INNSPUB

International Journal of Biosciences | IJB |
ISSN: 2220-6655 (Print), 2222-5234 (Online)
http://www.innspub.net
Vol. 14, No. 5, p. 450-459, 2019

REVIEW PAPER OPEN ACCESS

β-Aminobutyric acid (BABA) priming and abiotic stresses: a review

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Key words: β-Aminobutyric acid (BABA), Priming, Abiotic stresses.

http://dx.doi.org/10.12692/ijb/14.5.450-459 Article published on May 26, 2019

Abstract

The use of priming agents in combating the different plants' abiotic stresses has gained popularity over the years. β-Aminobutyric acid (BABA) is a non- protein amino acid, whose endogenous presence in plant has been lately discovered, is one of such priming agents that are employed for this purpose. While its efficacy against biotic stresses is well established by several pieces of research, its efficacy against abiotic stresses is relatively less pronounced. Although, its ability to independently induce stress tolerance has been reported, modulating plants' defence system as well as the production of ROS (reactive oxygen species) scavenging antioxidants to mitigate oxidative stresses are still the cardinal points to understanding BABA induced tolerance to abiotic stresses. Some of the changes (physiological, biochemical, molecular) effected by BABA priming against abiotic stresses include accelerated stomatal closure, water use efficiency, photosynthesis enhancement, solute content reorganisation, membrane stability, and stress-responsive gene expression. It is concluded that the effectiveness of BABA against abiotic stresses cannot be overemphasised, however studies regarding its effects against combined stresses and details of its activity, especially at molecular level are still much needed.

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Introduction

The decrease in global agricultural yield and productivity vis-a-vis the expanding population poses a challenge in the 21st century. The role of abiotic stresses in the fall of production efficiency is not minimal. Bray (2000) puts reduction in yield caused by abiotic stresses for most crops at 50%. According to Gao *et al.* (2007), abiotic stresses are the most harmful agents to crop yield and productivity. Abiotic stresses refers to environmental conditions leading to reduced growth and yield below optimum levels (Cramer *et al.*, 2011). Factors that predisposes abiotic stresses are numerous and usually naturally occurring and hence, non-avoidable. Some of these include intense sunlight, temperature and wind harmful to plants and animals in an affected area. Climate change as well as anthropogenic contributions (industrialisation and urbanisation) aggravates the severity of abiotic stresses (Fedoroff *et al.*, 2010; Nagajyoti *et al.*, 2010).

To overcome stress conditions (biotic and abiotic stresses) in plant cultivation, many approaches have and are been used, ranging from plant breeding (Bänziger *et al.*, 2006; Araus *et al.,* 2008), use of plant growth regulators (Taiz and Zeiger, 2006; Iqbal *et al.,* 2014), use of osmo-protectants (Lutts, 2000; Hua and Guo, 2002; Hussain, *et al.*, 2008), production of genetically modified plants (Garg *et al.*, 2002; Bahieldina *et al.*, 2005;), use of silicon (Hattori *et al.*, 2001; Hamayun *et al.*, 2010) priming and so on.

Priming or sometimes hardening is defined as the process whereby plants are treated with different agents (natural and synthetic) to prepare them for germination and early growth stage after sowing. In seed priming for example, seeds are exposed to mild stress conditions to equip them with the ability to withstand harsher conditions (Macarisin *et al.*, 2009). The primed seeds undergo first stage germination but the radicle does not protrude through the seed coat (Solang *et al.,* 2014). Seed priming treatments may be by soaking in water (hydropriming), salt solution (halopriming), osmotic solution (osmopriming), semi-solids (solid-matrix priming) hormones (hormonal priming), nutrients (nutrient priming) or even with inoculation with microorganisms (biopriming) (Chatterjee *et al.*, 2018; Jisha *et al.*, 2013; Raj and Raj, 2019).

The chemical agents involved in seed priming which are called seed primers or simply primers. Majorly, these seed primers have been well adopted in alleviating both biotic and abiotic stresses. Apart from effecting resistance to various biotic and abiotic stresses, priming also offer the advantage of reducing expensive energy investments in defence mechanism as plants full potential to stresses have not been fully exploited through it (Ton *et al.*, 2005). The main objective of this review is therefore, to evaluate the extent, prowess and mode of action of BABA against abiotic stresses in various plants.

