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Safal Rai
Ph.D., Research Scholar, Department of Vegetable and Spice Crops, Faculty of Horticulture, Uttar Banga Krishi Viswavidyalaya, Pundibari, Cooch Behar, West Bengal, India

Sindhu V
Ph.D., Research Scholar, Department of Vegetable and Spice Crops, Faculty of Horticulture, Uttar Banga Krishi Viswavidyalaya, Pundibari, Cooch Behar, West Bengal, India

Ram Krishna Sarkar
Assistant Professor, Department of Vegetable and Spice Crops, Faculty of Horticulture, Uttar Banga Krishi Viswavidyalaya, Pundibari, Cooch Behar, West Bengal, India

Santhoshkumar GM
Ph.D., Research Scholar, Department of Pomology and Post-Harvest Technology, Faculty of Horticulture, Uttar Banga Krishi Viswavidyalaya, Pundibari, Cooch Behar, West Bengal, India

Corresponding Author:
Safal Rai
Ph.D., Research Scholar, Department of Vegetable and Spice Crops, Faculty of Horticulture, Uttar Banga Krishi Viswavidyalaya, Pundibari, Cooch Behar, West Bengal, India

Role of polyamines in vegetable crop production: A review

Safal Rai, Sindhu V, Ram Krishna Sarkar and Santhoshkumar GM

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Abstract
Vegetables play a major role in human diet. They are enriched with various essential nutrients and therefore also called as protective food. For sustainable vegetable production and to meet the vegetable demand advancement in production techniques of vegetable crops is need of an hour. Use of polyamines as a tool for improving the vegetable production is found to be beneficial. Polyamines are the organic poly-cation compounds consisting of two or more amino groups found to improve growth and development of plants due to their effects on cell division and cell differentiation. Polyamines are also involved in various physiological processes in plants and also play major role in ion channels regulation and transportation of different molecules in cell membrane. Polyamines are associated with many fundamental processes such as DNA replication, RNA modification, synthesis of protein, modulation of enzyme activities and transcription in plants. Several studies have been conducted to study the effect of different polyamines (putrecine, spermidine, spermine etc.) on growth and development of vegetables for better outcome. Therefore, present review paper focuses on compilation of literature with respect to the effect of polyamines on growth and development of vegetables for sustainable and fruitful vegetable production.

Keywords: Polyamines, putrecine, spermidine, spermine, vegetables

Introduction
Vegetables are the rich source of vitamins, minerals, nutrients which are essential for balanced diet. They are consumed either raw or cooked. Consumption of vegetables has a vital role in prevention of several diseases, thus they are also called as protective food. It also holds its importance in foreign exchange curriculum of the nation aiming nation building. With respect to increase in population the vegetable demand has gained its momentum in fulfilling the balance diet and in such, advancement in vegetable production is need of an hour. Possible efforts are going on in advancing the quality vegetable production using various techniques and practices. Several research reports revealed that use of polyamines has a positive response in terms of production improvement in vegetables.

Polyamines are the organic poly-cation compounds consisting of two or more amino groups and are produced during metabolism (Xu *et al*., 2009; Vuosku *et al*., 2018) [154, 142] that are extensively distributed in the cells of eukaryotes and prokaryotes (Tabor and Tabor, 1984; Tiburcio *et al*., 1990; Liu *et al*., 2017; Mustafavi *et al*., 2018) [130, 138 77, 92]. Polyamines are involved in various physiological processes in plants (Xu *et al*., 2014b; Mustafavi *et al*., 2018) [156, 92] like embryogenesis, organogenesis (Xu, 2015) [155], senescence, flower development, fruit maturation, fruit development and responses to environmental stress (Vuosku *et al*., 2012; de Oliveira *et al*., 2016; Reis *et al*., 2016; Mustafavi *et al*., 2018) [142, 29, 108, 92] and are considered as new kind of plant bio-stimulants. They are also involved in plant growth and development, and ripening processes (Galston and Sawhney, 1995) [40].

