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Radiation use efficiency and instantaneous photosynthesis at different growth stages of wheat (*Triticum aestivum* L.) in semi arid ecosystem of Central Punjab, India

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ABSTRACT

The instantaneous canopy net photosynthetic rate (Ac) and photosynthetic radiation use efficiency (PhRUE) were investigated diurnally at different growth stages of wheat during two seasons 2009-2010 and 2010-11. Diurnal changes in Ac were synchronized with changes in incident photosynthetic photon flux density (PPFDo) throughout the experimental period during both the seasons. Regardless of growth stages, high Ac values were always observed around noon, when there was a high photosynthetic photon flux density (PPFD). In addition, the highest AC values were noticed at heading stage, when compared to other growth and development stages of wheat. With respect to PhRUE, the highest values occurred in the active tillering stage and decreased gradually upto soft dough stage during both the seasons. PhRUE was lowest after heading stage for wheat crop in both seasons, corresponding to decrease in photosynthetically active leaf area, another explanation for the decrease in RUE is a decrease in crop growth rate. Regarding diurnal changes in PhRUE, study revealed that it was always higher during early morning and evening time of the day at all the stages of the crop. The seasonal PhRUE of wheat was observed to be 1.21 g MJ^{-1} and 1.27 g MJ^{-1}, respectively during two seasons.

Key words: RUE, PhRUE, wheat, photon flux density and PAR

Wheat (*Triticum aestivum* L.) is a widely adapted crop. It is grown from temperate irrigated to dry and high rainfall areas, and from warm humid to dry cold environments. Undoubtedly this wide adaptation has been possible due to the complex nature of its genome, which provides a fantastic plasticity to the crop. Wheat is a C_3 plant and as such it thrives in cool environments.

Plant dry matter accumulation depends on the total C fixed by photosynthesis and fraction of that C converted to dry matter (Norman and Arkebauer 1991). Crop plants grow almost entirely by photosynthesis. Thus, plant productivity in terms of primary production of biomass is simply a measure of the total photosynthesis of the plants less respiration, which has occurred during its growth. In the absence of biotic and abiotic stresses, plant dry matter accumulation depends on the quantity of radiation absorbed by the canopy (Kiniry *et al*. 1989; Monteith 1977; Sinclair and Muchow 1999). The relationship between plant dry matter and radiation intercepted has been termed the radiation use efficiency.

Dry matter production has often been found to be linearly related to the photosynthetically active radiation (PAR) absorbed or intercepted by crops (Monteith 1972; 1977). The slope of this relationship is the radiation use efficiency (RUE), and has been used to model plant growth, especially in crops where growth is not limited by water or nutrient shortage, or by other adverse climatic conditions that may decrease RUE (Stockle and Kiniry 1990; Runyon *et al*. 1994; Ruimy *et al*. 1995).

RUE differs between crops (Sivakumar and Virmani 1984; Gosse *et al*. 1986), with plant nitrogen status (Green 1987; Sinclair and Horie 1989) and with phase of the crop cycle (e.g. vegetative versus reproductive growth) among other factors (Trapani *et al*. 1992).

Using biomass to study RUE implies long-term experiments since, on a short time scale (e.g. 1 d or less), biomass increases are difficult to measure. On a short time-scale, RUE can be studied by using gas exchange, though the results are difficult to compare with long-term changes in biomass since crop respiration needs to be assessed and accounted for. Although few studies have been performed linearity has been found between net CO_2 assimilation of the whole canopy, integrated over a day (daily canopy photosynthesis), and absorbed or incident

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PAR, implying constant photosynthetic RUE (PhRUE) on a daily basis (Sinclair 1991; Ruimy *et al*. 1995; Sinclair and Muchow 1999). However, instantaneous canopy photosynthesis tends to saturate at high irradiance, and instantaneous PhRUE varies with time of the day (Grace *et al*. 1995; Ruimy *et al*. 1995).

It has been suggested that the daily PhRUE can be calculated simply from the photosynthetic properties of a leaf at the top of the canopy and from the PAR incident on the canopy. The objective of this study was to investigate whether this portable photosynthetic system allows estimation of PhRUE of wheat crop and with daily incident PAR, and also during the crop growing season.

