The Importance of Phytohormones and Microbes in Biofertilizers

W.S. Wong, S.N. Tan, L. Ge, X. Chen and J.W.H. Yong

Abstract Plant growth is dependent on meristems where cell proliferations (cell division and growth) give rise to new plant structures and allow the plant to increase in size. We provided scientific linkages and evidence to show that the growth promoting factors in biofertilizers regulating cell proliferation and ultimately modulating plant growth and development are phytohormones. The known biological functions of phytohormones (cytokinins, auxins, gibberellins, etc.) are in tandem with the observed physiological characteristics and crop yield of plants. When light, water and mineral nutrients are not limiting, phytohormones especially cytokinins, in biofertilizers help to drive plant growth by progressing faster through the various plant cell cycle checkpoints leading to the production of more cells. In the soil matrices, PGPRs (Plant Growth Promoting Rhizobacteria) have the ability to promote plant growth via various mechanisms such as nitrogen fixation, phosphorus and zinc solubilization. Some PGPRs secrete phytohormones, especially cytokinins, and can be cultured and developed into a biofertilizer. In the near future, a hybrid approach of combining organic and conventional fertilization

---

W.S. Wong · J.W.H. Yong (✉)
Singapore University of Technology and Design, 8 Somapah Road,
Singapore 487372, Singapore
e-mail: jyong@sutd.edu.sg

S.N. Tan
Natural Sciences and Science Education Academic Group,
Nanyang Technological University, 1 Nanyang Walk, Singapore 637616, Singapore

L. Ge
Nanyang Environment & Water Research Institute, Nanyang Technological University,
1 CleanTech Loop, CleanTech One, #06-08, Singapore 637141, Singapore

X. Chen
College of Life Science, Zhejiang University, Hangzhou 310058, China

D.K. Maheshwari (ed.), *Bacterial Metabolites in Sustainable Agroecosystem*,
Sustainable Development and Biodiversity 12, DOI 10.1007/978-3-319-24654-3_6

regimes will be the likely scenario as we have achieved a better understanding of plant growth and development through the regulatory controls on the cell proliferation processes by phytohormones and mineral nutrients delivered by fertilizers. The futuristic green biofertilizer should come in the form of granules in which the active plant growth promoting and soil improving substances and/or suitable microbes, with carefully selected mineral nutrients, are embedded in the packing materials giving slow and sustained release over a desired period.

Keywords Phytohormones · Fertilizers · Biofertilizers · Mineral nutrition · Plant growth · Cell cycle · Cytokinins · Auxins · Microbes · PGPR · Rhizobacteria

1 Introduction

1.1 General Plant Growth and Mineral Nutrition

General plant growth and development require 16 chemical elements (Marschner 1995). These essential elements can be classified into groups of non-mineral and mineral elements. Non-mineral elements, hydrogen (H), oxygen (O) and carbon (C), are found in air and water. Plants require these elements as raw ingredients, in the form of carbon dioxide (CO_2) and water (H_2O), to produce their own food via photosynthesis. During photosynthesis, CO_2 and H_2O are converted into glucose and ultimately to complex sugars, starch and cellulose using the energy from the sun light. Starch and complex sugar in turn provide source of carbon, energy and polymeric substrates of the plant for their growth and biosynthesis processes (Rolland et al. 2002).

Unlike non-mineral nutrients, mineral nutrients are obtained from the soil (Bronick and Lal 2005). These nutrients can be classified into macronutrients and micronutrients according to their relative concentration in plant tissues (Shaviv and Mikkelsen 1993; Taiz and Zeiger 2010). Macronutrients can be further divided into primary and secondary nutrients. Amongst all the mineral nutrients, primary nutrients, nitrogen (N), phosphorus (P) and potassium (K), are utilized by plants in the largest amounts for growth and survival and thus these three components are most lacking in nutrient-depleted soil. The secondary macronutrients are calcium (Ca), magnesium (Mg) and sulfur (S). Under natural conditions, the soil contains sufficient amount of secondary macronutrients and hence supplementation through fertilization is not always necessary. Furthermore, large amounts of Ca and Mg are added when lime is applied to reduce soil acidity; while S content in the soil is maintained by those released from the organic matter that underwent slow decomposition.

Micronutrients, boron (B), copper (Cu), iron (Fe), chloride (Cl), manganese (Mn), molybdenum (Mo) and zinc (Zn), on the other hand are required by plants in much smaller (micro) amount (Hänsch and Mendel 2009). They are also commonly termed as trace elements. Like S, these elements are recycled from decomposed organic matter. The above-mentioned elements in the form of micronutrient and macronutrients are mandatory for plant growth and development. However, their availability for plant uptake is determined not only by the amount present in the soil; soil composition and physicochemical properties (e.g. soil texture, soil structure and soil pH) also determine the extent to which the nutrients are bioavailable to the plants.

1.2 Soil Properties and Nutrient Availability

The soil is a complex physical, chemical and biological substrate (Bronick and Lal 2005; Berendsen et al. 2012). It is the most common medium in which many plants grow, and thus good soil condition is the prerequisite for promoting favorable plant growth which subsequently affects crop yield.

The properties contributing to the soil's function and ability to support plant life are the soil structure, texture and pH. Many ecological and plant physiological processes are heavily influenced by these factors: nutrient cycling, erosion, root penetration and gas exchange are some of the processes more directly related to plant growth.

Soil texture refers to the proportion of sand, silt, clay and organic matter in the soil, which is influenced by the geographical location and seasons. Soil texture influences nutrient and water retention in the soil which in turn benefits the plants (Bronick and Lal 2005). Clay and organic soil have much better nutrients and water retention capacity than sandy soil. In soils with poor nutrient and water retention capacity, leaching and loss of soil nutrients into groundwater occur as nutrients drain away, along with the water that is not being retained. This results in less nutrients being available for plant uptake. When the soil has more clay and organic matter, then water might be retained for too long causing the soil to become waterlogged. Under waterlogged conditions, the oxygen content in the soil depletes, plant roots might also rot due to prolonged soaking in water and aerobic respiration at the roots ceases. Production of nitrates, N source for plants, is also inhibited by the anaerobic condition of waterlogged soil (Crawford and Glass 1998). Hence, soil that contains optimum portions of sand, silt, clay and organic matter is ideal for farming and agricultural use.

Apart from the soil composition, soil structure, i.e. aggregation of soil particles, is also an important property of productive soil. It is the key factor that determines the functioning of the soil and enables the soil to support plant life on top of moderating environmental quality with respect to soil carbon sequestration and water quality (Bronick and Lal 2005). The pore spaces created between the particles in the aggregates affect water and air movement within the rhizospheres, nutrient availability for plant root growth and microbial activity. Thus, favorable soil structure helps to improve soil fertility, agronomic productivity and enhance soil porosity while lowering erodibility of the soil (Bronick and Lal 2005).

Soil pH, a measure of the acidity or alkalinity of the soil, is another important property that directly affects the availability of nutrients for plant uptake. At low pH, macronutrients tend to be less available; while at high pH, micronutrients tend to be less available. Under most circumstances, most soil has low pH level due to the release of hydrogen ion from the reaction between soil water and carbon dioxide produced during organic matter decomposition. Lime application can raise the soil pH level to the ideal range of 6.0–6.5. This slightly acidic pH range promotes root growth, weathering of rocks that releases minerals (Ca, K, Mg and Mn), and increases the solubility of carbonates, sulfates and phosphates (Taiz and Zeiger 2010). Beneficial plant bacterial activities, such as microbial nitrogen fixation and conversion of sulfur to forms suitable for plant uptake, also become more prevalent. Furthermore, the added lime also contributes to the pool of Ca and Mg for plant use and enhances the soil structure which subsequently promotes water and air movement.

Although nutrients occur naturally in the soil, some nutrients should be added to the soil such as lime or fertilizer to sustain plant growth and especially under situations where there are significant biomass removal periodically (Shaviv and Mikkelsen 1993; Chen 2006).

1.3 Fertilizers

Sustainable agriculture ideally should produce good crop yields with minimal impact on important ecological factors such as soil fertility (Tilman 1998; Mäder et al. 2002; Chen 2006). Mäder et al. (2002) defined fertile soil as a soil that provides essential nutrients for crop plant growth, supports a diverse and active biotic community, exhibits a typical soil structure, and allows for an undisturbed decomposition. Such "ideal" fertile soil is, however, yet to be achieved widely in the current green revolution that practices high-intensity agriculture. Intensive agriculture, often referred to as conventional agriculture, has successfully increased crop yields to meet the demands of the growing global population, but it leads to serious environmental costs (Tilman 1998). These costs include contamination of groundwater, release of greenhouse gases, change in the natural soil structure, loss of crop genetic diversity, eutrophication of water bodies and aquatic ecosystems and alteration of aquatic food webs.

Over the years, an alternative agriculture practice known as organic farming, is steadily gaining wide acceptance and practice. Agriculture products from organic farming are also marketed globally. According to the survey conducted by Foundation Ecology and Agriculture (SÖL), 4.0 % (as of 2004) of the agricultural land in Asia is managed organically; a rapid rise from the 0.33 % in 2001 (Hsieh 2005). The survey also revealed that a significant percentage of agricultural land in other continents were also managed organically, e.g. Oceania: 42 %; Latin American: 24 %; North America: 6 %; Europe: 23 %; Africa: 1 % (as of 2004). The 21-year-long organic farming study conducted by Mäder et al. (2002) showed that this method is also environment friendly. Nutrient inputs (N, P, K) and energy required to produce a crop dry matter unit was significantly reduced to 34, 51, 20 and 56 %, respectively, as compared to the conventional practice. There was, however, 20 % less crop yield. But how sustainable is organic farming? Until today, the answer still remains elusive.

The success of both farming methods is highly dependent on soil fertility, i.e. mineral nutrients. Mineral nutrients from the soil are dissolved in water and absorbed through plant roots. These nutrients may occur naturally in the soil but the bioavailable amount may not be sufficient to support healthy and robust plant growth. Furthermore, farming (especially the conventional method) may also deplete the soil of nutrients, especially primary macronutrients—N, P and K. To overcome this nutritional limitation, farmers and gardeners add nutrients externally through the application of fertilizers to compensate for the shortage of mineral nutrients in the soil. Globally, fertilizer usage has been increasing steadily over the years; typically, 40–70 % of a food production company's operating cost is spent on fertilizer usage.

In general, fertilizers refer to the substances added to the soil to increase its fertility. While most fertilizers are applied to the soil, some are formulated to be sprayed on leaves and the other aerial plant parts. Fertilizers can be derived from either organic sources or can be chemically synthesized. Regardless of the route of application and how they are derived, fertilizers supply the plants with nutrients that are generally absorbed in the form of inorganic ions (Taiz and Zeiger 2010). Nevertheless, there is new evidence to demonstrate that plants are able to absorb proteins directly and without involving other organisms (Paungfoo-Lonhienne et al. 2008).

Fertilizers play a pivotal role in regulating the growth of crop plants, and thus the reliability of food supply. The application of fertilizers is important for plant growth via cell proliferation (cell division and enlargement; detailed mechanisms will be discussed in Sects. 2 and 3), and the periodic replenishment of essential nutrients, especially the primary macronutrients, N, P, K, which are most likely to be depleted in heavily utilized soil, and other trace micronutrient, is essential to maintain soil fertility.

N, P and K are the three major mineral nutrients essential for plant growth and development (Orhan et al. 2006). Among these three nutrients, N is the mineral nutrient needed in greatest abundance by plants (Crawford 1995). N is the key constituent of molecules such as amino acids, amides, proteins, nucleic acids, nucleotides, coenzymes that are essential for various biological functions and comprises about 1.5 % of a plant's dry weight (Taiz and Zeiger 2010). In addition to serving as a nutrient and as an osmolyte, N also functions as a signal that reprograms N and C metabolism and influences root and shoot growth (Crawford 1995; Wang et al. 2007). N level in the soil is often lowered due to plant uptake, leaching and microbial denitrification, resulting in the dependence on N fertilizers to sustain the productivity of any modern intensive agriculture (Crawford and Glass 1998).

After N, P is the second most frequently limiting macronutrient for plant growth (Schachtman et al. 1998). Making up about 0.2 % of a plant dry weight, P is a component of key molecules such as nucleic acids, phospholipids, sugar phosphates, coenzymes and ATP (Schachtman et al. 1998; Taiz and Zeiger 2010). Phosphorus in the form of orthophosphate (Pi), is also required in the regulation of metabolic pathways and enzymatic reactions (Theodorou and Plaxton 1993).

Potassium, K, generally constitutes 1 % of a plant dry weight and thus it is the nutrient to be absorbed in second largest amount, after N. It is essential as a cofactor for enzyme activities involved in nutrient absorption, respiration, transpiration and photosynthesis. Unlike N and P, K does not become a part of endogenous organic compounds but remain as a cation in the plant tissues. It is also the crucial for the establishment of cell turgor and maintenance of cell electroneutrality (Taiz and Zeiger 2010).

A wide variety of fertilizers are available commercially and they can be classified into chemical fertilizers and organic/green fertilizers. Another class of fertilizers, biofertilizers, is also gaining worldwide attention, due to the awareness of the detrimental effects of chemical fertilizers imposed on the environment globally and of the improved knowledge on the relationships between plants and microorganisms occurring in the soil (Malusá and Vassilev 2014). Thus, agricultural fertilizers currently available in the market can be classified traditionally into three broad categories, namely chemical fertilizers, organic fertilizers and biofertilizers.

Chemical fertilizers are chemically synthesized compounds that contain specific nutrients, macro and/or micronutrients. This group of fertilizers provides the plants with nutrients in inorganic forms. In this review, we refer chemical fertilizers specifically to synthetic fertilizers containing N, P and K in various ratios in terms of weight percentage, otherwise also known as NPK fertilizers or inorganic fertilizers (Shaviv and Mikkelsen 1993).

Organic fertilizers are fertilizers generally derived from natural sources such as plant and animal matter. The commonly known examples are composts (decomposed plant materials) and manure (animal excrement). Meat and bone meal is another form of organic material being used as organic fertilizers (Jeng et al. 2006). In this review, we consider composts and manures as organic fertilizers.

Biofertilizers are the new and emerging entities in the realm of agricultural fertilizers or “Biostimulants”. Biofertilizers are defined as fertilizers that enhance plant growth via the activities of microorganisms, i.e. conversion of nutritionally important elements/compounds from the “unavailable state” to (bio)available form(s) and production of active ingredients, particularly phytohormones (e.g. cytokinins, auxins, gibberellins etc.), amino acids and proteins. To date, the definition of biofertilizers is still unclear and remains highly debatable. No consensus has been agreed upon on the inclusion of indirect microbial activities, such as biocontrol properties targeting pathogens and conferring resistance against pathogens, as plant growth enhancing properties (Malusá and Vassilev 2014). Interestingly, there are also some people who do not consider biofertilizers as organic fertilizers. For the purpose of this review, we would, however, like to define biofertilizers as organic products containing biomass-based structural matrix, e.g. composts, humic acid and fulvic acid, with different types of useful (natural) microorganisms that enhance plant growth through their biological activities. Thus, in this review, our holistic classification of organic fertilizers is to include biofertilizers, unless otherwise stated.

In the following sections, we will discuss briefly on the advantages and disadvantages of chemical and organic fertilizers, while biofertilizers will be discussed in greater depth in Sect. 5.

1.3.1 Chemical Fertilizers

Chemical fertilizers are NPK-based formulation that has been widely used for over 100 years. Chemical fertilizers, e.g. urea, are the preferred choice as they are deemed to be highly effective and can be transported more economically. They supply the plants with mineral nutrients in the form of organic/inorganic salts that are easily and readily taken up by the plants via the roots, giving rise to immediate or quick plant growth improvement. Most importantly, chemical fertilizers supplement the soil with nutrients in desired ratios of N:P:K at a low cost.

Despite the advantages, a century-long usage of chemical fertilizers has seemed to reveal that these fertilizers are “losing” its growth promoting efficacy and increasingly, creating environmental problems. It has been reported that large fractions of N fertilizers applied to agriculture systems are lost as N_2, trace gases and nitrate leachate (Adesemoye et al. 2010), as the soil structure degrades and loses its mineral and water retention capacity. Larger amount of chemical fertilizers is thus required to achieve the same effect. The rampant use of chemical fertilizers in turn leads to eutrophication of water resources, pollution and contamination of soil, further degradation of soil structure, reduced soil fertility and reduced fertilizer efficiency (Vitousek et al. 1997; Tilman 1998; Mahdi et al. 2010; Xiang et al. 2012). Prolonged supply of high amount of N to plants also causes plant tissues softening, causing the plant to be more sensitive to pests and diseases (Chen 2006).

Chemical fertilizers also pose adverse effects on the biological properties of the soil. Its continuous application usually causes the soil to become acidic and repels earthworms, beneficial entity in fertile soil. Acidic soil also alters microbial species composition and diversity in the rhizosphere and results in the destruction and hindrance of beneficial microbial activities such as organic matter decomposition and symbiotic interaction with plants. Also, biologically inactive soil contains less organic matter and do not release as much nutrients as biologically active soil (Chandramohan et al. 2013). Over time, soil treated only with chemical fertilizers will lose its organic matter and disrupt the interactions with the living organisms, namely earthworms and microorganisms, which contribute immensely to soil “health” (Tilman 1998).

1.3.2 Organic Fertilizers

It is increasingly evident that the intensive agricultural methods employed as part of the conventional agriculture have been proven to be unsustainable (Tilman 1998; Mäder et al. 2002). Small but growing cohorts of farmers/growers have recognized this issue and have turned to utilize an alternate farming method, i.e. organic agriculture. Organic agriculture is defined by the FAO/WHO as "a holistic production management system which promotes and enhances agro-ecosystem health, including biodiversity, biological cycles and soil biological activity. It emphasizes the use of sustainable management practices in all aspects of the farm management and taking into account of the regional conditions and locally adapted systems. This is accomplished by using, wherever possible, agronomic, biological and mechanical methods, as opposed to using synthetic materials, to fulfill any specific function within the system" (FAO/WHO 2015). In comparison to conventional agriculture, organic agriculture is deemed to be an effective farming system with self-sustainability features.

Theoretically, organic agriculture is self-sustainable but it still requires the input of external fertilizers to replenish the nutrients that are quickly sequestered by the growing plants. To adhere to its organic practices, organic agriculture supply their soil with N by more natural means such as growing cover crops, mainly leguminous species that have the ability to fix atmospheric N. It makes use of organic fertilizers instead of chemical fertilizers. Organic fertilizers, also termed as green fertilizers, however, work on a different basis as compared to chemical fertilizers.

Organic fertilizers, including biofertilizers, supplement the soil with nutrients, but usually at a much lower concentration and slower release rate as compared to chemical fertilizers. N is released slowly from organic fertilizers (compost) due to its slow mineralization rate (Hernández et al. 2010) and its availability is dependent on soil properties (Fricke and Vogtmann 1993). P is contributed at a percentage of 20–40 % (Fricke and Vogtmann 1993) of its total low P content (vermicompost: 0.014 ± 0.0009 %; compost: 0.015 ± 0.0009 % (Hernández et al. 2010)). K is, however, contributed at an exceptionally higher percentage of 85 % (Fricke and Vogtmann 1993).

Generally, organic fertilizers have lower mineral nutrient contents which are often not well characterized and quantified, and may vary between production batches and methods when compared with chemical fertilizers (Shaviv and Mikkelsen 1993; Mäder et al. 2002; Chen 2006; Mahdi et al. 2010). Thus, within the plant industry, there is certainly a need to develop/produce organic fertilizers in a reproducible way in order to gain wider acceptance by farmers utilizing the conventional farming approach, i.e. quality control and assurance for organic fertilizers as a reliable commercial product. Furthermore, the rate of nutrient release in some poorly prepared organic fertilizers may not meet the needs of the vigorously growing plants, accustomed to conventional chemical fertilizers. Hence, larger amount of organic fertilizers has to be applied under certain situations. This in turn incurs more cost to the growers as compared with using the traditional chemical fertilizers.

Organic fertilizers are, however, desirable over chemical fertilizers due to its ability to improve the soil structure via the enhancement of soil biological diversity. As discussed earlier (Sect. 1.2), soil properties play a very vital role in determining plant growth and nutrient availability for plant uptake. Thus, organic fertilizers are more valued for their soil-improving qualities and to a lesser extent for their mineral nutrient, mainly N and P, contribution.

In comparison to chemical fertilizers, the environmentally friendly organic fertilizers (composts and manure) do appear to be the solution to attain sustainability in modern agriculture. However, due to our current limited understanding about the growth stimulating mechanism(s) of organic fertilizers on plant growth, we will not be able to achieve optimal and sustainable agriculture yield by relying solely on organic fertilizers at present. We believe that the combined use of chemical and/or organic fertilizer with the active ingredients obtained from biofertilizers, would help the present day farmers to achieve sustainable farming with maximal yield (Shafi et al. 2012; Qin et al. 2015; Song et al. 2015).

In order to understand how organic fertilizers and phytohormones work in tandem to govern plant growth and development, and the other associated useful plant performance characteristics such as conferring resistance against pathogens, the fundamentals of plant growth mechanisms and cell proliferation regulations by various substrates (sucrose, phytohormones, availability of nutrients, etc.) will be revisited and discussed in depth and in relation to fertilizers.

2 Plant Growth Mechanisms

Plant growth is dependent on meristems, groups of dividing cells that give rise to new plant structures (Steeves and Sussex 1989; Coen and Meyerowitz 1991; Wolters and Jürgens 2009) and enable the plant to increase in size continuously throughout its lifetime (Huala and Sussex 1993). In order to be competent and ready to divide, proliferative cells in the plant meristems have to undergo four distinctive phases of the cell cycle: postmitotic interphase (G1), DNA synthetic phase (S), postsynthetic interphase (G2) and mitosis (M phase); and subdivision phases of mitosis, cytokinesis and G1-phase (G0); all of which are governed by a series of checkpoints (Francis and Sorrell 2001) regulated by cyclin-dependent kinases (CDKs) (Den Boer and Murray 2000; Inzé 2003; Dewitte and Murray 2003) (Fig. 1). Cyclins, CDK inhibitors, retinoblastoma proteins, E2F/DP transcription factors, histones, sucrose and phytohormones (specifically cytokinins, auxins, gibberellin and abscisic acid) are some of the other factors involved in the regulation of the cell cycles (Inzé 2003; Souza et al. 2010).

Meristems have the ability to divide and differentiate but can only give rise to certain structures; for example, the root meristems give rise to roots while the shoot meristems may result in leaves, flowers, axillary buds and internodes (Huala and Sussex 1993). Primary shoot apical meristem (SAM) that arises during embryogenesis together with additional meristems formed after seed germination plays

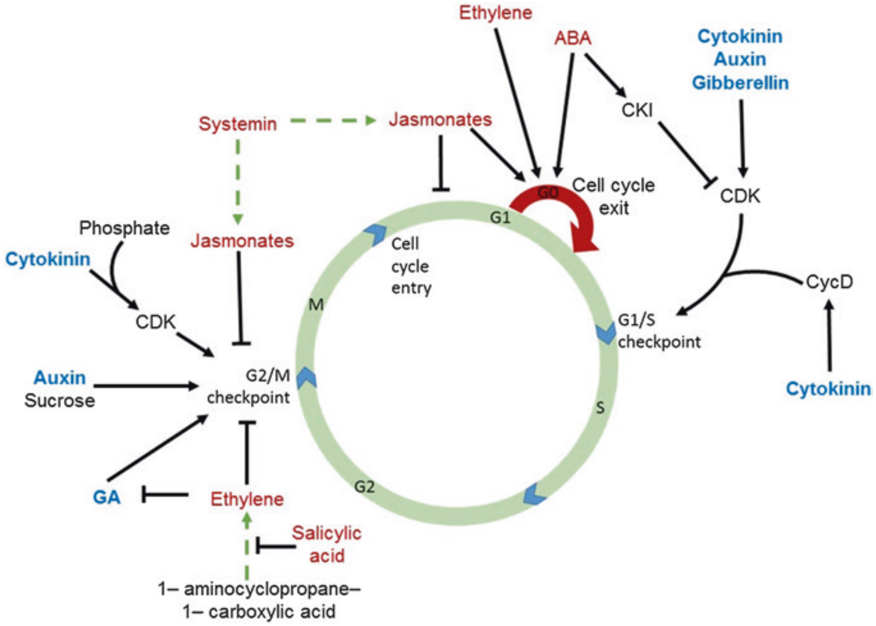


Fig. 1 Schematic diagram of the plant cell cycle and regulatory actions of phytohormones. Cell cycle has four distinct phases, G1 (postmitotic interphase), S (DNA synthetic phase), G2 (postsynthetic interphase) and M (mitosis); and subdivision phases of mitosis, cytokinesis and G1-phase (G0); all of which are governed by a series of checkpoints, mainly between G1 and S (G1/S checkpoint) and between G2 and M (G2/M checkpoint). The plant cell cycle is predominantly regulated by phytohormones while other factors exerting varying degrees of controls under different environmental (abiotic) and biotic circumstances in which the whole plant is exposed to. Generally, auxins, cytokinins and gibberellin play stimulatory roles; while abscisic acid (ABA), ethylene and jasmonates inhibit the progression of cell cycle. Systemin, a plant peptide hormone, down regulates cell cycle by promoting the biosynthesis of jasmonates, while salicylic acid up-regulates cell cycle progression by inhibiting the biosynthesis of ethylene

a crucial role in giving the plants its various forms (Steeves and Sussex 1989). Primary SAM provides the plant with the main axis while the other meristems determine the development of the shoot branches, and the brunches temporal and spatial development determines the complexity of the branching pattern (Shimizu-Sato and Mori 2001). Plant forms although plastic in nature, influenced by environmental cues, are still genetically governed and thus retain their species-specific forms (Shimizu-Sato and Mori 2001).

Axillary meristems are typically located on the adaxial (upper) region where the primary organ, such as leaf axil and stems join (Grbić and Bleecker 2000; Long and Barton 2000; Shimizu-Sato and Mori 2001). Being secondary meristems, axillary meristems are crucial for the continuous development of the plant morphology, such as lateral plant growth (Bennett and Leyser 2006). Lateral plant growth is, however, governed by a mechanism known as apical dominance. Apical dominance, broadly defined as the inhibitory control of the shoot apex over the outgrowth of lateral buds, is one of the mechanisms that ensure the plants survival with a reservoir of meristems to replace damaged primary shoot (Shimizu-Sato and Mori 2001). Apical dominance, however, can be released by development programs, hormonal and environmental cues (Turnbull et al. 1997; Bangerth el al. 2000; Shimizu-Sato and Mori 2001; Schmülling 2002). Increased cytokinin concentrations and changes in phytohormone ratio(s) (e.g. auxins:cytokinins) are some of the hormonal cues that enable the plant to overcome apical dominance.

3 Plant Growth Regulation

Plant growth is regulated by various abiotic and biotic factors such as temperature, light intensity, water availability, soil compositions and characteristics, nutrient availability, phytohormones (plant hormones) availability, interactions with the immediate organisms (microorganisms, fungi, other plants) in its surroundings, and other factors (for reviews, see Steeves and Sussex 1989; Mok 1994; Rolland et al. 2002; Van Loon 2007; Wolters and Jürgens 2009).

In this review, we will focus our discussion on sucrose and phytohormones availability in relation to fertilizer types and usage.

3.1 Regulation by Sucrose Availability

Photosynthesis is the fundamental process in plants and sugars are produced in the process. Sugars are essential for the plant growth as they are the source of carbon, energy and polymer substrates for biosynthesis (Rolland et al. 2002). They are transported via the plants phloem from the sites of photosynthesis (usually the leaves) to the various sink organs such as roots, flowers, developing fruits and seeds, mainly in the form of sucrose. Sucrose concentration plays an important role in regulating various plant growth processes. Low sucrose concentration stimulates leaf photosynthetic activities, nutrient mobilization and export from the sink organs, while high sucrose concentration inhibits photosynthetic activities but stimulate growth and storage in the sink organs (Wang and Ruan 2013). Before sucrose can be utilized for metabolism and biosynthesis, they are normally converted to simpler forms like glucose and fructose by invertase or UDP-glucose and fructose by sucrose synthase (Wang and Ruan 2013). In addition to their essential roles as source of carbon, energy and building blocks for plant growth, sucrose and its cleavage compound hexose have important hormone-like functions as signaling molecules that regulate specific gene expression (Rolland et al. 2002; Wang and Ruan 2013).

A close correlation was observed between the supply of sucrose and the expressions of cyclins, specifically d-type cyclins (CycD2 and CycD3), that induce the cell to progress beyond the G1 phase and become committed to complete the full plant cell cycle (Riou-Khamlichi et al. 2000) (Fig. 1). Expression of CycD2 only requires sucrose while CycD3 expression requires the presence of sucrose and phytohormones, specifically cytokinins and auxins (Koning 1994; Riou-Khamlichi et al. 2000). In other words, sucrose is essential in the upstream regulation prior to hormonal regulation of CycD3 expression. Sucrose is also required for the activation of mitotic entry by activating the transcription of key components that drives the G2 to M transition (Skylar et al. 2011) (Fig. 1). Thus, it is evident that sucrose could be involved in the reactivation of cell from the state of growth arrest (Souza et al. 2010). Apart from driving plant cell cycle transition indirectly, sucrose is also required for general plant growth such as tuberization in potato (Šimko 1994), to induce formation of adventitious roots in *Arabidopsis* seedlings (Takahashi et al. 2003), to induce flowering (Roldán et al. 1999) and various other growth processes (for a review, see Gibson 2005).

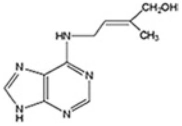
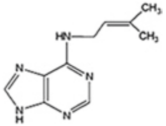
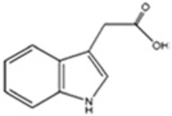
3.2 Regulation by Phytohormones Availability

Phytohormones are naturally occurring substances known to be crucial for regulating various aspects of physiology and development throughout the lifecycle (for reviews, see Bleecker and Kende 2000; Mok and Mok 2001; Pimenta Lange and Lange 2006; Matsubayashi and Sakagami 2006; Wolters and Jürgens 2009; Zhao 2010; Pacifici et al. 2015). Some of the growth regulatory functions include cell division and expansion, cell elongation, stem elongation, inhibition, root growth, activation of bud growth, branch development, promoting or delay in leaf senescence and chlorophyll production. Regulatory functions of cytokinins and auxins will be discussed in detail in the following sections. Other classes of phytohormones, such as gibberellins, ethylene, abscisic acid and strigolactones, are listed in Table 1 and will not be discussed in detail.

3.2.1 Cytokinins

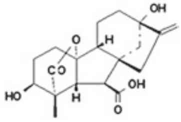
The vast majority of naturally occurring cytokinins are a group of adenine compounds with an isoprene, modified isoprene, or aromatic side chain attached to the N^6 amino group. Refer to Fig. 2a for the basic structure of cytokinins and Fig. 2b for the representative cytokinins. Cytokinins occur in both free and tRNA-bound forms, and are essential in regulating various physiological processes in plants (Letham and Palni 1983; Haberer and Kieber 2002; Stirk and Van Staden 2010). The biosynthetic gene *ipt*, which encodes the enzyme isopentenyltransferase, is responsible for the synthesis and expression of cytokinins (Kamínek et al. 1997). This enzyme is produced in the roots and shoots (Chen et al. 1985), with the root apical meristems being the major site of synthesis. Isopentenyltransferase is essential in the first step of cytokinin synthesis. It transfers the isopentenyl moiety from

Table 1 List of hormonal and non-hormonal plant growth promoters and their known biological functions

	Classes of plant growth promoters	Molecular structure	Biological functions	References
Hormonal	**Cytokinins** *trans*-zeatin (*t*Z) *trans*-zeatin riboside (ZR) Kinetin (K) N^6-[2-isopentyl] adenine (iP) N^6-isopentyladenosine (iPR) Dihydrozeatin	 *tz*	Activate cell division and regulate plant growth from the cellular level through to the tissue, organ and whole plant level	Letham and Palni (1983), Frank and Schmülling (1999), Francis and Sorrell (2001), Schmülling (2002), Sakakibara (2006)
			Upregulate CycD3 at the G1 checkpoint and the phosphoregulation of CDK at the G2/M checkpoint	Frank and Schmülling (1999), Francis and Sorrell (2001)
		 iP	Involved in formation of embryo vasculature, leaf expansion, branching, chloroplast development, root growth, seed germination and delay senescence	Letham and Palni (1983), Mok (1994), Schmülling (2002), Howell et al. (2003)
			Involved in the initiation and outgrowth of axillary buds, release from shoot apical dominance	Turnbull et al. (1997), Bangerth et al. (2000), Shimizu-Sato and Mori (2001), Yong et al. (2014)
			Function as signals	Leopold and Kawase (1964), Gersani and Kende (1982), Mauk and Noodén (1992), Yong et al. (2000), Emery and Atkins (2002), Ma et al. (2002), Schmülling (2002), Frugier et al. (2008), Stirk and Van Staden (2010); Yong et al. (2014)
	Auxins Indole-3-acetic acid (IAA) Indole-3-butyric acid (IBA) Naphthaleneacetic acid (NAA)	 IAA	Promote cell expansion/elongation, root growth, regulate cell cycle and inhibit growth of axillary buds	Zhao (2010)

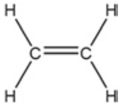
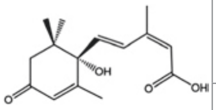
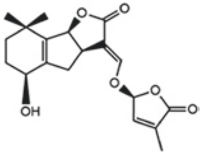
(continued)

Table 1 (continued)

	Classes of plant growth promoters	Molecular structure	Biological functions	References
			Induce the expression of CycD3 and CDKs	Wang and Ruan (2013)
			Interact with other phytohormones to regulate various plant growth processes	Shimizu-Sato and Mori (2001), Haberer and Kieber (2002), Wang and Ruan (2013), Zhou et al. (2013), Zhao et al. (2015)
			Regulate synthesis of other phytohormones	Al-Babili and Bouwmeester (2015)
			Involved in organ primordia initiation and the initiation and maintenance of organ founder cell populations	Wolters and Jürgens (2009)
	Gibberellin (GA) GA1 GA3 GA4 GA7	 GA1	Regulate plant growth, promote stem elongation, leaf expansion, trichome development, flower formation, sex expression, fruit setting, seed development and germination	Pimenta Lange and Lange (2006), Wolters and Jürgens (2009), Nelson et al. (2012), Pacifici et al. (2015)
			Transcriptional activation of G2/M checkpoint proteins that promote cell division	Sauter et al. (1995)
			Work in antagonism with ABA in the control of seed germination	Nelson et al. (2012)
			Inhibit fruit ripening by decreasing respiratory activity and delaying anthocyanin synthesis and chlorophyll degradation	Martínez et al. (1994)

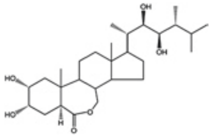
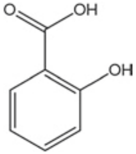
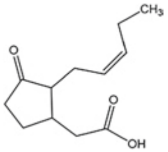
(continued)

Table 1 (continued)

	Classes of plant growth promoters	Molecular structure	Biological functions	References
	Ethylene		Inhibits cell proliferation	Herbert et al. (2001)
			Involved in stress response and activation of defense responses and resistance against certain pathogens	Klessig et al. (2000), Wolters and Jürgens (2009)
			Regulator of plant senescence	Bleecker and Kende (2000)
	Abscisic Acid (ABA)		Inhibit cell proliferation (cell division); prevent cells from entering S phase	Koning (1994), Francis and Sorrell (2001), Dewitte and Murray (2003)
			Inhibit bud growth	Shimizu-Sato and Mori (2001)
			Involved in stress response (closing of stomata)	Wolters and Jürgens (2009), Yoshida et al. (2010)
			Interact with auxin to regulate root development	Zhao et al. (2015)
			Downregulates GA signaling	Wolters and Jürgens (2009)
	Strigolactones	 Strigol	Carotenoid-derived phytohormones	Kretzschmar et al. (2012), Al-Babili and Bouwmeester (2015)
			Stimulate growth of arbuscular mycorrhizal (AM) fungi and seed germination of root-parasitic plants	Umehara (2011), Kretzschmar et al. (2012), Nelson et al. (2012)
			Coordinate root and shoot development in response to phosphorus starvation	Koltai (2011), Smith (2013)
			Interact strongly with the auxin signaling pathway to modulate auxin-dependent secondary growth, e.g. increasing stem thickness	Agusti et al. (2011)

(continued)

Table 1 (continued)

	Classes of plant growth promoters	Molecular structure	Biological functions	References
	Brassinosteroids		Regulate growth, xylem differentiation, disease resistance, stress tolerance and control of photomorphogenesis bending	Dewitte and Murray (2003), Müssig et al. (2006), Wolters and Jürgens (2009), Li et al. (2013), Pacifici et al. (2015)
			Required for the induction of a protein, ARGOS-LIKE (ARL), responsible for cell expansion during leaf growth	Wolters and Jürgens (2009)
			Required as signal for genes activation involved in a wide range of physiological processes	Müssig et al. (2006)
	Salicylic Acid		Involved in plant defense responses	Doares et al. (1995), Klessig et al. (2000), An and Mou (2011)
			Involved in cell growth, seed germination and establishment, flower formation, stomatal responses, thermotolerance, thermogenesis and nodulation	An and Mou (2011)
			Inhibits biosynthesis of ethylene	Raskin (1992)
			Induce production of plant phenolics	Raskin (1992)
	Jasmonates		Prevent DNA synthesis during the G1 phase and inhibit M phase progression	Dewitte and Murray (2003)

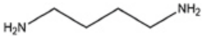
(continued)

Table 1 (continued)

