ s cm}^{-1}$ from cultivar Synthetic #1 at 900 MST. Among sampling periods, average diffusive resistance values for the older leaves ranged from $.84 \text{ s cm}^{-1}$ (measured at 900 MST) to 1.86 (measured at 1330 MST). Daily

Table 16. Individual and mean values of diffusive resistance in old leaves during six sampling periods on 3 August 1981.

		Diffusive Resistance (s cm ⁻¹)						
		Sampling Periods						
Cultivars	Blocks ¹	800 MST	900 MST	1000 MST	1100 MST	1330 MST	1430 MST	Means
300	3	.70	.57	.77	.81	.93	.98	.79
	5	.69	.76	.81	.75	.86	1.10	.83
(140 x 156) x 300	3	.94	.71	1.05	2.44	2.50	2.05	1.62
	5	2.55	1.29	2.04	2.90	2.38	2.15	2.22
Synthetic #1	3	1.46	1.75	1.29	1.64	1.19	1.31	1.44
	5	.51	.49	.78	.74	1.59	1.42	.92
250 x 300	3	.66	.51	.58	.86	2.42	.89	.99
	5	.56	.60	1.09	2.20	3.04	3.24	1.79
Sampling Period								
Means		1.01	0.84	1.05	1.54	1.86	1.64	1.32
C.V.%		68.3	54.2	43.8	57.1	44.6	48.9	
Grand Mean % C.V.								58.3

1. Single individual of each cultivar measured in each block

average rates of older leaves among cultivars ranged from 2.2 s cm^{-1} (140 x 156) x 300 to $.79 \text{ s cm}^{-1}$ (300).

The highest DR found for a young leaf (7.69 s cm^{-1}) exhibited by a plant from a cultivar (140 x 156) x 300 at 800 MST (Table 17). Although this DR was unusually high, this particular plant displayed the higher DR throughout the day compared to any other plant, indicating the values are probably correct. The high DR values may be the result of leaf damage rather than inherent genetic differences. The lowest DR value over the day for young leaves was $.46 \text{ s cm}^{-1}$ from an individual in cultivar Synthetic #1 at 900 MST. Daily average DR values of young leaves of individual plants ranged from 3.33 s cm^{-1} (140 x 156) x 300 to $.65 \text{ s cm}^{-1}$ (Synthetic #1) (Table 17).

In the afternoon, older buffalo gourd leaves reached much higher DR values than did younger leaves (Figure 9). The DR values for old leaves were much lower in the morning, but the average daily DR of old and young leaves were similar. The DR for both ages did not approach values of DR reported by Teare and Kanemasu (1972) for soybean and sorghum, while the average daily photosynthetic rates for buffalo gourd were only slightly higher. (Fig. 6 and 7). This suggests that leaf age in buffalo gourd does not strongly affect the DR of the leaf over the course of the day.

Table 17. Individual and mean values of diffusive resistance in young leaves during six sampling periods on 3 August 1981.

Cultivars	Blocks ¹	Diffusive Resistance (s cm ⁻¹)						Replicate Means
		Sampling Periods						
		800 MST	900 MST	1000 MST	1100 MST	1330 MST	1430 MST	
300	3	.56	.47	.72	.75	.72	1.10	.72
	5	.67	.82	1.11	.74	.71	.86	.82
(140 x 156) x 300	3	.62	.63	.80	.84	1.19	1.18	.88
	5	7.69	2.69	1.42	2.33	3.39	2.43	3.33
Synthetic #1	3	.73	1.28	1.90	1.28	1.08	1.29	1.26
	5	.57	.46	.96	.82	.59	.49	.65
250 x 300	3	.54	.62	.69	.79	.66	.88	.70
	5	.64	.57	.60	1.24	1.96	2.15	1.19
Sampling Period Means		1.50	.94	1.03	1.10	1.30	1.18	1.17
C. V. %		166.7	79.8	42.8	49.1	80.0	51.7	
Grand Mean % C.V.								100.0

