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The combined use of the antagonistic yeast *Hanseniaspora uvarum* with β-aminobutyric acid for the management of postharvest diseases of kiwifruit

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ABSTRACT

Significant losses in harvested kiwifruit can be directly attributed to decay fungi. In the present study, the use of an antagonistic yeast, *Hanseniaspora uvarum*, combined with β-aminobutyric acid (BABA), a non-proteinogenic amino acid, was evaluated as a treatment for controlling postharvest infections of kiwifruit, artificially-inoculated with either *Botrytis cinerea* or *Alternaria alternata*. Natural infection of treated kiwifruits was also assessed. *H. uvarum* or BABA as stand-alone treatment, significantly reduced gray mold (*B. cinerea*) and black rot (*A. alternata*) on kiwifruit, relative to untreated control fruit, and also reduced the level of natural infection. The combination of *H. uvarum* and BABA, however, provided a superior level of postharvest disease control compared to either treatment alone. The growth of *H. uvarum* growth in kiwifruit wounds was not affected by BABA. Treatment of kiwifruit with either *H. uvarum* or BABA individually or in combination induced the gene expression and enzyme activity of chitinase and β-1,3-glucanase in kiwifruit. The ability of BABA to enhance the biocontrol efficacy of *H. uvarum* may be partially attributed to the elicitation of defense response in kiwifruit. The combined use of *H. uvarum* and BABA represents a promising alternative approach to the use of synthetic fungicides for the control of postharvest diseases in kiwifruit.

1. Introduction

Harvested kiwifruit is subject to fungal infections that cause decay and result in significant postharvest losses (Chen et al., 2015; Koh et al., 2005). Gray mold, caused by *Botrytis cinerea*, is the most significant postharvest disease of kiwifruit worldwide (Liu et al., 2018; Michailides and Elmer, 2000). Black rot, caused by *Alternaria alternata*, can also cause decay in harvested kiwifruit (Kwon et al., 2011; Li et al., 2017a,b), although it is not as prevalent as gray mold. Although the current management of postharvest diseases of kiwifruit relies mainly on synthetic chemical fungicides, development of resistant biotypes of pathogens, environmental concerns, and food safety issues, have created great interest in exploring alternative strategies (Di Francesco et al., 2018; Hua et al., 2019; Zhang et al., 2018).

Among of the various alternative approaches, biological control utilizing antagonistic yeasts has been shown to be effective in managing postharvest diseases of fruits (Liu et al., 2013; Spadaro and Droby, 2016; Wisniewski et al., 2016). Recently, the antagonistic yeast *Hanseniaspora uvarum* has been reported to be an effective biocontrol agent for the control of postharvest diseases of citrus (Li et al., 2016; Taqarort et al., 2008), table grape (Apaliya et al., 2017; Qin et al., 2015), and strawberry (Cai et al., 2015; Qin et al., 2017) and chilli fruit (Ramanujam et al., 2012). The use of bio-elicitors to induce host resistance has also received increasing attention as a strategy for managing postharvest diseases (Romanazzi et al., 2016a). β-Aminobutyric acid (BABA), a non-proteinogenic amino acid, has been demonstrated to induce resistance in various fruits against fungal pathogens, including *Penicillium digitatum* on grapefruit (Porat et al., 2003), *Penicillium italicum* on orange (Tavallali et al., 2008), *Penicillium expansum* on apple (Zhang et al., 2011), *Colletotrichum gloeosporioides* on mango (Zhang et al., 2013), and *Alternaria alternata* on jujube (Yan et al., 2015).

While the use of antagonistic yeast or elicitors, such as BABA, has been shown to be effective in controlling postharvest diseases under laboratory and simulated, semi-commercial conditions, consistent and reliable performance has limited their commercial acceptance and use. Therefore, an integrated management strategy is needed to provide a more reliable alternative to chemical fungicides and meet commercial requirements under various environmental conditions (Romanazzi et al., 2016b; Wisniewski et al., 2016). While the use of antagonists and elicitors, alone and together, has been explored, considerable research is still needed to optimize the use of the combined approaches. Therefore, the objective of the present study was to evaluate the ability of BABA and the antagonistic yeast, *H. uvarum,* applied separately or in

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combination, to control gray mold and black rot of harvested kiwifruit. The effects of BABA on the defense response of kiwifruit, and on the population dynamics of *H. uvarum in planta* were also assessed.

2. Materials and methods

2.1. Antagonistic yeast

The antagonistic yeast, *H. uvarum* LQ65, was isolated from the surface of loquat fruit in our own lab. It was identified by its general morphology and the sequence of the ITS region of ribosomal DNA as described by Leaw et al. (2006). *H. uvarum* was cultured in 100 mL of yeast peptone dextrose (YPD) broth (10 g of yeast extract, 20 g of peptone and 20 g of dextrose in 1 L of water) in 500-mL conical flasks inoculated at an initial concentration of 10^5 cells/mL. Yeast cultures were incubated at 25 °C on a rotary shaker at 200 rpm for 48 h. *H. uvarum* cells were pelleted at 5000*g* for 3 min and washed twice with sterile distilled water to remove residual medium prior to their use in the biocontrol assay. The cell concentration was adjusted to 5×10^7 cells/mL with sterile distilled water using a hemocytometer.

2.2. Fungal pathogens

The fungal pathogens, *B. cinerea* and *A. alternata*, were isolated from infected kiwifruits and maintained on potato dextrose agar (PDA) at 4 °C. In order to reactivate the culture and verify their virulence, the pathogens were inoculated into kiwifruit wounds and re-isolated onto PDA once an infection was established. Spore suspensions of the two pathogens were obtained from two-week-old cultures growing on PDA at 25 °C. The spore concentration was calculated with a hemocytometer, and adjusted to 1×10^4 spores/mL with sterile distilled water prior to their use for inoculating wounded kiwifruit.

2.3. Fruit

Kiwifruits (*Actinidia chinensis* cv. Hongyang) were harvested at commercial maturity (average quality values: 7.0 °Bx of brix, 64 N of firmness, and 6.5 kg per 100 fruits of weight). Fruits without wounds or rot were selected based on uniformity of size, disinfected with 2% (v/v) sodium hypochlorite for 2 min, rinsed with tap water, and air-dried.

2.4. Effect of BABA and H. uvarum on the development of B. cinerea and A. alternata infection of kiwifruit

BABA was purchased from Sigma-Aldrich (Shanghai, China). The concentration-time treatment (50 mM, 5-min immersion) was based on previous studies (Jannatizadeh et al., 2018; Zhang et al., 2013) and our own preliminary experiments.

Following disinfection of the fruit as previously described, kiwifruits were divided into four groups as described by Tang et al. (2015).

Group I (BABA treatment): kiwifruits were immersed in 50 mM BABA solution containing 0.05% (v/v) Tween 80 for 5 min, then air-dried and wounded (one wound at the equator of each fruit) and inoculated with 5 μL of sterile water into each wound.

Group II (yeast treatment): fruits were wounded and inoculated with 5 μL of *H. uvarum* (5×10^7 cells/mL) by pipetting the cells into each of the wounds.

Group III (BABA + yeast treatment): fruits were immersed in 50 mM BABA solution containing 0.05% (v/v) Tween 80 for 5 min, air-dried, and then inoculated with 5 μL of *H. uvarum* (5×10^7 cells/mL) by pipetting the cells into a wound.

Group IV (Blank control): fruits were wounded and inoculated with sterile water. No BABA or yeast were administered to the fruit. After 24 h, all fruits in the four groups were inoculated with 5 μL of a spore suspension of either *B. cinerea* or *A. alternata* (1×10^4 spores/mL). Disease incidence and lesion diameter in kiwifruit stored at 25 °C were measured after 4 days. Each treatment had three replicates comprised of 40 fruits each, and the experiment was repeated three times.