The most common polyamines present in higher plants are putrescine, spermidine and spermine, thermospermine (Kim *et al*., 2014; Sobieszczuk-Nowicka, 2017; Takahashi *et al*., 2017b) [61, 125, 132] and cadaverine (Regla-Márquez *et al*., 2015; Nahar *et al*., 2016) [107, 93]. Among them, the major polyamines are putrescine, spermidine and spermine. Among these, putrescine is considered as diamine while spermidine and spermine are classified as higher polyamines and the classification is based on the strength of the amines which increase from putrescine to spermidine and spermine. Usually, the more the amino groups, the stronger the physiological activity. They are widely distributed in living organisms, found in actively proliferating cells in a very high concentration. These polyamines occur in different forms *i.e.* free living, conjugated and titer form (Tang *et al*., 2004) [134]. The activity of the conjugated form increase during flowering (Slocum *et al*., 1984; Tanguy, 2001) [121, 135], whilst the activity of titers increase during sprouting, seed germination, root formation and shoot formation (Galston and Flores, 1991; Mengoli *et al*., 1992) [37, 87]. Polyamines involve in many fundamental processes such as DNA replication, RNA modification, synthesis of protein, modulation of enzyme activities and transcription (Takashashi and Kakehi, 2010) [131]. The effects of polyamines have been mentioned in several studies (Besford *et al*., 1993; Galston *et al*., 1997) [14, 39, 40]. The present review aims at discussing the effects of exogenous and endogenous application of polyamines on plant growth and development in vegetable crop production.

Distribution, biosynthesis, degradation and conjugation of polyamines in plants

The distribution of polyamines in plants is tissue and organ specific. For instance, the most abundant polyamine present in the leaves is putrescine, while spermidine present most abundantly in other organs of the plant (Takahashi *et al*., 2017b) [132]. Within the cells, different types of polyamines show different localization patterns. For example, in carrot cells, putrescine accumulate in cytoplasm and spermine in cell well (Cai *et al*., 2006) [21]. Generally, vigorous plant growth is associated with higher biosynthesis of polyamines and higher level of polyamine content (Zhao *et al*., 2004; Cai *et al*., 2006) [161, 21].

The biosynthetic pathway of polyamines in plants (Fig 1) have been completely studied and reviewed here under in detail (Evans and Malmberg, 1989; Slocum, 1991; Martin-Tanguy, 2001) [134, 37, 81]. Putrescine is the main product of the biosynthetic pathway of polyamines. It is a synthetic precursor of spermidine and spermine (Xu *et al*., 2009) [154]. Putrescine is synthesized in plants by decarboxylation of ornithine or arginine which is catalyzed by ornithine decarboxylase or arginine decarboxylase respectively. Addition of two aminopropyl groups to putrescine in two reactions which is catalyzed by spermine synthase and spermidine synthase results in the formation of spermine and spermidine respectively. The aminopropyl groups arise from the decarboxylation of S-adenosylmethionine by S-adenosylmethionine decarboxylase (Groppa and Benavides, 2008) [47]. S-adenosylmethionine is a common common precursor for both polyamines and ethylene. There are four commonly used inhibitors for synthesis of polyamines. They are difluoromethylarginine, difluoromethylornithine, cyclohexylamine and methylglyoxyl-bis guanylhydrazone (Williams-Ashman and Schenone, 1972; Bey *et al*., 1987; Bitonti *et al*., 1987) [151, 15, 17].