1. Single individuals of each cultivar measured in each block.

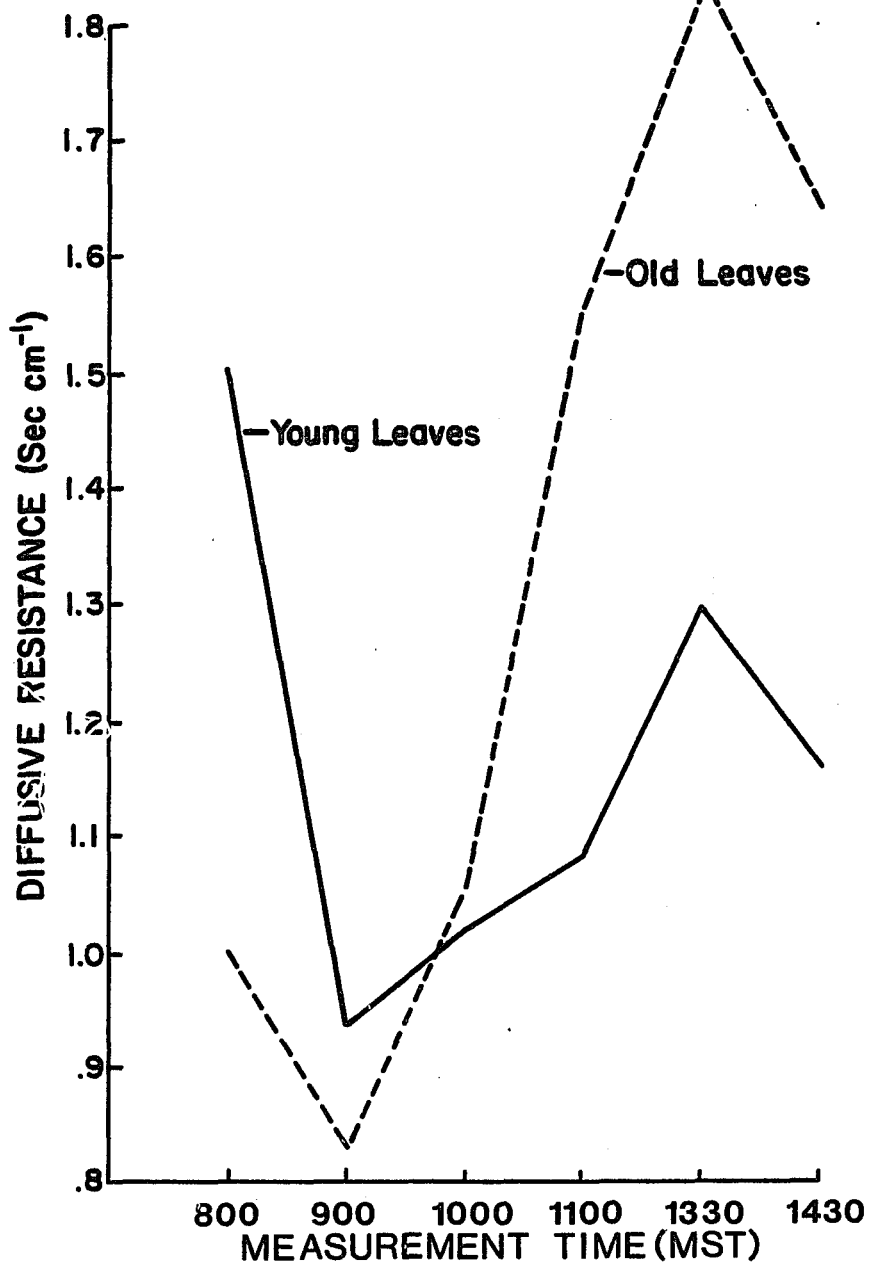


Figure 9. The Diffusive Resistance Means of Old and Young Leaves for Six Time Periods on 3 August 1981.

Comparison of Old and Young Leaves. Old leaves had a wider range in DR (Fig. 9), but the extent of variability within populations (as depicted by coefficients of variation) were higher for young leaves (Tables 16 and 17). Average DR overall sampling periods was higher for old leaves than for young (grand means of old and young leaf populations equal 1.32 and 1.17 s cm^{-1} respectively).

The average value of DR generally increased until 1330 MST in both young and old leaves. The pattern was disturbed by an unusually high DR displayed by a young leaf of $(140 \times 156) \times 300$ measured at 800 MST (Table 17). After peak stomatal resistance was reached at 1330 MST, values decreased again by 1430 MST.

The decrease in values observed here is similar to results found by Tenhunen et al. (1980). They found that the degree of closure depended largely on leaf temperature or the water potential gradient between leaf and air. Contrary to results in this study, they found that midday closure of stomata was sufficient to depress midday transpiration.

Among buffalo gourd individuals, young leaves did not exhibit lower transpiration at midday, as did older leaves. In Tenhunen's study of Arbutus unedo leaves, a midday increase in stomatal resistance resulted in a pronounced depression of net photosynthesis, which on some days reduced net photosynthesis to zero. In buffalo gourd net photosynthesis did reach $0 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ by midday for both old and young leaves (Figs. 6 and 7).

Temperature Differential

A leaf's ability to maintain a lower temperature during high ambient temperatures could prevent irreversible damage from degradation of the photosynthetic process. An increase in yield may also occur due to stomata's ability to stay open and allow CO₂ to enter and produce carbohydrates in the leaf during this critical time.

Among Cultivars. The range in temperature differential (TD) values previously discussed for sampling periods throughout the season was similar to that seen in the study of daily fluctuations (Table 6). Among cultivars, mean TD values varied over the whole day between 2.93 C (300) and 1.76 C (140 x 156) x 300 (Table 18). Variability within cultivars was high (Table 20); individual plant values recorded on both old and young leaves varied from 5.90 to -3.30 C (Fig. 10).

Among cultivars TD means over the day fell into the same range as sampling period means displayed during the season (Table 5). The population average for the whole day (2.45 C) resembled the seasonal average (2.70 C). The coefficient of variation among individuals in the seasonal study (23.90%) (Table 6) was only slightly greater than that in the whole day study (17.85%) (Table 19).

Among Sampling Periods. TD values were the highest and least variable at 800 MST the coolest and most humid time of day (Table 19). The least stable time was 1330 MST. TD values were most stable among

Table 18. Mean values of temperature differential during six periods on 3 August 1981 ^{1/}

Temperature Differential (degrees C)							
Cultivars	Sampling Periods						Cultivar Means
	800 MST	900 MST	1000 MST	1100 MST	1330 MST	1430 MST	
300	3.70	3.03	1.20	3.08	3.95	2.65	2.93
(140 x 156) x 300	2.63	3.10	1.73	.90	1.53	.95	1.76
Synthetic #1	2.73	2.52	.90	2.08	3.10	2.80	2.36
250 x 300	3.05	3.25	2.33	2.03	3.15	2.23	
Sampling Period Means	3.03	2.94	1.54	2.02	3.03	2.15	
Grand Mean							+ 2.45

1. Expressed in °C.

Table 19. Means, standard deviations, coded means and coded coefficients of variation for values of temperature differential during six periods on

Temperature Differential (degrees C)			
	Mean and S.D.	Coded Mean ¹	Coded C.V. ²
<u>Cultivar Means</u>			
300	2.93 \pm 1.39	7.93	17.53
(146 x 156) x 300	1.76 \pm 1.14	6.76	16.86
Synthetic #1	2.36 \pm 1.48	7.36	20.11
250 x 300	2.69 \pm 1.02	7.69	13.26
<u>Sampling Period</u>			
<u>Means</u>			
800 MST	3.03 \pm .82	8.03	10.21
900 MST	2.94 \pm 1.33	7.94	16.75
1000 MST	1.54 \pm 1.00	6.54	15.29
1100 MST	2.02 \pm 1.33	7.02	18.95
1330 MST	3.03 \pm 1.63	8.03	20.30
1430 MST	2.15 \pm 1.61	7.15	22.52
<u>Grand Mean</u>	2.45 \pm 1.33	7.45	17.85

