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Research Article

Biotic and Abiotic Stress Tolerance Induction by Salicylic and Abscisic Acid Phytohormones in Barley

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Abstract

Background and Objective: Unpredictable performance and short-term productivity of the newly released varieties under natural environmental conditions remains a major challenge in barley both at research and commercial production levels in Kenya. This is due to little understanding of the hormonal signalling and induction pathways under the influence of both biotic and abiotic stresses. The study was set to establish whether there is a synergistic and/or antagonistic effect of salicylic and abscisic acid phytohormones on net blotch disease, aluminium toxicity and drought stress in barley. **Materials and Methods:** Trait-specific barley genotypes were planted in a split-plot arrangement with phytohormone treatments as the main plot and barley genotypes as sub-plots in a completely randomized design with 3 repeated observations. The 50 µM SA, 20 µM ABA, 20 µM ABA+50 µM SA combination and double distilled water as control were supplied to each pot twice as a soil drench. Data on response to net blotch disease, aluminium toxicity and drought stress were collected and subjected to analysis of variance and descriptive statistics on genstat statistical software version 16.0. **Results:** Salicylic acid-enhanced tolerance to net blotch disease in a single application than when combined with abscisic acid. Contrary to disease, SA×ABA expressed a synergistic effect towards increased tolerance to aluminium toxicity and drought stress. **Conclusion:** Salicylic acid-enhanced tolerance to biotic stress while abscisic acid-enhanced tolerance to abiotic stress whose synergy is more expressed when combined with SA.

Key words: Salicylic acid, abscisic acid, synergy, antagonism, signalling, disease, aluminium, drought

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Competing Interest: The authors have declared that no competing interest exists.

Data Availability: All relevant data are within the paper and its supporting information files.

INTRODUCTION

The combined effects of net blotch, drought and aluminium cation toxicity together with genotype× environment interactions in barley is the major factor responsible for low yields and can cause up to 100% yield loss[1]. In Kenya, the actual yields remain low in barley growing zones which exhibit high frequencies of net blotch epidemics, unpredictable and intense droughts and soils that are increasingly becoming acidic and toxic to plants. However, the complex interaction effect among net blotch fungi, drought and aluminium toxicity in major barley growing zones of Kenya remains understudied despite soils in Kenya being mostly acidic[2,3].

In response to these stresses, plants produce varying levels of ABA, JA and SA phytohormones[4,5] which are either antagonistic or synergistic[6,7] to each other[8]. Additionally, upon synthesis, these phytohormones influence tolerance and/or susceptibility levels to biotic and abiotic stresses, with each having a distinct role in defence mechanism[4].

This scenario has not been scientifically studied and documented in winter and spring adapted barley genotypes commonly grown in Kenya and other countries where barley is grown despite varietal genetics, plant nutrition and environmental roles in the activation of pathways leading to synthesis and catabolism of these hormones[9]. This also may imply that the quantities of ABA, SA and JA produced in response to these stresses vary depending on plant stress and intensity.

This study aimed at determining the synergistic and antagonistic effects of exogenous phytohormones in barley concerning net blotch, aluminium cation toxicity and water deficiency (drought) stress factors using previously identified trait-specific barley genotypes adapted to winter and spring production conditions.

MATERIALS AND METHODS

Study area: This study was conducted at the Department of Seed, Crop and Horticultural Sciences in the School of Agriculture and Biotechnology at the University of Eldoret-Kenya within greenhouse and laboratory facilities due to the sensitivity of the treatments. The implementation commenced from August, 2016-2017, taking 12 months from the start to the end of the study.

Genotype selection: Barley genotypes previously selected for their response to drought, aluminium toxicity and net blotch disease were planted separately under drought, aluminium toxicity and net blotch, respectively then treated with the 4 phytohormones in the greenhouse. In each stress factor, a total of eight genotypes (4 winter and 4 spring genotypes) with 2 tolerant and 2 susceptible for each stress factor in each of the winter and spring groups and group codes were used in Table 1.

