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Diurnal and seasonal trends in photosynthetic performance of *Dalbergia sissoo* Roxb. and *Hardwickia binata* Roxb. from a semi-arid ecosystem

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Abstract

Diurnal and seasonal trends in net photosynthetic rate (P_N), stomatal conductance (g), transpiration rate (E), vapour pressure deficit, temperature, photosynthetic photon flux density , and water use efficiency (WUE) were compared in a two-year-old *Dalbergia sissoo* and *Hardwickia binata* plantation. Mean daily maximum P_N in *D. sissoo* ranged from 21.40±2.60 µmol m^{-2} s^{-1} in rainy season I to 13.21±2.64 µmol m^{-2} s^{-1} in summer whereas in *H. binata* it was 20.04±1.20 µmol m^{-2} s^{-1} in summer and 13.64±0.16 µmol m^{-2} s^{-1} in winter. There was a linear relationship between daily maximum P_N and g_s in *D. sissoo* but there was no strong linear relationship between P_N and g_s in *H. binata*. In *D. sissoo*, the reduction in g_s led to a reduction in both P_N and E enabling the maintenance of WUE during dry season thereby managing unfavourable environmental conditions efficiently whereas in *H. binata*, an increase in g_s causes an increase of P_N and E with a significant moderate WUE.

Additional key words: net photosynthetic rate; photosynthetic photon flux density; species differences; stomatal conductance; temperature; transpiration rate; vapour pressure deficit; water use efficiency.

Introduction

Depletion of forest cover in semi-arid regions has resulted in an environmental crisis. The extent and distribution of arid and semi-arid areas are subject to modification due to climate change, fire, and land use (Lenihan *et al.* 2003). Through augmenting fuel wood production large scale plantations of multipurpose agroforestry tree species such as *Dalbergia sissoo* and *Hardwickia binata* hold great potential in improving soil fertility (by symbiosis), controlling land degradation on one hand and meeting the demands for food, fodder, fibre (during the lean period), fuel wood, and timber on the other hand.

D. sissoo is a large deciduous tree that grows to an average of 25 m in height and 1.9 m in diameter. It is a premier timber species of rosewood genus because of its hardwood and high durability. Besides, it is important for firewood, shade, shelter, and fodder. Due to growing demand this economically important tree species has been planted and grown extensively outside its natural regions both in agricultural and marginal lands in Indian subcontinent. *H. binata* is also a deciduous, valuable indigenous multipurpose tree in India. It is a moderately-sized to large tree, up to 24–30 m tall, girth 1.8–3.0 m with a clean bole up to 12–15 m; graceful and dropping slender branches. The tree yields extremely hard, very heavy, and durable timber apart from high quality fuel-wood (Roy 1996) and rich fodder in terms of crude protein (Singh 1982). The use of *H. binata* as a main tree component in silvi-pasture (Hazra 1995) and an agro-silviculture (Gill 1998) has been studied extensively. The success of such multipurpose tree plantations depends on their productivity, which in turn is determined by the interaction of physiological factors with the environment. Physiological processes that determine productivity of a tree include photosynthesis, respiration, and partitioning of photosynthates within the tree, duration of active growth, and seasonal and diurnal patterns of CO_2 assimilation. Despite the considerable value of wood

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and timber, information is still scanty on the performance of young multipurpose tree plantations under natural conditions in the semi-arid eco-climatic regions of India.

Instantaneous measures of water use efficiency (WUE) are important for understanding short term plant water budget. It is often useful to model water use and loss over longer time scales using $\delta^{13}C$ stable isotopes (Sharifa Gullamhusein 2005). This integrative approach allows for tracing the source and fate of water and carbon dioxide at the ecosy stem level. Understanding seasonal changes in photosynthetic parameters and stomatal conductance (g_s) is crucial for modelling long-term carbon uptake and energy fluxes of an ecosystem. A prime focus of much research in the bio-geo-sciences is on the net carbon balance of an ecosystem (Xu and Baldocchi 2003). Such work requires the assessment of CO_2 fluxes on hourly, daily, seasonal, and yearly time scales and of leaves, individual plants, and array of plants (Baldocchi 2003).

