PHOTOSYNTHESIS AND RESPIRATION OF VEGETATIVE AND REPRODUCTIVE PARTS OF WHEAT AND BARLEY PLANTS IN RESPONSE TO INCREASING TEMPERATURE*†

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Net photosynthesis, dark respiration and the CO_2 compensation point were determined for several wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) cultivars at temperatures ranging from 5 to 35 C. Temperature optima for net photosynthesis were as follows: vegetative plants—wheat 25 C; barley 20 C; reproductive plants (leaves plus developing spikes)—wheat and barley 15 C. Temperature optimum for the flag leaf of wheat was 20 C while that for the spike was 10 C. Respiration rates increased with increasing temperatures giving a Q_{10} of between 1.4 and 2.3 for the range of 15 to 35 C; for 5 to 15 C the Q_{10} was between 1.9 and 3.7. The CO_2 compensation point averaged from 39 ppm at 7 C to 73 ppm at 30 C. Thus part of the reduction in temperature optimum for net photosynthesis can be attributed in the reproductive stage to the increasing volume of nonphotosynthetic tissue in the developing spike although there appears to be a lower optimum for the flag leaf as well. These declines in temperature optima very likely contribute to the lower wheat yields observed in many Great Plains wheat-growing areas where maximum daily temperatures during heading are often in the range of 25 to 35 C, temperatures that caused from 3 to 53% reduction in net photosynthesis in wheat plants in the reproductive stage and from 13 to 58% reductions in barley plants at a similar stage.

INTRODUCTION

Net assimilation in many higher plants is usually reduced at elevated temperatures because while the rate of photosynthesis increases modestly with increasing temperatures between 5 and 25 C, the rate of respiration usually doubles with each ten degree rise over the range of 5 to 35 C (1). The stored food in grain, for example, represents net photosynthate that was not used in other processes while the grain is being formed. A number of studies have been made of the overall accumulation process whereas few have studied the processes of photosynthesis and repiration during vegetative and reproductive development.

Friend, et al. (2) found dry matter accumulation in vegetative wheat (*Triticum aestivum* L.) plants to be maximal at 10 C and to drop to 50% of that value at 25 C. Flag leaf senescence was accelerated when plants were grown at higher temperatures.

Chinoy (3) measured yield in 260 wheat varieties and correlated these yields with maximum daily temperatures during heading under field conditions. Plants ripened during the period of time when maximum daily temperatures were 30 C or above gave about one-half the yield of plants that ripened under maximum daily temperatures of 24 C. He noted that some water stress during the ripening period was less detrimental to yield than higher temperatures during the same period.

Friend (4) found that the temperature optimum for ear development of 'Marquis' wheat was about 15 to 25 C with a substantial decline at 30 C. Asana and Williams (5) found that for 6 wheat varieties, grain weight per ear for main-shoot ears was greatest at 24/19 C (day/night temperatures), less at 27/22 C, and least at 30/25 C. The decrease in yield amounted to about 20 to 25% from most favorable to least favorable temperatures. During emergence of first ears, Owen (6) found that day/night temperature regimes of 32/16 C or 32/21 C reduced the number of florets per ear and grain weight per ear or per plant from that produced by plants grown at regimes of 27/16 C or 27/21 C. Thus, higher day temperatures during ripening cause decreased grain yields.

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Wardlaw, et al. (7) found that photosynthesis of intact ears of wheat at 30 C was 63% of that at 21 C (plants grown at day/night temperatures of 30/25 C and 21/25 C respectively). Yields of two cultivars grown at day/night temperatures of 30/25 C were reduced to 66% of that obtained at 21/16 C. The length of the growth period of the ear was reduced by 6 to 8 days out of a total of about 26 days at the higher temperature regime. Ford et al. (8) had previously shown that ear temperature was more important than flag leaf temperature. Maintaining ear temperature during development at 25 C as opposed to 15 C caused a 27% decrease in ear dry weight.