Research protocol: For net blotch, aluminium and drought stress experiment with phytohormones, 8 barley genotypes

Table 1: Trait specific winter and spring barley genotypes selected for phytohormonal studies

Genotype groups	Genotype names	Trait codes	Trait descriptions
Spring barley	Fanaka	DRT1	Drought tolerant
	NGUZO	DRT2	Drought tolerant
	HKBL 1805-3	DRS1	Drought sensitive
	HKBL 1862-5	DRS2	Drought sensitive
	NGAO	NBT1	Net blotch tolerant
	MALT1	NBT2	Net blotch tolerant
	SABINI	NBS1	Net blotch susceptible
	KARNE	NBS2	Net blotch susceptible
	HKBL 1663-3	ALT1	Aluminium tolerant
	HKBL 1805-3	ALT2	Aluminium tolerant
	HKBL 1674-4	ALS1	Aluminium sensitive
	NGAO	ALS2	Aluminium sensitive
Winter barley	GRACE	DRT1	Drought tolerant
	TITOUAN	DRT2	Drought tolerant
	BEATRIX	DRS1	Drought sensitive
	MARTHE	DRS2	Drought sensitive
	SHUFFLE	NBT1	Net blotch tolerant
	TITOUAN	NBT2	Net blotch tolerant
	QUENCH	NBS1	Net blotch susceptible
	BEATRIX	NBS2	Net blotch susceptible
	GRACE	ALT1	Aluminium tolerant
	ALICIANA	ALT2	Aluminium tolerant
	PUBLICAN	ALS1	Aluminium sensitive
	ANNABEL	ALS2	Aluminium sensitive

Aluminium: Degree of hematoxylin staining, Net blotch: 0-9 severity scale, Drought: Membrane stability index (MSI) previously selected for known tolerance and sensitivity to net blotch disease, aluminium cation toxicity and drought stress were raised in 2 L plastic pots filled with solarized forest soils (pH>6.0). The phytohormones treatments were randomized as main plots and trait-specific genotypes as sub-plots in a split-plot arrangement in a completely randomized design with 3 repeated observations.

For net blotch disease severity under the influence of phytohormones, 4 hormonal treatments at 50 μM SA[10], 20 μM ABA[11], 20 μM ABA+50 μM SA combination and double distilled water as control were supplied to each pot twice as soil drench immediately after seedling emergence and 2 weeks after the 1st hormone treatment. The 16-18 days old barley seedlings (Zadoks growth stage 15) initially treated with 4 phytohormones were transferred to inoculation chamber exhibiting temperatures and relative humidity then inoculated with 0.5 mL/plant of 5×10^3 conidia mL^{-1} spore concentration[12]. Disease severity data were collected on a 0-7 severity scale at 7 days intervals after inoculation up to 35th days after inoculation.

For aluminium toxicity versus phytohormones, the 4 hormonal treatments were supplied twice immediately after emergence and 2 weeks after the 1st hormonal treatment. The supply of 148 μM aluminium cation contained in a nutrient solution[13] commenced 1 day after the 1st hormonal treatment and this was used to maintain the genotypes at 80% FC up to physiological maturity. Data on height (cm), apical root length (cm), number of fibrous roots, root dry weight (g) and shoot dry weight (g) were recorded under the influence of phytohormones and aluminium cation toxicity.

Under drought stress versus phytohormones, water deficiency stress was introduced immediately after emergence and soil moisture was maintained at 20% field capacity till the end of the experiment. Phytohormone treatments were supplied to each pot twice as soil drench immediately after seedling emergence and 2 weeks after the 1st hormone treatment. Data on tillering ability and plant height (at physiological maturity) and total dry weight (at late vegetative growth stage) were recorded.

Statistical analysis: Data on the response of trait-specific winter and spring barley to drought, aluminium toxicity and net blotch disease severity under the influence of exogenous phytohormones were subjected to analysis of variance and descriptive statistics on Genstat statistical software release 16.0 VSN International Ltd. and Microsoft Excel at 5% level of significance.

RESULTS

Hormonal signalling effect on net blotch foliar infection in barley: Among the selected spring adapted barley genotypes, Salicylic Acid (SA) treatment at 50 μM induced disease resistance in barley with an average severity score of 2.2 on a 0-7 severity scale from 7-35 Days After Inoculation (DAI). Also, the combined application of SA and 20 μM abscisic acid (SA×ABA) did not enhance synergy in reduction of severity to net blotch foliar infection hence recorded an average of 2.3 on a 0-7 disease rating scale. However, a single application of ABA did not increase disease tolerance to net blotch where the genotype known to be the most susceptible to net blotch (NBS1) recorded the highest severity of 6.5 at 35 days after inoculation. Without hormonal treatment (control), the 2 known susceptible genotypes NBS1 and NBS2 expressed severities of 6.0 and 5.7, respectively as shown in Table 2 and Fig. 1.