β- Aminobutyric acid (BABA)

β- Aminobutyric acid (BABA) is a non-protein amino acid with chemical formula of C4H9NO2. It has two isomers: gamma-aminobutyric acid (GABA) and alpha-aminobutyric acid (AABA). BABA is generally regarded as being not common in nature (i.e. xenobiotic) however, Gamliel and Katan (1992) reported its occurrence in the root exudates of tomato plant grown on solarised soil. Thevenet *et al.* (2017) and Baccelli *et al.* (2017) also stated that the substance is naturally occurring in plants and its presence becomes more noticeable (i.e. increases in its endogenous level) with increasing stress condition. According to Baccelli and Mauch-Mani (2017), BABA can be considered a novel (priming) hormone due to its impressive ability in inducing tolerance and due to its levels in planta and its temporal dynamics.

BABA belongs to a group of endogenous substances that are released by neurons to act on receptor sites and eventually produce a functional change in the properties of the target cells.

They are known as neurotransmitters (Deutch, 2013). The properties of BABA also include its effectiveness at relatively low concentrations in an enantiomer-specific way (Jakab *et al.*, 2001).

Before 1958, the common methods for synthesising BABA involve the reduction of intermediate amino derivatives obtained by the reaction of the appropriate amine with ethyl acetoacetate, for example from crotonic acid and ammonia under pressure. However, in 1958, Zukha and Rivlin explained that BABA can be synthesise simply by catalytic hydrogenolysis of N-benzyl-DL- β -aminobutyric acid (Zukha and Rivlin, 1958). Later on, stereo-selective synthesis of BABA (optically pure form) gained more recognition owing to the biological significance of the substance (Liu and Sibi, 2002; Weiß *et al.*, 2010).

Modes of application Of BABA

BABA, like other chemical stress inducers, has been applied to different plants in more than one style. It has been employed using soil drenching (Jakab *et al.*, 2005; Shaw *et al.*, 2016; Javadi *et al.*, 2017), as foliar spray (Vaknin, 2016; Roylawar and Kamble, 2017), as fruit spray (Cohen *et al.*, 1994), and also as seed treatment (Jisha and Puthur, 2016a; Mostek *et al.*, 2016; Ziogas *et al.*, 2017). In all of these different modes of application, BABA proved generally valuable in mitigating the various stress conditions it has been used against. It is interesting to note that the mode of application of BABA may be vital to their performance as shown by different researches carried out by workers. Luna *et al* (2016), for example reported retardation in the growth of tomato plant treated with BABA applied as soil drench to the root while the growth was not affected with BABA applied as seed treatment. Quite rarely, the effect of the mode of action of BABA may be plant-specific as regards some parameters. For instance, while BABA applied as seed treatment against salt stress promoted the fresh and dry weight of all 3 varieties of rice tested by Jisha and Puthur (2016a), the same treatment was not effective with a certain line of barley plant under salt stress (Mostek *et al.*, 2016). Additionally, while soil drenching with BABA failed to increase the yield of wheat (Du *et al.*, 2012), it did increase the yield in potato (Sós-Hegedűs *et al.*, 2014).

The use of BABA as a plant activator or to induce defence against stress has been known for quite a long time as 1963 (Papavizas and Davey, 1963). Its prowess against stresses is more exploited in terms of biotic stresses than abiotic stresses. Cohen *et al.*, (2016), in his review, demonstrated how the substance has been used successfully in 40 different species against about 80 pathogens and pests. BABA induce resistance against biotic and abiotic stresses through a 'new physiological state' mediated by priming and not because remnants of the priming agent is left in the tissue of the emerging plant (Cohen *et al.*, 2016). More interestingly, the transgenerational effect discovered with BABA could be seen as an edge it has over other chemical priming agents (Slaughter *et al.*, 2012). This long term efficiency may however needs to be further tested with abiotic stresses.

BABA has been adopted in alleviating stress in a host of plants, majority of these being against biotic stress. The effectiveness of BABA against abiotic stresses like salinity, drought stress, heat stress, cold stress, and so on has been attributed to various factors and mechanisms including differences in environmental conditions. In other words findings now show, to an extent, that the common perception that BABA induced protection in plants follows a general mechanism is not an absolute fact. For example, following BABA treatment, there was a slight fall in aspartate accumulation in flax (Quéro *et al.*, (2015), whereas its accumulation was induced in Arabidopsis (Luna *et al.*, 2014).