	Classes of plant growth promoters	Molecular structure	Biological functions	References
			Involved in stress response by mediating the activation of defense response and resistance genes against certain pathogens and insects	Creelman and Mullet (1997), Klessig et al. (2000)
			Modulate growth processes, e.g. fruit ripening, production of viable pollen, root growth and tendril coiling	Creelman and Mullet (1997)
			Induce tuberization in potatoes	Pelacho and Mingo-Castel (1991)
			Regulation of genes encoding vegetative storage proteins	Creelman and Mullet (1997)
			Repress genes encoding proteins involved in photosynthesis	Creelman and Mullet (1997)
	Plant peptide hormones Systemin		Function as signals in the regulation of various growth processes, e.g. meristem organization, root growth regulation, leaf shape regulation, nodule development, callus growth, pollen tube growth and organ abscission	Matsubayashi and Sakagami (2006), Matsubayashi (2014)
			Involved in plant defense responses	Ryan (2000), Lindsey et al. (2002), Ryan and Pearce (2003), Matsubayashi and Sakagami (2006), Matsubayashi (2014)

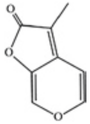
(continued)

Table 1 (continued)

	Classes of plant growth promoters	Molecular structure	Biological functions	References
	Polyamines Putrescine Spermidine Spermine	 Putrescine	Required for cell cycle progression	Weiger and Hermann (2014)
			Regulate fruit growth and ripening, leaf senescence, reproductive organ development and tuberization	Martin-Tanguy (2001)
			Involved in stress response	Groppa and Benavides (2008)
	Nitric oxide (NO)	$:N{=}O$	Function as signaling compound in regulatory pathways	Ya'acov (1996), Nelson et al. (2012)
			Stimulatory and inhibitory effects on plant growth	Ya'acov (1996), Durner and Klessig (1999)
			Regulate expression of genes related to metabolism, cellular detoxification, iron homeostasis, signaling, flowering, lignin biosynthesis and transport	Lamotte et al. (2005)
			Involved in plant defense gene activation upon pathogen attack	Durner et al. (1998), Klessig et al. (2000)
			Modulate the synthesis of salicylic acid, jasmonate and ethylene	Lamotte et al. (2005)

(continued)

Table 1 (continued)

	Classes of plant growth promoters	Molecular structure	Biological functions	References
	Karrikins	 Karrikinolide	Stimulate seed germination for certain plant species	Nelson et al. (2009, 2012), Scaffidi et al. (2012)
			Enhance light responses during germination and seedling development	Nelson et al. (2010)
Non-hormonal	**Humic substances** Humic acid Fulvic acid		Enhance plant growth and enhance root development	Rauthan and Schnitzer (1981), Piccolo et al. (1992), Atiyeh et al. (2002)
			Involved in cell respiration, oxidative phosphorylation, protein synthesis, photosynthesis and enzymatic reactions	Atiyeh et al. (2002)
			Improve nutrient uptake, e.g. iron and zinc	Atiyeh et al. (2002), Chen et al. (2004)
			Improve soil structure and accumulation of organic matter	Piccolo et al. (1992), Atiyeh et al. (2002), Piccolo (2002)

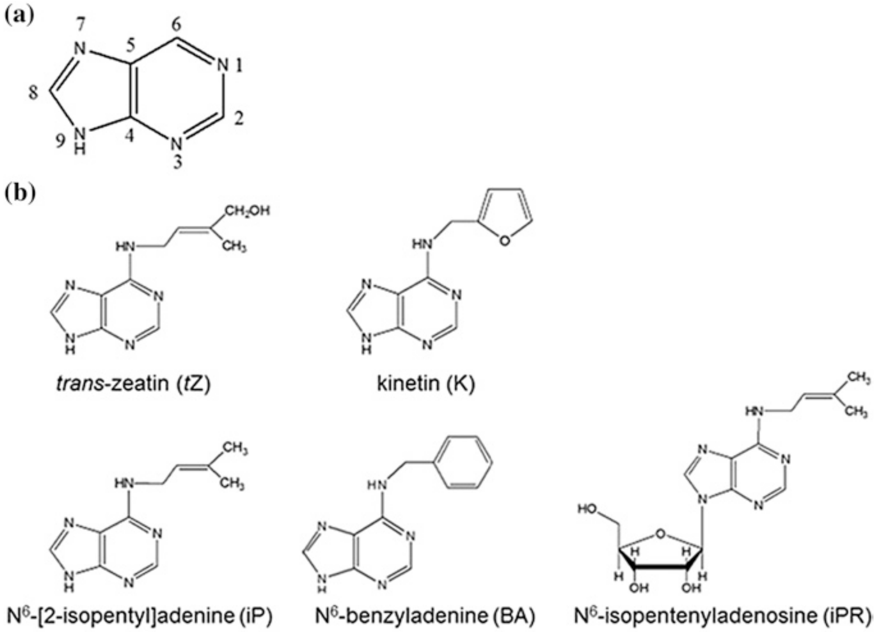


Fig. 2 Chemical structures of cytokinins and its basic structure. **a** Adenine structure and the numbering system for the nomenclature of cytokinins. **b** Representative cytokinins: *trans*-zeatin (*tz*), kinetin (K), N^6-[2-isopentyl]adenine (iP), N^6-benzyladenine (BA) and N^6-isopentyladenosine (iPR). Note that the isoprene, modified isoprene, or aromatic side chains are attached to the N^6 amino group of adenine compounds

dimethylallyl diphosphate (DMAPP) to ATP/ADP, which is more efficiently utilized by the plant isopentenyltransferase compared to AMP (Kakimoto 2001). In contrast, bacterial cytokinin synthesis, which shares a similar pathway, are able to start the first step by transferring isopentenyl moiety from 1-hydroxy-2-methyl-2-(E)-butenyl 4-diphosphate (HMBDP) to AMP (Ueda et al. 2012) (Fig. 3).

Cytokinins are classified according to their side-chain configurations as either isoprenoid or aromatic cytokinins (Stirk and Van Staden 2010) with the latter being the rarer form (Kakimoto 2003). Naturally occurring isoprenoid cytokinins are either isopentenyladenine (iP)-type, which carries an isopentenyl N^6 side chain, or zeatin-type, which carries hydroxylated isopentenyl N^6 side chain (Kakimoto 2003). Zeatin-type cytokinins can occur in *cis* or *trans* configuration, depending on the hydroxylation of the methyl group on the side chain; and *trans*-zeatin and its derivatives have higher biological activity than the *cis* forms. Zeatin-type cytokinins are also the main constituents in plants (Mok et al. 2000). Cytokinins also occur in different forms, namely in the form of free base, riboside, or ribotide (or nucleotide); with the free base form being biologically active and the riboside form being the form of transportation via the xylem system. The riboside type of cytokinins are later converted to their active form by another enzyme at the shoot (Sakakibara 2006).

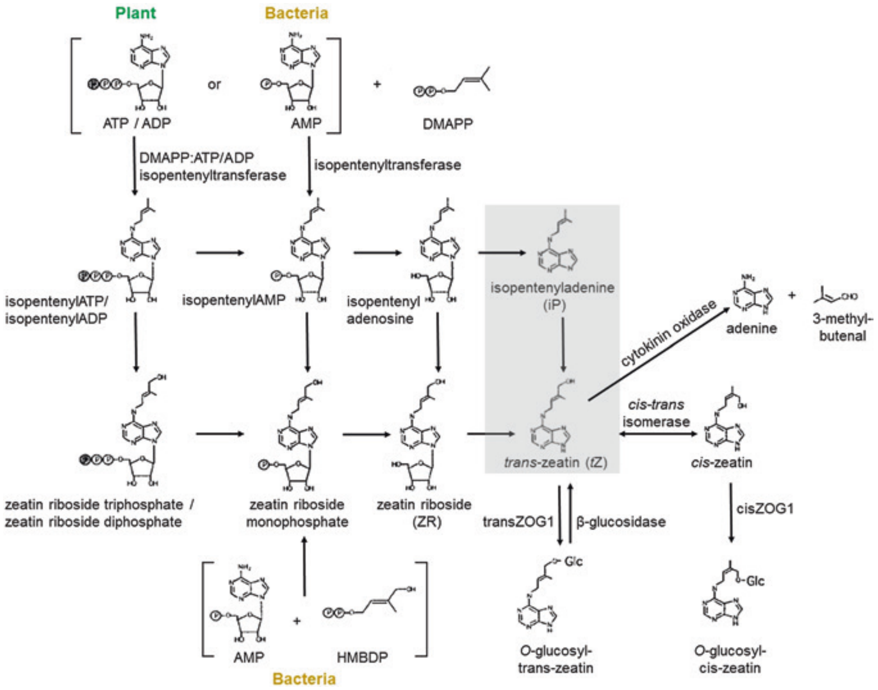


Fig. 3 A model for cytokinins biosynthesis and metabolic pathway in plants and bacteria. In plants, the isopentenyl moiety from dimethylallyl diphosphate (DMAPP) is transferred to ATP/ADP while the bacterial pathways start off with AMP. Bacteria cytokinin biosynthesis may also start by transferring isopentenyl moiety from 1-hydroxy-2-methyl-2-(E)-butenyl 4-diphosphate (HMBDP) to AMP. Active cytokinins are shaded (adapted from: Haberer and Kieber (2002), Kakimoto (2003), Sakakibara (2006), Tarkowski et al. (2009) and Frébort et al. (2011))

The biological concentrations of these phytohormones are closely regulated by the rates of biosynthesis, metabolism, inactivation and degradation with homeostasis under the influence of both internal and external factors (Sakakibara 2006). Any exchange or interconversion of cytokinins between plants and its various external components can potentially influence and even disrupt cytokinin homeostasis in the plant and alter its growth pattern as low concentrations of cytokinins are needed to elicit a physiological response (Letham and Palni 1983; Stirk and Van Staden 2010).

Role of Cytokinins in Plant Growth

Cytokinins are crucial for activating cell division and to regulate plant growth from the cellular level through to the tissue, organ and whole plant level (Letham and Palni 1983; Francis and Sorrell 2001; Schmülling 2002; Sakakibara 2006).

On the cellular level, cytokinins upregulate plant d-type cyclin (CycD3) at the G1 checkpoint and the phosphoregulation of the CDK at the G2/M checkpoint, thereby inducing a continuum of cell cycle activation that leads to plant growth (Francis and Sorrell 2001). The main cytokinin driver of the cell cycle is zeatin, which peaks its concentrations at the end of S phase, during the G2/M phase transition and in the late G1 phase.

Developmental processes such as formation of embryo vasculature, nutritional signaling, leaf expansion, branching, chlorophyll production, root growth, promotion of seed germination and delay of senescence are also heavily influenced by cytokinins (Letham and Palni 1983; Mok 1994; Schmülling 2002; Howell et al. 2003). The initiation and outgrowth of axillary buds, released from shoot apical dominance, were reported to be well correlated with the cytokinins levels (Turnbull et al. 1997; Bangerth et al. 2000; Shimizu-Sato and Mori 2001; Yong et al. 2014). It has been known that plants with reduced endogenous cytokinins have distinct morphological and developmental alterations such as shorter shoot internodes, delayed flowering, fewer flowers and reduced leaf surface area with smaller vasculature, smaller shoot apical meristems with reduced cell division, enhanced root growth and a larger root meristem (Schmülling 2002). Thus, any change in the levels of endogenous cytokinins could alter the regulation of the above-mentioned physiological processes and result in the disruption of normal plant growth (Letham and Palni 1983; Schmülling 2002). However, it is also important to note that different classes of phytohormones interact in a synergistic way for regulation of physiological processes and optimum plant growth. The roles of these phytohormones will be discussed in their respective sections.

Cytokinins have been reported to function as local and long-range chemical signals in plants. They are transported via the xylem and phloem (Hwang and Sakakibara 2006) and the transpiration stream from the root tips to aerial plant parts (Yong et al. 2000; Schmülling 2002; Stirk and Van Staden 2010; Yong et al. 2014). Studies conducted by Ma et al. (2002) showed that cytokinins synthesized in the embryo function as local signal for increased meristematic activity. Reallocation of nutrients, minerals and nonmetabolizable substances are also initiated with an increase in cytokinins concentrations in leaves (Leopold and Kawase 1964; Gersani and Kende 1982; Mauk and Noodén 1992), a phenomenon termed as cytokinin-induced nutrient mobilization. It has also been suggested by Frugier et al. (2008) that cytokinins may function as the central signal for controlling lateral organ differentiation. Their study revealed that a local increase in cytokinin concentrations within the roots induces nodule organogenesis while repressing lateral root formation (Fig. 4). Cytokinins functioning as long-range biochemical signals help to coordinate root–shoot development (Schmülling 2002; Stirk and Van Staden 2010), communicate root biotic interactions (e.g. with *Rhizobium*, Yong et al. 2014) and environmental stresses such as nutritional status, low temperatures, salinity and drought to the shoots (Goicoechea et al. 1996; Yong et al. 2000; Emery and Atkins 2002; Schmülling 2002), a phenomenon termed as root-to-shoot signaling.

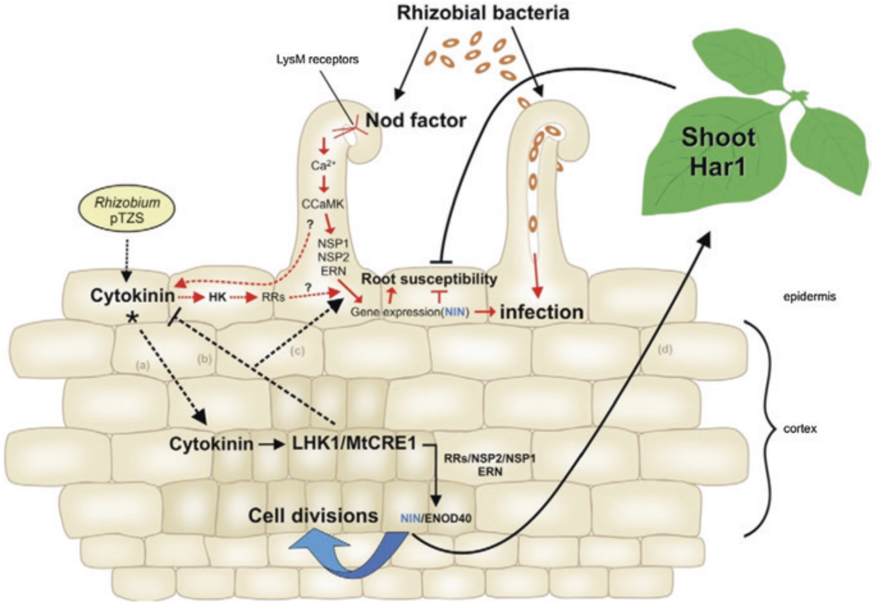


Fig. 4 Proposed role of cytokinin in nodulation and infection events. **a** Nod factor perception by lysin motif (LysM)-containing receptors elicits calcium signaling through a calcium- and calmodulin-dependent kinase (CCaMK). This in turn leads to localized biosynthesis and/or activation of cytokinin signaling by an as yet unknown mechanism. Part of this signaling cascade can be bypassed by bacterially produced cytokinins (*Rhizobium* pTZS) or cytokinin-like molecules, enabling Nod factor-independent nodulation. Epidermally produced cytokinin might be translocated to the cortex by diffusion and/or by selective transport from cell to cell. Alternatively, an intermediate messenger (*) might travel to the cortex to elicit de novo localized cytokinin signaling. **b** Cytokinin perception by LHK1 or ortholog MtCRE1, and signaling through cytokinin response regulators (RRs) leads to initiation of nodule organogenesis (cell divisions). This requires transcription factors such as NSP1, NSP2 and ERN, as well as downstream functions, such as NIN and ENOD40. In the epidermis, NIN is required for infection thread formation but also negatively regulates root susceptibility to rhizobial signaling. Hypothetically, cytokinin might participate in this process by signaling through an unknown histidine kinase receptor(s) (HK). In this scenario, cytokinin signaling contributes to, but is not fully responsible for, reprogramming of gene expression, possibly by regulating the activity and/or localization of transcriptional factors, such as NSP2, which is known to relocate from the nuclear envelope to the nucleus upon Nod factor signaling. Cytokinin might also be involved in both local and systemic feedback regulation of infection. In *Lotus*, LHK1 is not required for initiation and progression of infection events, but it participates in negative regulation of root susceptibility to infection. **c** In *M. truncatula*, both nodule inception and infection thread progression, but not initiation, are tightly linked to MtCRE1 function. **d** Cytokinin might also participate in systemic autoregulatory feedback mechanisms, possibly involving HAR1, to restrict nodule number (reprinted from Trends in Plant Science, 13, F. Frugier, S. Kosuta, J.D. Murray, M. Crespi, K. Szczyglowski, Cytokinin: secret agent of symbiosis, 115–120, Copyright (2008), with permission from Elsevier)

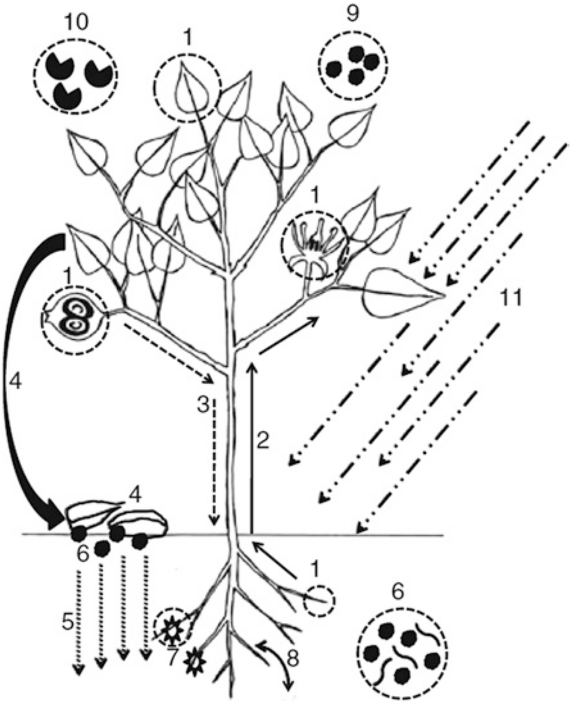


Fig. 5 Diagrammatic scheme showing the movement of cytokinins through the environment. *Dotted circles* indicate sites of cytokinins biosynthesis. *1* sites of cytokinin biosynthesis in vascular plants including roots, flowers and fruits; *2* cytokinin translocation via the xylem from the roots; *3* cytokinin translocation via the phloem from aerial plant organs; *4* cytokinins derived from degradation of leaf litter; *5* movement of cytokinins through the soil due to rainwater and irrigation; *6* free-living microorganisms (bacteria, fungi, Cyanophyta and Chlorophyta) in the rhizosphere; *7* microorganisms, including nematodes in a symbiotic relationship (either beneficial or parasitic) with the host plant's roots; *8* cytokinins released into the soil by root exudates and cytokinin uptake by the roots; *9* air-borne microorganisms (bacteria and fungi) in a parasitic relationship with the host plant; *10* insects infecting the host plant to form galls; *11* agricultural input including irrigation with water that contains cytokinins and application of natural (e.g. seaweed concentrates) and synthetic cytokinins for crop improvement (reprinted from Plant Growth Regulation, 62, 2010, 101–116, Flow of cytokinins through the environment, W.A. Stirk and J. Van Staden, Fig. 1, with kind permission from Springer Science and Business Media)

Flow of Cytokinins Through the Environment

Cytokinins are widely distributed throughout the plant kingdom (Stirk and Van Staden 2010), and are widely available and highly fluid within the environment (Fig. 5). In the following section, we will discuss the various plant-related sources of cytokinins and their distribution in the environment.

