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BABA-induced resistance: milestones along a 55-year journey

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Abstract β-aminobutyric acid (BABA) has been known as an inducer of disease-resistance since 1963, however, only in the recent two decades an increasing number of reports have been published shedding light on its spectrum of activity, physiological impacts, and mode of action. BABA has been shown to protect about 40 plant species against about 80 pathogens and pests, including a virus, protista, bacteria, oomycetes, fungi, nematodes and arthropods. Interestingly, it is also active against abiotic stress and enhances salt, heat and drought tolerance in several plant species. Although generally regarded as a xenobiotic, there are a few reports that mention its occurrence in plants. BABA-treated plants react faster and in a more robust manner to a stress situation, a phenomenon that has been termed priming. ^{14}C BABA is highly systemic, readily taken up by roots and leaves, and translocate both acropetally and basipetally. No metabolites of BABA are known. BABA is effective as a foliar spray, soil drench and seed treatment. Seeds derived from treated plants may produce primed progeny, making BABA the first agent with transgenerational efficacy. BABA induces numerous biochemical changes in treated plants. Among them are the induction of reactive oxygen species (ROS) and glycolate oxidase (GO) that are tightly linked to defense. ROS scavengers may alleviate the activity of BABA. Interestingly, only the R but not the S enantiomer of BABA primes for resistance. Unfortunately, BABA can also impose growth stress (and phytotoxicity) in some treated plants therefore BABA analogs with reduced stress effects are highly desirable for agricultural use.

Keywords Aspartyl tRNA synthetase · Abiotic stress · Biotic stress · β-aminobutyric acid · Induced-resistance · Priming

History

Lotan and Fluhr reported in 1990 (Lotan and Fluhr 1990) that application of DL-α-aminobutyric acid (AABA) to intact tobacco leaves gave comparable levels of elicitation of PR-proteins as achieved by TMV. We applied AABA to tobacco plants with the expectation that the induced PR proteins might protect against downy mildew caused by *Peronospore tabacina*. Since this was not the case, we tried the two other isomers of aminobutyric acid, DL-β-aminobutyric acid (BABA) and γ-aminobutyric acid (GABA). Surprisingly, BABA (but not GABA) provided excellent protection against downy mildew in tobacco and late blight

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in tomato caused by *Phytophthora infestans* with no adverse effect on spore germination on the leaf surface or penetration of the pathogen into the leaf epidermis (Cohen 1994a, b). BABA applied to tomato plants as a foliar spray induced PR proteins and provided 92 % protection against late blight. No activity was obtained with the isomers AABA, *iso*-AABA, *iso*-BABA, or GABA (Cohen 1994b). Additionally, BABA applied as a foliar spray, petiole dip, stem injection or soil drench to tobacco plants protected against downy mildew. Foliar spray induced PR protein accumulation but not the other modes of application. Interestingly, protection achieved by SA (sodium salicylate) or INA (2,6 dichloro-isonicotinic acid) was associated with PR-protein accumulation, regardless of the mode of application (Cohen 1994b).

Subsequent search of the literature revealed that Papavizas and Davey (1963) were the first to discover the activity of BABA against the root rot oomycete pathogen *Aphanomyces euteiches*. During the following 30 years, 1963–1994, no research was published on BABA. By 2016, a total of 147 papers were published (Fig. 1), including five review articles (Cohen 2001, 2002; Jakab et al. 2001; Piekna-Grochala and Kepczynska 2013; Baccelli and Mauch-Mani 2016) and three patents (Cohen 2000; Cohen et al. 2004; Oka et al. 2001) describing resistance induced by BABA against about 80 biotic and 6 abiotic stresses (Fig. 2; Table 1).

BABA induces resistance against numerous biotic and abiotic stresses

BABA induces resistance against a large variety of foliar, fruit and root pathogens as well as against abiotic stresses [drought, senescence, acid rain, cadmium, salt and heat (Table 1)]. It may be sprayed on leaf surfaces, injected into the stem, applied to fruits, drenched to the soil or applied to seeds. The mode of application may affect its efficacy and phytotoxicity.

BABA induces resistance against root and soil-borne pathogens (Chamsai et al. 2004; Li et al. 1996) but does not interfere with the colonization of tobacco roots with the arbuscular mycorrhizal (AM) fungus *Glomus intraradices* (David 1997) or of tomato roots with a mixture of five AM fungi (Luna et al. 2016).

BABA protects tomato and tobacco against late blight and downy mildew, respectively, even when applied 1- day post inoculation (Cohen 1994a, b). This seemed unusual at that time, since this finding did not fit the perception of classical SAR (systemic acquired resistance) that requires a lapse period of a few days between induction treatment and challenge inoculation. BABA induced resistance against downy mildew in lettuce, even when applied as late as 4 days' post-inoculation (dpi) (Cohen et al. 2011).

BABA induces the formation of small necrotic lesions when applied at a high concentration to

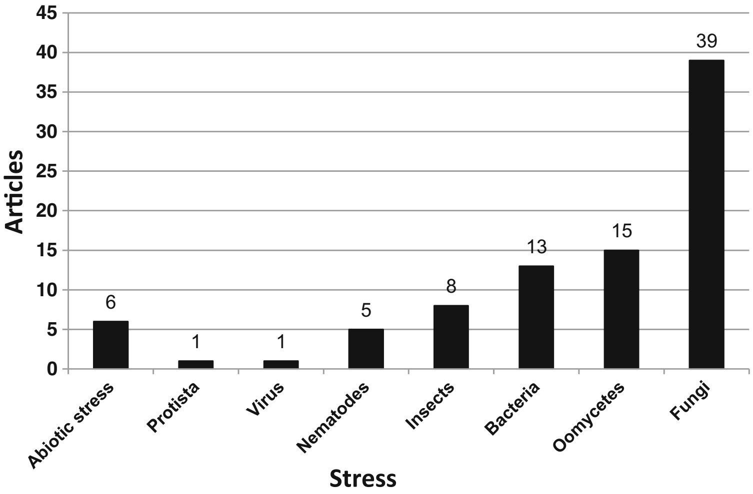

Fig. 1 Number of published articles describing abiotic and biotic stresses against which BABA induces resistance

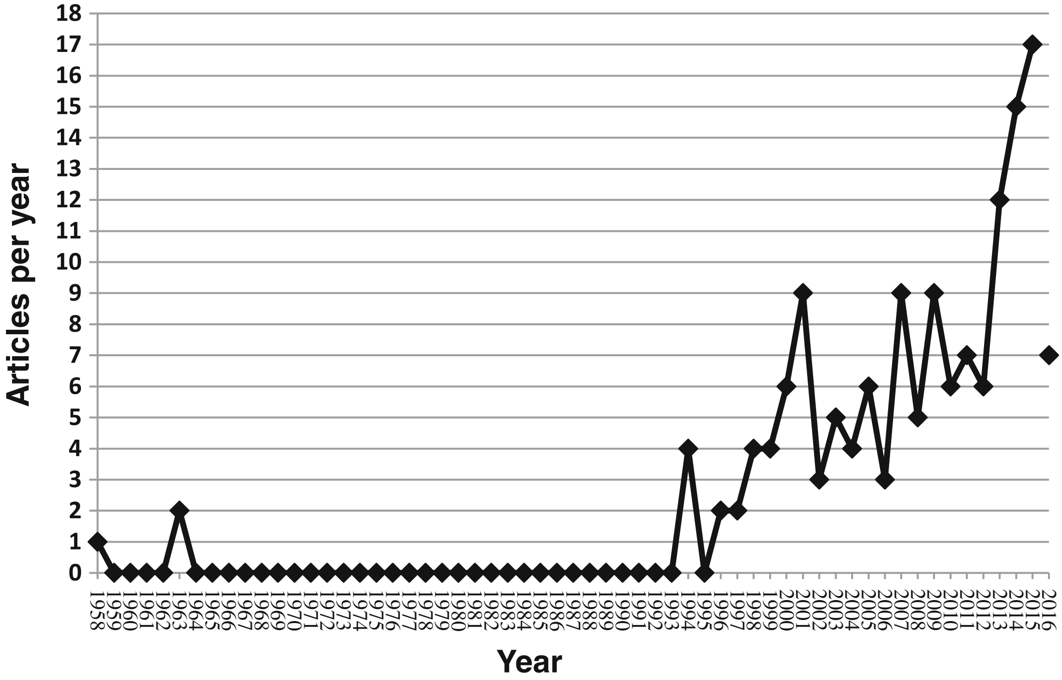

Fig. 2 Number of articles published per year during 1958–2016 describing abiotic and biotic resistances induced by BABA

leaves of tobacco, tomato, and potato (Cohen 1994a, b, 2002). No such lesions are produced when BABA is injected to the stem, applied as stem dip or petiole dip, or drenched to the soil (Cohen 1994a, b). All modes of application induced resistance but only foliar spray induced PR proteins (Cohen 2002).

The use of ^{14}C-BABA (kindly supplied by Syngenta, Basel, Switzerland) determined the relationship between translocation of BABA and resistance. It revealed that BABA moves in both directions in the plant. The level of protection against late blight was directly proportional to the amount of BABA translocated, suggesting that resistance depends on the actual presence of BABA in the leaf tissue (Cohen and Gisi 1994).