1. Coded mean = mean + 5

2. C.V. = standard deviation expressed as percentage of the coded mean

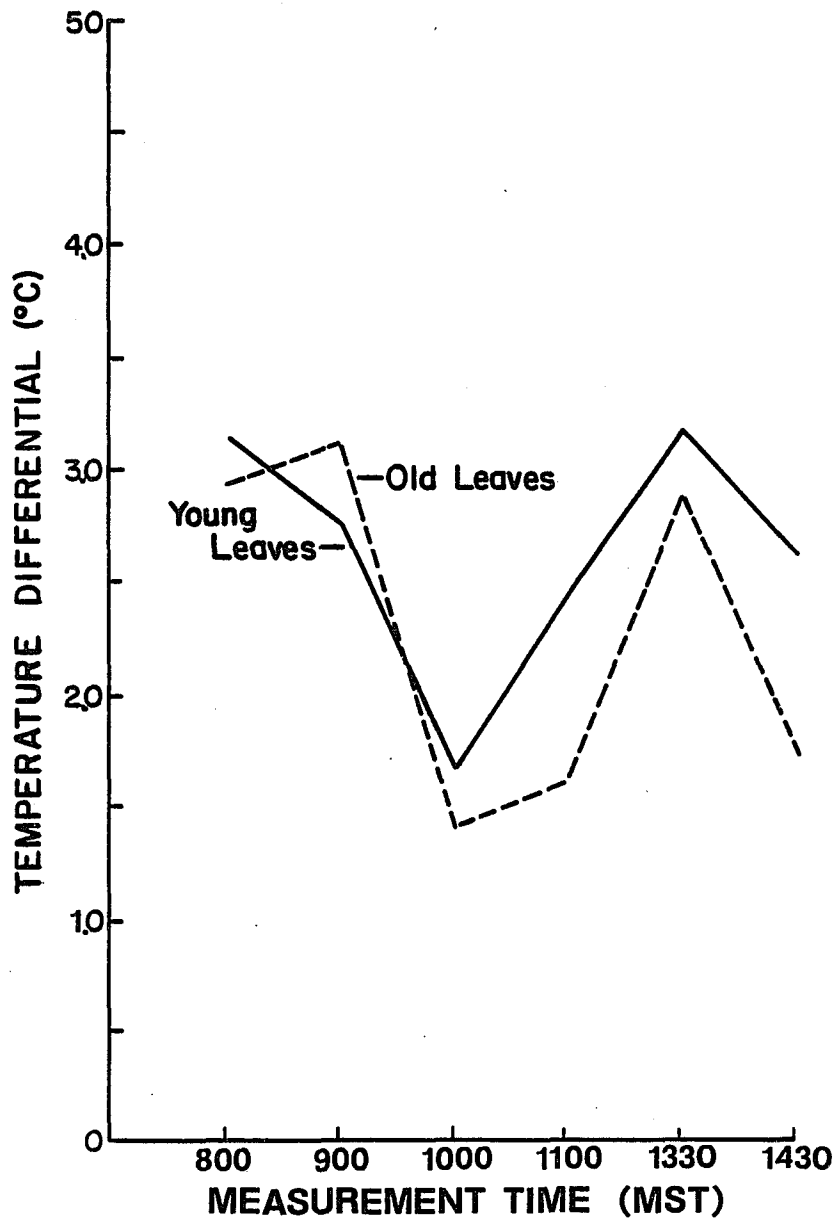


Figure 10. The Temperature Differential Means of Old and Young Leaves for Six Time Periods on 3 August 1981.

cultivars at this time. At 1000 MST the lowest average TD values were recorded.

In buffalo gourd, leaf resistance was high in the morning (around 900 MST) when ambient temperatures ranged from 33.80 to 35.40 C. Leaf temperatures at this time ranged from 29.90 to 32.90 C. Resistance was high again in the afternoon when temperatures ranged from 40.00 to 41.80 C and leaf temperatures ranged from 35.60 C to 39.80 C. The lowest diffusive resistance occurred at 1000 MST when ambient temperatures ranged from 35.40 to 36.20 C leaf temperatures ranged from 32.40 to 35.90 C. These results agree with Gates et al. (1964), who found that most plants became cooler than air in an ambient temperature between 30 and 40 C.

Old and Young Leaves Among Sampling Periods and Cultivars

The highest TD observed for an old leaf (4.90 C) was recorded at 900 MST from an individual in cultivar 300 (Table 20). The ambient temperatures ranged from 33.80 to 35.40 C, so leaf temperatures had cooled to around 30 C. Photosynthetic and diffusive resistance values were high and low, respectively. The lowest value recorded for an individual leaf of the same age was 0.10 C, measured at 1430 MST in an individual from cultivar (140 x 156) x 300. Ambient temperatures at this time ranged from 40.00 to 41.20 C. Mean diffusive resistance for old leaves in buffalo gourd at this time (i.e., 1430 MST) was 1.64 s cm^{-1} , which was among the highest TD values observed for this plant (Table 16). At these temperatures, old leaves could very well be wilting and the stomata closed, although the stomatal resistance seems low compared

Table 20. Individual and mean values of temperature differential in old leaves during six sampling periods on 3 August 1981. ¹

Cultivars	Temperature Differential (degrees C)							Replicate Means
	Blocks	Sampling Periods						
		0800 MST	0900 MST	1000 MST	1100 MST	1330 MST	1430 MST	
300	3	3.50	4.90	1.60	2.20	3.80	1.1	2.85
	5	3.60	1.30	1.90	2.40	4.00	3.2	2.73
(140 x 156) x 300	3	2.50	4.40	1.10	1.40	2.00	0.10	1.93
	5	2.70	1.10	1.80	0.50	1.11	1.80	1.50
Synthetic #1	3	1.80	3.50	0.80	1.00	2.60	0.60	1.72
	5	2.90	2.50	0.30	2.30	3.00	3.80	2.45
250 x 300	3	2.40	3.90	3.40	1.70	2.00	1.10	2.42
	5	4.00	3.30	0.40	1.30	4.60	2.30	2.65
Sampling Period Means		2.93	3.11	1.40	1.60	2.89	1.74	
Grand Mean								2.28

1. Two individuals of each cultivar measured in each block.

to other species. Daily average TD values of old leaves ranged from 2.85 C (300) to 1.50 C (140 x 156) x 300 for the day.

When the old leaves of individuals were averaged among sampling periods, the highest mean of 3.11 C was at 900 MST (Table 20). The lowest sampling period mean was 1.60 C at 1100 MST.