2.5. Effect of BABA and H. uvarum on natural infection of non-wounded kiwifruit

The effect of BABA, with or without of the addition of *H. uvarum*, on natural infection of kiwifruits was evaluated. Intact fruits were divided into the following four groups:

Group I (BABA treatment): kiwifruits were immersed in 50 mM BABA solution containing 0.05% (v/v) Tween 80 for 5 min.

Group II (yeast treatment): fruits were immersed in a water suspension of *H. uvarum* (5×10^7 cells/mL) containing 0.05% (v/v) Tween 80 for 5 min.

Group III (BABA + yeast treatment): fruits were first immersed in 50 mM BABA solution containing 0.05% (v/v) Tween 80 for 5 min, air-dried, and then immersed in a water suspension of *H. uvarum* (5×10^7 cells/mL) containing 0.05% (v/v) Tween 80 for 5 min.

Group IV (Blank control): fruits were immersed in sterile distilled water and then air-dried. No BABA or yeast were administered to the fruit.

After air-drying, the fruit in the four groups were stored at 25 °C for 14 days after which disease incidence was determined. Each treatment had three replicates comprised of 40 fruits each, and the experiment was repeated three times.

2.6. Determination of population dynamics of H. uvarum in fruit wounds

Kiwifruits were treated with BABA (50 mM for 5 min) as described above, while fruits without the BABA treatment served as a control. After air-drying, one wound (3 mm deep × 3 mm wide) was made at the equator of each kiwifruit. All wounds in treated and untreated fruit were inoculated with 5 μL of *H. uvarum* (5×10^7 cells/mL). Fruit was then stored at 25 °C. Samples of wounded tissues were subsequently collected every day over a period of 4 days and yeast populations were measured as described by Wang et al. (2018). Briefly, yeasts were recovered by removing sample tissues from 40 wounds with a cork borer (1 cm diameter × 1 cm deep). Samples were then ground with a mortar and pestle in 20 mL of sterile distilled water. Fifty microliters of ten-fold serial dilutions were spread on YPDA (YPDA: YPD with addition of 20 g of agar) plates. Samples taken at 1 h after treatment served as time 0. Colonies were counted after the YPDA cultures were incubated at 25 °C for 3 days and expressed as the log10 colony-forming units (CFU) per wound. Three biological replicates were used for each treatment at each specific time point. The experiment was repeated three times.

2.7. Assay of gene expression and enzyme activity of chitinase and β-1,3-glucanase in kiwifruit

Kiwifruits were immersed in BABA and/or yeast solution as described above, but pathogen inoculations were not subsequently conducted. Samples of kiwifruit tissues, consisting of both the pericarp and mesocarp, were collected from 40 fruits and pooled for use in the analysis of gene expression and enzyme activity. All tissue samples were immediately immersed in liquid nitrogen and then stored at −80 °C prior to subsequent analyses. Each treatment group had three biological replicates, and the experiment was repeated three times.

Total RNA was extracted from the collected kiwifruit tissue samples using PureLink™ Plant RNA Reagent (Invitrogen, Carlsbad, CA, USA) according to the manufacturer's instructions. The extracted RNA was treated with DNase and purified using an EasyPure Plant RNA Kit (TransGen Biotech, Beijing, China). First-strand cDNA synthesis was performed using 1 μg of total RNA in a final reaction volume of 20 μL using a TransScript® All-in-one First-Strand cDNA Synthesis SuperMix for qPCR (TransGen Biotech), following the manufacturer's protocol. Briefly, the 20-μL reaction was incubated at 42 °C for 15 min and 85 °C

Table 1
Primers used in RT-qPCR analysis of gene expression.

