EVALUATION OF PHOTOSYNTHESIS AND ROOT RESPIRATION OF WINTER WHEAT (*TRITICUM AESTIVUM* L. EM. THELL)

By

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RESPIRATION OF WINTER WHEAT

(TRITICUM AESTIVUM L.

EM. THELL)

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CHAPTER I

INTRODUCTION

The wheat (Triticum aestivum L. em. Thell) improvement program at Oklahoma has several objectives, one of which is increased grain yield through improved plant metabolism. Identification of key metabolic systems in the plant that can be used in achieving this objective has been a major goal of the wheat physiology project. Increased photosynthetic efficiency and a technique for evaluating root respiration should improve grain yields. The following reports are on research conducted in these two areas.

Chapter II is a definition of developmental stages in winter wheat. This information is used in later reports in reference to when data were taken. It is based on plant growth with respect to management practices and is simplified with respect to other systems presently being used.

The next chapter describes the system used to measure leaf photosynthesis. A modification of a leaf chamber developed by others was used to study diurnal variation in photosynthesis of wheat (Clegg and Sullivan, 1976; Huber, 1978). It is used in conjunction with an infrared gas analyzer to determine changes in CO_2 concentration resulting from photosynthesizing leaves.

The fourth chapter uses the system described in Chapter III to examine possible cultivar differences in photosynthetic rates. Five cultivars of contrasting yield and morphological characteristics were

used. Apparent photosynthesis per unit land area was determined and compared with grain yield. Photosynthetic efficiency was also determined from the ratio of grain yield to net carbon exchange per unit land area.

Chapter V is a comparison of root volume and root dry weight of the same cultivars used in the previous report. Plants were hydroponically grown and data collected shortly after germination was complete. Root volume was determined by water displacement and dry weight by oven drying excised roots. Comparison of root growth data with grain yield from a field study was made.

Chapter VI evaluates three techniques for studying root respiration in young wheat plants. Ion specific electrodes, one for measuring CO_2 release and the other for measuring O_2 uptake from nutrient solutions were used. Infrared gas analysis was the third technique and was used to measure gaseous CO_2 release by roots. Data are based on root volume as determined using the system described in Chapter V. The same five cultivars used in the two previous studies were used in this study. Comparison of respiration data with grain yield from a 1980 field experiment was made.

The final chapter presents a brief summary of results obtained in Chapters II through VI. These chapters are written in a form acceptable for publication by the Agronomy Journal (A.S.A., 1976).

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CHAPTER II

KEY DEVELOPMENTAL STAGES OF WINTER WHEAT (*TRITICUM AESTIVUM* L. EM. THELL)

H. A. BRUNS

ABSTRACT

Winter wheat (*Triticum aestivum* L.) is important as both a forage and grain crop in the central and southern Great Plains. A simpler system of describing winter wheat developmental stages than those currently being used is needed. Ten key developmental stages are described: 1-germination and emergence, 2-tillering, 3-leaf strongly erect, 4-node formation, 5-boot, 6-heading, 7-flowering, 8-grain filling, 9-ripening, and 10-maturity. All stages can be visually identified in the field and are important with respect to grazing management, fertilizer applications, pest control, forage yield, and grain harvesting. Often no time factors can be placed on the occurrence of these stages due to environmental and cultivar differences.

A discussion of stress influences on grain and forage yield is included.

Additional index words: Growth stages, forage, grazing management, fertilizer applications, pest control, physiological maturity, tillering, grain filling.

In much of the Great Plains winter wheat (Triticum aestivum L. em. Thell) is utilized as both a forage and grain crop. Identification of key developmental stages is essential in managing wheat with respect to timing of fertilizer and pesticide application, grazing, and forage or grain harvest.

Growth stages for various crop species have been identified and are frequently cited in the literature. Hanway (1963), described eleven growth stages in corn (Zea mays L.) which could be visually identified in the field. Similar work on grain sorghum (Sorghum bicolor (L.) Moench) was later reported by Vanderlip and Reeves (1972). The authors described ten distinct growth stages for the species ranging from emergence to physiological maturity. Soybeans (Glycine max (L.) Merr.) have also been characterized with respect to their developmental stages, (Hanway and Thompson, 1967).

The Feekes Scale for growth stages in cereals is one of the more frequently quoted in describing wheat plant development, (Feekes, 1941; Large, 1963). Jensen and Lund (1971), also reported a general method of defining growth stages in cereals. A quantitative system of wheat growth stages was later presented by Haun (1973). Recently Waldren and Flowerday (1979), described eleven developmental stages in winter wheat and the distribution of dry matter, N, P, and K as it relates to those stages.

I propose ten key developmental stages in winter wheat with respect to management for maximum forage and/or grain yield. (Fig. 1) The purpose of this report is to identify these stages and explain their significance as applied to grain and forage production in the central and southern Great Plains. No attempt was made to place a time element

(days after planting) on their occurrence due to the influence of environmental factors and possible cultivar variation.

Stage 1. Germination and Emergence. (Fig. 2)

This stage begins with inbibition of water by the kernel and continues until all stored nutrients in the grain are exhausted by the juvenile plant. Rapid growth of the coleoptile and radicle will occur under favorable moisture and temperature conditions. Adequate levels of nutrients applied at or before seeding can be benefical to the crop at this time for improved seedling vigor. Early seeding at uniform rates can result in increased tillering which will maximize fall grazing. This can also improve grain yields by increasing the number of head bearing tillers per unit land area (Knapp and Knapp, 1978). The use of large sound kernels can be of benefit by supplying a greater quantity of organic nutrition to the seedling.

Stage 2. Tillering. (Fig. 3)

Rapid expansion of lateral meristems occurs during this stage. Too often more tillers are produced by an individual plant than will reach maturity (Evans, Wardlow, and Fischer, 1973). However, economic benefit can be realized from fall and winter grazing of the excess tiller production. Drought stress during this stage has been observed to reduce the number of tillers produced (Gardner, 1942). Increased seeding rates and reduction in rates of N fertilization can also lower tiller number per plant. Vernalization induced by cold temperatures usually occurs when plants are of this stage, though it can occur in plants at Stage 1 or 3.

Stage 3. Leaf Strongly Erect. (Fig. 4)

Increasing temperatures and day length in late winter and early spring result in a flush of vegetative growth. Leaf sheaths elongate and cells become very turgid. Stem growth appears to be present, but upon close examination the true stem will still be near the soil surface. Grazing may be continued through this stage although close attention should be given to the crop and animals removed prior to node formation if grain is to be harvested.

During this stage the forage will be low in fiber and have a high water content. Animal health problems such as grass tetany and wheat pasture poisoning are usually most prevalent during this stage. However, they may occur anytime there is active plant growth.

Stage 4. Node Formation. (Fig. 5)

In early spring, vernalized tillers begin elongating as a result of rapid cell expansion in the internodes. Leaf primorida have completed development and blades will begin protruding from the whorls of tillers. Cold hardiness, developed during earlier stages is rapidly being lost and plants become susceptible to freeze damage. Stress during this stage can adversely affect the number of florets per head. Frequently, lateral tillers produced late in Stage 2 begin aborting from the parent plant in the latter portion of this stage. Application of supplemental N fertilizer is often benefical prior to or during this stage by stimulating the rate and amount of vegetative growth, resulting in increased photosynthetic area. Insect control measures are often initiated during this time also. Green bug aphids (Toxoptera graminum (Rond.)) can be a severe pest to plants in this stage.

Stage 5. Boot. (Fig. 6)

All leaves have emerged from the whorl by this stage. Flag leaves will be prominent on spike-bearing tillers and their sheaths are enlarged by the emerging ear. Rapid cell expansion is still occurring in the peduncle and upper most internodes. Drought stress during this stage can result in a reduction of viable florets which were previously set. Peduncle length may also be reduced if stress is increased. Maximum forage yields for hay can be obtained during the latter part of the boot stage.

Stage 6. Heading. (Fig. 7)

The onset of this stage is marked with the emergence of spikes from the flag leaf sheath. It is during the early part of the heading stage that total leaf area will reach its maximum (Evans, 1975). Drought and heat stress during this time can be detrimental to grain production in much the same way as it is in the boot stage. Hay may still be harvested but quality is beginning to decrease rapidly. Fiber content of the plant is beginning to increase and nutritional value for hay or pasture has peaked. Loose smut (Ustilago tritici) can infest crops at this time. Infested grain should not be used for seed the following season.

Stage 7. Flowering or Anthesis. (Fig. 8)

Vegetative growth has ceased by this stage and heads have fully protruded from the flag leaf sheath. Drought and particularly heat stress during this time can be devastating to grain yield by destroying viable pollen and reducing kernel set. Harvest for hay may still be

done although nutritional value has decreased due to increasing fiber content.

Stage 8. Grain Filling. (Fig. 9)

This stage begins upon completion of pollination and terminates at physiological maturity. Lower leaves have usually deteriorated to the extent that only three to four leaves per tiller remain. The bulk of photosynthate produced during this period is translocated and stored in the developing kernels. Drought stress and feeding damage by insects can severely damage grain quality and result in shrunken kernels by reducing the length of time plants remain at this stage. Ensilage crops should be harvested near the end of grain filling in order to obtain a desirable quality feed.

Stage 9. Ripening. (Fig. 10)

Leaves have all deteriorated and the peduncle begins to yellow at the onset of this stage. This is often referred to as physiological maturity. Kernels have accumulated all available carbohydrates and begin to harden. They usually appear plump and are difficult to separate from the lemma and palea. Plants allowed to reach this stage of development should only be harvested for grain due to a high amount of fiber in the straw. Ensiling at this stage is generally unsuccessful due to low moisture in the straw.

Stage 10. Maturity. (Fig. 11)

Kernels are usually easy to separate from the lemma and palea. They are generally very hard and can only be broken with considerable

force. Awns on some bearded cultivars may become less compact. It is during this stage that rainfall may be damaging to the crop by inducing conditions favorable for stem decay and shattering loose kernels from the heads. Weed control may be necessary if harvest is delayed at this time. Moisture content of the grain must be below 12.5% to be safely stored. Straw generally has value only as a roughage in most ruminate rations.

In summary, all these stages are visible and can be determined readily. These are key developmental stages in wheat growth with respect to timing of management practices.

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Table 1. Characteristics of Developmental Stages in Winter Wheat

Stage		
	1.	Germination and Emergence
		Coleoptile of the plant becomes visible. Only one primary culm is present.
	2.	Tillering
		Tillers are visible.
	3.	Leaf Strongly Erect
		Leaves strongly erect. Pseudo stem present.
	4.	Node Formation
		Tillers begin elongating. Nodes can be felt near base of main culms.
	5.	Boot
		Flag leaf is fully extended. Tops of heads on main culm may be visible. Sheaths of flag leaves are enlarged.
	6.	Heading
		Heads are visible above flag leaf collar and peduncles continue to elongate.
	7.	Flowering
		Heads are fully extended. Anthers protrude from the glume and pollination is evident.
	8.	Grain Filling
		Head, flagleaf and stem are green. Lower leaves begin to yellow and die.
	9.	Ripening
		Grain is firm but difficult to remove from the head. Leaves have senesced and peduncle begins to yellow.
	10.	Maturity
		Kernels separate easily from the head and are hard.

Fig. 1. Diagram of Developmental Stages in Winter Wheat

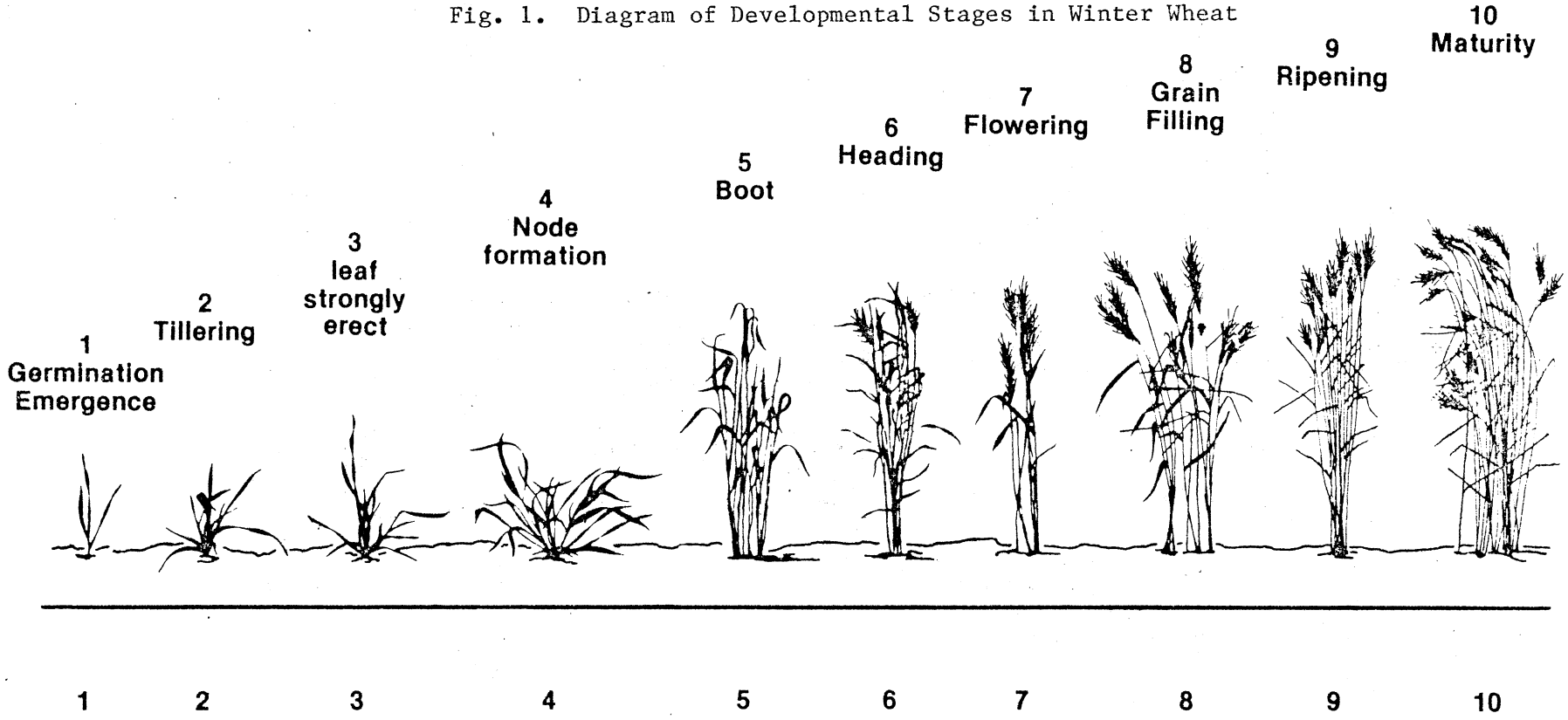

Fig. 2. Coleoptile and First 2-3 Leaves of Plant Appear.

