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Flowering synchronization in pineapples (*Ananas comosus* L. Merr): A review

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Abstract

Natural flowering in pineapple is precocious, lacks synchronization in reproductive phenology and consequently leads to significant losses due to fruits being harvested out of schedule. Several factors influencing the flower initiation in pineapple have been identified, including the cultivar, plant size, temperature, nutrients, and water stress. To increase the synchronization, pineapple flowering can be artificially induced by hormones such as auxin and ethylene. However, despite the artificial induction, the simultaneous full flowering emergence is still difficult to achieve in the industry. Thus, a greater understanding of factors affecting pineapple flowering before hormone application may help in enhancing flowering efficiency. This review discusses the initiation and development of pineapple flowering, as well as the use of exogenous hormones to improve efficacy and provide insight into better pineapple crop management.

Key words: Artificially induced flowering, flowering susceptibility, hormone efficiency, auxin, ethylene

Introduction

Pineapple (*Ananas comosus* L. Merr) is one of the important horticultural crops grown in more than 80 countries. It is perennial monocotyledonous, native to tropical and subtropical America, and mainly cultivated for its edible fruits through vegetative reproduction. It is also used for value added products, mainly in the forms of fresh, canned fruits and concentrated juice. Presently, five major groups have been introduced: Cayenne, Spanish, Queen, Abacaxi, and Maipure, as well as several clones and hybrids (Joy and Anjana, 2015). Although the morphological characteristics of each group are quite similar, the physiological needs typically vary.

The natural induction of flowering (NIF) causes the lack of synchronization in pineapple flowering. NIF is influenced by the cultivar, plant size, temperature, nutrients, and water stress (Bartholomew and Sanewski, 2018). Agronomic practice of artificially inducing flowering by using hormones may help in synchronization of the flowering of pineapples. The history of artificially induced flowering began in 1874 because of the unintended effects of smoking (Bartholomew, 2014). Later, the ethylene gas contained in the smoke was found to be the precursor that initiated this phenomenon (Rodriguez, 1932).

To date, the use of flowering hormones is vital for pineapple production; however, irregular flowering behavior of pineapples is still one of the primary concerns among farmers. Complete flowering uniformity has been reported to be challenging to achieve, consequently affecting crop production management. Thus, it is essential to evaluate the current practices among pineapple producers and determine the best practices to be shared.

Pineapple undergoes three stages in its life cycle: vegetative, reproductive, and propagative stages. A thorough understanding of the first two cycles can provide a better insight into its flowering behavior. The flowering process principally involves two phases: flowering initiation and flowering development (Parimalan *et al.*, 2005). The transition to the reproductive stage varies in timing due to a variety of internal and external factors. Therefore, understanding the transition process helps in planning the exact period in which to artificially induce the flowering. Several pineapple flowering hormones have been introduced, and their effectiveness depends on several factors that will be further explained. This review covers initiation and development of pineapple flowering, and exogenous hormone application to enhance its efficacy.

Initiation and development of pineapple flowering

Flowering involves many complex processes generated from the reprogramming of the identity of the shoot apical meristem (SAM). This reprogramming is initiated by the flowering stimulus that activates floral genes (Rainha *et al.*, 2013). Recent studies have revealed the association of specific genes during flowering transition (Li *et al.*, 2016; Espinosa *et al.*, 2017; Liu *et al.*, 2018). Moreover, the level of gene expressions varies at different concentrations of hormone application during flowering transition (Li *et al.*, 2016; Wang *et al.*, 2017) and flowering development (Liu and Fan, 2016). The competent state of leaves is also essential during this transition for generating and transporting the stimuli to the competent shoot apex (Lyndon, 1990).

The transition to flowering causes changes in the morphological structure of the SAM. It can be identified through microscopic observations, and the use of flowering hormones can easily determine this phenomenon. During the vegetative stage, the dome apex is flat and surrounded by leaf primordial. The transition to the reproductive stage subsequently causes an increase in the apex dimension for a certain period before a gradual decrease. The first evidence of transition may happen as early as 2 days after artificially induce the flowering by the

formation of the corpus. In the subsequent days, a distinct zone of tunica and corpus can be observed. Then, the bract appears on the meristem margin, and the bud, which is located on the bract axil, develops to a flower. It is then followed by formation of the sepal, petal, stamen, and pistil. This flowering initiation has been well documented by several studies (Gifford, 1969; Wee and Rao, 1979; Espinosa *et al.*, 2017). Additionally, Wee and Rao (1979) reported that the transition time varied with different types of flowering hormone applications.

In field observations, the natural flowering commonly occurs 12 to 18 months after planting (MPIB, 2017), and the emergence can vary from 0 to 100% (Kuan *et al.*, 2005). With a flowering hormone application, the plant is frequently induced 7 to 15 months after being planted depending on the cultivar, agronomic practices, and geographic region (Cunha, 2005). Inflorescence starts to appear approximately 30 to 60 days later.