Sources of Cytokinins

Cytokinins can be derived from various sources and the most prominent source would be from plants as they are called phytohormones. Cytokinins have been known to be released directly into the soil from plant roots (Van Staden 1976). Studies conducted by Arthur et al. (2001) showed that tomato seedlings metabolize the cytokinins taken up from their external environment before releasing them back to the external environment. Plant parts, such as cotyledons, flowers and leaf litter, are also sources of cytokinins (Letham and Palni 1983; Stirk and Van Staden 2010). Hence, root exudates and any plant parts that contain cytokinins are potential sources that may contribute to the pool of cytokinins available in the environment for the uptake by other plants.

Microalgae of both prokaryotic and eukaryotic nature, namely Cyanophyta and Chlorophyta, respectively, are also natural sources of cytokinins. Ördög et al. (2004), Stirk et al. (2003, 2009) and Burkiewicz (1987) have detected cytokinins and cytokinins-like activity in isolated microalgae samples. Stirk et al. (1999) had successfully proven the presence of cytokinins, specifically iP, in microalgae with the use of GC-MS. Also, studies on *Chlorella* had expressed highest biosynthetic rates for iPR, iP and cZ in samples harvested 8 h into the light period compared to samples harvested 8 h into the dark period (Stirk et al. 2011). These studies indicated that microalgae are capable of synthesizing cytokinins which might be released into the soil during cell decomposition, thereby further contributing to the pool of cytokinins available for plant uptake (Stirk and Van Staden 2010).

To date, various studies have proven that certain bacteria are important sources of cytokinins (Philip and Torrey 1972; Upadhyaya et al. 1991; Arkhipova et al. 2005; Kudoyarova et al. 2014) and harbor the potential for the discovery and extractions of cytokinins from nature for plant industry applications. Interestingly, there are novel cytokinins that are yet to be discovered and characterized from these microbial sources. Genetic studies have successfully identified biosynthetic gene responsible for the expression of cytokinins in various bacteria (Powell and Morris 1986; Crespi et al. 1992; Binns 1994; for a review, see Taylor et al. 2003). It has also been reported that bacteria enhance or promote plant cytokinin production. *Agrobacterium tumefaciens*, which induces crown galls in plants, was reported to be capable of transferring and integrating part of their Ti-plasmid DNA into the host plants' genome (Sakakibara et al. 2005). The integrated bacterial genome which encodes an enzyme, adenosine phosphate-isopentenyltransferase, confers the host plant with the ability to synthesize cytokinin via an alternative biosynthesis pathway leading to increased plant cytokinin production. Unlike plants, bacteria produce iP-type cytokinins. These iP-type cytokinins could be taken up by plants, gets converted to Z (Mok and Mok 2001) and subsequently to ZR. ZR is then transported within the xylem to target sites where it gets cleaved into the bioactive form (Z) to drive growth (active cell cycle) using NPK (raw materials) to achieve optimal growth. Studies conducted by Ueda et al. (2012), however, proved that *A. tumefaciens* was capable of efficient biosynthesis of *t*Z during tumor formation in infected galls. Thus, there is a possibility that other bacteria capable of synthesizing zeatin-type cytokinins remains to be discovered.

Apart from bacteria, other studies have also detected cytokinins production in various mycorrhizal fungi. Crafts and Miller (1974) had successfully obtained crystalized Z and ZR from the media in which *Rhizopogon roseolus* (Corda) Hollos, a fungus, had been cultured; presenting definite evidence for the production of cytokinins by the various mycorrhizal fungi screened. Studies conducted by Barea and Azcón-Aguilar (1982), Ng et al. (1982) and Kraigher et al. (1991) had also successfully detected substances with cytokinin-like activity and cytokinins in growth cultures of the various mycorrhizal fungi screened. Thus, it is possible that many cytokinin-producing fungi are contributing to the pool of cytokinins in the environment and these fungal species have yet to be identified.

Parasitic nematodes, root-knot nematodes (*Meloidogyne* species) and cyst nematodes (*Heterodera* species), the common cause of gall and cyst formation in plant roots (Stirk and Van Staden 2010) are known to be capable of exuding cytokinin-like substances (Bird and Loveys 1980). De Meutter et al. (2003) had detected the presence of cytokinins, specifically BA, iP and Z, from in vitro grown nematode exudates or lysates in concentrations high enough to be biologically active. The secretion of cytokinins together with host plant cytokinins had been reported to trigger a change in the nematodes' surface lipophilicity (Akhkha et al. 2002), which might be an infection strategy against the host plant's defense responses. It is also likely that the cytokinins help to establish and/or maintain the feeding cells as a nutrient sink (De Meutter et al. 2003) as roots with overexpressed cytokinins oxidase have reduced gall formation (Lohar et al. 2004).

Similar to nematodes, insect larvae had been reported to synthesize and secrete cytokinins into the plant tissues (Mapes and Davies 2001). Results from the experiments conducted by Van Staden and Bennett (1991) and McDermott et al. (1996) revealed an elevation in cytokinin concentrations in plant tissues that were infected with insect larvae compared to healthy tissue. Elevated concentration of up to 53 times was recorded in the cytokinin profile comparison between the insect larvae with the gall structure and the plant stem tissue. This observation suggested that the insect larvae are capable of synthesizing and secreting their own cytokinins (Mapes and Davies 2001).

Although the roles of cytokinins exuded by nematode and insect larvae are unclear, it is likely that high concentrations of cytokinins are secreted in the gall so that the feeding site remains as an active nutrient sink (Stirk and Van Staden 2010) as elevated concentration of cytokinins may function as local signal for the reallocation of nutrients and photoassimilates; similar to the cytokinin-induced nutrient mobilization phenomenon observed in plants. Thus, both nematodes and insect larvae are also potential sources of cytokinins which could contribute to the environmental cytokinins pool as exudates or lysates.

3.2.2 Auxins

Apart from cytokinins, auxins are another important class of phytohormones that play crucial roles in regulating various plant growth processes (for a review, see Zhao 2010). Auxins are synthesized at the root (Pacifici et al. 2015), in the shoot apex and young expanding leaves (Al-Babili and Bouwmeester 2015). From the site of biosynthesis, auxins are transported basipetally via auxin transporters, which in turn create an auxin gradient across the plant (Al-Babili and Bouwmeester 2015). Peaks of auxin concentration and gradient then act as positional information for auxin activity and maintenance of correct cell division, polarity and fates at the root apex (Sabatini et al. 1999; Al-Babili and Bouwmeester 2015). Auxins also regulate the synthesis of other hormones such as strigolactones (Al-Babili and Bouwmeester 2015), trigger organ primordia initiation and play a role in the initiation and maintenance of the organ founder cell populations (Wolters and Jürgens 2009).

At the cellular level, auxins induce the expression of CycD3 and CDKs, both play crucial roles governing the various checkpoints of the cell cycle, especially in the transition of G1/S phase (Wang and Ruan 2013). Auxin signaling is also required in the later phase of G2/M transition to complete the mitosis process (Wang and Ruan 2013). The mechanisms on how auxins are involved in the initiation of the various cell cycle stages have been reviewed by Wang and Ruan (2013).

Auxins are known to inhibit axillary bud growth, however, the mechanisms of axillary bud outgrowth are dependent on the ratio of cytokinins to auxin rather than the absolute concentration levels of either hormone (Shimizu-Sato and Mori 2001). Direct application of auxin to axillary buds, however, cannot prevent bud growth (Shimizu-Sato and Mori 2001). Apart from regulating axillary bud growth, cytokinin to auxin ratios also determine the development of roots and shoots. A balanced ratio of the two hormones keep the cells in undifferentiated state, while low cytokinin to auxin ratios promote root development and high ratios promote shoot development (Haberer and Kieber 2002). Apart from interacting with cytokinins, interactions between auxins and other phytohormones have been reported as well. Examples include interaction with ABA to regulate root growth (Zhao et al. 2015), with sugar for cell division and expansion regulation (Wang and Ruan 2013) and with brassinosteroids to regulate differential growth (Zhou et al. 2013).

Like cytokinins, auxins can be found in various fertilizer sources and these included vermicomposts (Zhang et al. 2015) and humic acids (Canellas et al. 2002). Hayat et al. (2010) provided a useful listing of bacteria (*Azospirillum*, *Azobacter*, *Bacillus*, *Kluyvera*, *Paenibacillus*, *Pseudomonas*, *Rhizobacteria*, *Rhizobium*) that produce auxins although not all the research described in the review paper provided unequivocal evidence for the occurrence of auxins using mass spectrometery. Interestingly, Patten and Glick (2002) provided scientific evidence for a direct role of auxins produced by *Pseudomonas putida* in regulating mung bean root development.

4 Non-hormonal Plant Growth Promoters (Humic Substances)

Humic substances are the major components of natural organic matter found in soil, water and organic deposits such as sediments, peats, coals, leaf litters and composts (for reviews, see Piccolo et al. 1992; Piccolo 2002; International Humic

Substances Society 2007). The bioactive components of humic substances are humic acid and fulvic acid. Fulvic acid is essentially a polymerized humic acid and thus this section will focus on humic substances in general as both humic acid and fulvic acid share similar if not the same chemical characteristics. Both humic and fulvic acids are available commercially in the forms of pellets.

Studies have often shown positive effects of humic substances on seed germination, root initiation and total plant biomass (Rauthan and Schnitzer 1981; Chen et al. 2004). This is achieved via their ability to improve soil structure and their hormone-like activity on plants (Piccolo et al. 1992; Atiyeh et al. 2002). In plants, humic acids are involved in cell respiration, oxidative phosphorylation, protein synthesis, photosynthesis and various enzymatic reactions (Atiyeh et al. 2002) by improving iron, and possibly zinc nutrition (Chen et al. 2004). At the roots, humic acids enhance root initiation, root hair proliferation and mineral nutrient uptake by increasing the permeability of membranes of the root cells (Atiyeh et al. 2002).

Piccolo (2002) stated that the beneficial effects which humic substances have on the physical properties of soil and their role in the soil environment are significantly greater than that attributed to their contributions to sustaining plant growth, and have provided a comprehensive review on how humic substances contribute to the soil properties and environment. Piccolo's review (2002) provided insights that the hydrophobic nature of humic components protects compounds that are easily degradable and enhance their persistence in soil. This contributes to the accumulation of organic matter which harbors beneficial effects on the rhizosphere and plant growth. Review by Bronick and Lal (2005) also corroborated this view that humic acids help improve the soil condition by increasing the aggregate stability of the soil structure which results in better plant growth and higher yield. Furthermore, humic acid, being a weak acid, could function as a buffer that keeps the soil at the optimal pH for both plant and microbial growth.

5 Biofertilizers

With the ever growing concerns in environmental-related issues and increasing efforts to promote more environmentally friendly farming practices in conventional farms and plantations, the usage of biofertilizers is gaining global acceptance. Unlike conventional chemically synthesized fertilizers that contain N, P and K, biofertilizers are biomass-based structural matrix (e.g. compost, humic acid, etc.) that contain live or latent cells of microorganisms that have the ability to augment nutrients for plant assimilation through microbial processes such as atmospheric nitrogen fixation, phosphate solubilization, cellulolytic degradation and production of phytohormones (Vessey 2003; Van Loon 2007; Lugtenberg and Kamilova 2009; Mishra et al. 2013; Ahemad and Kibret 2014; Owen et al. 2014). It has been reported that the application of biofertilizers to the seeds and the soil, has helped to increase nutrient availability for plant uptake, increased and/or improved plant growth parameters and increased crop yield up to 10–20 %

without any adverse effect on the environment (Bhattacharjee and Dey 2014). Thus, biofertilizers are plausible means to tap onto the natural nutrient cycle without posing any threat on the environment.

The use of biofertilizers in our modern farming practice should be encouraged so as to reduce the adverse effects of long-term chemical fertilizers usage. There is currently a wide range of biofertilizers available commercially (please refer to Table 2 for the mode of action of the various types of biofertilizers and their known microorganisms) and we will focus our discussion on PGPR and vermicomposts.

5.1 Plant Growth Promoting Rhizobacteria (PGPR)

PGPR are bacteria found within the rhizosphere and have the ability to promote plant growth (for reviews, see Kloepper et al. 1989; Vessey 2003; Hayat et al. 2010; Ahemad and Kibret 2014) via various mechanisms such as nitrogen fixation, phosphorus and zinc solubilization, which help to enhance the availability of plant nutrients for absorption (Çakmakçi et al. 2006; Mahdi et al. 2010). The use of PGPR has been reported to increase plant uptake of nitrogen from fertilizer (Adesemoye et al. 2010), and aid to sustain soil productivity and environmental health by reducing dependence on chemical fertilizers (Shaviv and Mikkelsen 1993). PGPR are also referred to as biocontrol agents due to their ability to reduce the incidence or severity of plant diseases (Beattie 2006). Applications of PGPR have been investigated in various plants and crops such as maize, wheat, oat, barley, peas, canola, soy, potatoes, tomatoes, lentils, radicchio, cucumber and chickpea (Gray and Smith 2005; Gopalakrishnan et al. 2015).

While some would consider bacteria localized on the epidermis of plant leaves to be PGPR (Maksimov et al. 2011), we consider PGPR to be the bacteria found within the rhizosphere, free-living or in association with plant roots. However, most PGPR are bacteria that form close association with the plants on the root surface (rhizoplane) or penetrate into the radicular tissues of the root. Most bacterial growth usually occurs at the junctions between epidermal cells and areas where side roots appear (Lugtenberg and Kamilova 2009). Some researchers speculated that PGPR must colonize the root surface efficiently, compete well against other microbes present within the same rhizosphere for nutrients secreted by the root and for sites that can be occupied on the root before being able to exert beneficial effects on the plants (Lugtenberg and Kamilova 2009).

In general, PGPR can affect plant growth in two different ways, directly or indirectly. Direct effects include the various positive influences that PGPR have on plant growth which occur in the absence of pathogens (Lugtenberg and Kamilova 2009). Minimizing or preventing deleterious effects of plant pathogenic organisms via production of antagonistic substances or induction of plant resistance against pathogens is referred to as indirect effects (Glick 1995). It is difficult to classify the effects of PGPR on plant growth into the two distinct groups as a direct effect

Table 2 Different types of biofertilizers and the known microorganisms

Biofertilizer	Mode of action	Microorganism	References
Symbiotic nitrogen fixers	Fix nitrogen only after colonizing host plants' roots	*Rhizobium* spp., *Azospirillum* spp	Steenhoudt and Vanderleyden (2000), Vessey (2003), Lugtenberg and Kamilova (2009), Mehboob et al. (2009), Mishra et al. (2013), Sivasakthivelan and Saranraj (2013)
Nonsymbiotic nitrogen fixer	Fix nitrogen without any symbiotic associations with plants	Cyanobacteria, *Azotobacter*	Johnstone (1967), Obreht et al. (1993), Zachmann and Molina (1993), Stirk et al. (1999), Mishra et al. (2013), Ahemad and Kibret (2014)
Phosphate solubilizers	Convert insoluble organic and inorganic bound phosphates into available forms for plant uptake and utilization	*Pseudomonas fluorescens*, *Thiobacillus* spp., *Aspergillus niger*, *Trichoderma* spp., *Paecilomyce* spp, *Bacillus* spp., *Rhizobium* spp., *Burkholderia* spp., *Achromobacter* spp., *Agrobacterium* spp., *Micrococcus* spp., *Aereobacter* spp., *Flavobacterium* spp. and *Erwinia* spp.	Handelsman and Stabb (1996), Vassilev et al. (2006), Berendsen et al. (2012), Mishra et al. (2013), Bhattacharjee and Dey (2014)
	May synthesize and release pathogen-suppressing metabolites (siderophores), phytohormones (IAA) and lytic enzymes		
Phosphate mobilizers	Form symbiotic associations with the plants at the roots and enhance uptake of phosphorous and other nutrients	Fungi	Torelli et al. (2000), Mishra et al. (2013)

(continued)

Table 2 (continued)

Biofertilizer	Mode of action	Microorganism	References
Zinc solubilizer	Convert zinc in the soil into suitable form for plant uptake and utilization	*Pseudomonas* spp., *Bacillus* spp., *Rhizobium* spp.	Mishra et al. (2013)
		Bacillus subtilis, *Thiobacillus thioxidans* and *Saccharomyces* sp.	
Plant growth promoting rhizobacteria (PGPR)	Fix nitrogen, solubilize phosphorus and zinc and enhance availability and uptake of plant nutrients	*Bacillus* spp., *Pseudomonas* spp., *Azospirillum* spp.	Phillips and Torrey (1972), Kloepper et al. (1989), Upadhyaya et al. (1991), Döbereiner (1992), Glick (1995), Glick and Bashan (1997), Okon et al. (1998), Ryu et al. (2003), Vessey (2003), Kravchenko et al. (2004), Gray and Smith (2005), Beattie (2006), Çakmakçi et al. (2006), Crowley (2006), Glick et al. (2007), Van Loon (2007), Lugtenberg and Kamilova (2009), Adesemoye et al. (2010), Hayat et al. (2010), Mahdi et al. (2010), Maksimov et al. (2011), Ahemad and Kibret (2014), Talaat et al. (2015)
	Confer biocontrol against plant diseases. Secrete bacterial phytohormones, e.g. cytokinins		
	Release volatiles and cofactor pyrrolquinoline quinone (PQQ) that stimulate plant growth		
	Reduce stress response in plants		
	Produce siderophores that help enhance plant iron uptake and remediate soil pollutants		

Adapted from Vessey (2003), Hayat et al. (2010), Mishra et al. (2013), Bhattacharjee and Dey (2014) might lead to an indirect influence. For example, production of phytohormones helps to enhance growth (direct effect) but may also induce disease resistance (indirect effect). Thus, our review will not classify the resultant effects into direct or indirect groups.

PGPR share similar functions with the other groups of biofertilizers. The common functions include converting atmospheric nitrogen (Döbereiner 1992) and facilitating the uptake of nutrients such as phosphorus and zinc via solubilizing inaccessible forms trapped in insoluble compounds. Unlike the other groups of biofertilizers that mainly exert one type of positive effect, PGPR enhance plant growth in many more ways. One of the most prominent enhancements is the secretion of bacterial phytohormones (Glick 1995), specifically cytokinins (Philip and Torrey 1972; Upadhyaya et al. 1991), which promotes plant growth. The phytohormones, specifically auxins which the bacteria synthesize using the tryptophan present in root exudates (Kravchenko et al. 2004), also promote better root system formation, thereby enhancing water and nutrient absorption (Patten and Glick 2002). These in turn help the plants to pass through the pathogen-sensitive early development stage more rapidly (Maksimov et al. 2011). This characteristic is especially important as studies with added inorganic nitrogen (to increase nitrogen fixation) suggested that plant growth promotion is caused by the production of plant growth factors such as phytohormones rather than nitrogen fixation (Okon et al. 1998).