Diurnal trends in gas exchange belong to the best indicators of the ability of plants to maintain their photosynthetic apparatus to readily respond to environment (Geiger and Servaites 1994, Li *et al.* 2007). We compared gas exchange of two multipurpose tree species and investigated (*1*) the extent to which net photosynthetic rate (P_N), g_s, transpiration rate (E), vapour pressure deficit (VPD), and WUE are affected by seasonal climatic changes, (*2*) diurnal trends in P_N, g_s, E, VPD, and WUE, and (*3*) the relationships between P_N and g_s, P_N and E, and P_N and photosynthetic photon flux density (PPFD).

Materials and methods

The study site was located at the Biomass Research Centre, Madurai Kamaraj University (latitude 10°00'N; longitude 78°10'E; elevation 133 m above m.s.l.) in Southern India. The mean annual rainfall was 600 mm (500–700 mm) during October–December while March, April, and the early May were virtually rainless. The soil at the experimental site is lateric loam with pH 8.5. Daily maximum and minimum atmospheric relative humidities ranged 50.3–63.5 % and 37.0–43.0 %, respectively.

Plants: Pods of *D. sissoo* and the seeds of *H. binata* were soaked in water at room temperature for 24 h and sown in mother beds. The germinated seedlings with two to four leaves were transferred to polythene bags of 30 cm height and 15 cm diameter filled with soil, sand, and farmyard manure (2 : 1 : 1). The seedlings were kept under tree shade for the first two months and then grown in nursery under open sunlight for six months. The seedlings in the polythene bags were placed on raised stands to prevent root penetration into soil. The seedlings were irrigated in the morning on every alternate day. After six months of nursery growth the seedlings were removed from polythene bags and planted at 2×2 m spacing (2 500 seedlings per ha). Irrigation was done every alternate day for about six months from the date of plantation to enhance seedling survival. The irrigation was stopped once the seedlings were established and acclimated. The study was carried out in a completely randomized sampling plot in three replicates of 3–5 plants. For each plant, measurements were made on a total of 3–5 leaves in both species, *i.e.* average of five plants was the average of several leaves.

Physiological measurements: Full diurnal and seasonal courses of P_N, g_s, E, VPD, and WUE were measured under ambient conditions using portable photosynthesis system (*LI-6400*, *Li-Cor*, Lincoln, NE, USA) equipped with a CO_2 control module. Monthly measurements of these parameters were conducted between July 2004 and June 2005, when the trees attained the age of two years. All measurements were made on clear sunny days. However, the experiments had to be precluded during November and December 2004 due to extended cloudy and rainy days. For all the measurements, healthy and fully expanded leaves were used. However, mature leaves undergoing senescence were often used during the months of February and March 2005 in *D. sissoo*. Diurnal measurements were made on a minimum of three leaves per sapling and five saplings for every two hour intervals between 06:00–18:00 h. Shorter sets of measurements were made during rainy season when it was nearly impossible to get a complete diurnal set of measurements on a given day because of heavy cloud built up almost every afternoon.

Statistical analysis: One way analysis (ANOVA) was used to determine the significant variation for each parameter at different time interval and season. Linear regression was used to analyze the relationship between P_N and g_s, P_N and PPFD, P_N and E, and g_s and E for both the species. Comparisons of two species during the season in P_N, g_s, E, VPD, and WUE were made using two-factor analysis in co-stat (Gomez and Gomez 1984).

Results

Mean daily changes in microclimatic parameters during the period of study were: the maximum air temperature of the day 27 °C (rainy season) to 44 °C (summer season) and night temperature of 20–23 °C. The maximum PPFD of the day ranged approximately from 1 200 (rainy season) to 2 000 (summer season) $\mu mol\ m^{-2}\ s^{-1}$ (Fig. 1).

