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Physiological and Biochemical Changes during Flowering of Mango (*Mangifera indica* L.)

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ABSTRACT

Physiological and biochemical changes in terms of chlorophyll *a*, chlorophyll *b*, total chlorophyll, total sugar, reducing sugar, protein level, nitrate reductase enzyme activity, and biophysical attributes such as internal leaf temperature, internal relative humidity, diffusion resistance and rate of transpiration were measured in two types of mango cultivars i.e., regular bearing 'Amrapali' and irregular bearing 'Chausa', 'Dashehari' and 'Langra' cultivars during flower bud differentiation stage (November) and flower bud swelling stage (January). The effect of paclobutrazol (PP_{333}), a growth retardant having anti-gibberellin activity on these parameters, was also studied. Physiological and biochemical changes associated with the flowering of mango leaves in 'Amrapali' at the flower bud differentiation stage contained higher chlorophyll content, total sugar, total protein, nitrate reductase activity and higher diffusion resistance capacity as compared to 'Chausa', 'Dashehari' and 'Langra'. High accumulation of these metabolites in the leaves of 'Amrapali' may possibly lead to floral induction even in the new shoot. A lower level of reducing sugar in regular bearing 'Amrapali' compared to irregular bearing 'Dashehari' at an advanced stage of the flower process (flower bud swelling stage) may indicate the capacity of this cultivar to form flower buds at a comparatively lower threshold level of reducing sugar content. The promotive effect of PP_{333} on sugar and protein content can be attributed to its flower regulatory role in mango.

Keywords: biochemical estimation, flower bud differentiation, *Mangifera indica*, paclobutrazol

INTRODUCTION

Mango (*Mangifera indica* L.) is the most important fruit crop in tropical and sub tropical regions of the world. The area under its cultivation has nearly three times within three decades and now it occupies an area of 20206×10^2 HA in the country producing 125379×10^2 MT. It accounts for 36.7% of total fruit area (5510×10^3 HA) and 21.3% of total production of fruits (58740×10^3 MT) in the country (Source: Indian Horticulture Database, NHB, 2006). However, the productivity of mango continues to remain below its potential level in India. This crop has a long-standing problem of alternate bearing which denotes yield variation in alternate years i.e. 'on' year of optimum or heavy fruiting is followed by 'off' year of little or no fruiting. Thus, it renders mango cultivation less remunerative to the orchardist and is one of the main hurdles in maximising mango production thus causing a major threat to the expansion of the mango industry. Besides, several factors, such as excessive vegetative growth and high gibberellin (GA) synthesis at the time of flower bud genesis are some of main reasons for erratic bearing in mango (Paulas and Shanmugavelu 1988). Thus, for increasing the reproductive growth of the tree there is a need to retard vegetative growth and to reduce GA biosynthesis during flowering.

The flowers of mango are small, monoecious and polygamous. The flowers have five sepals and petals and are highly pubescent. The floral discs are 4-5 lobed, fleshy and large, and located above the base of the petals. Although there are 5 stamens, only one of them is fertile, the remainder are sterile staminodes that are surmounted by a small gland. The gynoecium is monocarpellous having a single ovule.

Both male and hermaphrodite flowers are found within a single inflorescence. It is the hermaphrodite flowers that often undergo proper pollination and fertilization, and set fruit. In India, most of the cultivars are selections that were made from naturally occurring open pollinated seedlings. In spite of the many problems associated with mango breeding, intervarietal hybridization is now very common to develop new desired varieties.

Experimental evidence indicates that maturity of terminal shoots and accumulation of carbohydrates in the shoot apex are in some way associated with the synthesis of the floral stimulus, the absence of which can result in a lack of flowering or biennial bearing in many mango cultivars (Pandey 1988). Earlier researchers were also of the view that early initiation and cessation of growth followed by periodical quiescence or dormancy is necessary for proper physiological maturity of flower bud differentiation (Nakasone *et al*. 1955; Khan 1960). However, it has now been established that flower bud differentiation depends upon the 'on' and 'off' year phase of the tree rather than on the initial cessation of growth of shoots, which was later supported by the observations of Kulkarni (1983) and Reddy (1983). It was found that the activity of GA-like substances was greater in the 'off' year and was postulated that a high level of GA inhibits flowering while a high level of auxin-like substances may promote flowering either by reducing the effectiveness of GA or by decreasing the permeability of the cell membrane. It has been reported that potassium nitrate (KNO_3) is an effective flower inducer in mango by increasing the activity of nitrate reductase and stimulating the production of ethylene (Chadha and Pal 1994).