Apart from providing the plants with phytohormones, PGPR are also known to stimulate plant growth by releasing volatiles and cofactor pyrrolquinoline quinone (PQQ) (Ryu et al. 2003; Lugtenberg and Kamilova 2009). Volatiles are reported to increase photosynthetic efficiency and chlorophyll content in *Arabidopsis thaliana* through the modulation of endogenous signaling of glucose and abscisic acid sensing (Zhang et al. 2008). PQQ on the other hand functions as antioxidants and cofactor of enzymes involved in antifungal activity and induction of systemic resistance (Lugtenberg and Kamilova 2009; Choi et al. 2008).

Other major substances known to be synthesized by PGPR and are beneficial to the plants include antibiotics, siderophores and hydrolytic enzymes. PGPR antibiotics are oligopeptides that inhibit cell wall synthesis in pathogens at the cell wall synthesis initiation stage. The antibiotics disrupt the functions of ribosomes and inhibit the formation of initiation complex on small subunit of ribosomes (Maksimov et al. 2011). PGPR antibiotics are said to be effective against Gram-positive and Gram-negative bacteria and pathogenic fungi (Maksimov et al. 2011).

Microbial siderophores synthesis by PGPR is induced by low ferric ion level in the environment. Siderophores have high affinity to ferric ions and have the ability to solubilize and extract ferric ions from mineral or organic complexes (Wandersman and Delepelaire 2004). Thus, this increases the pool of iron available for plant assimilation. It was reported that microbial siderophores help to enhance iron uptake by plants that are able to recognize the bacterial ferric-siderophore complex (Masalha et al. 2000; Katiyar and Goel 2004; Dimkpa et al. 2009). Iron uptake by plants in the presence of other metals such as nickel and cadmium is also enhanced by siderophores (Burd et al. 1998; Dimkpa et al. 2008). By enhancing plant iron uptake, pathogens are deprived of the iron that is much needed for their growth and development and thus reducing the occurrence of plant diseases (Maksimov et al. 2011). Calcium assimilation by plants is also enhanced by siderophores.

The production of bacterial hydrolytic enzymes, e.g. chitinases, glucanases, proteases, lipases, that lyse fungal cells, volatile compounds and their toxins are also ways which PGPR help reduce and/or prevent pathogenic diseases (Neeraja et al. 2010; Maksimov et al. 2011) and suppress nematode populations within the rhizosphere (Youssef and Eissa 2014).

PGPR also help facilitate plant growth and development by reducing the stress response within plants via decreased ethylene levels. Ethylene precursor 1-aminocyclopropane-1-carboxylate (ACC) is converted into 2-oxobutanoate and ammonia by bacterial ACC deaminase (Glick et al. 2007), relieving the inhibition of root growth (Van Loon 2007) while rendering the plants to be more resistant against stress due to heavy metals (Ca^{2+} and Ni^{2+}), salt, draught and phytopathogenic bacteria (Glick and Bashan 1997; Lugtenberg and Kamilova 2009; Van Loon 2007). Studies by Talaat et al. (2015) also provide concrete evidence on the application of suitable microorganisms to help the plants gain tolerance against salinity stress via alteration of nutrient acquisition and accumulation of compatible solutes.

It is also noteworthy that PGPR play the role of rhizoremediator by degrading soil pollutants (Lugtenberg and Kamilova 2009). Siderophores produced by PGPR are able to aid in the bioremediation of soil pollutants (Crowley 2006) by isolating and degrading heavy metals and toxic organic matters such as metabolites of pathogenic origins (Maksimov et al. 2011) reducing the occurrence of contaminated crops that may pose adverse effects when consumed. Cleaner soil also allows more microorganisms and organisms (such as earthworms) to flourish, conferring beneficial effects on the plants.

Another way that plants benefit from the association with PGPR is the activation of defense mechanism—induced systemic resistance (ISR) against pathogens (Van Loon et al. 1998). Exudates produced by PGPR are able to stimulate ISR by activating components such as lipoxygenases, lipid peroxidases and reactive oxygen species (Maksimov et al. 2011) conferring protection against diseases caused by different organisms (Lugtenberg and Kamilova 2009) by reducing the rate of disease development in terms of severity or number of diseased plants (Van Loon 2007). ISR activation is dependent on jasmonic acid and ethylene signaling (Van Loon 2007). Systemic acquired resistance (SAR) which also enhances resistance against diseases is, however, induced by pathogens and dependent on salicylic acid (SA) signaling (Van Loon 2007). It is important to note that PGPR that elicit ISR in one plant species may not do so in another due to interaction specificity between rhizobacteria and plants (Van Loon 2007).

5.2 Vermicomposts

Another form of biofertilizer that is gaining widespread acceptance globally is vermicompost and vermicompost tea, a leachate of the vermicompost. Vermicompost is the highly valued compost produced by earthworms (for a review, see Edwards et al. 2010). Vermicomposting not only helps to reduce organic wastes in volume, but also turning them into humus-like substance that is finer than compost and generally contains high concentration of mineral matter. This makes vermicompost a very good fertilizer that is up to 70 times more efficient than conventional manure (Červená et al. 2013). The earthworm activity also stimulates and increases the diversity of microbial activity. Typically vermicompost is applied at low concentration to the plant growth medium or as soil drench or foliar spray.

Vermicomposts have been reported to have beneficial effects on plant growth such as improved seed germination, enhanced seedling growth and development, and increased plant productivity (Atiyeh et al. 2002; for a review, see Edwards et al. 2010). It enhances plant growth by improving the physical structure and moisture retention capacity of the soils (Arancon et al. 2004) while supplying the plants with N in stable form (Chaoui et al. 2003) and phytohormones or phytohormone-like compounds produced by the microorganisms present within.

Our group has been actively characterizing the phytohormones in vermicomposts and their leachate (vermicompost tea). Recently, a new method has been successfully established by our group for the analysis of phytohormones present within vermicompost (Zhang et al. 2015) and quantitative evidence of the various growth regulating factors, such as phytohormones, i.e. cytokinins, auxins, gibberellins and brassinosteroids, present in vermicompost tea and leachate have been provided by Zhang et al. (2014) and Aremu et al. (2015). Hopefully, the phytohormone screening approach developed for vermicomposts can be extended to all types of organic fertilizers. Aremu et al. (2015) have also provided insightful discussion on the importance of different phytohormones on their roles in regulating plant growth and development. Results from these studies indicated that vermicomposts harbor a rich diversity of plant growth promoting factors, specifically phytohormones. The origins of these "subterranean" phytohormones are likely to be linked to the symbiotic microbes living in the gut of the earthworms. There is also a possibility that vermicomposts may contain other factors that are beneficial for the plants that have yet to be detected. The beneficial effects of vermicomposts can also be attributed to the presence of humic acids or growth regulators associated with humic acids as demonstrated by Arancon et al. (2004) and Canellas et al. (2002).

Synergistic relationship between vermicompost and PGPR had been reported to improve plant growth, reduce plant mortality and increase microbial biomass (Sahni et al. 2008; Song et al. 2015). This could be due to the reason that vermicompost contains humus which allows PGPR to thrive well and multiply in population. Thus, farming practice can turn to a new biofertilization regime which utilizes both the vermicomposts and PGPR to reap the full synergistic benefits of these natural resources that are beneficial for the plants and to maintain good soil and environmental health.

6 How Biofertilizers Work in Tandem with Microorganisms and Phytohormones to Influence Plant Growth?

An extensive review of published literature (Gharib et al. 2008; Datta et al. 2009; Edwards et al. 2010; Hayat et al. 2010; Mahdi et al. 2010; Shafi et al. 2012; Ahemad and Kibret 2014; Bhattacharjee and Dey 2014; Qin et al. 2015; Sarma et al. 2015; Song et al. 2015) and our extensive field observations have shown that organic fertilizers, despite having low NPK value, can sometimes produce the same growth promoting effect and/or achieving comparable yields, when compared to plants grown using conventional chemical fertilizers with high NPK ratios (e.g. 10–21) (for reviews, see Shaviv and Mikkelsen 1993; Chen 2006). Hence, there must be some growth-promoting factors present in organic fertilizers and these positive factors are certainly not the NPK mineral nutrients per se, that are driving plant growth and development. These salient and positive growth enhancement observations had been noted by many farmers/growers in the plant industry and a plausible scientific explanation remains elusive. In this review, we provided scientific evidence that the growth promoting factors in biofertilizers modulating plant growth and development are phytohormones, and that the known biological functions of phytohormones are in tandem with the observed physiological characteristics and crop yield (Fig. 6).

At the whole plant level and in relation to the plant–soil continuum, the interactions between the whole plant and the microorganisms present in the soil can be best illustrated by Fig. 7. The soil and the entire subterranean root system form a diverse and intimate association of “biological networks and entities” comprising of plant roots, microbes (bacteria, fungi) and many very small organisms (nematodes, earthworms, etc.). Amidst the complex array of biological networks and entities is the soil matrix and water medium where multitudes of biological activities (e.g. microbial biochemical activities like enzyme production, plant exudations [allelopathic] and uptake, ingestion by earthworms, etc.) and interactions are taking place. It is therefore conceivable that the soil matrix and water medium contain many naturally produced substances, biological metabolites and these include the phytohormones and their precursors (see Sect. 5). From a holistic perspective, one may view the entire plant subterranean root system as a “receiver” of the multitudes of biochemical signals and this information allows the plants to “sense” the prevailing soil conditions for water, nutrient and phytohormone availability. The selected biochemical signals are “received” at the root tips, “assimilated” and sent to the various plant parts. These signals induce most responses at the actively growing areas within the plants. The actively growing areas within any plant are the plant meristems found mainly in the aboveground shoot system: shoot apices, axillary buds, flower buds and the root tips (belowground). The growth rates of these meristems are governed by the various phytohormonal chemical signals arriving there, from the roots. Most of these phytohormonal chemical signals have their origins in the subterranean soil and they normally travel with the

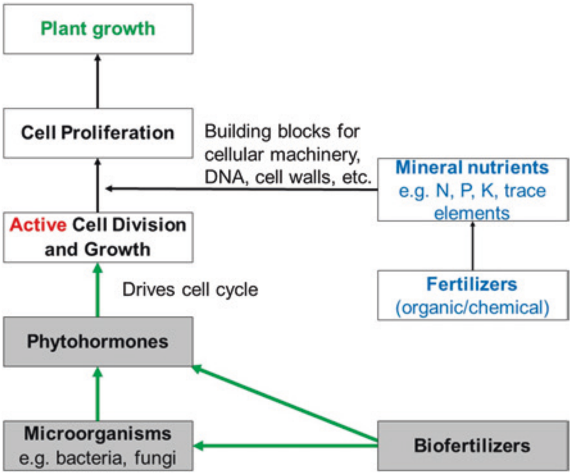


Fig. 6 The contribution of chemical, organic and biofertilizers to plant growth and development through cell proliferation. Chemical and organic fertilizers provide nutrients, e.g. N, P, K, that are essential for the basic cellular structural machinery and the biosynthesis of DNA, enzymes, cells walls, etc. These processes are active when the meristematic cells are dividing, i.e. cell undergoes the entire cell cycle process, and new cells are produced. Under normal conditions, plants grow at fairly predictable pace due in part to cell cycle regulation governed predominantly by the availability of resources (mineral nutrients, water), suitable environmental conditions (adequate sunlight, optimal temperature) and phytohormones. Thus, the addition of mineral nutrients via chemical fertilization will not necessarily increase the rate of plant growth per se, when there are other limitations imposed on the plant. The application of biofertilizers supplies the plants with phytohormones (in addition to those synthesized endogenously by the plants) that help the plant meristems to overcome the various cell cycle checkpoints' "restrictions" and to facilitate active cell proliferation. The calibrated and integrated usage of different fertilizers (both chemical and organic) to supply the plants with ample nutrients for their cellular structural needs and appropriate phytohormonal signals to proceed through cell cycle checkpoints will eventually lead to active plant growth

transpirational water flow through the xylem and onto many plant parts. Closer to the meristems where there may not be any functional conduits leading from the main transport tubes to the meristems, these chemical signals may travel via the phloem and/or through cell-to-cell linkages via diffusion and onto the meristems. Nevertheless, the xylem represents the main conduit for the root-to-shoot transmission of the phytohormonal signals for plant growth and development, and there are ample scientific evidence to support this growth regulatory mechanism (Yong et al. 2000, 2014; for reviews, see Schmülling 2002; Stirk and Van Staden 2010).

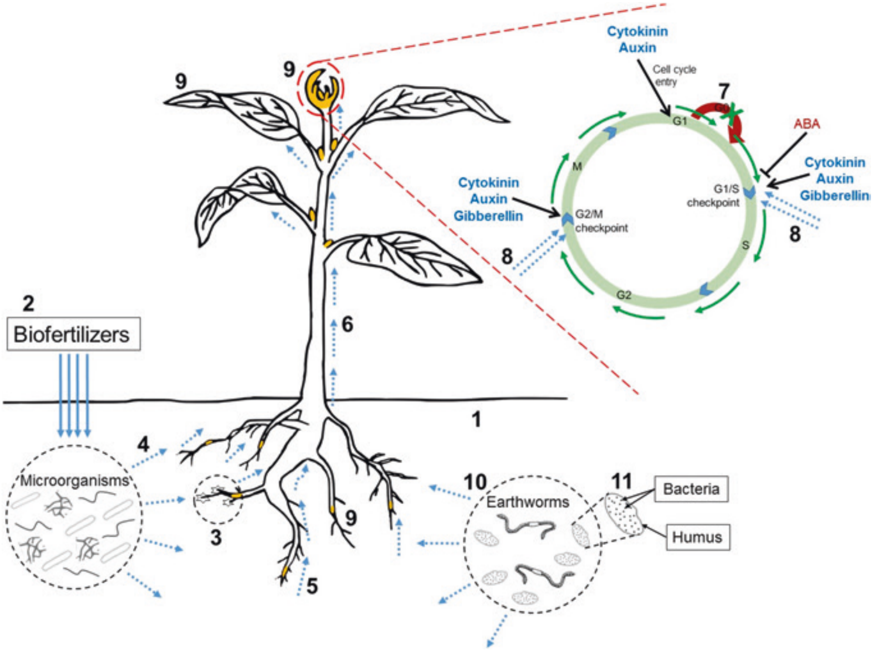


Fig. 7 Schematic diagram to describe how biofertilizers work in tandem with microorganisms and phytohormones to influence plant growth. *1* Soil provides the plants with general nutrients like N, P and K, that serve as cellular structural materials and building blocks for components such as nucleic acids, ATP and enzymes; and cofactors for enzyme activities. Fertilizers, either conventional or organic in origin, are added to restore the “nutrient loss” from biomass removal and/or through leaching or weathering processes. *2* Application of biofertilizers introduces microorganisms (e.g. bacteria and fungi) into the rhizosphere. *3* Microorganisms may be free-living or in symbiosis with the plants (at the roots). *4* Certain microorganisms produce various useful enzymes for improving soil availability of certain nutrients, and other useful substances including phytohormones or possibly, their precursors (mainly cytokinins and auxins). *5* The phytohormones (and/or their precursors), present in the soil, are then taken up by the plant, via the roots, and *6* transported to/or near the sites of active growth, i.e. shoot apices and axillary meristems, through the xylem. *7* The phytohormones help the cells to bypass the G0 phase and *8* proceed beyond the checkpoints (G1/S and G2/M) that results in active cell divisions, producing more cells at the meristems, and leading eventually to plant growth. *9* Phytohormones transported to the other parts of the plants also regulate various biological processes such as the opening of stomata, chloroplast production, release from apical dominance, flower development and root development. *10* Earthworms produce vermicompost that contains phytohormones (through earthworms’ intestinal microbial activities) that are released into the soil and can be taken up by the plants. *11* Vermicompost also contains humus that allows beneficial bacteria (either of earthworm gut origin and/or soil origin) to thrive and multiply, and thereby increasing the bioactivity of the soil. Humus also help to improve the soil structure that allow better water and air movement within the rhizospheres and thereby increasing soil fertility

6.1 *Improving Current Fertilizer Regime in Light of the Linkages Between Plant Growth and Microorganisms-Derived Phytohormones*

For the general plant industry at present, the sole application of each type of fertilizer (either chemical or organic) appears to be the current trend adopted by many growers/farmers. However, there is a gradual and progressive shift by some of the conventional farmers/growers toward using organic additives (organic fertilizers and biofertilizers) to supplement their chemically based NPK fertilizer applications in the farms/plantations. This is because many conventional farmers/growers have realized that the long-term and prolonged usage of chemical fertilizers on their lands had somewhat led to a drop in plant growth promoting efficacy and subsequently lower yield. Due to the complexity of these biotic and abiotic processes (some of which are still unclear) and interactions, it was often impossible to give farmers/growers adequate scientific explanations. Some research suggested a plausible link between lower yields (despite increasing chemical fertilization) and diminishing microbial activities ("poor soil health"). Such ambiguity paves the way for more intensive research toward understanding the role of soil microbes (and their associated phytohormonal content), in relation to plant growth and fertilizer formulations. Nevertheless, various scientific studies had been conducted on the use of a combination of fertilizers, chemical and organic (Shafi et al. 2012), organic and biofertilizers (Gharib et al. 2008; Sarma et al. 2015), vermicompost and PGPR (Song et al. 2015) and even a combination of all three types (chemical, organic and biofertilizers; Datta et al. 2009). The studies have proven that the integrated use of different fertilizers is highly beneficial in terms of crop yield and environmental friendliness.

Some conventional plant industries have started using humic acid (commercially available in pellet forms) and/or biocharcoal, in their farming practices. Humic acid pellets are known to improve the soil properties, which are likely to be degraded by prolonged chemical fertilizer application. Other conventional farmers/growers have used vermicomposts which not only improve the soil composition and structure but also introduce beneficial microorganisms. These microorganisms in turn provide the necessary phytohormones needed to support plant growth and development. While organic fertilizers and biofertilizers contain phytohormones (varying levels) and are environmentally friendly, they may fail to deliver stable and predictable growth stimulation comparable to chemical fertilizers as it is difficult to manage the batch–batch variation in microbial activities and missing mineral nutrients. Moving forward, plant industry that uses organic fertilizer or biofertilizers could consider fortifying their fertilizers with selected micro- and macromineral nutrients so as to supplement the low amount of nutrients, especially NPK and other trace elements, to improve or to maintain the yield.