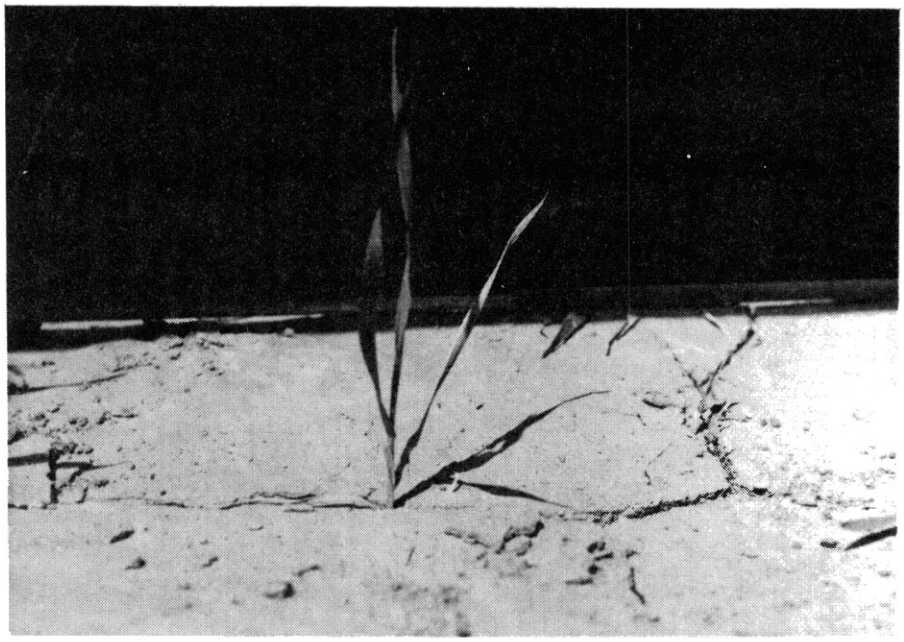

Fig. 3. Lateral Culms (Tillers) are Visible.

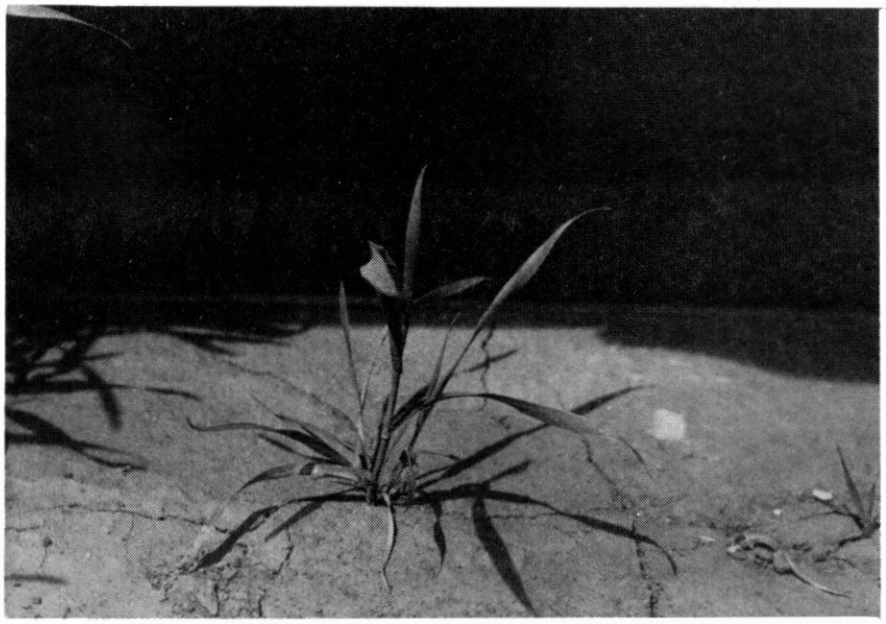

Fig. 4. Leaves Become Turgid and Stem Growth Appears to be Present.

Fig. 5. Tillers Begin Elongating and Nodes Can be Felt at About 2-3 cm Above Soil Surface.

Fig. 6. Flag Leaves are Fully Emerged and and Their Sheaths Appear Bloated.

Fig. 7. Heads Begin to Emerge.

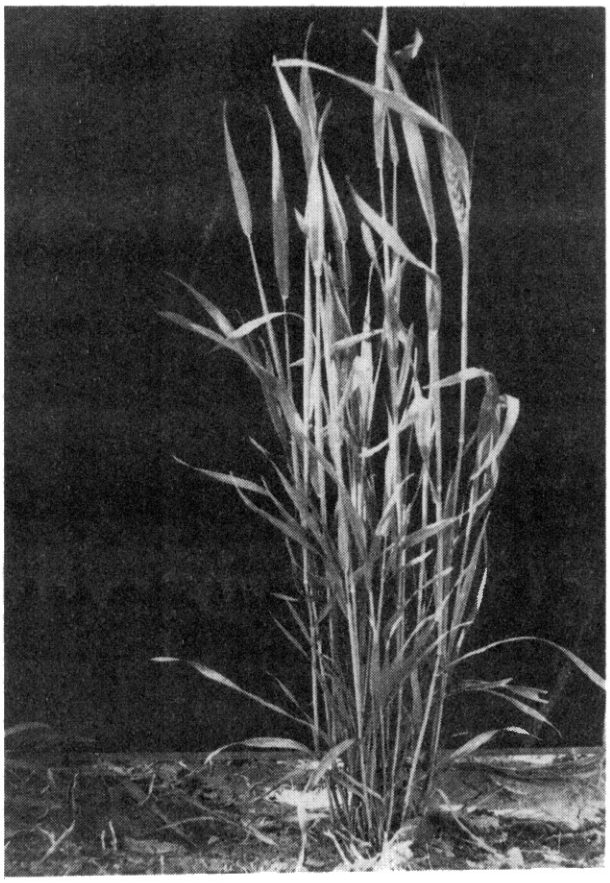

Fig. 8. Florets Protrude from the Glume.

Fig. 9. Head Begins to Enlarge and is Still Green Along With Flag Leaf and Stem.

Fig. 10. Leaves Have Deteriorated and the Penduncle Begins to Yellow.

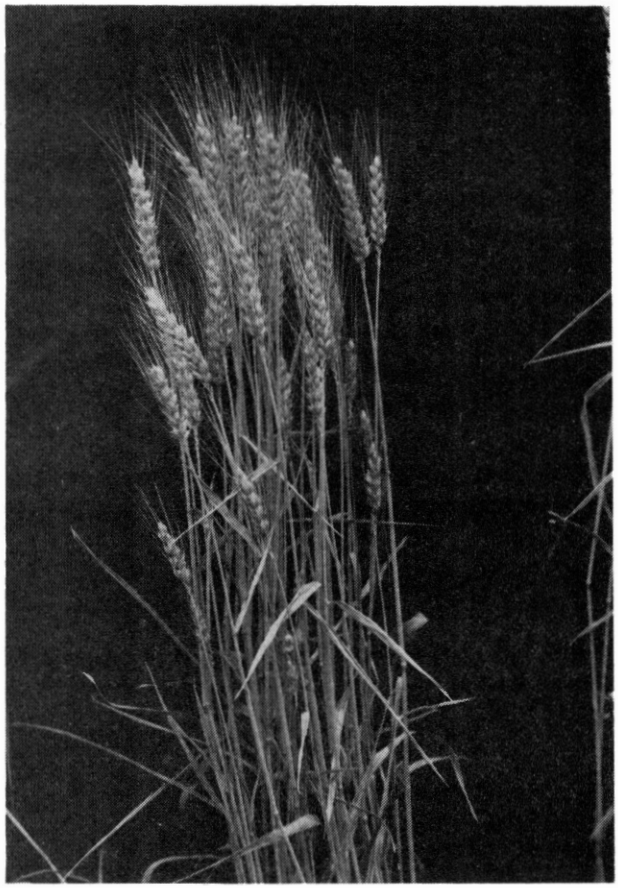

Fig. 11. Awns are Less Compact on Bearded Types and Kernels Separate Easily from the Head.

CHAPTER III

A LEAF CHAMBER FOR MEASURING DIURNAL VARIATION OF PHOTOSYNTHESIS IN WINTER WHEAT (*TRITICUM AESTIVUM* L. EM. THELL)

H. A. BRUNS

ABSTRACT

Previous leaf chamber designs used to evaluate photosynthesis through infrared gas analysis have limited the system's flexibility. A design is described that eliminates the need for transporting the analyzer to the field and allows repeated measurements. A study on diurnal variation was conducted to test the chamber's usefulness in taking repeated measurements on the same leaf. Three flag leaves were selected at random daily and evaluated for net carbon exchange. The study was conducted for three days. Rates of apparent photosynthesis increased rapidly in early morning then declined after 9:00 AM CST. Rates increased slightly again after 12:00 noon but then generally declined the remainder of the day.

Additional index words: Infrared gas analysis, net carbon exchange, apparent photosynthesis.

The use of infrared gas analysis for evaluating photosynthesis is well established. Several systems for obtaining data in the field from intact plants have been employed. Wolf et al. (1969), described a gas sealed leaf chamber that required a continuous flow of air of known CO_2 concentration. A modification of this chamber was later employed by Nelson et al. (1974), for evaluating photosynthesis in tall fescue (Festuca arundinacea Schreb.).

This system has disadvantages in that it requires transporting the analyzer and other instrumentation to the field. Considerable time can be consumed in the process and damage to delicate components can occur. Electricity necessary to power the equipment may also be difficult to obtain and can restrict the experimental location.

Clegg and Sullivan (1976), reported a chamber design that eliminated the need for transporting expensive instrumentation to the field. Their system used an air tight box chamber constructed of clear acrylic. The chamber hinged in the middle and the two chamber halves carefully fitted around the blade of a grain sorghum (Sorghum bicolor (L.) Moench) leaf. Photosynthesis was evaluated by measuring the change in CO_2 concentration inside the chamber before and after exposure to sunlight. To accomplish this, two gas samples (one before exposure and one after), were taken from inside the chamber by means of hypodermic syringes. The syringes were then transported to the lab and CO_2 content of the samples analysed by infrared gas analysis. Net carbon exchange was determined by relating the differences in CO_2 concentration to the surface area of the leaf tissue inside the chamber and the length of time it was exposed to light.

A later modification of this system proved successful for Huber (1978), in evaluating net carbon exchange in winter wheat (Triticum asetivum L. em. Thell). Huber's system used an air tight chamber constructed of clear acrylic tubing open at both ends and sealed with split rubber stoppers that were carefully fitted around a wheat leaf blade. For this system a balloon was attached to the under side of the chamber to serve as a reservoir of air and prevent outside air from being pulled inside during the sampling process. Photosynthesis was measured in much the same manner as that described by Clegg and Sullivan (1976).

Though Huber's (1978), system does eliminate the need for transporting a large amount of equipment to the field, it does have the disadvantage of being time consuming. An average of five minutes is required to affix a leaf blade and sample the internal gas. Also, a high vacuum grease is required to finish sealing the splits in the stoppers once the leaf is in place. This has been found to be phytotoxic to the leaf tissue and does not allow repeated measurements on the same blade over an extended period of time. For these reasons a second modification of this chamber was needed to extend the system's flexibility and reduce sampling time. A study is reported on diurnal variation of photosynthesis in wheat using the chamber.