About 96 % of the ^{14}C-BABA applied to 6-leaf tomato plants could be re-extracted after 6 days as pure BABA from the treated leaves (number 1–6) and from the newly-developed untreated leaves (number 7–8), suggesting that BABA was not metabolized (Cohen and Gisi 1994; Jakab et al. 2001). However, about 4 % of the label remained insoluble, bound to cell walls. This insoluble BABA was released by proteinase K, cellulase or pectinase, suggesting that it has incorporated into protein-carbohydrate complexes (Cohen and Gisi 1994). The oxygen burst induced by BABA (Cohen et al. 2011) may facilitate cross-linking of BABA to the cell wall matrix.

BABA isomers, enantiomers and derivatives

BABA is a unique inducer of plant defense. It is a simple, 4-carbon, non-protein amino acid with the formula CH_3-CH-(NH_2)-CH_2-COOH. Unlike natural amino acids whose amino group resides on carbon 2 (α position), in BABA it resides on carbon 3 (β position). This carbon is chiralic, allowing for R and S enantiomers. BABA is the only isomer of aminobutyric acid capable of inducing plant resistance. Aminobutyric acids that carry the amino group at α or γ position are inactive. The *iso* isomers of AABA and BABA are inactive. The R and S enantiomers of BABA (kindly synthesized by Syngenta) were tested against *Peronospora tabacina* in tobacco (Cohen 1994a) and against *Bremia lactucae* in lettuce (Cohen et al. 2011). The R, but not the S, enantiomer was active, suggesting stereospecific binding to a receptor in the plant cell. Longer β-amino acids,

Table 1 A list of host plants and their biotic and abiotic stresses against which BABA was reported to induce resistance

Host	Pathogen	Class	Reference
Apple	*Alternaria alternata*	Fungus	(Reuveni et al. 2003)
	Drought tolerance	Abiotic stress	(Macarisin et al. 2009)
			(Tworkoski et al. 2009)
	Dysaphis plantaginea	Insect	(Philippe et al. 2016)
	Erwinia amylovora	Bacterium	(Hassan and Buchenauer 2007)
	Penicillium expansum (postharvest)	Fungus	(Zhang et al. 2011)
			(Zhang et al. 2013a)
	Venturia inaqualis	Fungus	(MacLennan et al. 1963)
Arabidopsis	*Acid rain tolerance*	Abiotic stress	(Liu et al. 2011)
	Alternaria brassicicola	Fungus	(Ton and Mauch-Mani 2004)
			(Luna et al. 2012)
			(Flors et al. 2008)
	Botrytis cinerea	Fungus	(Zimmerli et al. 2001)
			(Koen et al. 2014)
	Brevicoryne brassicae	Insect	(Hodge et al. 2006)
	Cadmium tolerance	Abiotic stress	(Cao et al. 2009)
	Drought tolerance	Abiotic stress	(Jakab et al. 2005)
	Heat tolerance	Abiotic stress	(Zimmerli et al. 2008)
	Hyaloperonospora parasitica	Oomycete	(Ton et al. 2005)
	Hyaloperonospora arabidopsidis	Oomycete	(Luna et al. 2014b)
			(Luna et al. 2014a)
			(Van der Ent et al. 2009)
			(Luna et al. 2012)
			(Slaughter et al. 2012)
			(Ton et al. 2005)
	Myzus persicae	Insect	(Hodge et al. 2006)
	Pectobacterium carotovorum ssp. *carotovorum*	Bacterium	(Po-Wen et al. 2013)
	Peronospora parasitica	Oomycete	(Zimmerli et al. 2000)
	Plectospharella cucumerina	Fungus	(Ton and Mauch-Mani 2004)
			(Pastor et al. 2013)
	Plutella xylostella	Insect	(Hodge et al. 2006)
	Pseudomonas syringae pv. tomato	Bacterium	(Zimmerli et al. 2000)
			(Slaughter et al. 2012)
			(Luna et al. 2012)
			(Luna et al. 2014a)
			(Ton et al. 2005)
			(Flors et al. 2008)
	Salt tolerance	Abiotic stress	(Ton et al. 2005)
			(Jakab et al. 2005)
	Trichoplusia ni	Insect	(Hodge et al. 2006)
Artichoke	*Sclerotinia sclerotiorum*	Fungus	(Marcucci et al. 2010)

Table 1 (continued)

Host	Pathogen	Class	Reference
Barley	*Blumeria graminis f.sp. hordei*	Fungus	(Walters et al. 2014)
	Rhynchosporium commune	Fungus	(Walters et al. 2014)
	Heterodera avenae	Nematode	(Oka and Cohen 2001)
	Heterodera latipons	Nematode	(Oka and Cohen 2001)
	Salt tolerance	Abiotic stress	(Mostek et al. 2016)
Basil	*Peronospora belbahrii*	Oomycete	(Mersha et al. 2013) (Cohen et al. 2015)
Beans	*Acyrthosiphon pisum*	Fungus	(Hodge et al. 2005) (Hodge et al. 2011)
	Pseudomonas syringae pv. phaseolicola	Bacterium	(Martinez-Aguilar et al. 2016)
	Salt tolerance	Abiotic stress	(Jisha and Puthur 2016)
	Drought tolerance	Abiotic stress	(Jisha and Puthur 2016)
Brassica carinata	*Alternaria brassicae*	Fungus	(Chavan and Kamble 2014)
	Alternaria brassicae	Fungus	(Kamble and Bhargava 2007)
Broccoli, Kohlrabi	*Alternaria brassicicola*	Fungus	(Cohen 2000)
	Pseudomonas fluorescens	Bacteria	(Pajot and Silue 2005)
	Pseudomonas marginalis	Bacteria	(Pajot and Silue 2005)
Cauliflower	*Peronospora parasitica*	Oomycete	(Silue et al. 2002)
Cereals	*Heterodera avenae*	Nematode	(Oka et al. 2001)
	Heterodera lalipons	Nematode	(Oka et al. 2001) (Oka and Cohen 2001)
Cherry fruit	*Senescence inhibition, Increased fruit firmness*	Abiotic stress	(Wang et al. 2015)
Citrus	*Citrus Huanglongbing*	Bacterium	(Li et al. 2016)
	Diaphorina citri	Insect	(Tiwari et al. 2013)
	Penicillium digitatum (postharvest)	Fungus	(Panebianco et al. 2014)
	Penicillium italicum (postharvest)	Fungus	(Tavallali et al. 2008)
Cotton	*Verticillium dahliae*	Fungus	(Li et al. 1996)
Cucumber	*Botrytis cinerea*	Fungus	(Cohen 2000) (Ovadia et al. 2000)
	Cladosporium cucumerinum	Fungus	(Van Andel 1958)
	Colletotrichum lagenarium	Fungus	(Walz and Simon 2009)
	Colletotrichum orbiculare	Fungus	(Jeun and Park 2003) (Sang et al. 2014) (Jeun et al. 2004)
	Meloidogyne javanica	Nematode	(Oka et al. 1999) (Sahebani et al. 2011)
	Plectospharella cucumerina	Fungus	(Ton and Mauch-Mani 2004)
	Pseudoperonospora cubensis	Oomycete	(Baider and Cohen 2003) (Ovadia et al. 2000) (Walz and Simon 2009)
	Sphaerotheca fuliginea	Fungus	(Vogt and Buchenauer 1997)
Flax	*Drought tolerance*	Abiotic stress	(Quero et al. 2015)

Table 1 (continued)

Host	Pathogen	Class	Reference
Ginger	*Pythium aphanidermatum*	Oomycete	(Karmakar et al. 2003)
Grape	*Botrytis cinerea*	Fungus	(Csikász-Krizsics et al. 2013) (Fischer et al. 2009)
	Saccharomyces cerevisiae	Fungus	(Fischer et al. 2009)
	Leptosphaeria maculans	Fungus	(Sasek et al. 2012)
	Plasmopara viticola	Oomycete	(Cohen et al. 1999) (Cohen et al. 1994) (Hamiduzzaman et al. 2005) (Reuveni et al. 2001) (Slaughter et al. 2008)
Grapefruit	*Botrytis cinerea* (postharvest)	Fungus	(EL-Metwally et al. 2014)
	Penicillium digitatum	Fungus	(Porat et al. 2003)
Jujube	*Alternaria alternata* (postharvest)	Fungus	(Cao et al. 2013) (Yan et al. 2015)
	Monilinia fructicola (postharvest)	Fungus	(Cao et al. 2013)
Kimchi Cabbage	*Alternaria brassicicola*	Fungus	(Kim et al. 2013)
	Colletotrichum higginsianum	Fungus	(Kim et al. 2013)
Lettuce	*Bremia lactucae*	Oomycete	(Cohen et al. 2007) (Cohen et al. 2010) (Cohen et al. 2011) (Pajot et al. 2001)
Lime	*Xanthomonas citri ssp. citri*	Bacterium	(Sharifi-Sirchi et al. 2011)
Maize	*Drought tolerance*	Abiotic stress	(Shaw et al. 2016)
	Fusarium moniliforme	Fungus	(Cohen 2000)
Mango	*Colletotrichum gloeosporioides* (postharvest)	Fungus	(Zhang et al. 2013b)
Melon	*Drought tolerance*	Abiotic stress	(Macarisin et al. 2009)
	Fusarium oxysporum f. sp. melonis	Fungus	(Ovadia et al. 2000)
	Pseudoperonospora cubensis	Oomycete	(Ovadia et al. 2000)
Mung bean	*Salt tolerance*	Abiotic stress	(Jisha and Puthur 2016)
Onion	*Botrytis allii*	Fungus	(Polyakovskii et al. 2008)
	Botrytis cinerea	Fungus	(Polyakovskii et al. 2008)
Pea	*Aphanomyces euteiches*	Oomycete	(Papavizas and Davey 1963)
	Uromyces pisi	Fungus	(Barilli et al. 2010) (Barilli et al. 2015)
Peanut	*Cercosporidium personatum*	Fungus	(Zhang et al. 2001)
Pearl millet	*Sclerospora graminicola*	Oomycete	(Shailasree et al. 2001) (Shailasree et al. 2007) (Anup et al. 2015) (Shailasree and Melvin 2015) (Melvin et al. 2015)