6.2 The Novel Futuristic Green Biofertilizer—With Microbial Phytohormones

In our current plant industry and fertilization practices, the shortage of mineral nutrients can be assessed rapidly and easily overcome by adding fertilizers. However, the apparent shortage of phytohormones in promoting plant growth and development has never been recognized as an important tenet of whole plant nutrition. Ironically, the importance of phytohormones in promoting in vitro plant growth and development in the plant tissue culture industry is widely recognized and supplementing phytohormones within a desired mineral nutrient formulation is the standard practice (for reviews, see George and Sherrington 1984; George 1993). Unknown to many farmers/growers from the scientific perspective of plant cell cycle regulation through phytohormones, the use of organic fertilizers and biofertilizers (with their microbes and naturally occurring phytohormones and especially cytokinins) by either an organic farm (routinely) or as a periodic supplement to their conventional farming methods, help to increase the levels of growth promoting phytohormones in the subterranean root environment. With the new understanding about the pivotal role of phytohormones in regulating plant cell proliferation when mineral nutrients are sufficient, we believe that plant industry productivity or yield can be further enhanced with the supplementation (or natural occurrence) of phytohormones like cytokinins, auxins, gibberellins, etc., within the current fertilizer formulation, and possibly through microbial avenues with varying levels of controlled release technologies (Bashan et al. 2014).

Moving forward, we propose a new practice of introducing phytohormones, specifically cytokinins, in current agricultural/horticultural plant nutrition methodologies. Cytokinins appear to be one of the limiting factors in regulating plant growth due to its scarcity and fluidity in the fragile subterranean environment, as discussed in earlier sections. Thus, we believe that agricultural/horticultural yield/productivity can be greatly enhanced with the supplementation of cytokinins and other phytohormones in fertilizers. The preferred sources of cytokinins in any futuristic green biofertilizer should preferably be “natural” and originating from microorganisms (e.g. bacteria like *Azospirillum* and *Rhizobium*) and natural sources (coconuts, macroalgae, or seaweeds) that are widely available to the growers/farmers (for reviews, see Letham and Palni 1983; Stirk et al. 2003; Ördög et al. 2004; Yong et al. 2009). Microbial production of cytokinins has been well documented (Phillips and Torrey 1972; Ng et al. 1982; Burkiewicz 1987; Kraigher et al. 1991; Upadhyaya et al. 1991; Arkhipova et al. 2005; Kudoyarova et al. 2014) and could be cultured economically in large quantity using bioreactors and formulated for agricultural/horticultural use (Fig. 8). Thus, cytokinin-producing bacteria harbors the greatest potential for large-scale cytokinin production and can be developed into the next generation of green fertilizer for agricultural/horticultural applications.

The new generation of green biofertilizer is likely to come in the form of granules, and/or coated by natural/hydrophobic polymers or as matrices in which the

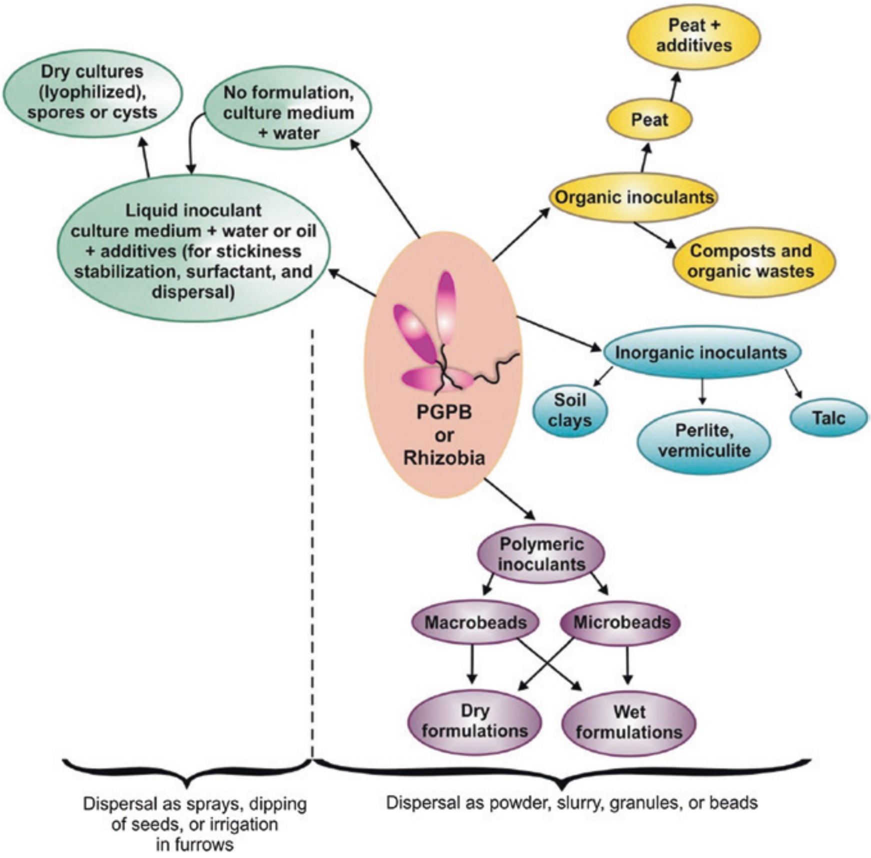


Fig. 8 Formulations of inoculants as biofertilizers for agricultural and environmental uses. (reprinted from Plant and Soil, 378, 2014, 1–33, Advances in plant growth promoting bacterial inoculant technology: formulations and practical perspectives (1998–2013), Y. Bashan, L.E. de-Bashan, S.R. Prabhu, Juan-Pablo Hernandez, Fig. 2, with kind permission from Springer Science and Business Media)

active plant growth promoting (e.g. cytokinins, auxins, gibberellins, etc.) and soil improving substances (e.g. humic acid), and/or suitable microbes, with carefully selected mineral nutrients, are embedded in packing materials (e.g. alginate) that restricts the rapid dissolution of the fertilizer, and consequently providing the plants with a sustained source of phytohormones, mineral nutrients, amino acids, proteins, etc. (Fig. 9). The current slow and controlled release or “stabilized” fertilizers is a useful design template to develop the futuristic fertilizer (for reviews, see Shaviv and Mikkelsen 1993; Bashan et al. 2014). The selection of specific mineral nutrients to be embedded in the novel futuristic green fertilizer should be formulated only after a proper chemical analysis of the targeted soil type or locality had been carried out. In situations where certain macro- and

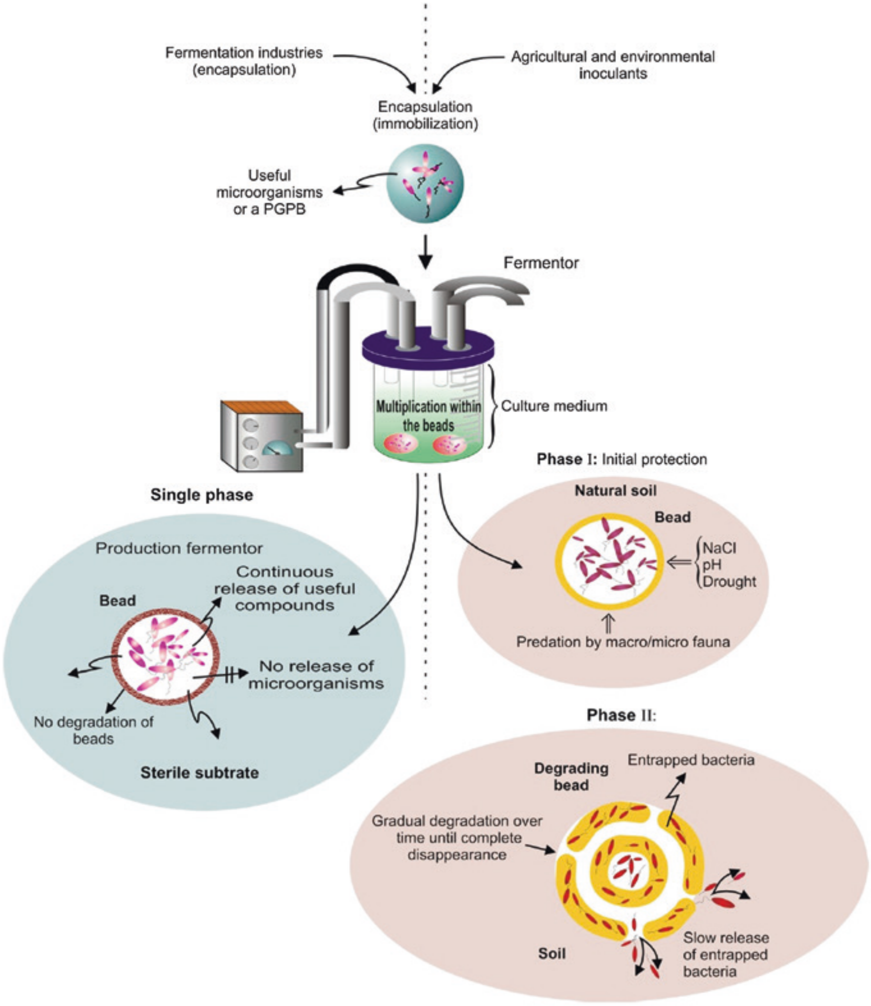


Fig. 9 Encapsulating bacteria for use in industrial fermentation and as an inoculant for agricultural/environmental use (reprinted from Plant and Soil, 378, 2014, 1–33, Advances in plant growth promoting bacterial inoculant technology: formulations and practical perspectives (1998–2013), Y. Bashan, L.E. de-Bashan, S.R. Prabhu, Juan-Pablo Hernandez, Fig. 3, with kind permission from Springer Science and Business Media)

micronutrients may be biologically unavailable, suitable and effective microbial populations for solubilizing the chemically fixed phosphorus and to improve the availability of other macro and micronutrients, could be added onto these granules. When there are threats to plant health, the novel fertilizer may be formulated to have some levels of biocontrol properties against certain pathogens. Some other organic compounds such as humic acids and vermicomposts with favorable soil structure improving properties (such as water and mineral nutrient retention) and soil microbial activity-enhancing properties, could also be added in order to augment the overall performance of the novel futuristic green biofertilizer. Bashan et al. (2014) provided interesting and useful methodologies toward designing varying levels of controlled release centered on either a seed (Fig. 10a) or a microbial pellet (Fig. 10b). These useful microbial-inoculant design conceptual templates

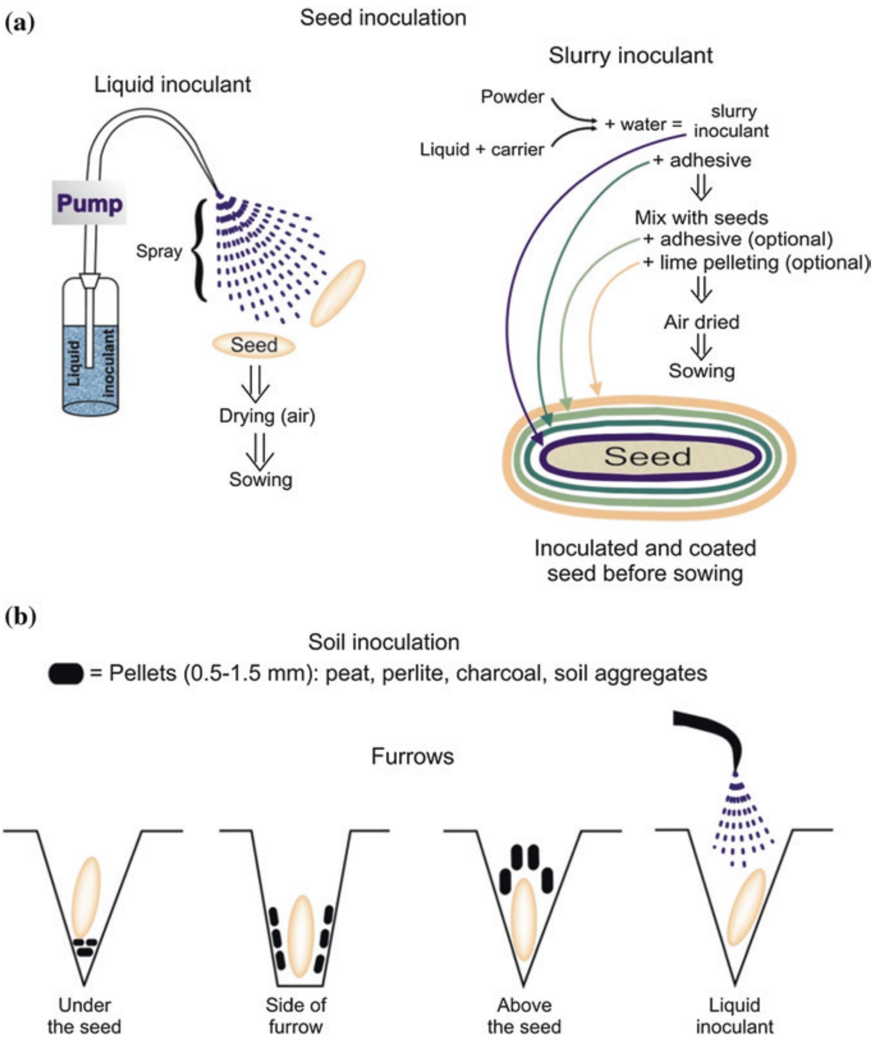


Fig. 10 Schematic representation of the various strategies available for **a** multilayered seed inoculation and **b** microbial pellets for soil inoculation (reprinted from Plant and Soil, 378, 2014, 1–33, Advances in plant growth promoting bacterial inoculant technology: formulations and practical perspectives (1998–2013), Y. Bashan, L.E. de-Bashan, S.R. Prabhu, Juan-Pablo Hernandez, Fig. 4, with kind permission from Springer Science and Business Media)

can be broaden further to include the futuristic green fertilizer granule design that may carry some useful substances (see Sects. 3.2 and 5) and perhaps, concomitantly embedding two different microbes with different biological functions in the soil. With above-mentioned benefits, together with a reasonable storage life (up to 3–6 months), the novel futuristic green biofertilizer in the form of granules is likely to be favored by the conventional farmers/growers.

The ideal fertilizers should have the following three characteristics:

- A single application should supply enough mineral nutrients and phytohormones throughout the entire growing season to meet plant demand for optimum growth;
- Maximal plant growth stimulation thus allowing the largest financial return for the cost of input;
- Minimum detrimental ecological effects on the soil, water and atmospheric environment.

7 Conclusion

Plant growth is dependent on meristems where cell proliferations give rise to new plant structures and allow the plant to increase in size. We provided scientific linkages and evidence to show that the growth promoting factors in biofertilizers regulating cell proliferation and ultimately modulating plant growth and development are phytohormones. The known biological functions of phytohormones (cytokinins, auxins, gibberellins, etc.) are in tandem with the observed physiological characteristics and crop yield of plants. When light, water and mineral nutrients are not limiting, phytohormones, especially cytokinins, in biofertilizers help to drive plant growth by progressing faster through the various plant cell cycle checkpoints leading to the production of more cells.

There is an enormous diversity of microbes found within the soil matrices of the subterranean environment where the plant root system exists. Within the rhizosphere, there is a group of PGPR bacteria that has the ability to promote plant growth via various mechanisms such as nitrogen fixation, phosphorus and zinc solubilization. Another prominent ability of some PGPR is the secretion of bacterial phytohormones, like cytokinins and auxins and other useful substances. Phytohormone-producing PGPR harbors the greatest potential for large-scale phytohormone (especially cytokinins) production and can be developed into the next generation of green fertilizer with microbial phytohormones and/or microbial inoculant for agricultural/horticultural applications.

Evidently, the above literature reviews and discussions reveal that biofertilizers bring about great advantages and improvements to our modern and intensive conventional agriculture practice. In addition, although not discussed in depth in this review, certain biofertilizers may also confer natural biocontrol property that would be useful for disease management. The long-term and fundamental sustainable criterion for any futuristic farmland/plantation is essentially soil health. Good soil provides the foundation for healthy plant growth with minimal external mineral nutrient addition. However, despite its environmental friendliness, any fertilizer regime that solely relies upon biofertilizer may not be feasible in terms of crop productivity per unit area when compared to conventional agriculture practice. Large amount of biofertilizers would be required as they generally contain lower mineral nutrient content, variable elemental composition and/or releasing nutrients at a much slower rate that is unable to sustain maximum plant growth over a limited time period (Chen 2006). Thus, for those involved solely in organic farming practices, we suggest that their organic fertilizers be fortified with selected macro- and micronutrients when there is a drop in horticultural productivity/crop yield. Conversely, for those involved in conventional farming practices, adding organic and biofertilizers periodically is the remedy to reduce chemical fertilizer usage while maintaining their expected yields. Under certain circumstances, selective biofertilizer application to support conventional farming practices is considered the best way to restore the effective microbial populations in order to solubilize chemically fixed phosphorus and to improve the availability of other macro- and micronutrients for plant uptake.

In the near future, we envisage that a hybrid approach of combining organic and conventional fertilization regimes will be widely accepted throughout the global plant industry. This is evident from the 15-year-long study conducted by Qin et al. (2015) which demonstrated that the combined application of organic fertilizers (manure was investigated in that study), together with chemical fertilizer are of great importance to improving agricultural economy as well as sustaining soil heath and quality. Moving forward, the new generation of green biofertilizer should come in the form of granules in which the active plant growth promoting (e.g. cytokinins, auxins, gibberellins, etc.) and soil improving substances (e.g. humic acid) and/or suitable microbes ("inoculants"), with carefully selected mineral nutrients, are embedded in the packing materials giving slow and sustained release over a desired period. The futuristic green fertilizers should provide the plants with a sustained source of phytohormones and mineral nutrients. In situations where certain macro- and micronutrients may be unavailable, suitable and effective microbial populations for solubilizing the chemically fixed phosphorus and to improve the availability of other macro- and micronutrients could be added onto these green fertilizer granules.