The highest TD found for a young leaf, 5.9 C was exhibited by a plant from cultivar Synthetic #1 at 1430 MST (Table 21). The lowest TD derived from an individual leaf was -3.3 C at 1100 MST from a plant in cultivar 300. The leaf surface was actually 3.3 C hotter than the cuvette temperature at that time. Daily averages of young leaves of individual plants ranged from 2.98 C (Synthetic #1) to 2.17 C (140 x 156) x 300.

Among sampling periods, the highest mean TD value for the younger leaves was 3.19 C at 1330 MST (Table 21). The lowest average TD value for the younger leaves, 1.68 C, was at 1000 MST. The average cuvette temperature at 1330 MST was 40.9 C, which means the average leaf temperature was 37.71 C at that time. The cuvette temperature at 1000 MST was 35.8 C which makes the average leaf temperature 34.12 C.

Comparison of Old and Young Leaves. Extremes in mean TD activity did not occur at identical sampling periods in old and young leaves (Table 22). Although young leaves were somewhat cooler in the afternoon than the older leaves, they both displayed their lowest TD (least difference in temperature between the leaf and the air) at

Table 21. Individual and mean values of temperature differential in young leaves during six sampling periods on 3 August 1981. ¹

Cultivars	Blocks ¹	Temperature Differential (degrees C)						Replicate Means
		Sampling Periods						
		0800 MST	0900 MST	1000 MST	1100 MST	1330 MST	1430 MST	
300	3	3.00	4.30	0.70	2.40	4.80	2.1	2.88
	5	4.70	1.60	0.60	-3.30	3.20	4.2	1.83
(140 x 156) x 300	3	3.50	3.80	2.40	2.00	3.30	1.10	2.68
	5	1.80	0.50	1.70	0.70	1.50	0.80	1.17
Synthetic #1	3	2.20	3.20	0.20	0.80	2.30	1.00	1.62
	5	4.00	2.90	2.30	4.30	4.50	5.90	3.98
250 x 300	3	2.70	1.80	2.60	2.40	3.60	3.30	2.73
	5	3.10	4.00	2.90	3.20	2.40	3.20	3.13
Sampling Period Means		3.13	2.76	1.68	2.44	3.19	2.63	
Grand Mean								2.62

1. Two individual of each cultivar measured in each block.

Table 22. Means, standard deviations, coded means and coded coefficients of variation for values of temperature differential of old and young leaves during six sampling periods on

Temperature Differential (C)					
Leaf Age	Sampling Periods	Mean and S.D.		Coded Mean ¹	Coded C.V. ²
Old	0800 MST	2.93	± .73	7.83	9.21
	0900 MST	3.11	± 1.38	8.11	17.02
	1000 MST	1.40	± 1.01	6.40	15.78
	1100 MST	1.60	± 0.76	6.60	11.52
	1330 MST	2.89	± 1.19	7.89	15.08
	1430 MST	1.74	± 1.26	6.74	18.69
	Grand Mean	2.28	± 1.25	7.28	17.17
Young	0800 MST	3.13	± 0.94	8.13	11.56
	0900 MST	2.76	± 1.34	7.76	17.27
	1000 MST	1.68	± 1.04	6.68	15.57
	1100 MST	2.44	± 1.67	7.44	22.45
	1330 MST	3.19	± 1.21	8.19	14.77
	1430 MST	2.63	± 1.93	7.63	25.29
	Grand Mean	2.63	± 1.40	7.62	18.37

1. Coded mean = mean + 5

2. C.V. = standard deviation expressed as a percentage of the coded means.

1000 MST. Both old and young leaves responded similarly during the day; transpiration was high in the early morning and again in the afternoon, with an observed midday slump at noon (Fig. 10). Ambient temperatures exceeded leaf temperatures at all measuring times throughout the day. Old and young leaves had similar ranges in their TD values for a strong variation in cultivar 300 for young leaves (Tables 20 and 21).

Variability within plots, as depicted by the coefficients of variation (Table 22), was similar. Combined measurements of TD over all sampling periods were also similar (grand means of old and young leaves were 2.28 C and 2.62 C, respectively).

CHAPTER 5

SUMMARY

Four physiological measurements: apparent photosynthesis, transpiration, diffusive resistance, and temperature differential, were studied on four dates during the season to determine the variability within and among buffalo gourd varieties. Plants from blocks three and five, containing all four varieties, were also examined at six consecutive time intervals throughout the day on 3 August 1981. All four parameters were measured on old and young leaves of each plant analyzed. Age of the leaf did not appear to affect values of the four parameters over the season or day.

Parameter differences among seed stocks were not statistically significant for either study, due in part to the high variability found within varieties. Substantial variation within seed stocks might be utilized in a breeding program to improve yield. All interactions of physiological measurements among sampling periods were significant at the .01 level for the four-day study. Significant variation among time intervals over the day was found only for photosynthesis. Table 23 displays the grand means, coefficients of variation, and mean ranges of all four parameters over both the four-day and the all-day study; the table includes variation in old and young leaves, which can be used to

Table 23. Summary of the means of the four physiological parameters and their coefficients of variations

	Grand Mean Over Season	C.V.	Grand Mean Over Day	C.V.	Grand Mean Old Leaves	C.V.	Grand Mean Young Leaves	C.V.	Range in Mean Rates Over The Day	Range in Mean Rates Over The Season
Apparent Photo- synthesis mg CO ₂ dm ⁻² hr ⁻¹	22.34	8.60	9.13	23.00	6.44	23.4	11.88	26.2	1.48-18.46	21.45-24.18
Transpiration u ₂ O cm ⁻² s ⁻¹	25.75	31.80	22.97	34.50	21.60	35.4	24.39	33.0	17.15-27.53	16.27-32.91
Diffusive Resistance cm s ⁻¹	.77	63.34	1.25	78.40	1.32	58.3	1.17	100.0	.73 - .82	.79 - 2.02
Temperature Differential degrees C	2.70	23.90	2.45	17.85	2.28	18.69	2.62	18.37	1.76 - 2.93	2.70 - 2.98

characterize buffalo gourd in relation to other crop plants. Rates of APS and transpiration were similar for buffalo gourd and conventional crops.

