Abstract  Field studies of gas exchange of *Populus deltoides*, *Prosopis juliflora* and *Acacia auriculiformis* showed large diurnal changes in net photosynthesis (A) and stomatal conductance (gₛ) during autumn. *P. deltoides* and *P. juliflora* undergo pronounced midday depression in A and gₛ while *A. auriculiformis* showed a one-peak response. Several factors indicative of photosynthetic performance were found to be reversibly affected during afternoon decline. These include (i) decrease in initial slope of the CO₂ response curve (carboxylation efficiency), (ii) substantial increase in CO₂ compensation point and (iii) decrease in overall quantum yield of photosystem II. The phenomenon can be duplicated in potted plants by simulating a typical daily pattern of PPFD and VPD. It is found that high VPD induces significant decline in A and gₛ at moderate temperature and saturating PPFD (800 µmol m⁻² s⁻¹) whereas these parameters are only marginally affected at high PPFD and low VPD. Fluorescence data show that the tree species under study have a high capacity for safe dissipation of excessive excitation energy. The activation of photorespiration, as evident from an increase in CO₂ compensation point, maintains constant internal CO₂ concentration (Cᵢ) which may aid in minimizing photoinhibition during stomatal closure at midday. In case of *P. deltoides* and *P. juliflora* the stomata seem to be quite sensitive to the changes in humidity whereas this does not appear to be essential in case of *A. auriculiformis* because of its phyllode structure that endows it with mechanisms for conserving water without undergoing large-scale stomatal changes.

Key words  *Acacia auriculiformis* · Gas exchange · Midday depression · *Populus deltoides* · *Prosopis juliflora*

Introduction  The studies of diurnal variations of light saturated net CO₂ assimilation in trees growing in Mediterranean and temperate climates were often reported to be associated with typical midday depression in A and gₛ. However very little, if any, information on such parameters on trees growing in tropical regions is available. We are studying the ecophysiology of few trees capable of growing on the marginal soils (of high pH and high salt content) and the extreme climates of north India, these include *Acacia auriculiformis*, *Prosopis juliflora* and *Populus deltoides*. *P. deltoides*, though native to temperate climates, was also found to be performing well on the marginal soils under field trials. The selected tree species also have different leaf types (*A. auriculiformis* has a phyllode, *P. juliflora* has compound leaves and *P. deltoides* has typical broad leaf). Seasonal studies of photosynthetic parameters showed that only in late monsoon *P. juliflora* and *P. deltoides* exhibited typical midday depression of gas exchange, while in case of *A. auriculiformis* only one peak response for photosynthesis and stomatal conductance was observed.

A number of possible causes of midday decline of gas exchange have been suggested including an increase in leaf-to-air VPD differences (Tenhunen et al. 1987; Roesler and Monson 1985; Raschke and Resemann 1986) and feedback inhibition of photosynthesis by carbohydrate accumulation (Azcon-Bieto 1986; Foyer 1988). It has also been suggested that the reason for midday decline of gas exchange could be long periods of high PPFD (Kuppers et al. 1986; Chaves et al. 1987; Correia et al. 1990). There are several reports indicating the involvement of photosynthetic apparatur in afternoon decline in gas exchange. It has been reported that carboxylation efficiency (CE) as well as photosynthetic capacity depressed during midday in species such as *Arbutus unedo* (Resemann and Raschke 1984; Belseylag et al. 1987; Demming-Adams et al. 1989), *Quercus suber* (Tenhunen et al. 1984) and *Vitis vinifera* (Correia et al. 1990). Photochemical studies carried out with techniques...
like chlorophyll fluorescence measurements and oxygen evolution by leaf discs revealed that photosynthesis was strongly and reversibly affected at chloroplast level during midday depression in *Arbutus unedo*, (Demming-Adams et al. 1989). Similar observations were reported for *Q. petraea* during drought under field conditions (Epron et al. 1992).

Our earlier studies have indicated that afternoon decline in photosynthesis observed in *A. auriculiformis*, *P. deltoides* and *P. juliflora* may either be associated with increase in VPD and/or high PPFD in absence of stressful temperatures. In the present study, we have attempted to analyze the relative contribution of light and VPD in midday depression using gas exchange techniques and portable fluorometer, which is capable of true in situ measurements under field conditions.

**Materials and methods**

The experiments were conducted during a warm-weather period after the last monsoon rains in the month of October, at the terrace garden of the institute. The study was carried out on 1-year-old plants of *P. deltoides*, *P. juliflora* and *A. auriculiformis*, grown in pots under natural conditions. All the experiments were carried out in a 30 day period to avoid seasonal changes.