The time of flowering emergence depends on several factors, such as the type of hormones used (Wee and Rao, 1979), hormone concentration (Palupri and Tri, 2018), plant age (Hussain *et al.*, 2008), and temperature (Julius *et al.*, 2017). The development of pineapple flowering is divided into six stages: i) green apex (begins from induction and prior to emergence of the red apex), ii) the red apex (central leaves become reddish and shortened), iii) inflorescence (capitulum continuously swells until it forms a spherical shape), iv) flower elongation (elongation of principal leaf axil), v) first flower bloom (flowers open by 10% starting from the bottom part of inflorescence), and vi) complete flower bloom (all petals are dry) (Zhang *et al.*, 2016; Julius *et al.*, 2017).

Inflorescence consists of approximately 50 to 200 individual hermaphrodite flowers, borne spirally in a tubular manner and capped by a crown (Bartholomew and Sanewski, 2018). However, the number of flowers depends on the cultivar, fertilization management (Rodriguez *et al.*, 2018), plant vigor at the time of artificial induction (Fassinou Hotegni *et al.*, 2014), hormone efficiency (Liu *et al.*, 2011b), and night temperature (Friend, 1981). Each flower consists of three sepals, three petals, six stamens, and a tricarpellate pistil with a hollow, trilobite and trifid style. A recent study has reported the genes involved in flower organ development (Wang *et al.*, 2020).

Exogenous hormones in pineapple flowering

Flower initiation in pineapples can be promoted by sufficient levels of ethylene in plant tissues (Liu *et al.*, 2011a) while in other plant species such as *Arabidopsis*, ethylene can delay flowering (Achard *et al.*, 2007). Increasing ethylene levels has resulted in an antagonistic behavior toward gibberellin production; thus, flowering promotion in pineapples can be stimulated (Espinosa *et al.*, 2017). Biosynthesis of ethylene involves a simple linear pathway regulated by several internal and external factors (Ma *et al.*, 2014). It is possible to artificially induce flowering with an application of an exogenous ethylene hormone as it can be directly absorbed through the plant tissues.

Another hormone, auxin, is also capable of influencing flowering by stimulating the ethylene pathway (Wee and Rao, 1979; Bartholomew, 2014). Auxin induces the expressions of RNA that form the labile enzymes required to synthesize ethylene (Kang *et al.*, 1971; Burg, 1973). The enzyme also known as 1-aminocyclopropane-1-carboxylic acid (ACC) synthase profoundly affects the transition activity from S-Adenosyl methionine to ACC (Yu and Yang, 1979; Hansen and Grossmann, 2000). The attempt to elucidate the role of this enzyme on pineapple flowering indicates that the flowering can be delayed by silencing the gene of this enzyme (Trusov and Botella, 2006).

Several types of growth regulators are efficient in initiating pineapple flowering. The most commercially used are ethylene, 2-chloroetilfosfonic acid (ethephon), α-naphthalene acetic acid (NAA), and calcium carbide (CaC_2). A number of factors may influence the flowering efficiency due to hormone application: i) type of hormone used, ii) assistance of additional substances or enhancers, iii) environmental conditions, iv) method of application, v) plant physiological state and planting materials, vi) cultivar or hybrid, and vii) nutrient management. Understanding the factors affecting natural flowering has provided significant benefits toward enhancing plant sensitivity to hormone induction, leading to higher flowering efficiency (Poel *et al.*, 2009).

Types of hormones used: According to Py *et al.* (1987), ethylene gas is more effective than ethephon in flowering induction because ethylene can be directly used by the plant, whereas ethephon should be liberated to form ethylene in plant tissues. Dass *et al.* (1975, 1976), Abdul and Yap (1992), and Butrat and Wangmuang (2004) found that ethephon application was more effective than NAA and CaC_2. However, several studies have also demonstrated that the NAA (Dass *et al.*, 1976) and CaC_2 (Raposo *et al.*, 2019) are comparable to ethephon. Induction by using NAA in the summer has reportedly failed, and it is not as effective as in autumn seasons, whereas ethylene is effective under both conditions (Cooper, 1942). This failure may be attributed to the differences in light intensity, with summer having higher intensity than autumn. Leeper *et al.* (1962) reported that the amount of NAA destroyed through decarboxylation increased in higher light intensity. Schonherr *et al.* (2000) also mentioned that NAA was sensitive toward light; therefore, the evening application of NAA is essential to enhance hormone efficiency.

Assistance of additional substances or enhancers: The effectiveness of hormones can be enhanced by adding substances such as calcium carbonate ($CaCO_3$) (Dass *et al.*, 1975), urea (Dass *et al.*, 1976; Malip, 2011), boron (Malip, 2011), activated charcoal (Poel *et al.*, 2009), ice cubes or cold treatment (Chang *et al.*, 2011), and oil-coated hormones (Onaha *et al.*, 1983). Besides that, adding these substances has an advantage of reducing the hormone concentration. Studies on hormone pH, especially ethephon, have contributed to significant flowering efficiency. This hormone is stable at acidic conditions of pH below 3.5, whereas it produces ethylene at higher pH values (Silva and Caputo, 2012). Since the pH of the pineapple leaf sap is in the range of 3.5 to 6.5 (Prigge and Gurierrez-Soto, 2014), the decomposition of ethephon happens once it penetrates through the leaf. In terms of the absorption rate through the leaf tissues, ethephon alone is rapidly absorbed compared to ethephon in alkaline conditions (ethephon mixed with sodium hydroxide); however, rapid absorption under this particular condition does not necessarily affect the flowering efficiency (Turnbull *et al.*, 1999). Moreover, several studies described in the following sections have found greater flowering efficiency under alkaline conditions compared with ethephon alone.

