

## Is dew useful for Himalayan plants?

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**Dew formation is a common phenomenon during October to February for plants growing in the tropical and subtropical Himalaya. Occurrence of dew for such a lengthy period may have important implications on ecophysiological responses that contribute to the growth, survival and productivity of plants. A perusal of the literature, however, shows conflicting reports on the impact of dew formation in plants. Further, such studies are also lacking for Himalayan plants. The present study was, therefore, undertaken with twin objectives: (i) to understand the effects of dew on photosynthetic rate, photochemical efficiency of photosystem II ( $F_v/F_m$  ratio), transpirational water loss, stomatal conductances for  $CO_2$  and water vapour, intercellular  $CO_2$  concentration, water use efficiency (WUE) and relative water content (RWC) in the leaves of three multipurpose evergreen tree species, viz. *Boehmeria rugulosa* Wed., *Grewia optiva* Drummond and *Olea glandulifera* Wall. ex G. Don, and (ii) to identify species on the basis of their response to dew for plantation programmes during winter season. The dew-exposed plants of all the three species showed significant ( $P < 0.05$ ) reduction in photosynthetic rate,  $F_v/F_m$  ratio, transpiration rate and stomatal conductances for  $CO_2$  and water vapour and WUE. The reduction was more prominent in *B. rugulosa* and *O. glandulifera* than *G. optiva*, indicating that *G. optiva* is less sensitive to dew compared to the other two species. Dew also did not improve RWC rather it decreased in the dew-exposed plants of *G. optiva*. Based on the results it may be suggested that dew, though a form of water, may not be useful to the Himalayan plants at least for the three species studied. Thus without providing protective measures from dew these plant species may not be successful in plantation programmes during winter season in the Himalayan region.**

**Keywords:** Himalayan plants, photosynthetic response, reactive water content.

WATER, the elixir of life, is vital for the survival and metabolism of all living organisms. Active life requires a minimum water content in organisms, which varies with cell type and physiological condition<sup>1,2</sup>. It is one of the most important factors influencing the occurrence, distribution, composition, growth and productivity of plants and vegetation, and the balance between evapotranspiration

and water ingress from precipitation and underground sources into an ecosystem is an important feature<sup>3-6</sup>. Further, a lack of adequate moisture leading to water stress has resulted in various degrees of land degradation across the globe<sup>7</sup>. It has been reported that about 60,000 km<sup>2</sup> of the earth's surface is becoming degraded land every year<sup>8</sup>. According to an estimate in India, about 8.3 mha of land is salt-affected and 92 mha of cultivable land is rainfed<sup>9</sup>. About 22 mha of land is degraded land out of 59 mha of land in the Indian Himalayan region<sup>10</sup>. The situation is further being aggravated due to changing patterns of rainfall by global climate change<sup>11</sup>. Over the years rainfall in the region has also become highly erratic and unpredictable, particularly during the winter season. Because of this seasonality of water availability in the rainfed region, most of the activities involving plants such as afforestation, reforestation and other plantation programmes are generally restricted to the rainy season. Further, precipitation, the most important source of moisture, occurs in various forms such as rainfall, snow and dew<sup>12</sup>. However, there is conflicting evidence with respect to the impact of dew formation on plants<sup>13</sup>. Dew can be an important source of water in certain regions of the world for part of the year<sup>14</sup>. Whereas artificial and/or natural dew has been reported to improve water potential, photosynthesis, growth and survival of plants<sup>15,16</sup>, negative effect of dew formation on photosynthesis and growth has also been reported<sup>17-19</sup>. However, such studies have not been undertaken for the Himalayan plants.