Any treatments which promote vigorous growth are known to antagonise flowering in mango. Among the plant growth regulators tested, anti-gibberellins growth retardants paclobutrazol [(2RS, 3RS)-1-(4-chlorophenyl)-4,4-dimethyl-2-(1H-1,2,4-triazol-1-yl) pentan-3-ol] (PP_{333}) is reported to promote flowering in mango (Singh and Bhattacher-

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jee 2005), apple (Quinlan and Richardson 1984) and plum (Webster and Quinlan 1984). The strategies for regulating flowering in these fruit crops have been previously described (Reddy 2004).

The present investigation was undertaken to understand the bienniality of mango in the light of some of the important physiological and biochemical differences in leaves of irregular bearing cultivars viz. 'Chausa', 'Dashehari', 'Langra' and regular bearing cultivar 'Amrapali' at the time of flower bud differentiation and flower bud swelling stages. The efficacy of PP_{333}, as a vegetative growth retardant and its role on physiological attributes such as the chlorophyll, total sugar content, protein level, transpiration rate, leaf internal temperature and diffusion rate was evaluated in two irregular flower bearing cultivars.

MATERIALS AND METHODS

Plant material

The experiment was conducted during 2003/2004 and 2004/2005 at the Central Institute for Subtropical Horticulture, Lucknow on 20 year-old biennial cultivars 'Chausa', 'Dashehari' and 'Langra' and regular cultivar 'Amrapali' mango (*Mangifera indica* L.) tree. The fully mature middle leaves of the twigs had the same orientation as standardized earlier for the measurement of photosynthesis (Yadav and Singh 1995) and were selected for measurement of gas exchange parameters and bio-chemical analysis.

Biochemical assay

Chlorophyll was estimated by Arnon's (1949) method. Sugar was estimated by a standard method (Ranganna 1977). Reducing sugar level was estimated by the method of Yemm and Willis (1954). Total protein in the leaves of different cultivars was estimated as described by Lowry *et al*. (1951). Nitrate Reductase (NR) activity *in vivo* was assayed in leaves according to the method of Srivastava (1975).

Gas exchange parameters

Leaf temperature (°C), relative humidity (%), diffusion resistance (mmol m^{-2} s^{-1}) and transpiration (µg cm^{-2} s^{-1}) were measured in the fully matured middle leaf of the twig as described above using a Steady State Porometer, Licor-1600 Lincoln, USA. The measurements of these parameters were performed simultaneously in different cultivars. All these gas exchange parameters were taken at the time of flower bud differentiation and flower swelling stages from five randomly selected leaves from each test cultivar.

PP_{333} response

Paclobutrazol was applied during September as a soil drench at 0.8 g a.i. (active ingredient) and 1.20 g a.i. m^{-1} canopy diameter of tree under a randomised block design (RBD) with three replications in 'Chausa' and 'Langra' mango as they are more prone to biennial bearing. Treatments without PP_{333} as a control were kept for comparison. The soil drench of PP_{333} was done inside the manuring ring at a 15 cm depth. The biochemical parameters in treated trees were estimated during the flower bud development stage (November–December).

Statistics

Experimental design was completely randomized and consisted of three independent experiments. All tests for significance were conducted at the $p \leq 0.05$ level. The software MSTAT-C was used for statistical analysis (1989).

RESULTS

Chlorophylls (Chl) *a* and *b* and total content 2.36 ± 0.09 mg g^{-1} FW was maximum at flower bud differentiation stage in cv. 'Amrapali' and minimum Chl content was found in cv. 'Dashehari'. Among the different Chl fractions, the Chl *a* in

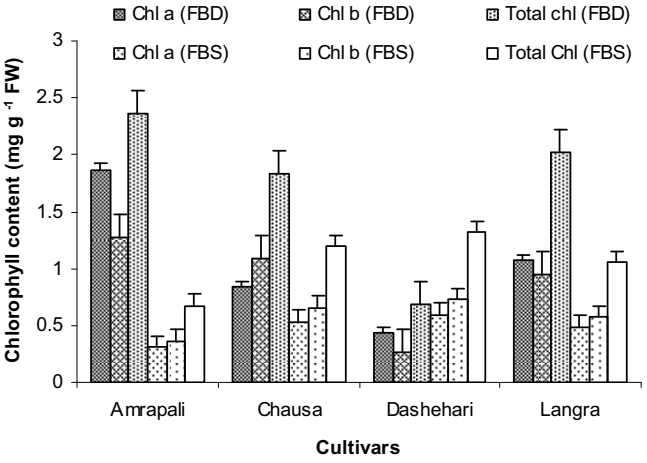

Fig. 1 Chlorophyll *a*, *b*, and total content during flower bud differentiation (FBD) and flower bud swelling (FBS) stages in different cultivars of mango (*Mangifera indica* L.).

