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REVIEW ARTICLE

# Mango (*Mangifera indica* L.) malformation: a malady of stress ethylene origin

**Mohammad W. Ansari · Varsha Rani · Alok Shukla · Gurdeep Bains · Ramesh C. Pant · Narendra Tuteja**

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**Abstract** Mango malformation is a major constrain in mango production worldwide causing heavy economic losses depending on cultivar type and susceptibility. The malady has variously been ascribed to be acarological, viral, fungal and physiological in nature. Here, we discuss the ethylene origin nature of malady. There are indications that most of the symptoms of mango malformation resemble with those of caused by ethylene effects. Multiple evidence reports of putative causal agents including *Fusarium mangiferae* to augment the endogenous pool of 'stress ethylene' are well documented. Therefore, over load of 'stress ethylene' impairs morphology malformed tissue and cyanide derived from ethylene biosynthesis causes necrosis and death of malformed cells. This review covers various factors eliciting 'stress ethylene' formation, role of ethylene in development of malady and regulation of ethylene action to reduce malformation in mango.

**Keywords** Abiotic and biotic stress · Cyanide · Ethylene · *Fusarium* · Mango malformation

## Introduction

Malformation is one of the most destructive malady of mango in nature (Joshi et al. 2014). It is a major constraint to mango production in India and other mango growing countries of the world (Crane and Campbell 1994). It causes 50 to 60 % economic loss every year and in severe cases it may extent up to 100 % (Misra et al. 2000). After its first report at Darbhanga district (Bihar) in India by Marries (Watt 1891a, b), this malady has been spread among other mango growing countries of the world found to be like Australia (Issarakraisila et al. 1997), Brazil (Flechtmann et al. 1970a, b), Cuba (Padron 1983), Egypt (Attiah 1955), Israel and Mexico (Malo and McMillan 1972), Middle east (Hassan 1944), Pakistan (Khan and Khan 1960), South Africa (Schwartz 1968), Sudan (Minessey, et al. 1971), United Arab Emirates (Burhan 1991), United States of America (Marasas et al. 2006), Bangladesh (Meah and Khan 1992), Sultanate of Oman (Kvas et al. 2008) and Southern Spain (Crespo et al. 2014). As much as Indian mango industry is taken into account, the malady of malformation is of meticulous significance to north India, because the majority of the commercial mango varieties developed here are at risk to severe malformation. The malady is practically missing from the southern and western areas of the country (Ansari et al. 2013a). There are indications that several species of *Fusarium* are probably associated with mango malformation (Kumar et al. 2014), while *F. mangiferae* has been reported to cause malformation via producing ethylene itself (Ansari et al. 2012, 2013b). Similarly, the characteristic symptoms evidenced by malformed plants may be ascribed to amplified production and accumulation of definite biochemical metabolites. Pant (2000) observed that mango malformation may be due to the production of 'stress ethylene', which refers a higher pace of ethylene biosynthesis upon perceiving a response from stressful environment. Further, various hormonal changes were also reported during malformation in mango plants (Singh and Dhillon 1989a). Symptoms of malformed panicle such as the occurrence of leaf epinasty, disorder in the normal orientation of shoots and panicles, containment of apical dominance,

Mohammad W. Ansari; Varsha Rani are contributed equally to this works

M. W. Ansari · N. Tuteja (✉)
Plant Molecular Biology Group, International Centre for Genetic Engineering and Biotechnology, New Delhi, India
e-mail: narendra@icgeb.res.in

V. Rani · A. Shukla · G. Bains (✉) · R. C. Pant
Department of Plant Physiology, College of Basic Sciences and Humanities, G.B. Pant University of Agriculture and Technology, Pantnagar 263145, Uttarakhand, India
e-mail: gurdeepbains123@rediffmail.com