Table 1 (continued)

Host	Pathogen	Class	Reference
Pepper	*Colletotrichum coccodes*	Fungus	(Hong et al. 1999)
	Phytophthora capsici	Oomycete	(Hwang et al. 1997)
			(Stamler et al. 2015)
			(Sunwoo et al. 1996)
			(Lee et al. 2000)
Pineapple	*Meloidogyne javanica*	Nematode	(Chinnasri et al. 2006)
Potato	*Drought tolerance*	Abiotic stress	(Sos-Hegedus et al. 2014)
	Fusarium sambucinum	Fungus	(Greyerbiehl and Hammerschmidt 1998)
	Fusarium sulphureum	Fungus	(Yin et al. 2010)
	Meloidogyne incognita	Nematode	(Mongae and Moleleki 2015)
	Pectobacterium carotovorum subsp. brasiliense	Bacterium	(Mongae and Moleleki 2015)
	Phytophthora infestans	Oomycete	(Cohen 2002)
			(Baider and Cohen 2003)
			(Jeun et al. 2000)
			(Jeun and Buchenauer 2001)
			(Eschen-Lippold et al. 2010)
			(Bengtsson et al. 2014)
			(Burra et al. 2014)
			(Andreu et al. 2006)
			(Altamiranda et al. 2008)
			(Lankinen et al. 2016)
			(Liljeroth et al. 2010)
			(Olivieri et al. 2009)
			(Olivieri et al. 2009)
	Fusarium solani f. sp. eumartii	Fungus	(Maldonado et al. 2015)
	Spongospora subterranea	Protista	(Rajaei and Mohamadi 2013)
Rape	*Drought tolerance*	Abiotic stress	(Sasek et al. 2012)
	Leptosphaeria maculans	Fungus	(Kamble et al. 2013)
	Verticillium longisporum	Fungus	(Ji et al. 2015)
Rice	*Meloidogyne graminicola*	Nematode	(Zhong et al. 2014)
Soybean	*Aphis glycines*	Insect	(Hossain et al. 2012)
	Cadmium tolerance	Abiotic stress	(Zeighaminejad et al. 2016)
Squash	*Podosphaera xanthii*	Fungus	(Wang et al. 2016)
	Botrytis cinerea (Postharvest)	Fungus	(Tosi et al. 1998)
Strawberry	*Peronospora halstedii*	Oomycete	(Amzalek and Cohen 2007)
Sunflower	*Puccinia helianthi*	Fungus	(Cohen 1994a)
	Peronospora tabacina	Oomycete	(Cohen et al. 1994)
Tobacco	*Peronospora tabacina*	Oomycete	(Siegrist et al. 2000)
	Tobacco mosaic virus	Virus	(Yun et al. 1999)
	Tobacco mosaic virus	Virus	(Cohen 2000)
	Alternaria solani	Fungus	(Roylawar et al. 2015)

Table 1 (continued)

Host	Pathogen	Class	Reference
Tomato	*Alternaria solani*	Fungus	(Maymoune et al. 2015)
	Botyrtis cineraea	Fungus	(Luna et al. 2016)
	Botyrtis cineraea	Fungus	(Chamsai et al. 1998)
	Clavibacter michiganensis	Bacteria	(Baysal et al. 2005)
	Clavibacter michiganensis ssp michiganensis	Bacterium	(Hassan and Buchenauer 2007)
	Clavibacter michiganensis ssp michiganensis	Bacterium	(Sos-Hegedus et al. 2014)
	Drought tolerance	Abiotic stress	(Li et al. 1996)
	Fusarium oxysporum f. sp. lycopersici	Fungus	(Ovadia et al. 2000)
	Fusarium oxysporum f. sp. lycopersici	Fungus	(Chamsai et al. 2004)
	Meloidogyne incognita	Nematode	(Mongae and Moleleki 2015)
			(Oka et al. 1999)
	Meloidogyne javanica	Nematode	(Oka and Cohen 2001)
	Meloidogyne javanica	Nematode	(Sahebani and Hadavi 2009)
	Oidium neolycopersici	Fungus	(Fatemy et al. 2012)
			(Moricova et al. 2014)
			(Farahani et al. 2016)
	Pectobacterium carotovorum subsp. carotovorum	Bacterium	(Baider and Cohen 2003)
	Phytophthora infestans	Oomycete	(Cohen 1994b)
	Phytophthora infestans	Oomycete	(Cohen and Gisi 1994)
	Pseudomonas syringae pv. tomato	Bacteria	(Cohen 2002)
			(Cohen 2001)
			(Baysal et al. 2007)
			(Hassan and Abo-Elyousr 2013)
	Ralstonia solanacearum	Bacterium	(Baysal et al. 2007)
	Salt tolerance	Abiotic stress	(Castaño Monsalve et al. 2015)
	Phytophthora infestans	Oomycete	(Du et al. 2012)
Tree tomato	*Phytophthora infestans*	Oomycete	(Castaño Monsalve et al. 2015)
Wheat	*Fusarium graminearum*	Fungus	(Cao et al. 2014)
	Sitobion avenae	Insect	(Oka and Cohen 2001)
	Heterodera avenae	Nematode	(Oka and Cohen 2001)
	Heterodera latipons	Nematode	(Hodge et al. 2006)
	Brevicoryne brassicae	Insect	(Hodge et al. 2006)
White mustard	*Myzus persicae*	Insect	(Hodge et al. 2006)
	Plutella xylostella	Insect	(Hodge et al. 2006)
	Trichoplusia ni	Insect	(Hodge et al. 2006)

with a backbone of 5, 6, 8 or 10 carbons, were ineffective in inducing resistance (Cohen 2000; Oka and Cohen 2001). Substitutions made in the amino group residing at the 3 (β) position of BABA hampered its activity, indicating specific binding of the amino group to its ligand. Acid salts of BABA were as effective as BABA in inducing resistance, suggesting hydrolysis of the molecule after uptake by the plant (Cohen 2000; Oka and Cohen 2001).

Natural occurrence of BABA

There are several reports in the literature that mention a natural occurrence of BABA. For example, it was found in Spanish wines (Barrado et al. 2009) and in root exudates of tomato plants grown in solarized soil (Gamliel and Katan 1992). Pfautsch et al. (2009) also reported its occurrence in the phloem and xylem exudates of *Eucalyptus regnans, Acacia dealbata* and *Acacia melanoxylon.*

Recently, Thevenet et al. (2016) reported on a reliable method to detect and quantify BABA in plant tissues using liquid chromatography-tandem mass spectrometry (LC-MS/MS) analysis. They showed that BABA is a natural product in *Arabidopsis thaliana*; Chinese cabbage (*Brassica rapa*), maize (*Zea mays*), teosinte (*Zea mays* ssp. mexicana) and wheat (*Triticum aestivum)* as well as in the moss *Physcomitrella patens*. Interestingly, the endogenous levels of BABA rapidly increase after infection with necrotrophic, biotrophic and hemibiotrophic pathogens, as well as after salt stress and submergence. BABA was also detected in leaves of tomato plants (Cohen, Gisi, Schalberger-Diethelm and Albrecht, unpublished data).

Activity against viruses and bacteria

BABA induces resistance against TMV in tobacco (Table 1). Csikász-Krizsics et al. (2013) reported that BABA induced resistance against the virus GLRaV1 in grapevines. No other viral diseases were reported to be affected by BABA. Whether this is due the lack of activity against other viruses or the lack of studies is not known.

BABA induces resistance against numerous bacterial diseases (Table 1) including *Pseudomonas syringae pv. tomato* in Arabidopsis (Zimmerli et al. 2000) and *Ralstonia solanacearum* in tomato (Fig. 3a) (Hassan and Abo-Elyousr 2013). Remarkably, BABA was recently reported to induce resistance against the HLB bacterial disease of citrus caused by *Citrus huanglongbing (citrus greening)*, not reported to have a cure (Li et al. 2016). This may be due to the resistance BABA induces against the vector itself or the causal bacterium, the Asian citrus psyllid, *Diaphorina citri* (Tiwari et al. 2013). BABA exerted no direct toxic effect on nymphs or adult *D. citri*.