MATERIALS AND METHODS

Study area

The present field investigation was conducted at the experimental farm, department of Agricultural Meteorology, Punjab Agricultural University, Ludhiana during the *rabi* season 2009-10 and 2010-11. Ludhiana is situated at 30°-54' N latitude and 75°-48' E longitude at a height of 247 m above the mean sea level. The meteorological observatory nearest to the present study is located in research farm, Department of Agricultural Meteorology, Punjab Agricultural University, Ludhiana.

Weather during crop growth period

Daily meteorology data, viz., rainfall, evaporation, relative humidity, maximum and minimum temperature, etc. were recorded from surface agrometeorology observatory, PAU, Ludhiana. The normal as well as prevailing weather conditions during two crop growth seasons (2009-10 and 2010-11) are given in Table 1. The study revealed that the mean monthly maximum temperature during crop growth period ranged from 38.7 ^{0}C in April to 15.7 ^{0}C in January during 2009-10 and 33.8 ^{0}C in April to 16.0 ^{0}C in January during 2010-11. As per the expected trend, the actual rainfall was meager during crop growth period. The rainfall amount of 54.9 mm, 100.2 mm occurred in the first, (2009-10) and second (2010-11) seasons, respectively. Study revealed that weather during crop growth periods was almost comparable with that of normal.

Soil of the experimental site

The soil of the experimental area was loamy sand. The soil was low in available N and organic carbon (OC), medium in available P and K.

Crop management

Wheat crop (cv. PBW 343) was sown with the row spacing of 22.5 cm on first week of November, during both the seasons 2009-10 and 2010-11. Four irrigations (75 mm water in each irrigation) were applied at four critical phenological stages of the crop *viz*., (i) CRI (ii) late tillering (iii) booting (iv) milking, which coincided with 20-25, 40-45, 70-75, 115-120 days after sowing, respectively in two different seasons. In regards to fertilizer application of the crop, 125 kg N, 62.5 kg P_2O_5 and 30 kg K_2O was applied. One third of the N and full dose of P_2O_5 and K_2O were applied as basal dose at the time of sowing by broadcasting method. Another 1/3rd dose of N was applied 21 days after sowing and remaining 1/3rd was applied 21 days thereafter.

Leaf area index (LAI) and mean tilt angle (MTA)

LAI and MTA of the crop was measured at every growth stage during crop growth season with a plant canopy analyzer (model LAI-2000 LICOR, Inc., Lincoln, NE, USA) following the standard procedure described by the manufacturer to avoid any row structure bias and the number of below canopy measurements needed .

Incident photosynthetically active radiation (IPAR)

Photosynthetically active radiation (PAR) is the general radiation term that covers both photon and energy terms. This is the number of photons in the 400-700 nm waveband incidents per unit time on a unit distance. Quantum sensor was used to measure the incident photosynthetically active radiation (IPAR) by the whole canopy.

Instantaneous leaf photosynthetic (Pr) and transpiration rates (Tr)

Instantaneous light-saturated photosynthetic rate (Pr) and transpiration rate (Tr) were measured on the leaves of selected plants. Measurements were made at ambient temperature and humidity, between 0800 and 1600 h, using portable gas exchange system (LI-6400, LICOR, Inc., Lincoln, NE, USA). Plants were selected on the average condition of the field (representative) and whole plant canopy were stratified into three layers (upper, middle and lower). Within a single plant canopy observations were taken from different strata with leaves of different ages (young, middle and old) as well as sunlit and shaded, a minimum of six leaves in a strata were

Table 1 : Normal as well as actual weather data during crop growth period

Parameters	Months					
	November	December	January	February	March	April
Total Rainfall (mm)						
2009-10	5.1	00	18.4	25.0	2.0	4.4
2010-11	00	17.6	5.4	44.2	6.5	26.5
Normal	9.4	16.9	25.4	29.9	26.1	18.3
Mean maximum air temperature (°C)						
2009-10	25.1	21.1	15.7	22.5	31.0	38.7
2010-11	27.1	20.5	16.0	21.2	27.9	33.8
Normal	26.7	20.4	18.9	21.6	26.6	34.2
Mean minimum air temperature (°C)						
2009-10	10.6	6.5	6.6	9.0	14.8	20.1
2010-11	11.4	5.6	5.2	9.4	13.4	17.6
Normal	10.1	6.1	5.3	7.2	11.3	16.9
Mean relative humidity (%)						
2009-10	67	71	86	72	65	45
2010-11	67	76	82	81	72	49
Normal	61	68	71	69	63	47

samples. A total of 5 plants were selected and observations were taken after every hour starting from 0800 h upto 1600 h at different growth stages of wheat during 2009-10 and 2010-11 and average value of total 5 plants were taken as the value.

