REVIEW ARTICLE

Role of gibberellins in regulation of source–sink relations under optimal and limiting environmental conditions

Noushina Iqbal, Rahat Nazar, M. Iqbal R. Khan, Asim Masood and Nafees A. Khan*

Department of Botany, Aligarh Muslim University, Aligarh 202 002, India

Gibberellins (GAs) are plant growth regulators that are known to stimulate physiological responses in plants and alter the source–sink metabolism through their effect on photosynthesis and sink formation. GAs promote fructose-1,6-biphosphatase and sucrose phosphate synthase and stimulate phloem loading. Photosynthate translocation from source to the developing sink is a major contributing factor towards increasing the sink strength, and GAs are the key regulators of the process through which the extracellular invertase involved in phloem unloading, carbohydrate partitioning and growth of sink tissues is induced. Gibberellic acid is the major contributor in the process of source and sink formation and is one of the most commonly studied GAs. Recent studies indicate that GA signalling is involved in adjustment of plants under limiting environmental conditions and maintains source–sink relation. This adjustment could be mediated through the influence of GA on the regulation of salicylic acid biosynthesis. Here we focus on the developments and understanding of integration of GA action with the metabolic process under optimal and limiting environmental conditions for maintaining source–sink relation. Further advances in the crosstalk between gibberellins and salicylic acid are discussed with reference to abiotic stress tolerance and source–sink relation.

Keywords. Gibberellins, invertase, phloem loading, sink, source, stress.

GIBBERELLINS (GAs) constitute a group of tetracyclic diterpenes best known for their influence on seed germination, leaf expansion, stem elongation, flower and trichome initiation, and flower and fruit development[1]. They play an important role in modulating diverse processes throughout plant development and are known to improve the photosynthetic efficiency of plants through their influence on photosynthetic enzymes, leaf-area index, light interception and enhanced use efficiency of nutrients[2]. The integrated mechanisms induced by gibberellic acid (GA_3) enhance the source potential and redistribution of photosynthates increases sink strength[2]. Plant growth and development are normally limited by photosynthetic resources, i.e. 'source-limited'. The source activity drives the sink metabolism and in turn is related to C and N metabolism. The supply of photoassimilate for growth and differentiation during plant development originates from leaves of the plants and the demand for photosynthate changes as plants grow, mature and senescence. The regulatory role of phytohormones in selective ion uptake and distribution in plants through their effect on membrane properties and transport of assimilates has been shown[3]. The role of GA has been shown in influencing the source–sink relationship by affecting various plant processes[4]. GA_3-mediated increase in photosynthesis and utilization of soil nitrogen (N) was the cause of increase in source–sink relation in mustard[5]. The action of GA promotes sucrose synthesis within the leaf through their positive effect on fructose-1,6-biphosphatase and sucrose phosphate synthase. In addition, GA stimulates phloem loading through its action on cell turgor, apoplast pH and hormone concentration[6]. Moreover, GAs also mediate assimilate translocation through increase in extracellular invertase which is responsible for phloem unloading into the sink, thereby increasing the strength.

GAs are also known to induce various physiological responses in plants and alter plant metabolism under stress. In addition to the role of GAs in the regulation of plant responses to biotic stress, recently, their role in early plant abiotic stress responses has been documented in *Arabidopsis* through modulation of salicylic acid (SA) levels[7]. GAs probably increase SA level through a member of the Gibberellic acid stimulated in *Arabidopsis* (GASA) gene family and thus show the existence of a crosstalk between these two plant hormones in *Arabidopsis* in the alleviation of abiotic stress[8]. GA action in alleviating oxidative stress generated due to the production of reactive oxygen species under stress conditions has been under focus recently[9]. GAs are found to enhance photosynthetic rate and invertase activity under stress[10], favouring

*For correspondence. (e-mail: naf9@lycos.com)

seedling growth under stress condition[9]. The present review focusses on the understanding of the developments in GA actions in the regulation of source–sink relation in plants under optimal and abiotic stress conditions and its impact on overall physiology and metabolism of plants.

Action of GAs in plants

GAs belong to a large family of diterpene acids. Over 136 naturally occurring GAs are known[11]. These are abbreviated as GA with a subscript such as GA_1, GA_2, GA_3, GA_4 and so on, of which GA_3, commonly known as gibberellic acid, is the most important GA in plants. GAs and GA-like substances have been found in almost all the representatives of the plant kingdom ranging from bacteria through fungi to angiosperms. They are produced in roots and younger leaves, but have their highest concentration in seeds of higher plants. GA_3 is the first widely available active form of commercial GAs. It is an economically important secondary metabolite[12] formed as the end-product of the GA pathway[13]. GA_3 acts as a hormone, regulating several processes of plant development[13]. It works with other hormones to promote rapid elongation and division of cells.

Receptor and binding proteins on the plasma membrane to perceive the hormones have been identified. GAs act on the outer face of the plasma membrane[14]. The involvement of G protein in the early GA signalling event in aleurone cells has been reported by Jones *et al.*[15]. GAs are synthesized from geranylgeranyl diphosphate produced mainly through the plastidial methylerythritol phosphate pathway[16]. Geranylgeranyl diphosphate is converted to bioactive GAs through the activity of terpene cyclases, P450 monooxygenases and 2-oxoglutarate-dependent dioxygenases[17]. Among the latter class of enzymes, GA20-oxidase and GA3β-hydroxylase catalyse the last steps of the synthesis of GA_4, the major GA in *Arabidopsis* shoots[18]. The genes encoding these enzymes were shown to be subjected to negative feedback regulation by the action of GA itself[17].

GA is known to affect plant morphology[19]. GA_3 increases shoot length by increasing its rate of elongation in majority of the plants, including *Brassica campestris*[20] and red sanders[21]. Root length was also observed to increase by GA_3 treatment in *Lupinus albus*[22]. GA_3 increased dry matter and leaf-area index in mustard plant[23], and photosynthetic rate in leaves of bean[24,25] and wheat[26]. Khan *et al.*[24] reported an increase in the activity of carbonic anhydrase (CA) in mustard leaves following the application of GA_3 treatment. GA induces the aleurone cells of barley seeds to produce α-amylase which is then transported to the endosperm, where it helps in the production of soluble sugars from starch. GA also activates cell division in the intercalary meristem assisting in the change of rosette plants in long stem and bolting.

In recent years, significant progress has been made in the identification of upstream GA signalling components and *trans* and *cis*-acting factors that regulate downstream GA-responsive genes in higher plants. GAs appear to derepress the signalling pathway by inducing proteolysis of GA signalling repressors (the DELLA proteins). Recent evidence indicates that the DELLA proteins are targeted for degradation by an E3 ubiquitin ligase SKP1–CULLIN–F-box (SCF) complex through the ubiquitin-26S proteosome pathway[27]. KNOX homeodomain proteins and MADS-box proteins (that determine plant architecture during the vegetative and reproductive phase) are transcription factors that preferentially accumulate in indeterminate cells around the shoot apical meristem (SAM), but not in determinate lateral organs such as leaves[28]. KNOX proteins are considered to play a role in the maintenance of the indeterminate meristematic identity of cells that constitute SAM[29]. The KNOX protein NTH15 from tobacco was shown to bind to the promoter sequence of the GA biosynthetic 20-oxidase gene *Ntc12* (ref. 30), involved in the oxidation steps leading to the formation of the bioactive GA_1 (ref. 17).