hypertrophied cells and additional gummosis in abnormal tissue are very much resembled to ethylene effects (Singh 2000; Bains and Pant 2003). Cells of malformed tissues were also evident along with black mitochondria and necrotic cells (Kukreja and Pant 2000; Kaushik 2002), which could be mediated via high cyanide in malformed tissue (Ansari et al. 2013a). Upto now, no evidence has been recorded for the involvement of programmed cell death in malformation, however the reactive oxygen species (ROS) as signaling molecules could realize programmed cell death (Singh et al. 2012), which may open new way toward execution of its role in mango malformation. Ethylene production, 1-amino-cyclopropane-1-carboxylic acid (ACC) oxidase, ACC synthase expression and ACC content were studied in mango to regulate ripening process (Nair et al. 2004) and the level of byproducts of ethylene biosynthesis in malformed tissues such as ascorbate, inorganic phosphate, methionine, cyanide (Kaushik 2002; Nailwal et al. 2006; Ansari et al. 2013a) explain that ethylene biosynthesis pathway (Yang Cycle) is conserved in mango plants. It is well known that the main enzymes in the pathway are ACC synthase and ACC oxidase which are positively/negatively altered by diverse environmental factors (Yang and Hoffman 1984). However, stress mediated modulation in ACC synthase and ACC oxidase expression in malformed tissues needs to be investigated further.

Furthermore, the putative causal agents of mango malformation such as excessive soil moisture, mite infestation, fungal infection, virus, herbicides and other toxic compounds seem to add to the production of ‘Stress ethylene’ (Rani et al. 2013). Recently, it has been reported that an augment in the endogenous ethylene level in malformed tissue under low temperature stress caused mango malformation (Ansari et al. 2013a). It has been ascribed as disease (Crespo et al. 2014) and a physiological disorder (Ansari et al. 2013b). The present review is intended to highlight various physiological aspects of malady with special emphasis to role of ‘stress ethylene’ in functioning potential etiologic agent.

## Malformation and its etiology

Numerous vegetative buds sprout producing hypertrophied growth which constitutes vegetative malformation. The condition of multi-branching of shoot apex with scaly leaves and shortened internodes is referred to as ‘Witches Broom’ (Gaur and Chakrabarti 2009). The production of excessive shoots (multi-branching) indicates the disturbance in the apical dominance. Leaves become dwarf and narrow and bend back towards the stem, which remain stunted and die (Kumar and Beniwal 1992) (Fig. 1a) as compared to healthy leaves (Fig. 1b). Floral malformation is considered more serious problem than vegetative malformation (Chakraborti and Misra 2014). During the development of floral malformation, primary, secondary and tertiary rachises become short, thick and hypertrophied with prominent nodes. Due to suppression of apical dominance, panicles become greener, heavier and highly branched (Kumar et al. 1993) on which flowers are crowded, enlarged with thicker pedicels, calices and enlarged petals and stamens consisting of deformed reproductive organs (Rani et al. 2013) (Fig. 1c) with respect to those of healthy panicles (Fig. 1d).

Study on biochemical characterization of various endogenous compounds such as mangiferin (1,3,6,7-tetrahydroxyxanthone-$C_2$-β-D-glucoside), phenolics, polyphenol oxidase (PPO), and phytoalexins provides tolerance/resistance in mango cultivars against malformation (Singh et al. 2012). The mango cultivars, namely, Langra, Ramkela and Chausa were found to be susceptible to malformation, whereas Amrapali, Bombay Green and Mallika were reported as highly susceptible cultivars particularly in regions of Delhi and north India (Yadav and Singh 1995; Singh et al. 2012). All the studied cultivars are completely resistant to mango malformation, however Ellaichi and Bhadauran cultivars are reported to be completely free from malformation (Kumar et al. 2011; Singh et al. 2012) (Table 1).

Due to mysterious nature of the malady its etiology has been strongly disputed for long time (Kumar et al. 2011). Diverse claims have been made for the cause and control of malformation (Rymbai and Rajesh 2011). There are indications that a number of abiotic and biotic factors are associated with the malady (Nailwal et al. 2006). The malady has variously been ascribed to be acarological, viral, fungal and physiological in nature (Rani et al. 2013). Recently, the association of ‘*F. mangiferae*’ and ‘ethylene’ has been suggested (Crespo et al. 2014; Singh et al. 2014). Here, we discuss the role of ethylene in the development of mango malformation.

## ‘Ethylene’ origin nature of malady

Several workers have implicated a role of ethylene in mango malformation (Singh et al. 1994; Pant 2000; Bains and Pant 2003; Nailwal et al. 2006; Krishnan et al. 2009; Rymbai and Rajesh 2011; Ansari et al. 2012, 2013a, b; Rani et al. 2013; Singh et al. 2014). Malformin-like substances are in some way concerned to cause malformation by stimulating ethylene production (Singh and Dhillon 1989a). Significantly higher levels of ethylene (46, 145, 67 and 34 %) were reported in malformed panicles of cultivar Dashehari at various developmental stages (i) fully swollen buds (ii) bud inception (iii) full grown panicle prior to full bloom and at full bloom. Similarly, shots bearing malformed panicles revealed significantly higher level of ethylene over those bearing healthy panicles (Singh and Dhillon 1990). Ethylene plays an important role in the causation of floral malformation in mango cultivars viz.,

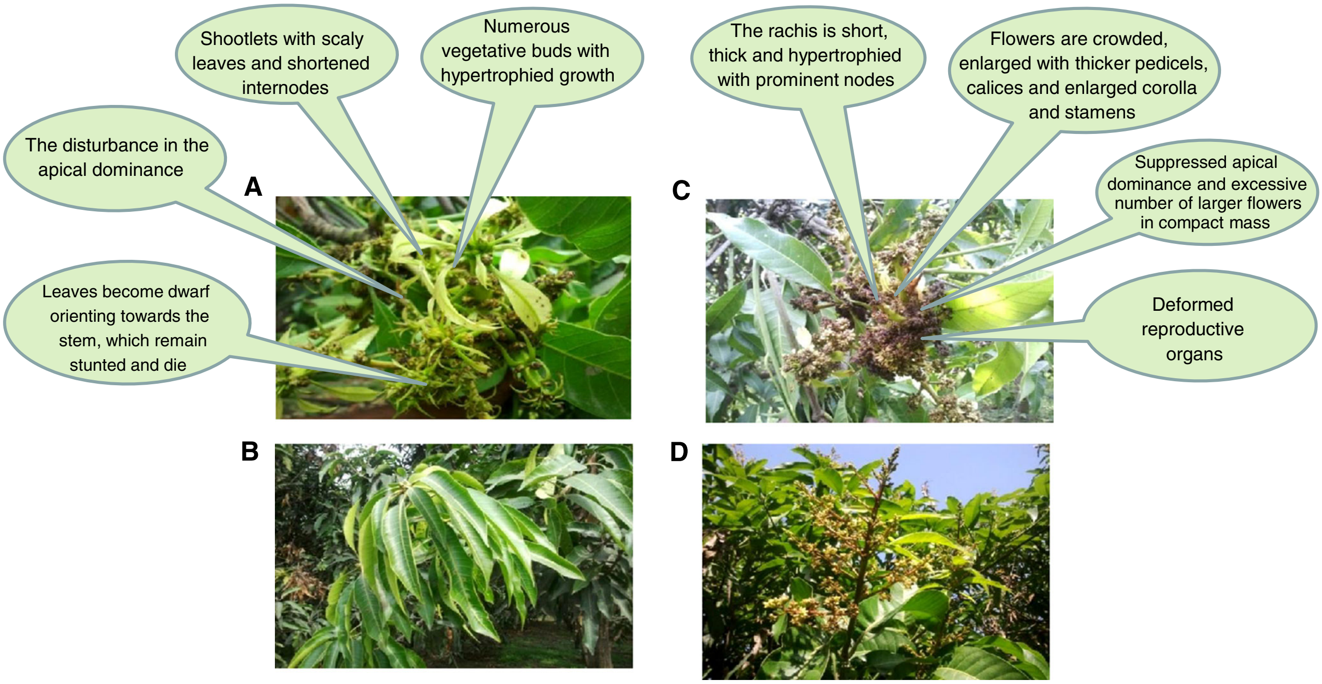


**Fig. 1** Vegetative and floral malformation in mango and effect of environmental factors on plant metabolites. Malformed (**a**) and healthy (**b**) vegetative shoot of mango. Mango compact mass of flower in malformed panicle (**c**) and normal healthy panicle (**d**)