Gene	Accession no.	Primer sequence (5′-3′)	Product size (bp)
CHI	Achn341891	F: GTCCCAAACAAGAACTACTAC R: TCCTCATCCAATACCACAA	106
GLU	Achn103301	F: ACTTCTTGACTCGGCATA R: GCTCCTTGTTATTCTCATCA	99
Actin	Achn107181	F: GCTTACAGAGGCACCACTCAACC R: CCGGAATCCAGCACAATACCAG	156
18S rRNA	AB253775	F: GTCGTAACAAGGTTTCCGTAGGT R: CAAAGGGAAGAAAGAGTAGGGTT	138

Target genes and *Actin* were identified from a kiwifruit genome database (http://bioinfo.bti.cornell.edu/cgi-bin/kiwi/home.cgi), while *18S rRNA* was identified from NCBI database.

for 5 s and then maintained at 4 °C. RT-qPCR analysis was performed using SYBR® Premix Ex Taq™ II (Tli RNase H Plus) (Takara Biomedical Technology, Beijing, China), and 200 nmol of each primer per reaction. The ABI StepOne Plus (Applied Biosystems, Carlsbad, CA, USA) was set to cycle as follows: 95 °C denaturation for 30 s, followed by 40 cycles of amplification (95 °C for 20 s, 58.5 °C for 20 s, 72 °C for 30 s). The expression level of the target defense-related genes, *chitinase* (*CHI*) and *β-1,3-glucanase* (*GLU*), was normalized to the internal control genes, *Actin* and *18S rRNA*, using the $2^{-\Delta\Delta CT}$ method (Tang et al., 2016). Melting curve analyses of amplification products were performed at the end of each PCR reaction to ensure that unique products were amplified. PCR products were cloned and sequenced to verify their identity. The gene-specific primer pairs listed in Table 1 are designed based on the previous studies (Tang et al., 2016; Zhang et al., 2018).

Extracts from the sampled kiwifruit tissues for the assay of CHI and GLU activity were prepared as described by Zhang et al. (2011). Approximately 10 g of kiwifruit tissue was homogenized in 30 mL of sodium acetate buffer (50 mM, pH 5.0) at 4 °C. The homogenate was centrifuged at 17,000*g* for 30 min at 4 °C, and the resulting supernatant was collected for the enzyme assay. CHI and GLU enzyme activity was measured as described by Zheng et al. (2011). One unit (U) of CHI activity was defined as the production of 1 μmol N-acetyl glucosamine per second, while U of GLU activity was defined as the production of 1 μmol glucose equivalents per second. The results are expressed as U per gram fresh weight.

3. Results and discussion

3.1. Effect of BABA and H. uvarum on control of B. cinerea and A. alternata on kiwifruit

Integrated management, based on combining elicitors (e.g., chitosan, harpin and plant growth regulators) with biocontrol agents, such as yeast antagonists, has been reported to result in better control of postharvest diseases of fruits including kiwifruit, compared to either treatment alone (Romanazzi et al., 2016b). In the present study, the use of BABA and *H. uvarum*, alone or in combination, significantly reduced disease incidence and lesion diameter of gray mold (*B. cinerea*) and black rot (*A. alternata*) on kiwifruit (Fig. 1A and B). BABA and *H. uvarum*, as stand-alone treatments, reduced disease incidence of gray mold from 100% in the untreated, control fruit to 93% and 53% in treated fruit, respectively. The combination of BABA and *H. uvarum* treatment, however, exhibited a synergistic effect, in which the disease incidence was as low as 35% (Fig. 1A). Correspondingly, the average lesion diameter of gray mold was 18.5 mm in control fruit and 15.3 mm or 11.7 mm in fruit treated with BABA or *H. uvarum* alone, respectively. Notably it was only 8.2 mm when the two treatments were combined (Fig. 1B).