Activity against oomycetes

BABA did not affect sporangial germination, zoospore release, encystment or cyst germination of *Phytophthora infestans* on tomato leaf tissue, nor mycelial growth on agar media (Cohen 1994b). In tomato, stem dip (Fig. 3b) or foliar spray were more effective than soil drench in protecting against late blight. R-BABA induced HR in tomato leaves when inoculated with sporangia of *P. infestans* whereas S-BABA allowed for abundant sporulation of the pathogen (Fig. 3c). Tomato leaves fed with 0.25 mg BABA through the petiole produced an HR upon inoculation with *P. infestans* while similarly-inoculated control leaves allowed for abundant sporulation of the pathogen (Fig. 3d). BABA was effective against oomycetes in NahG transgenic plants suggesting independence on salicylic acid signaling (Cohen 2002; Zimmerli et al. 2000). However, resistance against late blight in potato failed to occur in NahG plants (Eschen-Lippold et al. 2010).

Grape leaves treated with BABA show complete inhibition of sporulation of *Plasmopara viticola.* This is associated with a massive lignin accumulation (Cohen et al. 1999; Cohen 2002). In grape leaf discs the MIC values for R-BABA, DL-BABA and S-BABA were 4, 16 and >>32 ppm, respectively. BABA controls grape downy mildew in the field as effectively as commercial fungicides (Reuveni et al. 2001). In addition to lignin accumulation, Hamiduzzaman et al. (2005) showed that BABA protects grapevine through the potentiation of callose formation and acts via jasmonic acid signaling. It has also been shown that stilbene phytoalexins are induced by BABA leading to the protection of grapevine against downy mildew (Slaughter et al. 2008).

BABA applied to cucumber plants at 1-day before inoculation with *Pseudoperonospora cubensis* induces the formation of minute chlorotic lesions (Fig. 4a, b). Sporangiophore emergenge and sporangial production are suppressed in a dose-dependent manner (Fig. 4c-i) suggesting a post-penetration inhibition of the pathogen (Ovadia et al. 2000). Resistance is associated with encasement of the haustoria with callose (Fig. 4j-l). BABA applied curatively, at 1-day post inoculation, is as effective against downy mildew as when applied 1 day prior to inoculation. Lignin accumulation is associated with resistance.

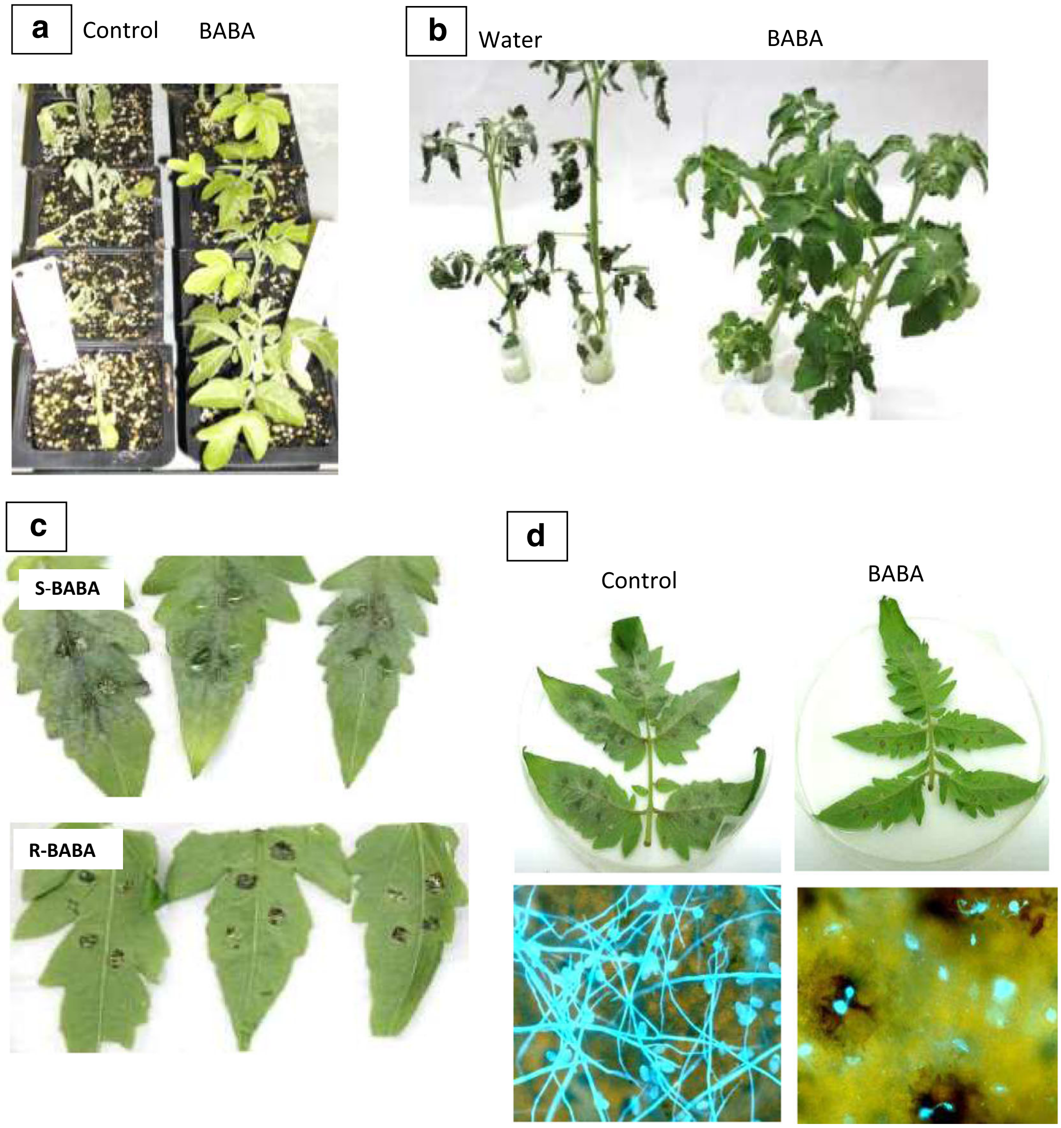

Fig. 3 **a** Resistance against *Ralstonia solanacearum* induced in tomato by BABA (soil drench). **b** Resistance against *Phytophthora infestans* induced in tomato by BABA (stem dip). **c** The R enantiomer of BABA, but not the S enantiomer, induces resistance in tomato against *Phytophthora infestans* (drop application). **d** Post-infection (1dpi) resistance induced by BABA (petiole feeding) against *Phytophthora infestans* in detached tomato leaves. Note heavy sporulation in the control leaves and HR in the treated leaves. For UV microscopy, leaves were clarified with ethanol and stained with calcofluor. Bar = 50 μ

Similar responses are observed in detached leaves of hop plants treated with BABA and inoculated with *Pseudoperonospora humuli* (Fig. 4m-o).

BABA protects lettuce against the biotrophic oomycete *Bremia lactucae* (Pajot et al. 2001) (Fig. 5a, b). It has no effect on spore germination, appressoria formation or penetration into the epidermis. BABA restricts *B. lactucae* soon after penetration by encasing the primary and secondary vesicles with a heavy layer of callose which prevents further growth of the pathogen (Cohen et al. 2010) (Fig. 5c). DAB staining shows that inhibition is associated with H_2O_2 production in the penetrated epidermal cells (Fig. 5d). Elevated activity of peroxisomal glyolate oxidase (GO) was found responsible for H_2O_2 production and external application of catalase as a scavenger, alleviates the protection induced by BABA (Vaknin 2016). This confirms