The winter adapted barley also responded to foliar infection by net blotch in a similar pattern just like the spring adapted barley by scoring an average of 2.1, 2.6, 3.0 and 3.7 under the exogenous treatment with 50 μM SA, 20 μM ABA, a combination of SA×ABA and control, respectively on a 0-7 severity rating scale. Contrary to the spring adapted barley, the winter barley recorded low disease severity under the influence of 20 μM ABA than when the 2 hormones are combined. At 35 DAI, application of SA induced resistance response in known susceptible and resistant genotypes which ranked 2.4 and 2.5 for NBS1 and NBS2 (known susceptible genotypes) and 1.6 and 1.9 for NBT1 and NBT2 (known tolerance genotypes). In contrast, these same genotypes exhibited higher disease severities under the influence of ABA alone and combined application of SA and ABA as shown in Table 3.

Hormonal signalling effect on aluminium cation toxicity in barley: Enhance increase in growth in terms of plant height, the number of fibrous roots, root dry weight and shoot dry weight was observed when spring adapted barley genotypes with known sensitivity and tolerance to aluminium toxicity were treated with 50 and 20 μM SA and ABA, respectively compared to an untreated set of the experiment. For example, when ALS1 known to be the most sensitive to aluminium toxicity was treated with SA alone, the height increased from 55 cm to slightly above 65 cm. A similar genotype expressed an enhanced increase in height from 65 cm under the influence of SA to 75 and 82 cm under the influence of ABA and SA×ABA combination hence indicating a synergistic

Table 2: Varying response of net blotch tolerant and susceptible spring adapted barley genotypes to foliar infections by *Pyrenophora teres* under the influence of exogenous phytohormones from 7-35 days after inoculation

		Net blotch severity (0-7 severity scale)-spring barley						
Phytohormone	Barley traits	7 DAI	14 DAI	21 DAI	28 DAI	35 DAI	Mean (trait)	Mean (phytohormone)
ABA	NBS1	1.8	2.8	5.8	6.0	6.5	4.6	3.1
	NBS2	1.7	2.7	3.2	3.5	3.8	3.0	
	NBT1	0.7	1.7	3.0	3.0	3.0	2.3	
	NBT2	1.0	1.8	2.7	2.7	3.2	2.3	
Control	NBS1	2.2	3.5	5.3	5.7	6.0	4.5	3.5
	NBS2	1.7	3.3	5.5	5.5	5.7	4.3	
	NBT1	1.2	2.0	3.2	3.3	3.3	2.6	
	NBT2	1.7	2.7	3.0	3.0	3.2	2.7	
SA	NBS1	1.5	2.3	3.7	3.7	3.8	3.0	2.2
	NBS2	1.0	1.7	2.3	2.0	2.3	1.9	
	NBT1	0.7	1.0	1.8	2.0	2.5	1.6	
	NBT2	1.2	1.7	2.3	2.7	2.8	2.1	
SA×ABA	NBS1	0.8	1.3	2.2	2.5	3.0	2.0	2.3
	NBS2	1.5	2.0	2.5	2.7	3.0	2.3	
	NBT1	1.7	2.3	3.0	3.2	3.5	2.7	
	NBT2	1.3	2.0	2.5	2.5	2.8	2.2	
Mean (DAI)		1.3	2.2	3.3	3.4	3.7	2.8	2.8

	Phytohormone (PH)	Trait (TR)	Time (TI)	PH×TR	PH×TI	TR×TI	PH×TR×TI
Probability	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
S.E.	0.1074	0.0876	0.0499	0.1859	0.1397	0.1251	0.2577
S.E.D	0.1519	0.1239	0.0706	0.2629	0.1975	0.1769	0.3645
CV (%)	12.5						

Table 3: Varying response of net blotch tolerant and susceptible winter adapted barley genotypes to foliar infections by *Pyrenophora teres* under the influence of exogenous phytohormones from 7-35 days after inoculation

		Net blotch severity (0-7 severity scale)-spring barley						
Phytohormone	Barley traits	7 DAI	14 DAI	21 DAI	28 DAI	35 DAI	Mean (trait)	Mean (phytohormone)
ABA	NBS1	1.5	2.2	2.5	3.2	3.7	2.6	
	NBS2	1.5	2.8	4.8	4.8	5.2	3.8	2.6
	NBT1	1.3	2.0	2.5	2.5	2.8	2.2	
	NBT2	0.8	1.2	2.2	2.5	2.5	1.8	
Control	NBS1	2.0	3.3	5.3	5.5	5.8	4.4	
	NBS2	1.7	3.0	5.8	6.0	6.0	4.5	3.7
	NBT1	1.2	2.5	3.2	3.3	3.8	2.8	
	NBT2	1.3	2.8	3.3	3.7	3.7	3.0	
SA	NBS1	1.7	2.0	2.5	2.7	3.0	2.4	
	NBS2	1.3	2.0	2.7	3.0	3.3	2.5	2.1
	NBT1	0.8	1.3	1.7	1.8	2.3	1.6	
	NBT2	1.3	1.7	2.0	2.2	2.5	1.9	
SA×ABA	NBS1	2.0	2.7	3.8	3.8	4.5	3.4	
	NBS2	2.0	3.0	4.5	4.8	4.8	3.8	3.0
	NBT1	1.7	2.2	2.7	2.7	3.2	2.5	
	NBT2	1.0	2.0	2.8	3.0	3.2	2.4	
Mean (DAI)		1.4	2.3	3.3	3.5	3.8	2.9	2.9