Quick release of ethylene by adding alkaline substances such as $CaCO_3$, urea, or a combination of both has resulted in higher flowering efficiency compared with ethephon alone (Dass *et*

al., 1975; Hazarika and Mohan, 1998). The addition of urea has reportedly been able to promote the penetration of other ionic substances through cuticular membranes (Wittwer *et al.*, 1967). Thus, ethylene availability in the plant tissues can be increased. The recommended rate of urea as an enhancer is 2%, and values higher than that may reduce hormone efficiency (Malip, 2011). Further increasing the pH of these combinations to 9 significantly reduces the ethephon usage to as low as 10 mg L^{-1} (Dass *et al.*, 1976). These authors also found a comparable effect when applying 100 mg L^{-1} ethephon alone and 25 mg L^{-1} ethephon mixed with urea and $CaCO_3$. Moreover, the estimation of cost by using a combination of 10 mg L^{-1} ethephon with urea and $CaCO_3$ can be reduced by up to 20% as compared with 100 mg L^{-1} ethephon alone. Malip (2011) also demonstrated that using 0.5% borax (15.2% boron) could substitute $CaCO_3$ because of its alkaline property.

A study found 0.5% activated charcoal with a 0.5 to 1.0% CaC_2 solution to be useful in inducing flowering in pineapples (Maruthasalam *et al.*, 2010), whereas 5% activated charcoal was required to supplement the ethephon solution at the commercial concentration (Poel *et al.*, 2009). Activated charcoal can absorb and retain the ethephon on its surface temporarily and then slowly release the ethylene gas toward the plant for a longer period. The concept of slow-release hormones has also been reported; the acetylene gas released by CaC_2 was prolonged by up to 8 hours by applying an oil coating (Onaha *et al.*, 1983). Additionally, the flowering percentage was relatively higher than the uncoated one in both cool and warm seasons.

The plants treated with 0.5 kg ice crystals alone by one and two applications have indicated an increase of ethylene levels by 100 %. However, flowering was not stimulated, probably because of the insufficient ethylene production to meet the initiation need (Lin *et al.*, 2009). Another study demonstrated that four applications of ice crystal or cold-water treatment were successful in stimulating the flowering (Maruthasalam *et al.*, 2010). Later, the combination of hormones prepared using cold water found a two-fold increase of flowering efficiency compared with a standard preparation (Chang *et al.*, 2011).

Environmental conditions: Plant sensitivity toward flowering can be triggered by environmental factors such as temperature, humidity, photoperiod, and precipitation. Hormone applications at high temperatures should be avoided because of the fast-drying effect, and it is better for them to be performed during the late evening to reduce the likelihood of flowering failure (Turnbull *et al.*, 1999). In natural flowering, pineapples grown at night temperatures of 15, 25 and 30°C were less responsive than those at 20°C (Friend, 1981). Min and Bartholomew (1997) also demonstrated that a night temperature of 20 °C significantly promoted ethylene biosynthesis compared to that of 30 °C. The flowering rate is also poor when the plant is exposed to the cold effects (12 °C -8 h/3 °C–16 h) for 3 to 5 days after 6 to 22 days of hormone application (Julius *et al.*, 2017).

Relative humidity (RH) is related to the drying effect, with drying being exacerbated under low RH conditions. Dry conditions may also cause less hormone absorption. Although Turnbull *et al.* (1999) demonstrated that low RH caused rapid hormone absorption in the first 2 h; the ethephon absorption was significantly lower in the subsequent 22 h compared to under high RH conditions. Schonherr *et al.* (2000) also confirmed that foliar penetration was better under high RH during the night.

The pineapple plant is a quantitative short-day plant that needs a relatively low photoperiod to accelerate the initiation of the flowering process. Prolonging the photoperiod to more than 15 h does not suppress the natural flowering (Gowing, 1961). Friend and Lydon (1979) concluded that an 8 h photoperiod was more inductive than a photoperiod of 10 to 16 h. Thus, planting regions that experience significant photoperiod changes require proper management of the planting schedule.

Exposing the pineapple plant grown in a subtropical drought period to water supply or the one grown in tropical conditions to drought stress may stimulate flowering initiation (Carr, 2014; Cunha, 2005). Therefore, understanding rainfall patterns could benefit the flowering hormone application by improving the efficacy of induction. This factor may influence the optimum growth size of the plant prior to hormone induction. William (2017) stated that the flowering induction affected by rainfall was due to stunted plant growth. Meanwhile, OGTR (2008) also reported that the larger or smaller plant was less susceptible towards flowering hormone. Besides that, interference of rainfall following hormone application may wash off or dilute the hormone, eventually resulting in reduced hormone efficacy.

Method of application: Poel *et al.* (2009) reported that the application of hormones directly to the central plant resulted in homogeneous flowering compared with spraying them on the whole plant. These authors added that the actual total amount of active ingredients that reached the SAM affected the efficiency of treatment. This result was corroborated by Turnbull *et al.* (1999), whom stated that the accumulation of hormones on basal white leaves showed higher hormone absorption compared with that on the green leaves. Additionally, reducing the commercial rate of ethephon by up to 80 % still exhibited full flowering when such method was used.