Instantaneous canopy net photosynthetic rate (Ac)

The fraction of the incident photosynthetic photon flux density (PPFDo) that was absorbed by the canopy (I_A) = 1-exp (-Cos (MTA) x LAI) ……………

(Rosati *et al*, 2004)

Where, MTA: Mean tilt angle (degree); LAI: Leaf area index

Now, sunlit leaf area in the crop canopy (LAIs) with units of m^2 leaf m^{-2} ground= I_A /Cos (MTA)

Therefore, Instantaneous canopy net photosynthetic rate (Ac)

Ac = LAIs x Instantaneous leaf photosynthetic rate (μmol CO_2 $m^{-2}s^{-1}$)

Photosynthetic radiation use efficiency (PhRUE)

The conversion efficiency of incident PAR to biomass was determined for wheat crop during different growth stages. Photosynthetic radiation use efficiency (PhRUE) is expressed as dry matter accumulation (g m^{-2} d^{-1}) per unit intercepted photosynthetically active radiations (PAR) (MJ m^{-2} d^{-1}).

Convert the canopy net photosynthetic rate or canopy gross CO_2 assimilation rate to a dry matter accumulation rate in g DM m^{-2} d^{-1}. For that the simplifying assumption that the new crop dry matter is made of carbohydrates with the stoichiometry of CH_2O. That implies 30 g of dry matter are accumulated for every mol of C (or, mol of CO_2) fixed (Rosati *et al*, 2004).

So, the rate of dry matter accumulation in g DM m^{-2} ground s^{-1} is

Ac x 30 g DM mol^{-1} CO_2

= μmol CO_2 m^{-2} ground s^{-1} x 10^{-6} mol μmol^{-1} x 30 g DM mol^{-1} CO_2

Note that this value has units of g DM m^{-2} s^{-1}. This is a crop growth rate (CGR), albeit one with a short time interval (one second).

Next, to determine how much PAR was absorbed by

Table 2 Instantaneous leaf photosynthetic (µmol CO_2 m^{-2} leaf s^{-1}) and transpiration rates (mmol H_2O m^{-2} leaf s^{-1}) at different growth stages of wheat (pooled data of 2009-2010 and 2010-11)

Time (hrs)	Growth stages									
	Active tillering		Jointing		Booting		Heading		Soft dough	
	Pr	Tr	Pr	Tr	Pr	Tr	Pr	Tr	Pr	Tr
8	16.50	3.03	17.40	3.64	19.85	3.84	21.85	3.97	19.15	3.66
9	19.50	3.98	19.90	3.87	23.20	4.20	23.40	4.27	21.35	4.09
10	20.60	4.53	21.55	4.74	25.85	5.56	27.60	5.80	23.95	4.52
11	21.80	5.12	23.95	6.42	29.00	6.42	30.15	6.93	29.05	6.36
12	24.35	6.48	25.45	7.55	35.60	7.86	37.05	8.22	33.35	7.73
13	22.15	5.25	24.50	6.00	33.60	7.11	34.50	7.99	30.85	7.33
14	20.40	4.82	22.55	5.63	31.05	6.30	32.45	7.18	28.9	5.99
15	19.05	4.07	20.05	5.00	27.85	5.39	29.50	6.73	26.45	5.29
16	18.55	3.19	19.10	4.11	21.60	4.72	24.15	4.40	20.9	4.39
Average	20.35	4.49	21.60	5.22	27.50	5.71	28.95	6.17	26.00	5.46

Pr: Instantaneous leaf photosynthetic rate; Tr: Instantaneous leaf transpiration rate

the crop canopy in order to produce that dry matter accumulation rate we just calculated, with units of MJ s^{-1}.

The incident PPFD, with units of µmol PPFD $m^{-2}s^{-1}$, and also the fraction of that incident PPFD that was absorbed by the canopy (I_A). One mol of PPFD contains approximately 217 KJ of energy (217 x 10^3 J).

So, energy of the absorbed radiation in J m^{-2} s^{-1} is:

PPFD x I_A x 217 x 10^3 J

= (µmol photon m^{-2} ground s^{-1}) x (10^{-6} mol µmol^{-1}) x (217 x 10^3 J mol^{-1} photon)

the RUE as:

CGR/PAR (absorbed) = g DM m^{-2} ground s^{-1}/MJ m^{-2} ground s^{-1} = g MJ^{-1}

Now that RUE was calculated on the basis of gross photosynthesis and respiration may be in the order of 30 per cent. Consequently, PhRUE would be estimated as 0.7 x PhRUE=PhRUE' in g MJ^{-1} (Azumendi *et al*, 2013).

RESULTS AND DISCUSSION

Diurnal changes in Pr with PPFDo

Diurnal changes in instantaneous leaf photosynthetic rate (Pr) were synchronized with changes in incident photosynthetic photon flux density (PPFDo) throughout the experimental period during the seasons, 2009-10 and 2010-11 (Fig. 1). Regardless of growth stages, high Pr values were observed around noon, when there was a high PPFDo (Fig. 2). Diurnal variation in Pr displayed increase Pr along the day, reaching maximum values at 12.00 noon followed by a progressive decline later in the day. In addition, the highest Pr values were noticed at heading stage, when compared to other growth and development stages of wheat.

Photosynthesis of individual leaves integrated over the day (daily photosynthesis) was linearly related to the daily PAR incident on the leaf (Fig. 1). The linear relationship agrees with the simulation of Haxeltine and Prentice (1996) and Dewar *et al*. (1998). Increased in Pr with the increase in PPFDo from 8.00 hrs to 12.00 noon and reached its peak value at 12.00 noon, when PPFDo was maximum at all the growth and development stages of wheat during both the seasons (Table 2). Out of the many observations, two observations dates coincided with active tillering and heading stage were taken for each crop season for studying the variation of Pr with PPFDo (Fig. 1). To study the critical factors influencing Pr of wheat, a stepwise regression correlation analysis between Pr and PPFDo was carried at active tillering and heading stages during both the seasons. Theoretical studies predict that nitrogen content (and thus photosynthetic properties) of leaves is distributed in a canopy in relation to the light gradient in such a way that daily canopy photosynthesis is optimized in relation to light (Hirose and Werger 1987).

Table 3 Instantaneous canopy photosynthetic rate (µmol CO_2 m^{-2} leaf s^{-1}) and Photosynthetic radiation use efficiency (g MJ^{-1}) at different growth stages of wheat during 2009-2010

Time (hrs)	Active tillering		Jointing		Booting		Heading		Soft dough	
	Ac	PhRUE	Ac	PhRUE	Ac	PhRUE	Ac	PhRUE	Ac	PhRUE
2009-10										
8	5.38	3.06	4.49	2.31	3.46	1.35	3.46	1.29	3.07	0.86
9	6.28	2.71	5.15	1.87	4.18	1.06	3.84	1.04	3.37	0.76
10	6.56	1.80	5.62	1.26	4.69	0.81	4.35	0.77	3.93	0.66
11	7.08	1.47	6.20	1.17	5.11	0.67	4.95	0.69	4.65	0.56
12	7.66	1.43	6.62	1.12	6.26	0.65	5.93	0.61	5.30	0.53
13	6.86	1.76	6.20	1.25	6.01	0.73	5.55	0.65	5.08	0.59
14	6.47	1.92	5.79	1.36	5.59	0.86	5.24	0.76	4.72	0.65
15	6.05	2.23	5.10	1.41	4.84	0.96	4.80	0.88	4.11	0.71
16	5.83	2.59	4.90	1.50	4.07	1.06	4.35	1.05	3.50	0.83
Average	6.46	2.11	5.56	1.47	4.91	0.91	4.72	0.86	4.19	0.68
2010-11										
8	5.19	3.26	4.60	2.37	3.81	1.52	3.81	1.44	3.25	1.07
9	6.23	2.63	5.24	1.82	4.32	1.15	3.94	1.16	3.68	0.90
10	6.62	1.68	5.64	1.17	4.78	0.85	4.82	0.80	3.98	0.65
11	6.89	1.56	6.30	1.12	5.51	0.80	5.07	0.66	4.93	0.61
12	7.94	1.50	6.67	1.10	6.78	0.70	6.38	0.61	5.71	0.58
13	7.34	1.91	6.59	1.25	6.30	0.74	5.92	0.67	5.10	0.56
14	6.60	2.08	5.98	1.46	5.79	0.84	5.55	0.86	4.82	0.69
15	6.15	2.27	5.37	1.57	5.37	1.06	5.00	0.94	4.62	0.77
16	6.05	2.70	5.07	1.74	3.85	1.18	3.67	1.23	3.40	0.89
Average	6.56	2.18	5.72	1.51	5.17	0.98	4.91	0.93	4.39	0.75

Ac: Instantaneous canopy photosynthetic rate; PhRUE: Photosynthetic radiation use efficiency

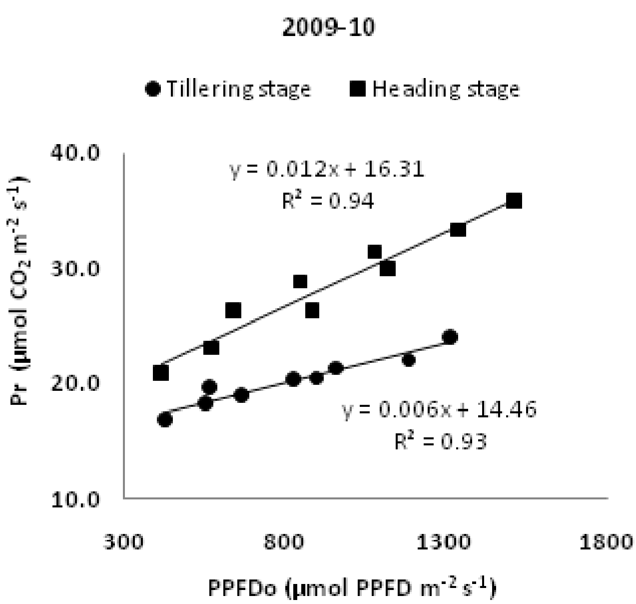

Fig. 1 : Relationship between Instantaneous leaf photosynthetic rate (Pr) and incident photosynthetic photon flux density (PPFDo)

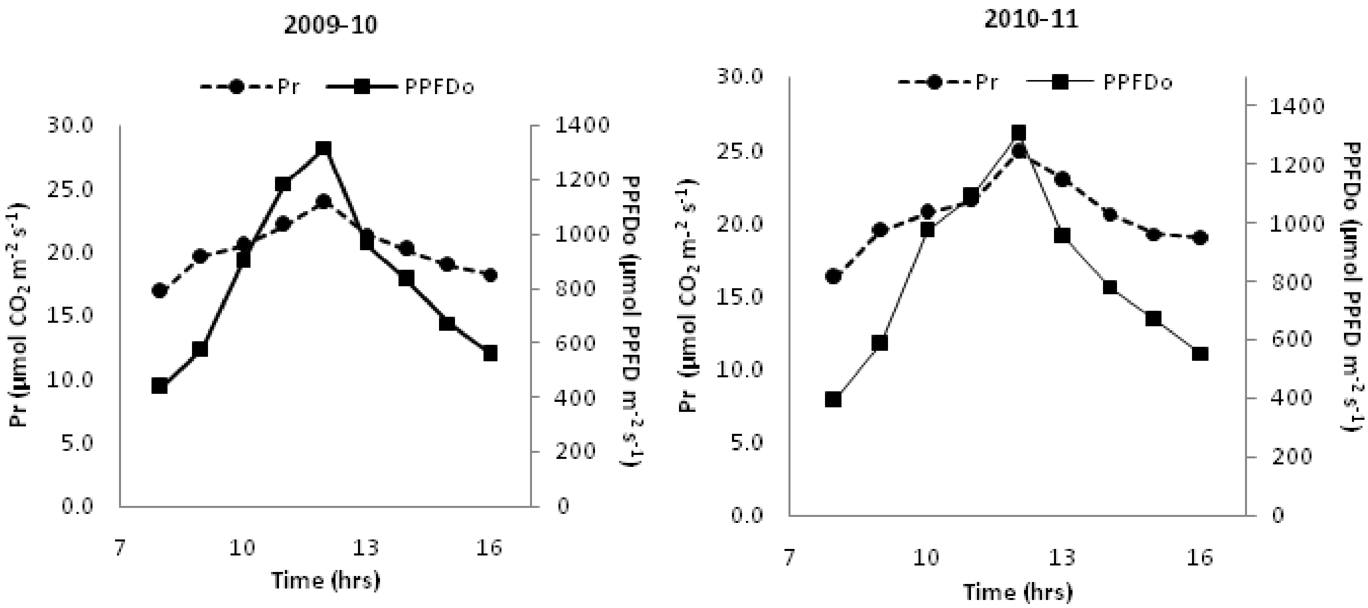

Fig. 2 : Diurnal variation in instantaneous leaf photosynthetic rate (Pr) and incident photosynthetic photon flux density (PPFDo) at active tillering stage