Amrapali, Bombay green, Chausa, Dushehri and Mallika. The endogenous ethylene content were elevated in malformed tissues as compared to healthy one under low temperature range during both the stages viz., 'prior to full bloom' and 'full bloom' (Ansari et al. 2013a). The cyanide is produced in an amount stoichiometrically equivalent to ethylene (Peiser et al. 1984) and is detoxified by conversion to β-cyanoalanine by β-Cyanoalanine synthase (β-CAS), an enzyme primarily responsible for cyanide detoxification in plants. Lower levels of β-CAS were reported in malformed tissues as compared to healthy tissues suggesting that a greater amount of HCN is being un-metabolized in healthy tissues (Kukreja and Pant 2000). Therefore, the death of malformed tissues of mango which sets in sooner or later may be nothing but necrosis arising due to excessive cyanide produced along with 'stress ethylene' (Ansari et al. 2013a). Further, the un-metabolized cyanide was detected in malformed tissues and its concentrations were observed to be higher during 11.00 a.m. to 1.00 p.m., a period which coincides with the period of maximum photosynthesis in the plant (Nailwal et al. 2006). These findings might be helpful in establishing a circadian rhythm of cyanide and ethylene production so that the effect of daily light and temperature variation and the effect of ethylene can be resembled with appearance of symptoms in malformed tissues.

**Table 1** Classification based on polyphenol oxidase activity, phenolic content and panicle formation

| Resistant/susceptibility | Varieties |
|---|---|
| Highly resistant | Bhadauran and H-8-1, Ellaichi and Rataul |
| Moderately resistant | Dashahari, Langra, Kurukkan and Fazli |
| Susceptible | Sensation, Eldon and Alphanso |
| Moderately susceptible | H-31-1, Lalsundari, Totapari, Red small, Himsagar, Neelum, Zill, Edward and Extreme |
| Highly susceptible | Tommy Atkins, Chausa, Zardalu, Ratna, Amrapali, Bomabay Green and Mallika |

## Symptoms of malady bear a resemblance to ethylene effects

Several functional characteristics of mango malformation such as changed morphology of panicles and shoots, increased radial growth of rachis and reduced length and broadening of secondary branches, thus amplified flowers mass seem to be caused by agumented 'ethylene' (Ansari et al. 2013a). The enlarged lenticels, so called hypertrophy (Larson et al. 1993), leaf epinasty and disturbance in the natural tendency of shoots and inflorescence in malformed trees, suppression of apical dominance, existence of vegetative and floral malformation in the same tree, degenerated root, flower fall from inflorescence, raised gummosis and necrosis have been attributed to ethylene effect in malformed trees (Rymbai and Rajesh 2011). Ethylene takes part in termination of apical dominance, leading to more radial growth of rachis in malformed inflorescence (Singh and Dhillon 1989b). Recently, in malformed panicles, fused lobed anther in the company of impaired pollen grains and hooked stigma through poor stigmatic receptivity are essentially accountable for obstructing the germination of pollen and consequently growth of pollen tube. The aborted morphology of each and every reproductive organ in mango inflorescence is due to amplified level of endogenous level of ethylene, which lead to malfunction in fruit development in mango, and also the added load of cyanide, resulted from ethylene biosynthesis, contribute to the progression of necrosis which responsible for dehydration of anther and pistil during oversensitive reaction of plants (Rani et al. 2013). Recently, a potential role of ethylene in floral malformation in mango was confirmed via its cross talk with purescine which could result in reduced malformation by mitigating the negative effects of ethylene in malformed mango flower (Singh et al. 2014). The ethylene formation can be elicited under various abiotic and biotic stresses.

## Stress stimulated ethylene formation

A large set of published paper over the last 30 years which support that ethylene production is induced in response to various environmental stresses (Ansari et al. 2013a) in both the 'mango malformation' and system other than mango malformation (Jouyban 2012). Several putative etiological agents of mango malformation mentioned earlier are summarized as a abiotic and biotic stress (Fig. 2). Multiple biotic or abiotic stresses offer signals which typically motivate ethylene formation in plants (Abeles and Abeles 1973; Apelbaum and Yang 1981; Yang and Hoffman 1984; Ansari et al. 2012, 2013a, b). The incident of elevated ethylene formation in effect to stress is usually called 'stress ethylene', which seems to be a paramount causal agent of malformation (Jouyban 2012). Further, the putative causal agents of malady viz., insect invasion, fungi, virus, flood, heat, chilling, physical damage and chemical incentives such as metal ions, herbicides and gases like $SO_2$ (Fig. 2) seem to stimulate production of 'stress ethylene' (Table 2).