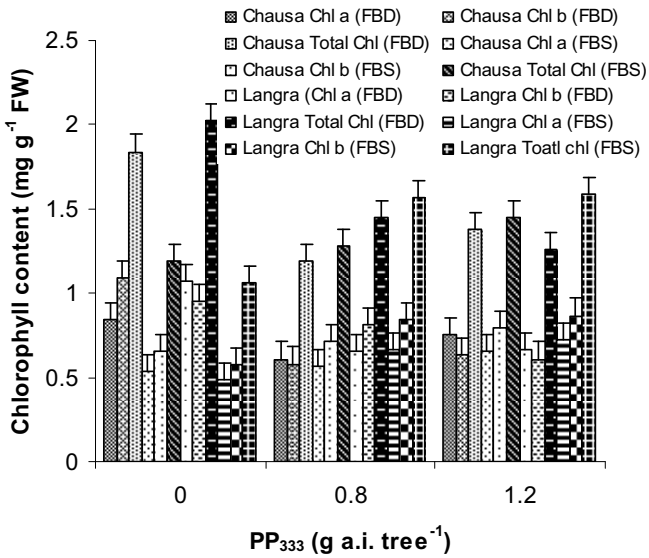

Fig. 2 Effect of PP_{333} concentrations on chlorophyll *a*, *b*, and total chlorophyll content during flower bud differentiation (FBD) and flower bud swelling (FBS) stages in two cultivars of mango (*Mangifera indica* L.).

'Amrapali' was >4 times higher (1.87 ± 0.1 mg g^{-1} FW) than cv. 'Dashehari' (0.43 ± 0.02 mg g^{-1} FW) (**Fig. 1**). In contrast to the flower bud differentiation stage, the total Chl content was higher in cv. 'Dashehari' at the flower bud swelling stage, although there was no marked change in Chl *a* content (**Fig. 1**). The pigment content (Chls *a*, *b* and total Chl level) in the leaves of PP_{333}-treated cvs. 'Chausa' and 'Langra' did not show significant differences in the two stages of flowering (**Fig. 2**). Total sugar content estimated at the flower bud differentiation stage was found to be significantly higher (13.69 ± 0.23 mg g^{-1} FW) in cv. 'Amrapali' than in cvs. 'Chausa' (8.63 ± 0.32 mg g^{-1} FW), 'Dashehari' (5.59 ± 0.35 mg g^{-1} FW) and 'Langra' (3.81 ± 0.13 mg g^{-1} FW) at the flower bud differentiation stage (**Fig. 3**). In contrast to that, there was no significant difference in total sugar content between these cultivars at the flower bud swelling stage, ranging from 24.10 ± 0.17 to 32.41 ± 0.13 mg g^{-1} FW (**Fig. 3**). The same pattern in sugar content was also observed in the PP_{333}-treated cvs. 'Chausa' and 'Langra' (**Fig. 4**). There was no significant difference in the reducing sugar level at the flower bud differentiation stage (**Fig. 5**). However, in contrast to the total sugar content, the reducing sugar level was found to be higher only at an advanced stage of flower bud differentiation stage in cv. 'Amrapali' (23.42 ± 0.17 mg g^{-1} FW), unlike cvs. 'Chausa' (14.98 ± 0.23 mg g^{-1} FW), 'Dashehari' (16.15 ± 0.13 mg g^{-1}