GAs in source–sink relations under optimal conditions

Several factors either endogenous or environmental conditions contribute to sink strength, but the sink activity can mainly be enhanced by GAs[31]. The influence of GA_3 on plant source is through increasing photosynthetic potential of plants, whereas its efficiency in assimilate transport helps enhance the sink strength, thus establishing its role in the source–sink system.

Sink potential is determined after growth and flowering, and phytohormones have a prominent role in modifying it. Phytohormones might function in enhancing sink potential via increasing cell number and/or regulating cell differentiation such as plastid biogenesis and DNA amplification, or by modifying the duration or rate of dry mass accumulation of developing reproductive organs[32]. Improvement in harvest index of many crops in response to phytohormones has been observed[24]. The source production is responsive to sink metabolism and this makes optimum use of C and N resources[33]. Photosynthesis is the main driving force influencing dry matter partitioning and organ formation. GAs are important in influencing the photosynthetic activity and consequently the source–sink relations. Higher net photosynthesis in leaves has been successfully attained by the exogenous application of GA_3 (ref. 2), through its stimulating effect on some enzymes of dark reaction and nutrient transport[5,24].

Khan *et al.*[5] reported that soaking of seeds in GA_3 manifested its effect at an early stage but was not carried

to the reproductive stage, whereas the spray application of GA_3, compensated the need for GA_3 requirement at a time when it was needed for photoassimilate formation, thus enhancing the sink strength and its redistribution towards seeds.

Role of GA_3 in photosynthesis

Studies have shown that GA_3 promotes growth[23,34], photosynthesis[23] and nitrogen utilization[24,34]. Plants treated with GA contain more soluble carbohydrate than controls, but this accounts only for a small part of the increased carbon assimilation. The increase in glucose content by GA application shows the efficiency of GA in increasing photosynthesis[35]. Khan *et al.*[34] have shown that GA_3 spraying on mustard plants at the pre-flowering stage contributed 35.5% more leaf area and eventually led plants to have a better chance of trapping sunlight and producing more dry matter. The 35.5% increase in leaf area contributed to a 27.1% increase in dry matter production. Spraying of plants with 10 μM GA_3 caused more cells to differentiate. As a result, leaf area and photosynthesis were enhanced by 29.6% and 31.1% respectively, whereas the same concentration applied through seed soaking could enhance leaf area and photosynthesis by 21.4% and 27.0% respectively[36].

Phytohormones have been employed to improve the physiological efficiency of plants by modifying the balance between photosynthesis and respiration[37], affecting stomatal aperture or the activity of photosynthetic enzymes[23]. GA_3 has been found to increase the photosynthetic rate in leaves of plants[26]. It has been suggested that GA_3 treatment could lead to changes in plastid development and chloroplast structure[38]. Contradictory reports are available showing the stimulatory[39] or inhibitory[40] effect of GA on ribulose-1,5-biphosphate carboxylase oxygenase (Rubisco) activity. Yuan and Xu[41] reported that the stimulatory effect on photosynthesis was due to increase in Rubisco content and activity, and GA_3 stimulates the synthesis of Rubisco protein at translational rather than transcriptional level. GAs were identified as one of the possible signals in the regulation of sucrose phosphate synthase (SPS) activity in soybean and spinach leaves. SPS plays an essential role in regulation of photosynthetic sucrose formation[42]. El-Shraiy and Hegazi[43] also found decrease in chlorophyll content with GA application. Application of GA_3 to red clover increased Rubisco activity and improved photosynthesis[44]. GA_3 has been found to increase the N-use efficiency and activities of nitrate reductase (NR) and CA of plants[23]. In a study on mustard, Khan *et al.*[24] reported that plants which were fed with sufficient N and treated with GA_3 showed higher activities of CA and NR, photosynthesis and leaf-area index. Increased N utilization by plants helped in increased photosynthesis.

Nutrient-use efficiency

Studies indicate that GA increases the use efficiency of nutrients. Eid and Abou-Leila[45] reported that GA treatment increased the N, P, K, Mg, Fe, Zn, Mn and Cu content, thereby increasing the mineral nutrient status of the plant. The increased nutrient content enhanced photosynthetic potential of leaves and source strength. GA_3 treatment increased the mineral nutrient levels of *Vigna unguiculata* roots and shoots[46]. Khan *et al.*[25] have shown that the increase in N uptake following GA_3 application was due to increase in shoot growth, which requires more utilization of soil N. GA_3 N uptake results in increased photosynthetic efficiency through maintenance of photosynthetic enzymes. They showed that application of GA_3 at 10 μM increased carbon dioxide exchange rate, plant N and seed N of plants grown at optimal N, but supra-optimal N applied to crop was not utilized. At optimal N, plants receiving GA_3 made maximum use of available N due to enhancement of vegetative growth and development of pods[25]. The utilization of N and S has been found to be interlinked, and GA_3 influences the uptake of these elements[2]. It has been suggested that leaf N was not utilized if mustard plants were grown with insufficient sulphur[5]. GA_3 increased carbon dioxide exchange rate, specific leaf area, leaf dry mass and dry mass of plants receiving 100 mg S kg^{-1} soil, and the gain in dry mass was associated with the increase in the efficiency of leaf. A two-fold increase in sulphur-use efficiency of GA_3-treated plants was noted at sufficient S, i.e. 200 mg S kg^{-1} soil (ref. 5). Thus optimum S is an essential requirement for increasing N utilization and consequently photosynthesis in GA_3-treated plants to enhance the source–sink relationship.

Sucrose synthesis and phloem loading

GAs have a strong influence on phloem loading and regulation of sucrose synthesis[47,48], and consequently on photosynthetic activity. GA-dependent activation of sucrose phosphosynthase has been shown[49], which is involved in the synthesis of sucrose. Sucrose symporter, a key player in apoplastic phloem loading, is regulated by the changes in level of sucrose in leaf. The sucrose-dependent transduction pathway is an important regulatory step in resource allocation. Sucrose is arguably the most important metabolite in this system of resource allocation, as it is generally the major end-product of photosynthetic carbon metabolism and, in most plants it is the predominant form of carbon transported to the heterotrophic tissues[50]. Moreover, in many plants energy-dependent sucrose accumulation in the phloem generates high hydrostatic pressure that drives the long-distance flow of resources. The proton-coupled sucrose symporter mediates phloem loading, the key transport step in assimilate partitioning

for many plants[51]. Chiou and Bush[52] provided evidence that this pivotal activity was regulated by a response pathway sensitive to sucrose levels in leaf. These characteristics are consistent with a sucrose-dependent signalling pathway that dynamically regulates phloem loading by responding to the sucrose levels in the phloem. Elevated sink demand would decrease sucrose levels in the phloem. This would upregulate transport activity and thus increase the capacity for phloem loading. Enhanced phloem loading would draw down the sucrose levels in the mesophyll, perhaps stimulating photosynthetic activity and also increasing the percentage of recently fixed carbon directed to sucrose synthesis versus starch accumulation[52]. In the source–path–sink continuum, phloem loading of organic solutes is a crucial step subject to regulation by phytohormones.