Seasonal trends: There were significant differences (p<0.001) in P_N, g_s E, VPD, and WUE in response to seasonal environmental change. Seasonal trends were similar for P_N, g_s, E, and WUE. In *D. sissoo*, maximum P_N (21.4±2.6 µmol m^{-2} s^{-1}) was observed in rainy season I (July–September 2004) but it declined significantly (p<0.001) (13.21±2.6 µmol m^{-2} s^{-1}) in summer (March–May 2005), whereas in *H. binata*, the maximum P_N was 20.04±1.2 µmol m^{-2} s^{-1} in summer and minimum in winter (January–February 2005), 13.64±0.16 µmol m^{-2} s^{-1}. The E in *D. sissoo* was highest in rainy seasons I and II (7.41±0.58 mmol m^{-2} s^{-1}) and lowest in winter (4.40±0.20 mmol m^{-2} s^{-1}). In *H. binata*, the maximum E was observed in rainy season I (8.07±1.60 mmol m^{-2} s^{-1}) and minimum in rainy season II (6.08±0.26 mmol m^{-2} s^{-1}). The maximum VPD of 3.76±1.00 kPa was observed in *D. sissoo* and 5.33±0.15 kPa in *H. binata* and the minimum of 2.50±0.04 kPa in winter in *D. sissoo* and 2.14±0.18 kPa in rainy season II in *H. binata*. Higher WUE (5.87±1.50 mmol m^{-2} s^{-1}) was observed in *D. sissoo* during summer compared to *H. binata* (5.55±0.79 mmol m^{-2} s^{-1}).

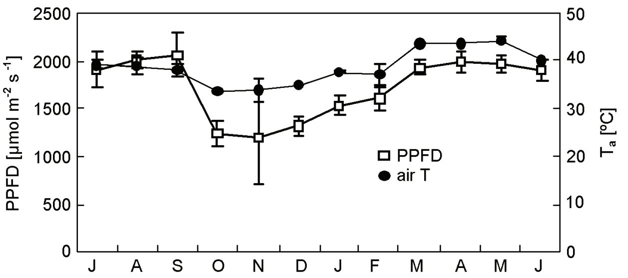

Fig. 1. Average daily maximum air temperature (T_a) and photosynthetic photon flux density (PPFD) from July 2004 to June 2005.

Diurnal physiological trends: There were significant (p<0.001) interactions between the two species with reference to time of the day for all the parameters such as P_N, g_s, E, VPD, and WUE. In both the species, maximum rates of P_N occurred around 10:00 h in all seasons except in rainy season II (October–December) when maximum rates were attained around 12:00 h.

In *D. sissoo*, two peaks were observed in summer, the first at 10:00 h (14.96±1.10 µmol m^{-2} s^{-1}) and the second