The combination of BABA and *H. uvarum* also resulted in better control of black rot, compared to either of the use of BABA or *H. uvarum* individually. Collectively, the results demonstrate that the combined use of BABA and *H. uvarum* provides the best control of gray mold and black rot of kiwifruit. The utilization of a combination of antagonistic yeasts with either harpin (Tang et al., 2015), or curing treatment (Cook et al., 1999) to manage *B. cinerea* and *P. expansum* on kiwifruit was previously reported. BABA has also been previously reported to be effective in controlling postharvest diseases on a variety of fruits, including orange (Tavallali et al., 2008), apple (Zhang et al., 2011) and mango (Zhang et al., 2013). The present study also demonstrated that the combined use of an antagonistic yeast (*H. uvarum*) and BABA can be used to more effectively manage postharvest diseases of fruit than the use of either agent alone.

3.2. Effect of BABA and H. uvarum on natural infection on kiwifruit

The predominant pathogens responsible for natural infections of kiwifruit are *B. cinerea*, *A. alternata*, *P. expansum,* and *Rhizopus stolonifera* (Tang et al., 2015; Thomidis and Prodromou, 2018). Consistent with the results obtained using artificially inoculated fruit, the combination of BABA and *H. uvarum* resulted in the greatest level of control of natural decay in kiwifruit as determined after 14-day storage at 25 °C (Fig. 2). Compared to control fruit with a natural decay incidence of 35%, BABA, *H. uvarum*, and the combined treatment decreased disease incidence to 23, 28, and 17%, respectively, all of which were significantly different from the control and from each other. The increased level of control resulting from the combined treatment may be the result of interactions occurring between BABA, kiwifruit host tissue and the antagonistic yeast, which collectively may affect pathogen development. Therefore, an assessment of yeast growth *in planta* was characterized by determining the rate of yeast growth in wounds of fruit previously treated with BABA.

3.3. Population dynamics of H. uvarum in kiwifruit wounds

H. uvarum multiplied rapidly in kiwifruit wounds stored at 25 °C (Fig. 3). The number of yeast cells increased more than ten-fold after one day of incubation and became gradually stable after three days when cells reached a stationary phase. Rapid growth and high population density of microbial antagonists colonizing fruit host are considered advantageous in competing for nutrients and space with the pathogen, and play a major role in biocontrol efficacy (Dukare et al., 2019; Jamalizadeh et al., 2011; Liu et al., 2013). Rapid multiplication of *H. uvarum* in fruit wounds indicates that this yeast is well-adapted to the microenvironment of fruit wounds, which is directly related to its biocontrol performance (Fig. 1). Importantly, the prior immersion of kiwifruit in BABA (50 mM for 5 min) did not markedly affect the colonization and growth of *H. uvarum* in wounds of kiwifruit (Fig. 3). These results provide support for using a combination of BABA and *H. uvarum* for the management of postharvest diseases of kiwifruit.

3.4. Effect of BABA and H. uvarum on gene expression and enzyme activity of CHI and GLU in kiwifruit

The defense response of host tissues to an invading pathogen plays an important role in the infection process. The induction of defense-related responses (e.g., activation of defense-related genes and enzymes) in host fruit tissues has been reported to be one of mechanisms of action of antagonistic yeasts (Sharma et al., 2009; Spadaro and Droby, 2016) and BABA (Chea et al., 2019; Jannatizadeh et al., 2018). Among defense-related enzymes, CHI and GLU have been suggested to play a crucial role in preventing the establishment of fungal pathogens in harvested fruit (Pétriacq et al., 2018). CHI catalyzes the hydrolysis of β-1-4-linkage of the N-acetyl glucosamine polymer of chitin, an essential cell wall component of fungal pathogens. GLU is a pathogenesis-related (PR) protein that directly degrades cell walls of pathogens or causes the release of oligosaccharides from fungal cell walls that elicit