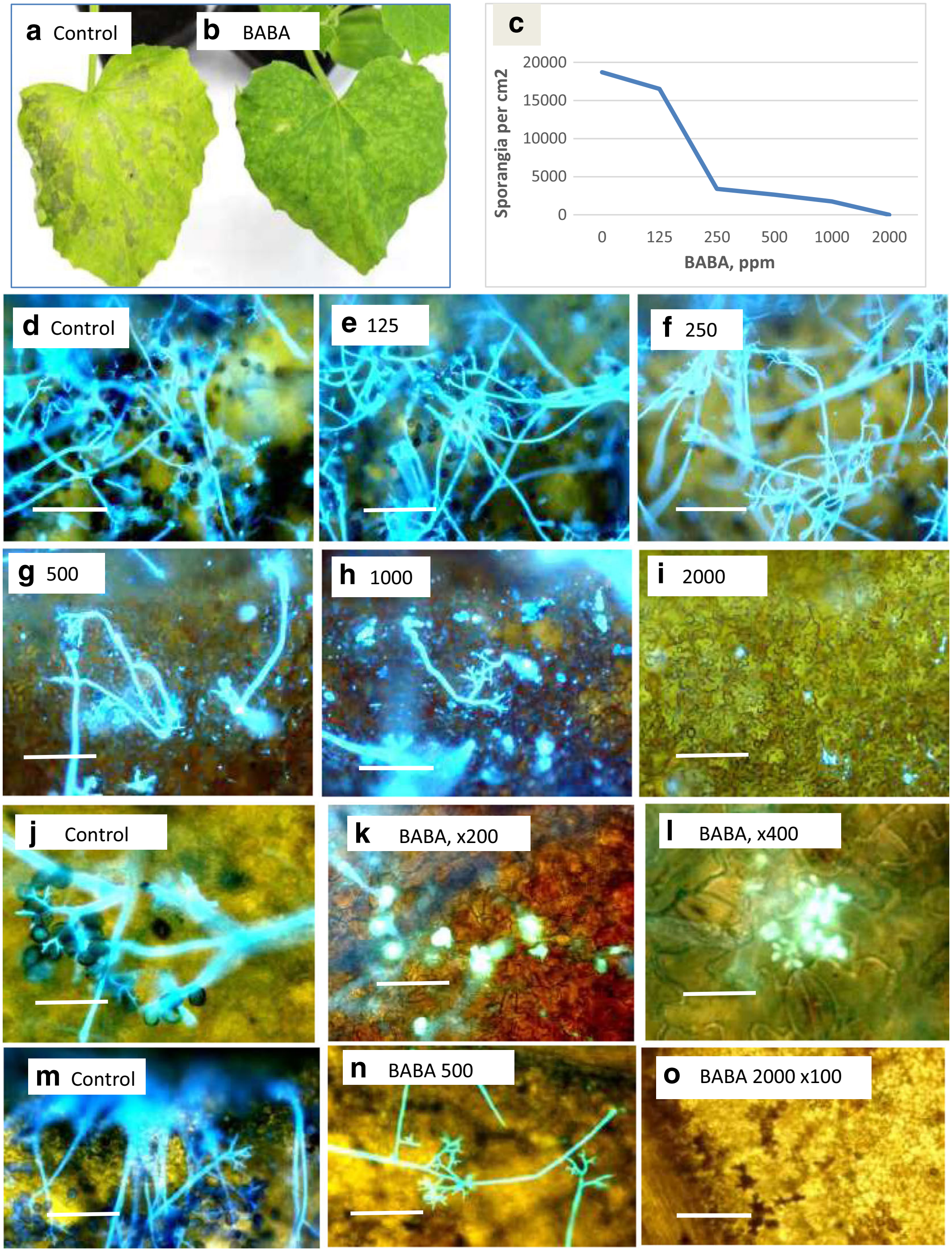

Fig. 4 **a, b** Resistance induced by BABA (foliar spray, 1 day before inoculation) against *Pseudoperonospora cubensis* in intact cucumber plants. **c** BABA (foliar spray, 1 day before inoculation) suppresses sporulation of *P. cubensis* in intact cucumber plants in a dose-dependent manner. **d-i** Microscopic observation of the resistance induced by 125–2000 ppm BABA (foliar spray, 1 day before inoculation) against *P. cubensis* in intact cucumber plants. Bars = 100 μm. **j-l** BABA (foliar spray 500 ppm) induces callose encasement of haustoria (*yellow* fluorescence in **k** and **l**) of *P. cubensis* in cucumber leaves. Bar in **j** and **k** = 50 μm; in **l** = 20 μm. **m-o** Microscopic observation of the resistance induced by BABA (foliar spray, 1 day before inoculation) against *Pseudoperonospora humuli* in detached leaves of hop. Bar in **m** and **n** =100 μm and in **o** = 50 μm

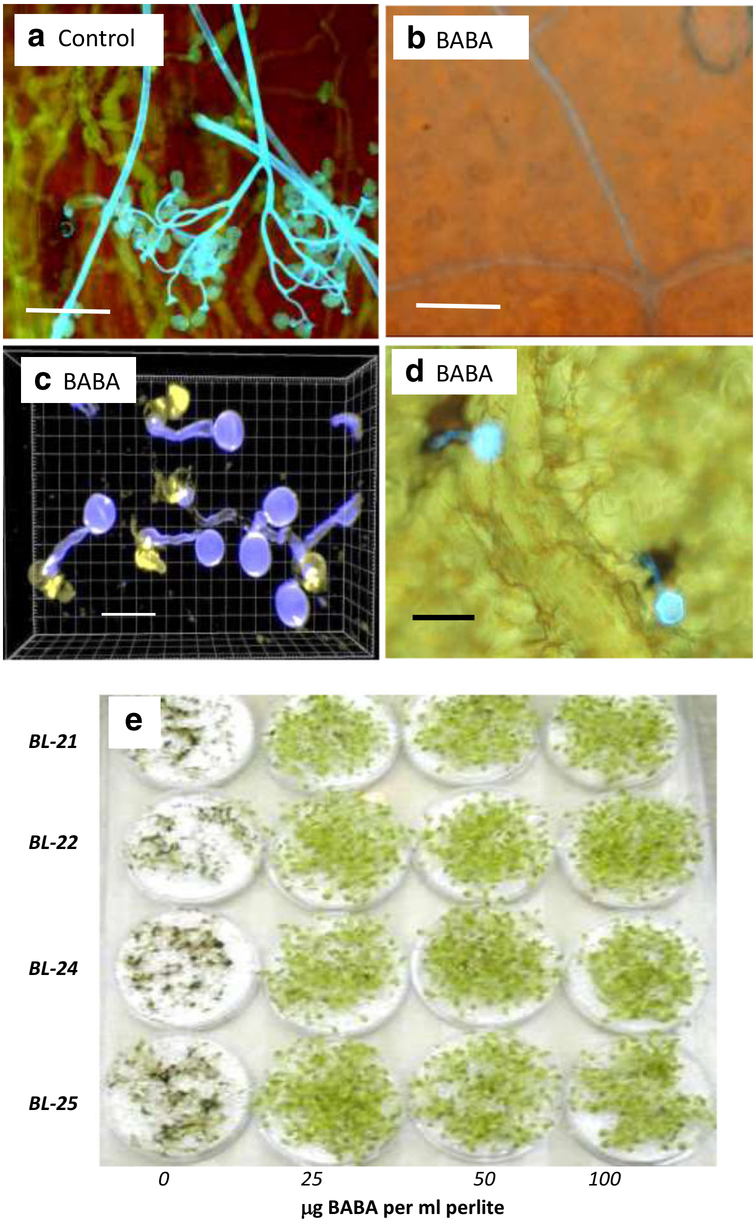

Fig. 5 Microscopic observation of the resistance induced by BABA against *Bremia lactucae* in detached leaves of lettuce. **a** Sporulation in a control leaf, bar = 50 µm. **b** No sporulation occurs in a treated leaf, bar = 50 µm. **c** Callose encasement (*yellow* fluorescence) of the primary and secondary vesicles of the pathogen inside the epidermal cell, bar = 20 µm. Basic aniline + calcofluor staining. **d** H_2O_2 accumulation (DAB staining) in a penetrated epidermal cell, bar = 20 µm. The Spore and germ-tube fluoresce blue. **e** BABA applied to perlite medium in Petri dishes induces resistance against different races of *B.lactucae*

that H_2O_2 is associated with BABA-induced resistance in lettuce. BABA was effective against all the tested isolates of *B. lactucae* in lettuce (Cohen et al. 2010) (Fig. 5e).

BABA-IR in tomato against late blight and lettuce against downy mildew is enhanced when plants are incubated in continuous light (Cohen 1994b; Vaknin 2016). The enhanced photosynthesis is associated with an elevated production of H_2O_2. This enhanced activity of BABA is alleviated by the photosynthesis inhibitor DCMU (Vaknin 2016), confirming the pivotal role of glycolate oxidase (GO) in BABA-induced resistance. GO was shown by Taler et al. (2004) to control resistance against downy mildew in melon.

When applied after inoculation, BABA protects against *B. lactucae* by inducing a range of responses, depending on application time. Application at 1 or 2 day post inoculation induces HR in the penetrated cells while application at 3 or 4 day post inoculation induces necrosis of the developing mycelium and accumulation of red (methanol-insoluble) pigment in the mesophyll (Fig. 6a-d). In both cases no sporulation occurred. However, when applied at 5 dpi, 1 day before completion of the asexual life cycle, BABA failed to prevent sporulation of the pathogen on the 6th day post inoculation (Cohen et al. 2011). Race specific resistance against *B. lactucae* is associated with HR while BABA-induced resistance is associated with callose encasement of the primary vesicles, regardless of the race used (Cohen et al. 2010). Unlike cultivated lettuce that responds to BABA with H_2O_2 accumulation in penetrated cells, the wild immune lettuce species *Lactucae saligna* and *Lactuca serriola* do not permit spore germination and/or germ-tube penetration (Fig. 6e-g) (Vaknin 2016).

Activity against basidiomycetes

Sunflower plants sprayed with BABA are protected against rust caused by *Puccinia helianthi* (Amzalek and Cohen 2007) (Fig. 7a, b). BABA protects pea against rust (*Uromyces pisi*) by enhancing phytoalexin production (Barilli et al. 2015). Marcucci et al. (2010) reported that foliar spray or soil drench with BABA induced a high level of resistance against the necrotrophic fungal pathogen *Sclerotinia sclerotiorum* in artichoke plantlets. BABA applied to potted lettuce plants or to detached cotyledons of lettuce, protects against *S. sclerotiorum* (Fig. 7c, d) but does not affect its growth on agar medium (Vaknin 2016).