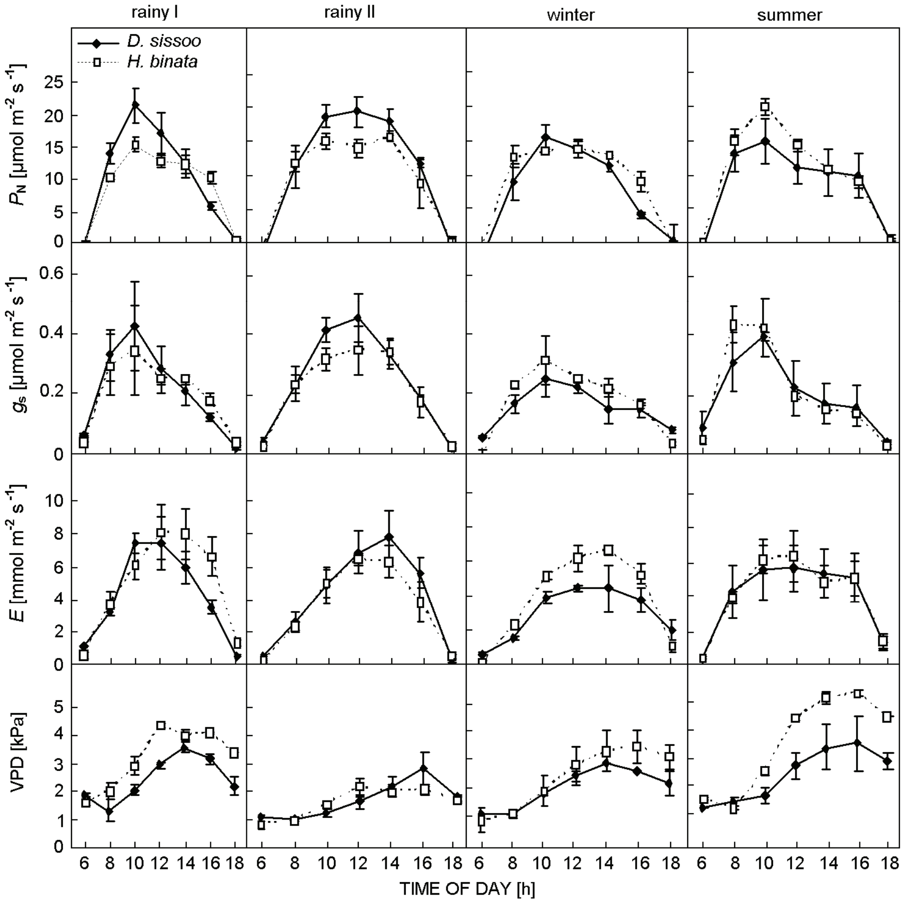

Fig. 2. Seasonal and diurnal trends in net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E), and vapour pressure deficit (VPD) in *D. sissoo* and *H. binata* measured in first rainy (June–August), second rainy (September–December), winter (January–February), and summer (March–May) seasons. Means±SE, n = 5.

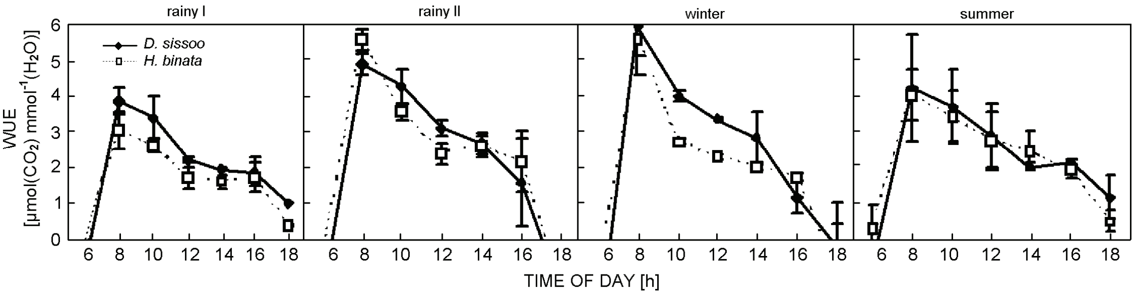

Fig. 3. Seasonal and diurnal trends in water use efficiency (WUE) in *D. sissoo* and *H. binata* measured between July 2004–June 2005. $n = 5$.