BABA priming against drought stress

From the foremost abiotic stresses BABA has been used against and has proved effective is drought stress. Jakab *et al.* (2005) showed that BABA delayed wilting, lowered the rate of water loss and accelerated stomatal closure in Arabidopsis under drought stress. A similar report was given by Macarisin *et al.* (2009) for drought stressed melon plant. In 2012, BABA promoted the water use efficiency and desiccation tolerance of two spring wheat cultivars under soil drying but did not improve the grain yield (Du *et al.*, 2012). Sós-Hegedűs *et al.* (2014) reported similarly for potato but with increase in tuber yield. Other plants where this efficacy of BABA against drought stress has been reported include flax (Quéro *et al.*, 2015), maize (Shaw *et al.*, 2016), rice (Jisha and Puthur, 2016a) beans (Jisha and Puthur, 2016b), rapeseed (Mohamadi *et al.*, 2017) and sweet cherry (Javadi *et al.*, 2017).

For drought stress, a number of approaches and ways have been exploited by workers in explaining how BABA alleviate the effects of the stress. BABA pre-treated plants under drought stress showed quickened stomata closure, enhancement in photosynthetic pigment content and in photosynthetic and mitochondrial activities with decreasing malondialdehyde content in seedling and accumulation of proline, total carbohydrate, total protein, and nitrate reductase activity (Jisha and Puthur, 2016a, 2016b). BABA did not induce accumulation of proline in the work of Shaw *et al.*, (2016) on maize plant under drought stress.

As a function of the stress applied, BABA induced tolerance takes different signaling (defence) pathways (Cohen *et al.*, 2016). Jakab *et al.*, (2005) solved the debate of whether BABA induced drought resistance is from salicyclic acid (SA) pathway or through Abscisic acid (ABA) pathway and proved that the drought tolerance induced by BABA is by following the ABA pathway system for drought stress protection as BABA treatment could not induce drought tolerance without the ABA signaling.

This result was similarly true for wheat plant as reported by Du *et al.*, (2012) but however less true for maize plant which followed majorly a (Jasmonic acid) JA-dependent pathway (Shaw *et al.*, 2016). In their own work on crab apple (*Malus pumila*), Macarisin *et al.*, (2009) claimed that although the assertion that BABA induced resistance is achieved by potentiating the ABA pathway is true to a large extent, it should however be noted that BABA is capable of inducing resistance in an ABA independent pathway. Owing to the nature of proteins that was observed from their proteomic analysis, they suggested that the BABA specific roles in inducing drought tolerance include changes in cell wall enzymes and suppression of lignin biosynthesis.

The analysis of metabolomics and ionomics profiling performed by Quéro *et al.*, (2015) revealed that BABA enhanced reorganisation in solute content leading to increased accumulation of non-structural carbohydrate and protein with a decrease in inorganic solutes. From Quéro *et al.*, (2015) experiment, there was slight fall in aspartate content as induced by BABA priming. Reduction in production of reactive oxygen species (like superoxide O_2^-, hydrogen peroxide H_2O_2) coupled with significantly intensified antioxidant activities; both enzymatic and non-enzymatic antioxidants (superoxide dismutase SOD, guaiacol peroxidase GPX, ascorbate peroxidase APX, ascorbic acid ASA, anthocyanins, flavonoids) are also involved with BABA priming (Du *et al.*, 2012; Jisha and Puthur, 2016b; Peyman and Neda, 2013). Shaw *et al.*, (2016) alluded maintenance of a balanced redox status against oxidative damage caused by drought to high increase in reduced glutathione (GSH) due to increase glutathione reductase (GR) activity and mRNA enhanced expression. In *Prunus avium*(sweet cherry), aside the improvement in morphological characters (like number of leaves, leaf area, fresh and dry weight), BABA was also shown to enhance membrane stability, relative water content, antioxidant enzymes (peroxidase POD, ascorbate peroxidase APX) activities under drought stress (Javadi *et al.*, 2017).

BABA priming against salt stress

Just like drought stress, quite a number of work have been carried out by researchers to investigate the ability of BABA in mitigating against the difficult condition of salt stress. BABA induced salt tolerance in Arabidopsis was reported by Ton *et al.*, (2005).

More effective response to salt stress was observed by Mostek *et al.* (2016) in his experiment with two barley lines. BABA was also effective against salt stress in rice (Jisha and Puthur, 2016a) and beans (Jisha and Puthur, 2016b).