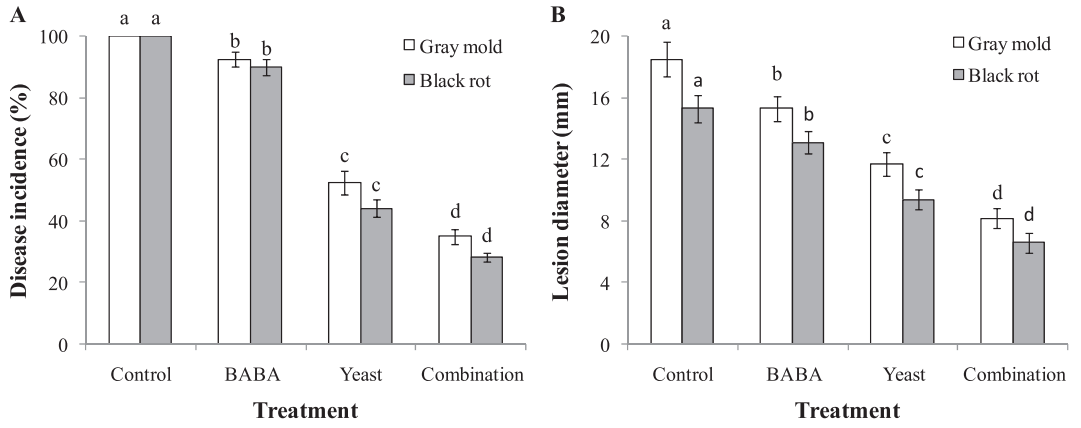

Fig. 1. Effect of BABA or an antagonistic yeast (*H. uvarum*) alone or in combination on disease incidence (A) and lesion diameter (B) of gray mold and black rot in kiwifruits stored at 25 °C for 4 days. The data presented are the mean ± SE of nine replicates pooled from three experiments. Columns with different letters in each disease are significantly different according to a Duncan's multiple range test at $P < 0.05$.

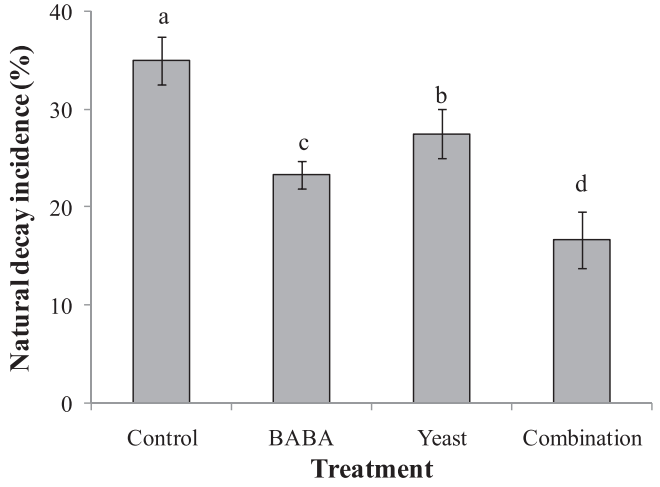

Fig. 2. Effect of BABA or an antagonistic yeast (*H. uvarum*) alone or in combination on natural infection of kiwifruits stored at 25 °C for 14 days, relative to an untreated control. The data presented are the mean ± SE of nine replicates pooled from three experiments. Columns with different letters are significantly different according to a Duncan's multiple range test at $P < 0.05$.

