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GA/ABA Antagonism in the Physiology of Seed Germination in the Recalcitrant and Vulnerable Tree- *Vateria indica* L.

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ABSTRACT

Background: Seed recalcitrance is a major problem associated with many tropical plants, limiting their natural regeneration. *Vateria indica* L. is a vulnerable and endemic tree species in South-Western Ghats of India, which is also recalcitrant. ABA and gibberellins are the most important plant hormones required for seed germination. It is the balance between ABA and GA which is responsible for desiccation tolerance in orthodox seeds. Exogenous hormones pretreatment has been also reported to influence seed germination. But such studies had been sparsely done in the case of recalcitrant seeds. This study aims to find out whether GA/ABA antagonism in recalcitrant plants is operating in the same way, like that in the orthodox seeds.

Methods: The effect of the exogenous pre-soaking application of phytohormones *viz.* GA_3 and ABA individually as well as their combinations on seed germination and growth of *Vateria indica* L. were carried out in the present work. The seeds were collected from April to July 2018 and the experiment was designed at Post Graduate and Research Department of Botany, Government College for Women, Thiruvananthapuram. When different concentrations of each phytohormone were externally given to the seeds, ABA reduced the germination and growth in almost all the concentrations. But GA_3 gave better results. When combinations of GA_3 and ABA were used, germination was poor in the sample where ABA was more than GA_3, But in samples with same concentrations of both the hormones and with more GA_3 gave better results.

Result: This study clearly showed that GA_3 when given externally along with ABA, might have affected the endogenous ABA in this recalcitrant seed and suppressed its retarding effect. Thus ABA/GA antagonism is working out, here, in the same way as in orthodox seeds. Since the germination of recalcitrant seeds is a less investigated area, the present study will form a basis and a lot more for further such studies.

Key words: ABA - