Indian J. of Agroforestry Vol. 17 No. 2 : 22-26 (2015)

Effect of temporal changes and plantation age on gas exchange characteristics of *Populus deltoides* in the Indo-Gangetic plains of India

Parveen Kumar*, Kailash Singh, Ajay Kumar Mishra, Ashwani Kumar, Rakesh Singh, Poornima Rai, S.K. Chaudhari and D.K. Sharma

ICAR-Central Soil Salinity Research Institute, Karnal- 132 001. Haryana, India

**Corresponding Author Email: pkumarcssri@gmail.com*

ABSTRACT: Temporal changes and plantation age have potential impact on gas exchange characteristics and soil respiration in *Populus deltoides* plantation, which is inferred in the present study. Temporal changes indicated statistically significant variation for gas exchange parameters and soil respiration. Plantation age showed decline trend in gas exchange parameters *viz.* net photosynthetic rate (Pn), transpiration (E), stomatal conductance (gs), intercellular CO_2 concentration (Ci) concentration and water use efficiency (WUE). Whereas, soil respiration (SR) increased with plantation age. During the early rainy season (May), poplar trees showed lowest Pn (8.06 ìmol CO_2 m^{-2} s^{-1}), while at the end of the rainy season (September) poplar showed highest Pn of 20.45 ìmol CO_2 m^{-2} s^{-1}, whereas, the same plant showed 18.03 ìmol CO_2 m^{-2} s^{-1} Pn during the early dry season (January). Significant and positive correlation was also observed between Pn and E (r = 0.803**), Ci and SR (r = 0.819**), gS and PAR (r = 0.753**), which reflected that these gas exchange attributes were correlated. Due to short rotation plantations, fast growth rate and adaptability to a range of environments, physiological and soil related parameters under *Populus deltoides* were significantly influenced by the temporal and plantation age changes which directly influenced the growth, biomass and ultimately the carbon sequestration.

Key words: Gas exchange parameters, *Populus deltoids*, plantation age, soil respiration and temporal changes

Received on: 21/10/2015 Accepted on: 15/12/2015

1. INTRODUCTION

Arid and semi-arid environments cover approximately one third of the world's land area and are among the world's most fragile ecosystems, a condition that is becoming accentuated due to periodic droughts and mounting overexploitation of scarce resources (Malagnoux *et al*., 2007). Global warming is predicted to affect arid lands through temperature increase and rainfall decrease all over the world with only a few exceptions (IPPC, 2007), leading to irremediable natural vegetation loss and a decrease of agriculture, rangeland and forest productivity, accompanied by loss of biodiversity, soil organic matter and soil fertility (Malagnoux *et al*., 2007). In India, fast growing exotic tree species have been introduced on-farm in order to obtain maximum monetary gains from a given land unit in a short period of time. But, the variability of the climate has been a topical issue in a sustainable environment as the crop yield and production is very important that depends on many physiological processes particularly photosynthesis. Photosynthesis alone contributes about 90 per cent of total dry matter production in plants. Globally, mean air temperatures are expected to increase 3 ^{0}C by the year 2100, with warming of up to 6.5 ^{0}C at higher latitudes (Christensen *et al*., 2007). Our ability to predict how this warming might alter terrestrial carbon uptake depends on determining the ability of plants to respond to increasing growth temperatures (Niu *et al*., 2012). We need an improved understanding of how the physiological processes involved in photosynthesis and respiration will acclimatize to warmer conditions, to provide a clear mechanistic framework for predicting future shifts in carbon fluxes from vegetation. *Populus deltoides* based agroforestry system is one of the viable alternate land use systems to prevent further degradation, to obtain biological production on sustainable basis, to ameliorate the environment and potential to mitigate climate change through higher carbon sequestration rate. Poplar (*Populus deltoides*) a winter deciduous tree, which proved to be the most promising tree in irrigated agro-ecosystems of northern India and is being raised either as block plantation or along field boundaries/windbreaks.

Physiological processes are very complex and are influenced by various factors in plants. Temporal aspect is an important factor due to its micro-environmental factors (such as solar radiation, temperature, and soil moisture) greatly affecting plant photosynthesis under field conditions (Kayama *et al.*, 2009). Plant photosynthesis is affected not only by environmental factors, but also by plant endogenous factors i.e. age. Plant age is a key factor which affects plant photosynthetic physiology (Munne-Bosch, 2008), but the effects of stand age on plant photosynthesis are not well understood. In Trans Gangetic plains of India, *Populus deltoides* play critical roles in fixing atmospheric CO_2 *via* photosynthesis. However, very limited information is available on how temporal aspects and plantation age affects the photosynthetic physiology of *Populus deltoides*. Therefore, the present study was conducted to compare the influence of different period of study (temporal) aspects on the photosynthetic physiology of *Populus deltoides*, and to analyze the differences of photosynthetic status in different stand age of *Populus deltoides*. The present study might be of great importance to improve our knowledge about the functioning of these plantations on the Trans-Gangetic plains of India, which can provide us with insights into understanding of photosynthetic acclimation for these communities to different microenvironments.

2. MATERIALS AND METHODS

The study was conducted to estimate physiological parameters (gas exchange characteristics) and soil respiration rate in *Populus deltoides* plantation at Hara Farm (30^0 7'55"N, 77^{0}22' 34"E, 255 m above sea level), Yamunanagar, Haryana (India). The district encompasses the Shivalik hills and foothill rolling plain in the North and North-East, and flood plain along the Yamuna river in the East and South-East. Yamunanagar has sub-tropical continental monsoon climate and experiences extreme conditions of the hottest months (May and June) and the coldest months (December and January). The average annual rainfall of the district is 1107 mm.

Estimation of Gas Exchange Characteristics and Soil Respiration

Leaf gas exchange attributes were studied on the mature and healthy leaves on the south branch at the middle layer of the tree canopy. These were selected to determine the response of net photosynthetic rate (Pn), transpiration (E), stomatal conductance (gs) photosynthetic active radiation (PAR), intercellular CO_2 concentration (Ci) and water use efficiency (WUE= P_N /E) with an infrared open gas exchange system (LI-6400, LICOR Inc., Lincoln, NE, USA). The soil respiration (SR, g CO_2 M^2 H^{-1}) and soil temperature (°C) was measured by an automated soil CO_2 flux system. Long-term soil chambers operating as closed systems were connected to an infrared gas analyzer through a multiplexer (LI-6400, LICOR Inc., Lincoln, NE, USA). PVC collars of 20 cm inner diameter and 11 cm height were inserted in the soil extending 3 cm above the soil surface.

Statistical Analysis

All the data were subjected to variance analysis using the SAS (Version 9.3, SAS Institute Inc., Cary, NC, USA). Duncans multiple test was applied at 5 per cent probability level to compare the mean differences. Correlation analysis was performed to determine the relationship between the traits using the Pearson coefficient procedure.

3. RESULTS AND DISCUSSION

The results of statistical analysis test showed the effect of temporal aspects and plant age on photosynthetic physiology. Significant variability ($p<0.05$) were observed in all studied parameters, as indicated by mean sum of squares.

Effect of Temporal Aspects on Gas Exchange Characteristics

Temporal change showed statistically ($p<0.5$) significant variability for photosynthetic rate (Pn). During the early rainy season (May), poplar trees showed lowest Pn (8.06 µ mol CO_2 m^{-2} s^{-1}) while at the end of the rainy season (September), poplar showed highest photosynthetic rate of 20.45 µ mol CO_2 m^{-2} s^{-1}, whereas the same plant showed 18.03 µ mol CO_2 m^{-2} s^{-1} Pn during the early dry season (January). Similar trend of increase and decrease in the rates of stomatal conductance (gS) and transpiration rate (E) was observed due to temporal variations. The lower photosynthetic rate might be due to lower stomatal conductance derived from higher vapour pressure and lower air temperature (Nishimura *et al.*, 2000; Hirai *et al.*, 2000). Temporal changes also showed significant variations for water use efficiency (WUE). WUE was highest in January (5.58) whereas it was 3.17 and 3.38 in the months of May and September, respectively. Effects of temporal variation on soil respiration and soil temperature were statistically significant. Soil respiration was highest (4.74 g CO_2 m^2 h^{-1}) during the month of January followed by May (3.19 g CO_2 m^2 h^{-1}) and least in the month of September (2.13 g CO_2 m^2 h^{-1}). The maximum soil temperature values were recorded during the month September (30.37 ^{0}C) and least during the month of January (18.96 ^{0}C). Results from the present study showed that with increase in PAR (photosynthetic active radiation) values, the rates of gas exchange attributes also increased. Maximum PAR values were observed in the month of September (863.9) followed during the month of January (854.33) and the minimum in the month of May (831.7). Same trend was recorded for other gas exchange attributes. This observation indicated that PAR was the main limiting factor to study the effects of temporal aspects on the photosynthetic characteristics in *Populus deltoides* (Table 1) which is probably because of the light super saturation phenomenon of photosynthetic rate, making the leaves not adequately absorb and utilize the high-intensity lights attributed to the limit of the enzymatic reaction.

Effect of Plantation Age on Gas Exchange Characteristics

The data related to the effect of plantation age on gas exchange parameters is given in Table 2. Measurements were done in 1- 4 year of poplar plantations to obtain information related to carbon pools, fluxes and carbon sequestration. Poplar trees showed decreased photosynthetic rate with progressive increase in plantations age but the decrease in Pn was not statistically significant. One year poplar tree showed Pn of 18.35 μ mol CO_2 m^{-2} s^{-1} which decreased with plantation age i.e. 16.34 μ mol CO_2 m^{-2} s^{-1} in 2nd year, 13.85 in 3rd year μ mol CO_2 m^{-2} s^{-1} and 13.5 μ mol CO_2 m^{-2} s^{-1} in 4th year poplar trees. Relative to juvenile trees of 1st year, decreases in photosynthetic capacities were also found in mature trees (Day *et al.*, 2001; Myung *et al.*, 2007). Previous studies also indicated that the longer distance between shoot apices and roots in mature trees could decrease the efficient transport of water, nutrients, carbohydrates, etc. between them (Greenwood *et al.*, 2008; Abdul-Hamid and Mencuccini, 2009). Overall, 36.3% reduction was observed in Pn from 1-4 year of plantation where as mean photosynthetic rate across the plantation age was 15.5 μ mol CO_2 m^2 s^{-1}. This drop in the photosynthetic capacity with increasing stand age could be associated with the increasing diameters and heights of poplar tree. Moreover, the nutrient status in the leaves of mature trees may also affect the vigor for photosynthesis (Munne-Bosch, 2008). The nitrogen content of leaves is closely correlated with the photosynthetic capacity (Liberloo *et al.*, 2007), reduced nitrogen contents in the leaves of mature trees might led to a lower photosynthetic capacity (Bond, 2000;

Table 1. Effect of plantation age on gas exchange characteristics (Pn- photosynthetic rate, gS- stomatal conductance, E- transpiration rate, PAR- photosynthetically active radiation, I CO_2 –intercellular CO_2, WUE- water use efficiency), soil respiration and soil temperature in *Populous* plantation

Source of variance	Degree of freedom	Analysis of variance among gas exchange characteristics of different aged Populus plantation (Means sum of squares)								
		P_n (μ mol $CO_2/m^2/sec$)	gS (m mol $CO_2/m^2/sec$)	E (μ mol $H_2O/m^2/sec$)	Leaf temp.	PAR (μ mol/m^2/sec)	I CO_2	WUE (μ mol/m mol)	Soil res p.(g CO_2 m^2 h^{-1})	Soil temp
Rep	2	0.007	0.0001	0.0004	0.097	0.079	0.541	0.000	0.0005	0.02
Time	2	46.645	1.1670**	3.8416	0.579	1620**	1324**	0.456	2.1770	8.67
Error	31	34.582	0.1036	2.7581	23.702	1211.6	1054.5	1.613	1.8688	28.46

Gas exchange characteristics of different aged Populus plantation

Plantation age (year)	P_n	gS	E	Leaf temp.	PAR	I CO_2	WUE	Soil resp.	Soil temp (^{o}C)
1	18.35	1.35^a	4.74	26.70	903.75^a	238.38^c	3.90	2.66	26.72
2	16.34	0.84^b	4.20	26.19	863.77^b	328.52^a	4.02	3.82	25.93
3	13.85	0.64^b	3.74	26.29	820.50^c	291.72^b	3.88	3.44	24.49
4	13.50	0.54^b	3.20	26.14	811.92^c	306.33^{ab}	4.37	3.49	25.05
Mean	15.51	0.84	3.97	26.33	849.98	291.24	4.04	3.35	25.55
CV (%)	37.92	38.27	41.84	18.49	4.10	11.15	31.42	40.78	20.88

Means with at least one letter common are not statistically significant ($p < 0.05$) using DUNCAN's Multiple Range Test

Table 2. Effect temporal variation on gas exchange characteristics (Pn- photosynthetic rate, gS- stomatal conductance, E- transpiration rate, PAR- photosynthetically active radiation, I CO_2 –intercellular CO_2, WUE- water use efficiency), soil respiration and soil temperature in *Populous* plantation

Source of variance	Degree of freedom	Analysis of variance among gas exchange characteristics of *Populus deltoides* (Means sum of squares)								
		P_n (µ mol $CO_2/m^2/sec$)	gS (m mol $CO_2/m^2/sec$)	E (µ mol $H_2O/m^2/sec$)	Leaf temp.	PAR (µ mol/m^2/sec)	I CO_2	WUE (µ mol/m mol)	Soil res p.(g CO_2 m^2 h^{-1})	Soil temp. (°C)
Rep	2	0.007	0.0001	0.0004	0.097	0.079	0.54	0.000	0.0005	0.020
Time	2	517.315**	0.3305	40.5987**	351.041**	3277.30	477.93	21.513**	20.748**	418.74**
Error	31	4.605	0.1919	0.4216	0.346	2528.50	2270.51	0.218	0.6806	1.369

Temporal variation in gas exchange characteristics of *Populus deltoides*

Treatments	P_n	gS	E	Leaf temp.	PAR	I CO_2	WUE	Soil resp.	ST
January	18.03^b	0.83	3.29^b	20.69^c	854.33	283.97	5.58^a	4.74^a	18.96^c
May	8.06^c	0.68	2.56^c	26.83^b	831.72	294.45	3.17^b	3.19^b	27.32^b
September	20.45^a	1.01	6.05^a	31.48^a	863.90	295.29	3.38^b	2.13^c	30.37^a
General Mean	15.51	0.84	3.97	26.33	849.98	291.24	4.04	3.35	25.55
CV (%)	13.84	52.08	16.36	2.23	5.92	16.36	11.55	24.61	4.58

Means with at least one letter common are not statistically significant ($p < 0.05$) using DUNCAN's Multiple Range Test

Feng *et al.*, 2004). Similar pattern of decrease was also recorded for gS and E. Statistical significant ($p<0.5$) variation were observed for gS with mean value of 0.84 mmol CO_2 m^{-2} s^{-1} across the plantation age. Mean transpiration rate was 3.97 mmol H_2O $m^{-2}s^{-1}$ whereas reduction was observed by 48% from 1st to 4th year of plantation age. The decrease in gas exchange attributes particularly gS (stomatal conductance) might be due to loss of integrity of chloroplast with the increase in plant age (Thornton and Wample, 1980). PAR values also decreased with plantation age and reduced by 11.3% from 1-4 year of plantation. WUE did not show any significant variation with plantation age (Table 2). Soil respiration and soil temperature were statistically similar among different age of poplar plantation.

Pearsons Correlation Analysis

Association analysis showed significant interaction among different traits in *Populus deltoids* (Table 3). Highest significant and positive correlation was observed between soil and leaf temp. (r = 0.954**). Significant and positive correlation was also observed between Pn and E (r = 0.803**), Internal CO_2 and soil respiration (r = 0.819**), gS and PAR (r = 0.753**) which reflected that these gas exchange attributes were correlated. Significant and negative correlation of leaf temp was observed with soil respiration (r = -0.862**) and WUE (r = -0.828).

4. CONCLUSION

Results concluded that PAR was the main limiting factor for the photosynthetic characteristics that make the leaves adequately not absorb and utilize the high-intensity lights attributed to the limit of the enzymatic reaction in *Populus deltoides*. Whereas, stand age also cause drop in the photosynthetic capacity due increasing diameters and heights of poplar tree.

Table 3. Pearsons correlation association analysis of temporal variation and stand age in *Populous* plantation

Traits	P_n	gS	E	Leaf temp.	PAR	I CO_2	WUE	SR	ST
P_n	1	-0.055	0.803**	0.111	0.513**	-0.168	0.331*	-0.112	-0.016
gS		1	-0.050	0.068	0.753**	-0.582**	-0.055	-0.152	0.099
E			1	0.662**	0.433**	-0.131	-0.283	-0.613**	0.538**
Leaf temp.				1	0.064	0.063	-0.828**	-0.862**	0.954**
PAR					1	-0.453**	0.135	-0.132	0.184
WUE						1	-0.014	0.323	0.031
I CO_2							1	0.819**	-0.841**
SR								1	-0.806**
ST									1

**Correlation is significant at the 0.01 level, *Correlation is significant at the 0.05 level.

ACKNOWLEDGEMENTS

We express our sincere gratitude to the Department of Science and Technology, New Delhi, for providing financial support to conduct the study. We convey our thanks to late Sh. Surinder Singh Hara, Mr. Kuldeep Singh Rana and Mr. Vishwas Tyagi and other staff of Hara farm for providing us research platform and logistics support for the present study. We thankfully acknowledge the help and support of Director and Head, Division of Soil and Crop Management, CSSRI, Karnal, Haryana. Thanks to Mr. Girraj Prasad Meena for assistance in lab and field work.

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