Dew formation is a common phenomenon during October to February for plants growing in the tropical and subtropical Himalayas. Occurrence of dew for such a lengthy period may have important implications on physiological processes such as photosynthetic rate, transpiration rate, stomatal conductance and water-use efficiency (WUE) that contribute to the growth, survival and productivity of plants. It would therefore be useful to better understand the impact of dew on photosynthetic characteristics of important plant species in the Himalayan region. Further, such studies are also useful for selection of plant species that could be successfully used for the rehabilitation of degraded lands during winter season. The present study was therefore undertaken with twin objectives: (i) to understand the effects of dew on photosynthetic rate, photochemical efficiency of photosystem II ( $F_v/F_m$  ratio) transpirational water loss, stomatal conductances for  $CO_2$  and water vapour, intercellular  $CO_2$  concentration ( $C_i$ ), WUE and relative water content (RWC) of three multipurpose evergreen tree species in central Himalaya, viz. *Boehmeria rugulosa* Wedd., *Grewia optiva* Drummond and *Olea glandulifera* Wall.ex.G. Don, which are extensively used in plantation programmes, and (ii) to identify species on the basis of their response to dew for plantation programmes during winter season.

Seedlings of *B. rugulosa*, *G. optiva* and *O. glandulifera* were grown singly in earthen pots (28 cm dia.; 25 cm

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depth) containing a mixture of farmyard manure, sand and garden soil (1:1:1). The plants were kept in the botanic garden of the High Altitude Plant Physiology Research Centre, Srinagar-Garhwal (altitude 550 m; lat. 30°13'N; long. 74°48'E). Two-year-old healthy seedlings of the same size were divided into two sets of 60 plants each during November. One set of plants of each species was shifted to a large glasshouse (28 m length, 15.5 m width, 7.5 m height in the middle and 4.6 m on the sides; hereafter referred to as control plants) and the other set was left in the botanic garden (hereafter referred to as dew-exposed plants). Both sets of plants were watered regularly.

Photosynthetic measurements were made on the youngest fully expanded leaves of five randomly selected plants for each species from each condition during January and February using climate-controlled compact minicuvette system (Heinz Walz GmbH, Effeltrich, Germany) with cuvette temperature of 10°C and photosynthetic photon flux density (PPFD) of 0–2000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  using an artificial light source (Type LA4) with neutral density filters.

In another experiment, 20 seedlings of *G. optiva* with almost identical total leaf area were selected. Of these, 10 seedlings were protected from dew by keeping them beneath the outer extension of the laboratory wall during night and shifting them to the garden in the morning (control plants) every day for five consecutive days in the last week of November. The other 10 seedlings were maintained in the botanic garden (dew-exposed plants). In this way plants kept in the garden experienced dew formation, whereas those shifted to beneath the outer extension of the laboratory wall during night did not. Both sets of plants were not watered during photosynthetic measurements made on the youngest, fully expanded leaves of five randomly selected plants from each condition for five consecutive days, to understand the impact of dew on photosynthetic characteristics using climate-controlled compact minicuvette system with cuvette temperature of 10°C and PPFD of 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (this light intensity was found to be optimum for these species). The dark respiration rate was measured by maintaining the leaf in the cuvette at zero light intensity.

In both the experiments, the cuvette air temperature was recorded with a thermocouple during measurements. Cuvette humidity was maintained at around 65–70%. All measurements were recorded under steady-state conditions. The recording was done for a period of 30–45 min for obtaining steady-state conditions. The photosynthetic rate, transpirational water loss, dark respiration rate and stomatal conductances for  $\text{CO}_2$  and water vapour and  $C_i$  were calculated according to the equation of Von-Caemmerer and Farquhar<sup>20</sup>. Instantaneous WUE was also computed as the ratio of photosynthetic and transpiration rate. The data were analysed statistically according to Mather<sup>21</sup>.

Youngest, fully expanded leaves of 5–8 plants for each species were darkened in the leafclips of a Hansatech Plant Efficiency Analyser (Hansatech Ltd, UK) for a period of 30 min for measurement of photochemical efficiency of photosystem II ( $F_v/F_m$  ratio) on cloudless days. Fluorescence was excited by red (actinic) light with 650 nm peak wavelength obtained from light-emitting diodes<sup>22,23</sup>. The chlorophyll fluorescence measurements were made during November, January–February and March–April.

