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Physiology of flowering in litchi (*Litchi chinensis*): A review

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ABSTRACT

Lychee or litchi (*Litchi chinensis* Sonn.) is most popular fruit of South-East Asia, produces leaf flushes, flowers and fruits on terminals of new growth. The reproductive phase is associated with the ability to alternate between the production of vegetative and reproductive buds. The stress factors like water stress, cold winter are the triggering factors to induce dormancy which promotes flowering. The trees must experience one flush of vegetative growth during summer immediately after harvest and require a minimum number of three flushes for adequate fruit production. The flushes maturing earliest (before the winter period) produce floral shoots, while trees flushes maturing quite late produce vegetative shoots. The stem must take rest for 4 to 6 weeks prior to winter-spring flush for panicle formation in same flush. High leaf N is conducive for frequent flushes of vegetative growth and concentration less than 1.70 percent discourages initiation of vegetative flushes in the fall period. The vegetative flushing just prior to floral induction results in poor or no initiation and often vegetative shoots. The transition from vegetative to floral development is the consequence of changes in the physical and genetical expression in the shoot apex (with high cytokinin concentration). One month before flower bud formation, abscisic acid increases markedly and total cytokinin content increased in the xylem sap reaching maximum during flower bud formation and full bloom. The chlorophyll concentration dependent photosynthesis rate of lychee leaves on younger flushes and adjacent to fruit, is greater than that on shaded older flushes. The available total non structural carbohydrates or starch is found to be accumulated before flower initiation and leaf flushing. Girdling (generally done when post harvest flushes are matured) and spray of paclobutrazol (PBZ) and/or KNO_3 induced flowering in *China* litchi.

Key words: Floral induction, Flushing, Litchi, Photosynthesis, Shoot maturity

Flowering is the single most important event in the survival of angiosperms. Woody tree species in this phylum have adapted a variety of mechanisms to ensure the success of this event. Fruit bearing arboreal species have been selected for cultivation primarily because of their palatable fruit characteristics and qualities that make them attractive. They can be broadly categorized into two main groups, deciduous fruit tree species that grow in temperate climates and evergreen species that thrive in both tropical and subtropical climates. These two groups display phenologies that incorporate adaptations to each climate, including timing of flowering to avoid injurious conditions such as freezing (winter) temperatures in temperate regions and the desiccating conditions present during dry seasons in the tropics and subtropics (Davenport 2000, Malhotra 2017).

Flowering is a complicated developmental process of physiological and morphological stages under the control of a number of external signals and internal factors. The time of floral transition is influenced by endogenous and environmental factors which trigger or repress the change of the shoot meristem from generating leaves to the development of reproductive organs (Hanke *et al.* 2007). Some aspects of flowering in trees make them especially challenging for physiologists, breeders, and growers. First, the juvenile phase, which lasts for several years during which, no flowering or fruiting occurs; second, interactions between vegetative growth, flowers, and fruit of the previous year on floral initiation in the current year that affect growers through phenomena such as biennial bearing, and make interpretation of research data difficult for scientists (Wilkie *et al.* 2008).

Litchi or lychee (*Litchi chinensis* Sonn.) is a subtropical fruit tree as well as typical sun-loving species. It’s production constraints are, alternate bearing habit and low productivity. The litchi flower buds are initiated and develop at the apex of mature current-season shoots. Litchi orchard management includes watering, fertilizer application, girdling, growth regulators and pruning which have a large impact on tree growth, yield and profitability but physiology of growth, flowering and cropping needs to be described as the lack of flowering is usually not only related to the weather or the timing of shoot growth but its [shoot] maturity, physiology, biochemical, nutritional and hormonal status of shoot buds

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during flower initiation/and vegetative phase, a critical period of production cycle (Singh 2015, Malhotra 2016, Srivastava *et al.* 2014).

Although growers have no control over the weather, they can optimize flowering by managing the vegetative vigour of the trees (Li *et al.* 2001), pruning, irrigation, and balancing carbohydrate to nitrogen ratio, endogenous hormones (exposure to ethylene) (Davenport 2009) and polyamines during flowering. Modern research tends to concentrate on force flushing during desirable period, balancing nutrient levels as well as high carbohydrate levels needed for good flowering. If these two levels are sufficiently high, the trees appear to need a triggering factor to actually start the floral emergence. When the soil is dry or low in nutrients, carbohydrates continue to build up all through the year and a heavy crop depletes the nutrient/carbohydrate levels considerably and the trees have a relatively short time to recover, subsequently trees have to replenish their nutrients to complete one or two flushes, harden off and settle down to a dormant period in to build up carbohydrate levels before flowering (Nath and Singh 2014).

This review will briefly summarise the basic mechanism of litchi flushing, phase changes, floral bud initiation and induction of flowering, recent advances in our knowledge of regulation and management of flowering and more focussed on how this information can be utilized to control reproductive and vegetative growth of this crop. Further, detailed understanding of flower formation mechanisms during lychee tree development is necessary to develop appropriate techniques to shorten the juvenile phase which is especially important for breeders and production scientists.

Flushing pattern, growth and maturity of shoots

Litchi is an evergreen, recurrently flushing tree (Olesen *et al.* 2002, Davenport and Stern 2005), and vegetative characters are very susceptible to environment and can change with differences in climate, soil or culture practices. Tree growth occurs as periodic, ephemeral flushes of shoots emerging from apical or lateral resting buds before returning to a quiescent state. Periods of stem dormancy are short in young plants but can last more than 8 months between flushing episodes in mature trees (Davenport 2000).