MATERIALS AND METHODS

Clear acrylic tubing measuring 2.54 cm outside diameter is first cut into 6 cm segments (Fig. 1). Ends of the tubing are polished and 2.54 X 2.54 X 0.3 cm squares of acrylic are cemented to each end. Chloroform or other suitable solvent may be used to make the bonds.

Once the bonds have thoroughly dried the tubing is carefully cut into two halves. Handles constructed of 6 mm thick acrylic are then bonded to the chamber. Each handle is in two separate pieces, with each piece cemented to one half of the chamber. The lower portion of the handle spans the length of the chamber at the point of attachment and is flush with the end of the tubing. The top portion must be cemented to the chamber at an angle in order to assure a good seal between the two chamber halves. To obtain an air-tight seal, pieces of weather stripping are cemented on the cut edge of both chamber halves. A hinge mechanism, constructed of small pieces of acylic, is bonded to both handle halves. A spring mechanism is then placed in the handle between the chamber and the hinge. Tension can be adjusted by a wingnut just above the spring. Holes through the handle need to be larger than the bolt so the chamber can be opened and closed easily.

A small hole is drilled midway in the top half of the leaf chamber to accomodate a small ampul stopper from which to collect gas samples. Another hole is drilled in the bottom half and a small piece of 1.5 cm acrylic tubing cemented over it so a balloon can be attached.

In order to prevent photosynthesis during attachment of the chamber to a leaf blade, a sunshade constructed of light weight aluminum is placed over the upper half of the chamber. The sunshade is covered with

black electrical tape on the underside and is permanently attached to the chamber. A hinge allows the shade to be readily folded back so the leaf tissue may be exposed to light.

To test the chamber's effectiveness on repeated measurements, a study on diurnal variation of photosynthesis in wheat was made. The study was conducted on the cultivar Scout 66 which was growing in the field on the Agronomy Research Center at Stillwater, Oklahoma in 1981. Three tillers were selected at random on three separate days and carbon exchange measurements begun shortly after sunrise (6:00 AM CST). Measurements were taken on an hourly basis using the flag leaves and continued until dusk (7:00 PM CST). This procedure was conducted on May 11, 14, and 18, 1981. Plants were in Stage 8 as defined in an earlier report (Bruns, 1981).

Gas samples from inside the leaf chamber were taken using 10 cc hypodermic syringes. Sample size for each was 6.0 cc. Five cubic centimeters of gas from each syringe was injected into a Beckman Model 865 Infrared Gas Analyzer via a stream of lamp grade nitrogen gas flowing at 1 liter min^{-1}. A Beckman Model 1005 chart recorder was used to record data. Photosynthesis was determined by the following equation:

$$NCE = \frac{ppm * C * V}{A*T}$$

where:

NCE=Net carbon exchange

ppm=Sample 1 ppm CO_2 minus Sample 2 ppm CO_2

C=constant conversion factor (0.0109 $mgdm^{-2}hr^{-1}$)

V=volume of chamber(ml)

A=area of leaf in cm^2

T=time of exposure in minutes.

Area of leaf segments were determined after each day using a LI-COR LI 3000 leaf area meter. Light levels were monitored during sampling using a LI-COR quantium meter with sensor.

RESULTS

The portable leaf chamber is easy and inexpensive to construct. Time required to sample an individual leaf blade for net carbon exchange is approximately two minutes. In field experiments one person can sample 30 individual leaves an hour thus, reducing varibility that might be introduced by changing sun angle, temperature, or other environmental factors. Because of the small amount of equipment required to take field samples with this system, less time is needed in preparation than with others. By not having to move the infrared gas analyzer and related equipment the chance of damage to expensive instruments is greatly reduced.

Another advantage to this system is the increased utility of the infrared gas analyzer. With systems in which the analyzer is transported to the field, data on one study are all that can be collected within a given time. By using the portable leaf chambers data have been collected on as many as four different studies concurrently, limited only by the number of chambers and personnel available.

Repeated measurements on a leaf blade are possible with this chamber. No visible damage was observed on individual blades sampled for diurnal variation in net carbon exchange. Blades remained turgid throughout the day and no crushed cells were noticed. Standard deviation of the means for individual times ranged from 0.37 to 0.76 (Table 1). These compare with a standard error of 1.47 on data from tall fescue using a continous flow system (Nelson, et al., 1974).

Light levels during the study were constant on all three days. At 6:00 AM levels were found to be approximately 600 $\mu Em^{-2}sec^{-1}$. By 7:00 AM light levels were up to 2000 $\mu Em^{-2}sec^{-1}$ and remained steady until

6:00 PM. A decrease to 1000 $\mu Em^{-2}sec^{-1}$ was then observed and by 7:00 PM readings were approximately 500 $\mu Em^{-2}sec^{-1}$.

Apparent photosynthesis was low at 6:00 AM then rapidly increased by 7:00 to 10.92 $mgCO_2dm^{-2}hr^{-1}$ (Fig. 2). Net carbon exchange peaked near 8:00 AM at 12.50 $mgCO_2dm^{-2}hr^{-1}$ but begin declining by 10:00 AM. A decline to 9.27 $mgCO_2dm^{-2}hr^{-1}$ was observed at 11:00 AM. Rates remained steady until 1:00 PM then declined the rest of the day. Water was not considered a factor as substantial rainfall occurred just two days prior to the study. However, diffusive resistance measurements were not taken to verify leaf water potential. Possible product or feed back inhibition of the carboxylating enzymes or other systems are probably resulting in a decrease on net photosynthesis.

CONCLUSIONS

Various types of leaf chambers have been developed for measuring photosynthesis using infrared gas analysis. Some require transporting the analyzer and other equipment to the field which limits the system's usefulness. A modification of a portable chamber designed by Huber (1978), for use in winter wheat reduces time required for making measurements of apparent photosynthesis to two minutes per sample.

A study of diurnal variation in winter wheat net carbon exchange was conducted to test the design's effectiveness at repeated sampling on the same leaf. Three tillers of the cultivar, Scout 66, were randomly selected each day. The study was conducted for three days, beginning at 6:00 AM CST. Gas samples were taken hourly throughout the day.

Rates of net carbon exchange increased rapidly from first light until 8:00 AM CST. A decline began after 9:00 AM and continued until 12:00 noon. A steady state in apparent photosynthesis was observed until 1:00 PM followed by a general decline for the remainder of the day. Possible product or feed back inhibition of the carboxylating enzymes or some other system in photosynthesis is probably responsible.

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TABLE 1

DIURNAL VARIATION IN PHOTOSYNTHESIS
OF WINTER WHEAT

Time (CST)	Net Carbon Exchange[1] $mgCO_2dm^{-2}hr^{-1}$	Standard Deviation of Mean Value
6:00 AM	3.38	0.59
7:00 AM	10.92	0.55
8:00 AM	12.50	0.37
9:00 AM	12.42	0.48
10:00 AM	10.70	0.56
11:00 AM	9.27	0.38
12:00 Noon	9.44	0.73
1:00 PM	9.81	0.74
2:00 PM	8.05	0.51
3:00 PM	8.67	0.76
4:00 PM	7.06	0.72
5:00 PM	6.92	0.73
6:00 PM	5.25	0.67
7:00 PM	2.30	0.41

[1]Mean of three tillers selected at random daily for three days.

Fig. 1. Leaf Chamber for Measuring Photosynthesis of Winter Wheat Leaf Blades Using Infrared Gas Analysis.

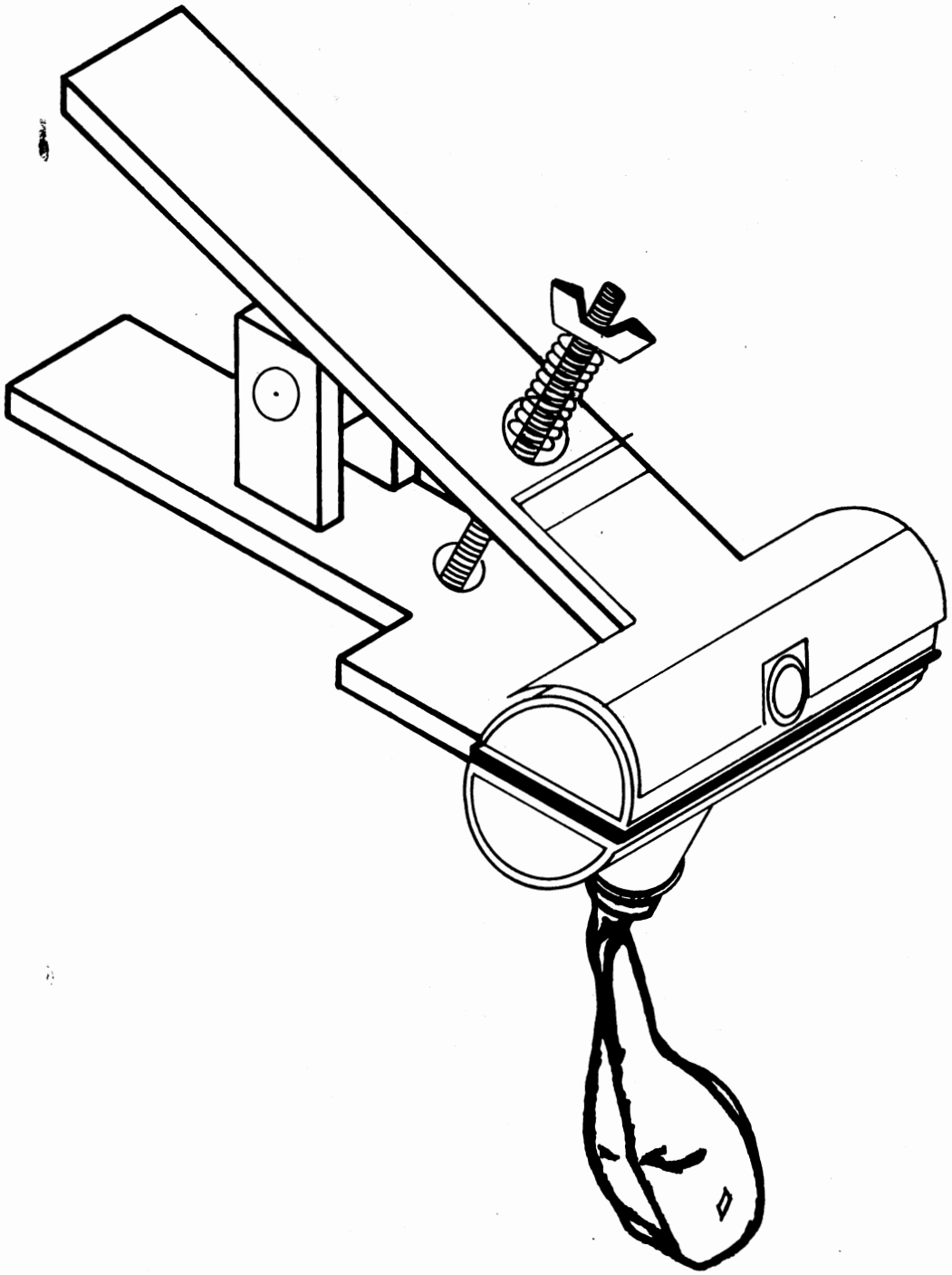
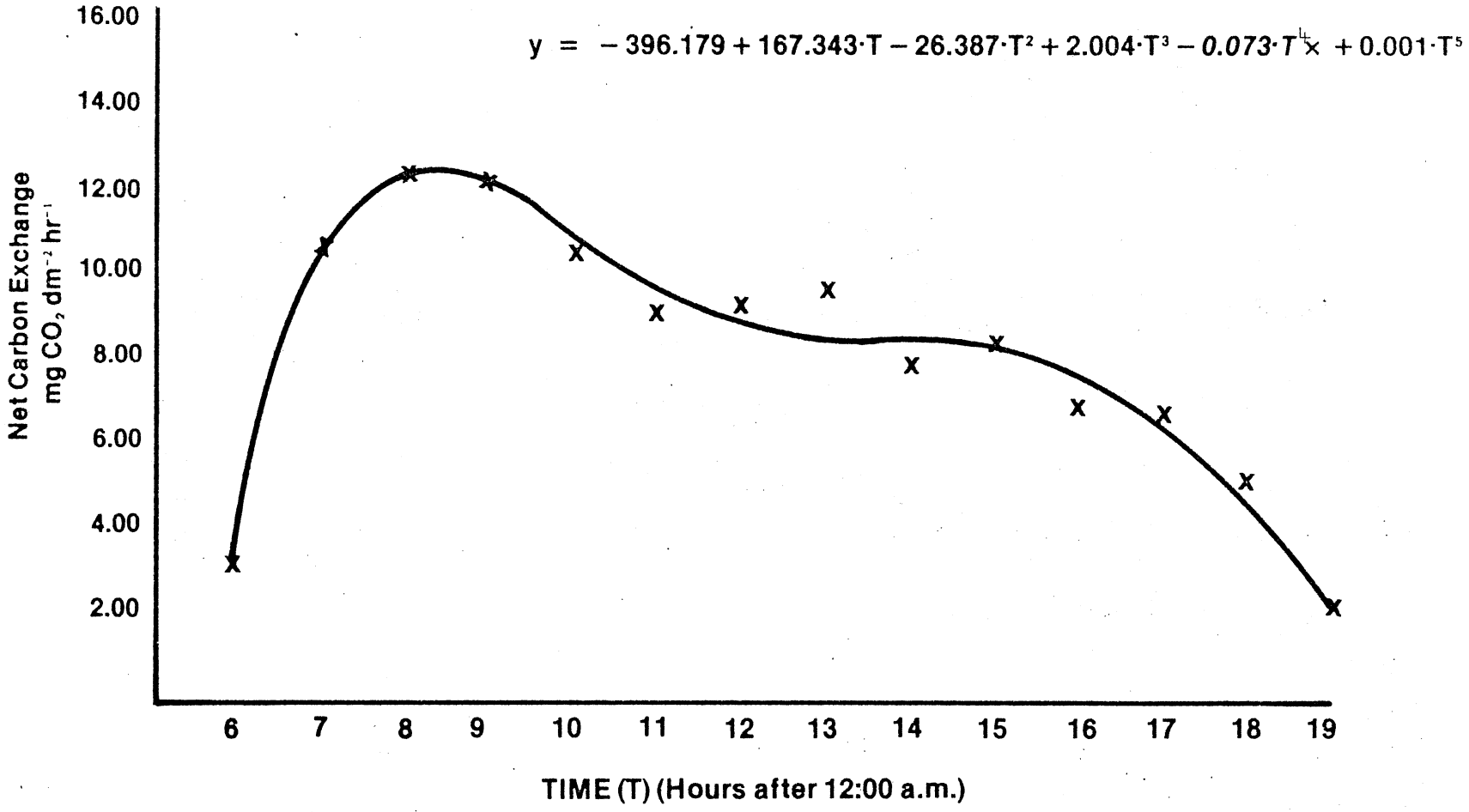