This study was initiated to determine the vegetative and reproductive temperature optima for photosynthesis in hard red winter wheats. Both vegetative and reproductive stages were examined because of the wide range of temperatures to which winter wheat is normally subjected during the winter and spring in the Great Plains. In addition, the effect of temperature on dark respiration was determined since it has a direct effect on net photosynthesis.

METHODS AND MATERIALS

Seeds of hard red winter wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) were obtained from the Agronomy Department, Oklahoma State University (cultivars listed in tables). Seeds were soaked in petri dishes in tap water at room temperature for 2 days, then vernalized for 6 weeks at 4 C. Seedlings were transplanted to 15.3-cm pots with a sand-soil-peat mixture (2:1:2), watered daily, and grown in a controlled environment under 20 k-lux Gro-lux fluorescent plus incandescent light and with 14-hour photoperiod and 25/20 C day-night temperature. Plants grown for 3 weeks under the above conditions were vegetative. Six weeks after the vernalization period they began their reproductive stage. Measurements on reproductive plants were performed 2 to 3 weeks after anthesis (milk or soft dough stages).

Measurements of CO_2 concentration were made with a Beckman Model 15A Infrared Gas Analyzer (calibrated from 0 to 400 ppm). Shoots of intact vegetative plants or flag leaf plus spike of reproductive plants were enclosed in 2.8 × 28 cm cylindrical tubes having a volume of 156 m*l*. The total volume of the closed system was 0.85 *l* with a flow rate of 2 *l*/min. Illumination for photosynthesis measurements was the light in the growth chamber plus a 150-W incandescent spot lamp which gave light intensities of about 10^5 lux. Temperature of the growth chamber was adjusted so as to give the desired temperature in the plant enclosure during measurements. Leaf temperature was monitored with a thermistor probe.

TABLE 1. *Characteristics of plants used for photosynthesis measurements.*

CULTIVAR	Apparent photosynthesis at optimum temperature (mg CO_2 g^{-1} hr^{-1})	Leaf and stem wt. (mg)	Spike weight (with awns) (mg)
VEGETATIVE			
Wheat			
KanKing	36.7 @ 25 C	189	—
Scoutland	42.1 @ 25 C	156	—
Barley			
Kerr	41.3 @ 20 C	158	—
REPRODUCTIVE			
Wheat			
KanKing	34.4 @ 15 C	46	82
Scoutland	35.0 @ 15 C	77	84
Ponca	34.7 @ 15 C	49	86
Triumph 64	35.7 @ 15 C	34	98
Sturdy	34.7 @ 15 C	28	102
Agent	30.2 @ 15 C	69	143
Barley			
Will	32.0 @ 15 C	15	167
Rogers	30.8 @ 15 C	114	170
Kerr	28.9 @ 15 C	81	219

The plants were allowed to adjust to the experimental conditions for 20 to 30 min. Rates of photosynthesis were determined by using an initial CO_2 concentration of 320 ppm (obtained by flushing with outside air) and the concentration changes followed for 2 min. Dark respiration was determined by extinguishing the light after the CO_2 concentration was reduced to 220 ppm and measuring the increase in concentration. Air temperature was initially 5 C and measurements were made at 5-C intervals to 35 C, then the temperature was reduced in 5-C intervals back to 5 C.

For CO_2 compensation concentration determinations, intact shoots were enclosed in a sealed chamber and exposed to 10 k-lux Gro-lux fluorescent light. The CO_2 concentration of the enclosed system (same as described before) was determined after equilibrium had been reached (normally less than one hour).

Plants were harvested after completion of measurements and dry weights determined (80 C for 48 hr).