	Phytohormone (PH)	Trait (TR)	Time (TI)	PH×TR	PH×TI	TR×TI	PH×TR×TI
Probability	0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.003
S.E	0.1376	0.0997	0.0468	0.2208	0.1611	0.1301	0.2771
S.E.D	0.1946	0.1409	0.0662	0.3122	0.2278	0.1841	0.3918
CV (%)	11.4						

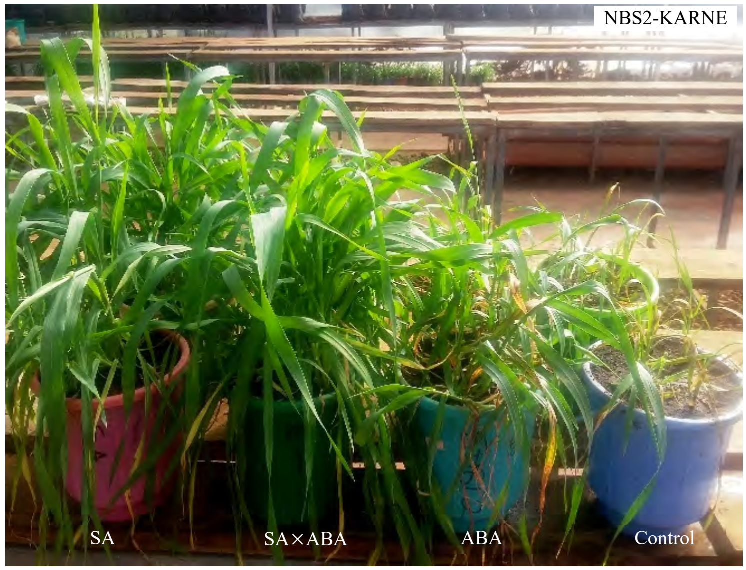

Fig. 1: Response to net blotch foliar infection by a susceptible barley genotype (KARNE) after: SA: 50 µM, SA×ABA: 50 µM SA plus 20 µM ABA, ABA: 20 µM ABA and Control: No hormone