Fig. 2. Diurnal Variation in Photosynthesis of Winter Wheat (Triticum aestivum L. em. Thell)



CHAPTER IV

EVALUATION OF PHOTOSYNTHETIC EFFICIENCY IN WINTER WHEAT (*TRITICUM AESTIVUM* L. EM. THELL)

H. A. BRUNS

ABSTRACT

Five winter wheat cultivars were evaluated for photosynthetic activity using infrared gas analysis in field and growth chamber studies. Photosynthetic efficiency was determined by the ratio of fixed CO_2 contained in the grain to net carbon exchange per unit land area. Mean net carbon exchange per unit leaf area failed to be significantly different among cultivars in both field and growth chamber experiments. Thus, no relationship to grain yield could be established. Net carbon exchange per unit land area did yield significant differences across cultivars but no relationship to yield was observed. Photosynthetic efficiency differed significantly among cultivars. High grain yield was not necessarily associated with high NCE per unit land area. Further study into source-sink relationships is needed before improvements in grain yield through increased photosynthesis can be made.

Additional index words: Infrared gas analysis, net carbon exchange, leaf area index, wheat grain yield.

Several researchers have suggested increased economic yields of C_3 crops by elevated rates of photosynthesis. This was concluded by Krenzer and Moss (1975), from research with wheat (Triticum aestivum L. em. Thell). They reported that a screening procedure to classify wheat genotypes based upon their rates of photosynthesis would probably benefit a breeding program aimed at increased yields. Shibles and Weber (1966), reported three approaches to maximize soybean (Glycine max (L.) Merrill) seed yields; two of which were increasing the efficiency of utilization of intercepted solar radiation and selecting for a greater diversion of photosynthesis to seed production. Brun and Cooper (1967), also suggested that improved soybean yields could possibly be obtained by selecting cultivars with increased photosynthesis.

Increased rates of photosynthesis by either CO_2 enrichment or increased light intensity, has resulted in greater economic yields of several C_3 species. A yield increase of 43% in wheat was observed by Gifford (1977), when plants, growing in a growth chamber, were subjected to a CO_2 concentration 65% greater than ambient. Cooper and Brun (1967) found that by increasing CO_2 levels from 350 to 1350 ppm, soybean seed yields were substantially increased. This improvement, they concluded, was due primarily to an increase in the number of pods per plant. Fischer and Aguilar (1976), reported improved grain yields in dwarf spring wheat grown in the field under elevated levels of CO_2. They concluded the greatest yield limitation by crop photosynthesis occurred two months preceding grain filling. During this time the number of grains per unit land area is being set according to their observations. Asana (1968), previously concluded that photosynthesis levels in early stages

of growth in wheat may be very important in determining number and size of heads per unit land area, with a resulting influence on grain yield. Krenzer and Moss (1975), reported increases in kernel weights and kernels per plants in wheat grown in a CO_2 enriched environment. However, their data showed no improvement in these yield components occurred until floral development.

Light levels below those of full sunlight have been demonstrated to be detrimental to photosynthesis and thus yield. Asana' et al. (1969), reported decreases in grain yield and sugar content of wheat with decreasing light levels. These findings were in agreement with those of Pendleton and Weibel (1965) who reported, that with varying degrees of shading, correlated reductions in yield occurred. They concluded light was very critical during heading and that even slight reductions in intensity for short periods could reduce yields.

A relative increase in rate of leaf emergence and tillering in wheat was observed by Friend (1965), as light intensity was increased from 200 fc to 2500 fc. Though its influence on yield was not reported the increase in tillering could conceivably improve grain yield by resulting in more spikes being produced per unti area. Soybean yields have been shown to benefit from supplemental lighting. Johnston, Pendleton, Peters, and Hicks (1969), found the lower one-third of the canopy produced 30% more seed when exposed to supplemental light.

Leaf photosynthesis is the ultimate factor involved in crop yield. Some researchers have investigated possible differences in photosynthesis across cultivars of several C_3 species. Osada and Murata (1965), reported relatively stable cultivar differences in photosynthesis of rice (Oryza sativa L.) in both young and mature tissue. Investigating

the influence of cold hardening on photosynthesis in wheat, Barta and Hodges (1970), found higher rates of net carbon exchange occurred in a more winterhardy cultivar. A spring cultivar, included for comparison, had a lower rate of photosynthesis than winter types when exposed to low temperatures.

Genotypic variation in photosynthesis of nine soybean cultivars was reported by Dreger et al. (1969). They found a large amount of variability existed in plant to plant observations within a cultivar. But, after adjusting for this they were able to distinguish significant differences in net carbon exchange among cultivars. Izhar and Wallace (1967), identified differences in net carbon exchange of several dry bean (Phaseolus vulgaria L.) cultivars. They concluded for this species, that the genetic mechanism controlling these differences is quantitative, that there may be relatively few genes involved in its control, and that there is some dominance for lower photosynthetic efficiency.

A few studies on rates of photosynthesis in wheat have been reported. Gale, Edrich, and Lupton (1974), found net carbon exchange to range from 12.4 to 19.2 $mgCO_2dm^{-2}hr^{-1}$ across eight cultivars of wheat. Using five winter wheat cultivars, Ruckenbauer (1975), found photosynthesis of the flag leaves at anthesis to range from 28.0 to 39.0 $mgCO_2dm^{-2}hr^{-1}$. He also found cultivars with the highest yield per spike had the highest rate of photosynthesis.

Information on efficiency of photosynthesis in winter wheat is limited. It is the purpose of this report to define procedures for determining photosynthetic efficiency and relate it to possible cultivar differences.

MATERIALS AND METHODS

General

Five winter wheat cultivars (Turkey, Bezostaia 1, Priboy, TAM-W101, and Hart), were selected for this study based upon their contrasting yield and morphological characteristics. Apparent photosynthesis was determined in both experiments by the rate of net carbon exchange (NCE) per unit leaf area using infrared gas analysis. The instrument used in this study was a Beckman Model 865 Infrared Gas Analyzer with a Beckman Model 1005, 10 inch Chart Recorder attached to permanently retain data.

Sampling air surrounding photosynthesizing leaves was accomplished by a technique described by Huber (1978). This system employed a portable air-tight leaf chamber that was affixed midway of the newest fully extended leaf. The leaf chamber used in this study was modified from one used by Huber (1978). A complete description can be found in an earlier report (Bruns, 1981b). During attachment of the chamber the leaf segment was covered to prevent photosynthesis or at least hold it at a very low level. A gas sample was withdrawn from the chamber by means of a hypodermic syringe. The cover was then removed and the leaf segment exposed to light for a specific time. Then a second gas sample was withdrawn.

Syringes containing gas samples were brought to the laboratory and injected into the infrared analyzer via a stream of lamp grade nitrogen for determination of CO_2 concentration. Flow rate of the nitrogen was adjusted to 1 liter min^{-1}.

Net carbon exchange for a leaf was calculated using the following formula:

$$NCE = \frac{\Delta ppm * C * V}{A * T}$$

where;

NCE=net carbon dioxide exchange

$$\Delta ppm = \frac{\text{ppm } CO_2 \text{ in sample 1 minus sample 2}}{\frac{[\text{ppm } CO_2 \text{ in sample 1 plus sample 2}]}{2}} * 350$$

C=constant conversion factor (0.0109 $mgCO_2dm^{-2}hr^{-1}$)
(based on change of 1 ppm CO_2 standard condition)

V=volume of gas in leaf chamber (cc)

A=leaf segment area cm^2

T=time in minutes

Based on data by Huber (1978) and random samples of air from the Agronomy Research Center mean CO_2 concentration of ambient air at the field site is 350 ppm. All data, therefore, were adjusted relative to this level.

Field Experiments

Five wheat cultivars were planted in 1979 and 1980 in randomized complete block designs with four replications on the Agronomy Research Center in Stillwater, Oklahoma. Soil type was a Abruptic Pachic Paleustolls (Kirkland silt loam). Plots were planted on November 12, 1979 and October 24, 1980 in four rows 4.3 m long with 30.5 cm between rows. Seeding rate for all cultivars was 114.4 $kgha^{-1}$ to insure sufficient stands. Supplemental irrigation was applied to the plot area prior to planting in 1980 and twice during the following spring due to drought conditions. Nitrogen fertilizer was applied in early spring both seasons.

Net carbon dioxide exchange measurements were begun in early spring at growth Stage 4, as defined in an earlier report (Bruns, 1981a). Measurements were continued through the remainder of the growing season on a weekly basis, weather permitting. Six sampling dates were completed both years, each beginning at 10:00 CST. The last fully extended leaf of three tillers, selected at random, from each plot were sampled. Sampled leaf segments were detached for area determination using a LiCor LI-3000 leaf area meter.

Data on leaf area index were obtained during mid-grain filling (Stage 8) (Bruns, 1981a). Data on kernels per spike and kernel weight were collected at maturity and total grain yield also obtained by harvesting a 2.4 m section of the two middle rows. Photosynthetic efficiency is defined as the ratio of fixed CO_2 contained in the grain to mean net carbon exchange per unit land area. Fixed CO_2 contained in the grain is assumed to be 90% of total dry weight based on data from Mitchell (1970). Mean net carbon exchange per unit land area was determined by:

$$\text{Mean } kgCO_2ha^{-1} = \text{Mean NCE } (mgCO_2dm^{-2}) * LAI$$

Growth Chamber Experiment

Five wheat cultivars were planted on October 14, 1980 and January 6, 1981 in 11 cm plastic pots filled with a 1:1 vermiculite-perlite mixture at the rate of six seeds per pot. Four weeks after planting stands were thinned to three plants per pot. The pots were arranged in randomized complete block designs with four replications in a W. H. Curtin Biotronette Mark III environmental chamber. Temperature varied with daily fluctuations in room temperature of the laboratory. An

initial sub-irrigation of half strength modified Hoagland's solution was applied at planting with follow-up topical irrigations of 50 ml weekly. Additional irrigations with distilled water were applied when needed.

Net carbon exchange measurements were taken at weekly intervals beginning when plants were six weeks of age and ending on the ninth week after which each experiment was terminated. Data were collected on the newest fully extended leaf of each plant. Area of sampled segments was estimated by measuring the width at mid-point and multiplying by segment length. Light level within the chamber during sampling was 200 μEm^{-2} sec^{-1}.

RESULTS

Differences in yield were observed only between Turkey and the other four cultivars. Turkey's grain yield was significantly lower at the 1% level of probability even though tiller number was not different other cultivars (Table 1). Data on kernel numbers per spike and kernel weight revealed Turkey to have a significantly lower kernel weight than the other four cultivars (Table 1). With respect to kernels per spike it was not significantly different from Hart, Bezostaia 1, or Priboy, but did produce slightly less. This combined with lower kernel weight was responsible for its low yield. TAM-W101 was significantly (at the 1% level) lower in kernels per spike than the others. But, it tillered more than all others and produced heavier kernels which helped to stabilize its yield. Hart is a soft red wheat, containing more starch and less protein, thus it would be expected to have a low kernel weight compared to most hard cultivars.