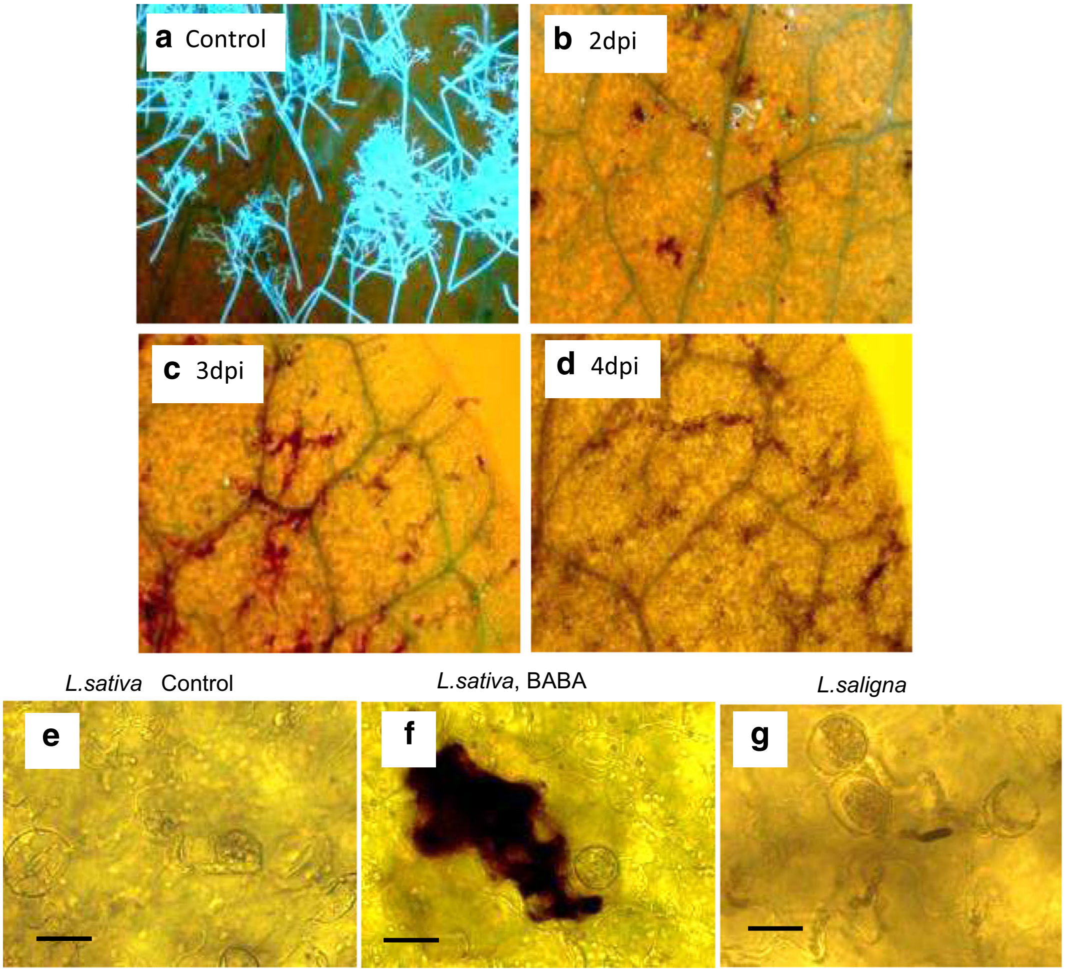

Fig. 6 Post-infection (2–4 dpi) resistance induced by BABA against *Bremia lactucae* in intact lettuce plants. **a** Heavy sporulation occurs in the control leaves. **b** HR develops in leaves treated with BABA at 2 dpi. **c, d** Necrotic hyphae are seen in leaves treated with BABA at 3dpi and 4 dpi. **e-g** Resistance induced by BABA in *Lactuca sativa* against *B.lactucae* is associated with H_2O_2 accumulation but not in the genetically-resistant wild lettuce *Lactuca saligna*. Bars = 20 µm

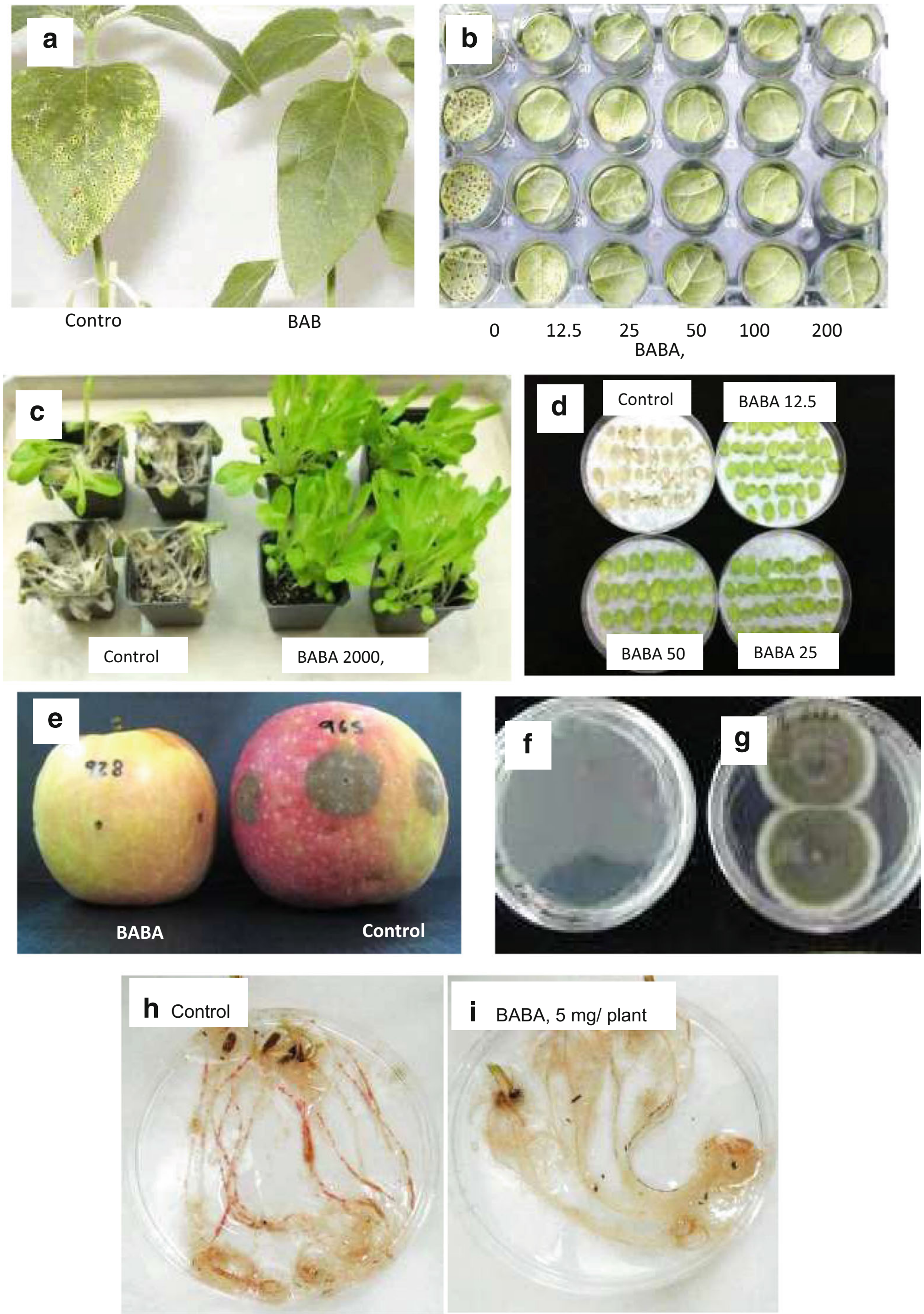

Fig. 7 Resistance induced by BABA (foliar spray, 1 day before inoculation) against *Puccinia helianthi* in intact sunflower plants (**a**) and in floating leaf discs (**b**). **c, d** BABA applied to the soil or dropped onto detached cotyledon leaves protects lettuce against *Sclerotinia sclerotiorum*. **e** BABA injected to apple fruits protects against *Alternaria alternata* apple type. **f** The fungicide Score is fully inhibitory at 5 ppm against the pathogen in vitro. **g** BABA at 2000 ppm has no effect on the growth of the pathogen in vitro. **h-i** BABA applied to the soil protects wheat against the root knot nematode *Meloidogyne marylandi*. Nematode galls in the control roots stain *red*

Activity against ascomycetes

In the field BABA effectively protects apples from moldy-core decay (Reuveni et al. 2003) and from blotch caused by *Alternaria alternata* apple type (Gur et al. 2013) (Fig. 7e). No inhibition of this fungus was induced by BABA in vitro (Gur 2013) (Fig. 7f, g). BABA performed in the field as effectively as the recommended commercial fungicides against both apple diseases (Gur et al. 2013; Reuveni et al. 2003). BABA induced resistance against *Alternaria brassicae* in *Brassica juncea* (Kamble et al. 2013) and *Verticillium longisporum* in *Brassica napus* (Kamble et al. 2013). Several papers report the control of *Botrytis cinerea* with BABA (Zimmerli et al. 2001; Maymoune et al. 2015; Luna et al. 2016). Koen et al. (2014) showed that the protective effect induced by BABA against *B. cinerea* is mimicked by Fe deficiency. Wang et al. (2016) showed direct inhibition of *B. cinerea* at BABA of >1000 ppm. They immersed strawberry fruits in BABA for 15 min and then wound-inoculated them with *B. cinerea*. Fruits induced for resistance exhibited higher sucrose, fructose and glucose contents, sweetness index and sensory scores. Direct toxicity of BABA to *B. cinerea* in culture was also reported by Fischer et al. (2009). Vogt and Buchenauer (1997) showed that BABA protects cucumber from powdery mildew and Zeighaminejad et al. (2016) confirmed it in squash. Walz and Simon (2009) showed protection of cucumber against the biotroph *P. cubensis* and the necrotroph *Colletotrichum lagenarium*.