Induction of extracellular invertase and phloem unloading

Extracellular invertase is the key enzyme of an apoplasmic phloem unloading pathway and catalyses the hydrolytic cleavage of sucrose released into the apoplast. This mechanism contributes to long-distance assimilate transport, helps the substrate sustain heterotrophic growth and generates metabolic signals known to affect various processes of primary metabolism and defence responses[53]. Extracellular invertase is particularly suited as a key regulator of apoplasmic phloem unloading due to its enzymatic activity. The K_m value of hexose transporters is in the micro-molar range, and the K_m value of extracellular invertase is in the millimolar range and thus are limiting in phloem unloading. In addition, extracellular invertase catalyses the only irreversible step of the apoplasmic phloem-unloading pathway. An increase in acid invertase activity in response to exogenous GA has been observed in many elongating plant tissues such as *Avena* internodes[54], *Phaseolus vulgaris* internodes[55] and elongating dwarf *Pisum sativum* shoots[56]. Increased acid invertase activity in response to GAs in these tissues was also accompanied by increased hexose concentrations and rapid elongation growth. Wu *et al.*[56] showed an increase in acid invertase mRNA levels within 4 h after GA treatment in dwarf pea seedling. This indicated that enhanced invertase expression was an initial response to GAs causing increased hexose sugar availability and growth elongation. Since unloading of sucrose from the phloem into the apoplast follows the concentration gradient and hexose transport into the sink cells is mediated by high-affinity monosaccharide transporters, extracellular invertase with a high K_m value in the millimolar range is expected to be the limiting step for phloem unloading and thus a potential target for regulation. Studies demonstrate an essential function of extracellular invertase for phloem unloading, carbohydrate partitioning and growth of sink tissues[57]. Extracellular invertase has been shown to be specifically expressed under conditions that require a high carbohydrate supply such as pathogen infection or wounding, and upregulated by a number of stimuli that affect source–sink relations[58]. GAs play an important role in expressing higher acid invertase activity during the rapid elongation phase, enabling the cleavage of imported sucrose to hexoses that are utilized in elongating cells[59]. Tymowska-Lalanne and Kreis[57] have shown that GA_3 plays a significant role in regulating invertase levels. Invertase mRNA from shoots of dwarf *P. sativum* was induced after GA_3 treatment, indicating that the expression of the pea shoot cell-wall invertase gene could be regulated by GA_3 at transcriptional and/or translational levels[56]. In suspension cultured tomato cells (*Lycopersicon esculentum* L.), the addition of GA_3 had no effect on the mRNA for the two invertase genes expressed in flower organs. This finding suggests that the function of GAs in flower induction seems to be unrelated to sucrose metabolism[60]. However, a solely tissue-specific GA induction of the corresponding invertase genes cannot be ruled out.

The long-term GA_3 exposure might enhance growth in the sink leaf (symplastic unloading), where sucrose is rapidly utilized in growth and metabolism. Here, GA may enhance export to the sink leaf by increasing the assimilate concentration gradient between source and sink leaf. GAs increase sink demand by the enhancement of phloem unloading or/and metabolism of carbon assimilates[61].

Assimilate partitioning and sink strength

The assimilate partitioning to sink organ increases the sink strength. Sink strength is defined as the competitive ability of an organ to receive or attract assimilates[62], and is regulated by phytohormones through stimulating nutrient transport and increasing phloem unloading, or acting on metabolism and compartmentalization of sucrose and sorbitol[31]. The systemic distribution of photosynthate is known as 'assimilate partitioning', and it is a major determinant of plant growth and productivity[63]. Phytohormones have been found to be engaged in the assimilate translocation towards reproductive parts of plants[24]. They enhance the partitioning of carbon assimilates to developing fruits by several mechanisms. GAs likely enhance either cell division or enlargement, and increased cell numbers or size results in more sites for assimilate deposition increasing dry matter accumulation. Photosynthate translocation in phloem controlled by the pressure gradient between source and sink is driven through osmosis[64], or the active process of phloem loading or unloading[65]. Partitioning of photosynthetic metabolites between leaf and stem is an important factor in yield determination[66]. Komor[67] reported that total plant productivity relied on appropriate C assimilation rate and the export of C from source leaves. Moreover, phytohormones have

been proposed as mobilizers of assimilates to fruits and modulators for many of the rate-limiting components in the overall process of C partitioning[31]. Recently, it has been suggested that apoplasmic phloem unloading existed in developing apple fruit and invertase was critical for this process[68]. Studies on the activity of NAD^+-dependent sorbitol dehydrogenase (NAD-SDH) and invertase in 'Kousui' fruit after GA application also confirmed the above finding[69]. The mechanism of GA action seems to be more complex than the stimulation of assimilate transport, i.e. phloem loading and unloading. GA-dependent stimulation of SPS activity, a key enzyme in sucrose synthesis, as well as invertases degrading sucrose has been defined[70]. GA and kinetin influence assimilate transport at the site of hormone application[71]. GA affected the source–sink relationship in trans-location and carbohydrate storage in alfalfa[72]. Sucrose concentration in the elongating internodes fell substantially after treatment with GA_3, whereas the concentration of hexose sugars increased. It has been suggested that GA_3 stimulated acid invertase synthesis in the elongating internodes, and established a more favourable sucrose gradient between sink and source[72]. Under source-limiting conditions this, in turn, will lead to a reduced rate of assimilate translocation to competing sinks in the root system. GA_3 promotion of photosynthate accumulation by the pith tissues is a minor contributing factor to GA_3 regulation of phloem translocation. The GAs may stimulate the photosynthetic activity from the beginning of shoot growth and are thus responsible for the enhancement of yield[49]. The possible role of GA in increasing source–sink relation is depicted in Figure 1, where it is shown that GA affects SPS-enhancing sucrose synthesis and is involved in phloem loading of sucrose. Further, apoplastic unloading is also under the influence of GA, through its role in increasing invertase activity. Invertase converts sucrose to hexose, forming a concentration gradient that favours the unloading of sucrose into the sink cell. The hexose in the sink cell is responsible for sink strength. Thus GA indirectly affects sink strength through this pathway and directly through cell expansion that governs sink size. Besides, the phytohormones may stimulate transport of nutrients through the phloem and modify the sink strength by stimulating its growth and increasing the ability for sugar unloading from the phloem. GA increases sink demand by the enhancement of phloem unloading or/and metabolism of C assimilates. A larger fruit size and increased sink demand were closely correlated with changes in the activity of sugar-metabolizing enzymes induced by GA application. Also, Zhang *et al.*[61] found that increased sink demand by GA application was closely related to the activation of invertase cell wall (Inv-CW) bound in the core and invertase neutral (Inv-N) and NAD-SDH in the pulp during rapid growth in fruits. The supply of the transport sugar, sucrose, is a limiting step for the growth of sink tissues[73] and sucrose-metabolizing enzymes are important determinants of sink capacity by generating a sucrose gradient to support unloading of sucrose from the phloem. Thus, the sink strength can be increased through GA, which increases extracellular invertase and sucrose gradient through the conversion of sucrose to glucose. This helps in phloem unloading of carbohydrate in sink organ, subsequently increasing plant yield. Hence, the enzymes responsible for the first metabolic reaction of sucrose are probably critical links between photosynthate production in source leaves and growth capacity of sink organs[73].