For the measurement of RWC, leaves were harvested and their middle portions, excluding midribs were used for the estimation of RWC. The RWC was recorded at 4 h intervals for two consecutive days for diurnal recordings and daily between 1100 and 1300 h for five consecutive days in the second experiment, following the method of Weatherley<sup>24</sup>.

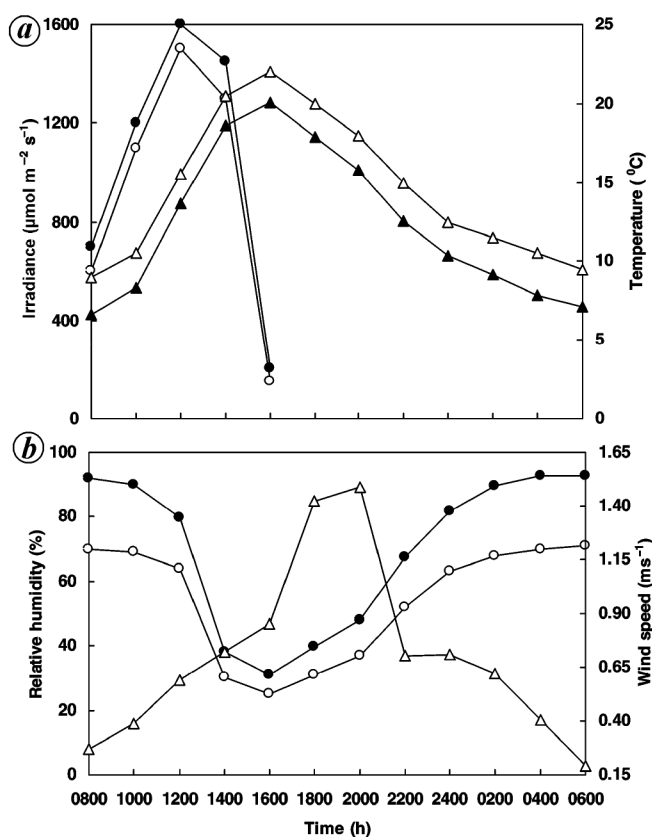
Meteorological data like irradiance, air temperature, relative humidity and wind speed on the day of observation were recorded for ambient conditions using an automatic weather station and data logger (Campbell Scientific, USA). The same parameters, except wind speed were also recorded manually at 2 h intervals inside the glasshouse, and beneath the outer extension of the laboratory wall during night.

The tropical and subtropical plants of the Himalayan region experience dew formation during winter months characterized by low temperature and high humidity; the two basic requirements for dew formation<sup>25,26</sup>. Dew-exposed plants experienced 2.0–2.5°C lower temperature in comparison to control plants and those kept beneath the outer extension of the laboratory wall during night in addition to higher humidity, particularly during the period of maximum dew formation (Figure 1a and b). Several workers have shown that dew promotes growth and survival of plants probably by improving the water status of plants either directly by absorption<sup>27</sup> or indirectly by reducing transpiration<sup>28</sup>. In the present study, dew did not seem to improve the water status of plants as RWC of dew-exposed plants did not differ from that of control plants<sup>23</sup> (Table 1), but adversely affected both photosynthetic and transpiration rates. However, the extent of reduction was species-specific. Both photosynthetic and transpiration rates were significantly reduced in dew-exposed plants of all the three species. The reduction was more prominent in *B. rugulosa* and *O. glandulifera*. The dew-exposed plants of *B. rugulosa* and *O. glandulifera* showed a decrease of 67% and 69% in photosynthetic rate, and 54% and 69% in transpiration rate at maximum light intensity (Figure 2a and b) respectively compared to their respective control plants. This resulted in poor WUE of dew-exposed plants (Figure 3b). Of the two species, WUE of *B. rugulosa* was poorer. Existence of differences in WUE of plants is well known in the literature<sup>29,30</sup>. On the other hand, dew-exposed plants of *G. optiva* showed considerably less reduction in photosyn-