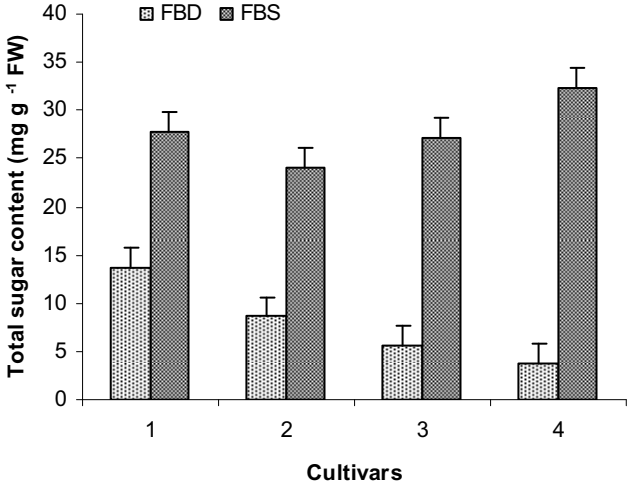

Fig. 3 Total sugar content during flower bud differentiation (FBD) and flower bud swelling (FBS) stages in different cultivars of mango (*Mangifera indica* L.).

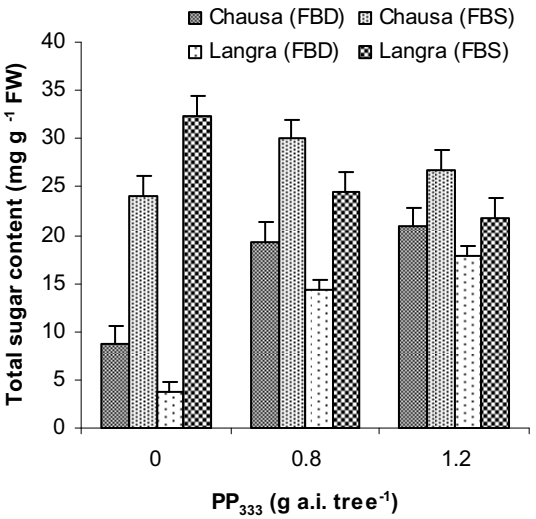

Fig. 4 Effect of PP_{333} on total sugar content during flower bud differentiation (FBD) and flower bud swelling (FBS) stages in two cultivars of mango (*Mangifera indica* L.).

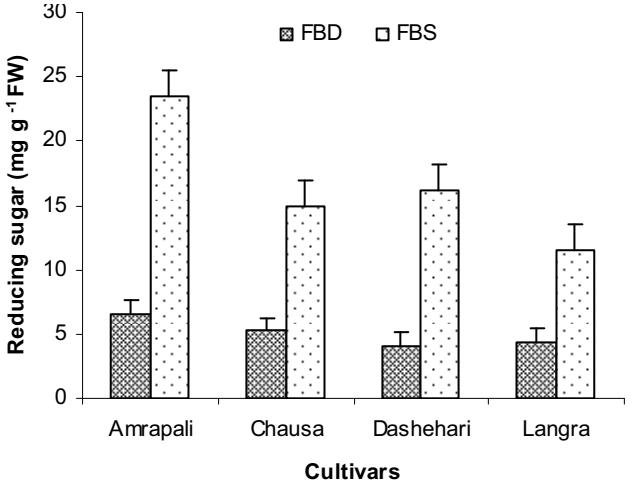

Fig. 5 Reducing sugar level during flower bud differentiation (FBD) and flower bud swelling (FBS) stages in different cultivars of mango (*Mangifera indica* L.).

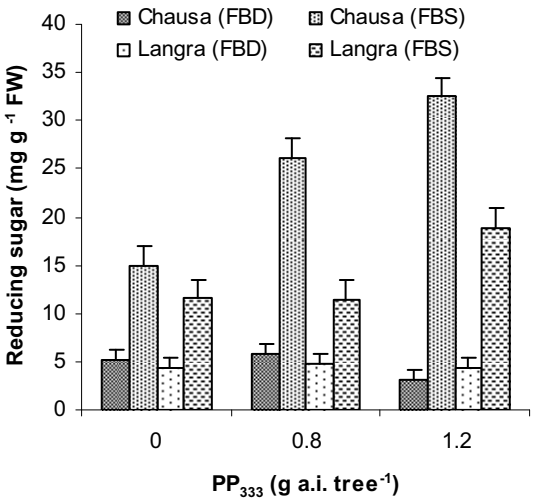

Fig. 6 Effect of PP_{333} on reducing sugar level during flower bud differentiation (FBD) and flower bud swelling (FBS) stages in two cultivars of mango (*Mangifera indica* L.).