**Gas exchange measurements in the field**

Diurnal exchange of CO₂ and water vapour was measured on attached fully expanded leaves, using a Li-Cor model 6200 portable photosynthesis system, incorporating a model 6250 infra-red gas analyzer and 1-l chamber (Li-Cor). Diurnal measurements were made on the mature leaf of three trees of each species. The same leaf was analysed for each sampling time throughout the day. The measurements were made for 2 days during the season. Each leaf was fully exposed and oriented normal to light during measurements to ensure the measurements of gas exchange at the highest possible PPFD. The instrument also gives online measurements of possible PPFD. The equation used for calculation are those reported by von Caemmerer and Farquhar (1981) as detailed in Li-Cor technical reference manual (1987). Calibration of the IRGA was performed using authentic gases from Li-Cor, Neb., USA.

Diurnal changes in CO₂ response curve (AC) were measured according to McDermitt et al. (1989). A baseline response curve was measured by placing fully expanded leaf/leaflets in a 1-l chamber and allowing CO₂ to deplete until the compensation point was reached. During measurements care was taken to moderate the temperature increase as described by McDermitt et al. (1989). The data for A, g, and Ci were computed approximately every 5 ppm as the mole fraction of CO₂ in the chamber declined. Since each measurement of AC requires 30–45 min only five measurements could be made under saturating light over the entire day.

**Fluorescence measurements**

Fluorescence measurements were made using a newly developed modular fluorescence system (PAM-2000, Walz, Germany) which combines the advantages of the Walz PAM-101 system with easy portability. The system is incorporated with all the required light sources such as modulated red, actinic red (=650) or white (<710 nm), saturation pulse (halogen) up to 12 000 μmol m⁻² s⁻¹ and far-red (peak wavelength =735 nm) and could be operated via a notebook computer. The fluorescence parameters initial fluorescence yield (F₀), maximum fluorescence yield (Fm′), variable fluorescence yield (Fv′), Fv′/Fm′, 1-YIELD/YIELDmax, photochemical quenching (qP) and nonphotochemical quenching (qN) are displayed or calculated online (for nomenclature see Van Kooten and Snel 1990). The measurements area, depending on the distance of the glass fiber optics, covers only 0.3–0.5cm² of the leaf and hence several measurements (10–12) were made covering the area used for gas exchange measurements using the Li-Cor 1-l leaf chamber. In case of *P. juliflora* at least 15 measurements were made on different leaflets of a single plant.

Ideally, Fv′ should be determined under conditions where all PSI reaction centers are in the oxidized state. This is difficult to accomplish for leaves which have reached steady state in light under field conditions, even when the light energy from the “measuring” beam is kept as low as possible. The effect of imposing a background of far-red (to oxidize any PSI centers by preferential excitation PSI) was therefore determined routinely. The minimum value of fluorescence emission (F₀), whether obtained with or without far-red was taken as a measure of Fv′. The fraction of PSI reaction centers that were in the reduced state (“closed” centers), or the reduction state of the primary acceptor, Q₀ was calculated according to Dietz et al. (1985) as Q₀/Q = (1-qP).

**Laboratory measurements**

For studying the effect of light and VPD the potted plants were transferred to a greenhouse and gas exchange was measured under controlled conditions of light and VPD. The temperature was not controlled but under laboratory conditions it only varied between 30 and 33°C. The light was provided from a halogen lamp of a projector using neutral density filters. The VPD in the 1-l chamber was adjusted using a dew point generator (model Li 610). The gas exchange was measured with a Li-Cor model 6200 portable photosynthesis system, incorporating an analog output for the recorder. During measurements the fully expanded leaf was exposed to given light and VPD, the system was equilibrated in open mode and when no change was detected on recorder for the air vapour pressure inside the chamber, the system was closed and measurements were taken. Inside the greenhouse the ambient CO₂ levels were maintained the same as outside using exhaust fans and proper ventilation to facilitate the measurements of photosynthesis in a closed system. Secondly, while gas exchange rates were being determined with one leaf, the other leaves of the plant were kept in dim light and at room temperature. This ensured low whole plant transpiration rates and therefore, prevented the development of a plant internal water deficit.

**Results**

In order to establish the midday depression of photosynthetic CO₂ uptake occurring in plants which were chosen for this investigation, diurnal patterns of CO₂ exchange were measured on a number of leaves. Typical daily patterns of A and g for *P. deltoides*, *P. juliflora* and *A. auriculiformis* during autumn are shown in Fig. 1. A pronounced midday depression in both A and g was clearly evident in *Prosopis* and *Populus*. In *A. auriculiformis* depression is slight with partial recovery. In both *Prosopis* and *Populus* maximum values for A and g were observed in the morning between 0800 and 0900 hours and then a sharp decline occurred so that by early afternoon (1130–1400 hours) A decreased to 20–30% and g to 25% of the morning maxima. The Ci remained mostly unaltered from 0800–1600 hours in all three species. PPFD was saturating for most of the day. Leaf tempera-