References

Adesemoye AO, Torbert HA, Kloepper JW (2010) Increased plant uptake of nitrogen from ^{15}N-depleted fertilizer using plant growth-promoting rhizobacteria. Appl Soil Ecol 46:54–58

Agusti J, Herold S, Schwarz M, Sanchez P, Ljung K, Dun EA, Brewer PB, Beveridge CA, Sieberer T, Sehr EM, Greb T (2011) Strigolactone signaling is required for auxin-dependent stimulation of secondary growth in plants. Proc Natl Acad Sci USA 108:20242–20247

Ahemad M, Kibret M (2014) Mechanisms and applications of plant growth promoting rhizobacteria: current perspectives. J King Saud Univ—Sci 26:1–20

Akhkha A, Kusel J, Kennedy M, Curtis R (2002) Effects of phytohormones on the surfaces of plant-parasitic nematodes. Parasitology 125:165–175

Al-Babili S, Bouwmeester HJ (2015) Strigolactones, a novel carotenoid-derived plant hormone. Annu Rev Pl Biol 66:161–186

An C, Mou Z (2011) Salicylic acid and its function in plant immunity. J Integr Plant Biol 53:412–428

Arancon NQ, Edwards CA, Bierman P, Welch C, Metzger JD (2004) Influences of vermicomposts on field strawberries: 1. Effects on growth and yields. Bioresour Technol 93:145–153

Aremu AO, Strik WA, Kulkarni MG, Tarkowská D, Turečková V, Gruz J, Šubrtová M, Pěnčík A, Novák O, Doležal K, Strnad M, Van Staden M (2015) Evidence of phytohormones and phenolic acids variability in garden-waste-derived vermicompost leachate, a well-known plant growth stimulant. Plant Growth Regul 75:483–492

Arkhipova TN, Veselov SU, Melentiev AI, Martynenko EV, Kudoyarova GR (2005) Ability of bacterium *Bacillus subtilis* to produce cytokinins and to influence the growth and endogenous hormone content of lettuce plants. Plant Soil 272:201–209

Arthur GD, Jäger AK, Van Staden J (2001) Uptake of [$_{3}$H]DHZ by tomato seedlings. S Afr J Bot 67:661–666

Atiyeh RM, Lee S, Edwards CA, Arancon NQ, Metzger JD (2002) The influence of humic acids derived from earthworm-processed organic wastes on plant growth. Bioresour Technol 84:7–14

Bangerth F, Li CJ, Gruber J (2000) Mutual interaction of auxin and cytokinins in regulating correlative dominance. Plant Growth Regul 32:205–217

Barea JM, Azcón-Aguilar C (1982) Production of plant growth-regulating substances by the vesicular-arbuscular mycorrhizal fungus *Glomus mosseae*. Appl Environ Microbiol 43:810–813

Bashan Y, de-Bashan LE, Prabhu SR, Hernandez JP (2014) Advances in plant growth-promoting bacterial inoculant technology: formulations and practical perspectives (1998–2013). Plant Soil 378:1–33

Beattie GA (2006) Plant-associated bacteria: survey, molecular phylogeny, genomics and recent advances. In: Gnanamanickam LJ (ed) Plant-associated bacteria. Springer, Netherlands, pp 1–56

Bennett T, Leyser O (2006) Something on the side: axillary meristems and plant development. Plant Mol Biol 60:843–854

Berendsen RL, Pieterse CMJ, Bakker PAHM (2012) The rhizosphere microbiome and plant health. Trends Plant Sci 17:478–486

Bhattacharjee R, Dey U (2014) Biofertilizer, a way towards organic agriculture: a review. Afr J Microbiol Res 8:2332–2343

Binns AN (1994) Cytokinin accumulation and action: biochemical, genetic, and molecular approaches. Annu Rev Plant Biol 45:173–196

Bird AF, Loveys BR (1980) The involvement of cytokinins in a host–parasite relationship between the tomato (*Lycopersicon esculentum*) and a nematode (*Meloidogyne javanica*). Parasitology 80:497–505

Bleecker AB, Kende H (2000) Ethylene: a gaseous signal molecule in plants. Annu Rev Cell Dev Biol 16:1–18

Bronick CJ, Lal R (2005) Soil structure and management: a review. Geoderma 124:3–22

Burd GI, Dixon DG, Glick BR (1998) A plant growth-promoting bacterium that decreases nickel toxicity in seedlings. Appl Environ Microbiol 64:3663–3668

Burkiewicz K (1987) Active substances in the media after algae cultivation. Acta Physiol Plant 9:211–217

Çakmakçi R, Dönmez F, Aydın A, Şahin F (2006) Growth promotion of plants by plant growth-promoting rhizobacteria under greenhouse and two different field soil conditions. Soil Biol Biochem 38:1482–1487

Canellas LP, Olivares FL, Okorokova-Façanha AL, Façanha AR (2002) Humic acids isolated from earthworm compost enhance root elongation, lateral root emergence, and plasma membrane H^+ -ATPase activity in maize roots. Plant Physiol 130:1951–1957

Červená K, Lyčková B, Kučerová R (2013) Vermicompost—an effective natural fertilizer. In: Proceedings in EIIC-The 2nd electronic international interdisciplinary conference. http://www.eiic.cz/archive/?vid=1&aid=3&kid=20201-110&q=f1. Accessed 13 Nov 2014

Chandramohan A, Sivasankar V, Ravichandran C, Sakthivel R (2013) A probe on the status of microorganisms in the air, soil and solid waste samples of Ariyamangalam dumping site at Tiruchirappalli district, South India. In: Velu RK (ed) Microbiological research in agroecosystem management. Springer, India, pp 1–9

Chaoui HI, Zibilske LM, Ohno T (2003) Effects of earthworm casts and compost on soil microbial activity and plant nutrient availability. Soil Biol Biochem 35:295–302

Chen CM, Ert JR, Leisner SM, Chang CC (1985) Localization of cytokinin biosynthetic sites in pea plants and carrot roots. Plant Physiol 78:510–513

Chen Y, Clapp CE, Magen H (2004) Mechanisms of plant growth stimulation by humic substances: the role of organo-iron complexes. Soil Sci Plant Nutr 50:1089–1095

Chen JH (2006) The combined use of chemical and organic fertilizers and/or biofertilizers for crop growth and soil fertility. In: International workshop on sustained management of the soil-rhizosphere system for efficient crop production and fertilizer use, vol 16. Land Development Department Bangkok, Thailand, p 20

Choi O, Kim J, Kim JG, Jeong Y, Moon JS, Park CS, Hwang I (2008) Pyrroloquinoline quinone is a plant growth promotion factor produced by *Pseudomonas fluorescens* B16. Plant Physiol 146:657–668

Coen ES, Meyerowitz EM (1991) The war of the whorls: genetic interactions controlling flower development. Nature 353:31–37

Crafts CB, Miller CO (1974) Detection and identification of cytokinins produced by mycorrhizal fungi. Plant Physiol 54:586–588

Crawford NM (1995) Nitrate: nutrient and signal for plant growth. Plant Cell 7:859–868

Crawford NM, Glass AD (1998) Molecular and physiological aspects of nitrate uptake in plants. Trends Plant Sci 3:389–395

Creelman RA, Mullet JE (1997) Biosynthesis and action of jasmonates in plants. Annu Rev Plant Biol 48:355–381

Crespi M, Messens E, Caplan AB, Van Montagu M, Desomer J (1992) Fasciation induction by the phytopathogen *Rhodococcus fascians* depends upon a linear plasmid encoding a cytokinin synthase gene. EMBO J 11:795–804

Crowley DE (2006) Microbial siderophores in the plant rhizosphere. In: Barton LL, Abadia J (eds) Iron nutrition in plants and rhizospheric microorganisms. Springer, Netherlands, pp 169–198

Datta JK, Banerjee A, Sikdar MS, Gupta S, Mondal NK (2009) Impact of combined exposure of chemical, fertilizer, bio-fertilizer and compost on growth, physiology and productivity of *Brassica campestries* in old alluvial soil. J Environ Biol 30:797–800

De Meutter J, Tytgat T, Witters E, Gheysen G, Van Onckelen H, Gheysen G (2003) Identification of cytokinins produced by the plant parasitic nematodes *Heterodera schachtii* and *Meloidogyne incognita*. Mol Plant Pathol 4:271–277

Den Boer BG, Murray JA (2000) Triggering the cell cycle in plants. Trends Cell Biol 10:245–250

Dewitte W, Murray JA (2003) The plant cell cycle. Annu Rev Plant Biol 54:235–264

Dimkpa C, Svatoš A, Merten D, Büchel G, Kothe E (2008) Hydroxamate siderophores produced by *Streptomyces acidiscabies* E13 bind nickel and promote growth in cowpea (*Vigna unguiculata* L.) under nickel stress. Can J Microbiol 54:163–172

Dimkpa CO, Merten D, Svatoš A, Büchel G, Kothe E (2009) Siderophores mediate reduced and increased uptake of cadmium by *Streptomyces tendae* F4 and sunflower (*Helianthus annuus*), respectively. J Appl Microbiol 107:1687–1696

Doares SH, Narvaez-Vasquez J, Conconi A, Ryan CA (1995) Salicylic acid inhibits synthesis of proteinase inhibitors in tomato leaves induced by systemin and jasmonic acid. Plant Physiol 108:1741–1746

Döbereiner J (1992) History and new perspectives of diazotrophs in association with non-leguminous plants. Symbiosis 13:1–13

Durner J, Klessig DF (1999) Nitric oxide as a signal in plants. Curr Opin Plant Biol 2:369–374

Durner J, Wendehenne D, Klessig DF (1998) Defense gene induction in tobacco by nitric oxide, cyclic GMP, and cyclic ADP-ribose. Proc Natl Acad Sci USA 95:10328–10333

Edwards CA, Arancon NQ, Sherman R (2010) Vermiculture technology: earthworms, organic wastes, and environmental management. CRC Press, Boca Raton

Emery RJN, Atkins CA (2002) Roots and cytokinins. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant roots—the hidden half. Marcel Dekker Inc, New York, pp 417–434

FAO/WHO (2015) What is organic agriculture. http://www.fao.org/organicag/oa-faq/oa-faq1/en/. Accessed 3 Jan 2015

Francis D, Sorrell DA (2001) The interface between the cell cycle and plant growth regulators: a mini review. Plant Growth Regul 33:1–12

Frank M, Schmülling T (1999) Cytokinin cycles cells. Trends Plant Sci 4:243–244

Frébort I, Kowalska M, Hluska T, Frébortová J, Galuszka P (2011) Evolution of cytokinin biosynthesis and degradation. J Exp Bot 62:2431–2452

Fricke K, Vogtmann H (1993) Quality of source separated compost. BioCycle 34:64–70

Frugier F, Kosuta S, Murray JD, Crespi M, Szczyglowski K (2008) Cytokinin: secret agent of symbiosis. Trends Plant Sci 13:115–120

George EF (1993) Plant propagation by tissue culture, part 1: the technology, 2nd edn. Exegetics Ltd, Edington

George EF, Sherrington PD (1984) Plant propagation by tissue culture-handbook and directory of commercial laboratories. Exegetics Ltd, Edington

Gersani M, Kende H (1982) Studies on cytokinin-stimulated translocation in isolated bean leaves. J Plant Growth Regul 1:161–171

Gharib FA, Moussa LA, Massoud ON (2008) Effect of compost and bio-fertilizers on growth, yield and essential oil of sweet marjoram (*Majorana hortensis*) plant. Int J Agr Biol 10:381–382

Gibson SI (2005) Control of plant development and gene expression by sugar signalling. Curr Opin Plant Biol 8:93–102

Glick BR (1995) The enhancement of plant growth by free-living bacteria. Can J Microbiol 41:109–117

Glick BR, Bashan Y (1997) Genetic manipulation of plant growth-promoting bacteria to enhance biocontrol of phytopathogens. Biotechnol Adv 15:353–378

Glick BR, Cheng Z, Czarny J, Duan J (2007) Promotion of plant growth by ACC deaminase-producing soil bacteria. Eur J Plant Pathol 119:329–339

Goicoechea N, Antolin MC, Strnad M, Sánchez-Díaz M (1996) Root cytokinins, acid phosphatase and nodule activity in drought-stressed mycorrhizal or nitrogen-fixing alfalfa plants. J Exp Bot 47:683–686

Gopalakrishnan S, Srinivas V, Alekhya G, Prakash B, Kudapa H, Rathore A, Varshney RK (2015) The extent of grain yield and plant growth enhancement by plant growth-promoting broad-spectrum *Streptomyces* sp. in chickpea. SpringerPlus 4:31. doi:10.1186/s40064-015-0811-3

Gray EJ, Smith DL (2005) Intracellular and extracellular PGPR: commonalities and distinctions in the plant–bacterium signaling processes. Soil Biol Biochem 37:395–412

Grbić V, Bleecker AB (2000) Axillary meristem development in *Arabidopsis thaliana*. Plant J 21:215–223

Groppa MD, Benavides MP (2008) Polyamines and abiotic stress: recent advances. Amino Acids 34:35–45

Haberer G, Kieber JJ (2002) Cytokinins. New insights into a classic phytohormone. Plant Physiol 128:354–362

Handelsman J, Stabb EV (1996) Biocontrol of soilborne plant pathogens. Plant Cell 8:1855–1869

Hänsch R, Mendel RR (2009) Physiological functions of mineral micronutrients (Cu, Zn, Mn, Fe, Ni, Mo, B, Cl). Curr Opin Plant Biol 12:259–266

Hayat R, Ali S, Amara U, Khalid R, Ahmed I (2010) Soil beneficial bacteria and their role in plant growth promotion: a review. Ann Microbiol 60:579–598

Herbert RJ, Vilhar B, Evett C, Orchard CB, Rogers HJ, Davies MS, Francis D (2001) Ethylene induces cell death at particular phases of the cell cycle in the tobacco TBY-2 cell line. J Exp Bot 52:1615–1623

Hernández A, Castillo H, Ojeda D, Arras A, López J, Sánchez E (2010) Effect of vermicompost and compost on lettuce production. Chil J Agr Res 70:583–589

Hsieh SC (2005) Organic farming for sustainable agriculture in Asia with special reference to Taiwan experience. Research Institute of Tropical Agriculture and International Cooperation, National Pingtung University of Science and Technology, Taiwan. http://www.agnet.org/htmlarea_file/library/20110801133519/eb558.pdf. Accessed 23 Oct 2014

Howell SH, Lall S, Che P (2003) Cytokinins and shoot development. Trends Plant Sci 8:453–459

Huala E, Sussex IM (1993) Determination and cell interactions in reproductive meristems. Pl Cell 5:1157–1165

Hwang I, Sakakibara H (2006) Cytokinin biosynthesis and perception. Physiol Plant 126:528–538

International Humic Substances Society (2007) What are humic substances? http://www.humicsubstances.org/whatarehs.html. Accessed 24 Oct 2014

Inzé D (2003) Why should we study the plant cell cycle? J Exp Bot 54:1125–1126

Jeng AS, Haraldsen TK, Grønlund A, Pedersen PA (2006) Meat and bone meal as nitrogen and phosphorus fertilizer to cereals and rye grass. Nutr Cycl Agroecosys 76:183–191

Johnstone DB (1967) Isolation of *Azotobacter insignis* from fresh water. Ecology 48:671–672

Kakimoto T (2001) Identification of plant cytokinin biosynthetic enzymes as dimethylallyl diphosphate: ATP/ADP isopentenyltransferases. Plant Cell Physiol 42:677–685

Kakimoto T (2003) Biosynthesis of cytokinins. J Plant Res 116:233–239

Kamínek M, Motyka V, Vaňková R (1997) Regulation of cytokinins content in plant cells. Physiol Plant 101:689–700

Katiyar V, Goel R (2004) Siderophore mediated plant growth promotion at low temperature by mutant of fluorescent pseudomonad. Plant Growth Regul 42:239–244

Klessig DF, Durner J, Noad R, Navarre DA, Wendehenne D, Kumar D, Zhou JM, Shah J, Zhang S, Kachroo P, Trifa Y, Pontier D, Lam E, Silva H (2000) Nitric oxide and salicylic acid signaling in plant defense. Proc Natl Acad Sci USA 97:8849–8855

Kloepper JW, Lifshitz R, Zablotowicz RM (1989) Free-living bacterial inocula for enhancing crop productivity. Trends Biotechnol 7:39–44

Koltai H (2011) Strigolactones are regulators of root development. New Phytol 190:545–549

Koning RE (1994) Cell cycle. Plant Physiology Information Website. http://plantphys.info/plant_physiology/cellcycle.shtml. Accessed 24 Oct 2014

Kraigher H, Grayling A, Wang TL, Hanke DE (1991) Cytokinin production by two ectomycorrhizal fungi in liquid culture. Phytochem 30:2249–2254

Kravchenko LV, Azarova TS, Makarova NM, Tikhonovich IA (2004) The effect of tryptophan present in plant root exudates on the phytostimulating activity of rhizobacteria. Microbiology 73:156–158

Kretzschmar T, Kohlen W, Sasse J, Borghi L, Schlegel M, Bachelier JB, Reinhardt D, Bours R, Bouwmeester HJ, Martinoia E (2012) A petunia ABC protein controls strigolactone-dependent symbiotic signalling and branching. Nature 483:341–344

Kudoyarova GR, Melentiev AI, Martynenko EV, Timergalina LN, Arkhipova TN, Shendel GV, Kuz'mina LY, Dodd IC, Veselov SY (2014) Cytokinin producing bacteria stimulate amino acid deposition by wheat roots. Plant Physiol Biochem 83:285–291

Lamotte O, Courtois C, Barnavon L, Pugin A, Wendehenne D (2005) Nitric oxide in plants: the biosynthesis and cell signalling properties of a fascinating molecule. Planta 221:1–4

Leopold AC, Kawase M (1964) Benzyladenine effects on bean leaf growth and senescence. Am J Bot 51:294–298

Letham DS, Palni LMS (1983) The biosynthesis and metabolism of cytokinins. Ann Rev Plant Physiol 34:163–197

Li P, Chen L, Zhou Y, Xia X, Shi K, Chen Z, Yu J (2013) Brassinosteroids-induced systemic stress tolerance was associated with increased transcripts of several defence-related genes in the phloem in *Cucumis sativus*. PLoS ONE 8:e66582. doi:10.1371/journal.pone.0066582

Lindsey K, Casson S, Chilley P (2002) Peptides: new signalling molecules in plants. Trends Plant Sci 7:78–83

Lohar DP, Schaff JE, Laskey JG, Kieber JJ, Bilyeu KD, Bird DM (2004) Cytokinins play opposite roles in lateral root formation, and nematode and rhizobial symbioses. Plant J 38:203–214

Long J, Barton MK (2000) Initiation of axillary and floral meristems in *Arabidopsis*. Dev Biol 218:341–353

Lugtenberg B, Kamilova F (2009) Plant-growth-promoting rhizobacteria. Annu Rev Microbiol 63:541–556

Ma QH, Lin ZB, Fu DZ (2002) Increased seed cytokinin levels in transgenic tobacco influence embryo and seedling development. Funct Plant Biol 29:1107–1113

Mäder P, Fliessbach A, Dubois D, Gunst L, Fried P, Niggli U (2002) Soil fertility and biodiversity in organic farming. Science 296:1694–1697

Mahdi SS, Hassan GI, Samoon SA, Rather HA, Dar SA, Zehra B (2010) Bio-fertilizers in organic agriculture. J Phytol 2:42–54

Maksimov IV, Abizgil'Dina RR, Pusenkova LI (2011) Plant growth promoting rhizobacteria as alternative to chemical crop protectors from pathogens (review). Appl Biochem Microbiol 47:333–345

Malusá E, Vassilev N (2014) A contribution to set a legal framework for biofertilisers. Appl Microbiol Biot 98:6599–6607

Mapes CC, Davies PJ (2001) Cytokinins in the ball gall of *Solidago altissima* and in the gall forming larvae of *Eurosta solidaginis*. New Phytol 151:203–212

Marschner H (1995) Mineral nutrition of higher plants, 2nd edn. Academic Press, London

Martínez GA, Chaves AR, Añón MC (1994) Effect of gibberellic acid on ripening of strawberry fruits (*Fragaria annanassa* Duch.). J Plant Growth Regul 13:87–91

Martin-Tanguy J (2001) Metabolism and function of polyamines in plants: recent development (new approaches). Plant Growth Regul 34:135–148

Masalha J, Kosegarten H, Elmaci Ö, Mengel K (2000) The central role of microbial activity for iron acquisition in maize and sunflower. Biol Fert Soils 30:433–439