One of three primary types of shoots (i.e. *actively growing branch tips or laterals regardless of type of growth*), is typically induced to develop from initiated buds: vegetative (leaves only), generative (determinate panicles or indeterminate inflorescences), or mixed (composed of both leaves and lateral inflorescences inserted at each node or, in general, a mixture of flower and leaves) (Davenport 2003). Vegetative flushes (i.e. *growth occurring in numerous shoots, usually in sections of tree canopy or throughout the entire tree*) of growth typically occur one to several times per year on individual stems (i.e. *branch tips that are in rest*). The frequencies of flushes that occur annually depend upon cultivar, size of the tree, and growing conditions (especially related to nitrogen and water availability). Reproductive flushes generally occurs after extended periods of stem rest in the low-latitude tropics or immediately following periods of cool night temperatures in the higher latitude in tropics and subtropics (Davenport 2000). The low temperature coupled with low soil moisture is required during pre-flowering period to provide the physiological changes required for flower bud initiation/induction in litchi (Menzel 1983). Rainless cool winter months are favourable for successful flowering in litchi.

Vegetative growth occurs as a series of flushes alternating with period of rest. The growth rhythm for high yields is one or two flushes after harvest, followed by another one in winter (Menzel 2001). The flushing enlarges tree size and produce leaves for utilizing sunlight for carbohydrates synthesis which supports fruit development in the following seasons. Moreover, leaf flushing is one of the factors that counteract flowering process (Menzel and Simpson 1992).

Fig 1 (a) Flush emergence on secondary branches and (b) Mature flush of litchi on which flowering is expected in upcoming season.

The flushing of shoots in litchi is recurrent with cyclic flush growth (Davenport and Stern 2005). When new shoots emerge, they elongate, and the new leaves expand, subsequently, the terminal bud becomes dormant and leaves continuing to mature and accumulate chlorophyll (O'Hare 1989). The flushes maturing earliest before the winter period tended to produce a high proportion of floral shoots, while trees maturing quite late in the season produced a high proportion of vegetative shoots. Flushes that matured approximately 2 months before winter (midway between the above flushes) however produced a high proportion of dormant buds (O'Hare 2002) (Fig 1b). Flush growth after harvest is crucial for tree recovery and productivity for next season. New growth of shoot responds to low temperatures in winter and forms reproductive flushes (Batten and Mc Conchie 1995). However, new growth occurs only from a fully mature shoot (Yang *et al.* 2013). The maturity of flush in winter exerts a large influence on the flowering (Davenport and Stern 2005, Menzel 1983, O'Hare 2002, Olesen *et al.* 2002). The flush cycle is managed in such a way that the latest flushes are fully matured before winter, which maximizes flowering success. The trees that flushes vegetatively in autumn are less likely to flower than those remain dormant (Menzel and Simpson 1992), hence, prediction of the flush cycle is needed so that precise and effective measures can be taken to manipulate/or force it and is necessary to determine the progress of flush maturation, which is reflected by maturity of the new leaves. As leaves mature, they attain their full size, typical green colour, hard texture and optimal photosynthetic function.

Litchi leaves have a definite lifetime and shed periodically. With a situation of winter vegetative growth flush, selective pinching/or pruning of the growth flush by leaving some new leaves to support fruit development can be done for better flowering. A better strategy is to time your postharvest pruning so as to ensure bud break during the cooler season (Folino and Mee 2004). Floral initiation as the first step in the productivity of litchi plants in warm subtropical region (Das *et al.* 2004) is governed by shoot maturity and sufficient nutrient reserve in the shoots. When a litchi tree flowers, the flowering panicle emerges 4-6 weeks after initiation, as showy multi flowered cluster, known as a panicle on the end of branches (terminal inflorescence). It is believed that litchi needs a period of vegetative dormancy to initiate floral buds. Fruit from the trees which flower very late in the cycle often do not fully mature.

Flushes of vegetative growth occur on groups of stem borne on scaffolding branches in isolated section of tree canopy. Flushing stems are usually connected at some common branch point within the tree limbs (Davenport 2009) (Fig 1a). Appearance of enlarged leaf primordia and lateral meristems on the elongating main axis are the first indications of floral differentiation in litchi. The emerging inflorescence is initially similar to a vegetative flush and when the lateral meristem develop into secondary inflorescences or start producing small leaves (as in the case of mixed shoots), each panicle produces ten to hundreds of small flowers (Menzel and Waite 2005).

Out of three flushes in litchi, early (after harvest) and mid (August to October) season flushing influence the yield, and late season (after November) do not contribute towards yield. Thus, the mid-season flush is of more significance in cultivars *Bedana*, *Bombai* and *Deshi*, whereas the early season flush (appearing in July) is the desirable vegetative flush in the rest of the cultivars with respect to yield (Pereira *et al.* 2005), i.e. all the shoots with second flush (in August) and third flush (in November) bears panicles in upcoming season (Das *et al.* 2004) (Fig 2c).

Leaf flushing is the dominant factor controlling panicle initiation (Menzel and Simpson 1992). A minimum cycle would be 6 to 8 weeks for flushing and 4 to 6 weeks between flushes; consequently, bearing shoot rarely completes more than two flushes between harvest and flower initiation in Australia (Batten and Lahav 1994). Flush growth should be restricted to 0.6 – 2.0 cm in October-November and that leaves should be removed from flush growth of more than 10 cm. These practices prevent alternate fruit set and stabilise yield (Chen and Huang 1994).