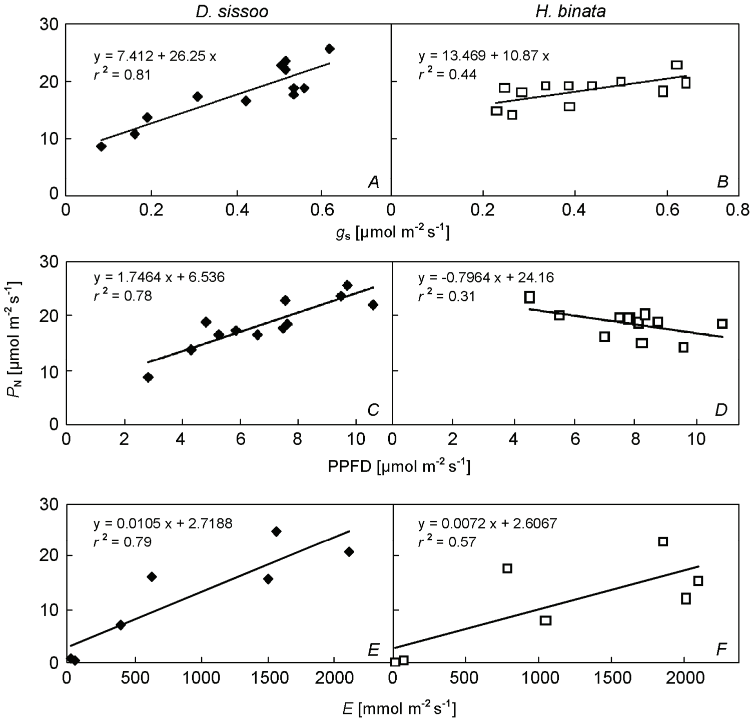

Fig. 4. The relationships between stomatal conductance (g_s; *A, B*), transpiration rate (*E*; *C, D*), or photosynthetic photon flux density (PPFD; *E, F*) and net photosynthetic rate (P_N) in *D. sissoo* (*A, C, E*) and *H. binata* (*B, D, F*) by plotting individual values from each measurement day against concurrent values ($p<0.001$). $n = 5$.

one at 14:00 h (12.60±0.90 μmol m^{-2} s^{-1}). There was significant ($p<0.001$) decline in P_N in summer after 08:00–10:00 h with a slight increase around 14:00 h. *H. binata* also showed double peaks, the first one at 10:00 h and the second at 14:00 h during rainy season I (15.41±1.08 μmol m^{-2} s^{-1}; 12.89±1.50 μmol m^{-2} s^{-1}) and II (15.06±1.17 μmol m^{-2} s^{-1}; 15.71±0.70 μmol m^{-2} s^{-1}), respectively.

In *D. sissoo*, P_N and g_s measured in the afternoon were always lower than those in the morning, whereas in *H. binata*, g_s slightly increased during the late afternoon. In all the months, PPFD was a limiting factor for P_N before 08:00 h and after 16:00 h for both the species. In *D. sissoo*, the maximum *E* was observed in rainy seasons I and II at 12:00 h but in winter and summer it showed significant reduction ($p<0.001$). Almost similar trends were observed in *H. binata* also. In *H. binata*, the maximum *E* was reached at 12:00 h and continued till 14:00 h in all months except for few months.

The VPD varied between 0.80 (morning) and 1.30 (afternoon) kPa in rainy season and between 1.30 (morning) and 3.76 (afternoon) kPa in summer in *D. sissoo* whereas in *H. binata* VPD varied between 0.90 (morning) and 1.40 (afternoon) kPa in the rainy season and between 1.54 (morning) and 5.33 (afternoon) kPa in summer (Fig. 2).

WUE was always higher in the morning (08:00 h) than in the afternoon in both the species. Significant ($p<0.001$) reduction in WUE was observed during summer when compared to the other seasons (Fig. 3).

Leaf temperature (T_l) also varied greatly during the day. Increase in air temperature (T_a) gradually increased T_l throughout the day along with the increase in VPD until the respective maximum values of 41 °C and 5.17 kPa were reached. The maximum P_N was reached at a T_l of about 33–36 °C and then it decreased as T_l and T_a increased ($p<0.001$) for both the species.