RESULTS

Effect of Temperature on Apparent Photosynthesis

Leaf and stem weights and apparent photosynthesis at the optimum temperature are presented in Table 1. Apparent photosynthesis values given in Table 2 for different temperatures are percentages of the highest rate obtained. Thus different cultivars and stages of development can be compared more easily. Vegetative wheat showed an optimum apparent photosynthesis at 25 C. Temperature optima for reproductive wheat plants for four cultivars were 15 C and two were at 20 C. While no significant differences were found between 15 and 20 C, the optimal values were definitely skewed toward a lower temperature for the reproductive plants. A statistical analysis comparing cultivars KanKing and Scoutland at both developmental stages confirmed that plants in the vegetative state had a significantly higher temperature optimum for photosynthesis (probability $p < .01$). Shoots having smaller spikes trended toward a higher optimal temperature for photosynthesis than those with larger spikes. Photosynthesis in all cases was markedly reduced at 5 C and 35 C from rates at the temperature optimum. An inverse relationship was noted between spike weight and at 35 C. For example, wheat cultivar Agent, with a spike weight of 143 mg, exhibited a photosynthesis rate reduction of 53%, whereas the rate for KanKing, with a spike weight of 82 mg, was reduced only 22%.

The temperature optimum for apparent photosynthesis in barley plants in the re-

TABLE 2. *Effect of temperature on apparent photosynthesis of wheat and barley (% of optimal value).*

	Temperature (C)						
Cultivar	5	10	15	20	25	30	35
Reproductive							
KanKing	52	73	97	100	97[a]	87	78
Scoutland	68	85	96	100[a]	90	87	77
Ponca	67	90	100	97	94[a]	91	75
Triumph 64	64	97	100	96[a]	91	82	72
Sturdy	76	93	100	86[a]	78	68	53
Agent	68	88	100	93[a]	77	64	47
Vegetative							
KanKing	49	77	85	90	100	73	68
Scoutland	47	71	89	93	100[a]	83	64
Reproductive Barley							
Kerr	74	87	100	85	73	68	42
Rogers	66	88	100	90	72	65	50
Will	61	87	100	92	87	74	69
Vegetative barley							
Kerr	60	85	93	100[a]	70	65	30

[a]Means conducted by horizontal lines are not significantly different at the 5% level using Duncan's multiple range test.

productive stage was also 15 C for all cultivars, with substantial reductions at 5 and especially 35 C. The greatest reduction was for the cultivar having the largest spike weights. There were insufficient data to show a significant difference between the optimum temperature for apparent photosynthesis of vegetative and reproductive stages in barley although the maximum rate for cultivar Kerr in the reproductive stage was 15 C as opposed to a vegetative optimum closer to 15 C vs. 20 C.

Respiration measurements

As the plants develop from the vegetative to the reproductive stage there is an increasing mass of reproductive tissue that does not carry on photosynthesis. This tissue mass carries on respiration at a rate dependent upon external temperature. Dark respiration was determined on several of the cultivars used (Table 3). Reproductive wheat plants had higher Q_{10} values than vegetative plants at all temperature ranges examined (Table 4), with the highest values for the range of 15/5 C. Reproductive barley gave lower Q_{10} values than wheat. The larger Q_{10} values for reproductive plants could have contributed to the observed decreased optimum temperature for apparent photosynthesis in the reproductive plants.

TABLE 3. *Effect of temperature on dark respiration of wheat cultivars as percent of rate at 35 C.*

Cultivar	Temperature (C) 5	10	15	20	25	30	35	Respiration rate at 35 C (mg CO_2 hr^{-1} dry wt^{-1})
Reproductive								
Scoutland	6	17	24	42	58	77	100	9.8
Ponca	6	9	21	33	47	74	100	7.6
Vegetative								
Scoutland	19	29	36	49	58	77	100	11.2
KanKing	16	31	44	52	64	84	100	11.1

TABLE 4. *Calculated Q_{10} values for dark respiration of barley and wheat shoots. (Numbers following averages are standard deviations.)*

	Q_{10} Temperature Ranges (C) 15/5	25/15	35/25
Wheat (2 cultivars)			
Vegetative	1.89 ± 0.07	1.37 ± 0.21	1.98 ± 0.08
Reproductive	3.74 ± 0.68	2.28 ± 0.17	2.04 ± 0.29
Barley (3 cultivars)			
Reproductive	2.03 ± 0.39	2.04 ± 0.80	1.76 ± 0.29