Vegetative flushing prior to the usual period of floral initiation (in December and January) results in poor or no floral initiation. The vegetative flushing in the last week of November hardly produced any panicle in March apparently due to immaturity of these shoots to differentiate flower buds in the month of December and January (Shukla and Bajpai 1974) and vegetative growth after September led to erratic bearing in litchi (Kanwar and Nijjar 1985). The duration and interval of growth in litchi are strongly related to environmental conditions, with optimum leaf area production occurring at about 29°C (Batten and Lahav 1994). Variation in leaf flushing and reproductive activity of litchi may be due to variation in microclimate, soil nutrient (especially N) and insect attack which influences the endogenous rhythm of each tree (Menzel and Simpson 1992). Vegetative flushing in the 4-6 weeks period before the time of panicle emergence eliminates flowering in spring (Menzel *et al.* 1988).

The poor fruit retention in litchi results from insufficient flushes on the bearing shoot, whereas poor flowering could occur when the bearing shoots produce immature flush and leaves in winter (Chang 2004). The emerging inflorescence is initially similar to a vegetative flush and it is only when the lateral meristems develop into secondary inflorescences or start producing small leaves in the case of mixed shoots, it is possible to identify the shoot. Each panicle produces ten to hundreds of small flowers (Menzel and Waite 2005). Limited data suggested that cultivars with early fruit ripening had a lower alternate-bearing tendency than late ripening cultivars (Smith *et al.* 1986).

Factors influencing floral initiation and induction

Lychee flowering is very much related to various morphological (flushing time, shoot maturity), physiological and biochemical status of shoots especially C: N ratio, balance of endogenous hormones and floral initiation process especially in warm subtropical region. The lack of profuse and regular flowering has been attributed to several factors such as juvenility, environment (temperature and soil moisture), tree manipulations (nutrition, cincturing and growth regulators), crop competition, photoperiod, genotype and interaction of factors. Lychee trees do not display concurrent vegetative and reproductive growth on the same shoot (Menzel and Simpson 1991). The vegetative growth after September is at the expense of fruiting in the following year (Mustard and Lynch 1959). The relationship between flowering and vegetative flushing activity during winter is well established (Menzel *et al.* 1988) and floral initiation takes place only after the shoot has undergone a period of vegetative dormancy. Resting period during early winter is conducive to floral initiation in litchi i.e. continuous vegetative flushing during winter and the absence of a dormant or resting phase during this period reduce flowering (Nagao *et al.* 2000).The growers are achieving more reliable flowering, especially in low-production cultivars by discouraging fall vegetative flushes thereby insuring adequate age of the stems when the cool night temperatures occur in winter (Menzel 1983). Litchi bears heavy crop in one year and light or no crop in the adjoining year. The flushing habit of litchi varieties is intimately connected with irregular bearing. Problem is generally due to failure of flower initiation which puts forth vegetative growth prior to panicle emergence and flowering eliminates the crop completely (Singh *et al.* 2012). Although there is competition between fruit and shoots during flowering and early fruit growth which may limit initial fruit set, but leaves are required for latter fruit development (Hieke *et al.* 2002d).

A range of factors (environmental conditions and plant factors), as they are involved in the expression of genes are associated with flowering. These are temperature, drought and plant factor as cultivar, tree and panicle within a tree, nutrients, carbohydrates, and phyto-hormones contents etc. Chilling as a continuous spell is more effective than appearing in scattered manner. Soil moisture stress cannot replace chilling over induction process. Floral induction occurs when the apical meristem is quiescent whereas floral initiation starts from the 'millet stage' when cell division in the apical meristem become active (Huang and Chen 2005).

Induction of reproductive or vegetative shoots is thought to be governed by the ratio of a temperature-regulated florigenic promoter and an age regulated vegetative promoter at the time of shoot initiation (Davenport 2007). The ration of these two putative component at the time that shoot are evoked from resting buds determines the fate of the resulting new shoots (Davenport *et al.* 1999).

The vegetative (V) or generative (G) shoot types can be reversed in lychee during shoot morphogenesis. Transition shoots (V>G or G>V) are evoked when containerized trees transferred from warm-to-cool or cool to-warm temperatures, respectively, during early bud development (Batten and McConchie 1995). The flower bud induction process is followed by differentiation and flower expansion preceding anthesis. The subsequent fruit set process usually involves 2 major drop periods, one at bloom and another some weeks later when crop load is reduced as excess fruitlets are shed (Gene Albrigo and Saúco 2004).

The flower bud differentiation in tropical species such as mango and lychee often use a predictable environmental stimulus, cool winter temperatures, to induce flowering (Wilkie *et al.* 2008). Floral induction is a function of internal plant hormone levels, and prevailing environmental conditions. When the buds first emerge, they are a mixture of flower and leaf buds. As the bud continues to grow, the leaves fall off and an inflorescence develops if the temperatures remain low. If the temperatures remain high, a mixed inflorescence with both flowers and leaves can develop (Folino and Mee 2004). Temperature is undoubtedly an essential factor in the entire flower-bud formation process of subtropical fruit crops and the lack of sufficiently low temperatures (<15°C) is one of the main reasons for the irregular bearing habit of these plants under natural conditions. The lack of flowering is usually related to the weather or the timing of shoot growth during the cooler months of the year. Litchi must experience bud break (of 2 mm to 4 mm) during an extended period of cool weather (Folino and Mee 2004). Litchi used to flower during the spring months (northern India) and September (southern India) when the mean temperatures in preceding months are consistently below 20° threshold which is required for bloom formation during March–April in the northern hemisphere and August-September in the southern hemisphere. During warm winter (average temperatures above 20°C), most litchi trees will grow vegetative and not produce flowers. It has been generally established that if the mean daily temperature is above 20°C, new growth will be vegetative (i.e. leaves and branches) whereas if the mean temperatures are below this temperature flowering panicles will be formed from emergent buds (Singh *et al.* 2012).

