COMMUNICATIVE & INTEGRATIVE BIOLOGY
2017, VOL. 10, NO. 2, e1290019 (3 pages)
http://dx.doi.org/10.1080/19420889.2017.1290019

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ARTICLE ADDENDUM

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When the story proceeds backward: The discovery of endogenous β-aminobutyric acid as the missing link for a potential new plant hormone

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ABSTRACT

The capacity of β-aminobutyric acid (BABA) to induce resistance in plants against biotic and abiotic stresses has been known for more than 50 y. In the beginning reports were mainly descriptive of the phenomenon, but it became clear with the discovery of BABA insensitive mutants in Arabidopsis that there was definitely a genetic basis underlying BABA-induced resistance. The study of these mutants, along with the use of regular hormone mutants, allowed establishing the defense pathways activated upon defense induction. To date it is clear that BABA potentiates the defense pathway more appropriate to counteract the upcoming stress situation, through a phenomenon termed priming. Interestingly, plants possess a receptor for BABA, but up to recently there was a general consensus on the fact that BABA was a xenobiotic molecule. The development of an accurate non-destructive assay for measuring aminobutyric acid isomers in planta and the finding of plant-produced BABA, thus seems to represent the missing link for the discovery of a novel plant hormone. Differences and similarities with some of the classical plant hormones are presented here.

ARTICLE HISTORY
Received 18 January 2017
Accepted 30 January 2017

KEYWORDS
induced resistance; non-protein amino acid; plant hormones; priming; stress

A short history of β-aminobutyric acid (BABA)

Research with Arabidopsis has allowed dissection of the events taking place following treatment with BABA.[1,2] In summary, the stress encountered determines the events following it, and the treatment with BABA can potentiate (prime) the most appropriate to counteract it.[3,4] For example, bacterial infection by *Pseudomonas syringae* pv *tomato* (*Pst*) DC3000 and attack by the fungal pathogen *Botrytis cinerea* are both combatted through potentiation of salicylic acid (SA)-dependent defenses,[5,6] while defense against *Plectosphaerella cucumerina* is obtained through an enhanced callose deposition depending on a functional abscisic acid (ABA) signaling pathway.[7] Enhanced ABA signaling also occurs for BABA-induced protection against high salinity.[8]

BABA does not usually induce directly defense responses, but primes the plant to react faster and/or stronger to a given stress.[3] Interestingly, the priming state induced by BABA can also be transmitted to the descendants of a plant via its seeds.[9]

A few years ago a perception mechanism for BABA was found in Arabidopsis.[10] BABA perception involves an aspartyl-tRNA synthetase,[10] and this could be interpreted as a first clue to the possibility that BABA might play a natural role in a plant's physiology. The recent discovery of BABA as natural molecule synthesized by plants and induced by stress[11] sheds new light on the research presented until now, and many phenomena known up to date have to be seen and interpreted in the light of this new finding. In particular, BABA seems now to possess the features of a novel plant stress hormone.

Similarity and differences with classical plant hormones

The finding of endogenous BABA in plants raises 2 questions: a) Is the amount of BABA produced by plants comparable to main plant stress hormones? and b) How do the temporal dynamics of its induction relate to those of hormones? In this addendum, we will try to answer these questions.

In our last paper we measured the levels of BABA in *A. thaliana* plants before and after exposure to several biotic and abiotic stressors.[11] Unstressed Columbia-0 plants at the age of 5 weeks showed a basal level of

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Addendum to: Thevenet D, Pastor V, Baccelli I, Balmer A, Vallat A, Neier R, Glauser G, Mauch-Mani B. The priming molecule β-aminobutyric acid is naturally present in plants and is induced by stress. New Phytol 2017; 213:552-9; http://dx.doi.org/10.1111/nph.14298

BABA in leaves usually lower than 10 ng/g of fresh weight (FW).[11] Is this amount too low to be considered biologically significant? If we compare with SA, which can be found, as the free form, in amounts between 30 and 500 ng/g FW in unstressed *A. thaliana* leaves,[12–16] BABA can be considered less present than SA.

However, the molecular weight of BABA is the lowest when compared, for example, to SA, ABA, jasmonic acid (JA) or indole-3-acetic acid (IAA). Therefore, in comparison to ABA and JA, which are similarly found in amounts lower than 10 ng/g FW,[12,15,17,18] or IAA, which is present in amounts around 20 ng/g FW,[19,20] the basal amount of BABA in *A. thaliana* leaves can be considered in line with, or in some cases higher than these hormones.

Depending on the stress applied, BABA accumulated from about 3- to 15-fold.[11] How and how much do plant hormones vary in similar circumstances? By making comparisons with the literature it is possible to observe, for example, that ABA has been reported to accumulate during the first 48 hours after *P. cucumerina* infection[21] with a similar pattern to BABA.[11] In that study, García-Andrade et al.[21] report that ABA levels increased about 2.5–fold after 48 hours of infection, and the ABA peak was reached at that time point.[21] In our study, BABA similarly accumulated 2.5-fold after 48 hours, although it kept increasing up to 5-fold after 72 hours.[11] In a different study with *P. cucumerina*, SA and JA have also been reported to increase,[22] but neither hormone was found to increase over 2-fold after 48 hours.[22]

During *Pst* DC3000 infection, BABA showed a continuous increase over time until reaching 15-fold the control value after 48 hours,[11] whereas in a study by Gao et al.[15] both ABA and SA increased about 25-fold during a period of 36 hours.[15] In addition to *P. cucumerina* and *Pst* DC3000 infection, we also tested the levels of BABA after infection with a virulent strain of *Hyaloperonospora arabidopsidis*.[11] Interestingly, 3 d of infection with this biotrophic pathogen were not enough for BABA to significantly accumulate,[11] as similarly reported by other authors for free SA.[23] Finally, salt stress led BABA to increase already after 24 hours of treatment,[11] whereas Ellouzi et al.[24] report on ABA accumulation in leaves of *A. thaliana* after 3 d of NaCl treatment to the roots.

In conclusion, although the biologic role of the endogenous production of BABA during stress has still to be clarified, its levels in planta and its temporal dynamics suggest, along with its outstanding efficacy in inducing resistance, that BABA may be a novel plant (priming) hormone.

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

Acknowledgments

The authors are grateful to all the colleagues which contributed to establishing the methodology to measure BABA.

Funding

This work was supported by Swiss National Foundation Grant 31003A_140593 to B.M.M.

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