Low oxygen (hypoxia) conditions, a feature of flooded soils, triggers ethylene accumulation in mango which leads to lenticel hypertrophy (Larson et al. 1993). Ethylene production was stimulated by viral infection (Abeles et al. 1992). Most plants release ethylene in reaction to insect's infestation and elicitors of ethylene are oral oozing-specific compounds while hitting insect feeds (Dahl and Baldwin 2007). Ethylene release was significantly promoted by the presence of chemical stimuli such as metal ions (Ievinsh 2012), herbicides and gases like $SO_2$ etc. (Rymbai and Rajesh 2011). Several species of *Fusarium* are found to produce ethylene themselves (Swart and Kamerbeek 2010). Recently, the contribution of *Fusarium mangiferae* to add ethylene to endogenous 'stress ethylene pool' in mango plants was realized (Ansari et al. 2013a, b). Nailwal et al. (2006) established a circadian rhythm of cyanide and ethylene production during 11.00 a.m. to 1.00 p.m. and reported that the effect of daily light and temperature variation could be correlated with the ethylene. More recently, the over production of ethylene under low temperature regime (10–16 °C) suggests its potential role in development of malady (Ansari et al. 2013a) (Table 2).

## Physiological effects of ethylene in 'malformation' system

In the ethylene biosynthetic pathway, ACC synthase catalyzes the final reaction where ethylene is produced from 1-aminocyclopropane-1-carboxylic acid (ACC) and is accompanied with cyanide (HCN) production on a one to one basis derived from C-1 of ACC. An important characteristic of ACC oxidase is its requirement of ascorbic acid, $Fe^{2+}$ and oxygen (Yang and Hoffman 1984). The overall reaction is summarized below:

$$ACC + O_2 + Ascorbate \xrightarrow{Fe^{2+}} C_2H_4 + CO_2 + Dehydroascorbate + HCN + H_2O$$

The accumulation of toxic levels of cyanide (Nailwal et al. 2006) due to lower levels of β-Cyanoalanine synthase (β-CAS) (Kukreja and Pant 2000) during higher pace 'ethylene' biosynthesis under stress (Ansari et al. 2013a, b; Ansari et al. 2013a) affects respiration and results in necrosis and death of

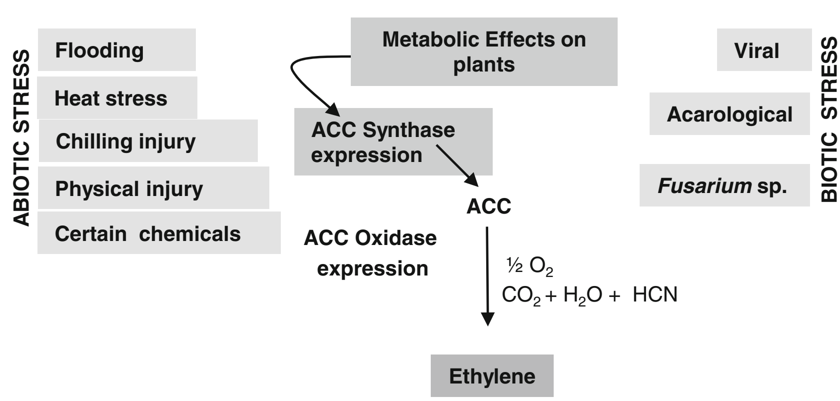


**Fig. 2** Abiotic stresses such as flooding, heat chilling, physical injury and certain chemicals, and biotic stresses viz., viral, fungal and acarological which positively modulate 1-amino cyclopropane-1-carboxylic acid (ACC) synthase expression leading to overproduction of ethylene and toxic cyanide (HCN)

**Table 2** Putative causal agents of mango malformation are known to produce 'stress ethylene' in 'mango malformation system' and in the system other than 'mango malformation'

| Causal agents | 'Stress ethylene' production | | References |
|---|---|---|---|
| | In mango malformation system | In system other than 'mango malformation' | |
| Flooding stress | No | Yes | Larson et al. 1993 |
| Viral infection | No | Yes | Abeles et al. 1992 |
| Insect infestation | No | Yes | Dahl and Baldwin 2007 |
| Chemical stimuli such as metal ions, herbicides and gases like $SO_2$ etc. | No | Yes | Rymbai and Rajesh 2011 Ievinsh 2012 |
| *Fusarium* spp. | No | Yes | Swart and Kamerbeek 1976, 2010 |
| *Fusarium mangiferae* | Yes | Yes | Ansari et al. 2013a, b |
| Temperature stress | Yes | Yes | Nailwal et al. 2006 |
| Temperature stress | Yes | Yes | Ansari et al. 2013a, b |