Cunha (2005) stated that two applications of NAA or ethylene with 2 or 3 days of intervals might promote higher flowering efficiency, whereas ethephon and CaC_2 application was repeated in case of rainfall occurring within 6 h from its first application. Nevertheless, excessive hormone concentration at 1,000 mg L^{-1} NAA retards flowering initiation (Clark and Kerns, 1942). Although ethylene biosynthesis is highly stimulated at a high concentration of NAA, the details of flowering inhibition mechanism are not well understood (Bartholomew, 2014). Meanwhile, Pal *et al.* (2010) stated that the combination of 100 mg L^{-1} ethephon with 10 mg L^{-1} NAA caused a longer flowering initiation period and a lower flowering percentage than 50 mg L^{-1} ethephon alone. Several reported studies of pineapple flowering induced by hormones are presented in Table 1.

Plant physiological state and planting materials: Hormones should be applied when the plant reaches its maturity or adequate developmental stages. When the plant leaves are fewer than 10, the plant do not respond to flowering hormones, and at least 21 leaves are required to induce full flowering (Das and Baruah, 1965). Poel *et al.* (2009) reported that the susceptibility to the flowering hormone could be as early as 3 months after planting, but it significantly resulted in an uneconomical yield. Chan and Lee (2001) demonstrated that hormone induction with an economic yield size could be attained as early as 6 months after planting. However, hormone application is more suitable for flowering when it is applied close to the natural flowering season (Wariboko *et al.*, 2013).

Table 1. Reported flowering hormone application in pineapple from previous studies

Hormone	Cultivar/Hybrid	Recommendation	Remarks	Reference
Ethephon	Singapore Spanish	200 to 1, 200 mg L^{-1}	Quicker and higher flowering emergence than CaC_2	Wee and Ng (1971)
	Maspine	240 mg L^{-1} + 2% urea	Full flowering emergence within 45 days	Malip (2011)
	Phuket	100 mg L^{-1} + 1.5% urea	Full flowering emergence within 32 days	Butrat and Wangmuang (2004)
	i) Tainon 20, Comte de Paris, Pearl. ii) Smooth Cayenne	i) 200 to 400 mg L^{-1} ii) 400 to 600 mg L^{-1}	Cool seasons need higher concentration than warm seasons. Different cultivars have different requirements	Liu *et al.* (2010)
	Smooth Cayenne	1,000 mg L^{-1}	Higher flowering emergence than 750, 500 and 200 mg L^{-1}	Rojas and Solidum (1990)
	Kew	25 mg L^{-1} + 2 % urea + 0.04 % $CaCO_3$	Higher flowering emergence than 100 mg L^{-1} ethephon, 10 mg L^{-1} planofix, and 1 g per plant CaC_2	Hazarika and Mohan (1998)
	Kew	10 to 25 mg L^{-1} + 2 % urea + $CaCO_3$ (adjusted to pH 9.0)	Flowering emergence more than 90% within 40 days	Dass *et al.* (1976)
	Kew	50 mg L^{-1}	Reduce flowering duration	Pal *et al.* (2015)
	Perola	200 mg L^{-1}	Full flowering emergence and comparable to 800 mg L^{-1}	Li *et al.* (2016)
CaC_2	Tainon 17	1 % dilution	Full flowering emergence by cold water than 50% flowering emergence by 25 °C water	Chang *et al.* (2011)
	Tainon 17	1 % dilution	Full flowering emergence within 49 days by two applications at 48 h intervals	Maruthasalam *et al.* (2010)
	Perola	0.5 % dilution	More than 90% of flowering emergence	Raposo *et al.* (2019)
	Smooth Cayenne	1 to 2 g per plant	Flowering emergence up to 70% within 60 days on 10 months old plant, while less than 50% on 8 and 9 months old plant	Wariboko *et al.* (2013)
	Phuket	1 g per plant	Almost 80% of flowering emergence within 40 days by two applications while less than 50% by single application	Butrat and Wangmuang (2004)
NAA	Kew	10 mg L^{-1}	Maximum flowering	Pal *et al.* (2015)
	Kew	222 mg L^{-1}	Flowering emergence more than 95% within 60 days, and comparable to 100 mg L^{-1} ethephon	Dass *et al.* (1976)
	Phuket	0.5 mg per plant	Flowering emergence up to 90% within 38 days.	Butrat and Wangmuang (2004)

The selection of good planting material may help increase flowering efficiency. Generally, pineapple plants propagate through their sucker, slip, or crown. However, these planting materials result in different periods of the crop cycle. Reinhardt *et al.* (2018) mentioned that the vegetative stage of the suckers is relatively shorter than those of the slips and crowns. These are also associated to planting size, with the sucker being normally larger (300 g to 500 g) than the slip (intermediate) and crown (≤200 g). Therefore, the use of suckers and slips seems to achieve higher flowering efficiency because the plant is ready for the induction at the standard period.