GAs in source–sink relations under limiting environmental conditions

Phytohormones are active members of the signal compounds involved in the induction of plant stress responses[69]. They not only regulate plant growth and development, but also increase plant resistance to various environmental stress conditions[74]. Partitioning of assimilates and its effect on dry matter distribution is influenced by several environmental factors such as temperature, drought, salinity and nutrient availability[70]. The photoassimilates produced under salt stress are used to support crucial processes such as growth and osmotic adjustment. In general, salinity causes a reduction in sink enzyme activities, leading to an increase in sucrose in source leaves, with a decrease in photosynthesis rate by feedback inhibition[75]. Application of GA is found to induce extracellular invertase, which acts on sucrose to form hexose. The hexose formed is easily transported to the sink, thereby increasing sink strength (Figure 2). The induction of extracellular invertase by both abiotic and biotic stress stimuli supports the suggestion that extracellular invertase is not only a key modulator of assimilate partitioning, but is also an important component of various stress responses. Similarly, GA increases photosynthetic rate under stress and thus enhances the source potential (Figure 2).

Reduced plant growth under stress conditions could result from an altered hormonal balance and phytohormone application provides an attractive approach to cope with stress[9]. An intimate relationship has been suggested to exist between GA levels and the acquisition of stress protection in barley (*Hordeum vulgare*)[9]. Overexpression of Dwarf and Delayed Flowering 1 (DDF1) causes a reduction in GA_4 content and dwarfism in *Arabidopsis*[76]. There is a correlation among the survival of salt toxicity and the function of DELLA proteins[77]. These results suggest that the salt-inducible DDF1 gene is involved in growth responses under high salinity conditions in part through altering GA levels and improves seed germination[78]. Kumar and Singh[79] reported increased growth and grain yield under saline condition on GA treatment. Archard *et al.*[77] reported that salt-treated *Arabidopsis*

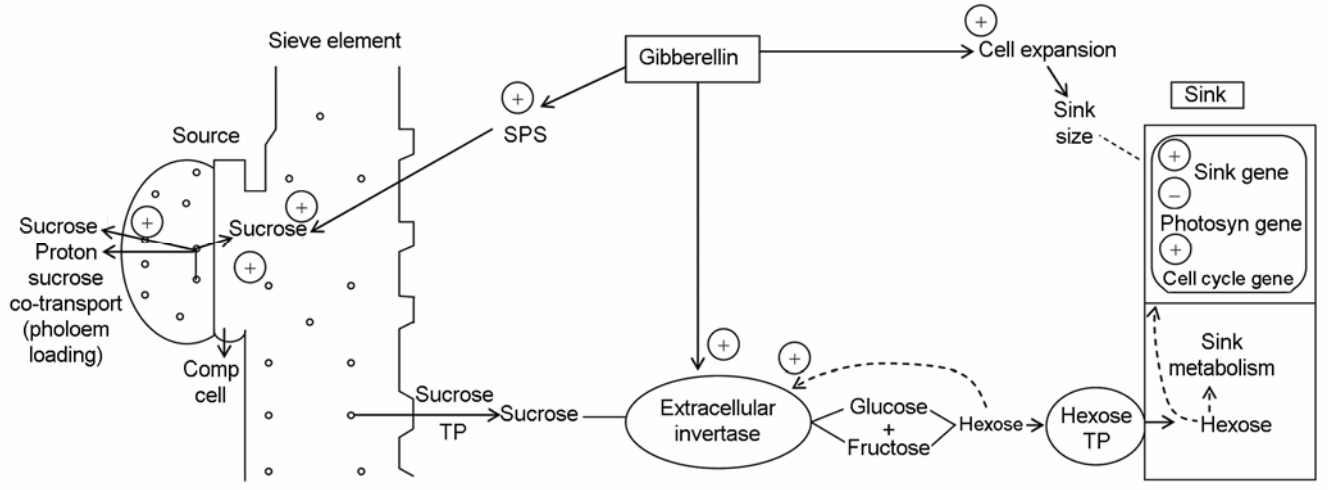

Figure 1. Phloem loading in sieve element and apoplastic phloem unloading mediated by regulation of extracellular invertase. Sucrose is loaded into the sieve element by proton sucrose co-transport and the apoplastic unloading occurs by the action of extracellular invertase on sucrose to form hexose. Hexose is transported through hexose transportor. TP, Transportor; SPS, Sucrose phosphate synthase; Comp cell, Companion cell; Photosyn., Photosynthetic; +, Positive effect; –, Negative effect.

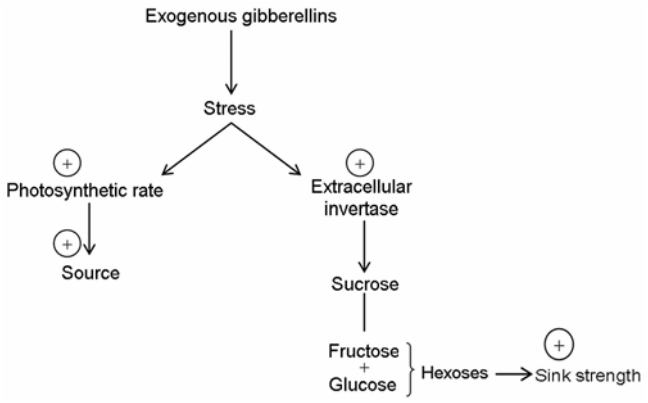

Figure 2. Action of gibberellins on source–sink relation under stress. Extracellular invertase is regulated by both gibberellins and stress, and invertase acts on sucrose to form hexose that increases sink strength. The increase in photosynthetic rate by gibberellin under stress increases source potential.

plants contain reduced levels of bioactive GAs, supporting the idea that salt slows down the growth by modulating the GA metabolism pathway.

Salt stress generally decreases the GA content. However, a remarkable increase in GA_3 content was reported in the leaves of salt-tolerant wild tomato, *L. pennellii*[80]. Exogenous application of GAs overcomes the effect of salinity stress and improves seed germination under saline conditions[78]. GA_3 has also been shown to alleviate the effects of salt stress on pigment content, Hill activity[81] and water-use efficiency[82]. GA_3 treatment of salt-stressed wheat plants resulted in an increased photosynthetic capacity, which was discussed as a major factor for greater dry matter production[23]. The increase in pigment content, photosynthetic capacity and growth through GA treatment under salinity stress indicates its potential in the regulation of source–sink metabolism. Mohammed[83] suggested that the multiple effects of GA_3 which could be involved in alleviating the adverse effect of salinity on mungbean seedlings include the stimulation of growth parameters, increase in photosynthetic pigments concurrent with the marked increase in reducing sugars and sucrose, increase in protein synthesis, including *de novo* synthesis of proteins and accumulation of certain existing proteins, increase in the activities of catalase and peroxidase and decreases in the activities of the ribonuclease and polyphenol oxidase. The promoting effect of GA_3 on seed germination may be attributed to an increase in α-amylase activity, thus increasing soluble sugars, and this might enable the embryo to germinate and accelerate the mobilization of reserves from the endosperm[84]. Siddique *et al.*[85] found ameliorating effect of GA_3 and N in *Brassica juncea* salinity stress. The ameliorative effect of GA and N was on the primary growth potential, activities of NR and CA enzymes, membrane permeability and N-use efficiency. The available nutrients in the growth medium were absorbed more rapidly as reflected by increased leaf N and K concentration, and this led to maximum utilization of absorbed nutrients, resulting in enhancement of vegetative growth and development of more pods (sink).