Data on net carbon exchange per unit leaf area failed to show significant differences among cultivars in both field and growth chamber experiments. No consistant relationship was observed in either field or growth chamber data nor could conclusions be drawn from it with respect to grain yield. No cultivar by date of sampling interaction was found significant in any experiment. Using Stein's two stage sampling procedure, the number of sampling dates could have been reduced to four and maintained a standard error among cultivars of $\pm$ 0.75 $mgCO_2dm^{-2}$ with 95% confidence. Variation between dates of sampling was significant at the 1% level in all experiments. But, upon examination of weather data these tend to be related to rainfall periods in field experiments. In

the growth chamber experiments it is probably related to ambient CO_2 concentrations within the laboratory. Variation probably occurred due to the differences in numbers of people near and in the lab on various days. Random samples of ambient air during the study showed CO_2 levels to range from approximately 375 ppm to 900 ppm.

Yield, the result of photosynthesis, is commonly expressed in terms of weight per unit land area. Thus, expressing photosynthetic activity on a per unit land area basis may be more meaningful than expressing it on a per unit leaf area basis. Analysis of mean net carbon exchange per unit land area ($kgCO_2ha^{-1}$) revealed TAM-W101 to be significantly (at the 1% level) higher than three of the other cultivars (Table 2). The major contributing factor was a significantly (at the 5% level) higher leaf area index (LAI) for TAM-W101 (Table 2). Turkey also had a high LAI and was not significantly different from TAM-W101.

Bezostaia 1 was significantly lower in NCE per unit land area than TAM-W101 or Turkey. Again, leaf area index played a major role in determining this value. Judging from these data it would appear photosynthesis per unit land area may not be strongly related to grain yield.

Evaluation of photosynthetic efficiency revealed Hart to be significantly (at the 5% level) more efficient at translocating photosynthate to grain than all others tested except Bezostaia 1 (Table 3). Lower levels of protein and greater quantities of starch being stored in kernels probably contributed to this. Less energy input is required to produce a gram of long chained carbohydrate such as amylose or amylopectin than a gram of protein.

Turkey was significantly lower in photosynthetic efficiency than Hart or Bezostaia 1. Its low grain yield (see Table 1) combined with high NCE per unit land area (see Table 2) resulted in its low efficiency. Turkey is a tall statured cultivar making it subject to lodging as well as a poor yielder. For these reasons it is no longer grown commercially. An appreciable amount of photosynthate probably goes to stem growth and maintenance limiting the amount available for grain. In 1980, Turkey severely lodged just before maturity which contributed to its low yield that year. It was also generally 5-7 days later in maturing than the other four cultivars.

TAM-W101 though significantly lower in photosynthetic efficiency than Hart, did not compare well with Priboy and Bezostaia 1. It had the highest rate of NCE per unit land area of all cultivars (see Table 2), but, yielded comparable to Hart, Priboy, and Bezostaia 1. At present it is one of the more popular cultivars in the southern Great Plains. It is a semi-dwarf that resists lodging. However, a large quantity of photosynthate appears to be going to other sinks beside developing kernels. Respiration necessary for cell maintenance may be a factor involved in using much of the photosynthate.

From these data it can be concluded that high rates of net carbon exchange, either on a per unit leaf area or land area basis, are not necessarily associated with high grain yields. Increasing photosynthesis without a corresponding increase or at least maintainance of efficiency will not result in increased yields. Further study into the mechanism of translocation of photosynthate from source leaves to developing grain is definitely needed. When the factors involved in translocation are better understood and controlled then improving grain yields with increased photosynthesis may be possible.

CONCLUSIONS

Five winter wheat cultivars were planted in field experiments for evaluation of photosynthesis and its relation to grain yield using infraed gas analysis. Growth chamber studies were also conducted for support of some conclusions. Data on apparent photosynthesis was reported on both net carbon exchange per unit leaf area and per unit land area. Yield and yield component data on kernels per spike and kernel weight were also collected from field experiments. Photosynthetic efficiency was defined as the ratio of grain yield to NCE per unit land area.

Data on NCE per unit leaf area of both growth chamber and field experiments failed to show any significant differences among cultivars. No relationship with grain yield could be determined from these data. Sampling dates differed significantly in NCE but no significant sampling date by cultivar interactions were noted. Four sampling dates are probably sufficient in determining possible cultivar differences. Differences between sampling dates were probably related to environmental factors such as soil moisture in field experiments and ambient CO_2 level for growth chamber studies.

Significant differences at the 1% level were observed across cultivars in data on NCE per unit land area. These appear directly related to differences in leaf area index as it is used in data determination. However, no relationship with grain yield was apparent in these either.

Data on photosynthetic efficiency showed significant differences at the 1% level among the cultivars. High grain yield was not necessarily associated with high efficiency. Hart, a soft red cultivar, was most

efficient probably because of the lower protein and higher starch content characteristic of these types. Less photosynthate is used to produce an equivalent weight of starch than protein. Turkey was found least efficient due to its relatively poor yield and high NCE per unit land area. An appreciable amount of its photosynthate is probably going for stem growth and cell maintenance due to its tall stature. Though not significantly different from Priboy or Bezostaia 1, TAM-W101 did not appear to compare favorably in efficiency.

In summary, it appears photosynthesis expressed as net carbon exchange per unit land area is more meaningful than on a per unit leaf area basis. Before improvements in grain yield through increased photosynthesis can be made, a better understanding of mechanisms controlling photosynthetic efficiency is required. More information on translocation of photosynthate from source leaves to developing grain is needed. Attempts at increasing grain yields through increased NCE may be futile unless efficiency is improved or at least maintained.

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LIST OF TABLES

TABLE 1

GRAIN YIELD, KERNELS PER SPIKE, AND KERNEL WEIGHT OF FIVE WINTER WHEAT CULTIVARS

Cultivar	Grain Yield (Q ha^{-1})	Kernels/Spike	Kernel Weight (mg)	Tillers/meter length of row
Turkey	26.8	28	35.8	210
Bezostaia 1	38.6	32	43.8	141
Priboy	40.2	30	45.5	173
TAM-W101	40.1	23	45.5	236
Hart	42.7	30	38.8	202
lsd @ 0.01	3.5	5	2.8	64

TABLE 2

LEAF AREA INDEX (LAI) AT MID-GRAIN FILLING AND NET CARBON EXCHANGE (NCE) PER UNIT LAND AREA OF FIVE WINTER WHEAT CULTIVARS

Cultivars	LAI	NCE ($kgCO_2ha^{-1}$)
Turkey	2.44	24.82
Bezostaia 1	1.69	17.23
Priboy	1.96	19.38
TAM-W101	2.66	28.15
Hart	2.04	20.56
	lsd @ 0.05 = 0.61	lsd @ 0.01 = 7.67

TABLE 3

PHOTOSYNTHETIC EFFICIENCY OF FIVE
WINTER WHEAT CULTIVARS

Cultivar	Grain CO_2:NCE
Turkey	108.9
Bezostaia 1	215.3
Priboy	196.3
TAM-W101	134.4
Hart	234.1

lsd @ 0.05 = 90.1

CHAPTER V

COMPARISON OF ROOT VOLUME AND ROOT DRY WEIGHT OF FIVE WINTER WHEAT (*TRITICUM AESTIVUM* L. EM. THELL) CULTIVARS

H. A. BRUNS

ABSTRACT

Information on root growth in winter wheat is limited. Five winter wheat cultivars were grown hydroponically until 12 days of age. Root volume was determined by water displacement and root dry weight was measured on excised roots dried at 70 C for 48 hrs. Significant differences (at the 1% level), were observed across experiments for both root volume and dry weight. These were probably due to slight age differences in plants when data were collected. Cultivars were also significantly different (at the 1% level) in volume and dry weight. Turkey, which was low in grain yield in 1980 field data, had significantly lower volume and dry weight values. Regression analysis of both parameters vs. yield showed a moderate relationship. Correlation of root volume and dry weight though did not yield conclusive information.

Additional index words: hydroponics, grain yield.

Much is still to be learned about root growth in our agronomic crops. Techniques for studying roots of plants grown in the field are difficult. Extracting roots from the soil is often destructive to the experimental site and usually results in extensive losses of root tissue. Musick et al. (1965), studied differences in root volume of corn (Zea mays L.) hybrids with contrasting root lodging characteristics. Plants were field grown then extracted from the soil and washed to remove foreign matter. They stated that some of the root tissue was undoubtedly lost before volume measurements were made using water displacement.

Hurd (1964), reported on a technique in which he grew wheat (Triticum aestivum L. em. Thell) in sloped boxes. A glass plate was used on the sloped side so he could observe the effects of soil cracking on root growth. In later work he used this technique to study the rooting patterns of seven spring wheat cultivars (Hurd, 1968).

Some work done on root growth has been conducted with hydroponically grown plants. Blum et al. (1977), studied root growth and morphogenesis in grain sorghum (Sorghum bicolor (L.) Moench) that was hydroponically grown. Data were collected on root volume, root length, and leaf area. They concluded plants having a larger leaf area are more likely to have a larger root volume.

Methods of evaluating root growth are varied. Root dry weight has been used in some studies. However, it is questioned whether this is a true measure of growth (McKee, 1967; Blum et al., 1977; Murphy and Long, 1979). McKee (1967), observed considerable changes in root volume:dry weight ratios of two varieties of tobacco (Nicotiana tobacum L.). In his study root volume:dry weight ratios ranged from 24:1 at two weeks

of age to 5:1 after 10 weeks. He concluded dry weight as a measure of total root quantity could be misleading. Blum et al. (1977), concluded that in grain sorghum, dry weight of seminal and adventitious roots do not appear to be a good basis for selection of improved rooting characteristics. Murphy and Long (1979), found for oats (Avena sativa L.) that root weight was only moderately correlated with root volume and root length.

Differences in root development across cultivars of various species are observed. Blum et al. (1977), compared hybrids and their parental lines. They found that hybrid grain sorghums developed a larger root volume than parental lines of similar leaf area and adventitious root length. In later work on grain sorghum, Jordan et al. (1979), concluded genetic varibility exists for growth within root systems. Musick et al. (1965), observed differences in root volume of corn genotypes when planting was delayed. Root volume decreased in lodging resistant hybrids as planting was delayed. Susceptable hybrids, on the other hand, showed no significant changes. Derera et al. (1969), found cultivars of spring wheat differed in size and distribution of roots produced. They stated that length per unit weight of roots needs improvement in order to develop more drought tolerant cultivars.

It was the purpose of this study to compare the root volume and root dry weight of five winter wheat cultivars in the early stages of growth. Plants were hydroponically grown and comparisons of these parameters with yield data from the field are made.

MATERIALS AND METHODS

Five cultivars of winter wheat (Turkey, Bezostaia 1, TAM-W101, Priboy, and Hart) were selected for this study. The study consisted of six growth chamber plantings each with five plants of each cultivar arranged in a 5 X 5 latin square. The study was conducted during the summer of 1980 in the Crop Physiology Laboratory of Oklahoma State University. Ten to twenty kernels of each cultivar were first germinated in approximately 300 mls of distilled water. Continuous aeration was supplied by an aquarium air pump with an air stone placed in the water.

After 4-5 days five healthy plants were selected for each cultivar and their roots suspended in half-strength modified Hoagland's solution. The modification consisted of doubling the calcium nitrate, tripling the monopotassium phosphate, and substituting 0.5M dibasic ammonium phosphate for monobasic. Twenty-five milliliter erlenmeyer flasks were used to contain the plants and solution. Flasks were covered with aluminium foil to prevent algae formation and chlorophyll development in the roots.

Plants were placed in a Percival Model E-54B growth chamber set at 24.0-15.5 C day-night temperature and received a 12 hr photoperiod. Nutrient solutions were changed every 48 hrs. At 12 days of age, plants were removed from the growth chamber and root volume determined by water displacement. Roots were then detached and placed in a drying oven set at 70 C for 48 hrs. Afterwards, dry weight was determined to the nearest 0.1 mg.

The chamber used for volume determinations was constructed of clear acrylic tubing 5 cm long and 3.8 cm in diameter (Fig. 1). One end of

the tube was cemented to a 5 X 5 cm flat piece of acrylic for a base. A tuberculin syringe, graduated in 0.01 cc, was inserted through an ampul stopper located in a hole drilled near the base of the chamber. The chamber top was covered by two flat pieces of acrylic 5 X 2 1/2 cm in size which served as a lid. Small notches were cut in one edge on each lid half to accomodate an intact plant. The chamber was filled with distilled water and the syringe drawn back. Plant roots were then placed in the chamber and the lid reclosed. Water in the syringe was forced back into the chamber to its original level. Remaining water in the syringe was interpreted as root volume.

RESULTS

Significant differences at the 1% level were observed for both root volume and root dry weight across plantings (Table 1). With respect to root volume, the major difference in the various means was between planting six and all others. The mean root volume for that planting was significantly higher. The mean value for planting three was significantly higher than planting five also. These differences are probably due to a slight variation of 4-6 hrs in age from planting to planting at the time measurements were made.

Mean values for root weight across plantings show two distinct differences. Mean root weight in planting one was significantly lower than all others and plantings five and six were significantly higher. Again, slight differences of a few hours in plant age may be a contributing factor. Root growth occurs as a result of both cell division and cell enlargement. In the process of cell enlargement the relative amount of dry matter, usually cellulose, tends to increase while the quantity of protoplasm remains constant. Differences in root dry weight across plantings is probably due to whether root growth occurred mostly as cell division or cell enlargement a few hours prior to harvest.