In warm weather, the pre-existing primordial leaves develop to form true compound leaves. If favourable conditions persists, through the initiation and differentiation of new nodes, the new primordial leaves develop into compound leaves at the distal part of the shoot (Batten and McConchie 1995) but vegetative shoot takes 6 weeks or longer, depending on the weather (Olesen *et al.* 2002). During this period, the apex produces about eight leaves before returning to rest. In contrast to vegetative shoots in which true compound leaves arise from the primordial leaf tissues, the leaf primodia remain relatively quiescent and the lateral meristems at each node are instead evoked elongation of the articulated thyrosoidal structures at each node terminates in dichasial floral structures (Fig 2d). The litchi exhibits dichogamy, in which the peak time of functionally male flowers does not synchronize with that of the functionally female flowers. The production of functional female flowers varies between 10 and 60%. Flowers are usually produced in later winter or early spring and there are three types of flowers which open in succession on the same panicle (Singh *et al.* 2012).

Fig 2 (c) Post harvest flush emergence, (d) Flowering on September flush, (e) Flowers ready for pollination.

Phenology

The relationship between flowering and vegetative flushing activity in winter is well established in litchi (Olsen *et al.* 2013). In most perennial fruit, trees do not flower when they are in vegetative growth. Good floral initiation in litchi is erratic, resulting in low and irregular fruit yields. The failure of flower initiation is clearly related to failure of induction of vegetative dormancy on the tree.

Litchi bearing shoot comprised three to four flushes and its carbohydrate reserves are essential for adequate cluster production. The age of the vegetative flush, or the degree of dormancy, appears to have a strong influence on the subsequent shoot development of litchi (Shigeura 1948). Bearing tree of litchi should have maximum vegetative growth between July-September and least during winter months (January-March) (Ray 2004). The shoot must be of high quality i.e. must have plenty of leaves, good built up of carbohydrates and above all matures on time (Huang and Chen 2014). The winter flushes are not allowed as these do not flower in upcoming season. Failure of shoot to bloom is generally attributed to an insufficient degree of dormancy required for initiation of flower bud formation (Nath and Singh 2014) (Fig 2c). The time window for flower induction is a function of flush maturity and chilling period. The duration and interval of successive flushes in litchi seems to be strongly dependent on the vigour of the tree, orchard management (e.g. pruning, irrigation, radiation, and temperature) (Menzel 2005, Olesen *et al.* 2002)

During two phenological stages of the reproductive cycle, *viz.* floral initiation and flowering and fruit set, the floral initiation is a problem in warm tropics, whereas poor fruit set is a problem of the subtropics (Das *et al.* 2004). Vegetative growth, flowering and fruit growth reduced starch reserves while rest periods, such as the end of fruit growth (until new vegetative flushing) and the winter rest period, starch reserves again increased. The transition of the bud from the vegetative stage to the reproductive one is accompanied directly with changes in the nucleic acid metabolism because the flower differentiation is based on synthesis of a specific ribonucleic acid (Hanke *et al.* 2007).

Pruning, tree synchronization, girdling and use of paclobutrazol

Litchi is an evergreen fruit tree that grows up to 15 m (30 m under favourable conditions) tall and removal of older growth stimulate new growth in all of the meristematic terminal ends which helps to achieve hemispherical growth habit. The clipping off of a branch tip with each cluster of fruits is sufficient to promote new growth for the next crop (Anonymous 2003). Pruning stimulates growth of the axillary buds (Olesen *et al.* 2002). Flush removal/ tip removal (*pruning prior at the onset of an extended cold period*) is desired for getting forced flower panicles during the winter months through bud break, has been quite effective but cumbersome and tedious. At the same time, the remaining leaves left after the pruning is too old to support a good crop because the photosynthetic capacity and nutrient and energy output of the leaves diminishes with age. The vegetative flushing during the winter reduced flowering of *Kaimana* trees and that pruning of young flushes, which emerged during early December, stimulate flowering (Nagao *et al.* 2000).The pruning of fruit from the lychee tree at harvest should be accompanied by pruning of non-productive, vegetative stems as well, to better insure a single synchronized flush of growth at the proper time (Davenport 2003). There is strong relationship between flowering and shoot development in litchi and developing fruit are dependent on current photosynthates produced by the leaves behind the inflorescences (Olesen *et al.* 2013) i.e. fruits are mainly dependent on mature leaves behind the panicles, but could also utilize reserve stored in the branches (Hieke *et al.* 2002d).

Girdling (or cincturing) suppresses vegetative flush (in winter) (Ramburn 2001) increased flowering intensity in lychee (Menzel 1983, Menzel and Simpson 1987, Ramburn 2001) by manipulating growth cycle (so that new buds develop during cool weather and similar to the drought treatments) and redirect assimilate that normally supported stem and root growth. Closed girdling, spiral girdling led to increase in flowering in litchi with increases in soluble sugars and starch content in the shoot. Girdling of trunks or primary branches inhibits the downward transport of photosynthates, and promotes accumulation in the upper canopy (Li and Xiao 2001). In China, it is practiced only when trees are about to flush after heavy rainfall in autumn (Menzel and Simpson 1987) and flowering could be induced by girdling 3 mm wide strip of bark around the main branches (Morse and Ooosthuizen 1993). The branch girdling in *O-Hea* litchi variety during September to December results in an increase in percent of flowering with the maximal flowering percentage obtained when the branches are girdled in October in the south portion and November in the north portion of the tree. Total non structural carbohydrates (TNC) content in leaves and terminal shoots of the girdled branches tended to be higher than those of the un-girdled ones. Total nitrogen (TN) content in branches increased progressively from August to December and slightly decreased in October. The higher the TN content in branches the lower the flowering percentage. C/N (TNC/TN) ratio of leaves and terminal shoots increased prior to flowering (Duang 1984).