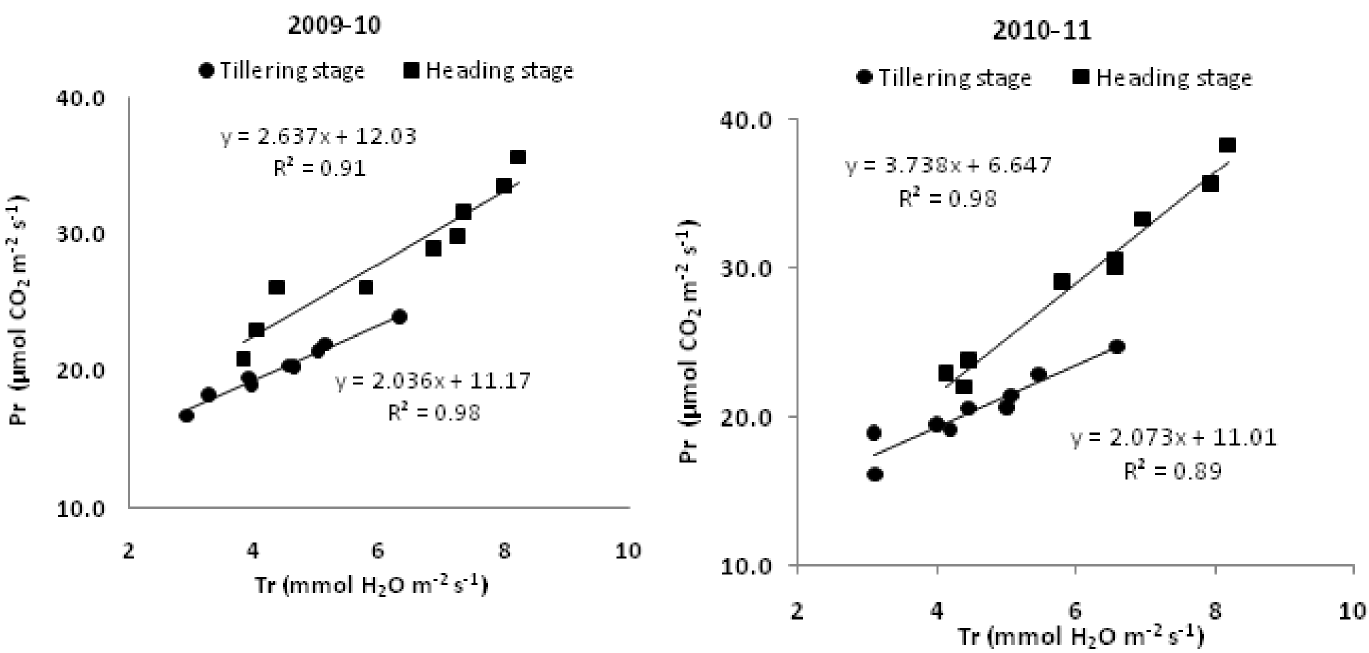

Fig 3 : Relationship between instantaneous leaf photosynthetic rate (Pr) and transpiration rates (Tr)

There is then a linear relationship between daily canopy photosynthesis and intercepted PAR (De Witt 1965; Kull and Jarvis 1995).

Instantaneous leaf photosynthetic rate (Pr) and transpiration rates (Tr)

Instantaneous leaf photosynthetic rate increased linearly with increase in leaf transpiration rate at all the growth and development stages of wheat. Out of several observations, during active tillering and heading stage the positive relationship were obtained between leaf photosynthetic rate and leaf transpiration rate (Fig. 3) with R^2 ranging from 0.91 to 0.98 at both that stages in both the years. Similar results were found at all growth and development stages of wheat (Table 2).