When photosynthesis in buffalo gourd was observed over the season, the highest rates were found to occur during flowering and seed fill (3 August). This same sampling period displayed the highest variability among individuals (C.V. = 50.6%). Selection for high photosynthesizing genotypes would most easily be accomplished during this period due to the large range in apparent photosynthesis. Over the day, photosynthetic rates among varieties were highest and least variable at 800 MST (Table 8), and lowest and most variable in the afternoon.

The highest mean rate for transpiration over the season occurred on the first measuring date (17 July 1981), during vegetative growth. TR decreased as the season progressed as a result of environmental and growth stage factors. Variation among individuals was greatest during the final sampling period (C.V. = 30.9%). Over the day, transpiration rates among varieties were most stable at 1000 MST; the average rate was lowest at 800 MST (Table 10). The highest rate deviation occurred at 1330 MST, while the highest average rate was noted at 1430 MST.

Mean diffusive resistance appeared to increase dramatically on the final sampling date, 8 September 1981 (Table 4). Variation among varieties was also greatest on this date (C.V. = 66.4%), perhaps due in part to senescence in some individuals (Table 4). Gases were exchanged

most freely during the earliest sampling period, and plants were most similar on this date; DR values generally increased as the season progressed. Over the day, diffusive resistance values among cultivars were highest at 1330 MST and most variable at 900 MST (Table 15). The average lowest DR value among sampling periods occurred at 900 MST. The mean DR values were least variable at 800 MST. Average daily DR values of old and young leaves were similar (Figs. 6 and 7). The average value for diffusive resistance generally increased until 1330 MST in both young and old leaves. After peak stomatal resistance was reached (1330 MST), values decreased again by 1430 MST. This characteristic midday closure of stomata occurred simultaneously with a depression in photosynthetic rate (Figs. 6, 7, and 9), but only transpiration in older leaves were affected (Figure 8). Environmental factors such as above-optimum temperature and/or humidity may play a larger role than diffusive resistance in the photosynthetic process of buffalo gourd over the day.

Temperature differential values over all cultivars of buffalo gourd were the least stable on 8 September 1981 (Table 6). Temperatures were highest for leaves on 3 August 1981, during flowering and seed fill. On this date plants deviated substantially in their ability to maintain lower-than-ambient leaf temperatures (Table 6), which suggests the possibility of breeding for this trait. Temperature differential values were highest and most stable at 800 MST. The least stable time period was 1330 MST. At 1000 MST, the lowest average values were

recorded for temperature differential. Both old and young leaves behaved similarly during the day, transpiring in the early morning and again in the afternoon after a decrease in transpiration at noon.

When all cultivars of buffalo gourd were considered as one group over the season, there was a significant negative correlation between diffusive resistance and both transpiration ($r = -.462^{***}$) and temperature differential ($r = -.560^{***}$) but not photosynthesis ($r = -.087$). Transpiration and temperature differential were also significantly correlated ($r = .376^{***}$). No correlation was found with photosynthesis and either transpiration or temperature differential. Although photosynthesis and transpiration are both controlled somewhat by the stomatal aperture, they did not appear to be related to each other in buffalo gourd over the season, as shown by mean values among sampling periods (Tables 2 and 3) ($r = -.191$). This suggests a possible control of transpiration, independent of effects upon photosynthesis, through limitation of stomatal number.

Average ambient temperatures were above average leaf temperatures at all measuring times throughout the day and season. Buffalo gourd possesses highly pubescent leaves that may cut down on the amount of solar absorbance and transpiration losses in the leaf. Measurements of leaf temperature may have promise as a screening technique due to the ease of measuring a large number of leaves during maximum high temperature stress. More tests should be initiated to verify the above trends and to determine the relationship, if any, of these parameters and yield potential in buffalo gourd.

LITERATURE CITED

- Alexandrov, V. Y. 1964. Cytophysiological and cytoecological investigations of heat resistance of plant cells toward the action of high and low temperature. *Quart. Rev. Biol.* 39: 35 - 77.
- Barrs, H. C. 1968. Effect of cyclic variations in gas exchange under constant environmental conditions on the ratio of transpiration to net photosynthesis. *Physiologia Pl.* 21: 918 - 929.
- Beadle, C. L., K. R. Stevenson, H. H. Newmann, C. W. Thurtell, and K. M. King. 1973. Diffusive resistance, transpiration and photosynthesis in single leaves of corn and sorghum in relation to leaf water potential. *Can. J. Plant Sci.* 53: 537 - 544.
- Beardsell, M. F., P. G. Jarvis, and B. Davidson. 1972. A null-balance diffusion porometer suitable for use with leaves of many shapes. *J. Appl. Ecol.* 9: 677 - 690.
- Bemis, W. P., J. W. Berry, M. J. Kennedy, D. Woods, M. Monan, and A. D. Deutschman. 1967. Oil composition of Cucurbita. *J. Am. Oil Chem. Soc.* 44: 429 - 430.
- Bemis, W. P., J. W. Berry, and C. W. Weber. 1979. The buffalo gourd, a potential arid land crop. p. 65 - 87. In G. A. Ritchie (ed.) *New Agricultural Crops*. Westview Press, Boulder, Colorado.
- Berry, J. W., W. P. Bemis, C. W. Weber, and T. Philip. 1975. Cucurbit root starches: isolation and some properties of starches from Cucurbita foetidissima H.B.K. and Cucurbita digitata Gray. *J. Agric. Chem.* 23: 825 - 826.
- Berry, J. W., J. C. Scheerens, and W. P. Bemis. 1978. Buffalo gourd roots: chemical composition and seasonal changes in starch content. *Agric. and Food Chem.* 26: 344 - 356.
- Berry, J. W., C. W. Weber, M. L. Dreher, and W. P. Bemis. 1976. Chemical composition of buffalo gourd, a potential food source. *J. Food Sci.* 41: 465 - 466.
- Berry, J. and Bjorkman. 1980. Photosynthetic response and adaptation to temperature in higher plants. *Ann. Rev. Plant Physiol.* 31: 491 - 543.