At harvest, regardless of the time of branch girdling, fruit yield and quality increased with increasing number of flushes; shoots with three flushes were similar to un-girdled controls (Chang and Lin 2008). Girdling of branches having 3 to 4 cm diameter or foliar application of 0.5 g paclobutrazol + 0.4 g of ethephon per litre with hardened flush in September (northern hemisphere) promote flowering in unproductive litchi trees (Ramburn 2001). Application of paclobutrazol and ethephon (1000: 500 ppm), reduces the percentage of leaf flushing about 10% compared to the untreated ones (Chaitrakulsub *et al.* 1981).

The paclobutrazol (PBZ) induced flowering in China because after 2 months of treatment, paclobutrazol treatment records higher amount of total non-structural carbohydrates (TNC), reducing sugars (RS) in the branches and leaves whereas the total nitrogen content (TN) decreases, thus resulting in a higher ratio of TNC/TN in the treated trees than in the control. The TN content of the leaves at a stage of 1 month before flower initiation is lower. Phosphorus and potassium contents of the branches and leaves at one month after the treatment are found to be lower than in the control (Angsananiwat 1990). There is an increase in C: N ratio and leaf water potential, by the paclobutrazol with drastic increase at the bud break. C: N ratio in shoot is positively related to abscisic acid (ABA) content in buds. The doses of 1.0 and 1.5 g of PBZ resulted in the reduction in the concentration of nitrogen and carbon in leaves and, therefore increase C: N Ratio. Liang and Yu (1991) found an increase in the proportion of pure panicles by 4-fold with 0.1 g paclobutrazol spray in litchi cv. Xiangli. Paclobutrazol besides affecting gibberellins also increases ABA and cytokinin contents concomitant with C: N ratio and leaf water potential in mango buds to elicit flowering responses (Upreti *et al.* 2013).

Abiotic stress including water relations and temperature

Climatic conditions (cool temperatures or water stress), bud age and tree vigour are usually associated with the flower bud induction process, whereas climatic stress and internal limitations from lack of pollination, adverse hormonal levels or competition for carbohydrate and/or nutrients may lead to unsuccessful fruit-set (physiological drop) (Gene Albrigo and Saúco 2004).

The litchi trees should suffer some stress during panicle and floral development to prevent vegetative flushing which is thought to compete with flowering (Cull and Paxton 1983). In litchi, it is generally accepted that high soil moisture in autumn is inductive to vegetative growth and suppresses flowering, while low soil moisture restricts vegetative growth and promotes flowering (Menzel 1983). The drought may have a negative effect on photosynthetic capacity as it limit phosphorylation, RuBP regeneration, or carboxylation by Rubisco are the more often reported. All enzymes related to these main processes of photosynthesis may have a decreased activity or amount.

Among the possible causes of photosynthesis inhibition, accumulation of carbohydrate and subsequent lower *Rubisco* activation state and repression of photosynthetic genes expression is likely the better known (Paul and Foyer 2001). Water stress can also act indirectly to promote floral initiation by checking vegetative flushing in lychee (Stern *et al.* 1998) but there is no conclusive evidence that water stress is directly involved in inductive processes as has been found in citrus (Menzel 1983). The water stress is required to induce dormancy, which promotes flowering (Thunyarpar 1998). If there is dry period before flower bud differentiation, it is beneficial to litchi (Mitra 2004). Drought prevents new leaf growth which normally competes with the developing fruit for the tree resources. The trees droughted for flowering have double the number of fruits per panicle at harvest compared with control plants (Batten *et al.* 1994).

Temperature also has a strong influence on shoot development, with high temperatures conducive to vegetative growth and low temperatures appearing necessary for floral initiation. Litchi being subtropical fruits crop, cool temperature became a key trigger of flower induction (FI). Due to cool temperature treatment a clear raise of cytokinins (CKs) in buds is opposed by a drop in gibberellins (GAs) and auxin (IAA) (Hegele *et al.* 2010). Deficit irrigation can enhance fruit quality by raising dry-matter percentage and sugar content. Furthermore, controlled water deficit has been used as a technique to stimulate blossoming in litchi. Higher concentration of *malondialdehyde (*MDA), (which is the product of membrane lipid peroxidation) in the leaves after drought stress indicated an increased on oxidative stress in the leaves. Total amylase activity increased 3 to 7 folds and acid invertase activity increased 7 folds in K-deficient leaves. Higher acid invertase activity was recorded during emergence of panicles, and increased amylase activity was observed during pre-swelling stage.

Initiation of mixed shoots in litchi occurs in mild weather, at temperature lower than those needed for purely vegetative shoots and higher than those for purely floral shoots. Both leaf primordial and lateral meristems develop, resulting in shoots with a leaf and an inflorescence at each node. Transition shoots commonly appear in litchi when shoot emerge during rapidly changing temperatures. These initiate one type of shoot, either vegetative or generative, which finish as the generative (Batten and McConchie 1995).