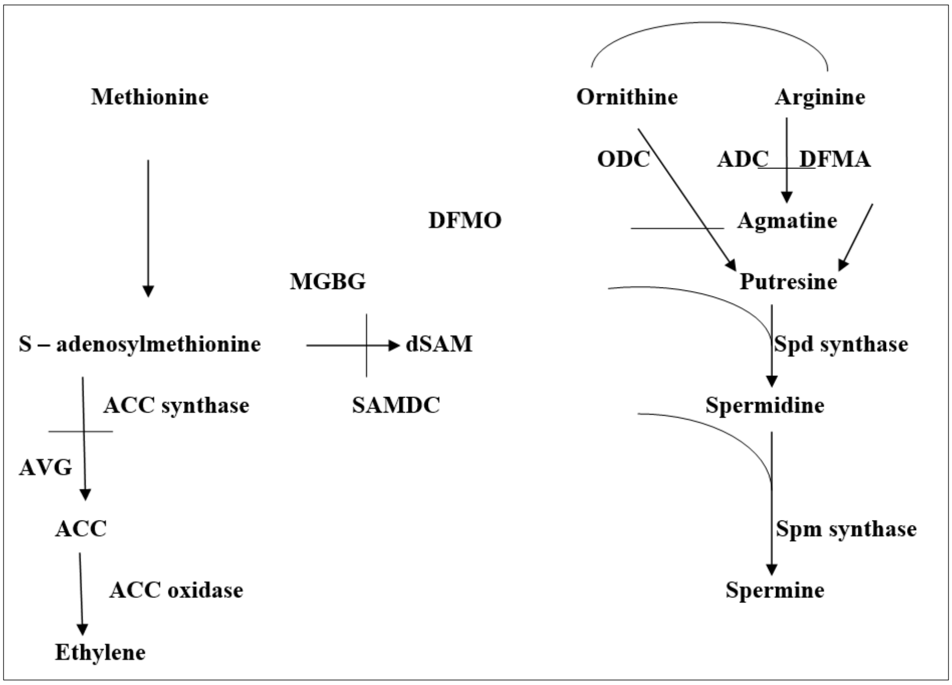

Fig 1: Polyamine biosynthetic pathway linkage to ethylene biosynthetis. Biosynthetic enzymes are ADC, ODC and SAMDC and the inhibitor DFMA, DFMO and MGBG. Sawhney *et al.* 2003 [112]

In plant cells, the level of free polyamines not only depends on their synthesis but also on their degradation and conjugation. Degradation of putrescine is catalyzed by a copper containing enzyme, diamine oxidase which oxidizes the diamine at the primary amino group while spermine and spermidine are oxidized by a flavin containing polyamine oxidase at secondary amino groups (Flores and Filner, 1985) [36]. Polyamines are conjugated to small molecules like antibiotics, phenolic acids (mostly hydroxyl cinnamic acid) and proteins (Martin-Tanguy, 2001) [81].

Role of polyamines in plants

In plants, polyamines involve in a wide range of processes, which include growth and development, embryogenesis, stem elongation, floral initiation and development (Masgrau *et al*., 1997; Hanzawa *et al*., 2000; Panicot *et al*., 2002a) [83, 51, 97], root growth (Watson *et al*., 1998) [147], tuber development (Kumar *et al*., 1996; Rafart-Pedros *et al*., 1999) [66, 105], fruit development and ripening (Khan *et al*., 2008) [60], leaf senescence (Evans and Malmberg, 1989; Galston *et al*., 1997; Bais and Ravishankar, 2002) [134, 39, 40, 10] and abiotic stresses (Minocha and Sun, 1997; Soyka and Heyer, 1999; and Roy and Wu, 2001) [88, 127, 110]. The polyamines have regulatory effect for enhancing the productivity of the plants (Gharib and Ahmed, 2005). Polyamines are found to be anti-senescent agents (Khan *et al*., 2007) [59] and are considered as nitrogen and carbon reserves, new group of growth regulators that acts as second hormonal messengers (Nahed *et al*., 2009) [94] and helps in the synthesis of RNA and protein (Kim and Jin, 2006) [62]. Also, they are involved in the buffering mechanism in order to maintain ion homeostasis and cellular pH (Smith, 1971; Young and Galston, 1983) [122].

Fate of polyamines in plants

The relationship between polyamines and plant development has been clearly mentioned in few studies. In general, the level of polyamines is high during the initial stages of plant development. Although, it depends mainly on the plant species and polyamine content present in the plant (Liu *et al*., 2006) [75]. Active cell divisions during the early stages of plant growth needs higher level of polyamines while, the decline at the later stages (*i.e.*, end of the developmental stages) which acts as signal for the beginning of senescence and death of the part of the plant or whole plant. Though, the opposite results have been noticed in tomato (Saftner and Baldi, 1990) [111].

Few studies have indicated the concentration of polyamines during growth, development and senescence of plants. In pepper, there were no major changes in free polyamines in endogenous spermidine and spermine, whilst spermidine in tomato fruits during developmental stage. Although, spermine in tomato fruit and putrescine in bell pepper fruit increased very early until about 30-38 days from fruit set and reached to low level at maturity and ripening stages. There was a consistent increase in the concentration of putrescine in tomato fruit (Yahia *et al*., 2001) [157].