CO_2 compensation concentration

Vegetative intact seedlings of wheat and barley responded similarly, with increasing temperatures approximately doubling the equilibrium CO_2 concentration between 7 and 30 C (Table 5). The increased photorespiration at 30 C would also contribute to a lowering of net photosynthesis at the higher temperature. Maize and sorghum tested in the same system gave values of between 2 and 4 ppm with no change with temperature.

Apparent photosynthesis and dark respiration of flag leaf blade and spike

To more thoroughly investigate the temperature effects on the different parts of the reproductive wheat plants, measurements were made by separately enclosing the spike or flag leaf blade on intact plants. Apparent photosynthesis of the flag leaf blade was maximal around 20 C, whereas the spike maximum was clearly at 10 C (Figure 1). Dark respiration on a dry weight basis was higher for the leaf blade than the spike, presumably owing to the large amount of stored material accumulated. Apparent photosynthesis in a spike of Barsoy barley also was maximal at 10 C (data not shown).

Table 5. *Effect of temperature on CO_2 compensation concentration (ppm) on vegetative plants.*

	7	15	20	25	30 C
Rogers barley	44	56	59	62	75
Ponca wheat	39	46	54	58	72
KanKing wheat	34	48	51	56	72

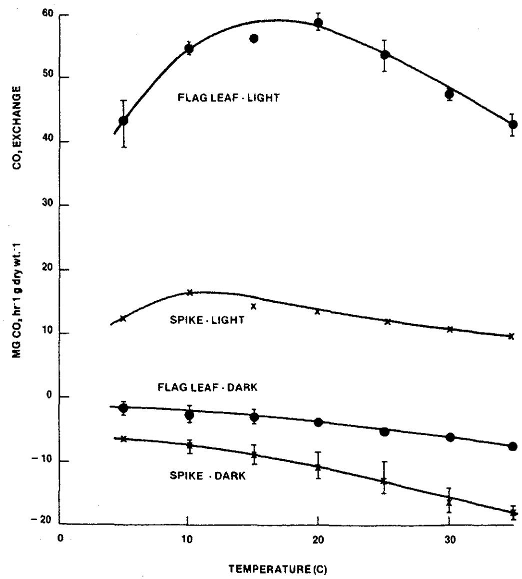

Figure 1. Effect of temperature on net photosynthesis and dark respiration of the spike and flag leaf individually of Agent wheat plants. Vertical bars represent the standard deviation.

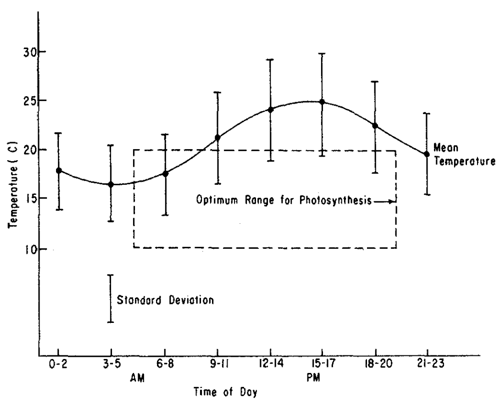

Figure 2. Mean temperatures for Oklahoma City derived from hourly averages for the years 1943-1967 for the month of May compared to the optimum temperature for photosynthesis of reproductive wheat shoots. Vertical bars represent the standard deviation.

Wheat production in Oklahoma

A trend toward a lower temperature optimum for apparent photosynthesis of reproductive wheat plants than for vegetative plants has some interesting implications for wheat production in Oklahoma. Outdoor temperatures during heading and grain filling continually increase whereas at the same time photosynthesis is declining and respiration is increasing. The combined effect must result in less accumulation of photosynthetic end products and therefore yield of grain. Others have also observed that elevated temperatures reduce the length of the grain filling period (7).