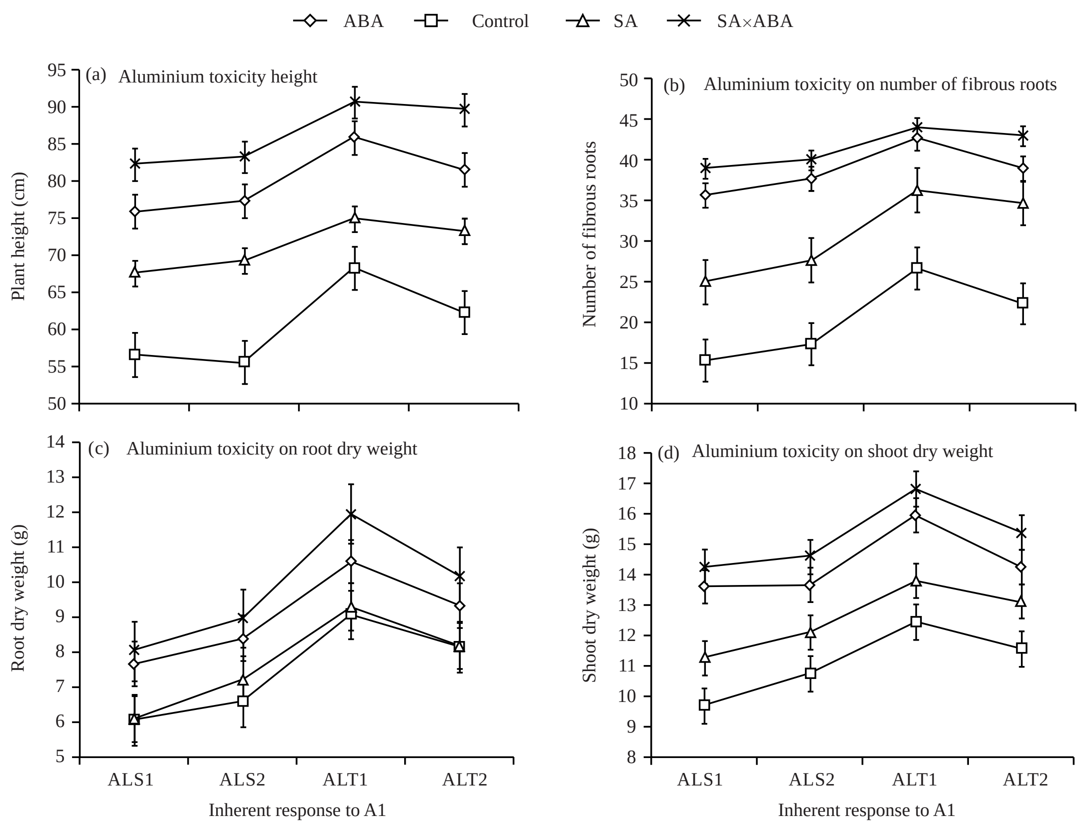

Fig. 2(a-d): Synergistic effect of combined application of SA and ABA in enhancing tolerance to aluminium toxicity in spring adapted barley with known sensitivity (ALS1 and ALS2) and tolerance (ALT1 and ALT2), (a) Enhanced effect of SA, ABA and SA×ABA on barley height, (b) Enhanced effect of SA, ABA and SA×ABA number of fibrous roots, (c) Enhanced effect of SA, ABA and SA×ABA root dry weight and (d) Enhanced effect of SA, ABA and SA×ABA shoot dry weight
Error bars represent standard error bars for mean