Role of polyamines in growth and development of vegetables: The role of polyamines in growth and development of plants (Table 1) have been studied by few researchers. Polyamines are known to improve growth and development of plants due to their effects on cell division and cell differentiation. Such effects were noticed in bean plants (Altman *et al*., 1982) [5]. It is found that putrescine have significantly enhanced the productivity in many vegetable crops like tomato (Cohen *et al*., 1982) [25], sweet pepper (Talaat, 2003) [133] and peas (Gharib and Hanafy, 2005) [44]. It is a fact that growth of plant is encouraged by an organic carbon source that alters the rate of growth, whilst its direction is controlled by plant growth regulators (Jimenez-Cervantes *et al*., 1998) [56]. Few studies reported that increased effect of polyamine on growth rate is due to the fact that, they helps in uptake of minerals (N, P and K) from soil (Shawky, 2003) [116]. Due to the application of polyamines, there was an increased growth rate and the uptake of nutrients in leaves of pepper (Shawky, 2003) [116]. Also, Evans and Malmberg (1989) [134] reported that putrescine has found to be a substitute for inorganic nitrogen for enhancing the growth of *in vitro* explants of Jerusalem artichoke.

Table 1: Effect of exogenous application of polyamines on growth, quality and shelf life of vegetables

Crop	Polyamines	Effect on crops	References
Tomato	Spermidine, Spermine	Improved the germination of pollen and growth of pollen tube *in-vitro* under high temperature stress, helped in amelioration of NaCl stress stimulation	Song *et al*. (1999) [126] and Slathia *et al*. (2012) [119]
Radish	Putrescine, Spermidine, Spermine	Acted as antioxidant protectors against damage of cotyledons to paraquat	Kim and Jin (2006) [62]
Cucumber	Putrescine, Spermidine	Increased the tolerance to chilling through modulating the antioxidative system	Shen *et al*. (1999b) [117]
Cucumber	Spermidine	Improved the salt tolerance in seedlings	Wu *et al*. (2018) [152]
Muskmelon	γ-aminobutyric acid	Improved seedling tolerance to Ca(NO3)2 stress	Hu *et al*. (2015) [55]
Melon	Putrescine, Spermidine, Spermine	Delayed senescence by increasing the antioxidant enzymes activity and increased marketable life	Lester (2000) [71]
Zucchini squash	Spermidine, Spermine	Decreased the activity of polygalacturonase and the incidence of chilling injury	Martinez-Tellez *et al*. (2002) [82]
Globe artichoke	Putrescine	Increased growth, productivity and quality	El-Abagy *et al*. (2010) [33]
Alfalfa	Putrescine	Reduced the sensitivity to drought stress	Zeid and Shedeed (2006) [162]

Source: Abbasi *et al*., 2017 [7]

Role of polyamines in flowering, fruit setting and fruit retention

Flower bud differentiation is a complex process which is triggered by nutrition, photoperiod, water status and vernalization, and is achieved by the interaction of hormones and polyamines (Xu, 2015) [155]. Exogenous application of polyamines to poorly flowering plants substantially increased their response to flowering (Applewhite *et al*., 2010) [7]. In rapeseed, lower level of polyamines were found to be beneficial for the initiation of flower bud differentiation and an higher level of polyamines were useful for development of flower bud (Ai *et al*., 2011) [3]. Crop yield is directly related to the fruit set after the pollination. Poor fruit set due to heavy post-bloom and pre-harvest drop rarely produce economic crop (Lombard *et al*., 1971; Callan, 1977; Lombard and Richardson, 1982) [79, 22, 78]. Also, low level of self-fruit fullness due to the short effective pollination might be the reason for the poor fruit set (Williams, 1966) [150]. Furthermore, ethylene was developed from pollinated flowers, which suggests that ethylene has a role of in fertilization. The metabolism of polyamine during ripening of tomato was studied (Rastogi and Davies, 1990) [106]. Application of putrescine during anthesis time increased fruit set and yield in vegetable crops (Crisosto *et al*., 1988) [28]. Application of polyamines increased nutrient content in leaves in pepper seedlings (Shawky, 2003; Nahed *et al*., 2009 and Wu *et al*., 2010) [116, 94, 153].