Matsubayashi Y (2014) Posttranslationally modified small-peptide signals in plants. Annu Rev Plant Biol 65:385–413

Matsubayashi Y, Sakagami Y (2006) Peptide hormones in plants. Annu Rev Plant Biol 57:649–674

Mauk CS, Noodén LD (1992) Regulation of mineral redistribution in pod-bearing soybean explants. J Exp Bot 43:1429–1440

McDermott J, Meilan R, Thornburg R (1996) Plant–insect interactions: the hackberry nipple gall. World Wide Web J Biol 2 http://epress.com/w3jbio/vol2/mcdermott/mcdermott.html

Mehboob I, Naveed M, Ahmad Z (2009) Rhizobial association with non-legumes: Mechanisms and applications. Crit Rev Plant Sci 28:432–456

Mishra DJ, Singh R, Mishra UK, Kumar SS (2013) Role of bio-fertilizer in organic agriculture: a review. Res J Recent Sci 2:39–41

Mok MC (1994) Cytokinins and plant development–an overview. In: Mok DWS, Mok MC (eds) Cytokinins: chemistry, activity and function. CRC Press, Boca Raton, pp 155–166

Mok DW, Mok MC (2001) Cytokinin metabolism and action. Annu Rev Plant Biol 52:89–118

Mok MC, Martin RC, Mok DW (2000) Cytokinins: biosynthesis, metabolism and perception. In Vitro Cellular Dev-Plant 36:102–107

Müssig C, Lisso J, Coll-Garcia D, Altmann T (2006) Molecular analysis of brassinosteroid action. Plant Biol 8:291–296

Neeraja C, Anil K, Purushotham P, Suma K, Sarma PVSRN, Moerschbacher BM, Podile AR (2010) Biotechnological approaches to develop bacterial chitinases as a bioshield against fungal diseases of plants. Critl Rev Biotechnol 30:231–241

Nelson DC, Riseborough JA, Flematti GR, Stevens J, Ghisalberti EL, Dixon KW, Smith SM (2009) Karrikins discovered in smoke trigger *Arabidopsis* seed germination by a mechanism requiring gibberellic acid synthesis and light. Plant Physiol 149:863–873

Nelson DC, Flematti GR, Riseborough JA, Ghisalberti EL, Dixon KW, Smith SM (2010) Karrikins enhance light responses during germination and seedling development in *Arabidopsis thaliana*. Proc Natl Acad Sci USA 107:7095–7100

Nelson DC, Flematti GR, Ghisalberti EL, Dixon KW, Smith SM (2012) Regulation of seed germination and seedling growth by chemical signals from burning vegetation. Annu Rev Plant Biol 63:107–130

Ng PP, Cole ALJ, Jameson PE, McWha JA (1982) Cytokinin production by ectomycorrhizal fungi. New Phytol 91:57–62

Obreht Z, Kerby NW, Gantar M, Rowell P (1993) Effects of root-associated N_2-fixing cyanobacteria on the growth and nitrogen content of wheat (*Triticum vulgare* L.) seedlings. Biol Fert Soils 15:68–72

Okon Y, Bloemberg GV, Lugtenberg BJJ (1998) Biotechnology of biofertilization and phytostimulation. In: Altman A (ed) Agricultural biotechnology. Marcel Dekker, New York, pp 327–349

Ördög V, Stirk WA, Van Staden J, Novák O, Strnad M (2004) Endogenous cytokinins in three genera of microalgae from the chlorophyta. J Phycol 40:88–95

Orhan E, Esitken A, Ercisli S, Turan M, Sahin F (2006) Effects of plant growth promoting rhizobacteria (PGPR) on yield, growth and nutrient contents in organically growing raspberry. Sci Hortic 111:38–43

Owen D, Williams AP, Griffith GW, Withers PJA (2014) Use of commercial bio-inoculants to increase agricultural production through improved phosphorus acquisition. Appl Soil Ecol 86:41–54

Pacifici E, Polverari L, Sabatini S (2015) Plant hormone cross-talk: the pivot of root growth. J Exp Bot 66:1113–1121

Patten CL, Glick BR (2002) Role of *Pseudomonas putida* indoleacetic acid in development of the host plant root system. Appl Environ Microb 68:3795–3801

Paungfoo-Lonhienne C, Lonhienne TG, Rentsch D, Robinson N, Christie M, Webb RI, Gamage HK, Carroll BJ, Schenk PM, Schmidt S (2008) Plants can use protein as a nitrogen source without assistance from other organisms. Proc Natl Acad Sci USA 105:4524–4529

Pelacho AM, Mingo-Castel AM (1991) Jasmonic acid induces tuberization of potato stolons cultured *in vitro*. Plant Physiol 97:1253–1255

Phillips D, Torrey J (1972) Studies on cytokinin production by *Rhizobium*. Plant Physiol 49:11–15

Piccolo A (2002) The supramolecular structure of humic substances: a novel understanding of humus chemistry and implications in soil science. Adv Agron 75:57–134

Piccolo A, Nardi S, Concheri G (1992) Structural characteristics of humic substances as related to nitrate uptake and growth regulation in plant systems. Soil Biol Biochem 24:373–380

Pimenta Lange MJ, Lange T (2006) Gibberellin biosynthesis and the regulation of plant development. Plant Biol 8:281–290

Powell GK, Morris RO (1986) Nucleotide sequence and expression of a *Pseudomonas savastanoi* cytokinin biosynthetic gene: homotogy with *Agrobacterium tumefaciens* tmr and tzs loci. Nucleic Acids Res 14:2555–2565

Qin H, Lu K, Strong PJ, Xu Q, Wu Q, Xu Z, Xu J, Wang H (2015) Long-term fertilizer application effects on the soil, root arbuscular mycorrhizal fungi and community composition in rotation agriculture. Appl Soil Ecol 89:35–43

Rauthan BS, Schnitzer M (1981) Effects of a soil fulvic acid on the growth and nutrient content of cucumber (*Cucumis sativus*) plants. Plant Soil 63:491–495

Raskin I (1992) Role of salicylic acid in plants. Annu Rev Plant Biol 43:439–463

Riou-Khamlichi C, Menges M, Healy JS, Murray JA (2000) Sugar control of the plant cell cycle: differential regulation of *Arabidopsis* D-type cyclin gene expression. Mol Cell Biol 20:4513–4521

Roldán M, Gómez-Mena C, Ruiz-García L, Salinas J, Martínez-Zapater JM (1999) Sucrose availability on the aerial part of the plant promotes morphogenesis and flowering of *Arabidopsis* in the dark. Plant J 20:581–590

Rolland F, Moore B, Sheen J (2002) Sugar sensing and signaling in plants. Plant Cell 14:S185–S205

Ryan CA (2000) The systemin signaling pathway: differential activation of plant defensive genes. Biochim Biophys Acta 1477:112–121

Ryan CA, Pearce G (2003) Systemins: a functionally defined family of peptide signals that regulate defensive genes in Solanaceae species. Proc Natl Acad Sci USA 100:14577–14580

Ryu CM, Farag MA, Hu CH, Reddy MS, Wei HX, Paré PW, Kloepper JW (2003) Bacterial volatiles promote growth in *Arabidopsis*. Proc Natl Acad Sci USA 100:4927–4932

Sabatini S, Beis D, Wolkenfelt H, Murfett J, Guilfoyle T, Malamy J, Benfey P, Leyser O, Bechtold N, Weisbeek P, Scheres B (1999) An auxin-dependent distal organizer of pattern and polarity in the *Arabidopsis* root. Cell 99:463–472

Sahni S, Sarma BK, Singh DP, Singh HB, Singh KP (2008) Vermicompost enhances performance of plant growth-promoting rhizobacteria in *Cicer arietinum* rhizosphere against *Sclerotium rolfsii*. Crop Prot 27:369–376

Sakakibara H (2006) Cytokinins: activity, biosynthesis, and translocation. Annu Rev Plant Biol 57:431–449

Sakakibara H, Kasahara H, Ueda N, Kojima M, Takei K, Hishiyama S, Asami T, Okada K, Kamiya Y, Yamaya T, Yamaguchi S (2005) *Agrobacterium tumefaciens* increases cytokinin production in plastids by modifying the biosynthetic pathway in the host plant. Proc Natl Acad Sci USA 102:9972–9977

Sarma I, Phookan DB, Boruah S (2015) Influence of manures and biofertilizers on carrot (*Daucus carota* L.) cv. *Early Nantes* growth, yield and quality. EFAJ 10:25–27

Sauter M, Mekhedov SL, Kende H (1995) Gibberellin promotes histone H1 kinase activity and the expression of cdc2 and cyclin genes during the induction of rapid growth in deepwater rice internodes. Plant J 7:623–632

Scaffidi A, Waters MT, Bond CS, Dixon KW, Smith SM, Ghisalberti EL, Flematti GR (2012) Exploring the molecular mechanism of karrikins and strigolactones. Bioorg Med Chem Lett 22:3743–3746

Schachtman DP, Reid RJ, Ayling SM (1998) Phosphorus uptake by plants: from soil to cell. Plant Physiol 116:447–453

Schmülling T (2002) New insights into the functions of cytokinins in plant development. J Plant Growth Regul 21:40–49

Shafi M, Shah A, Bakht J, Shah M, Mohammad W (2012) Integrated effect of inorganic and organic nitrogen sources on soil fertility and productivity of maize. J Plant Nutr 35:524–537

Shaviv A, Mikkelsen RL (1993) Controlled-release fertilizers to increase efficiency of nutrient use and minimize environmental degradation—a review. Fert Res 35:1–12

Shimizu-Sato S, Mori H (2001) Control of outgrowth and dormancy in axillary buds. Plant Physiol 127:1405–1413

Smith SM (2013) Plant biology: Witchcraft and destruction. Nature 504:384–385

Šimko I (1994) Sucrose application causes hormonal changes associated with potato tuber induction. J Plant Growth Regul 13:73–77

Sivasakthivelan P, Saranraj P (2013) *Azospirillum* and its formulation. Int J Microl Res 4:275–287

Skylar A, Sung F, Hong F, Chory J, Wu X (2011) Metabolic sugar signal promotes *Arabidopsis* meristematic proliferation via G2. Dev Biol 351:82–89

Song X, Liu M, Wu D, Griffiths BS, Jiao J, Li H, Hu F (2015) Interaction matters: synergy between vermicompost and PGPR agents improves soil quality, crop quality and crop yield in the field. Appl Soil Ecol 89:25–34

Souza BM, Molfetta-Machado JB, Freschi L, Figueira A, Purgatto E, Buckeridge MS, Van Sluys M, Mercier H (2010) Axillary bud development in pineapple nodal segments correlates with changes on cell cycle gene expression, hormone level, and sucrose and glutamate contents. In Vitro Cell Dev-Plant 46:281–288

Steenhoudt O, Vanderleyden J (2000) *Azospirillum*, a free-living nitrogen-fixing bacterium closely associated with grasses: genetic, biochemical and ecological aspects. FEMS Microbiol Rev 24:487–506

Steeves TA, Sussex IM (1989) Patterns in Plant Development, 2nd edn. Cambridge University Press, London

Stirk WA, Van Staden J (2010) Flow of cytokinins through the environment. Plant Growth Regul 62:101–116

Stirk WA, Ördög V, Van Staden J (1999) Identification of the cytokinin isopentenyladenine in a strain of *Arthronema africanum* (Cyanobacteria). J Phycol 35:89–92

Stirk WA, Novák O, Strnad M, Van Staden J (2003) Cytokinins in macroalgae. Plant Growth Regul 41:13–24

Stirk WA, Novák O, Hradecká V, Pěnčík A, Rolčík J, Strnad M, Van Staden J (2009) Endogenous cytokinins, auxins and abscisic acid in *Ulva fasciata* (Chlorophyta) and *Dictyota humifusa* (Phaeophyta): towards understanding their biosynthesis and homoeostasis. Eur J Phycol 44:231–240

Stirk WA, Van Staden J, Novák O, Doležal K, Strnad M, Dobrev P, Sipos G, Ördög V, Bálint P (2011) Changes in endogenous cytokinin concentrations in *Chlorella* (Chlorophyceae) in relation to light and the cell cycle. J Phycol 47:291–301

Taiz L, Zeiger E (2010) Plant physiology, 5th edn. Sinauer Associates Inc, Sunderland

Takahashi F, Sato-Nara K, Kobayashi K, Suzuki M, Suzuki H (2003) Sugar-induced adventitious roots in *Arabidopsis* seedlings. J Plant Res 116:83–91

Talaat NB, Ghoniem AE, Abdelhamid MT, Shawky BT (2015) Effective microorganisms improve growth performance, alter nutrients acquisition and induce compatible solutes accumulation in common bean (*Phaseolus vulgaris* L.) plants subjected to salinity stress. Plant Growth Regul 75:281–295

Tarkowski P, Ge L, Yong JWH, Tan SN (2009) Analytical methods for cytokinins. Trend Anal Chem 28:323–335

Taylor NJ, Stirk WA, Van Staden J (2003) The elusive cytokinin biosynthetic pathway. S Afr J Bot 69:269–281

Theodorou ME, Plaxton WC (1993) Metabolic adaptations of plant respiration to nutritional phosphate deprivation. Plant Physiol 101:339–344

Tilman D (1998) The greening of the green revolution. Nature 396:211–212

Torelli A, Trotta A, Acerbi L, Arcidiacono G, Berta G, Branca C (2000) IAA and ZR content in leek (*Allium porrum* L.), as influenced by P nutrition and arbuscular mycorrhizae, in relation to plant development. Plant Soil 226:29–35

Turnbull CG, Raymond MA, Dodd IC, Morris SE (1997) Rapid increases in cytokinin concentration in lateral buds of chickpea (*Cicer arietinum* L.) during release of apical dominance. Planta 202:271–276

Ueda N, Kojima M, Suzuki K, Sakakibara H (2012) *Agrobacterium tumefaciens* tumor morphology root plastid localization and preferential usage of hydroxylated prenyl donor is important for efficient gall formation. Plant Physiol 159:1064–1072

Umehara M (2011) Strigolactone, a key regulator of nutrient allocation in plants. Plant Biotechnol 28:429–437

Upadhyaya NM, Letham DS, Parker CW, Hocart CH, Dart PJ (1991) Do *Rhizobia* produce cytokinins? Biochem Int 24:123–130

Van Loon LC (2007) Plant responses to plant growth-promoting rhizobacteria. Eur J Plant Pathol 119:243–254

Van Loon LC, Bakker PAHM, Pieterse CMJ (1998) Systemic resistance induced by rhizosphere bacteria. Annu Rev Phytopathol 36:453–483

Van Staden J (1976) The release of cytokinins by maize roots. Plant Sci Lett 7:279–283

Van Staden J, Bennett PH (1991) Gall formation in crofton weed. Differences between normal stem tissue and gall tissue with respect to cytokinin levels and requirement for in vitro culture. S Afr J Bot 57:246–248

Vassilev N, Vassileva M, Nikolaeva I (2006) Simultaneous P-solubilizing and biocontrol activity of microorganisms: potentials and future trends. Appl Microbiol Biot 71:137–144

Vessey JK (2003) Plant growth promoting rhizobacteria as biofertilizers. Plant Soil 255:571–586

Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG (1997) Human alteration of the global nitrogen cycle: sources and consequences. Ecol Appl 7:737–750

Wandersman C, Delepelaire P (2004) Bacterial iron sources: from siderophores to hemophores. Annu Rev Microbiol 58:611–647

Wang L, Ruan YL (2013) Regulation of cell division and expansion by sugar and auxin signaling. Front Plant Sci 4:1–9

Wang R, Xing X, Crawford N (2007) Nitrite acts as a transcriptome signal at micromolar concentrations in *Arabidopsis* roots. Plant Physiol 145:1735–1745

Weiger TM, Hermann A (2014) Cell proliferation, potassium channels, polyamines and their interactions: a mini review. Amino Acids 46:681–688

Wolters H, Jürgens G (2009) Survival of the flexible: hormonal growth control and adaptation in plant development. Nat Rev Genet 10:305–317

Xiang W, Zhao L, Xu X, Qin Y, Yu G (2012) Mutual information between beneficial microorganisms and the roots of host plants determined the bio-functions of biofertilizers. Am J Plant Sci 3:1115–1120

Ya'acov YL (1996) Nitric oxide in biological systems. Plant Growth Regul 18:155–159

Yong JWH, Wong SC, Letham DS, Hocart CH, Farquhar GD (2000) Effects of elevated [CO_2] and nitrogen nutrition on cytokinins in the xylem sap and leaves of cotton. Plant Physiol 124:767–780

Yong JWH, Ge L, Ng YF, Tan SN (2009) The chemical composition and biological properties of coconut water. Molecules 14:5144–5164

Yong JWH, Letham DS, Wong SC, Farquhar GD (2014) *Rhizobium*-induced elevation in xylem cytokinin delivery in pigeonpea induces changes in shoot development and leaf physiology. Funct Plant Biol 41:1323–1335

Yoshida T, Fujita Y, Sayama H, Kidokoro S, Maruyama K, Mizoi J, Shinozaki K, Yamaguchi-Shinozaki K (2010) AREB1, AREB2, and ABF3 are master transcription factors that cooperatively regulate ABRE-dependent ABA signaling involved in drought stress tolerance and require ABA for full activation. Pl J 61:672–685

Youssef MMA, Eissa MFM (2014) Biofertilizers and their role in management of plant parasitic nematodes. A review. EJBPR 5:1–6

Zachmann JE, Molina JAE (1993) Presence of culturable bacteria in cocoons of the earthworm *Eisenia fetida*. Appl Environ Microbiol 59:1904–1910

Zhang H, Xie X, Kim MS, Kornyeyev DA, Holaday S, Paré PW (2008) Soil bacteria augment *Arabidopsis* photosynthesis by decreasing glucose sensing and abscisic acid levels in planta. Plant J 56:264–273

Zhang H, Tan SN, Wong WS, Ng CYL, Teo CH, Ge L, Chen X, Yong JWH (2014) Mass spectrometric evidence for the occurrence of plant growth promoting cytokinins in vermicompost tea. Biol Fert Soils 50:401–403

Zhang H, Tan SN, Teo CH, Yew YR, Ge L, Chen X, Yong JWH (2015) Analysis of phytohormones in vermicompost using a novel combinative sample preparation strategy of ultrasound-assisted extraction and solid-phase extraction coupled with liquid chromatography–tandem mass spectrometry. Talanta 139:189–197

Zhao Y (2010) Auxin biosynthesis and its role in plant development. Annu Rev Plant Biol 61:49–64

Zhao FY, Cai FX, Gao HJ, Zhang SY, Wang K, Liu T, Wang X (2015) ABA plays essential roles in regulating root growth by interacting with auxin and MAPK signaling pathways and cell-cycle machinery in rice seedlings. Plant Growth Regul 75:535–547

Zhou XY, Song L, Xue HW (2013) Brassinosteroids regulate the differential growth of *Arabidopsis* hypocotyls through auxin signaling components IAA19 and ARF7. Mol Plant 6:887–904