- Bhagsari, A. S., D. A. Ashley, R. H. Brown, and H. R. Boerma. 1977. Leaf photosynthetic characters of determinate soybean cultivars. *Crop Sci.* 17: 929 - 932.
- Bidwell, R.G.S. 1979. Photosynthesis. p. 146 - 191. In A. T. Jaden-dorf, W. T. Jackson, and I. A. Tamos (eds.). *Plant Physiology*. MacMillan Publishing Co., Inc. New York
- Blum, A. 1974. Genotypic responses in sorghum to drought stress. I. Responses to soil moisture stress. *Crop Sci.* 14: 361 - 364.
- Bolley, D. S., R. H. McCormick, and L. C. Curtis. 1950. The utilization of seeds of the wild perennial gourds. *J. Am. Oil Chem. Soc.* 29: 571 - 574.
- Boyer, J. S. 1970. Differing sensitivity of photosynthesis to low leaf water potentials in corn and soybean. *Plant Physiol.* 46: 236 - 239.
- Boyer, J. S. 1976. Photosynthesis at low water potentials. *Phil. Trans. R. Soc. Lond. B.* 273: 501 - 512.
- Boyer, J. S. and B. L. Bowen. 1970. Inhibition of oxygen evolution in chloroplasts isolated from leaves with low water potentials. *Plant Physiol.* 45: 612 - 615.
- 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. *Proc. 11th Int. Grassland Congr. Queensland, Austr.* p. 248 - 251.
- Clegg, M. D. and C. Y. Sullivan. 1975. A rapid method for measuring carbon dioxide concentrations. *Agron. Abstr.* p. 70.
- Clegg, M. D., C. Y. Sullivan and J. D. Eastin. 1978. A sensitive technique for the rapid measurement of carbon dioxide concentrations. *Plant Physiology.* 62: 924 - 926.
- Cossack, Z., L. B. Waymack, C. W. Weber, and J. C. Scheerens. 1979. Nutritional availability of buffalo gourd (*Cucurbita foetidissima*) residue for sheep. *Am. Soc. Am. Sci. Proc., W. S.* 30: 156 - 158.
- Curtis, L. C. 1946. The possibility of using species of perennial cucurbita as a source of vegetable fats and proteins. *Chemurgic Dig.* 5: 221 - 224.

- Curtis, P. E., W. L. Ogren, and R. H. Hageman. 1969. Varietal differences in soybean photosynthesis. *Crop Sci.* 9: 323 - 327.
- Curtis, L. C. and N. Rebeiz. 1974. The domestication of a wild, perennial, xerophytic gourd: Cucurbita foetidissima, the buffalo gourd. Report of the Arid Lands Agricultural Development Program. The Ford Foundation.
- Dastur, R. H. 1925. The relation between water content and photosynthesis. *Ann. Bot.* 39: 769 - 786.
- Delaney, R. H., A. K. Dobrenz. 1974. Morphological and anatomical features of alfalfa leaves as related to CO₂ exchange. *Crop Sci.* 14: 444 - 447.
- Delaney, R. H., A. K. Dobrenz, and H. T. Poole. 1974. Seasonal variation in photosynthesis, respiration, and growth components of nondormant alfalfa (Medicago sativa, L.). *Crop Sci.* 14: 58 - 61.
- Dittmer, H. J. and M. L. Rosen. 1963. The periderm of certain Cucurbitaceae. *Southwestern Naturalist* 8: 1 - 9.
- Dittmer, H. J. and B. P. Talley. 1964. Gross morphology of tap roots of desert cucurbits. *Bot. Gaz.* 125: 121 - 126.
- Donald, C. M. 1962. In search of yield. *J. Austr. Inst. of Ag. Soc.*, Sept., p. 171 - 176.
- Dornhoff, G. M. and R. M. Shibles. 1970. Varietal differences in net photosynthesis on soybean leaves. *Crop Sci.* 10: 42 - 45.
- Dornhoff, G. M. and R. M. Shibles. 1976. Leaf morphology and anatomy in relation to CO₂ exchange rate of soybean leaves. *Crop Sci.* 16: 377 - 381.
- Dossey, B. F., W. P. Bemis, and J. C. Scheerens. 1981. Genetic control of gynoecey in the buffalo gourd. *J. Hered.* 72: 355 - 356.
- Dreger, R. H. 1967. The effect of genotype on the photosynthetic rate of Glycine max. (L.) M.S. Thesis, Univ. of Minnesota, St. Paul, Minnesota.
- Dreger, R. H., W. A. Brum, and R. L. Cooper. 1969. Effect of genotype on photosynthetic rate of soybean (Glycine max. (L.) Men.) *Crop Sci.* 9: 429 - 431.

- Dreher, M. L., A. M. Tinsley, J. C. Scheerens, and J. W. Berry. 1983. Buffalo gourd root starch II: Rheologic behavior, freeze thaw stability for use in food products. *Starch/Stärke* 35: 157 - 162.
- Ehrler, W. L. and C. H. Van Bavel. 1968. Leaf diffusion, resistance, illuminance, and transpiration. *Plant Physiol.* 43: 208 - 214.
- El-Sharkawy, M. A. and J. D. Hesketh. 1964. Effects of temperature and water deficit on leaf photosynthetic rates of different species. *Crop Sci.* 4: 514 - 518.
- Evans, L. T., and R. L. Dunstone. 1970. Some physiological aspects of evolution in wheat. *Aust. J. Biol. Sci.* 23: 725 - 741.
- Fry, K. E. 1970. Some factors affecting hill reaction activity in cotton chloroplasts. *Plant Physiol.* 45: 465 - 469.
- Frydrych, J. 1976. Photosynthetic characteristics of cucumber seedlings grown under two levels of CO₂. *Photosynthetica* 10: 335 - 338.
- Gates, D. M. and L. E. Papias. 1971. In *Atlas of Energy Budgets of Plant Leaves*. Academic Press, New York.
- Gates, D. M., W. M. Heisey, H. W. Milner and M. A. Nabs. 1964. Temperatures of mimulus leaves in natural environments and in a controlled chamber. *Ann. Rep. Carnegie Institution of Washington Year Book*, 63: 418 - 430.
- Gathman, A. C. and W. P. Bemis. 1982. The History, Biology, and Chemistry of buffalo gourd, *Cucurbita foetidissima* H.B.K. In R. Robinson (ed.) *The Biology and Chemistry of The Cucurbitaceae*. Cornell University Press, Ithaca, New York, In Press.
- Good, N. E. and D. H. Bell. 1980. Photosynthesis, plant productivity and crop yield. p. 39. In Peter S. Carlson (ed.) *The Biology of Crop Productivity*. Michigan State Univ., Academic Press, New York.
- Heichel, G. H. and R. B. Musgrave. 1969. Varietal differences in net photosynthesis of *Zea mays* (L.) *Crop Sci.* 15: 516 - 518.