Role of polyamines in stomatal movements

Stomata play an important role in the exchange of gases between the environment and plant (Ward *et al*., 1995). Potassium ions play significant role in controlling the opening and closing of stomata. Several studies have shown the inward potassium ions channel inhibiting factors (polyamines, abscisic acid and Ca^2+ levels) usually inhibit the opening of stomata (Liu *et al*., 2000) [76]. Like abscisic acid, polyamines also have role in regulation of stomata with different mechanism, while abscisic acid brings out turgor loss by outward potassium ion channels and activating anion channels (Pei *et al*., 1997) [100]. In contrast, polyamines do not affect the anion channels or inward potassium ion channels, thus indicating the capability of some other targets of polyamine besides potassium ion channels in guard cells for initiation of closure of stomata. Regulation of stomata is one of the most reviewed plant response mechanisms to stresses. Several stress factors are well-known to elate polyamines. Bruggemann *et al*. (1998) [20] showed that the polyamines block fast activating channels of vacuolar cation in higher plants. Amongst the ion channels in the guard cells, the inward channels of potassium ion are important in regulation of stomata and factors blocking the inward channels of potassium ion inhibiting the opening of stomata. Liu *et al*. (2000) [76] studied the involvement of polyamines in regulation of inward channels of potassium ion in plasma membrane of guard cells in broad bean (*Vicia faba*) leaves. Whole-cell patch clamp analysis showed that the intracellular applications of all natural polyamines (spermine, spermidine, putrescine and cadaverine) induced the stomatal closure by inhibiting the inward potassium ion current across the plasma membrane of guard cells. Furthermore, an effort was made for the identification of the target channel at molecular level, which showed that the spermidine induced stomatal closure due to the inhibition of inward potassium ion current carried by KATI channel. Single channel recording analysis suggested that the regulation of channels of potassium ion by polyamines needs unknown cytoplasmic factors/ processes (Liu *et al*., 2000) [76]. They suggested that the polyamines target KATI like inward potassium ion channels in guard cells to modulate movement of stomata and therefore provide a link between polyamine levels, stress conditions and regulation of movements of stomata.

Role of polyamines in extension of shelf life

After physiological maturity, sharp increase in the ethylene is the key feature of climacteric fruits. During ripening of climacteric fruits, ethylene production occurs with increased activities of 1-aminocyclopropane-1-carboxylic acid oxidase and 1-aminocyclopropane-1-carboxylic acid synthase enzymes (Lelievre *et al*., 1997) [70]. The enzymatic changes that cause fruit softening are also associated with the fruit ripening. Major enzymes responsible for softening of the fruits are polygalacturonase and polyestrase (Huber, 1983) [53]. Ethylene is a senesce promoting hormone and promotes ripening of fruits. Several studies have showed the slowdown of ethylene production particularly in the climacteric fruits, which helped to extend the shelf life and maintain the quality for the longer period of time. Both ethylene and polyamine has the same precursor i.e. S-adenosyl methionine, hence polyamines biosynthesis inhibit the biosynthesis of ethylene by competing for the common precursor (Pandey *et al*., 2000) [96], because both ethylene and polyamine have opposite effect on the senescence and fruit ripening. Many studies have indicated that the polyamines could inhibit the synthesis of 1-aminocyclopropane-1-carboxylic acid (precursor of ethylene) which reduces production of ethylene (Li *et al*., 2004) [72]. The inhibition of ethylene has been reported in many horticultural crops including tomatoes by the exogenous application of polyamines (Suttle, 1981) [129]. Application of polyamines, their precursors and metabolites (putrescine, spermine, spermidine, γ-aminobutyric acid, methionine and diaminopropane) prolonged the storage life of tomato fruits (Law *et al*., 1991) [69]. Post-harvest application of spermine at 1.0 mM most effectively improved the shelf-life of tomato fruits (Bhagwan *et al*., 2000) [16]. Putrescine is responsible for maintaining post-harvest quality in vegetables. Pre-harvest application of putrescine enhanced shelf life and quality of Punjab Ratta cultivar of tomato during storage (Babu *et al*., 2014) [9]. Similarly, the treatment of tomato fruits with putrescine have resulted in increased keeping qualities (Dibble *et al*., 1988; Grierson and Kader, 1986) [30, 46]. Putrescine treatment reduced the loss of moisture and respiration rate during storage and therefore helped in prolonging storage life of the tomato fruits. Pre-storage application of polyamines retarded ethylene production and fruit softening by reducing the activities of both ethylene producing and fruit softening enzymes (1-aminocyclopropane-1-carboxylic acid, 1-aminocyclopropane-1-carboxylate oxidase, 1-aminocyclopropane-1-carboxylate synthase and polygalacturonase) during low temperature storage, thereby enhancing the shelf life of the tomato fruits (Ahmad *et al*., 2007) [2].