Similarly, heavy metals alter the hormone content in plants and the application of phytohormones to heavy-metal stressed plants reduces the uptake of these metals[86]. GAs strongly inhibited Cd and Ni incorporation into plants[43]. Picazo *et al.*[87] found that GA increased the sugar content in roots, second and third leaves, and also modified the carbohydrate distribution pattern of rice plants grown with Cd or Ni. GA_3 probably reverses the effect of Ni stress in soybean seedlings by decreasing the Ni uptake by roots to some extent and by enhancing

antioxidant enzyme activities[88], thereby promoting growth. The enhancement of growth rate by GA might result in an increase in leaf area, stimulation of photosynthetic rate, modified partitioning of photosynthates, or their combination[10]. GA-mediated elongation of shoots of various plants results from activation of cell division and/or cell elongation. The GA_3-mediated invertase activity in elongating shoots could result in significant accumulation of hexoses required for primary cell-wall biosynthesis[11], thus favouring seedling growth under stress condition[9].

GA applications effectively promoted the development of flowers during normally inhibitory high temperatures. This was due to the promotion of longitudinal growth of the flower primordium by GA application[50]. Treatment of *Phalaenopsis* flowering shoots with GA at warmer temperatures increased the levels of the active GA required for the promotion of flower development to the same extent as that found in flowering shoots grown in cool temperatures[89].

Recently, it has been reported that GAs interact with other phytohormones such as salicylic acid, abscisic acid and jasmonic acid and influence various plant developmental processes[7,8,90].

The regulation of source–sink relations under abiotic stress could be attributed to GA-enhanced SA production. Transgenic plants overexpressing a GA-responsive gene from beechnut (*Fagus sylvatica*), coding for a member of the GASA family (FsGASA4), showed reduced GA dependence for growth and improved responses to salt, oxidative and heat stress at the level of seed germination and seedling establishment[7]. This finding was further substantiated by the reversal of inhibitory effect of salt, oxidative and heat stress by the exogenous application of GA_3 in the germination and seedling establishment of *Arabidopsis thaliana*. This effect of GA_3 was accompanied by an increase in SA levels[8]. GAs and the overexpression of a GA-responsive gene were able to increase not only the endogenous levels of SA, but also the expression of *ics1* and *npr1* genes involved in SA biosynthesis and action respectively. Furthermore, this hypothesis is supported by the finding that sid2 mutants, impaired in SA biosynthesis, are more sensitive to salt stress than the wild type and are not affected by exogenous application of GA_3.

In contrast, Hamayun *et al.*[90] reported that SA content decreased under the influence of elevated GA_3, whereas it increased in NaCl-treated plants. It suggested that SA biosynthesis was upregulated to strengthen the systemic acquired resistance mechanism under stress conditions. As GA_3 application relieved plants from salt stress, a decline in endogenous SA content was observed. The role of SA as an anti-stress hormone is evident from SA-induced synthesis of heat shock proteins in tobacco plants[91], accumulation of wheat lectins[92], and fast activation of 48-kDa protein kinase in suspension cell culture of tobacco[93]. However, the mechanisms of molecular signalling and their regulation of plant resistance to unfavourable environmental conditions induced by SA are still not clear. Generally, deficiency or a high level of SA increases the plant susceptibility to abiotic stress[94], and probably GA functions in inducing stress tolerance through its influence on SA. Notably, SA also induces genes encoding GA biosynthetic enzymes. These observations indicate that SA promotes seed germination under high salinity by modulating biochemical and molecular mechanisms signalling a crosstalk with GA[95].

Conclusion

GA_3 enhances source and sink potential through increasing photosynthetic enzymes, increasing leaf area for higher interception of photosynthetically active radiation and enhancing nutrient use efficiency. The integrated mechanisms enhance the source potential and redistribution of photosynthates by GA_3 results in increased sink strength. GAs are known to induce extracellular invertase, and phloem loading and unloading. It activates SPS resulting in sucrose formation, which is loaded into the phloem and is acted upon by invertase before being unloaded into the sink. The whole process is under the control of GA.

Besides increasing source–sink potential under optimum growth conditions, the role of GA in increasing source–sink relations under limiting environmental conditions is equally important. The exogenous application of GA helps the plant to ameliorate the abiotic stress conditions. GAs increase the photosynthetic potential of plants under stress resulting in more photosynthate production (source) and this in turn enhances the sink strength. Extracellular invertase also increases under stress. Thus, there could be a role for extracellular invertase in increasing source–sink potential under various abiotic stress conditions. Extracellular invertase may be considered as a central modulator of assimilate partitioning and defence response based on the following four different functions: supplying carbohydrates to sink tissues; regulation of source–sink transitions; amplification of signals that regulate source–sink relations, and integration of signals that regulate source–sink relations and defence responses.

Exogenous application of growth hormones may be useful to return metabolic activities to their normal levels. At a certain concentration GA_3 has been shown to be beneficial for the physiology and metabolism of many plants under abiotic stress, since it may provide a mechanism to regulate the metabolic process as a function of sugar signalling and antioxidative enzymes. There also exists a crosstalk between GAs and SA in the regulation of source–sink relation under abiotic stress. Although GA_3 is the most studied GA, the importance of other GAs

needs to be emphasized. In general, it is GA as a whole that influences the source–sink relation.

Genetic manipulation of GA biosynthesis or degradation has become an alternative approach to the widespread use of chemical regulators to modify source–sink relation, since most of the biosynthetic genes have been identified. Additionally, expression of these genes is under environmental and developmental control. Manipulation of GA biosynthesis not only affects plant growth and morphology, but also biomass accumulation and thus the source–sink potential. Thus by manipulation of the GA biosynthesis pathway or the exogenous application of an adequate quantity of GA at an appropriate time, plant source–sink potential can be regulated to get maximum yield under both optimum and limiting environmental conditions.