The greatest level of flowering of litchi occurred when low temperature continued after floral induction. Flowering is much more consistent in areas where day temperature in winter falls below 20ºC for a few weeks (Batten and McConchie 1994). High temperature after panicle emergence reduced the proportion of leafless panicles and increases the proportion of leafy panicles and some panicle reverts to vegetative growth (Menzel and Simpson 1991). Both temperature and flush maturity can influence subsequent shoot structure of lychee. In the absence of either a strong floral temperature (18/13˚C) or strong vegetative temperature (28/23˚C), slight differences in initial flush maturity have greater impact on the type of emerging shoot formed (O'Hare 2002).The flowering in lychee is best after ten weeks at 15°C, while periods of 8 hour or more per 24 hour above 20°C are detrimental (Menzel and Simpson 1995). The high root temperatures can inhibit floral initiation in lychee even when shoots are exposed to florally inductive temperatures (O'Hare 2004), implicating either perception by the roots and long-distance signalling or heat transfer via the transpirational stream (Wilkie *et al.* 2008).

Source-sink relationship and crop load

The relation between developing fruits (sink) with mother soil base (source) is well established in litchi. The development and transfer of nutrients from source to ultimate sink (fruit) has been very crucial. Generally, most perennial fruit trees do not flower when they are in vegetative growth. The intra-plant variation in flushing and shoot growth pattern influences the overall floriferousness of the litchi plants (Singh *et al.* 2004).

Under normal circumstances, one of three shoots initiates growth from apical or axillary buds in resting stem. Vegetative shoots produce only leaves at each node; generative shoots give rise to inflorescences; and mixed shoot bear both leaves and inflorescences at each node. There is importance of flushing management in terms of the bearing shoot for flowering and fruiting in litchi, and poor fruit retention would result from insufficient flushes on the bearing shoot, whereas poor flowering occurs when the bearing shoots produce immature flush and leaves in winter. The inability of shoots emerging after harvest from the fruiting terminals to bear fruits in the next spring was probably due to depletion of food reserves in the supporting tissues as a result of which the new shoots could not mature enough in time to differentiate to flower buds for the next crop (Kanwar 2002).

Nitrogen and carbohydrate reserves

In litchi, the available carbohydrate as total non structural carbohydrate or starch is accumulated before flower initiation and leaf flushing (Thunyarpar 1998). Vegetative growth, flowering and fruit growth reduces starch reserves while rest periods, such as the end of fruit growth until new vegetative flushing and the winter rest period, increases starch reserves again (Cronje and Mostert 2010). Starch concentration in the leaves is higher than that in the terminal shoots of the light flowering trees. It is suggested that carbohydrate distribution pattern may serve as an indication for the judging of the floral induction effect in litchi. The carbohydrate content of previous season flush appears to be contributing towards the emergence of third flush (during November) and ultimately the panicle as the content was found to decrease during the third flushing. The phenol content of all the flushes is found to increase during the initiation of new flushes (Das *et al.* 2004).

Leaf nitrogen (N) can also play a critical role in regulating flushing just prior to panicle emergence. It has direct effect on flowering, high N reduced flowering while low N promotes flowering (Thunyarpar 1998). By restricting leaf N level to below 1.75 to 1.85% prior to panicle emergence, flowering can be promoted in subtropical environment (Menzel *et al.* 1988). The leaf N content decreased with the growth of panicle and blossom as the leaf N mainly transferred toward the reproductive growth centre. However, in the flower bud differentiation to early fruit expansion period, the potassium (K) content drastically decreased. As the litchi grows, the leaf calcium (Ca) content experience a declining–increasing–declining development, but eventually reaches a certain maximum value after fruit picking and a second maximum value during blossoming and fruit setting. The demand for carbohydrates during litchi flowering and fruit development is evident. The lack of carbohydrates in the mid- and late-fruit development is closely related to the second physiological fruit drop, which has become the main factor affecting production (Deng *et al.* 1993).

Starch accumulation (more related to vegetative growth) found low in flushing tree and higher in dormant tree or tees with floral buds, i.e. starch concentrations are higher in all parts of flowering lychee trees than in non-flowering but vegetatively flushing trees (Menzel *et al.* 1995a). It is suggested that carbohydrate distribution pattern may serve as an indication for the judging of the floral induction effect in litchi and concentration of soluble sugars increases from November to December and then decreased in January while the starch concentration increases progressively, (especially in the upper parts of the canopy). Starch concentrations in the heavy flowering trees are highest in small branches and decreased acropetally and basipetally, whereas the concentrations of soluble sugars record highest in the terminal shoots (Houbin *et al.* 2004). During the period from June to November, litchi leaves produce large amounts of carbohydrates that accumulate in branches and trunks, with starch concentration the highest in small branches (Chen *et al.* 2004). This provides the necessary energy for floral formation and flowering in early spring.

Sucrose and its metabolizing enzymatic activities increased during flowering, indicating their decisive role in the flowering process. During the bud swelling stage, the maximum reducing sugars contents are recorded, while higher *chlorophyll a* and *b* values recorded during bud break stage in mango (Shivu Prasad *et al.* 2014). In contrast, Menzel *et al.* (1995a) reported that high carbohydrate content was not necessary for flower initiation in the lychee. Accumulation of total non structural carbohydrates (TNC) content occurred before a week of leaf flushing and decreased at leaf flushing. TNC accumulated in leaves and stem apices, one month before panicle emergence or leaf flushing and then depleted (Chaitrakulsub 1981). TNC concentration, and particularly starch concentration, in the roots has been linked to bearing consistency. Carbohydrate concentrations during the winter markedly affected subsequent flowering.