Role of polyamines in abiotic and biotic stress

A stress affects the normal metabolic processes of plants in a negative way. Physiological processes of horticultural crops are modified by the stress (biotic or abiotic), therefore the plant gets affected and productivity is decreased which in turn leads to economic losses. Major abiotic stress factors are extreme temperature, frost, drought, salinity and pollutants. While biotic stress factors are the pathogens. It is a well-known fact that all types of stresses produce species of reactive oxygen in the biological system which is highly toxic and leads to oxidative stress (Alexieva *et al*., 2003) [4]. The extent of the stress consequences depends on the time period to which the plant species remain exposed to the stress conditions. When pathogens invade plant cells, they induce PA accumulation and PA oxidase activity which leads to increased H_2O content resulting in prevention of pathogen from infecting cells (Yordanova *et al.*, 2003) [158]. Higher putrescene content was found to be associated with greater insect resistance in Chinese cabbage (Wang, 2007) [145]. Polyamines are well known to be associated with various biotic and abiotic stresses (Richard and Coleman, 1952; Smith, 1982; Young and Galston 1983; Mc-Donald and Kushad, 1986; Tang *et al*., 2004) [109, 123, 134, 84]. Several research workers have observed the role of polyamines in reducing the consequences of different stresses, as they are considered to be radical scavengers (Kim and Jin, 2006) [62]. On the contrary, several researchers reported that the cell counteraction with the stresses is due to the increase in the antioxidant defence systems by the polyamines application (Velikova *et al*., 2000) [139].

Role of polyamines in high temperature stress

High temperature stress causes lower yield of crops and adaptability of the crops throughout the world, particularly when the crop is at its critical stage of growth and development (Mc Williams, 1980; Chen *et al*., 1982; Paulsen, 1994; Maestri *et al*., 2002) [85, 135, 99, 80]. Even the short term exposure of plants to high temperature (45 to 50^0C) makes alteration in the physiological processes (Bauer and Senger, 1979) [12]. Heat shock protein synthesis is one of the responsive mechanisms by the plant to prevent the harmful effects caused due to high temperature stress. Polyamines directly affect the synthesis of heat shock proteins by affecting the properties of cell membrane (Konigshofer and Lechner, 2002) [63]. S-adenosyl-methionine decarboxylase is the major regulatory enzyme in the synthesis of polyamines. Under heat stress condition, transgenic tomato plants having S-adenosyl-methionine decarboxylase produced 1.7 to 2.4

times higher spermidine and spermine than non-transgenic tomato plants. Increased activity of antioxidant enzyme and the protection of membrane lipid peroxidation were also observed in transgenic tomato plants. Under heat stress condition, polyamines can enhance photosynthesis, antioxidant capacity and osmotic adjustment capacity of plants (Tian, 2012) [136, 137]. Foliar application of spermidine improved the antioxidant enzymes activity in cucumber seedlings, which reduced the effects of high temperature (Tian *et al*., 2012) [136, 137]. The heat tolerance of alfalfa was related to higher content of spermidine and lower content of putrescine and spermine (Shao *et al*., 2015) [115]. These studies revealed that improving biosynthesis of polyamines in plants have led to the resistance against high temperature stress (Cheng *et al*., 2009) [24]. Application of spermidine at 4 mM in two cultivars of tomato improved the heat tolerance, pollen growth and tube germination under high temperature stress condition (Song *et al*., 1999; Murkowski, 2001) [126, 91].