1. Yamaguchi, S., Gibberellin metabolism and its regulation. *Annu. Rev. Plant Biol.*, 2008, **59**, 225–251.
2. Khan, N. A., Singh, S., Nazar, R. and Lone, P. M., The source–sink relationship in mustard. *Asian Aust. J. Plant Sci. Biotechnol*., 2007, **1**, 10–18.
3. Steveninck, R. F. M. V., Effect of hormones and related substances on transport. In *Encyclopedia of Plant Physiology* (eds Lüttge, U. and Pitman, M. G.), Springer-Verlag, Berlin, 1976, pp. 307–342.
4. Marschner, H. (ed.), Growth. In *Mineral Nutrition of Higher Plants*, Academic Press, New York, 1986, pp. 269–340.
5. Khan, N. A., Mobin, M. and Samiullah, The influence of gibberellic acid and sulphur fertilization rate on growth and S-use efficiency of mustard (*Brassica juncea* L.). *Plant Soil*, 2005, **270**, 269–274.
6. Zamski, E. and Schaffer, A. A., *Photoassimilate Distribution in Plants and Crops: Source–Sink Relationships*, CRC Press, Boca Raton, 1996.
7. Alonso-Ramírez, A. *et al.*, Evidence for a role of gibberellins in salicylic acid-modulated early plant responses to abiotic stress in *Arabidopsis* seeds. *Plant Physiol*., 2009, **150**, 1335–1344.
8. Alonso-Ramírez, A. *et al.*, Cross-talk between gibberellins and salicylic acid in early stress responses in *Arabidopsis thaliana* seeds. *Plant Signal. Behav*., 2009, **48**, 750–751.
9. Vettakkorumakankav, N. A., Crucial role for gibberellin in stress protecting of plants. *Plant Cell Physiol*., 1999, **40**, 542–548.
10. Ghorbanli, M., Kaveh, S. H. and Sepehr, F. M., Effects of cadmium and gibberellin on growth and photosynthesis of *Glycine max*. *Photosynthetica*, 1999, **17**, 627–631.
11. MacMillan, J., Occurrence of gibberellins in vascular plants, fungi and bacteria. *J. Plant Growth. Regul*., 2002, **20**, 387–420.
12. Martin, G. C., Commercial uses of gibberellins. In *The Biochemistry and Physiology of Gibberellins* (ed. Crozier, A.), Praeger, New York, 1983, pp. 395–444.
13. Takahashi, N., Yamaguchi, I. and Yamane, H., Gibberellins. In *Chemistry of Plant Hormones* (ed. Takahashi, N.), CRC Press, Boca Raton, 1986, pp. 57–151.
14. Gilroy, S. and Jones, R. L., Perception of gibberellin and abscisic acid at the external face of the plasma membrane of barley (*Hordeum vulgare* L.) aleurone protoplasts. *Plant Physiol*., 1994, **104**, 1185–1192.
15. Jones, R. L., Smith, S. J., Desikan, R., Plakidou-Dymock, S., Lovegrove, A. and Hooley, R., Heterotrimeric G proteins are implicated in gibberellin induction of amylase gene expression in wild oat aleurone. *Plant Cell*, 1982, **10**, 245–253.
16. Kasahara, H., Hanada, A., Kuzuyama, T., Takagi, M., Kamiya, Y. and Yamag, S., Contribution of the mevalonate and methylerythritol phosphate pathways to the biosynthesis of gibberellins in *Arabidopsis*. *J. Biol. Chem*., 1982, **277**, 45188–45194.
17. Hedden, P. and Kamiya, Y., Gibberellin biosynthesis: enzymes, genes and their regulation. *Annu. Rev. Plant. Physiol. Plant. Mol. Biol*., 1997**, 48**, 431–460.
18. Talon, M., Koorneef, M. and Zeevaart, J. A., Endogenous gibberellins in *Arabidopsis thaliana* and possible steps blocked in the biosynthetic pathways of the semi dwarf ga4 and ga5 mutants. *Proc. Natl. Acad. Sci. USA*, 1997, **87**, 7983–7987.
19. Chauhan, J. S., Tomar, Y. K., Badoni, A., Singh, N. I., Ali, S. and Debarati, Morphology, germination and early seedling growth in *Phaseolus mungo* L. with reference to the influence of various plant growth substances. *J. Am. Sci*., 2010, **6**, 34–41.
20. Pressman, E. and Shaked, R., Regulation of stem elongation in Chinese cabbage by inflorescence removal and application of growth regulators. *J. Plant Growth Regul*., 1991, **10**, 225–228.
21. Venkataramaiah, V. and Swamy, P. M., Effect of gibberellic acid on growth and net assimilation rate of *Pterocarpus samtalinus* L. *Indian J. For*., 1981, **4**, 91–94.
22. Sidiras, N. and Karsioti, S., Effects of seed size and seed substances of lupins on seedling emergence and root system development in relation to sowing depth, soil water and gibberellin. *J. Agron. Crop Sci*., 1996, **177**, 73–83.
23. Khan, N. A., Effect of gibberellic acid on carbonic anhydrase, photosynthesis, growth and yield of mustard. *Biol. Plant*., 1996, **38**, 145–147.
24. Khan, N. A., Ansari, H. R. and Mobin, M., Effect of gibberellic acid and nitrogen on carbonic anhydrase activity and mustard biomass. *Biol. Plant*., 1996, **38**, 601–603.
25. Khan, N. A., Mir, R., Khan, M., Javid, S. and Samiullah, Effects of gibberellic acid spray on nitrogen yield efficiency of mustard grown with different nitrogen levels. *Plant Growth Regul*., 2002, **38**, 243–247.
26. Ashraf, M., Karim, F. and Rasul, E., Interactive effects of gibberellic acid (GA_3) and salt stress on growth, ion accumulation and photosynthetic capacity of two spring wheat (*Triticum aestivum* L.) cultivars differing in salt tolerance. *Plant Growth Regul*., 2002, **36**, 49–59.
27. Sun, T. P. and Gubler, F., Molecular mechanism of gibberellins signalling in plants. *Annu. Rev. Plant Biol*., 2004, **55**, 197–223.
28. Nishimura, A., Tamaoki, M., Sato, Y. and Matsuoka, M., The expression of tobacco knotted 1-type class1 homeobox genes correspond to regions predicted by the cytohistological zonation model. *Plant J*., 1999, **18**, 337–347.
29. Reiser, L., Sánchez-Baracaldo, P. and Hake, S., Knots in the family tree: evolutionary relationships and functions of KNOX homeobox genes. *Plant Mol. Biol*., 2000, **42**, 151–166.
30. Sakamoto, T., Kamiya, N., Ueguchi-Tanaka, M., Iwahori, S. and Matsuoka, M., KNOX homeodomain protein directly suppresses the expression of a gibberellin biosynthetic gene in the tobacco shoot apical meristem. *Genes Dev*., 2001, **15**, 581–590.
31. Kuiper, D., Sink strength: established and regulated by plant growth regulators. *Plant Cell Environ*., 1993, **16**, 1025–1026.
32. Davies, P. J., *Plant Hormones, Physiology, Biochemistry, and Molecular Biology*, Kluwer, Dordrecht, 1995.
33. Paul, M. J. and Foyer, C. H., Sink regulation of photosynthesis. *J. Exp. Bot*., 2001, **2**, 1383–1400.
34. Khan, N. A., Ansari, H. R. and Samiullah, Effect of gibberellic acid spray during ontogeny of mustard on growth, nutrient uptake and yield characteristics. *J. Agron. Crop Sci*., 1998, **181**, 61–63.
35. Brian, P. W., Elson, G. W., Hemming, H. G. and Radley, M., The plant-growth-promoting properties of gibberellic acid, a metabolic product of the fungus *Gibberella fujikuroi*. *J. Sci. Food Agric*., 2006, **5**, 602–612.
36. Khan, N. A. and Samiullah, Comparative effect of modes of gibberellic acid application on photosynthetic biomass distribution