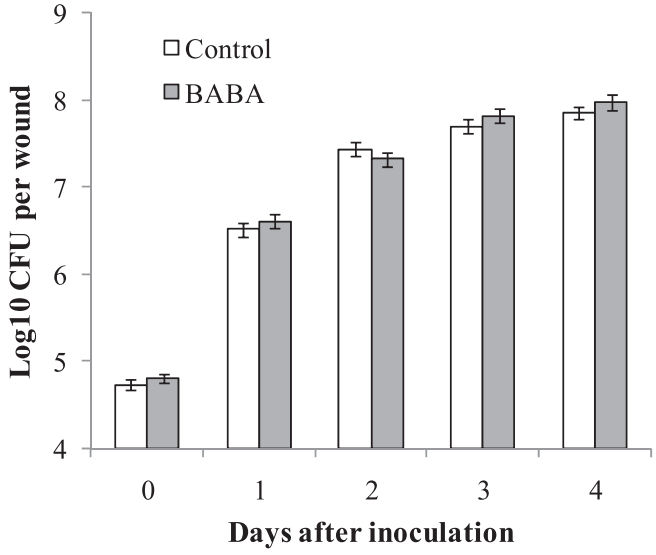

Fig. 3. Population dynamics of *H. uvarum* in wounds of BABA-treated and non-treated control kiwifruits stored at 25 °C. The data presented are the mean ± SE of nine replicates pooled from three experiments. No significant difference ($P > 0.05$) in the growth rate was observed between BABA-treated and non-treated control kiwifruits at each time point, according to a Student's *t*-test.

host defense response (Zavaliev et al., 2013). In the current study, the pattern of *CHI* expression in control and treated fruit were similar, although the specific levels of activity varied (Fig. 4A). *CHI* expression remained relatively stable in control fruit (non-treated) over the time course of four days of storage at 25 °C. In contrast, all treated fruit (BABA, yeast, or a combination of both) exhibited significantly higher levels of expression than control fruit at all time points. The highest level of *CHI* expression was observed in fruit that received the combined BABA/*H. uvarum* treatment. Both BABA and *H. uvarum* also induced a higher level of *GLU* expression in treated fruit than in non-treated, control fruit (Fig. 4B). Notably, the highest level of *GLU* expression during the first three days of storage was observed in fruit that received the BABA/*H. uvarum* treatment.

Corresponding to the pattern of gene expression observed for the two defense-related genes, BABA and *H. uvarum* induced an increase in the activity of CHI and GLU enzymes in kiwifruit stored at 25 °C (Fig. 5). The highest level of enzyme activity was observed in fruit that received the combined BABA/*H. uvarum* treatment. The activity of CHI in the non-treated, control fruit remained relatively low at all time points. CHI activity in fruit treated with the combination of BABA and *H. uvarum* peaked at 3 days of storage, and was over two-fold greater than the CHI activity in control fruit (Fig. 5A). Fruit treated with the combination of BABA and *H. uvarum* also exhibited significantly higher GLU activity than non-treated, control fruit over the whole four days of storage. Fruit treated with BABA or yeast alone exhibited significantly higher levels GLU activity than control fruit over the first three days of storage (Fig. 5B). These results are consistent with previous reports on the effect of these agents in other horticultural crops. Postharvest treatment of BABA induced CHI and GLU enzyme activity in apple, mango and jujube fruits **(Yan et al., 2015; Zhang et al., 2011, 2013), while *H. uvarum* induced the activity of GLU and other defense-related enzymes in grape berry (Apaliya et al., 2019; Liu et al., 2010) and strawberry (Cai et al., 2015). In the present study, *H. uvarum* or BABA treatment alone induced the gene expression and enzyme activity of CHI and GLU in kiwifruit stored at 25 °C, relative to untreated fruit, while the combined treatment of fruit with both BABA and the yeast induced the greatest increase.

4. Conclusions

The use of the yeast *H. uvarum* combined with prior treatment of kiwifruit with BABA was more effective in managing postharvest