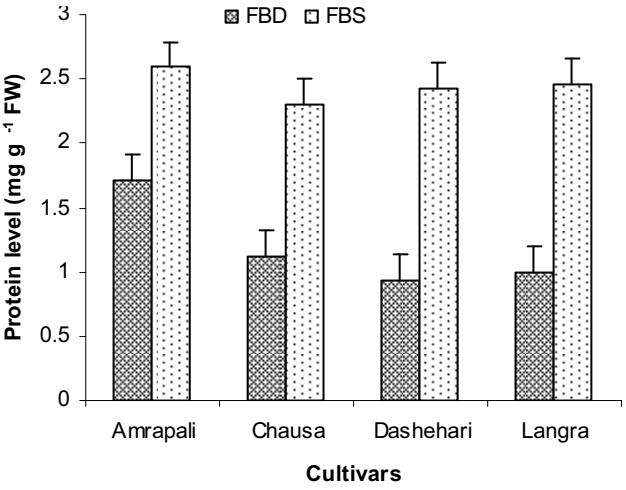

Fig. 7 Total protein content during flower bud differentiation (FBD) and flower bud swelling (FBS) stages in different cultivars of mango (*Mangifera indica* L.).

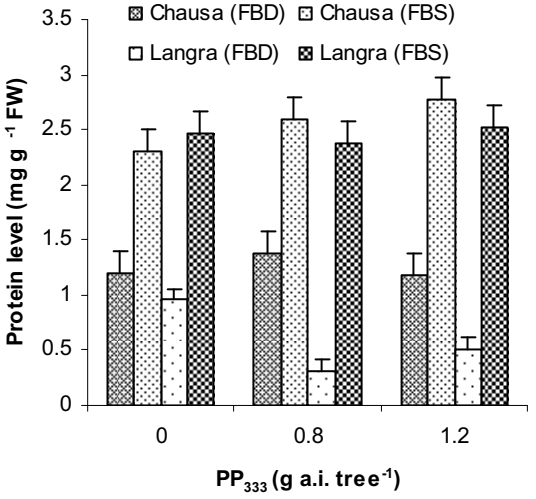

Fig. 8 Effect of PP_{333} on protein level during flower bud differentiation (FBD) and flower bud swelling (FBS) stages in two cultivars of mango (*Mangifera indica* L.).

FW) and 'Langra' (11.55 ± 0.21 mg g^{-1} FW) (**Fig. 5**). The concentration of reducing sugar was also higher in the PP_{333}-treated tree of cvs. 'Chausa' and 'Langra' at an advanced stage of flower bud development in comparison to the early flower bud differentiation stage (**Fig. 6**). There was a significant difference among the different cultivars

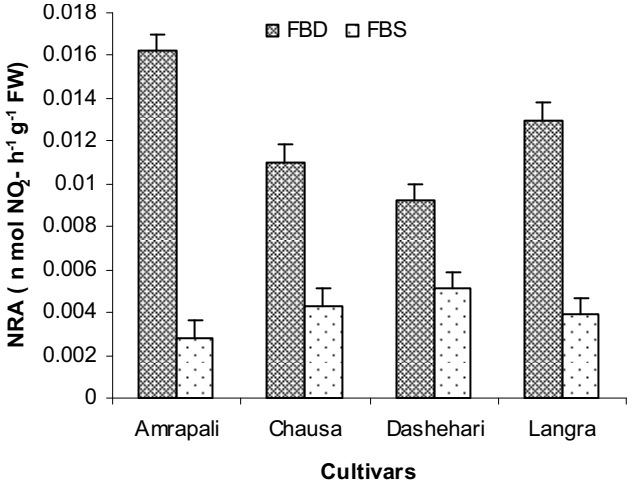

Fig. 9 Nitrate reductase activity (NRA) during flower bud differentiation (FBD) and flower bud swelling (FBS) stages in different cultivars of mango (*Mangifera indica* L.).

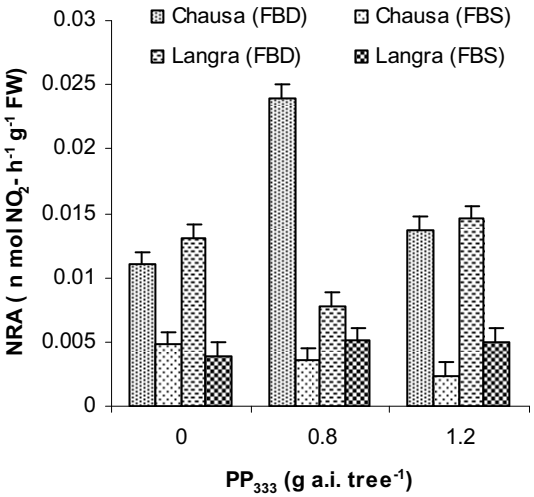

Fig. 10 Effect of PP_{333} on Nitrate Reductase activity (NRA) during flower bud differentiation (FBD) and flower bud swelling (FBS) stages in two cultivars of mango (*Mangifera indica* L.).