Activity against nematodes

Oka and associates were the first to show that BABA applied as a foliar spray or root drench protects cucumber and tomato against the root knot nematode *Meloidogyne javanicum* (Oka and Cohen 2001; Oka et al. 1999) and wheat against the root knot nematode *Meloidogyne marylandi* (Oka and Cohen 2001) (Fig. 7h, i). ^{14}C-BABA applied to nematode-inoculated cucumber plants was shown to translocate from the treated leaves into the nematode galls (Oka et al. 1999).

BABA applied as a soil drench protects tomato against *M. ingognita* (Anter et al. 2014). Fatemy et al. (2012) showed that seed treatment with BABA is effective against *M. javanicum* in tomato. Ahmed et al. (2009) reported efficacy of BABA against *M.javanica* in mung bean. Mongae and Moleleki (2015) showed efficacy of BABA in protecting potato from the disease complex exerted by *Meloidogyne incognita* and *Pectobacterium carotovorum* subsp. *brasiliense* (Pcb). Sahebani and Hadavi (2009) concluded that the protection BABA provided to tomato against *M. javanica* resulted from ROS production by the enzymes SOD and POX.

Ji et al. (2015) showed that BABA induces resistance in rice against the root knot nematode *M. graminicola* while having no direct toxicity against the nematode. BABA applied to rice plants inhibits nematode penetration and results in delayed nematode and giant cell development. BABA-induced resistance is still functional in mutants or transgenic plants defective in salicylic acid biosynthesis and or abscisic acid (ABA) response. Pharmacological inhibition of jasmonic acid (JA) and ethylene (ET) biosynthesis indicated that BABA-IR against rice *M. graminicola* is independent of JA and ET. Protection resulted from the activation of basal defense mechanisms such as ROS accumulation, lignin formation, and callose deposition.

Activity against insects

Hodge et al. (2005) were the first to show that BABA induces resistance against insects. When applied as a root drench to six legume plant species it reduced the performance of the pea aphid *Acyrthosiphon pisum*. When applied to Brassicaceae plants, BABA suppressed the growth of the phloem-feeding insects *Myzus persicae* and *Brevicoryne brassicae* as well as chewing insects *Trichoplusia ni* and *Plutella xylostella* (Hodge et al. 2006). Tiwari et al. (2013) reported that BABA induced citrus resistance to the Asian citrus psyllid, *Diaphorina citri* the vector of *Citrus Greening*. They found no direct toxicity of BABA to this insect in leaf-dipping bioassays. BABA effectively protected soybean from *Aphis glycines* (Zhong et al. 2014). In contrast, Cao et al. (2014) reported that resistance of wheat to the grain aphid *Sitobion avenae* resulted from direct toxicity of BABA. *Sitobion avenae* growth rates were also reduced on artificial diet containing BABA. Philippe et al. (2016) showed that BABA protected apples against the rosy apple aphid *Dysahis plantaginea* with no direct toxicity to the aphid.

Seed treatment with BABA

Stirring seeds of pearl millet for 6 h in BABA of 50 mM protected emerging seedlings by up to 75 % from downy mildew caused by *Sclerospora graminicola* without affecting seed germination or seedling vigor (Shailasree et al. 2001). Downy mildew in BABA-protected plants was reduced by 90 % relative to control plants. Such seed treatment was long-lasting, effective against *S. graminicola* during the vegetative and reproductive growth periods of the plant.

In a later study, Shailasree et al. (2007) showed a close association between BABA-induced protection and increased accumulation of defense-related proteins such as phenylalanine ammonia lyase, peroxidase, β-1,3-glucanase and cell wall hydroxyproline-rich glycoproteins. Melvin et al. (2015) and Shailasree and Melvin (2015) suggested that BABA-induced resistance in pearl millet is a JA/SA mediated phenomenon. By using a proteomic approach Anup et al. (2015) revealed that the majority of the 63 differentially accumulated proteins in pearl millet seeds that were treated with BABA and inoculated with *S. graminicola* were associated with energy and metabolism, followed by stress and defense proteins. The over-representation of proteins pertaining to glucose metabolism suggested that seed priming ensures plant protection against disease without compromising its normal growth and development.

BABA seed priming improves drought and salinity stress tolerance potential of *Vigna radiate* (Jisha and Puthur 2016). These authors showed that BABA increases photosynthetic pigment content and photosynthetic and mitochondrial activities. Moreover, BABA seed priming reduces malondialdehyde content in the seedlings and enhances the accumulation of proline, total protein, total carbohydrate, nitrate reductase activity, and activities of antioxidant enzymes such as peroxidase and superoxide dismutase.

Worrall et al. (2012) showed that BABA seed treatment provided an 8 week-primed defense period against powdery mildew caused by *Oidium neolycopersici*. Priming responses are associated with enhanced defense gene expression during pathogen attack. No significant antagonism was seen between different forms of defense in plants grown from seeds treated with a combination of JA and BABA. Long-term defense priming by seed treatment is not accompanied by reductions in growth, and may therefore be suitable for commercial exploitation (Shailasree et al. 2001).

Luna et al. (2016) germinated tomato seeds for 1 week in BABA formulated in carboxy-methyl cellulose. Such treatment promotes seed germination efficiency, does not affect plant growth, does not affect colonization with arbuscular-mycorrhizal fungi and induces resistance against *Botrytis cinerea* in 4-week-old plants.

Mostek et al. (2016) soaked barley seeds in BABA for 24 h and thereafter allowed the seeds to germinate under salt stress conditions for 7 days. BABA induced the up-regulation of antioxidant enzymes (catalase, peroxidase and superoxide dismutase), PR proteins (chitinase, endo-1,3-β-glucosidase) and chaperones (cyclophilin, HSC 70). BABA induces defense and detoxification processes that may enable faster and more effective responses to salt stress, increasing the chances of plant survival under adverse environmental conditions.

The long-term protection against biotic and abiotic stresses induced by seed treatment is not derived from the actual presence of BABA in the tissues of the emerging plants but rather from a new physiological state primed by BABA.

Combination with other compounds

In field experiments, Cohen (2002) found that BABA provided significant control of late blight of potato. Baider and Cohen (2003) reported that using a mixture of BABA and mancozeb was significantly more effective in controlling late blight in potato and downy mildew in cucumber compared to BABA or mancozeb alone. Mixtures made of BABA and one or two anti-oomycete fungicides exhibited synergistic activity against late blight in potato, downy mildew in grapes and downy mildew in tobacco (Baider and Cohen 2003; Cohen et al. 1999). Liljeroth et al. (2010) showed that BABA used together with a reduced fungicide dose in the field gave the same level of late blight control as a full dose of the standard fungicide treatment. Walters et al. (2014) used a combination of three elicitors: BABA, Bion and cis-jasmonate with fungicides for the control of two barley diseases caused by *Blumeria graminis* f.sp. *hordei* and *Rynchosporium* *commune* in the field. They found that such combination provided disease control and increased yields which were equal to, and in some cases better than, that provided by the best fungicide treatment alone.

Plant stress induced by BABA

BABA applied to Arabidopsis caused female sterility due to accumulation of callose in the pistil (Jakab et al. 2001). Arabidopsis root growth is inhibited by BABA but this inhibition is alleviated by L-glutamine (Wu et al. 2010). Soil drench with BABA to 5-day Arabidopsis seedlings reduced their mass by about 60 %. However, the weight was recovered when plants were transplanted to BABA-free soil (Luna et al. 2014b). In tomato, three sprays of BABA applied to flowering plants in the field at weekly intervals resulted in a strong reduction in fruit set (Vaknin 2016). Lettuce seedlings growing on BABA-amended agar medium showed reduced growth of the main root (Fig. 8). Root growth was not restored by L-glutamine (Vaknin 2016).

Luna et al. (2016) showed that BABA applied to tomato seedlings as a root drench repressed plant growth whereas seed treatment did not. Kim et al. (2013) observed that treatment of kimchi cabbage seedlings with BABA protected against *Alternaria brassicicola* and *Colletotrichum higginsianum* but significantly reduced primary root elongation and cotyledon development. BABA does not inhibit spore germination nor mycelial growth of either fungus in vitro.

Other reports showed a positive effect of BABA on yield. BABA improved tuber late blight resistance (Olivieri et al. 2009) but the degree of reduction in disease severity depended on the basic level of resistance in each cultivar. Four foliar applications of BABA increased amounts of tubers per plant and total dry matter of tubers in both the moderately resistant and the highly susceptible cultivars. Four weekly sprays of BABA applied to Carignan grapevines during flowering had no effect on yield or sugar content compared to control untreated trees (Cohen, unpublished results). According to Luna et al. (2014b) stress and defense induced by BABA are controlled by different pathways and therefore can be separated.