Cultivar/Hybrid: The determination of hormone concentration is imperative for the flowering sensitivity of the planted cultivar. Smooth Cayenne and some of the spineless hybrids, such as MD-2, are less susceptible to flowering compared to Queen and Spanish groups (Bartholomew, 2014; Liu *et al.*, 2018). A molecular study revealed that the sensitivity was associated with the ethylene signal transduction (Liu *et al.*, 2018). Bartholomew added that the environmental stresses were crucial for stimulation of flowering on less susceptible cultivar. Moreover, Reinhardt *et al.* (2002) suggested that a high concentration of the hormone was needed to enhance flowering stimulation on such cultivars.

Nutrient management: Iqbal *et al.* (2013) concluded that several nutrient adjustments are capable of influencing ethylene biosynthesis. However, for the pineapple plant, an emphasis of the effect of carbohydrate or carbon (C) and nitrogen (N) on flowering sensitivity has been extensively addressed. Oliveira *et al.* (2015) reported that lower hormone efficiency was caused by N application. N is closely related to vigorous vegetative growth; consequently, a vigorous growth may reduce flowering efficiency (Cunha *et al.*, 2003; OGTR, 2008; Suwanti *et al.*, 2017). The manipulation of C : N dynamic can be achieved by controlling the N source application (Lin *et al.*, 2015). Valleser (2018) observed that the natural flowering on MD-2 occurred at a C:N ratio above 50, and no flowering occurred at ratio below 40. Thus, the use of flowering hormones is more efficient when the plant experiences N stress or no fertilizer application within 30 to 45 days before the hormone application (Suwanti *et al.*, 2017).

Lack of flowering uniformity has become a significant concern in the pineapple industry as it can lead to significant financial loss. Several studies have been conducted to tackle this issue. One of the most important studies is on hormone application. Although flowering hormones can successfully stimulate flower initiation, simultaneous and full flowering emergence is still difficult to obtain. Therefore, to ensure that the flowering in response to hormones can be enhanced, an integrated study of flowering efficiency factors, as highlighted in this paper, is believed to help improve the flowering efficiency.

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References

Abdul, R.H. and B.H. Yap, 1992. Effect of hormones on flowering of pineapple (cv. moris) grown on mineral soil. *Trans. Malays. Soc. Plant Physiol.*, 3: 158-160.

Achard, P., M. Baghour, A. Chapple, P. Hedden, D. Van Der Straeten, P. Genschik, T. Moritz and N.P. Harberd, 2007. The plant stress hormone ethylene controls floral transition *via* DELLA-dependent regulation of floral meristem-identity genes. *Proc. Natl. Acad. Sci. U. S. A.*, 104(15): 6484-6489.

Aldrich, W.W. and H.Y. Nakasone, 1975. Day versus night application of calcium carbide for flower induction in pineapple. *J. Am. Soc. Hort. Sci.*, 100: 410-413.

Bartholomew, D.P. 2014. History and perspectives on the role of ethylene in pineapple flowering. *Acta Hort.*, 1042: 269-284.

Bartholomew, D.P. and G.M. Sanewski, 2018. Inflorescence and fruit development and yield, p. 233-268. In: *The Pineapple: Botany, Production and Uses*, G.M. Sanewski., D.P. Bartholomew. and R.E. Paull (2nd ed.). CABI, Boston, U.S.

Burg, S.P. 1973. Ethylene in plant growth. *Proc. Natl.Acad.Sci. U.S.A.*, 70(2): 591-597.

Butrat, P. and A. Wangmuang, 2004. Effects of flowering chemicals application on flowering and fruit quality of pineapple (*Ananas comosus* L. Merr. cv. Phuket). *Songklanakarin J. Sci. Technol.*, 26(3): 339-345.

Carr, M.K.V. 2014. *Advances in Irrigation Agronomy: Fruit Crops.* Cambridge Univ. Press, Cambridge, U.K.

Chan, Y.K. and H.K. Lee, 2001. Response of four pineapple hybrids to early flower induction. *J. Trop. Agric. Food Sci.*, 29(2): 145-150.

Chang, J.C., Y.L. Liu, S. Maruthasalam and C.M. Sun, 2011. Forcing of Tainon17 pineapple with calcium carbide (CaC_2) and/or ice-cold stress under field conditions. *Acta Hort.*, 902: 327-335.

Clark, H.E. and K.R. Kerns, 1942. Control of flowering with phytohormones. *Science*, 95(2473): 536-537.

Cooper, W.C. 1942. Effect of growth substances on flowering of the pineapples under Florida conditions. *Proc. Am. Soc. Hort. Sci.*, 41: 93-98.

Cunha, G.A.P., J.T.A. Costa and D.H. Reinhardt, 2003. Natural flowering in pineapple: Inhibition by growth regulators. *Fruits*, 58(1): 27-37.

Cunha, G.A.P. 2005. Applied aspects of pineapple flowering. *Bragantia*, 64(4): 499-516.

Das, N. and A. Baruah, 1965. Induction of flowering and fruit formation of pineapples with the aid of acetylene and calcium carbide. *Indian Agric.*, 9: 15-23.

Dass, H.C., G.S. Randhawa and S.P. Negi, 1975. Flowering in pineapple as influenced by ethephon and its combinations with urea and calcium carbonate. *Sci. Hort.*, 3(3): 231-238.

Dass, H.C., G.S. Randhawa, H.P. Singh and K.M. Ganapathy, 1976. Effect of pH and urea on the efficacy of ethephon for induction of flowering in pineapple. *Sci. Hort.*, 5(3): 265-268.

