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

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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. Photosynthetic 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. 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. The integrated mechanisms induced by gibberellic acid (GA3) enhance the source potential and redistribution of photosynthates increases sink strength. 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 photosyntheate 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. The role of GA has been shown in influencing the source–sink relationship by affecting various plant processes. GA3-mediated increase in photosynthesis and utilization of soil nitrogen (N) was the cause of increase in source–sink relation in mustard. 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. 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. 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. GA action in alleviating oxidative stress generated due to the production of reactive oxygen species under stress conditions has been under focus recently. GAs are found to enhance photosynthetic rate and invertase activity under stress, favouring...
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 gibberelic 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\(_1\) 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\(^{14}\). 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\(^{22}\). 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 GA3\(_\beta\)-hydroxylase catalyze the last steps of the synthesis of GA\(_1\), 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\(^{19}\).

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\(^{24}\) and wheat\(^{25}\). Khan et al.\(^{26}\) 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 \(\alpha\)-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\(^{33}\). The source production is responsive to sink metabolism and this makes optimum use of C and N resources\(^{34}\). 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\(^{34}\).

Khan et al.\(^{3}\) reported that soaking of seeds in GA\(_3\) manifested its effect at an early stage but was not carried
Role of GA in photosynthesis

Studies have shown that GA promotes growth\textsuperscript{23,34}, photosynthesis\textsuperscript{23} and nitrogen utilization\textsuperscript{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\textsuperscript{35}. Khan et al.\textsuperscript{34} have shown that GA\textsubscript{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\textsubscript{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\textsuperscript{36}. Phytohormones have been employed to improve the physiological efficiency of plants by modifying the balance between photosynthesis and respiration\textsuperscript{37}, affecting stomatal aperture or the activity of photosynthetic enzymes\textsuperscript{23}. GA\textsubscript{3} has been found to increase the photosynthetic rate in leaves of plants\textsuperscript{26}. It has been suggested that GA\textsubscript{3} treatment could lead to changes in plastid development and chloroplast structure\textsuperscript{38}. Contradictory reports are available showing the stimulatory\textsuperscript{39} or inhibitory\textsuperscript{40} effect of GA on ribulose-1,5-biphosphate carboxylase oxygenase (Rubisco) activity. Yuan and Xu\textsuperscript{41} reported that the stimulatory effect on photosynthesis was due to increase in Rubisco content and activity, and GA\textsubscript{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\textsuperscript{42}. El-Shraiy and Hegazi\textsuperscript{43} also found decrease in chlorophyll content with GA application. Application of GA\textsubscript{3} to red clover increased Rubisco activity and improved photosynthesis\textsuperscript{44}. GA\textsubscript{3} has been found to increase the N-use efficiency and activities of nitrate reductase (NR) and CA of plants\textsuperscript{23}. In a study on mustard, Khan et al.\textsuperscript{24} reported that plants which were fed with sufficient N and treated with GA\textsubscript{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\textsubscript{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\textsubscript{3} treatment increased the mineral nutrient levels of Vigna unguiculata roots and shoots\textsuperscript{46}. Khan et al.\textsuperscript{23} have shown that the increase in N uptake following GA\textsubscript{3} application was due to increase in shoot growth, which requires more utilization of soil N. GA\textsubscript{3} N uptake results in increased photosynthetic efficiency through maintenance of photosynthetic enzymes. They showed that application of GA\textsubscript{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\textsubscript{3} made maximum use of available N due to enhancement of vegetative growth and development of pods\textsuperscript{25}. The utilization of N and S has been found to be interlinked, and GA\textsubscript{3} influences the uptake of these elements\textsuperscript{2}. It has been suggested that leaf N was not utilized if mustard plants were grown with insufficient sulphur\textsuperscript{4}. GA\textsubscript{3} increased carbon dioxide exchange rate, specific leaf area, leaf dry mass and dry mass of plants receiving 100 mg S kg\textsuperscript{−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\textsubscript{3}-treated plants was noted at sufficient S, i.e. 200 mg S kg\textsuperscript{−1} soil (ref. 5). Thus optimum S is an essential requirement for increasing N utilization and consequently photosynthesis in GA\textsubscript{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\textsuperscript{47,48}, and consequently on photosynthetic activity. GA-dependent activation of sucrose phosphosynthase has been shown\textsuperscript{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\textsuperscript{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\textsuperscript{51}. Chiu and Bush\textsuperscript{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 signaling 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\textsuperscript{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 apoplastic 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\textsuperscript{53}. Extracellular invertase is particularly suited as a key regulator of apoplastic 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 apoplastic 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\textsuperscript{54}, *Phaseolus vulgaris* internodes\textsuperscript{55} and elongating dwarf *Pisum sativum* shoots\textsuperscript{56}. Increased acid invertase activity in response to GAs in these tissues was also accompanied by increased hexose concentrations and rapid elongation growth. Wu \textit{et al.}\textsuperscript{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\textsuperscript{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\textsuperscript{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\textsuperscript{59}. Tymowska-Lalanne and Kreis\textsuperscript{57} have shown that GA\textsubscript{3} plays a significant role in regulating invertase levels. Invertase mRNA from shoots of dwarf *P. sativum* was induced after GA\textsubscript{3} treatment, indicating that the expression of the pea shoot cell-wall invertase gene could be regulated by GA\textsubscript{3} at transcriptional and/or translational levels\textsuperscript{56}. In suspension cultured tomato cells (*Lycopersicon esculentum* L.), the addition of GA\textsubscript{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\textsuperscript{60}. However, a solely tissue-specific GA induction of the corresponding invertase genes cannot be ruled out.