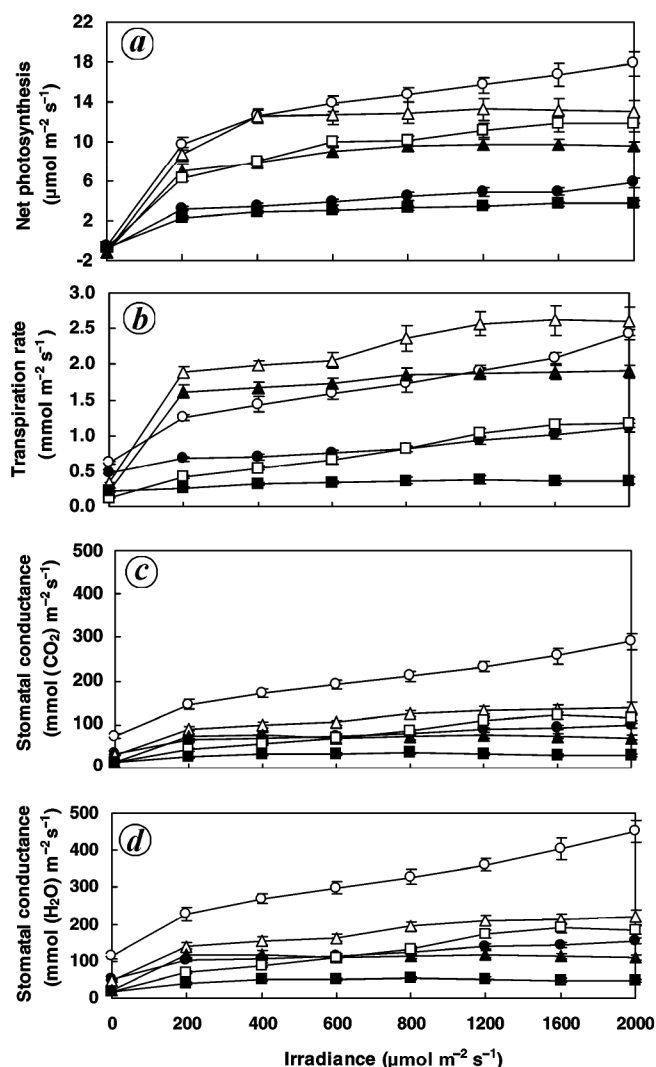
thetic (26%) and transpiration rate (27%), but there were no significant differences in WUE between dew-exposed and control plants (Figure 3 b), probably indicating that *G. optiva* is less sensitive to dew compared to *B. rugulosa* and *O. glandulifera*. It has been shown that plants with high rate of photosynthesis and WUE have the potential to grow faster and yield more than species with low photosynthetic rate and WUE<sup>31,32</sup>. Thus one would expect relatively better growth performance by dew-exposed *G. optiva* plants. It has also been reported that the application of artificial dew at night prolongs the survival of *Pinus* seedlings under water stress conditions<sup>33</sup>. However, in the present study, the most striking visual consequences of dew in non-irrigated plants under field conditions were leaf-shedding in *B. rugulosa* and yellowing of leaves in *O. glandulifera*. This visual finding is supported by WUE data of the present study, suggesting that WUE is critical relative to photosynthesis for the performance of plants under limited water availability, as in the rainfed areas<sup>31</sup>. Further, the dew-exposed plants of *B. rugulosa* and *O. glandulifera* showed higher respiration rate compared to their respective control plants, whereas there was no significant difference in dark respiration rate between dew-exposed and control plants of *G. optiva* (Figure 2 a

and Table 2). Reduced rates of photosynthesis and increased rates of respiration are reported to limit the productivity in some plant species<sup>34,35</sup>. Significant increase in diameter growth was recorded in *G. optiva* plants when grown inside the polyhouse during winter months characterized by frost formation<sup>36</sup>. This supports the negative impacts of frost/dew in plants.