To illustrate the relationship between P_N and g_s, we related leaf P_N to g_s. In *D. sissoo*, for all seasonal measurements the regressions were significant ($p<0.001$) ($r^2 = 0.81$) (Fig. 4*A*) whereas in *H. binata,* the relationship was not so strong ($r^2 = 0.44$) (Fig. 4*B*). In *D. sissoo*, P_N and E were under strong stomatal control ($r^2 = 0.78$) over a large range of environmental conditions, whereas in *H. binata* ($r^2 = 0.31$), the stomatal control was not as strong as in *D. sissoo* (Fig. 4*C,D*).

During all the diurnal measurements in summer, a decline in P_N and g_s associated with high PPFD and increase in VPD was observed. In *D. sissoo* except for summer, P_N and g_s followed the PPFD ($r^2 = 0.79$) better than in *H. binata* ($r^2 = 0.57$) (Fig. 4*E,F*).

Discussion

We used leaf-level photosynthetic measurements to compare the physiological responses of *D. sissoo* and *H. binata* to daily and seasonal micro-climatic changes. Replications of photosynthetic observations measured allowed quantify the relative magnitude of the effect of diurnally and seasonally varying environmental conditions on *in-situ* photosynthesis. P_N, g_s, E, and WUE varied considerably across the day reaching maximum in the mid-morning and minimum in the afternoon during which the T_l and T_a, VPD, and PPFD increased considerably. In *D. sissoo*, P_N and g_s were maximum with the significant positive correlation between P_N and g_s which is consistent with the results of Rawat and Singh (2000). In *H. binata*, there was no such strong positive correlation between P_N and g_s. This is similar to the results of Caemmerer *et al.* (2004) in which g_s did not correlate with photosynthetic capacity in transgenic tobacco containing reduced amounts of ribulose-1,5-bisphosphate carboxylase/oxygenase. In *D. sissoo*, the average P_N and g_s over the site decreased significantly in March due to summer drought (Xu and Baldocchi 2003). However, in *H. binata* the increased g_s along with increased P_N and E and moderate WUE were observed in high VPD, temperature, and PPFD. The values of P_N are determined largely by the characteristics of the photosynthetic machinery, including the capacity which is not fixed but changes with irradiance, temperature, and nutrient supply during plant growth so that P_N changes both diurnally and seasonally (Lawlor 2001). Our results are consistent with the previous reports as far as *D. sissoo* is concerned: g_s was closely related to P_N, environmental VPD, and soil water status (Franks *et al.* 1997, Sellin 1999). Under dry soil conditions the stomatal limitation to CO_2 influx into mesophyll is the primary cause of photosynthetic depression observed in mature tissue (Ishida *et al.* 1999). We showed that D. *sissoo* had mature leaves the senescence of which might have caused the reduction in P_N. In addition, the decreased g_s may be the result rather than the cause of decreased photosynthesis (Fiscus *et al.* 1997). Like other plant species, *H. binata* experiences a pronounced midday depression in P_N under semi-arid conditions. Excess radiant energy often occurs with a high T_l and T_a, and water deficit is a major environmental stress and causes midday depression of photosynthesis (Tenhunen *et al.* 1981). This could also be attributed to the variation in high PPFD along with a substantial increase in VPD (Pathre *et al.* 1998). However, *H. binata* did show a two-peaked response characterizing afternoon recovery after midday depression in P_N. Whitehead (1998) demonstrated that for large woody plants the short-term responses of stomata are probably brought about by hydraulic signals that affect g_s by triggering the release of abscisic acid in leaves thereby reducing P_N. Stomatal closure and photo-inhibitory damage are the major physiological factors responsible for the midday depression (Mott and Parkhurst 1991). Raising transpiration demand may also result in deeper midday depression in *H. binata*.

Stomatal closure can be induced by a large leaf–air VPD and low leaf water potential (Mott and Parkhurst 1991) would decrease the CO_2 concentration in the intercellular spaces (C_i) (Tenhunen *et al.* 1981). We may presume that *H. binata* grown under low VPD (rainy/monsoon season) when exposed to a relatively dry environment (summer) shows strong stomatal response to dry air atmosphere with double-peaked diurnal activity.