Phosphorous and other mineral nutrient contents

The leaf phosphorus (P) content increased after the fruit picking period to the early flower bud differentiation period and then reached the maximum level in the early flower bud differentiation period. Subsequently, the P content decreased in the blossoming and fruit setting periods. Generally, the flower bud differentiation in litchi starts in December and completed by the end of January. After harvest, the N contents in leaves and stalks rose while P and K contents in them continued to decline. The N content in xylem significantly increased at the pre-heading stage, but the P and K contents significantly decreased, and only P content significantly declined at the pre-blossoming stage, while N and P contents significantly rose after harvest. K affects photosynthesis in litchi (Deng *et al.* 1993). Potassium is essential for photosynthesis, carbohydrate and protein synthesis, and enzyme activation. Deficiency in both micronutrients B and Zn results in growth depression, reduced flower induction and fruit set as well as decreased fruit quality in litchi. The association of Ca deficiency with leaf senescence fits very well with the loss of chlorophyll, total protein, and *Rubisco* protein, which have been found to be characteristic of Ca deficiency. Zn deficiency caused bronzing of litchi leaflets and smaller fruits with reduced flesh recovery and sugar content.

Endogenous hormones

The higher level of IAA in the shoot promotes flower bud initiation in litchi (Liang *et al.* 1987) and high auxin: gibberellins ration promotes flower bud differentiation in the shoots (Das *et al.* 2004), i.e. reduced levels of endogenous GA have been correlated with floral initiation in lychee (Chen 1990). There is an increase in cytokinin activity in the buds during flower bud differentiation in litchi. In dormant buds, the endogenous cytokinin content remains low, and the buds do not respond to exogenous cytokinin application. However, application of kinetin promotes flower bud differentiation after completion of bud dormancy. Thus it can be referred as an indication that the increase in endogenous cytokinin levels during flower bud differentiation may be correlative rather than the cause of flower bud initiation (Chen 1991).

It is also suggested that apart from the minimum nutritional and carbohydrate levels, floral initiation in litchi is controlled by a dynamic balance among auxins, gibberellins, cytokinins and abscisic acid in the leaves and terminal buds about four weeks prior to and during the period of floral initiation. Four cytokinins, zeatin, zeatin riboside, N6-(62-isopentenyl) adenine, and N6-(56-isopentenyl) adenine riboside, were detected in buds (Chen 1990). Gibberellin content was high at the period of leaf flushing and then the level decreased when the flower bud was formed, however, the indole acetic acid (IAA) content was nearly the same level in both stages of leaf flushing and flowering. Ethylene concentration in stem apex of lychee increased at the 3rd week before leaf flushing and remains constant till leaf flushing time (Lerslerwong and Thunyarpar 2001). The kinetin is more effective for promoting flower bud differentiation than other types of cytokinins and the level of cytokinin and abscissic acid in shoot tip of litchi cv. Heh Yeh at the period of leaf flushing is lower than that at flowering.

In Thailand, ethephon decreased flowering of Ohia and had no effect on Hong Huay litchi (Stern and Gazit 2003). The ethephon, kinetin (Chen and Ku 14), and auxins increased flower bud formation (Menzel 1983). In contrast, gibberellins increased the proportion of male to female flowers and delayed the appearance of female flowers . The GA levels in xylem sap dropped, cytokinin-like activity increased, and that IAA and ABA in shoot tips never change prior to flower initiation (Chen 1990). Low GAs levels in litchi shoot tips occurred during floral initiation (Liang *et al.* 1987).

Other biochemical factors influencing flowering

Assessing changes in biochemical constituents in shoots, viz. carbohydrates, phenols, soluble protein and amino acids in relation to flushing and panicle initiation helps in developing a proper understanding of the panicle initiation process in litchi (Das *et al.* 2004). Higher level of RNA, phenols, and reduced level of amino acids, N, P, K, content favour flowering. Non-reducing sugars, total soluble sugars, alcohol insoluble N, total N and nitrate reductase activity recorded higher in floral shoots. Respiration rate, carotenoids content, xanthophylls is found higher at floral bud differentiation (FBD) stages, while total free amino acids reduced during FBD. Storage protein accounted for most of the nitrogen used during the initial spring growth flush and flowering in pistachio.

Little changes in contents of chlorophyll before flowering may indicate that chlorophyll contents may not be a factor in the flower induction of litchi. There is an 8.5-fold increase in total chlorophyll concentration during development from young red leaves to mature dark green leaves. There is no increase in chlorophyll content and significantly lower Fv/Fm values indicate a possible decrease of photosynthesis. Fv/Fm ratio of Hong Huay litchi is similar and higher than 0.700, which indicate that leaves are non-stressed (Hetherington *et al.* 1989). As the concentration of growth retardants increased, Fv/Fm values decreased and decreases in Fv/Fo, indicating possible structural damage to the thylakoid membranes of the chloroplasts (Pereira *et al.* 2000). Chlorophyll fluorescence (Fv/Fm ratio) and chlorophyll content in leaves increases with leaves age.

Leaf gaseous exchange

Photosynthesis, one of the most fundamental metabolic processes in plants, is directly related to the abundance of chlorophylls, which absorb light energy that drives carbon-fixing reactions. Hence, leaf greenness may be closely related to photosynthetic performance. There is a sigmoid growth pattern of leaf expansion and an exponential pattern of net CO_2 assimilation (A) and stomata conductance with leaf age. The fruit are mainly dependent on current photosynthesis. Photosynthesis in the leaves behind the fruit cluster is more important than photosynthesis in older shaded leaves (Hieke *et al.* 2002a, b). Fullness of leaf expansion is another index of leaf development. However, litchi is a typical "delayed greening" tree, whose leaves are immature and accumulates chlorophylls when they are fully expanded (Hieke *et al.* 2002a, O'Hare 1989). Fruit set and final yield in most fruit crops can be described as a function of tree photosynthetic efficiency. Initial fruit set in litchi increased with increasing leaf area. The new leaves on one branch do not reduce fruit growth on adjacent branches (Hieke *et al.* 2002b). Leaves next to inflorescence are more important for yield than older leaves (Hieke *et al.* 2002a). Young litchi shoot has relatively low rates of photo assimilation until the leaves are fully expanded and dark green, and depends on assimilates from elsewhere in the plant. During leaf expansion, translocation of assimilates to the shoot occurs at the expense of the roots (Hieke *et al.* 2002c).The A of new leaves maintains below zero before they reach their 50% of full size (Hieke *et al.* 2002a). The light green fully expanded new leaves have A about 1/3 of the dark green fully matured leaves (Hieke *et al.* 2002c). Starch concentrations of the lower stem and roots decreases as the young red leaves expanded, and increased as the fully expanded leaves turned dark green. Chlorophyll concentrations and net CO_2 assimilation rate are high in the fully expanded dark green leaves (Hieke *et al.* 2002c).