Espinosa, M.E.A., R.O. Moreira, A.A. Lima, S.A. Sagio, H.G. Barreto, S.L.P. Luiz, C.E.A. Abreu, E. Yanes-Paz, Y.C. Ruiz, J.L. Gonzalez-Olmedo, 2017. Early histological, hormonal and molecular changes during pineapple (*Ananas comosus* [L.] Merrill) artificial flowering induction. *J. Plant Physiol.*, 209: 11-19.

Fassinou Hotegni, V.N., W.J.M. Lommen, E.K. Agbossou and P.C. Struik, 2014. Heterogeneity in pineapple fruit quality results from plant heterogeneity at flower induction. *Front. Plant Sci.*, 5(670): 1-13.

Friend, D.J.C. 1981. Effect of night temperature on flowering and fruit size in pineapple (*Ananas comosus* [L.] Merrill). *Botanical Gazette*, 142(2): 188-190.

Friend, D.J.C. and J. Lydon, 1979. Effects of daylength on flowering, growth and CAM of pineapple (*Ananas comosus* [L.] Merrill). *Botanical Gazette*, 140(3): 280-283.

Gifford, E.M. 1969. Initiation and early development of the inflorescence in pineapple (*Ananas comosus* "Smooth Cayenne") treated with acetylene. *Am. J. Bot.*, 56(8): 892-897.

Gowing, D.P. 1961. Experiments on the photoperiodic response in pineapple. *Am. J. Bot.*, 48(1): 16-21.

Hansen, H. and K. Grossmann. 2000. Auxin-induced ethylene triggers abscisic acid biosynthesis and growth inhibition. *Plant Physiol.*, 124(3): 1437-1448.

Hazarika, D.N. and N.K. Mohan. 1998. *Artificial Flower Induction in Pineapple During Off Season.* 3rd Int. Pineapple Symp., Pattaya, Thailand, 17-20 Nov.

Hussain, M.J., M.A. Ulla, M.M.R. Salim, M.M. Rahman and M.M.R. Sarker, 2008. Effect of different application time of ethrel on off-season pineapple production at Srimongal, Sylhet. *Int. J. Sustain. Crop Prod.*, 3(6): 68-71.

Iqbal, N., A. Trivellini, A. Masood, A. Ferrante and N.A. Khan, 2013. Current understanding on ethylene signaling in plants: The influence of nutrient availability. *Plant Physiol. Biochem.*, 73: 128-138.

Joy, P.P. and R. Anjana, 2015. Evolution of pineapple, In: *Evolution of Horticultural Crops*, K.V. Peter (ed.). Astral International. New Delhi, India.p. 1-39.

Julius, I.P., H.H. Tseng and H.L. Lin, 2017. Low temperature effect on flower and fruit development of Tainung No 17 pineapple. *Acta Hort.*, 1166(1166): 131-136.

Kang, B.G., W. Newcomb and S.P. Burg, 1971. Mechanism of auxin-induced ethylene production. *Plant Physiol.*, 47(4): 504-509.

Kuan, C.S., C.W. Yu, M.L. Lin, H.T. Hsu, D.P. Bartholomew and C.H. Lin, 2005. Foliar application of aviglycine reduces natural flowering in pineapple. *HortScience*, 40(1): 123-126.

Leeper, R.W., D.P. Gowing and W.S. Stewart, 1962. Decarboxylation of alpha-naphthaleneacetic acid by pineapple leaves in sunlight. *Int. J. Appl. Radiat. Isot.*, 13(7-8): 399-402.

Li, Y.H., Q.S. Wu, X. Huang, S.H. Liu, H.N. Zhang, Z. Zhang and G.M. Sun, 2016. Molecular cloning and characterization of four genes encoding ethylene receptors associated with pineapple (*Ananas comosus* L.) flowering. *Front. Plant Sci.*, 7(710): 1-15.

Lin, C.H., S. Maruthasalam, L.Y. Shiu, W.C. Lien, M. Loganathan, C.W. Yu, S.H. Hung, Y. Ko and Y.Y. Chen, 2009. Physical and chemical manipulation of flowering in pineapple. *Acta Hort.*, 822(822): 117-124.

Lin, M.T., A.M. Chen, T.S. Lin, C.S. Kuan, C.L. Lee and W.J. Yang, 2015. Prevention of natural flowering in pineapple (*Ananas comosus*) by shading and urea application. *Hort. Environ. Biotechnol.*, 56(1): 9-16.

Liu, C.H. and C. Fan, 2016. De novo transcriptome assembly of floral buds of pineapple and identification of differentially expressed genes in response to ethephon induction. *Front. Plant Sci.*, 7(203): 203.

Liu, S.H., M.A. Dou, X.P. Zang and G.M. Sun, 2010. *Flower Forcing Technique by Ethephon in Pineapple*. 7th Int. Pineapple Symp., 13-15 July. Johor Bharu, Malaysia.

Liu, S.H., X.P. Zang and G.M. Sun, 2011a. Changes in endogenous hormone concentrations during inflorescence induction and development in pineapple (*Ananas comosus* cv. Smooth Cayenne) by ethephon. *Afr. J. Biotechnol.*, 10(53): 10892-10899.