Further, a comparison of changes in photosynthetic characteristics between dew-exposed and control plants of *G. optiva* for five consecutive days shows that dew does not improve the water status of plants, but both photosynthetic and transpiration rates are decreased in dew-exposed plants (Tables 2 and 3). This finding suggests that dew is not beneficial to *G. optiva* plants, as the plants exposed to dew did not show improvement in their photo-



**Figure 1.** Diurnal time course of change in environmental parameters: (a) irradiance (circle) and air temperature (triangle), (b) relative humidity (circle) and wind speed (triangle) outside (closed symbols) and inside (open symbols) the glasshouse.



**Figure 2.** Net photosynthesis (a), transpiration rate (b) and stomatal conductances for  $\text{CO}_2$  (c) and water vapour (d) in dew-exposed (closed symbols) and control (open symbols) leaves of *Boehmeria rugulosa* (circle), *Grewia optiva* (triangle) and *Olea glandulifera* (square) plants as a function of irradiance. Each value is the mean of five replicates. Vertical bars show standard deviation.

**Table 1.** Diurnal changes in relative water content (RWC) and  $F_v/F_m$  ratio of dew-exposed and control plants of *Grewia optiva* during January–February and April

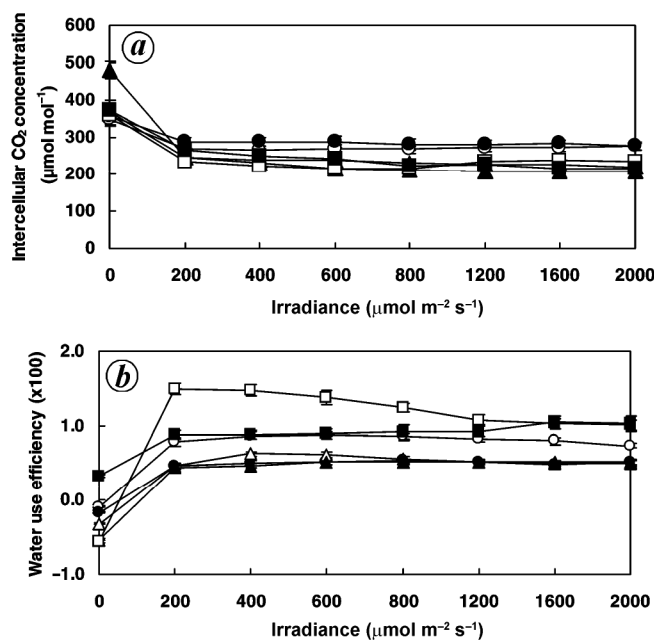
Time (h)	RWC (%)		$F_v/F_m$ ratio (January–February)		$F_v/F_m$ ratio (April)	
	Control	Dew-exposed	Control	Dew-exposed	Control	Dew-exposed
0800	91 ± 7.43	92 ± 6.60	0.80 ± 0.02	0.78 ± 0.05	–	–
1200	85 ± 5.19	86 ± 7.57	0.80 ± 0.03	0.76 ± 0.04	0.80 ± 0.03	0.80 ± 0.04
1600	88 ± 6.15	89 ± 7.12	0.80 ± 0.03	0.75 ± 0.04	–	–
2000	89 ± 4.84	90 ± 5.16	0.80 ± 0.02	0.77 ± 0.05	–	–
2400	90 ± 6.82	90 ± 7.14	0.80 ± 0.03	0.78 ± 0.03	–	–
0400	90 ± 5.00	92 ± 4.48	0.80 ± 0.03	0.78 ± 0.05	–	–

±, SD; –, not given.

**Table 2.** RWC,  $F_v/F_m$  ratio and dark respiration rates of control and dew-exposed *G. optiva* plants for five consecutive days