- Hofmann, W. 1982. The physiology of stressed and non-stressed sorghum. Ph. D. Thesis, University of Arizona, Tucson, Arizona.
- Hsiao, T. C. 1973. Plant responses to water stress. *Ann. Rev. Plant Physiol.* 24: 519 - 570.
- Huffaker, R. C., T. Radin, G. E. Kleinkopf, and E. L. Cox. 1970. Effects of mild water stress on enzymes of nitrate assimilation of carboxylative phase of photosynthesis in barley. *Crop Sci.* 10: 471 - 474.
- Irvine, J. E. 1975. Relation of photosynthetic rates of leaf and canopy characteristics to sugar cane yield. *Crop Sci.* 15: 671 - 676.
- Johns, G. G. and A. Lazenby. 1973. Defoliation, leaf area index and water use of four temperate pasture species under irrigated and dryland conditions. *Aust. J. Agric. Res.* 24: 783 - 795.
- Jones, H. C. 1973. Limiting factors in photosynthesis. *New Phytol.* 72: 1089 - 1094.
- Keuneman, F. A., D. H. Wallace, and P. M. Ludfort. 1979. Photosynthetic measurements of field-grown dry beans and their relation to selection for yield. *J. Amer. Soc. Hort. Sci.* 104: 480 - 482.
- Lange, O. L. 1959. Untersuchungen über Warmehaushalt und Hitzeresistenz mauretanischer Wusten- und Savannenpflanzen. *Flora* 147: 595 - 651.
- Lange, L. and R. Lange. 1963. Untersuchungen über Blattemperaturen Transpiration und Hitzeresistenz an Pflanzen mediterraner Standorte (Costa Brava, Spanien). *Flora* 153: 387 - 425.
- Leavitt, J. R. C., A. K. Dobrenz, and J. E. Stone. 1979. Physiological and morphological characteristics of large and small leaflet alfalfa genotypes. *Agro. J.* 71: 529 - 532.
- Linacre, E. T. 1964. Determinations of heat transfer coefficient of leaf. *Plant Physiol.* 39: 687 - 690.
- Lott, J. N. A. 1970. Changes in the cotyledons of *Cucurbita maxima* during germination. I. General characteristics. *Can. J. Bot.* 48: 2227 - 2231.
- Mahon, J. D., S. B. Lowe and L. A. Huni. 1975. Photosynthesis and assimilate distribution in relation to yield of cassava grown in controlled environments. *Can. J. Bot.* 54: 1322 - 1331.

- Milthorpe, F. L. and J. Moorby. 1974. An introduction to Crop Physiology. p. 202. In Plant Physiology. Cambridge Univ. Press, Cambridge, Mass.
- Miskin, K. E., D. C. Rasmusson, and D. N. Moss. 1972. Inheritance and physiological effects of stomatal frequency in barley. *Crop Sci.* 12: 780 - 783.
- Murata, Y. 1961. Studies on the photosynthesis of rice plants and its cultural significance. *Bull Nat. Inst. Agr. Sci. Series D.* No. 9. Nishigahara, Tokyo, Japan.
- Murata, Y., J. Iyama and T. Honma. 1966. Studies on the photosynthesis of forage crops IV. Influence of air temperature upon the photosynthesis and respiration of alfalfa and several southern type forage crops. *Proc. Crop Sci. Soc. Japan* 34: 154 - 158.
- Musgrave, R. B. and D. N. Moss. 1961. Photosynthesis under field conditions. I. A portable, closed system for determining net assimilation and respiration of corn. *Crop Sci.* 1: 37 - 41.
- Nelson, C. J., K. H. Asay, and G. R. Hoist. 1975. Relationship of leaf photosynthesis to forage yield of tall fescue. *Crop Sci.* 15: 476 - 478.
- Nelson, J. M., J. C. Scheerens, J. W. Berry and W. P. Bemis. 1983. Effect of plant density and planting date on root and starch production of buffalo gourd grown as an annual. *J. Amer. Soc. Hort. Sci.* 108: 198 - 201.
- Nie, C. H., J. G. Hull, K. Jenkins Steinbrenner and D. H. Bent. 1975. In Statistical Package for the Social Science. McGraw Hill, Inc. N.Y.
- Ojima, M. 1972. Improvement of leaf photosynthesis in soybean varieties (Japanese, English summary). *Bull. Natl. Inst. Agric. Sci. (Japan) Series D.*, No. 23, p. 97 - 154.
- Osment, J. V. 1978. Photorespiration, apparent photosynthesis, specific leaf weight and leaf anatomy of selected alfalfa (Medicago sativa L.) clones. M. S. Thesis, University of Arizona, 1978.
- Parkhurst, D. F., O. L. Loucks. 1970. Optimal leaf size in relation to environment. *J. Ecol.* 60: 505 - 537.
- Paur, Sherman. 1952. Four native Mexican plants of promise as oilseed crops. New Mexico Agricultural Experiment Station, College of Agriculture and Mechanical Arts. Press Bull. 1064.