Instantaneous leaf (Pr) and canopy photosynthetic rates (Ac)

Diurnal trends for instantaneous leaf and canopy

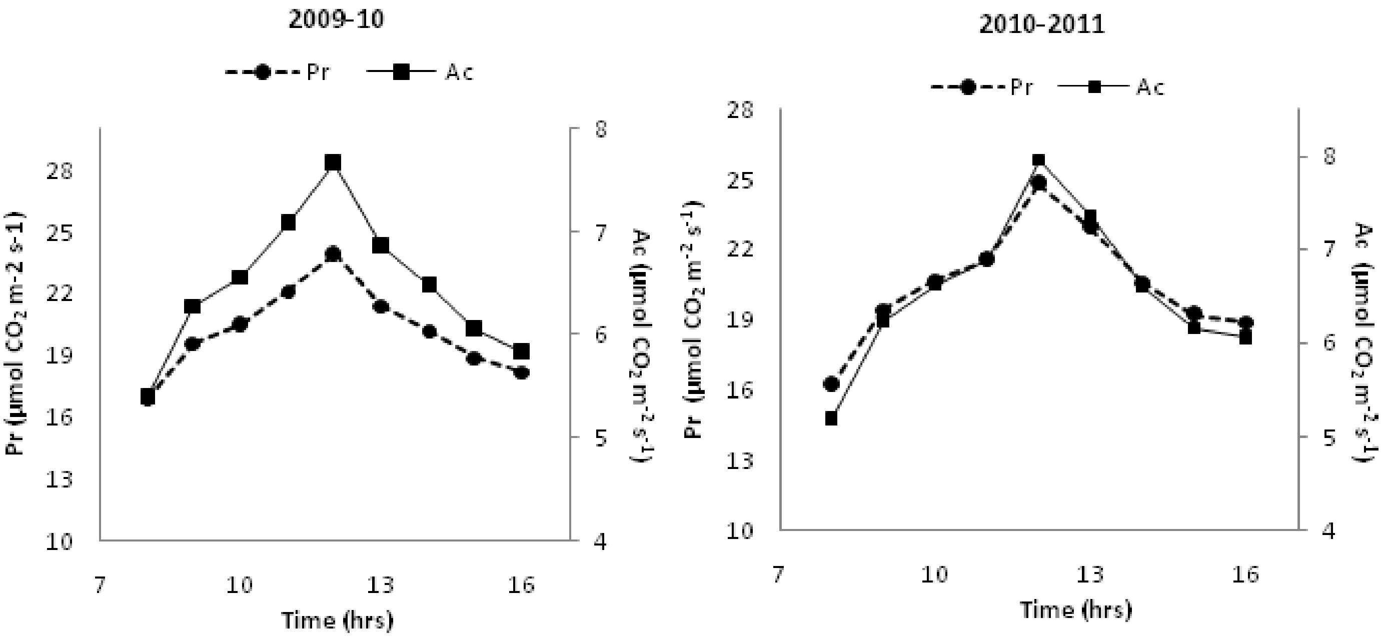

Fig. 4 : Diurnal variation instantaneous leaf photosynthetic rate (Pr) and instantaneous canopy photosynthetic rate (Ac) at active tillering stage