Toxicity to mice

BABA added to the drinking water (10 mM) of mice had no effect on their behavior during an experimental period of 4 weeks. BABA was secreted in their urine but

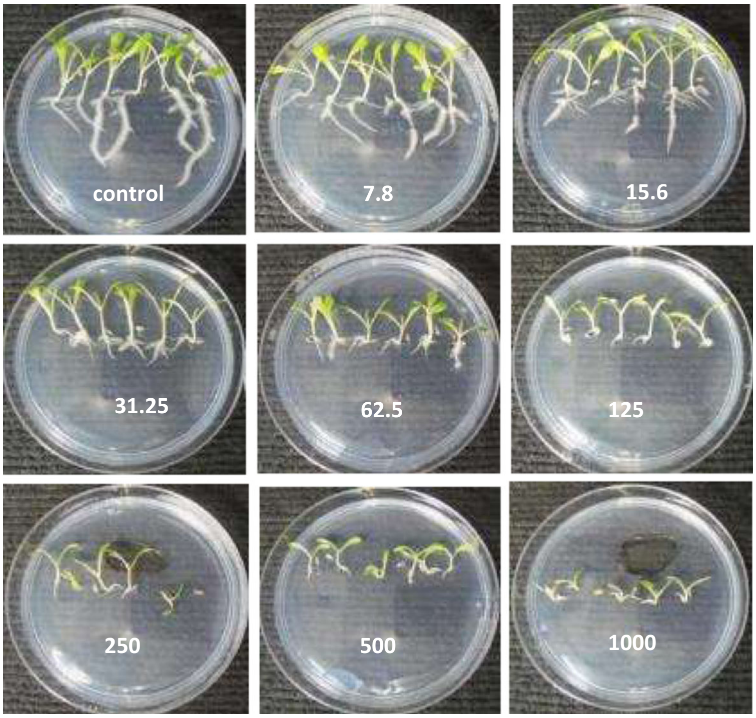

Fig. 8 The adverse effect of BABA, applied to agar medium at various doses (7.8-1000 ppm), on growth of lettuce seedlings

was not detected in their brains (Y. Buganim, M. Bitton and Y. Cohen, unpublished data). These findings may encourage further studies to enable registration of BABA for agro use.

Physiological and molecular changes induced by BABA

In Arabidopsis BABA-triggered resistance to pests is associated with a major metabolic shift that includes pipecolic acid (PA) accumulation. PA is considered a critical endogenous signal for priming (Conrath et al. 2015). BABA significantly increased anthocyanin content of purple basil and its potential anti-inflammatory activity (Zlotek et al. 2015). BABA delayed senescence of sweet cherry fruits (Wang et al. 2015) due to depressed membrane permeability and malondialdehyde content, reduced activities of polygalacturonase and pectinmethylesterase, enhanced cell-wall polysaccharide content, and integrated sub epidermal cell structure. Wang et al. (2016) showed that treating strawberry fruits with BABA enhanced activity of sucrose phosphate synthase, sucrose-6-phosphate phosphatase and sucrose synthase, thus increasing sweetness of the fruits.

Sos-Hegedus et al. (2014) reported that BABA increased drought tolerance of potato. Burra et al. (2014) compared the transcriptomes induced in potato foliage by phosphite and BABA. Phosphite treatment triggered induced resistance responses at the transcriptomic level similar to that induced by BABA treatments.

Maymoune et al. (2015) provided evidence that prior exposure of tomato plants to abiotic stress (leaf wounding, water stress or nitrogen deficiency) altered the protection efficacy of BABA (and other elicitors) against *B. cinerea*, suggesting an antagonistic interaction between the tomato responses to abiotic stresses and BABA treatment.

BABA-treated citrus plants are characterized by significantly lower levels of iron, magnesium, phosphorus, sodium, sulphur and zinc as compared with control plants (Tiwari et al. 2013). Koen et al. (2014) showed that BABA chelates iron in vivo. They believed that Fe deficiency response caused by BABA could induce the plant to a defense ready state participating in plant resistance against the pathogens.

Molecular genetic aspects of BABA-induced resistance

Involvement of various defense pathways

By testing various defense mutants of *Arabidopsis* for their ability to express BABA-IR (induced resistance), it became clear that BABA-IR is not controlled by a single defense signaling pathway but by various ones, depending on the type of stress applied. For example, BABA-IR against the bacterial pathogen *Pseudomonas syringae* pv. *tomato* DC3000 and the fungal pathogen *B. cinerea* resembling pathogen-induced SAR, in that it requires endogenous accumulation of SA and a functional NPR1/NIM1 protein (Zimmerli et al. 2000; Zimmerli et al. 2001). BABA-IR against *P. infestans* in potato (Eschen-Lippold et al. 2010) and TMV infection in tobacco (Siegrist et al. 2000) has also been shown to depend on a functional SA-signaling pathway. For the protection of grapevine against downy mildew, the JA-pathway is of importance. Here, BABA treatment leads to the potentiation of JA-regulated genes such as *LOX-9* and *PR-4* (Hamiduzzaman et al. 2005). In drought-stressed potato pre-treated with BABA, the ethylene receptor ETR1 was expressed longer than in the corresponding controls, suggesting an involvement of the ethylene-defense pathway (Sos-Hegedus et al. 2014).

BABA-IR against *Hyaloperonospora arabidopsidis*, as well as the necrotrophic fungi *Alternaria brassicicola* and *Plectosphaerella cucumerina*, is fully functional in *Arabidopsis* genotypes impaired in SA-, JA-, and ET-dependent signaling (Zimmerli et al. 2000; Ton and Mauch-Mani 2004), whereas mutants affected in the production or sensitivity to the abiotic stress hormone abscisic acid (ABA) are unable to express BABA-IR against *P. cucumerina* (Ton and Mauch-Mani 2004). Similarly, BABA-induced protection against drought and salt stress is unaffected in genotypes affected in SA-, JA-, and ET-dependent signaling pathways, but blocked in genotypes impaired in ABA signaling (Jakab et al. 2005). Hence, BABA-IR functions through different defense pathways, depending on the stress applied.

Priming

BABA-IR is tightly associated with primed expression of defense mechanisms. BABA-IR against *P. syringae* pv. *tomato* and *B. cinerea* coincides with primed transcription of the SA-inducible *PR-1* gene (Zimmerli et al. 2000, 2001). In contrast, BABA-IR against *H. arabidopsidis*, *P. cucumerina*, as well as against *A. brassicicola*, was found to correlate with primed accumulation of callose-containing papillae at the sites of infection (Ton and Mauch-Mani 2004) and such primed callose deposition is controlled by an ABA-dependent pathway, since ABA signaling mutants do not develop BABA-IR against *P. cucumerina* and concomitantly fail to express primed callose accumulation (Flors et al. 2008). ABA has also been implicated in the priming of defense during BABA-induced protection against osmotic stress. BABA-treated *Arabidopsis* showed a faster and higher induction of ABA-inducible marker genes upon salt stress (Jakab et al. 2005).

A screen to select *Arabidopsis* mutants that are impaired in BABA responsiveness (Toquin et al. 2002) yielded several *ibs* (*impaired in BABA-induced sterility*) mutants impaired in priming (Ton et al. 2005). Using subtraction suppression hybridization, a BABA-inducible gene, *PRLIP1*, was isolated and characterized. The predicted PRLIP1 amino acid sequence has regions of similarity to Ser hydrolases (eukaryotic lipases and esterases) similar to PAD4 (Jirage et al. 1999) and EDS1 (Falk et al. 1999). The expression profile of this lipase-like gene family has been described (Jakab et al. 2003) and it was shown to be primed in grapevine during defense against powdery mildew (Szalontai et al. 2012).

The BABA receptor

The stereospecific mode of action of BABA (see above) has long hinted to the presence of a specific receptor for this molecule. Such a receptor has been recently suggested in the form of an aspartyl-tRNA synthetase (Luna et al. 2014b). The receptor was identified in a screen of *A. thaliana* mutants impaired in BABA-induced immunity that yielded the mutant *ibi1*. Binding of R-BABA to the IBI1 protein leads to priming for non-canonical defense signaling upon pathogen attack.

Transgenerational inheritance of BABA priming

Research on the duration of BABA-IR over time revealed that the primed state in *Arabidopsis thaliana* is still functional in the next generation without additional treatment. When comparing the reactions of Arabidopsis plants that had been either primed with BABA or treated with water alone, it became apparent that the descendants of primed plants reacted much faster to inoculation with virulent Pseudomonads. Subjecting trans-generationally BABA-primed plants to an additional BABA-priming treatment leads to an even enhanced primed phenotype in their descendants (Slaughter et al. 2012). Interestingly, transgenerational inheritance of BABA-priming has also been observed in the weed *Solanum physalifolium* expressed as late blight resistance (Lankinen et al. 2016). Current evidence concerning the functioning of transgenerational priming points to epigenetic mechanisms (Luna et al. 2012).

Summary

BABA is a unique β-amino acid with major effects on plant physiology. It appears only rarely in nature. BABA moves systemically in the plant and induces resistance against soil borne, foliar and fruit pathogens belonging to different kingdoms. It also induces resistance against abiotic stresses. Of all the isomers of aminobutyric acid, BABA is the only active molecule, and of the two enantiomers, R-BABA is active. BABA is the only priming agent with long-lasting efficacy capable of causing also trans-generation resistance. It binds to a specific target in the plant cell, aspartyl-tRNA synthetase. The agro industry is seeking to develop new innovative products, such as BABA, for plant defense based on induced resistance.

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