- 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.
- Peet, M. M., A. Bravo, D. H. Wallace, and J. R. Ozbun. 1977. Photosynthesis, stomatal resistance and enzyme activities in relation to yield of field-grown dry bean varieties. *Crop Sci.* 17: 287 - 293.
- Plaut, Z. 1971. Inhibition of photosynthetic carbon-dioxide fixation in isolated spinach-chloroplasts exposed to reduced osmotic potentials. *Plant Physiol.* 48: 591 - 595.
- Rogers, C. A., R. D. Powell, and P.J.M. Sharpe. 1979. The relationship of temperature of stomatal aperture and potassium accumulation in gourd cells. *Plant Physiol.* 63: 388 - 391.
- Saeki, T. 1959. Variation of photosynthetic activity with aging of leaves and total photosynthesis in a plant community. *Bot. Mag. Tokyo* 72: 104 - 108.
- Santarius, K. A. 1967. Assimilation of CO₂, NADP and PGA reduction and ATP synthesis in intact leaf cells in relation to water content. *Planta* 73: 228 - 242.
- Santarius, K. A. and R. Earnst. 1967. Hill reaction and phosphorylation of isolated chloroplasts in relation to water content 1. Removal of water by means of concentrated solutions. *Planta* 73: 91 - 108.
- Santarius, K. A. and U. Heber. 1967. Hill reaction and photophosphorylation of chloroplasts in relation to water content Part 2. Removal of water by CaCl₂. *Planta* 73: 109 - 137.
- Scheerens, J. C., W. P. Bemis, M. L. Dreher and J. W. Berry. 1978. Phenotypic variation in fruit and seed characteristics of buffalo gourd. *J. Am. Oil Chem. Soc.* 55: 523 - 525.
- Schulze, E. D., O. L. Lange, M. Evanari, S. Kappen, U. Buschbom. 1974. The role of air humidity and leaf temperature in controlling stomatal resistance of *Prunus armeniaca* (L.) under desert conditions. Part A. Simulation of the daily course of stomatal resistance. *Oecologia (Berl.)* 17: 159 - 170.
- Shahani, H. S., F. G. Dollear, K. S. Markley and J. R. Quinby. 1951. The buffalo gourd, a potential oilseed crop of the southwestern drylands. *J. Am. Oil Chem. Soc.* 28: 90 - 95.

- Shimshi, D. and J. Ephrat. 1975. Stomatal behavior of wheat cultivars in relation to their transpiration, photosynthesis, and yield. *Agron. J.* 67: 326 - 331.
- Sisson, W. B. 1981. Photosynthesis, growth, and U-V light irradiance absorbance of Cucurbita pepo (L.) leaves exposed to ultraviolet B-radiation (280 - 315 nm). *Plant Physiol.* 67: 120 - 124.
- Slavik, B. 1963. On the problem of the relationship between hydration of leaf tissue and intensity of photosynthesis and respiration. p. 390 - 406. IN A. J. Rutter and F. H. Whitehead (eds). *The water relations of plants.* Blackwell, Oxford.
- Slavik, B. 1965. The influence of decreasing hydration level on photosynthetic rate in the thalli of the hepatic Conocephallum conicum. p. 195 - 322. In B. Slavik (ed.) Water Stress in Plants. Proc. Symp. Prague, 1963. Czech. Acad. Scil, Prague.
- Smith, W. K. 1978. Temperatures of desert plants: another perspective on the adaptability of leaf size. *Science* 201: 614 - 616.
- Smith, W. K. and G. N. Geller. 1980. Leaf and environmental parameters influencing transpiration: Theory and field measurements. *Oecologia (Berl.)* 46: 308 - 313.
- Sullivan, C. Y., M. D. Clegg and J. M. Bennett. 1976. A new portable method for measuring photosynthesis. *Agron. Abstr.* p. 77.
- Sullivan, C. Y., N. V. Norico, and J. Eastin. 1977. p. 301 - 317. In A. Muhammed, R. Aksel, and R. C. von Borstel, (eds.). Genetic Control of Diversity in Plants. Plenum Co., New York.
- Sullivan, C. Y. and W. M. Ross. 1979. Selecting for drought and heat resistance in grain sorghum. p. 263 - 301. In Harry Mussel and Richard C. Staples (eds). Stress Physiology in Crop Plants. John Wiley and Sons, N.Y.
- Tatum, L. A. 1954. Breeding for drought and heat tolerance. p. 22 - 28. In W. Heckendorn and J. Joragory (eds.) Hybrid Corn. Hybrid Corn Ind. Res. Conf., Chicago. Pub. 9 Dec. 1 - 2, 1954.
- Teare, I. A. and E. T. Kanemasu. 1972. Stomatal-diffusion resistance and water potential of soybean and sorghum leaves. *New Phytol.* 71: 805 - 810.

- Tenhunen, J. D., O. L. Lange, M. Braun, A. Meyer, R. Losch and J. S. Pekeira. 1980. Midday stomatal closure in Arbutus unedo leaves in a natural macchia and under simulated habitat conditions in an environmental chamber. *Oecologia* 47: 365 - 367.
- Thompson, S. A., C. W. Weber, J. W. Berry, and W. P. Bemis. 1978. Protein quality of buffalo gourd seed and seed fractions. *Nut. Rep. Int.* 18: 515 - 519.
- Thorne, G. N. 1966. In F. L. Milthorpe and J. D. Ivins, (eds.) *The Growth of Cereals and Grasses*. Butterworths, London.
- Throen, J. H. and H. R. Koller. 1974. Influence of assimilate demand on photosynthesis, diffusive resistance, translocation and carbohydrate levels of soybean leaves. *Plant Physiol.* 54: 201 - 207.
- Turgeon, R. 1973. Leaf development and phloem transport in Cucurbita pepo: carbon economy. *Planta (Berl.)* 113: 179 - 191.
- Turner, N. C., J. E. Begg, H. M. Rawson, S. D. English, and A. B. Hearn. 1978. Agronomic and physiological responses of soybean and sorghum crops to water deficits. III. Components of leaf water potential, leaf conductance, 14 CO_2 photosynthesis and adaptation to water deficits. *Aust. J. Plant Physiol.* 5: 179 - 194.
- Vasconcellos, J. A., W. P. Bemis, J. W. Berry, and C. W. Weber. 1981. The buffalo gourd, Cucurbita foetidissima H.B.K., as a source of edible oil. *Ref. Amer. Oil Chem. Soc.* 9: 55 - 60.
- Vasconcellos, J. A., J. W. Berry and C. W. Weber. 1980. The properties of Cucurbita foetidissima seed oil. *J. Am. Oil Chem. Soc.* 57: 310 - 313.
- Verduin, J. and W. E. Loomis. 1944. Absorption of CO_2 by maize. *Plant Physiol.* 19: 278 - 293.
- Willmer, C. M. 1983. Stomatal responses to environmental factors which control stomata. p. 64 - 88. In D. A. Baker (ed.) *Stomata*. Longman, Inc., New York.