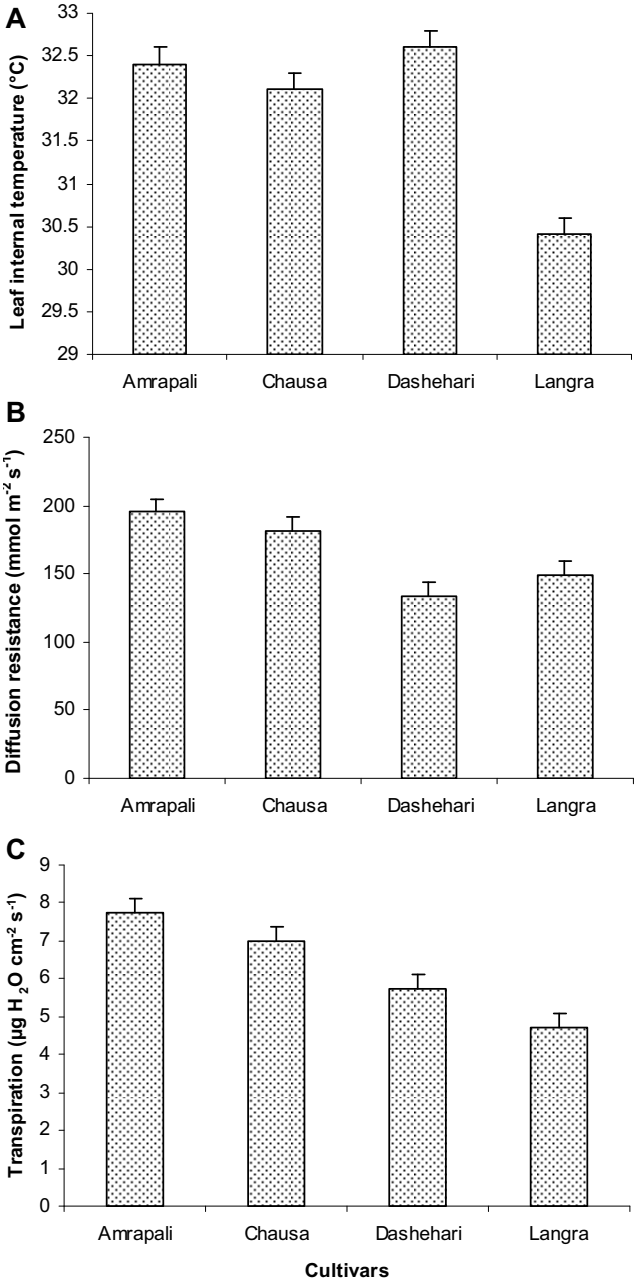

Fig. 11 Variation in biophysical parameters (leaf internal temperature (A), diffusion resistance (B) and transpiration (C)) during flower bud differentiation (FBD) stage in different cultivars of mango (*Mangifera indica* L.).

with respect to total protein content at the early flower bud differentiation stage and its maximum level (1.71 ± 0.14 mg g^{-1} FW) was recorded in cv. 'Amrapali' unlike lower levels in cvs. 'Chausa' (1.12 ± 0.12 mg g^{-1} FW), 'Dashehari' (0.94 ± 0.03 mg g^{-1} FW) and 'Langra' (0.99 ± 0.01 mg g^{-1} FW). In contrast, a significant difference in protein content among the different cultivars could not be observed at an advanced stage of flower bud differentiation (**Fig. 7**). The protein content in the leaves of PP_{333}-treated tree was higher than in both untreated ones in cvs. 'Chausa' and 'Langra' at the flower bud differentiation stage (**Fig. 8**). NR activity at the flower bud differentiation stage was significantly higher in all cultivars than at an advanced stage of flower differentiation with maximum activity occurring in cv. 'Amrapali' (1.62 ± 0.14× 10^{-2} n mol NO_2^- $h^{-1}g^{-1}$ FW) and minimum in cv. 'Dashehari' (0.92 ± 0.03 × 10^{-2} n mol NO_2^- $h^{-1}g^{-1}$ FW) (**Fig. 9**). On the other hand, no definite pattern in NR activity was obtained in the leaves of PP_{333}-treated cvs. 'Chausa' and 'Langra' (**Fig. 10**).