Day	RWC (%)		$F_v/F_m$ ratio		Dark respiration ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	
	Control	Dew-exposed	Control	Dew-exposed	Control	Dew-exposed
0	85 ± 4.16	88 ± 5.63	0.78 ± 0.01	0.78 ± 0.03	1.06 ± 0.08	1.10 ± 0.06
1	86 ± 5.17	87 ± 4.98	0.78 ± 0.02	0.77 ± 0.02	1.07 ± 0.07	1.12 ± 0.09
2	84 ± 2.78	83 ± 6.19	0.78 ± 0.03	0.77 ± 0.04	1.05 ± 0.09	1.10 ± 0.07
3	82 ± 2.56	79 ± 3.61	0.78 ± 0.02	0.75 ± 0.04	1.04 ± 0.06	1.08 ± 0.04
4	79 ± 3.45	75 ± 4.77	0.78 ± 0.03	0.73 ± 0.05	1.02 ± 0.07	1.06 ± 0.07
5	72 ± 4.66	66 ± 5.92	0.78 ± 0.01	0.71 ± 0.04	1.00 ± 0.09	1.06 ± 0.08

± SD.

**Figure 3.** Intercellular  $\text{CO}_2$  concentration (a) and water use efficiency (b) in dew-exposed and control leaves of *B. rugulosa*, *G. optiva* and *O. glandulifera* plants as a function of irradiance. Symbols and other details as in Figure 2.

synthetic rate which is known to be greatly affected by the water status of the plants<sup>29,37</sup>. This finding is in conformity with the results of some researchers who have found negative effect of dew on photosynthetic rate and

growth of plants. In context to WUE and photochemical efficiency of photosystem II ( $F_v/F_m$  ratio), plants of *G. optiva* kept beneath the outer extension of laboratory wall during night and shifted to the garden during daytime showed slight improvement in their WUE and no reduction in  $F_v/F_m$  ratio in contrast to dew-exposed plants (Tables 2 and 3). The slight improvement in WUE was primarily because of less decrease in their photosynthetic rate (Table 3).

In the present study, dew-exposed plants showed a decrease in photosynthetic rate. A number of factors can be ascribed to this reduction as photosynthesis is a combination of complex steps involving diffusive, photochemical and biochemical processes. Further analysis of photosynthetic data showed that both apparent quantum yield (initial slope of the curve) and photosynthetic capacity decreased in plants exposed to dew, as evidenced from their light response curves (Figure 2a). Similar observations have been reported by Ishibashi and Terashima<sup>18</sup> for *Phaseolus vulgaris* subjected to artificial rain. A sharp decline in the photosynthetic rate on artificial or natural wetting (dew) in species with wettable leaf surfaces was also observed by Smith and McClean<sup>38</sup>. Significant reduction in stomatal conductances for  $\text{CO}_2$  and water vapour was observed in dew-exposed plants of all the three species (Figure 2c and d). The reduction in stomatal conductance for  $\text{CO}_2$  was minimal (49%) in *G. optiva* and maximum (74%) in *O. glandulifera*; *B. rugulosa* (66%) showed an intermediate response. However, despite decrease in stomatal conductance, corresponding decrease in transpi-

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**Table 3.** Changes in photosynthetic rate, transpiration rate, stomatal conductance to water vapour, water-use efficiency and intercellular CO<sub>2</sub> concentration (% initial) in control and dew-exposed *G. optiva* plants during winter for five consecutive days

Day	Treatment	Photosynthetic rate	Transpiration rate	Conductance to water vapour	Water use efficiency	Intercellular CO <sub>2</sub> concentration
0	Control	100.00 ± 5.70	100.00 ± 6.30	100.00 ± 7.10	100.00 ± 7.17	100.00 ± 5.40
	Exposed	100.00 ± 4.50	100.00 ± 4.30	100.00 ± 5.60	100.00 ± 6.23	100.00 ± 4.30
1	Control	100.23 ± 6.10	98.36 ± 4.50	98.35 ± 6.10	102.00 ± 4.26	101.00 ± 5.70
	Exposed	98.43 ± 5.10	97.06 ± 4.70	94.00 ± 4.80	102.00 ± 6.67	97.46 ± 4.70
2	Control	97.67 ± 4.30	95.08 ± 5.30	92.88 ± 5.40	102.00 ± 7.40	95.26 ± 5.50
	Exposed	86.38 ± 4.80	88.66 ± 5.10	83.99 ± 3.50	98.11 ± 5.77	95.34 ± 3.50
3	Control	95.03 ± 3.50	89.75 ± 4.60	84.88 ± 7.30	106.00 ± 9.29	89.22 ± 5.40
	Exposed	82.76 ± 5.30	83.19 ± 4.00	79.85 ± 5.20	100.00 ± 7.74	95.34 ± 5.10
4	Control	92.31 ± 7.00	84.84 ± 5.80	79.55 ± 6.10	108.00 ± 6.30	85.78 ± 5.10
	Exposed	78.03 ± 5.20	77.31 ± 3.80	69.84 ± 5.50	102.00 ± 4.26	98.31 ± 4.70
5	Control	88.89 ± 6.20	79.92 ± 3.59	76.77 ± 5.70	111.00 ± 6.95	80.17 ± 5.40
	Exposed	72.05 ± 4.70	75.63 ± 3.33	56.99 ± 4.60	96.00 ± 5.88	100.00 ± 4.30