Cultivars were found signficantly different (at the 1% level) for both root volume and root dry weight (Table 2). Turkey was observed to be significantly lower in root volume than TAM-W101 or Hart. In root dry weight it was significantly lower than TAM-W101, Hart, and Priboy. Bezostaia 1 was also found to be significantly lower than TAM-W101 in root dry weight. Yield data on these cultivars from the Agronomy Research Center at Stillwater, Oklahoma in 1980, showed Turkey to be

significantly lower (at the 1% level) in yield than all others (Table 2). Though data from this study do not reflect root growth rates throughout the season, it is interesting to speculate that early trends in root growth may give clues as to a cultivar's performance. Regression analysis using the above mentioned yield data of root volume vs. grain yield and root dry weight vs. grain yield across varieties produced r=0.83 and r=0.73 respectively (Fig. 2 & 3).

Correlations of root volume and root dry weight did not show conclusive information. Across cultivars the relationship was high (r=0.96) (Fig. 4). However, across plantings there was only a moderate relationship (r=-0.69) (Fig. 5). Its negative r value probably resulted from data in planting five. The lowest mean root volume occurred in this planting. Yet root dry weight was higher than most. Probably considerable cell expansion and relatively little cell division had occurred prior to harvest. Thus, the major form of root growth was due to dry matter accumulation in this planting. Despite the above results, no significant planting X cultivar interaction was observed in either root volume or root dry weight data.

CONCLUSIONS

Five winter wheat cultivars were hydroponically grown and their root dry weights determined after 12 days of age. The cultivars were Turkey, Bezostaia 1, TAM-W101, Priboy, and Hart. Root volume was determined by water displacement and root dry weight after excised roots were oven dried at 70 C for 48 hours.

Significant differences at the 1% level were observed in both root volume and root dry weight across plantings. However, these differences were probably due to slight age differences of a few hours in plants at the time data were taken. Differences in the relative amount of cell expansion vs. cell division just prior to harvest probably contributed to differences in dry weight (Table 1).

Cultivars were found to be significantly different at the 1% level of probability in both root volume and root dry weight. When compared with yield data from a 1980 field experiment, it was found the cultivar with the lowest root volume and root dry weight was also lowest in grain yield. Regression analysis of these data showed a moderate correlation to exist.

No conclusive information was gained on correlations of root volume with root dry weight. Across cultivars there appeared a strong relationship ($r=0.96$). However, across experiments data were not strongly related ($r=-0.69$). According to Murphy and Long (1979), in oats there was only a moderate relationship of root volume with root dry weight. Further study of root growth throughout the growing season may result in a better understanding of its relationship to crop yield. A need still exists to determine which method, volume or dry weight, is better for measuring root growth.

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TABLE 1

ROOT VOLUME AND DRY WEIGHT OF FIVE WINTER WHEAT CULTIVARS ACROSS SIX PLANTINGS

Planting No.	Root Volume cm^3	Root Dry Weight (mg)
1	0.111	2.96
2	0.120	6.11
3	0.135	6.26
4	0.130	6.08
5	0.101	8.53
6	0.171	11.05
lsd .01	0.032	1.58

TABLE 2

ROOT VOLUME, DRY WEIGHTS, AND GRAIN YIELD OF FIVE WINTER WHEAT CULTIVARS

Cultivar	Root Volume cm^3	Root Dry Weight mg	Grain Yield[1] Q/ha
Turkey	0.106	5.59	28.2
Bezostaia 1	0.118	6.19	40.0
TAM-W101	0.139	7.82	38.9
Priboy	0.133	7.20	42.5
Hart	0.143	7.35	44.10
lsd @ 0.01	0.030	1.47	7.9

[1]Yield data from 1980 field study Agronomy Research Center, Stillwater, Oklahoma.

Fig. 1. Chamber for Measuring Root Volume in Winter Wheat

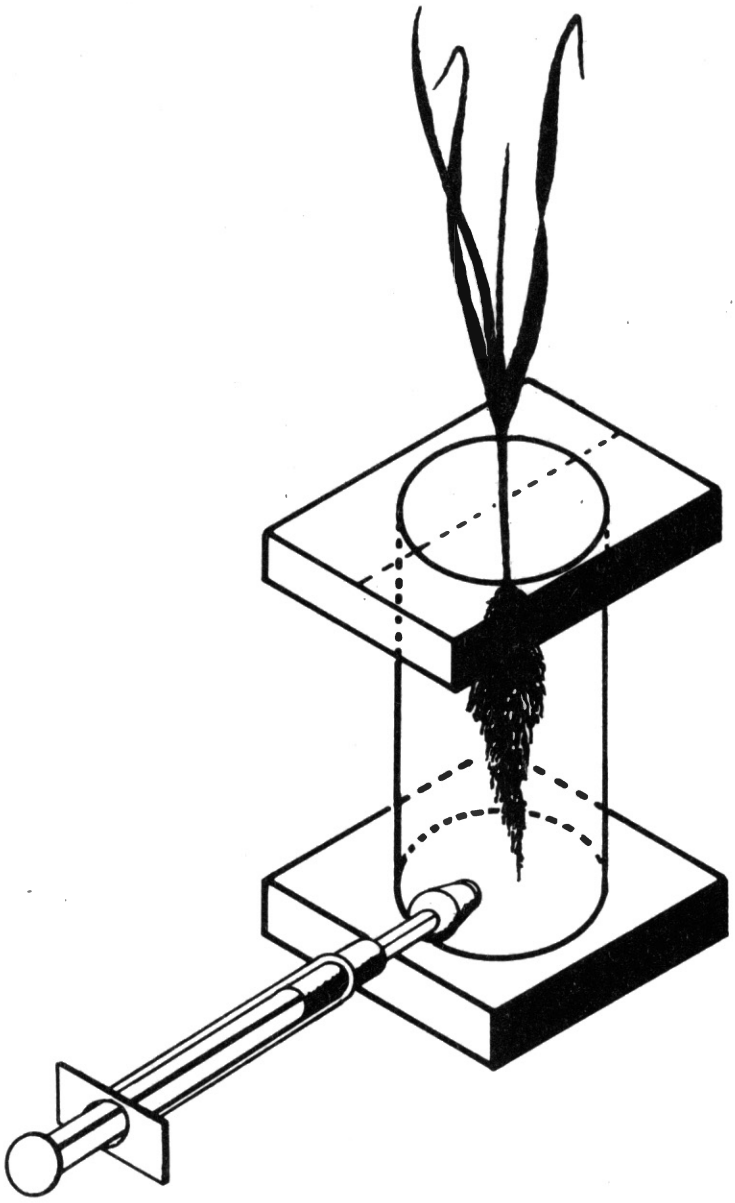
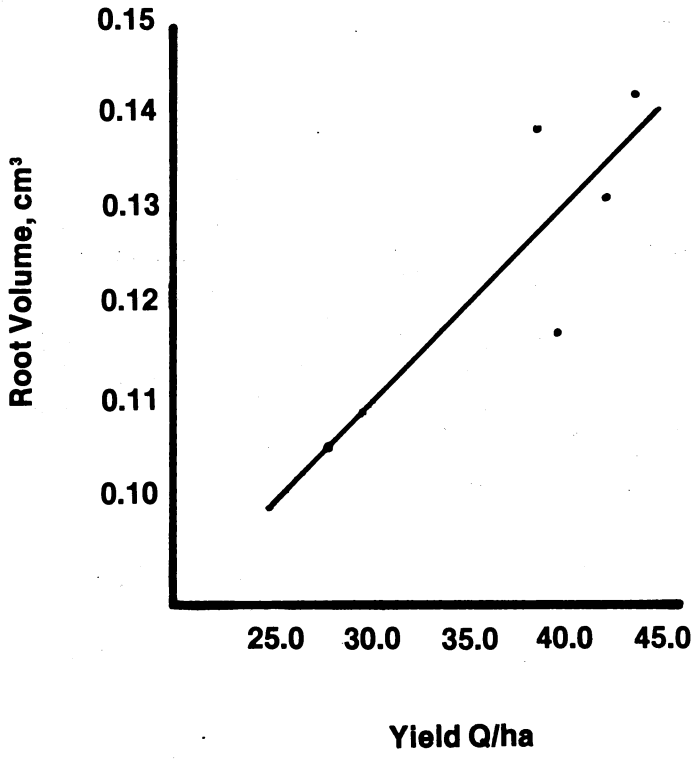


Fig. 2. Root Volume vs. Grain Yield of Five Winter Wheat Cultivars



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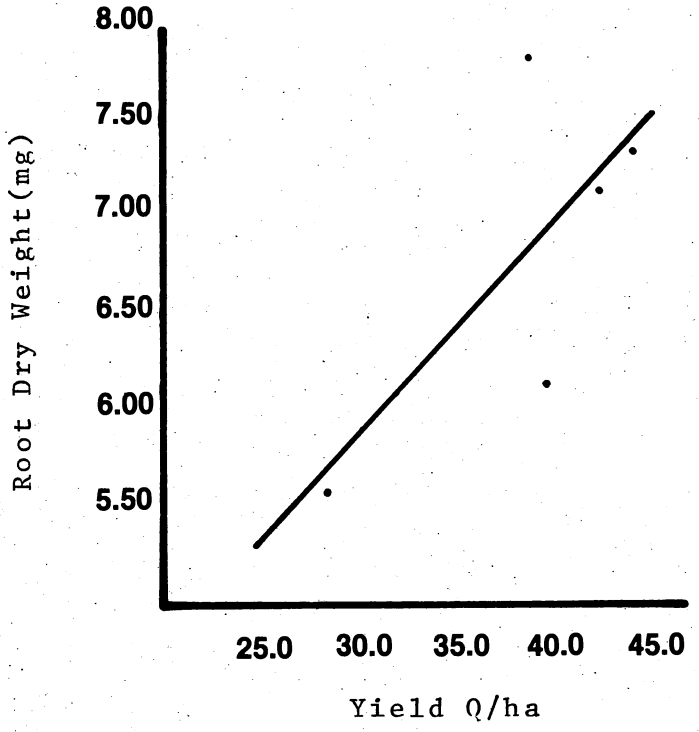
$r = 0.83$