The long-term GA\textsubscript{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\textsuperscript{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\textsuperscript{62}, and is regulated by phytohormones through stimulating nutrient transport and increasing phloem unloading, or acting on metabolism and compartmentalization of sucrose and sorbitol\textsuperscript{51}. The systemic distribution of photosynthate is known as ‘assimilate partitioning’, and it is a major determinant of plant growth and productivity\textsuperscript{63}. Phytohormones have been found to be engaged in the assimilate translocation towards reproductive parts of plants\textsuperscript{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\textsuperscript{64}, or the active process of phloem loading or unloading\textsuperscript{65}. Partitioning of photosynthetic metabolites between leaf and stem is an important factor in yield determination\textsuperscript{66}. Komor\textsuperscript{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. Recently, it has been suggested that apoplastic phloem unloading existed in developing apple fruit and invertase was critical for this process. Studies on the activity of NAD-dependent sorbitol dehydrogenase (NAD-SDH) and invertase in ‘Kousui’ fruit after GA application also confirmed the above finding. 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. GA and kinetin influence assimilate transport at the site of hormone application. GA affected the source–sink relationship in trans-location and carbohydrate storage in alfalfa. Sucrose concentration in the elongating internodes fell substantially after treatment with GA3, whereas the concentration of hexose sugars increased. It has been suggested that GA3 stimulated acid invertase synthesis in the elongating internodes, and established a more favourable sucrose gradient between sink and source. Under source-limiting conditions this, in turn, will lead to a reduced rate of assimilate translocation to competing sinks in the root system. GA3 promotion of photosynthetic activity from the beginning of shoot growth and are thus responsible for the enhancement of yield. 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 increasing the ability for sugar unloading from the phloem. GA increases sink demand by the enhancement of phloem unloading 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. 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 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 photosynthetic production in source leaves and growth capacity of sink organs.

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. They not only regulate plant growth and development, but also increase plant resistance to various environmental stress conditions. Partitioning of assimilates and its effect on dry matter distribution is influenced by several environmental factors such as temperature, drought, salinity and nutrient availability. The photoasimilates 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. 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. An intimate relationship has been suggested to exist between GA levels and the acquisition of stress protection in barley (Hordeum vulgare). Overexpression of Dwarf and Delayed Flowering 1 (DDF1) causes a reduction in GA4 content and dwarfism in Arabidopsis. There is a correlation among the survival of salt toxicity and the function of DELLA proteins. 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. Kumar and Singh reported increased growth and grain yield under saline condition on GA treatment. Archard et al. 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 transporter. 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 GA₃ content was reported in the leaves of salt-tolerant wild tomato, L. pennellii. Exogenous application of GAs overcomes the effect of salinity stress and improves seed germination under saline conditions. GA₃ has also been shown to alleviate the effects of salt stress on pigment content, Hill activity and water-use efficiency. GA₃ treatment of salt-stressed wheat plants resulted in an increased photosynthetic capacity, which was discussed as a major factor for greater dry matter production. 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 suggested that the multiple effects of GA₃ 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 GA₃ 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. Siddique et al. found ameliorating effect of GA₃ 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. GAs strongly inhibited Cd and Ni incorporation into plants. Picazo et al. 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. GA₃ 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, 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. 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, thus favouring seedling growth under stress condition.

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. 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.

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.

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. 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. 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 ics$1$ and npr$1$ 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. 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, accumulation of wheat lectins, and fast activation of 48-kDa protein kinase in suspension cell culture of tobacco. 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, 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.

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.

16. Kasahara, H., Hanada, A., Kuzuyama, T., Takagi, M., Kamiya, Y. and Yamag, S., Contribution of the mevalonate and mehtylenyri-


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