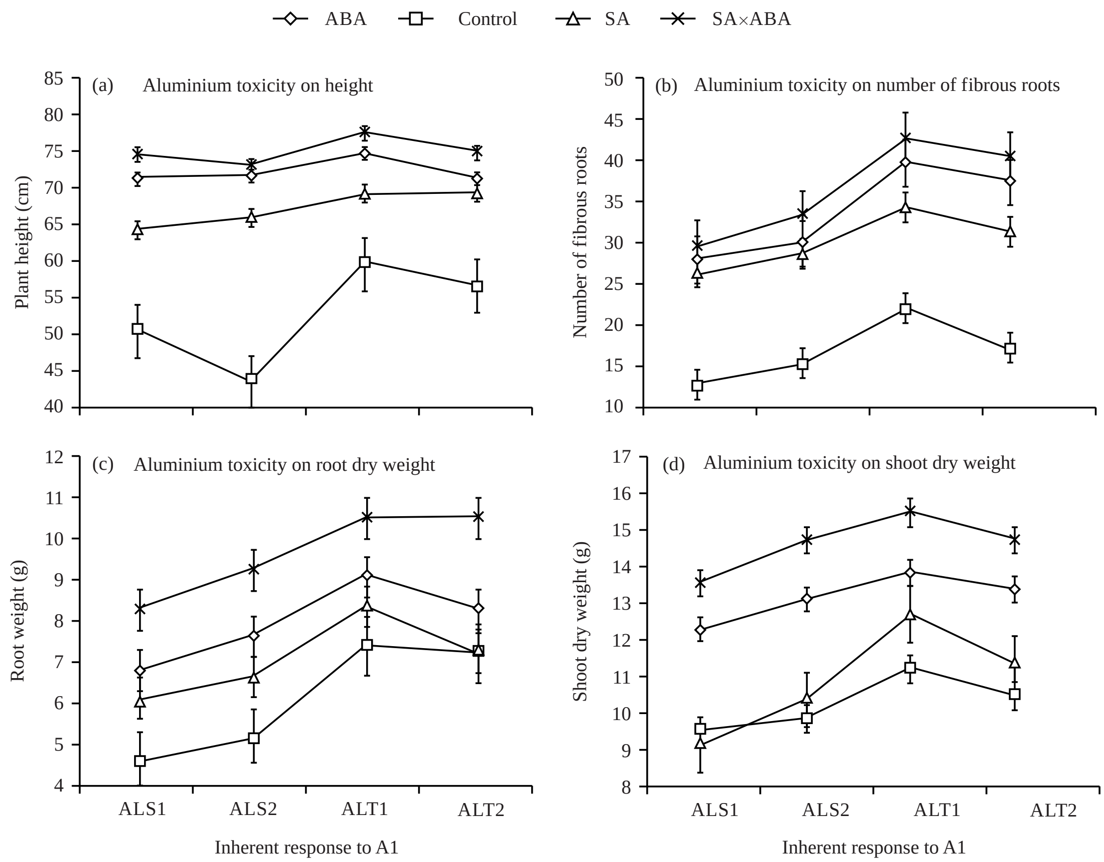

Fig. 3(a-d): Synergistic effect of combined application of SA and ABA in enhancing tolerance to aluminium toxicity in winter adapted barley with known sensitivity (ALS1 and ALS2) and tolerance (ALT1 and ALT2), (a) Enhanced effect of SA, ABA and SA×ABA on barley height, (b) Enhanced effect of SA, ABA and SA×ABA number of fibrous roots, (c) Enhanced effect of SA, ABA and SA×ABA root dry weight and (d) Enhanced effect of SA, ABA and SA×ABA shoot dry weight
Error bars represent standard error bars for mean

Fig. 4: Root and shoot growth enhancement effect by phytohormones in aluminium sensitive (a) spring and (b) winter barley genotypes under 148 μM Al toxicity, more root growth enhancement under SA×ABA