Fig. 3. Root Dry Weight (mg) vs. Grain Yield of Five Winter Wheat Cultivars



$Y = 2.6624621 + 0.1076883.X$

$r = 0.73$

Fig. 4. Root Volume vs. Root Dry Weight Across Five Wheat Cultivars

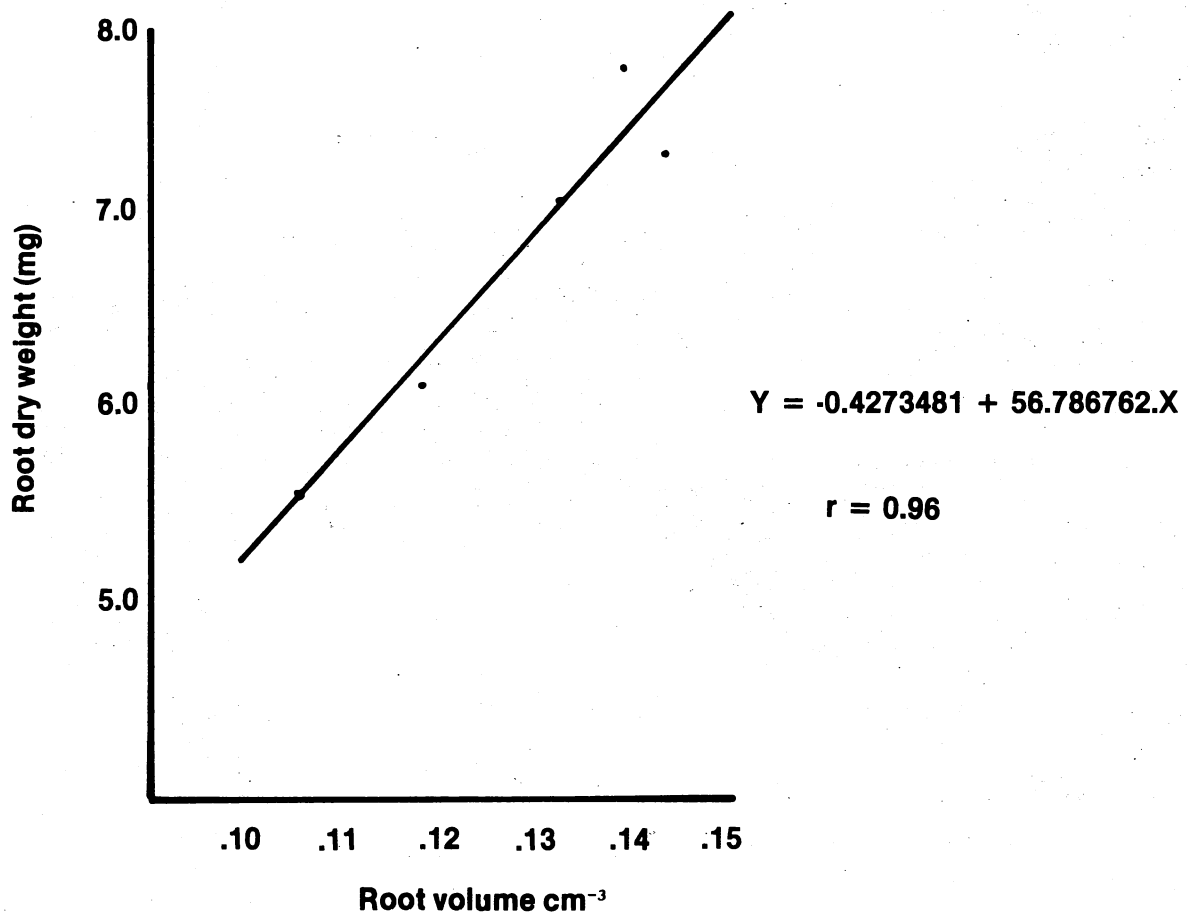
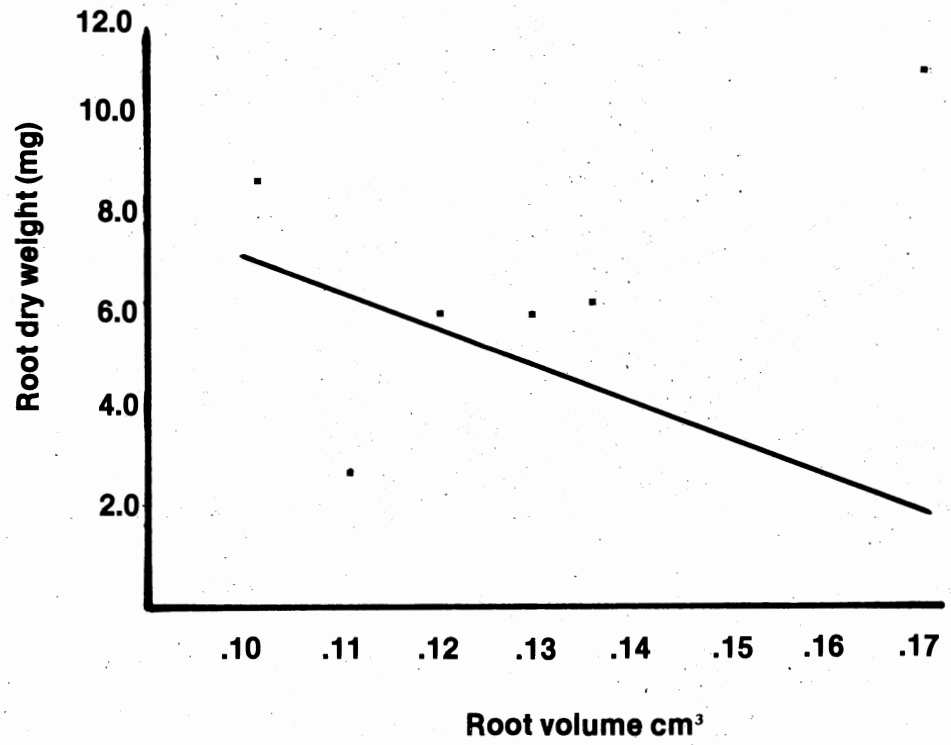


Fig. 5. Root Volume vs. Root Dry Weight Across Six Experiments of Five Wheat Cultivars



$Y = 14.854764 - 75.63982X$

$r = -0.69$

CHAPTER VI

TECHNIQUES FOR EVALUATING ROOT RESPIRATION IN WINTER WHEAT (*TRITICUM AESTIVUM* L. EM. THELL)

H. A. BRUNS

ABSTRACT

Root respiration in winter wheat is not well described. Three instruments, a carbon dioxide specific electrode, infrared gas analyzer, and galvanic electrode were used to evaluate root respiration rates on five hydroponically grown wheat cultivars. Four plantings were made for study of each instrument with three observations made on each planting. Respiration rates were found to decrease with increasing plant age. In the infrared gas analysis study and the galvanic electrode experiments cultivar differences in root respiration were observed. The cultivar with the highest rate or respiration was also the lowest in grain yield. All techniques were effective in measuring root respiration but need refinement.

Additional index words: Carbon dioxide specific electrode, galvanic electrode, infrared gas analyzer, hydroponics, root volume.

Roots play a vital role in production of economic yield. Hurd (1964, 1968), stated that a good root system was necessary for grain production in spring wheat (Triticum aestivum L. em. Thell) grown in droughty soils. He also described methods on evaluating root development in this crop. Roots absorb mineral nutrients and water for growth, they anchor the plant to the earth's surface, and in some species provide sites of storage for energy reserves. Because of difficulty encountered in obtaining field samples, studies on roots are limited. Destruction of both plants and soil profile at the experimental site forces most research on roots to be conducted in a laboratory with hydroponically grown plants.

Root respiration in plants is not well documented relative to other metabolic processes. Yet it is a vital process in production of economic yield and essentially the sole source of energy for root cells. Of the total carbon dioxide fixed by photosynthesis it has been estimated that in garden peas (Pisum sativium L.) 35% was respired into the soil profile as a result of cell maintenance. Another 7% was estimated to be used for root growth (Minchin and Pate, 1973). This was separate from the carbon dioxide respired by the root nodules formed by nitrogen fixing rhizobium.

Uptake of nutrient ions has been demonstrated to be closely linked to root respiration. Bange (1965), stated potassium uptake by roots of corn (Zea mays L.) was either directly or indirectly associated with metabolic energy. Assimilate supply to roots from photosynthesizing leaves has been demonstrated to affect ion absorption. Bowling (1968), observed a reduction in root respiration and potassium uptake when sunflower (Helianthus annus) plants were girdled, reducing the

translocation of soluble sugars downward. Nitrate uptake by Italian ryegrass (Lolium multiflorum) was observed by Hansen (1980), to closely correspond to diurnal variations in root respiration. Andre´ and others (1978), found corn root respiration rates to be slightly higher during daylight hours than at dark.

Factors that adversely affect root growth usually do so by impairing root respiration (Goss, 1973). Soils that are waterlogged or high in clay can restrict gas exchange and result in sub-optimal oxygen levels. The permeability of membranes is usually impaired. Adenosine triphosphate (ATP) produced during oxidative phosphorylation has been shown to be important in active transport across the plasmalemma (Goodwin and Mercer, 1972).

Methods used for evaluating root respiration are varied. Andre´ et al. (1978), evaluated root respiration in corn by measuring CO_2 production with infrared gas analysis. Plants were grown in nutrient culture and a controlled flow rate of air was bubbled through the culture. The resulting increase in CO_2 concentration of air was reported as $CO_2 ml hr^{-1}$. This method was similar to one employed by Hansen and Jensen (1977), for measuring whole plant respiration in Italian ryegrass. Their system consisted of a chamber separating the roots from the top growth and allowing continuous monitoring of respiration and photosynthesis. Their data were expressed as gCH_2O $pot^{-1} day^{-1}$ and based on daily gross photosynthesis. Lambers (1979), measured root respiration in several plant species by determining oxygen consumption of excised roots placed in nutrient solution. Oxygen consumption was determined over a thirty minute time span and reported in mg O_2/hrgm dry roots.

Little is known about root respiration in wheat and how it may relate to grain yield. It is the purpose of this research to investigate methods for such study. Instruments used are a carbon dioxide and galvanic electrode for measuring respectively CO_2 release and O_2 uptake and an infrared gas analyzer to measure gaseous CO_2 release. Possible cultivar differences are examined. Hydroponically grown plants were used in order to study the feasibility of repeated sampling.

MATERIALS AND METHODS

General

Five winter wheat cultivars (Turkey, Bezostaia 1, TAM-W101, Priboy, and Hart) were selected for these studies. In all plantings 10-20 kernels of each variety were first germinated in approximately 300 ml of distilled water with continuous aeration being supplied by an aquarium air pump. After 4-5 days five healthy plants were selected and their roots suspended in half strength, modified Hoagland's solution. The modification consisted of doubling the calcium nitrate, tripling the monopotassium phosphate, and substituting 0.5M dibasic ammonium phosphate for monobasic. Initial pH after modification was 6.5 ± 0.5.

For the CO_2 specific electrode and infrared gas analysis studies, 25 ml erlenmeyer flask were used to contain the plants. Test tubes of 50 ml volume were used in the galvanic electrode study. Nutrient solutions were changed every 48 hours and no aeration was supplied as this would have interfered with results. Containers were covered with aluminum foil to prevent chlorophyll formation in the roots and inhibit algal growth.

Plants were placed in a growth chamber set at 24.0-15.5 C day-night temperature. For the CO_2 electrode and infrared gas analysis experiments, plants received 12 hours light. Fourteen hours of light were given plants in the galvanic electrode study to facilitate data collection.

All studies consisted of four plantings with the five cultivars arranged in 5 X 5 latin squares. Data were collected three separate times on each planting. Data on root respiration began once all plants

had exhausted stored nutrients in the kernel, usually 10-12 days after germination. Prior to data collection the remaining portion of the spent kernel was detached from the plant to prevent its interference with root volume determinations.

Root volume was measured by means of water displacement, using an acrylic chamber and tuberculin syringe previously described (Bruns, 1981). Volume measurements were taken each time respiration data were collected and recorded as cm^3.

Carbon Dioxide Electrode Study

The purpose of this study was to determine if a carbon dioxide specific electrode could be used to measure CO_2 release by wheat roots into the nutrient solution. Instruments used in this study were an Orion Model 95-02 Carbon Dioxide Specific Electrode attached to a Beckman Model 4500 pH Meter with millivolt (mV) capability. Readings in mV were converted to $\mu moles CO_2 cm^{-3} hr^{-1}$ by means of a standard curve developed from varing concentrations of $NaHCO_3$.

Prior to adding nutrient solutions, from which data were collected, a 50 ml sample was analyzed for CO_2 concentration. No measurable amounts of CO_2 were detected in any of the test samples of nutrient solution. All plants then received 25 mls of fresh nutrient solution. After 48 hours a 20 ml sample was removed and analyzed for CO_2 concentration. Samples were acidified to pH 4.5 with a 1M $Na_3C_6H_5O_7 \cdot 2H_2O$:HCl buffer to convert any bicarbonate and carbonate to CO_2. Two mls of buffer were added to each sample to complete acidification.

Infrared Gas Analyzer Study

The principle behind this study was to determine changes in gaseous

CO_2 levels resulting from respiring wheat roots. Data are reported in $\mu moles CO_2 cm^{-3} hr^{-1}$.

In order to sample air immediately surrounding roots for CO_2 concentration, a chamber was designed to contain plant roots during the sampling process. The chamber was constructed of 2.5 cm acrylic tubing 7 cm long, and wrapped with black electrical tape to exclude light. One end of the chamber was cemented to a 7.5 X 7.5 cm base. The other end was left open and a split rubber stopper inserted to hold the plant and maintain an air-tight seal during sampling. A grove was cut in the stopper to prevent the crushing of plant tissue. Two holes were bored into the chamber, one in which a small ampul stopper was fitted for sample collection and the other for forcing CO_2 free air into the chamber between samples.

Carbon dioxide free air was obtained by bubbling ambient air through two 500 ml erlenmeyer flasks filled with 1M KOH. A balloon was placed in the line leading from the second KOH carbon dioxide scrubber to the chamber. This helped to maintain atmospheric pressure inside the chamber and prevent sample contamination by outside air during sampling. The CO_2 free air was continually forced into the chamber except during the time between first and second gas samples for a particular plant. During this period CO_2 produced by respiring roots was allowed to accumulate in the chamber.

Gas samples from inside the chamber were withdrawn by means of two 10 ml hypodermic syringes. A six ml sample was first withdrawn as soon as the plant was affixed in the chamber and the grove in the center of the rubber stopper sealed with modeling clay. Immediately after one minute another six ml sample was withdrawn. Five ml's of both samples

were injected into a Beckman Model 865 Infrared Gas Analyzer with 10 inch chart recorder for CO_2 concentration determinations. Carbon dioxide exchange rates were calculated using the following formula:

$$CER = \frac{ppm * C * V_c}{V_r * T}$$

where:

CER=Carbon Dioxide Exchange Rate

ppm=ppm of CO_2 in sample 1 minus ppm CO_2 in sample 2.

C=Constant conversion factor ($1.09 * 10^{-4}$ mg CO_2 hr^{-1})

V_c=Volume of chamber in cc

V_r=Volume of roots in cm^3

T=Time in minutes.

Galvanic Electrode Study

This study was conducted to evaluate the use of a galvanic electrode in determining oxygen consumption by wheat roots from an oxygen saturated nutrient solution. The instrument used was a Precision Scientific Galvanic Cell Oxygen Analyzer. Data are reported as $\mu moles O_2$ $cm^{-3} hr^{-1}$.

Before filling test tubes containing plants with 45 mls of air-saturated nutrient solution, a sample of fresh solution was analyzed for O_2 content. Saturation of replacement solution with O_2 was accomplished by continuous aeration with an aquarium air pump and an air stone placed in the bottom of replacement solution.

Test tubes were filled with fresh solution at the beginning of the light period. Plants were placed back in the growth chamber for 12

hours then removed and the O_2 concentration determined. Differences between initial and final O_2 concentrations were interpreted as O_2 consumption. All readings were adjusted to a standard temperature.