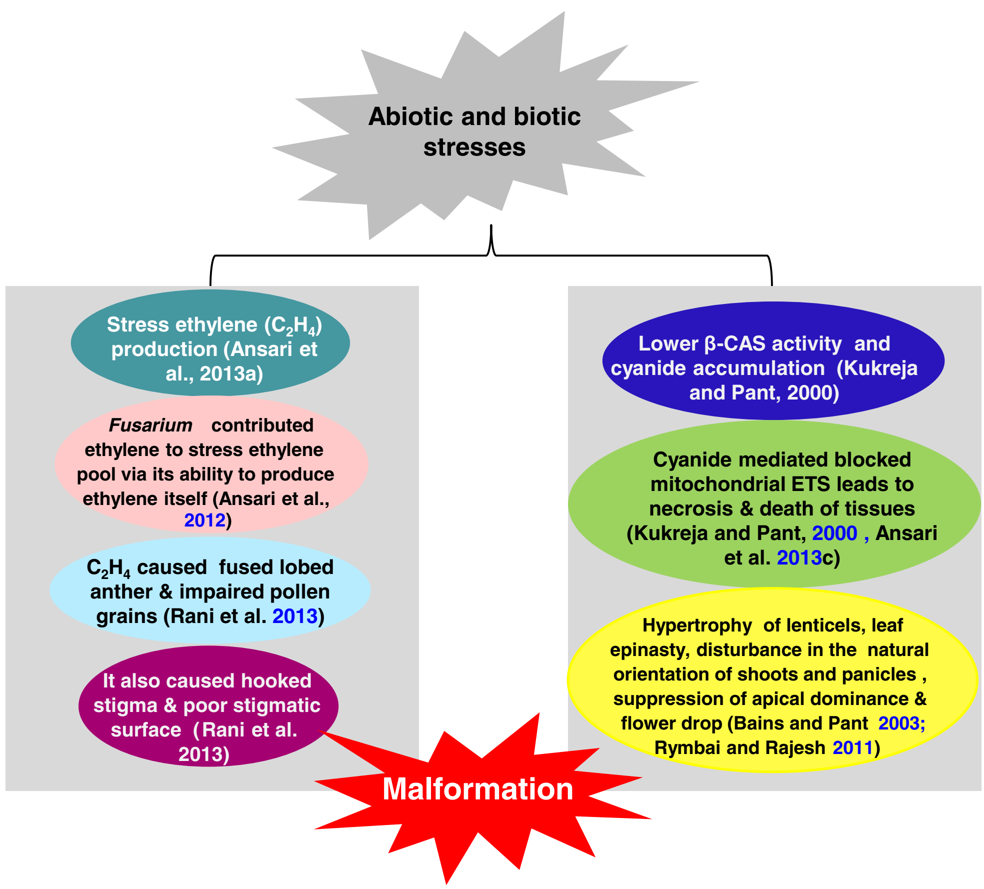


**Fig. 3** Abiotic and biotic stresses-induced ethylene caused malformation in mango. 'Stress ethylene' production affects raproductive organs (anther and stigma) of mango panicle which resulted into falure of fertilization and fruit set. Low temperature stimulated 'stress ethylene' formation and ethylene produced by *Fusarium mangiferae* iteself. The various adverse effects on mango tissues such as hypertrophy of lenticels, leaf epinasty, disturbance in the natural orientation of shoots and panicles, suppression of apical dominance and flower drop are mediated via ethylene. Lower activity of β-CAS and higher cyanide level led to death of tissues and necrosis. *Fusarium* conidial germination in vitro under PGR and anti-MF treatments and its restricted mycelial growth at temperature to which malformation is most severe do not authenticate its involvement in malady development. *β-CAS*, β-cyanoalanine synthase; *ETS*, electron transposrt cahin; *PGR*, plant growth regulators; *Anti-MF*, antimalformin