Liu, S.H., X.P. Zang, X.M. Zhang and G.M. Sun, 2011b. Integrated effects of ethylene absorbents on flower forcing of yellow Mauritius pineapple. *Newsletter of the Pineapple Working Group, Int. Soc. Hort. Sci.*, 18: 24-26.

Liu, C.H., Y. Liu, X.H. Shao and D. Lai, 2018. Comparative analyses of the transcriptome and proteome of Comte de Paris and Smooth Cayenne to improve the understanding of ethephon-induced floral transition in pineapple. *Cell. Physiol. Biochem.*, 50(6): 2139-2156.

Lyndon, R.F. 1990. *Plant Development: The Cellular Basis*. Unwin Hyman, London, U.K.

Ma, B., H. Chen, S.Y. Chen and J.S. Zhang, 2014. Roles of ethylene in plant growth and responses to stresses. In: *Phytohormones: A Window to Metabolism, Signaling and Biotechnological Applications*, L.S. Tran and S. Pal (eds.). Springer-Verlag, New York, U.S. p. 81-118.

Malip, M. 2011. A new formulation for the flowering of Maspine pineapple. *Acta Hort.*, 902(902): 257-261.

Maruthasalam, S., L.Y. Shiu, M. Loganathan, W.C. Lien, Y.L. Liu, C.M. Sun, C.W. Yu, S.H. Hung, Y. Ko and C.H. Lin, 2010. Forced flowering of pineapple (*Ananas comosus* cv. Tainon 17) in response to cold stress, ethephon and calcium carbide with or without activated charcoal. *Plant Growth Regul.*, 60(2): 83-90.

Min, X.J. and D.P. Bartholomew, 1997. Temperature affects ethylene metabolism and fruit initiation and size of pineapple. *Acta Hort.*, 425: 329-338.

MPIB. 2017. Pineapple farm management. <http://www.mpib.gov.my/en/pineapple-farm-management/>.

OGTR. 2008. The biology of *Ananas comosus* var. Comosus (Pineapple). <http://www.ogtr.gov.au/internet/ogtr/publishing.nsf/Content/pineapple-3/$FILE/biologypineapple08_2.pdf>.

Oliveira, A.M.G., R.C.C. Rosa, D.T. Junghans and W. Natale, 2015. NK fertilization in 'BRS imperial' pineapple, I - Effect on development and plant flowering. *Rev. Bras. Frutic*, 37(3): 755-763.

Onaha, A., F. Nakasone and H. Ikemiya, 1983. Induction of flowering with oil-coated carbide in pineapples. *J. Jpn. Soc. Hort. Sci.*, 52(3): 280-285.

Pal, S., P. Subba, S. Seletsu, P.K. Paul, N. Bhowmick, B. Mathew and C.P. Suresh, 2010. Induction of flowering in pineapple (*Ananas comosus* [L.] Merr.) by NAA and ethrel. 7th Int. Pineapple Symp., 13-15 July. Johor Bharu, Malaysia.

Pal, R., S.K. Mahato, B. Chhetri and C.P. Suresh, 2015. Growth regulators influencing yield and quality of pineapple (*Ananas comosus* [L.] Merr.). *Ecol. Environ. Conserv.*, 21(2): 885-890.

Palupri, P. and K. Tri, 2018. Pengaruh beberapa dosis etilen pada pembungaan tanaman nanas (*Ananas comosus* L. varietas Queen). *J. Viable Pertan*, 12(2): 11-19.

Parimalan, R., P. Giridhar, A.J. Joel and S. Jagadeesan, 2005. Molecular basis of flower initiation - A review. *Indian J. Biotechnol.*, 4: 455-565.

Poel, B.V.D., J. Ceusters and M.D. Proft, 2009. Determination of pineapple (*Ananas comosus*, MD2 hybrid cultivar) plant maturity, the efficiency of flowering induction agents and the use of activated carbon. *Sci. Hort.*, 120(1): 58-63.

Prigge, M. and M.V. Gurierrez-Soto, 2014. Pineapple photosynthesis and leaf sap pH as a surrogate of CAM performance in the field. A Research Advance. *Newsletter of the Pineapple Working Group, Int. Soc. Hort. Sci.*, 21: 18-23.

Py, C., J.J. Lacoeuilhe and C. Teisson, 1987. *The Pineapple: Cultivation and Uses*. Maisonneuve G.P. and Larose. Paris, France.

Rainha, N., V.P.D. Medeiros, A.B.D. Silva and C. Cruz, 2013. The molecular mechanisms of flowering. Is pineapple flowering totally understood?. *Newsletter of the Pineapple Working Group, Int. Soc. Hort. Sci.*, 20: 16-23.

Raposo, R., G.A.M. Pereira, C.C. Matos, L.H. Barcellos, D.F. Paula and A.A. Silva, 2019. Use of 2,4-D in mixture with ethephon and calcium carbide in pineapple crop. *Planta Daninha*, 37: 1-10.

Reinhardt, D.H., R.S.C. Jose, F.S.S. Luiz, N.F. Sanches and P.M. Aristoteles, 2002. Perola and Smooth Cayenne pineapple cultivars in the state of Bahia, Brazil: Growth, flowering, pests, diseases, yield and fruit quality aspects. *Fruits*, 57(1): 43-53.