Biophysical parameters

Biophysical parameters (leaf temperature, diffusion resistant, transpiration rate) were measured at the time of flower bud differentiation stage in cvs. 'Amrapali', 'Chausa', 'Dashehari' and 'Langra'. Cv. 'Amrapali' leaves showed maximum diffusion resistance (195.30 ± 0.16 m mol m^{-2} s^{-1} FW) while cv. 'Dashehari' had the lowest value (133.30 ± 0.18 m mol m^{-2} s^{-1}). There was no significant difference in other compared biophysical parameters among the cultivars (**Fig. 11A-C**). The trees treated with PP_{333}, however, exhibited a higher level of diffusion resistance than untreated trees (**Fig. 12A-C**).

DISCUSSION

Understanding the various external and internal factors involved in flower induction in mango is crucial for developing suitable orchard management practices and thus helps in achieving regular high yield. The low efficiency experienced in commercial mango orchards is mainly due to erratic flowering and biennial bearing. Studies on the various factors influencing flowering were initiated long back, but most of them were aimed at developing suitable agro-techniques to induce regular cropping or control biennial bearing and therefore did not provide much knowledge on the physiology of flowering (Singh 2006). We conducted

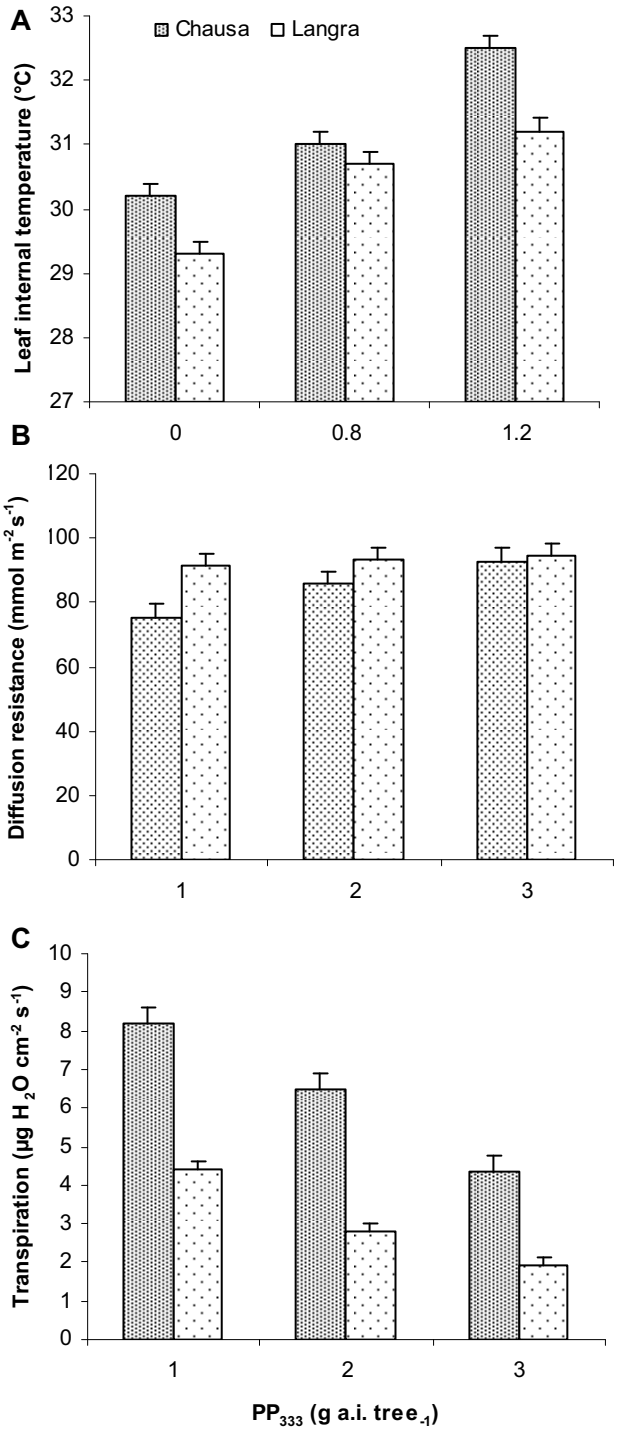

Fig. 12 Effect of PP_{333} on biophysical parameters (leaf internal temperature (A), diffusion resistance (B) and transpiration (C)) during flower bud differentiation (FBD) in two cultivars of mango (*Mangifera indica* L.).

this study to elicit information on the physiological and biochemical changes involved at critical stages (flower bud differentiation, flower bud swelling) of mango flower development (**Fig. 13**).