BABA treated plants showed reduction in wilting rate during salt stress in Arabidopsis (Jakab *et al.*, 2005). The activity of antioxidants enzymes is boosted with BABA treatment under salt stress (Qingli *et al.*, 2015a). Like in drought stress, Jakab *et al.*, (2005) held that the SA pathway signaling is dispensable in BABA induced resistance against salt stress. Photosynthesis under salt stress was also aided with BABA priming (Jisha *et al.*, 2016b). With BABA priming in rice under salt stress, relative membrane permeability was reduced considerably and with increase in content of soluble sugar, there was no significant increase in proline accumulation (Yong-ming *et al.*, 2010). Conversely in the same rice plant, Jisha *et al.*, (2016a) reported proline accumulation with BABA treatment under salt stress.

Ton *et al.*, (2005) suggested from their work on Arabidopsis that the inability of BABA to induce salt tolerance in the plant was because of the impaired priming for ABA-inducible gene expression. What this means is that augmented expression of ABA-dependent defences is vital to BABA induced tolerance to salt stress. This potentiation of defence mechanism is in corroboration of the previous findings of Jakab *et al.*, (2001).

Experiments in proteomics involving the use of 2D gel electrophoresis and MALDI-TOF mass spectrometry revealed that BABA induce defence and detoxification process involving the up regulation of antioxidant enzymes (catalase, peroxidase and superoxide dismutase), chaperones and pathogen-related (PR) proteins (Mostek *et al.*, 2016). BABA was similarly observed to induce salt acclimation in citrus through alternation of specific proteins like citrin (Ziogas *et al.*, 2017).

BABA priming against other abiotic stresses

The efficacy of BABA priming has also been tested against other abiotic stresses with varying degrees of success. Zimmerli *et al.*, (2008) tested its effect on heat stress in Arabidopsis plant and recorded its significance in enhancing thermotolerance. ABA was the only hormone that played a role in this amelioration. With the same Arabidopsis plant, BABA was found effective against cadmium (heavy metal) stress by alleviating the root growth inhibition caused by the metal. It was suggested from the results of the study that the alleviation followed a glutathione (GSH) dependent pathway (Cao *et al.*, 2009). Using biophoton analysis and proteomics techniques, cellular detoxification activation and plants' defence modulation were the reasons proffered in combating cadmium challenge in soybean with BABA (Hossain *et al.*, 2012). Similar trend of effectiveness of BABA was reported by Liu *et al.*, (2011) in their experiment, also, with Arabidopsis when the plant was subjected to simulated acid rain. While BABA did not only account for serious metabolism change, it also activated the antioxidants systems, the salicyclic, jasmonic and abscisic acid signaling pathways (Liu *et al.*, 2011). By increasing fruit firmness, activating antioxidants activities and reducing membrane permeability, post-harvest application of BABA has helped to enhance senescence inhibition and confers decay tolerance in sweet cherry (Wang *et al.*, 2015), strawberry (Jannatizadeh *et al.*, 2018) . Pre-harvest treatment of BABA to fruits of 'Bluecrop' highbush blueberry yielded similarly (Chea *et al.*, 2019). The use of BABA against low Potassium stress has also been experimented, with BABA proving handy in increasing potassium (K^+) uptake under low K^+ condition through modulation of appropriate genes (Cao *et al.*, 2008; Jiang *et al.*, 2012). By promoting the activity of antioxidant enzymes (SOD, APX, CAT and POD), synthesis of organic acid and with the expression levels of appropriate genes, BABA was effective in alleviating the challenge of copper stress (Kuizheng *et al.*, 2014), cadmium stress (Song *et al.*, 2016), zinc stress (Xuelian *et al.*, 2015), heat stress (Qingli, *et al.*, 2015b) and alkaline stress in tobacco (Benwu *et al.*, 2017). Under $NAHCO_3$ stress, BABA significantly boosted net photosynthesis and antioxidant system activity in Rhododendron (Xu *et al.*, 2018).

Future prospects

Like many other chemical inducers, BABA induced priming needs to be studied more, especially in omics, in order to elucidate the internal agents (genes, proteins, metabolites) involved in its activity and their reactions against the various abiotic stresses (studying their areas of intersection and difference) and in order to seek ways to alteration or adjustment using biotechnology. This will work hand in hand in promoting developing more tolerant cultivars of different crops and in enhancing new agricultural strategies. The environmental effects of BABA and its potential phytotoxicity are also areas that should be equally more researched.

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