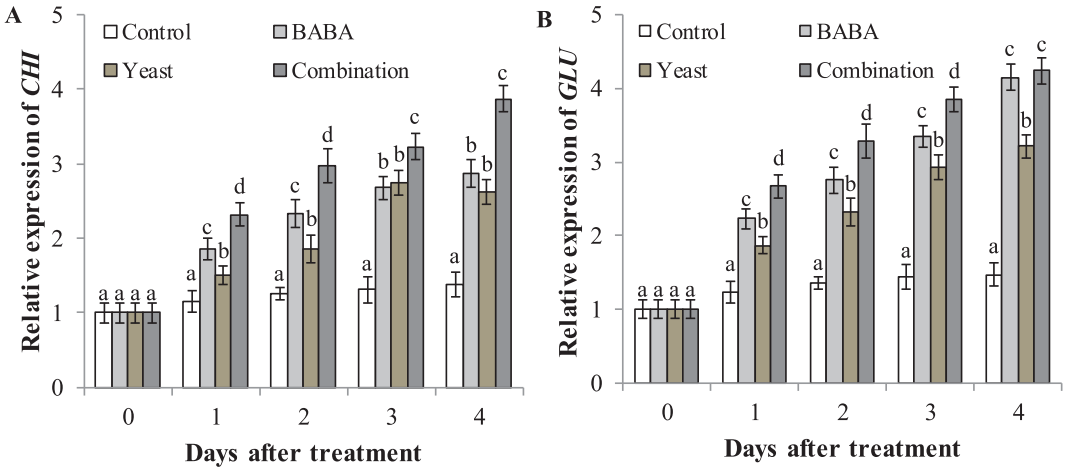

Fig. 4. Effect of BABA and an antagonistic yeast (*H. uvarum*), applied alone or in combination on gene expression of *chitinase* (*CHI*, A) and *β-1,3-glucanase* (*GLU*, B) in kiwifruits stored for four days at 25 °C. The data presented are the mean ± SE of nine replicates pooled from three experiments. Values with different letters at each time point are significantly different according to a Duncan's multiple range test at $P < 0.05$.

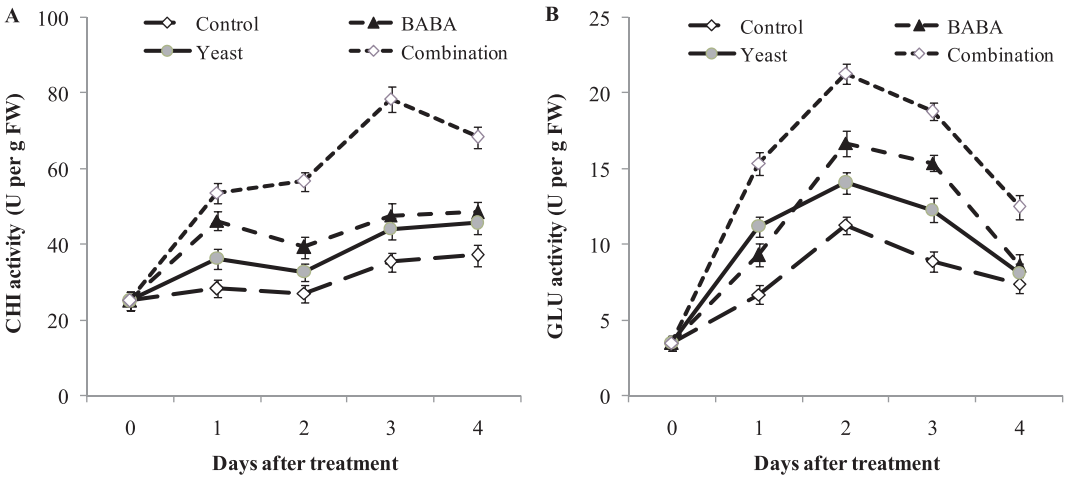

Fig. 5. Effect of BABA and an antagonistic yeast (*H. uvarum*), applied alone or in combination on the enzyme activity of chitinase (CHI, A) and β-1,3-glucanase (GLU, B) in kiwifruits stored for four days at 25 °C. The data presented are the mean ± SE of nine replicates pooled from three experiments.

diseases of kiwifruit than either treatment alone. An integrated strategy utilizing a biocontrol agent with an elicitor represents a promising approach for the management of postharvest diseases of fruit crops, especially for highly perishable commodities such as kiwifruit. The research on optimization of the combined approach like the treatment concentration/time at commercial scale, however, will be further investigated.

Author contributions

All authors read and approved the final manuscript. X. Nie conceived and designed the experiments; L. Cheng, X. Nie and C. Jiang performed the experiments; S. Li analyzed the data; X. Nie and S. Li drafted the manuscript.

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