It was obvious from the experimental results that chlorophyll fractions *a*, *b* and total were higher in cv. 'Amrapali' when flower bud differentiation was started and its content decreased as flowering advanced. Cv. 'Amrapali' is a regular bearing tree and higher photosynthetic pigment content at this stage clearly suggested its more photosynthetic efficiency than 'Chausa', 'Dashehari' and 'Langra', which are prone to irregular bearing. A higher total sugar, protein content and NR enzyme activity at the flower bud differentiation stage, particularly in cv. 'Amrapali'were found and thus could be the possible factor in inducing more flower in the new shoots. A higher accumulation of total carbohydrates, acid hydrolysable polysaccharide and protein content during floral initiation has been reported in mango (Sen *et al*. 1969). A lower level of reducing sugar content in the leaves of 'Amrapali' (regular) at an early flower bud differentiation stage compared leaves of 'Chausa', 'Dashehari' and 'Langra' (irregular) during this stage may be attributed to the fact that regular bearing varieties are capable of forming flowering buds at a comparatively lower threshold level of reducing sugar content in their shoot. NR is the first enzyme of nitrogen metabolism and is substrate inducible, so the variation in its activity might be due to inherent variation of the cultivars. However, induction of flowering in mango by stimulating NR activity (NRA); NR was the most important enzyme in the production of ethylene in mango (Saidha *et al*. 1983). Ethylene has been implicated individually and collectively with other hormones in the flowering mechanism (Anez *et al*. 2000; Singh and Garg 2008). Biophysical characters recorded in regular and irregular cultivars did not show any significant difference among the cultivars except diffusion resistance, which was significant higher in 'Amrapali'. The high level of diffusion resistance in this cultivar suggests its superior stomatal behavior at the time of flower bud induction in comparison to irregular cultivars, 'Chausa', 'Dashehari' and 'Langra'. PP_{333} has been used as a broad spectrum growth retardant and has been reported to exert a profound effect on vegetative and flowering behaviour in mango and other fruit crops. Significant variation by PP_{333} on these attributes was also recorded in irregular flower bearing cvs. 'Chausa' and 'Langra'. PP_{333} is a triazole compound having anti-GA activity that was found to effectively induce flowering even in the 'off' year of bearing by inhibiting vegetative growth of shoots and promote flowering in mango (Singh and Saini 2001). Its profound effect on vegetative and flowering behaviour in apple and other plant species have also been reported (Steffens *et al*. 1985; Davenport and Nuntz-Elisea 1997). An increase in flowering with PP_{333} was found to be associated either its direct effect on flower bud differentiation by inhibiting GA biosynthesis (Hedden and Graebe 1982) or by altering the assimilation partitioning pattern in plants during flowering (Kokate and Thakur 2000). It has already been demonstrated that PP_{333} alters the relative sink strength and assimilate partitioning in temperate fruit crops (Anonymous 1984). However, that study was insufficient to point out how ex-

Fig. 13 Different developmental stages of flowering in mango (*Mangifera indica* L.).

actly this is brought about. An alteration in the proportions of phloem and xylem tissue in response to PP_{333} (Kurian and Iyer 1992) could be important in restricting the vegetative growth and enhancing flowering by altering the assimilate partitioning and pattern of nutrient supply for new growth. The response of PP_{333} on diffusion resistance and transpiration was similarly reported in *Lycopersicon* spp. (Fleteher and Hofstra 1985) and *Phaseolus* spp. (Boamah *et al*. 1986). An increased in gas exchange parameters by PP_{333} was reported in apple (16%) and pecan (7.54%) (Fletcher and Gilley 2000). On the basis of maximum carbohydrate, protein level in 'Amrapali' during flower bud differentiation, it may be concluded that a faster rate of synthesis of carbohydrates and proteins in leaves of regular bearing compare to irregular bearing cultivar of mango at the time of flower bud differentiation and flower bud swelling stage are the possible factors to complete the reproductive phase and thereby regular fruit production. The present study also elucidates the role of PP_{333} in controlling irregular flowering in mango.

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