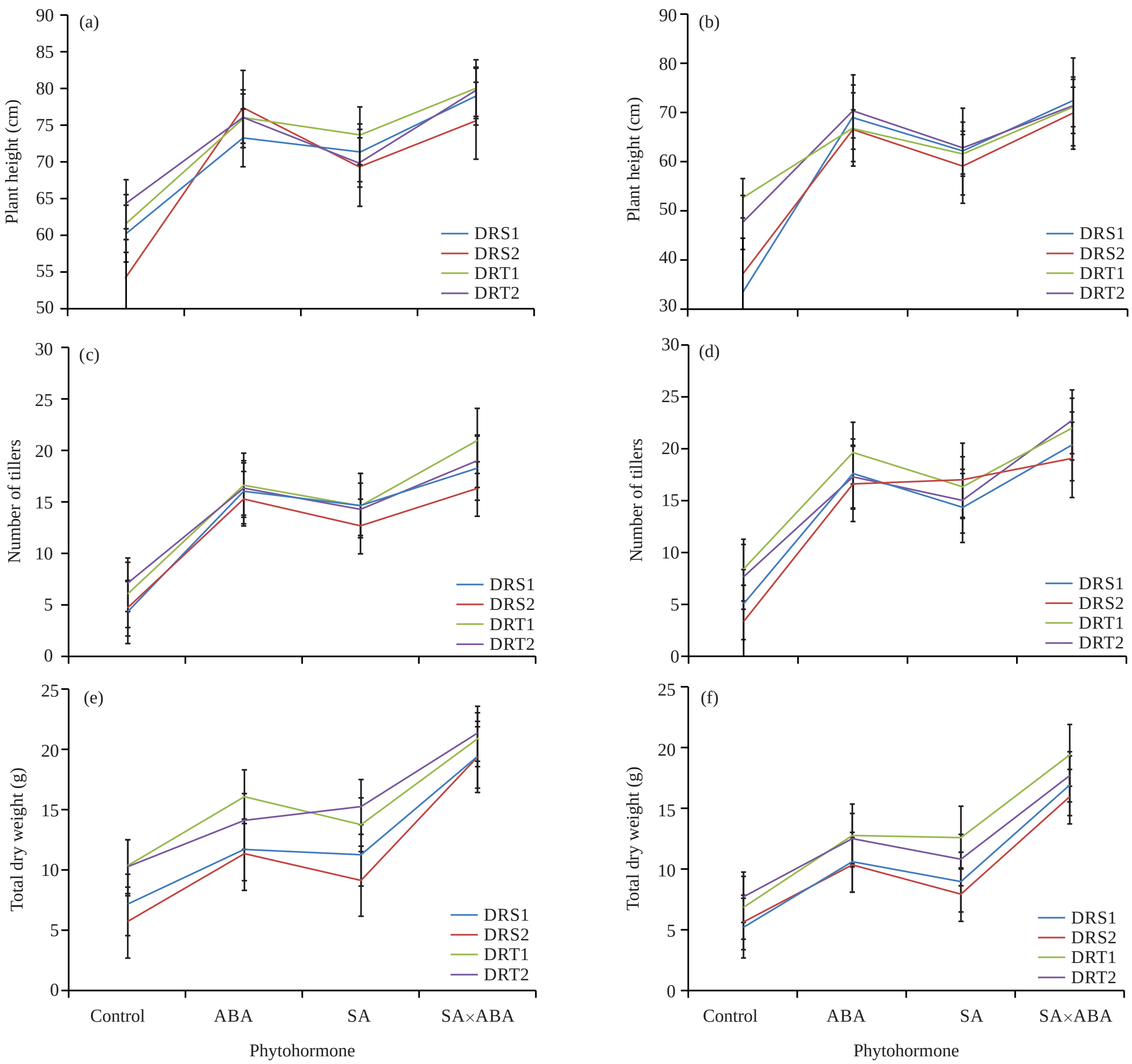

Fig. 5(a-f): Hormonal signalling effect on growth characteristics of winter and spring barley exhibiting different tolerance (DRT1 and 2) and susceptibility (DRS1 and 2) levels to drought stress under controlled conditions of 20% field capacity, (a) Effect of drought and phytohormone on plant height (spring barley), (b) Effect of drought and phytohormone on plant height (winter barley), (c) Effect of drought and phytohormone on tillering ability (spring barley), (d) Effect of drought and phytohormone on tillering ability (winter barley), (e) Effect of drought and phytohormone on total dry weight (spring barley) and (f) Effect of drought and phytohormone on total dry weight (winter barley)
Error bars represent standard error bars and overlap shown no significant difference in means

effect of the 2 hormones on tolerance to aluminium toxicity as indicated in Fig. 2a. The same synergistic effect was also observed on other parameters such as the number of fibrous roots which increased from 15-40 g in Fig. 2b, root dry weight from 6-8 g in Fig. 2c and shoot dry weight from 9.5-14 g in Fig. 2d for genotype ALS1 under the influence of SA×ABA in comparison with control. Additionally, all the aluminium tolerant genotypes expressed higher growth rate and dry matter accumulation both under the influence of phytohormones and under control compared to the aluminium sensitive genotypes.

Despite showing similar trends in terms of response to aluminium toxicity under the influence of hormonal treatment compared to the spring adapted barley, the winter adapted barley proved to be very sensitive to this cation more especially when not treated with hormones. Specifically, the most sensitive winter barley (ALS1) recorded approximately 51 and 75 cm in Fig. 3a in terms of height under no hormone

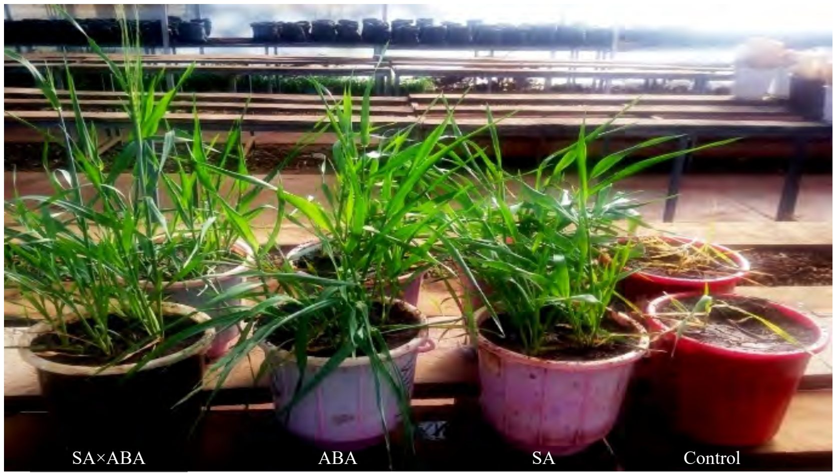

Fig. 6: Hormonal signaling effect on growth parameters of barley (WDRT1-SCRABBLE) under controlled condition (20% field capacity) in the greenhouse. Higher tolerance observed under SA×ABA treatment

(control) and SA×ABA treatments, respectively. A similar synergy of SA×ABA was observed for the same genotype in terms of the number of fibrous roots, root dry weight and shoot dry weight which recorded between 14 and 30 in Fig. 3b, 4.5 and 8.5 g in Fig. 3c and 9.5 and 13.5 g in Fig. 3d, respectively for genotype ALS1 under the influence of SA×ABA compared to control.

Phenotypic comparisons between spring and winter adapted barley further revealed that winter genotypes were more sensitive to aluminium toxicity and expressed more root stunting when untreated with phytohormones than when treated. For instance, a single treatment of the sensitive spring (SALS1) in Fig. 4a and winter (WALS1) in Fig. 4b genotypes with 50 µM SA and 20 µM ABA did not differ significantly in terms of fibrous root growth and development compared to the combined effect of the 2 hormones.