Role of polyamines in eliminating the chilling injury

Polyamines can be used to inhibit the chilling injury in vegetable crops which enhances the marketable life and quality of the produce. Increase in the membrane permeability is due to the deleterious effects of chilling injury because it modifies the membrane phase transition (from a liquid crystalline state to a solid gel state) of the membrane proteins and lipids, which in turn increases the ions and electrolyte leakage (Stanley, 1991; Gomez-Galindo *et al*., 2004) [128, 124]. Chilling injury not only affects the shape of the produce but also deteriorates its quality. The imbalance occurred during the stress condition leads to the acidification of the cytoplasm with serious effects on the homeostasis and the metabolic regulation of living cells (Smith, 1984) [124]. Studies suggest that the increase in polyamines during stress condition have a direct role in maintaining the thermostability of cell membrane against changes in solute leakage and fluidity (Smith, 1982) [123]. Application of spermine or putrescine at 1 to 10 mM protected lysis of isolated protoplasts and reduced the breakdown of macromolecules (Altman *et al*., 1977; Galston and Kaur-Sawhney, 1980) [6, 38]. Some studies have reported that the accumulation of polyamines has maintained the cell membrane integrity (Smith, 1982; Guye *et al*., 1986; Smith, 1971) [122, 123]. Exogenous application of polyamines reduces the chilling injury in various vegetable crops during storage. Post-harvest dipping of polyamines reported to reduce the chilling injury in cucumber (Zhang *et al*., 2009) [24] and zucchini squash (Kramer and Wang, 1989) [65]. Therefore, polyamines not only considered as scavengers of reactive oxygen species but also as activates of the expression of the genes encoding antioxidant enzymes (peroxidase, superoxide dismutase and catalase) (Hiraga *et al*., 2000; Aronova *et al*., 2005) [52, 8]. Furthermore, changes in the cell membrane lipid during chilling injury are also reported, which leads to increased permeability and leakage of ions (Stanley 1991, Gomez-Galindo *et al*., 2004) [128, 124]. Polyamines act as free radical scavengers (Drolet *et al*., 1986, Bors *et al*., 1989; Velikova *et al*., 2000) [32, 189, 139]. As polyamines are poly-cationic in nature, they interact with membrane, providing the stability to membrane against various stresses (Besford *et al*., 1993; Borrell *et al*., 1997) [14, 18].

Role of polyamines in drought and salinity stress

Drought and salt stress are the two major abiotic stresses in crop production. Both of them causes reduced water potential in the plants. Drought adversely affects the growth and productivity of the plant (Parida and Das, 2005) [98]. Endogenous application of spermine was strongly related to drought resistance in cherry tomato (Montesinos-Pereira *et al*., 2014) [90]. Means of irrigation is very important for the successful production of plants in dry zones. Not only insufficient irrigation, but also the poor quality of irrigation water i.e. the presence of disproportionate concentration of ions is another big problem in dry areas. Among different crop species, horticultural commodities are very sensitive to drought and soil salinity. An electric conductivity of 4 mS/cm (40 mM NaCl or 0.27% salt) of the saturation extract is regarded as critical in orchards. The exogenous application of polyamines reduced the effects of NaCl stress and reduced damage in various vegetable crops (Verma and Mishra, 2005; Li *et al*., 2008) [140, 73]. Generally, the plants rich in polyamines show strong tolerance to salt. It was indicated that the spemidine level in plants is an important indicator of salt tolerance (Li and He, 2012) [74]. Application of polyamines in tomato plants was effective in amelioration of NaCl stress. Exogenous application of spermine and spermidine increased photosynthesis and reactive oxygen metabolism, which enhanced the growth of plant and reduced the inhibitory effects of salt stress (Meng *et al*., 2015; Baniasadi *et al*., 2018) [86, 11] in soybean seedlings (Wang and Bo, 2014) [146]. Buildup of cadaverine and putrescine was noted in pea and bean plants grown under high salt conditions (Shevyakova *et al*., 1981) [118]. Similar study was done in broad bean (*Vicia faba*) (Priebe and Jager, 1978) [102, 103].