and productivity of rapeseed-mustard. *Physiol. Mol. Biol. Plant*, 2003, **9**, 141–145.
37. Arteca, R. N. and Dong, C. N., Stimulation of photosynthesis by application of phytohormones to the root systems of tomato plants. *Photosyn. Res*., 1981, **2**, 243–249.
38. Wellburn, F. A. M., Welburn, A. R., Stoddart, J. L. and Trehane, K. J., Influence of gibberellic acid and abscisic acid and the growth retardant CCC, upon plastid development. *Planta*, 1973, **111**, 337–346.
39. Nath, N. and Mishra, D., Changes in RUBP case activity of developing and sensing barley leaves and its alteration by plant growth regulators. *Indian J. Exp. Biol*., 1990, **28**, 665–670.
40. Huber, W. and Sankhla, N., Effect of gibberellic acid on the activities of photosynthetic enzymes and $^{14}CO_2$ fixation products in leaves of *Pennisetum typhoides* seedlings. *Z. Pflanzenphysiol.*, 1974, **71**, 275–280.
41. Yuan, L. and Xu, D.-Q., Stimulation effect of gibberellic acid short-term treatment on the photosynthesis related to the increase in rubisco content in broad bean and soybean. *Photosyn. Res*., 2001, **68**, 39–47.
42. Cheikh, N., Brenner, M. L., Huber, J. L. and Huber, S. C., Regulation of sucrose phosphate synthase by gibberellins in soybean and spinach plants. *Plant Physiol*., 1992, **100**, 1238–1242.
43. El-Shraiy, A. M. and Hegazi, A. M., Effect of acetylsalicylic acid, indole-3-butyric acid and gibberellic acid on plant growth and yield of pea (*Pisum sativum* L.). *Aust. J. Basic Appl. Sci*., 2009, **3**, 3514–3523.
44. Treharne, K. J. and Stoddart, J. L., Effects of gibberellin on photosynthesis in red clover (*Trifolium pratense* L.). *Nature*, 1968, **220**, 457–458.
45. Eid, R. A. and Abou-Leila, B. H., Response of croton plants to gibberellic acid, benzyl adenine and ascorbic acid application. *World J. Agric. Sci*., 2006, **2**, 174–179.
46. Al-Rumaih, M. M., Rushdy, S. S. and Warsy, A. S., Effect of cadmium stress in the presence and absence of gibberellic acid on mineral nutrition of cowpea (*Vigna unguiculata* L.) during ontogenesis. *Agric. Sci*., 2003, **15**, 141–151.
47. Aloni, B., Daie, J. and Wyse, R. E., Enhancement of [^{14}C] sucrose export from source leaves of *Vicia faba* by gibberellic acid. *Plant Physiol*., 1986, **82**, 962–966.
48. Chen, W. S., Liu, Z. H., Yang, L. and Chen, W. H., Gibberellin and temperature influence carbohydrate content and flowering in *Phalaenopsis*. *Physiol. Plant*., 1994, **90**, 391–395.
49. Kozłowska, M., Rybus-Zając, M., Stachowiak, J. and Janowska, B., Changes in carbohydrate contents of *Zantedeschia* leaves under gibberellin-stimulated flowering. *Acta Physiol. Plant*, 2007, **29**, 27–32.
50. Avigad, G., Sucrose and other disaccharides. In *Encyclopedia of Plant Physiology* (eds Loewus, F. A. and Tanner, W.), Springer Verlag, Berlin, 1982, pp. 217–347.
51. Riesmeier, J. W., Willmitzer, L. and Frommer, W. B., Evidence for an essential role of the sucrose transporter in phloem loading and assimilate partitioning. *EMBO J*., 1994, **13**, 1–7.
52. Chiou, T. J. and Bush, D. R., Sucrose is a signal molecule in assimilate partitioning. *Proc. Natl. Acad. Sci. USA*, 1998, **95**, 4784–4788.
53. Roitsch, T., Balibrea, M. E., Hofmann, M., Proels, R. and Sinha, A. K., Extracellular invertase: key metabolic enzyme and PR protein. *J. Exp. Bot*., 2003, **54**, 513–524.
54. Kaufman, P. B., Ghosheh, N. S., LaCroix, J. D., Soni, S. L. and Ikuma, H., Regulation of invertase levels in *Avena* stem segments by gibberellic acid, sucrose, glucose, and fructose. *Plant Physiol*., 1973, **52**, 221–228.
55. Morris, D. A. and Arthur, E. D., Effects of gibberellic acid on patterns of carbohydrate distribution and acid invertase activity in *Phaseolus vulgaris*. *Physiol. Plant*., 1985, **65**, 257–262.
56. Wu, L., Mitchell, J. P., Cohn, N. S. and Kaufman, P. B., Gibberellin (GA_3) enhances cell wall invertase activity and mRNA levels in elongating dwarf pea (*Pisum sativum*) shoots. *Int. J. Plant Sci*., 1993, **154**, 280–289.
57. Tymowska-Lalanne, Z. and Kreis, M., Expression of the *Arabidopsis thaliana* invertase gene family. *Planta*, 1998, **207**, 259–265.
58. Roitsch, T., Source–sink regulation by sugars and stress. *Curr. Opin. Plant Biol*., 1999, **2**, 198–206.
59. Ranwala, A. P. and Miller, W. B., Gibberellin-mediated changes in carbohydrate metabolism during flower stalk elongation in tulips. *Plant Growth Regul*., 2008, **55**, 241–248.
60. Godt, D. E. and Roitsch, T., Regulation and tissue-specific distribution of mRNAs for three extracellular invertase isoenzymes of tomato suggests an important function in establishing and maintaining sink metabolism. *Plant Physiol*., 1997, **115**, 273–282.
61. Zhang, C., Tanabe, K., Tamura, F., Itai, A. and Yoshida, M., Roles of gibberellins in increasing sink demand in Japanese pear fruit during rapid fruit growth. *Plant Growth Regul*., 2007, **52**, 161–172.
62. Farrar, J. F., Sink strength: what is it and how do we measure it? Introduction. *Plant Cell Environ*., 1993, **16**, 10–15.
63. Gifford, R. M., Thorne, J. H., Hitz, W. D. and Giaquinta, R. T., Crop productivity and photo assimilate partitioning. *Science*, 1984, **225**, 801–808.
64. Weatherley, P. E. and Jhonson, R. P., The form and function of sieve tubes: a problem of reconciliation. *Int. Rev. Cytol*., 1968, **24**, 149–192.
65. Ho, L. C. and Baker, D. A., Regulation of loading and unloading in long distance transport systems. *Physiol. Plant*., 1982, **56**, 225–230.
66. Misra, A., Srivastava, N. K., Srivastava, A. K. and Khan, A., Influence of etherel and gibberellic acid on carbon metabolism, growth, and alkaloids accumulation in *Catharanthus roseus* L. *Afr. J. Pharm. Pharmacol.*, 2009, **3**, 515–520.
67. Komor, E., Source physiology and assimilate transport: the interaction of sucrose metabolism, starch storage and phloem export in source leaves and the effects on sugar status in phloem. *Aust. J. Plant Physiol*., 2000, **27**, 497–505.
68. Zhang, L. *et al.*, Evidence for apoplasmic phloem unloading in developing apple fruit. *Plant Physiol*., 2004, **135**, 574–586.
69. Zhang, C., Tanabe, K., Tamura, F., Matsumoto, K. and Yoshida, A., ^{13}C-photosynthate accumulation in Japanese pear fruit during the period of rapid fruit growth is limited by the sink strength of fruit rather than by the transport capacity of the pedicel. *J. Exp. Bot*., 2005, **56**, 2713–2719.
70. Wardlaw, I. F., The control of carbon partitioning in plants. *New Phytol*., 1990, **116**, 341–381.
71. Patrick, J. W. and Mulligan, D. R., Gibberellic-acid-promoted transport of assimilates in stems of *Phaseolus vulgaris*. Effects on assimilate accumulation by the sink. *Ann. Bot*., 1989, **63**, 581–587.
72. Cole, D. F., Dobrenz, A. K. and Massengale, M. A., Effect of gibberellic acid on alfalfa (*Medicago sativa* L.). *Crop Sci*., 1972, **12**, 674–676.
73. Farrar, J., Regulation of shoot–root ratio is mediated by sucrose. *Plant Soil*, 1996, **185**, 13–19.
74. Ewais, E. A., Regulation of cadmium, cobalt, nickel and lead accumulation by plant growth regulators in *Ricinus communnis* L. cotyledon cultured *in vitro*. *Egypt. J. Biotechnol*., 2004, **16**, 228–240.
75. Poljakoff-Mayber, A. and Lerner, H. R., Plants in saline environments. In *Handbook of Plant and Crop Stress* (ed. Pessarakli, M.), Marcel Dekker Inc, New York, 1994, pp. 65–96.
76. Magome, H., Yamaguchi, S., Hanada, A., Kamiya, Y. and Oda, K., Dwarf and delayed-flowering 1, a novel *Arabidopsis* mutant deficient in gibberellin biosynthesis because of overexpression of a putative AP2 transcription factor. *Plant J*., 2004, **37**, 720–729.