Hormonal signalling effect on drought stress in barley: Application of phytohormones on drought-sensitive barley significantly enhanced tolerance levels which resulted in increased plant height, tillering ability and biomass accumulation. In spring adapted barley, treatment with 50 µM SA, 20 µM ABA and a combination of SA and ABA resulted in an increased plant height from approximately 54 (when untreated with hormones) to 70, 77 and 75 cm, respectively for DRS2 genotype in Fig. 5a. Similarly, for the winter adapted, the synergistic effect when SA is combined with ABA was more evident and resulted in enhanced tolerance plant height from 35 cm under control to 70 cm under SA×ABA compared to single doses of SA and ABA which scored 58 and 64 cm, respectively for genotype DRS2 in Fig. 5b. Similar enhancement effects of SA×ABA were for tillering ability in Fig. 5c and d and total dry weight in Fig. 5e and f for both spring and winter adapted barely compared to a single application of SA and ABA.

The phenotypic expressions when drought-tolerant genotypes were treated SA, ABA and a combination of SA and ABA corresponds to the descriptive analysis, with SA×ABA exhibiting enhanced synergistic effect on height and shortened time flower compared to ABA and SA alone in Fig. 6. Under severe water deficiency, even the drought-tolerant genotypes were negatively affected with majority drying before attaining vegetative growth stage especially when no hormonal application was done.

DISCUSSION

For net blotch disease, the low disease severity among the known susceptible genotypes could be due to induction of resistance mechanisms within the plants treated with hormones and this corresponds to the past research where SA signalled the induction of immune system in other plants[14]. Increased disease tolerance among the susceptible barley treated with phytohormones could also imply that upon application, these hormones activated the Systemic Acquired Resistance (SAR) to net blotch in barley as previously observed in the distal (systemic) tissues of other plants[15]. Contrary to SA, the ABA did not signal the induction of disease resistance hence higher disease severity and this could also mean that ABA expressed negative regulation on disease resistance[16].

Based on the antagonistic interaction between ABA and SA previously confirmed with *P. syringae*[17], the exogenous application of ABA prevent SA accumulation and this suppressed the resistance to *P. teres* in several barley genotypes. This further explains why there was no significant difference between SA and SA×ABA combinations in terms of induction of disease tolerance in barley. However, compared to the control, barley treated with ABA expressed low disease and this could be due to previous reports that ABA regulates defense response through its effect on production of reactive oxygen[18], cellulose deposition[19] and regulation of defence gene expression[20].

Concerning aluminium cation toxicity, enhanced tolerance implies that these hormones induced the activation of biochemical mechanisms, signalling pathways and genes needed for abiotic stress tolerance to be expressed in plants[21]. For example, when treated with SA×ABA, root elongation and formation of fibrous roots increased significantly than those treated with SA or no hormone at all. The observed tolerances especially under the influence of SA×ABA and ABA could also imply that exogenous application of these hormones may have triggered the expression of specific genes within the barley plant to signal their production in large quantities[22,23] hence higher tolerance to aluminium than barley not treated with phytohormones.

For both drought stress and aluminium toxicity, SA×ABA, ABA and SA ranked 1st, 2nd and 3rd in terms of the level of tolerance, an indication of the synergistic effect of SA×ABA combination towards abiotic stresses but antagonistic effect towards biotic stresses[16]. For instance, the application of ABA and SA×ABA might have triggered the activation of numerous physiological processes which induced adaptation to drought stress conditions[24]. In particular, ABA application may have induced stomatal closure to conserve water and also up-regulated the endogenous ABA levels to magnify the lowering transpiration rates[25] under water deficiency stress conditions.

CONCLUSION

Salicylic acid is the key phytohormone in inducing tolerance to net blotch foliar infection among barley while abscisic acid is the best in terms of abiotic stress tolerance in barley concerning drought and aluminium cation toxicity stresses. The combination of SA and ABA seems to be synergistic in inducing tolerance abiotic stresses but the same combination proves antagonistic net blotch disease severity hence higher disease levels.

SIGNIFICANCE STATEMENT

The findings of this study fill the gap by providing the answers as to why there are inconsistencies in the productivity and expression of true traits by several barley varieties in Kenya. The first major finding is that phytohormones take a key influence on the observed traits and this influence several physiological processes within plants. Secondly, it is now apparent that the phenotypic response of barley to net blotch, drought and aluminium toxicity or a combination of either of the three is influenced by the hormone produced by the plant itself as induced by the genetic make-up.

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