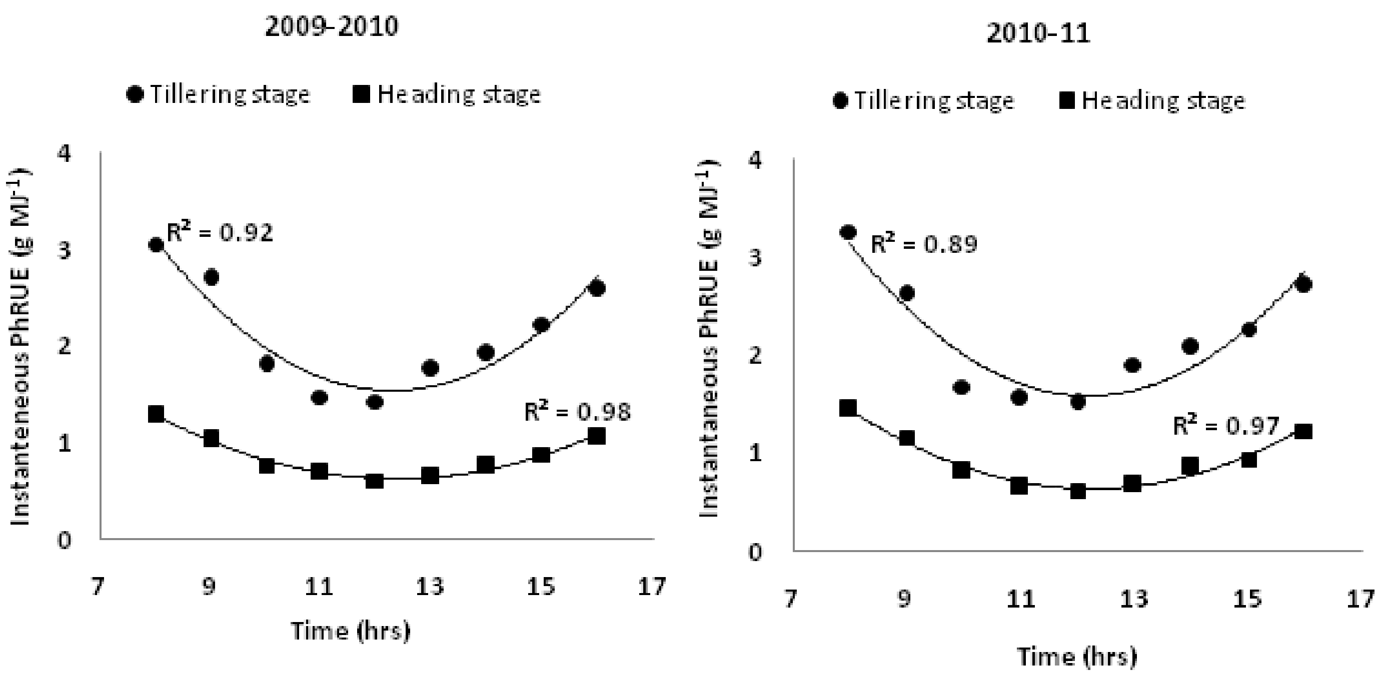

Fig. 5 : Diurnal variation in instantaneous photosynthetic radiation use efficiency (PhRUE)

photosynthetic rates for different growth stages are shown in Table 2. The diurnal trend of instantaneous leaf and canopy photosynthetic rate (Fig. 4) during active tillering stage showed that Ac closely tracked the pattern of Pr during the day. A similar pattern was observed for all the growth and development stages during the course of the crop growth season (Peri *et al,* 2006).

Instantaneous photosynthetic radiation use efficiency (PhRUE)

Values of Instantaneous photosynthetic radiation use efficiency (PhRUE) changed considerably during crop growth period (Table 3). The highest PhRUE occurred early in the active tillering stage and decreased gradually after tillering stage upto soft dough stage during both the seasons of crop growth. During reproductive growth, RUE was lower than during middle and late stages of vegetative growth (Green 1987; Fischer 1993; Calderini *et al*. 1997).

PhRUE was lowest after heading stage for wheat crop in both seasons, suggesting a physiological change in carbon uptake. PhRUE decreased considerably after tillering stage, corresponding to decrease in photosynthetically active leaf area, another explanation for the decrease in PhRUE is a decrease in crop growth rate. Regarding diurnal changes, study revealed that PhRUE was higher during early morning and evening time of the day at all the growth and development stages of the crop (Table 3), which may be due to increase in the proportion of diffuse radiation during those periods (Sinclair and Muchow 1999). During active tillering and heading stage the diurnal variations of PhRUE (Fig. 5). PhRUE decline from 8.00 hrs and minimum value was reached at 12.00 noon at all the growth stages during both seasons, when PPFDo was maximum. The seasonal average PhRUE of wheat crop observed in the present study amounted to 1.21 g MJ^{-1} and 1.27 g MJ^{-1}, during season 2009-10 and 2010-2011, respectively. This corresponds to the potential RUE of 1.38 g MJ^{-1} solar radiation as summarized by Sinclair and Muchow (1999).

CONCLUSION

Results provided physiological insights of wheat. PhRUE was lowest after heading stage for wheat crop in both seasons, suggesting a physiological change in carbon uptake. PhRUE decreased considerably after tillering stage, corresponding to decrease in photosynthetically active leaf area. Another explanation for the decrease in PhRUE is a decrease in crop growth rate. Results showed the relationship between daily Ac of individual leaves and daily incident PAR. Maximum PhRUE and PhRUE decay can be extrapolated from daily PAR.

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