77. Achard, P. *et al.*, Integration of plant responses to environmentally activated phytohormonal signals. *Science*, 2006, **311**, 91–94.
78. Kaya, C., Tuna, A. L. and Yoka, I., The role of plant hormones in plants under salinity stress. In *Salinity and Water Stress: Improving Crop Efficiency* (eds Ashraf, M., Ozturk, M. and Arthur, H. R.), Springer, 2009.
79. Kumar, B. and Singh, B., Effect of plant hormones on growth and yield of wheat irrigated with saline water. *Ann. Agric. Res*., 1996, **17**, 209–212.
80. Yurekli, F., Turkan, I., Porgali, Z. B. and Topcuoglu, S. F., Indoleacetic acid, gibberellic acid, zeatin, and abscisic acid levels in NaCl-treated tomato species differing in salt tolerance. *Isr. J. Plant Sci*., 2001, **49**, 269–277.
81. Aldesuquy, H. S. and Gaber, A. M., Effect of growth regulators on *Vicia faba* plants irrigated by seawater, leaf area, pigment content and photosynthetic activity. *Biol. Plant*., 1993, **35**, 519–527.
82. Shah, S. H., Effects of salt stress on mustard as affected by gibberellic acid application. *Gen. Appl. Plant Physiol*., 2007, **33**, 97–106.
83. Mohammed, A. H. M. A., Physiological aspects of mungbean plant (*Vigna radiata* L. Wilczek) in response to salt stress and gibberellic acid treatment. *J. Agric. Biol. Sci*., 2007, **3**, 200–213.
84. Martin, C. C., The role of glumes and gibberellic acid in dormancy of *Themda triandra* spikelets. *Physiol. Plant*., 1975, **33**, 171–176.
85. Siddiqui, M. H., Khan, M. N., Mohammad, F. and Khan, M. M. A., Role of nitrogen and gibberellin (GA_3) in the regulation of enzyme activities and in osmoprotectant accumulation in *Brassica juncea* L. under salt stress. *J. Agron. Crop Sci*., 2008, **194**, 214–224.
86. Rubio, M. I., Escrig, I., Martinez-Cortina, Lopez-Benet, F. J. and Snaz, A., Cadmium and nickle accumulation in rice plants. Effects on mineral nutrition and possible interactions of abscisic and gibberellic acids. *Plant Growth Regul*., 1994, **14**, 151–157.
87. Picazo, I., Ros, R. and Moya, J. L., Heavy metal hormone interactions in rice plants: effect on growth, net photosynthesis and carbohydrate distribution. *J. Plant Growth Regul*., 2007, **14**, 61–67.
88. Saeidi-Sar, S., Khavari-Nejad, R. A., Fahimi, H., Ghorbanli, M. and Majd, A., Interactive effects of gibberellin and ascorbic acid on lipid peroxidation and antioxidant enzyme activities in *Glycine max* seedlings under nickel stress. *Russ. J. Plant Physiol*., 2007, **54**, 74–79.
89. Su, W. R. *et al.*, Changes in gibberellin levels in the flowering shoot of *Phalaenopsis* hybrida under high temperature conditions when flower development is blocked. *Plant Physiol, Biochem*., 2001, **39**, 45–50.
90. Hamayun, M., Shin, J. H., Khan, S. A., Ahmad, B., Shin, D. H., Khan, A. L. and Lee, I. J., Exogenous gibberellic acid reprograms soybean to higher growth and salt stress tolerance. *J. Agric. Food Chem*., 2010, **58**, 7226–7232.
91. Burkhanova, E. A., Fedina, A. B. and Kulaeva, O. N., Effect of salicylic acid and (2′–5′)-oligoadenylates on protein synthesis in tobacco leaves under heat shock conditions: a comparative study. *Russ. J. Plant Physiol.*, 1999, **46**, 16–22.
92. Shakirova, F. M. and Bezrukova, M. V., Induction of wheat resistance against environmental salinization by salicylic acid. *Biol. Bull*., 1997, **24**, 109–112.
93. Mikolajczyk, M., Awotunde, O. S., Muszynska, G., Klessig, D. F., Dobrowolska, G., Osmotic stress induces rapid activation of a salicylic acid-induced protein kinase and a homolog of protein kinase ASK1 in tobacco cell. *Plant Cell*, 2000, **12**, 165–178.
94. Yuan, S. and Lin, H. H., Role of salicylic acid in plant abiotic stress. *Z. Naturforsch. C*, 2008, **63**, 313–320.
95. Lee, S. and Park, C. M., Modulation of reactive oxygen species by salicylic acid in *Arabidopsis* seed germination under high salinity. *Plant Signal. Behav*., 2010, **5**, 1534–1536.

Received 20 July 2010; revised accepted 3 February 2011