A comparison of the photosynthesis temperature optimum with average maximum and minimum temperatures at Oklahoma City is provided in Figures 2 and 3. These figures show that during the period of grain development in Oklahoma the average daily maximum temperatures are considerably above the optimum for photosynthesis (temperature extremes for the month of May at Oklahoma City are: maximum 36 C; minimum 4 C). Thus wheat yields in years having a lower mean temperature should be enhanced provided that all other factors (moisture, sunlight, etc.) remain comparable.

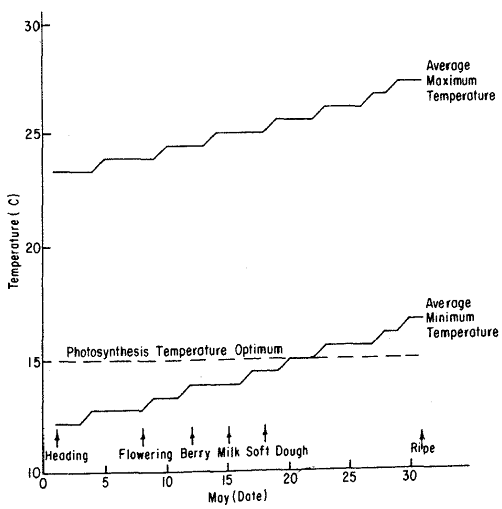

Figure 3. Maximum and minimum average temperatures by date at Oklahoma City (1931-1960) compared with the optimum temperature for photosynthesis of reproductive wheat shoots. Approximate dates for various growth stages are for Stillwater, Oklahoma, 105 km NNE of Oklahoma City.

DISCUSSION

Net photosynthesis values appeared to be greatly affected by the amount of respiration taking place in the developing grain. Photosynthesis is largely confined to the surfaces of the spike whereas the increasing volume of grains does not photosynthesize but continues to respire. Todd, et al. (9) reported that net photosynthesis in the developing lemon fruit declined as the fruit grew in size because of the addition of tissues in the fruit that respire but do not photosynthesize.

The optimum temperature for apparent photosynthesis in vegetative winter wheat was 25 C whereas the optimum for reproductive plants was around 15 C. [Friend (1) reported a temperature optimum of 20 C for apparent photosynthesis of 5-week-old plants of Marquis wheat.] Reproductive barley was similar to wheat. Owen (6) reported a greater reduction in yield when higher temperatures were imposed during the reproductive stage; thus part of the decreased yield may be accounted for by decreased photosynthesis.

Respiration rate increases about twofold for each 10 degree C rise in temperature and may also be responsible for decreased net accumulation of stored materials in the developing seed. Comparative studies on C-3 versus C-4 plants indicated that photorespiration in wheat and barley appeared to increase sharply as temperature increases.

The optimum temperature for apparent photosynthesis in the attached spike was 10 C as opposed to the flag leaf blade, where it was around 20 C. Ford, et al. (8) had noted that temperature fluctuations of the ear had more influence on yield than changes in the flag leaf temperature.

Other internal factors may contribute to decreased wheat and barley yields at the higher temperatures. Higher temperatures caused a reduction in leaf area per plant (2) as well as earlier senescence (5, 7). Very low concentrations of carbohydrate were present at higher temperatures in bluegrass leaves (11). If wheat plants behave in a similar manner, this could also be consistent with the observed decline in grain yield.

Maximum day temperatures in Oklahoma show a steady upward progression during the period of reproductive development. Average daily maximum tmperatures substantially exceed those for maximum photosynthesis. Thus higher temperatures usually experienced during this time undoubtedly limit the yield potential. In addition to reducing photosynthesis, higher temperatures were demonstrated to reduce the period of grain filling by causing premature senescence (7), thus compounding the yield reduction problems. Selection of wheat cultivars that perform better at higher temperatures might be a useful approach to increase wheat yields in Oklahoma.

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