The increase in A is associated with increased chlorophyll concentrations and higher stomatal conductance (*gs*), but lower internal CO_2 concentrations. The increase in A during leaf maturation was strongly related to changes in *gs* and chlorophyll concentration. Leaves close to inflorescences records lower rates of mitochondrial respiration (Rd) and net photosynthesis (A_{net}), and lower stomatal conductance (*g*s) and quantum efficiency of photosystem II under actinic light than vegetative shoot leaves. Leaf nitrogen concentration, (generally decreased from the beginning until the end of flowering), reduces, near to inflorescences than in vegetative shoot leaves. However, these differences and changes are counterbalanced by an increase in leaf-mass to area ratio so that leaf nitrogen per unit leaf area (*N*a) remained nearly constant during the whole flowering period, except in leaves close to panicles bearing set fruits. Low A_{net} in leaves close to inflorescences is neither due to changes in *N*a nor to a decrease in *Rubisco* activity induced by low *gs*, but rather to a decrease in electron flow in PS II. This decrease is not directly associated with higher starch or soluble sugar contents (Urban *et al.* 2004). Mature leaves on younger flushes located in the outer canopy had greater net CO_2 assimilation (A_{CO2}), *gs* and transpiration (*E*) but smaller internal CO_2 concentration (*Ci*) than older leaves on old flushes or woods located inside the canopy and contributes majority of carbohydrate production. Leaves on the last flushes adjacent to fruit clusters had greater A_{CO2}, gs and E than leaves on similar position of a de-fruiting shoots (Chang and Lin 2007). The primary source of photosynthates for new leaves are the older leaves on the same shoot, whereas fruit are able to import assimilate from other branches (Hieke *et al.* 2002d).

A decline in leaf relative water content (RWC) initially causes stomatal closure, which in turn leads to a decrease in the supply of CO_2 to the mesophyll cells and thus reduces leaf photosynthetic rate (Restrepo-Diaz *et al.* 2010). Increases or decreases in net photosynthetic assimilation in the presence of developing flowers may result either from modification of leaf nitrogen per unit leaf area (*Na)* caused by a change in leaf nitrogen concentration or in leaf mass-to-area ratio, or from an increase or decrease in one or more of the limiting biochemical factors of net photosynthesis, mainly ribulose-1,5-bisphosphate carboxylase/oxygenase (*Rubisco*) activity, ribulose bisphosphate (RuBP) regeneration, and mitochondrial respiration rate (Urban *et al.* 2004).

The light compensation point (LCP), light saturation point (LSP) and apparent quantum yields (AQY) of litchi indicated that it was a heliophilous plant (Zhang *et al.* 2014). A_{CO2} at leaf temperature at $< 24^{\circ}C$ is only half of the maximum values, indicating a potential shortage of carbohydrate supply during blooming season and early fruit set in the spring (Chang and Lin 2007). The contribution of fruit photosynthesis to reproductive growth varies across species, environment and fruit type, but ranges from 5 to 15% for many fruit trees (Birkhold *et al.* 1992). The relatively low photosynthetic efficiency of litchi could contribute to its sensitivity to environmental stresses (Menzel *et al.* 1995b). The leaf photosynthesis on younger flushes and adjacent to fruit is greater than that on shaded older flushes (Chang and Lin 2007). The developing fruit of Tai So litchi depends primarily on current CO_2 assimilation from leaves rather than on stored carbohydrates (Roe *et al.* 1997). Carbohydrate accumulation, which may derive from tree reserves, canopy photosynthesis, or photosynthesis by the fruit (Hieke *et al.* 2002a), is essential for fruit development. The individual branches of litchi generally act independently and supply assimilates to fruit only when there is a severe local shortage of fixed CO_2, therefore it appears that the bearing shoot is the major source of carbohydrates for fruit growth, mainly through leaf CO_2 assimilation, but also through its carbohydrate reserves when needed (Menzel 2005). Net CO_2 assimilation in litchi, under high irradiance and high ambient CO_2 concentrations, increased at high application rates of K.

CONCLUSION

Although low temperature appears a pre-requisite for floral induction in lychee but there is strong relationship between flowering and shoot development. The flush maturity has a strong influence on determining shoot development when shoots are mature enough but slight fluctuation in temperature and rainfall pattern disturb phasic changes. Harvesting of fruits with few leaves, post harvest cincturing, use of paclobutrazol or KNO_3, exogenous application of kinetin (applied after dormancy) has been used effectively in the sub-tropics to induce synchronous flowering. Foliar and leaf tissue analyses are complementary and should be used as a basis for a fertilization in a litchi flowering management program. Foliar nitrogen levels should not exceed 1.7% to discourage vegetative flushes during winter. Armed with the basic information provided here, growers can manage flowering to occur at any desired week of the year. Local environmental conditions may alter the expected responses, but scrutiny of all of the factors should bring consistent success.

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