Role of polyamines in mitigating atmospheric pollutants

Common atmospheric pollutants like sulphur-di-oxide increased bound and free polyamines as in case of pea plants. This might be due to the release of hydrogen ions as sulfur dioxide absorption into cells forms acids (Priebe *et al*., 1978) [102, 103]. Moreover, beans treated with cadmium chloride increased putrescine content (Weinstein *et al*., 1986) [149]. Ozone is another important air pollutant which adversely affects the crop growth and development, and its yield. Exogenous application of polyamines reduced the deleterious effects of ozone in the tomato plants (Ormrod and Beckerson, 1986; Bors *et al*., 1989) [95, 189]. Foliar application of polyamines protected paraquat damage in radish (Kim and Jin, 2006) [62] and UV radiation effect in cucumber plants (Kramer *et al*., 1991) [64] by invoking the antioxidant protector enzymes (superoxide dismutase and ascorbate peroxidase). These studies indicate that the polyamines can be useful in reducing the environmental pollutants which are one of the major problems in the production of crops in recent days.

Role of polyamines in control of disease

The protection of horticultural commodities from attack of fungal pathogens is largely due to the activation of biochemical and structural defense systems that helps to prevent the spread of pathogens (Schroder *et al*., 1992; Lawton *et al*., 1996) [114, 70]. Chitinase and β-1,3- glucanase hydrolyze fungal cell wall polymers, which are involved in the defense mechanism of plants against infection of fungus (Schlumbaum *et al*., 1986; Collinge *et al*., 1993) [113, 26]. Phenylalanine ammonia-lyase is an enzyme involved in the first step of the phenylpropanoid pathway, which is associated with the defense system of plant (Dixon and Paiva, 1995). The activity of peroxidase produces the oxidative power for cross linking of phenylpropanoid radicals and proteins which leads to the reinforcement of cell walls against penetration of fungus (Huckelhoven *et al*., 1999) [54]. Several findings have also indicated that peroxidase, β-1, 3-glucanase and phenylalanine ammonia-lyase are associated with influencing resistance in plants (Hammerschmidt *et al*., 1982; Pellegrini *et al*., 1994; Mohammadi and Kazemi, 2002; Qin *et al*., 2003) [50, 101, 89, 104]. Application of polyamines or their precursors to the leaves of plants increased the activity of peroxidase and polyphenol oxidase in bean plant (Haggag, 2005) [49], which is related to the increased resistance against the attack of disease causing pathogens (Kumar and Balasubramanian, 2000) [67]. Application of polyamines increased free and conjugated phenols, and pathogen related proteins. Moreover, phenol synthesis is very important in various forms of resistance (Garriz *et al*., 2003) [42]. The pathogen related protein activity develops resistance against viral and fungal infections in plants. Hiraga *et al*. (2000) [52] reported that the polyamines might have a role in developing resistance against infection in plants by activating the protein gene. The formulation of phytopathogenesis related protein gene resulted in decreased viral infection (Hiraga *et al*., 2000) [52]. The disease spread is dependent on the response of plants in interacting with the disease causing organisms (pathogens) (Walters, 2000; Cowely and Walters, 2002; Walters, 2003) [27, 143, 144]. Polyamines coupled with phenolic compounds (hydroxycinnamic acid amides) accumulated in incompatible interactions between plants and pathogens, whilst changes in the diamine catabolic enzyme (diamine oxidase) indicated a role in hydrogen peroxidase production during plant defense responses (Walters, 2003) [143, 144]. The increase in the ethylene activity during pathogen infection reduces the polyamines concentration which also represents the role of polyamines in controlling fungal and viral infection (Jose *et al*., 1991) [57]. Biotic stress is a vast field as very little literature is available on the role of polyamines in controlling the disease and infection in vegetable crops.

Conclusion
Vegetables are the rich source of vitamins, minerals, nutrients and are essential for balanced diet. Major problem during transportation of vegetables is their poor shelf life, which is causing huge post-harvest losses. Recently, a new group of compounds called polyamines (putrescine, spermine, spermidine etc.) have been involved in increasing the shelf life of vegetable crops. Along with enhancing the shelf life, they also promote growth and development of vegetable crops, and plays significant role in tolerating the effects of various stresses (biotic and abiotic stresses). They help in inducing the resistance against diseases, but only a little work is done in vegetable crops regarding this aspect. Still a lot of research is required to understand the proper mechanism of action of polyamines and their role in vegetable crops.

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