Reinhardt, D.H.R.C., D.P. Bartholomew, F.V.D. Souza, A.C.P.Pd Carvalho, T.R.Pd Pádua, D.T. Junghans and A.Pd Matos, 2018. Advances in pineapple plant propagation. *Rev. Bras. Frutic.*, 40(6): 1-22.

Rodriguez, A.G. 1932. Influence of smoke and ethylene on the fruiting of the pineapple (*Ananas sativus* shult). *J. Agric. Univ. P.R.*, 16(1): 5-18.

Rodriguez, R., E. Caceres, G.Y. Lorente, R. Avila, O. Perez, O. Garcia, Y. Dominguez, F. Barrios, L., Licor, C. Carvajal, *et al.*, 2018. Effects of potassium chloride and potassium sulphate on MD-2 pineapple fruit yield and quality. *Newsletter of the Workgroup Pineapple, Int. Soc. Hort. Sci*., 25: 8-12.

Rojas, W.U. and P.P. Solidum., 1990. Effects of different ethrel concentrations on the flowering and fruit setting of pineapple (*Ananas comosus* L.). *CMU J. Sci.*, 3(2): 25-32.

Schonherr, J., P. Baur and B.A. Uhlig, 2000. Rates of cuticular penetration of 1-naphthylacetic acid (NAA) as affected by adjuvants, temperature, humidity and water quality. *Plant Growth Regul.*, 31: 67-74.

Silva, M.D.A. and M.M. Caputo, 2012. Ripening and the use of ripeners for better sugarcane management. In: *Crop Management: Cases and Tools for Higher Yield and Sustainability.* F.R. Marin (eds.). InTech, Rijeka, Croatia. p. 3-24.

Suwanti, S., B.M. Joko and P.W. Karuniawan, 2017. Response of flowering and yield of pineapple cv. Smooth Cayenne for fertilizer reduction and ethylene application. *J. Prod. Tanam*, 5(8): 1346-1355.

Turnbull, C.G.N., E.R. Sinclair, K.L. Anderson, R.J. Nissen, A.J. Shorter and T.E. Lanham, 1999. Routes of ethephon uptake in pineapple (*Ananas comosus*) and reasons for failure of flower induction. *J. Plant Growth Regul.*, 18(4): 145-152.

Trusov, Y. and J.R. Botella, 2006. Silencing of the ACC synthase gene ACACS2 causes delayed flowering in pineapple [*Ananas comosus* (L.) Merr.]. *J. Exp. Bot.*, 57(14): 3953-3960.

Valleser, V.C. 2018. Plant age and rate of flower inducer affects flower initiation of 'MD2' pineapple (*Ananas comosus* L.). *Int. J. Res. Rev.*, 5(4): 25-72.

Wee, Y.C. and J.C. Ng, 1971. The effects of ethrel on the Singapore Spanish pineapple. *Malays. Pineapple*, 1: 5-10.

Wee, Y.C. and A.N. Rao, 1979. Development of the inflorescence and crown of *Ananas comosus* after treatment with acetylene, NAA and ethephon. *Am. J. Bot.*, 66(4): 351-360.

Wang, J., Z. Li, M. Lei, Y. Fu, J. Zhao, M. Ao and L. Xu, 2017. Integrated DNA methylome and transcriptome analysis reveals the ethylene-induced flowering pathway genes in pineapple. *Sci. Rep*., 7(17167): 1-11.

Wang, L., Y. Li, X. Jin, L. Liu, X. Dai, Y. Liu, L. Zhao, P. Zheng, X. Wang, Y. Liu, D. Lin and Y. Qin, 2020. Floral transcriptomes reveal gene networks in pineapple floral growth and fruit development. *Commun. Biol.*, 3(1): 500.

Wariboko, C., I.A.I. Ogidi and L.D. Gbaranch, 2013. The effect of chemical hormone (calcium carbide) application on pineapple flower induction in the Nigeria Delta of Nigeria. *Acta Agron. Nigeria*, 13(1): 26-34.

Williams, P.A., O. Crespo, C.J. Atkinson and G.O. Essegbey, 2017. Impact of climate variability on pineapple production in Ghana. *Agric. Food Secur.*, 6(1): 1-14.

Wittwer, S.H., M.J. Bukovac, W.H. Jyung, Y. Yamada, R. De, H.P. Rasmussen, S.N.H. Haile Mariam and S. Kannan, 1967. Foliar absorption - Penetration of the cuticular membrane and nutrient uptake by isolated leaf cells. *Qual. Plant. Mater. Veg.*, 14(1-2): 105-120.

Yu, Y.B. and S.F. Yang, 1979. Auxin-induced ethylene production and its inhibition by aminoethyoxyvinylglycine and cobalt ion. *Plant Physiol.*, 64(6): 1074-1077.

Zhang, H.N., W.S. Sun, G.M. Sun, S.H. Liu, Y.H. Li, Q.S. Wu and Y.Z. Wei, 2016. Phenological growth stages of pineapple (*Ananas comosus*) according to the extended Biologische Bundesantalt, Bundessortenamt and Chemische Industrie scale. *Ann. Appl. Biol.*, 169(2): 311-318.

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