Our results for *D. sissoo* are consistent with the measurements over ecosystems in Mediterranean climates (Wilson *et al.* 2003). Influenced by extremely high T, high VPD, and low soil moisture content, photosynthesis peaked at 10:00 h and shut down quickly during the course of the day in the dry summer period (March). The lower P_N in the afternoon must be the result of intrinsic changes in the efficiency of the photosynthetic apparatus and also due to the increase in T_l; even plants adapted to tropical environment are often exposed to daytime temperature higher than optimum one (Prior *et al.* 1997).

Leaves of *D. sissoo* could withstand higher PPFD (up to 2 200 μmol m^{-2} s^{-1}) than their saturating limit (1 600 μmol m^{-2} s^{-1}) without much reduction in P_N which substantially provided VPD was favourable. Except for summer, P_N and g_s followed the PPFD, which indicated the absence of severe water stress; this has also been demonstrated experimentally in other plant species (Pathre *et al.* 1998). High VPD may have reduced g_s and subsequently P_N. This may be quantified as an indirect effect of VPD on P_N (Bassow and Bazzaz 1998). Our field data obtained from *D. sissoo* highlighted a trend towards lower g_s during summer which is consistent with the results of studies made by Kaiser (1987) and Mott and Parkhurst (1991). In view of strong g_s mean value drop, a reduction in E was possible, thereby helping to maintain the leaf water status in dry season which prevails with high VPD values. This indicates that sensitive control of transpiration could be carried out by narrowing the stomatal pore thereby disagreeing with free transpiration hypothesis. The *E* also increased with increase in VPD and then decreased gradually at higher VPD; the phenomenon is known as feed forward response which may be associated with patchy stomatal closure for limited CO_2 supply to chloroplast (Kaiser 1987, Mott and Parkhurst 1991). The significant reduction in P_N and *E* allows the maintenance of WUE. Stomatal aperture responds to transpiration demand which varies with T_l and VPD (Mott and Parkhurst 1991). This greater control of g_s upon *E* may have been effective for maintenance of water potential in dry season by reducing water loss to atmosphere (Chaves *et al.* 2002). Similar results were obtained by Cui *et al.* (2004) in *Syringa pinnatifolia* where a low g_s along daytime did benefit to obviously reduce *E* and promote instantaneous WUE. This altered the efficiency of conversion of intercepted radiant energy to photoproducts which becomes more strongly influenced by atmosphere, environmental conditions, and time of the day.

In conclusion, the significant differences between *D. sissoo* and *H. binata* in all leaf gas exchange parameters, both in diurnal and seasonal trends, were apparent especially during the dry summer season. As in many Mediterranean and tropical species, the stomatal closure in *D. sissoo* during summer constitutes a mechanism to cope with diurnal and seasonal water deficits. *H. binata* remained with open stomata during the summer season, influencing the CO_2 assimilation. The net carbon gain was comparatively higher in *D. sissoo* than in *H. binata*. Even though both the species are deciduous, *H. binata* has obvious advantages in avoiding unfavourable periods, for instance, the midday depression of photosynthesis as it is likely to be one of the most important factors to understand acclimation of photosynthesis to irradiance in natural environment. But in *D. sissoo* the major adaptation to seasonal severe drought appears to be leaf senescence which was observed during the dry summer time (March). The seasonal course of carbon gain and water turnover exhibited in *D. sissoo* shows that stomatal acclimation to the weather patterns may change either by increasing carbon gain on the one hand or limiting water loss on the other. As long as there is no water stress, stomata may acclimate to allow higher P_N, together with a higher water loss especially during and after the rainy season when the soil water content is large. On the other hand, during periods of persistent high atmospheric evaporative demand due to high temperature, VPD, and depleted soil water buffering, acclimation limits excessive water loss as a first priority, thereby allowing lower carbon gain.

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