± SD.

rational water loss was not observed in dew-exposed plants. This indicates greater dependence of transpirational water loss of dew-exposed plants on leaf-to-air vapour pressure difference than stomatal conductance, as transpiration rate is known to depend on stomatal conductance to water vapour and leaf-to-air vapour pressure difference<sup>34</sup>. Further, no decrease in Ci was observed despite reduction in stomatal conductance in dew-exposed plants; rather Ci values were slightly higher than or at par with those of control plants. These findings indicate that stomatal closure is not the major cause of decreased photosynthetic rate in the plants. Similar results were also obtained for dew-exposed plants of *G. optiva* in another experiment. Photosynthesis is known to be limited by both stomatal and non-stomatal components. However, the relative contribution of these components varies with plant species and environmental conditions<sup>37,39</sup>. A significant reduction in the photochemical efficiency of photosystem II ( $F_v/F_m$  ratio) was observed in all the three species studied<sup>23</sup> (Table 2). A considerable reduction in  $F_v/F_m$  ratio has been reported in *Pinus sylvestris*<sup>40</sup> and spruce<sup>41</sup> plants grown in the field during winter season. However, the recovery of dew-exposed plants which were watered regularly during winter months measured in terms of  $F_v/F_m$  ratio in March–April<sup>23</sup> (Table 1) reveals that the photosynthetic system of these plants is revocable.

In summary, based on the results it may be suggested that dew, though a form of water, may not be useful to the Himalayan plants at least for the three species studied, as the dew-exposed plants of the three species showed considerable reduction in photosynthetic rate,  $F_v/F_m$  ratio, transpiration rate, stomatal conductances for CO<sub>2</sub> and water vapour, and WUE. The reduction in these parameters was more prominent in *B. rugulosa* and *O. glandulifera* than *G. optiva*. Thus without providing protective measures from dew these plant species may not be successful in plantation programmes during winter season in the Himalayan region.

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## Altered gibberellin and auxin levels in the ovaries in the manifestation of genetic parthenocarpy in tomato (*Solanum lycopersicum*)

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**Precocious ovary development and altered gibberellin (GA) and auxin levels in the ovary of the *pat-2* gene-induced facultative parthenocarpic line of tomato (*Solanum lycopersicum* L.) Oregon Pride was studied. Unpollinated ‘Oregon Pride’ ovaries showed marked development with 2.78-fold higher GA content at anthesis and 10.48-fold higher auxin content at 2–3 days before anthesis stage, than the ovaries of the non-parthenocarpic line Patharkuchi at the corresponding stages of the flower which might have triggered the precocious onset of cell division and elongation in the pericarp. Very low selfed and crossed seeds in the fruits of Oregon Pride indicated that marked higher GA and auxin concentration in the ovary leading to anticipated ovary growth and parthenocarpy might have resulted in impaired fertilization by either enhancing ovule abortion or reducing the pollen tube growth.**

**Keywords:** Auxin, facultative parthenocarpy, gibberellic acid, ovary, tomato.

PARTHENOCARPY, the alternative pathway to normal fruit-set and development, has a genetic basis and in tomato it

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