malformed tissue due to generation of cyanide insensitive respiration (Rychter et al. 1988, Kukreja and Pant 2000). Further, over production of cyanide as a result of stress induced ethylene formation in mango plants inhibits vital cell functions such as carbohydrate metabolism, carbon dioxide fixation and nitrate reduction. Cyanogenic compounds are present in plants in form of stable compounds like cyanogenic glycosides. In case of tissue disruption and infection hydrogen cyanide is released from cyanogenic compounds, (Yip and Yang 1988; Ansari et al. 2013a). Over production of stress ethylene causes fused lobed anther with weakened pollen grains and curved stigma with poor stigmatic face, which limits successful fertilization and thereby no fruit set (Rani et al. 2013). Hypertrophy resulted due to enlargement of lenticels, leaf epinasty, disorder in the natural direction of shoots and inflorescence, reduced apical dominance and flower drop (Bains and Pant 2003; Rymbai and Rajesh 2011). In acute response, 'stress ethylene' exerts adverse effects on the physiology of floral and vegetative tissue leading to loss of function at later stage and thereby mango malformation (Rani et al. 2013). Further, ethylene and polyamine cross talk in response to abiotic and biotic stress in cell signaling net work of metabolic processes leading to change in functional morphology in malformed tissues has been established (Singh et al. 2014), which fine tune at biochemical and molecular levels might be useful in further research to strengthen the stress physiology in mango malformation (Singh et al. 2012; Ansari et al. 2013a; Singh et al. 2014) (Fig. 3).

## Mango malformation can be reduced by regulating the ethylene action in plants

Growers in Philippines and India sometimes maintain smoky fires in mango orchards for several days during a vegetative flush to incite good flowering (Valmayor 1972). This results in reduced malformation. Smokes elevate both temperature and carbon dioxide which in turn mitigates ethylene production (Abeles and Abeles 1973). Further, treatment of malformed panicles with 600 ppm $AgNO_3$ helped plants to bear normal panicles with fruits borne on them (Bist and Ram 1986; Ansari et al. 2013b). The cause may undoubtedly be due positive regulation of $Ag^+$ towards ethylene action (Ansari and Tuteja 2013). Also malformation could be reduced by misting 100-200 ppm naphthalene acetic acid (NAA) in the first week of October (Majumdar et al. 1970) and floral malformation could be reduced by spaying 400 ppm 2-chloroethyl-phosphonic acid (CPA) prior to flower bud differentiation and at the bud inception stage (Ansari et al. 2013b). It may be due to auto inhibition of ethylene (Riov and Yang 1982). Anti-ethylene produces such as aminovinylglycine (AVG) and 1-methylcyclopropene (1-MCP) might be exploited to reduce the adverse effect of ethylene on morphology of mango panicles (Zaharah and Singh 2011; Rani et al. 2013). The exogenous application of putrescine caused a channeling of S-adenosyl methionine (SAM) towards polyamine synthesis, which resulted into slowing down the higher pace of ethylene biosynthetic pathway and thereby a drop in ethylene endogenous pool and reduction in panicle malformation (Singh et al. 2014). Therefore, further research should be focused in order to nullify the 'stress ethylene' to cope its adverse effects on mango tissues.

## Conclusion

In spite of rigorous research for finding out the cause and control of mango malformation, the problem has not been resolved yet. Till date its symptoms and cultivar susceptibility has been revealed but its etiology is not well understood. Abiotic and biotic stresses are important determinants of normal growth and development of mango plants through their life cycle. In the present scenario, nature of malady has been explained due to imbalance in ethylene in response to stress. Involvement of diverse *Fusarium* spp. in causing abnormal morphology of vegetative and floral tissues i.e. malformation is out of question if its growth and severity of malformation incidence are not correlated with each other. Recent study provides direct evidence that amplified with level of endogenous ethylene due to stress during flowering is, almost certainly, the cause of malady. In conclusion, hardly any recent article has covered the physiological consequences of ethylene at the molecular level to explain the nature of malady and the challenge to develop control measures against malformation malady is still daunting. Therefore, attempts to control ethylene action in plants are of paramount importance to rescue from malformation mediated loss of mango fruits.

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**Authors' contributions** NT, and RCP proposed the study. MWA, VR and AS participated in collection and Figures preparation. MWA, GB, AS and CPS reviewed the contents of the manuscript under the guidance of NT, RCP. All authors contributed to the intellectual context and approved the final version.

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