RESULTS AND DISCUSSION

Carbon Dioxide Electrode Study

Differences at the 1% level of probability were observed for the overall means of each planting. Values were inconsistant and ranged from 40.8 to 75.8 $\mu moles CO_2 hr^{-1}$ (Table 1). Time alotted for CO_2 accumulation may have been too long. Reducing reaction time to one day or 12 hours may improve repeatability. Further study is warranted to determine this.

Observations across plantings were also found to be significantly different at the 1% level of probability. The initial reading taken on a planting was higher than the subsequent two (Table 2). Levitt (1969), stated that in developing tissue an initial drop in respiration probably occurs because of cell enlargement and a subsequent drop in the relative amount of protoplasm.

No significant differences in root respiration were observed across cultivars (Table 3). Comparison of these data with grain yield will not be meaningful. Also, no significant cultivar X planting or cultivar X observation interaction was observed.

Infrared Gas Analysis Study

Observations across plantings and the observation X plantings interaction were significant at the 1% level of probability. With respect to increasing plant age the third observation was significantly lower than the other two (Table 2). Again the fact that cell enlargement tends to decrease the relative amount of protoplasm probably caused a decrease in respiration rates.

Significant interaction of observation X planting mean squares occurred primarily because the mean value for the first observation in the first planting was much higher than the other two (Table 4). Also, in experiment two, the mean for observation one was significantly lower than for observation two. This did not fit data in plantings three and four. Observation means of these plantings were not significantly different. Because of this it is reasonable to question the validity of the significance of observations across plantings. Overall means for each planting were not significantly different (Table 1). However, because of the nature of the significant observation X planting interaction further study is needed. This would be to test the system's reliability with respect to time of sampling and determine if a decrease in root respiration rates does in fact occur with increasing plant age.

Cultivars within plantings were significantly different at the 10% level of probabilty (Table 3). The cultivars Hart and TAM-W101 had significantly lower rates of carbon dioxide exchange than Turkey. According to yield data from the Agronomy Research Center at Stillwater, Oklahoma in 1980, Turkey yielded significantly (at the 1% level) less grain than the other four varieties (Table 3). Higher rates of root respiration may well be a contributing factor to lower grain yield. If photosynthesis is limited for some reason, the demand for fixed carbon by roots could limit that available for grain production. It could also be causing a reduction in stem strength because of the high photosynthate demand. Turkey is noted for being highly susceptable to lodging, which is detrimental to yield.

Comparing data from this study with that of the CO_2 electrode shows close to 20 times more CO_2 per volume of roots detected by infrared gas

analysis. During the scrubbing process ambient CO_2 is removed and not available to initially inhibit the respiratory process. Thus, no appreciable product inhibition is occurring during the short time span of sampling. In the CO_2 electrode study the reaction time, being much greater, allowed for some CO_2 to be lost to the atmosphere before data were collected.

Galvanic Electrode Study

Means across plantings were significantly different at the 1% level of probability (Table 1). The mean value for O_2 consumption in planting four was significantly lower than the first two experiments. Data on root volumes showed plants in planting four to have a higher mean value than the others (0.94 cm^3 vs. 0.65, 0.73, 0.81 cm^3 for plantings 1, 2 and 3 respectively). Though plants were near the same age at the time data were collected, slight age differences of a few hours probably contributed to planting four having the largest volume of roots. This was probably due to considerable cell expansion and a relative decrease in protoplasm. Thus, a decrease in repiration per volume of roots occurred as reflected in oxygen consumption.

Means across observations were significantly different at the 1% level (Table 2). First and second observations were higher than the final ones in experiments one, two, and four. Data in planting three showed a response in the opposite manner (Table 4). Though its values across observations were not significantly different, it did result in a significant planting X observation interaction.

Cultivars differed significantly (at the 1% level) in their mean values of oxygen consumption (Table 3). Turkey showed a significantly

higher rate of oxygen consumption per volume of roots than the other cultivars. This is further evidence that less grain yield may result in this cultivar due to respirational losses of photosynthate in roots.

Compared with the other systems the galvanic electrode took less time to collect individual datum. Coefficients of varibility were also lowest with the galvanic electrode (56% vs. 78% for CO_2 electrode and 72% for infrared gas analysis). However, temperature correction tables supplied by the manufacturer were somewhat difficult to interpolate. All three systems though, seem effective in determining root respiration, but refinement of procedures is advisable.

CONCLUSIONS

Three studies were conducted to evaluate possible techniques for measuring root respiration in winter wheat. Five cultivars, Turkey, Bezostaia 1, TAM-W101, Priboy, and Hart were hydroponically grown in a modified Hoagland's solution. Each study consisted of four plantings with three separate observations on 5 plants per cultivar. The studies utilized one of the following instruments: 1) a carbon dioxide specific electrode for measuring CO_2 release by roots into the nutrient solution, 2) an infrared gas analyzer for measuring gaseous CO_2 production by roots, and 3) a galvanic electrode for measuring oxygen consumption by plant roots from the nutrient solution.

Mean values across plantings were significantly different in the CO_2 electrode study and the galvanic electrode study. Differences in the CO_2 electrode study were inconsistant and probably related to reaction time. In the galvanic electrode study differences across plantings appear to be related to root volume as influenced by plant age.

Observations across plantings in all studies generally showed a decrease in respiration per volume of roots with increasing plant age. Root growth by cell enlargement is noted not to cause an increase in cell protoplasm (Levitt, 1969). Thus, a relative decrease in the symplastic portion occurs and lower respiration rates per volume of tissue results.

Significant differences in respiration rates were noted across cultivars in the infrared gas analysis and galvanic electrode studies. The most noteworthy observation from these data is that the cultivar Turkey, was significantly higher in its gaseous CO_2 output and its O_2 consumption. This same cultivar, when compared with the other four for

grain yield, was lowest in a 1980 field experiment in Stillwater, Oklahoma. These observations are consistent with the idea that high rates of root respiration may be detrimental to yield.

In comparing and contrasting the three techniques used to study root respiration, all appear to have promise in studies of these kinds. Better data may have been obtained from the carbon dioxide specific electrode if the time of reaction were shortened to one day or 12 hours instead of 48 hours. The instrument itself is easy to use but one should practice with it before taking critical data.

The infrared gas analyzer has proven its effectiveness in measuring CO_2 in many studies on photosynthesis. In evaluating root respiration, the system is easy to use and quick. It may allow more versitility than the two electrodes because of different size root chambers that could be adapted and the amount of gas sample could also be altered. It could also be used to monitor root respiration throughout a plant's life cycle. Reaction times may need expanding to better reflect respiration rates.

The galvanic electrode is easy to use once calibrated. It is slightly more difficult to calibrate than the carbon dioxide electrode. But, it does allow adjustment for differences in sample temperature, which the CO_2 electrode does not. We did find the correction tables sent with the instrument somewhat difficult to interpolate.

With regards to root respiration in wheat, further study is warranted. Information on respiration rates throughout the growing season is lacking. Characterization of root respiration rates across genotypes may be of value in developing high yielding cultivars. Refinement of the techniques described above may be used in discerning these possible differences.

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TABLE 1

ROOT RESPIRATION OF WINTER WHEAT ACROSS FOUR PLANTINGS AND USING THREE TECHNIQUES

	Type of Study		
Exp. No.	CO_2 Electrode ($\mu moles CO_2 cm^{-3} hr^{-1}$)	Infrared gas analysis ($\mu moles CO_2 cm^{-3} hr^{-1}$)	Galvanic Electrode ($\mu moles O_2 cm^{-3} hr^{-1}$)
1	75.8	35.0	2.8
2	40.8	30.7	2.4
3	52.4	33.8	2.2
4	45.1	35.4	1.8
lsd @ 0.01	0.4	---	0.6

TABLE 2

ROOT RESPIRATION OF WINTER WHEAT WITH INCREASING PLANT AGE AS DETERMINED BY THREE METHODS OF EVALUATION

	Type of Study		
Plant age[1]	CO_2 Electrode ($\mu moles CO_2 cm^{-3} hr^{-1}$)	Infrared Gas Analysis ($\mu moles CO_2 cm^{-3} hr^{-1}$)	Galvanic Electrode ($\mu moles O_2 cm^{-3} hr^{-1}$)
1	66.4	35.2	2.5
2	45.8	36.2	2.4
3	48.4	29.9	2.1
lsd @ 0.01	16.1	6.4	0.2

[1]Plant Age: 1 = 10-12 days 2 = 12-14 days 3 = 14=16 days

TABLE 3

ROOT RESPIRATION BY THREE TECHNIQUES AND GRAIN YIELD OF FIVE WINTER WHEAT CULTIVARS

Cultivar	Type of Study			Grain Yield[1] (Q/ha)
	CO_2 Electrode ($\mu moles CO_2 cm^{-3} hr^{-1}$)	Infrared Gas Analysis ($\mu moles CO_2 cm^{-3} hr^{-1}$)	Galvanic Electrode ($\mu moles O_2 cm^{-3} hr^{-1}$)	
Turkey	60.4	40.2	3.1	28.2
Bezostaia 1	47.9	34.5	2.1	39.9
TAM-W101	51.6	30.1	2.0	42.5
Priboy	56.2	33.2	2.2	38.9
Hart	51.5	30.7	2.2	44.0
		lsd @ 0.01 = 7.3	lsd @ 0.01 = 0.6	lsd 0.01 = 7.9

[1]Data from 1980 field experiment at Stillwater, OK.

TABLE 4

ROOT RESPIRATION IN WINTER WHEAT AS MEASURED BY CO_2 RELEASE AND O_2 CONSUMED IN FOUR PLANTINGS WITH INCREASING PLANT AGE

Exp. No.	Plant age[1]	Type of Study: CO_2 Electrode ($\mu moles CO_2 cm^{-3} hr^{-1}$)	Infrared Gas Analysis ($\mu moles CO_2 cm^{-3} hr^{-1}$)	Galvanic Electrode ($\mu moles O_2 cm^{-3} hr^{-1}$)
1	1	92.5	47.1	3.3
	2	65.3	27.7	2.9
	3	69.7	30.1	2.3
Mean		75.8	35.0	2.8
2	1	57.7	25.4	2.7
	2	30.4	41.0	2.6
	3	36.3	25.9	2.0
Mean		40.8	30.7	2.4
3	1	71.8	32.9	2.1
	2	41.9	38.0	2.2
	3	43.3	30.5	2.3
Mean		52.4	33.8	2.2
4	1	45.6	35.2	2.0
	2	45.2	37.9	1.9
	3	44.1	32.9	1.7
Mean		45.1	35.3	1.8
		lsd 0.01 = 13.6		lsd 0.01 = 0.4

[1]Plant age: 1 = 10-12 days, 2 = 12-14 days, 3 = 14-16 days

CHAPTER VII

SUMMARY

Studies were conducted to evaluate possible cultivar differences in photosynthesis and root respiration of winter wheat. A comparison of root volume and root dry weight to grain yield was also made as well as investigations on diurnal variation of photosynthesis. Apparent photosynthesis was determined in both field and growth chamber experiments using infrared gas analysis. Root respiration was measured using hydroponically grown plants and three different techniques: 1) a CO_2 specific electrode for measuring CO_2 release by wheat roots into a nutrient solution, 2) a galvanic electrode for measuring O_2 uptake by roots from a nutrient culture, and 3) infrared gas analysis to measure gaseous CO_2 release by respiring roots. Root volume in all studies was determined by water displacement. A description of key developmental stages of wheat preceeds the above reports and is referenced as to when some data are taken.

Diurnal variation of photosynthesis in wheat showed rates of net carbon exchange to be highest two to three hours after sunrise. Rates then declined until 12:00 noon CST, after which a steady state was observed until after 1:00 pm CST. A fairly steady decline in net carbon exchange then occurred for the remainder of the day.

Net carbon exchange per unit of leaf area on five wheat cultivars failed to yield significant differences in photosynthesis for both field

and growth chamber experiments. Calculating net carbon exchange per unit of land area did yield significant cultivar differences but no relationship to grain yield was observed. Photosynthetic efficiency was defined as the ratio of grain CO_2 to net carbon exchange per unit land area. Significant cultivar differences were observed and high grain yield was not necessarily associated with high efficiency. Further study of source-sink relationships is warranted.

Significant differences (at the 1% level) in root volume and root dry weight were observed among the same five cultivars at 12 days age. The cultivar with both lowest root volume and dry weight was lowest in grain yield in a 1980 field experiment. Regression analysis of both parameters vs. yield showed a moderate relationship. Conclusive data however was not obtained from correlations of root volume and root dry weight.

Of the three methods used to study root respiration, all seem effective in obtaining data. However, refinement in the techniques is needed. Increasing plant age was found to result in decreasing respiration rates. Statistically significant cultivar differences were observed in the infrared gas analysis and galvanic electrode studies. The cultivar with the highest rate of root respiration was also lowest in grain yield according to 1980 field data.

VITA

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Doctor of Philosophy

Thesis: EVALUATION OF PHOTOSYNTHESIS AND ROOT RESPIRATION IN WINTER WHEAT (TRITICUM AESTIVUM L. EM. THELL)

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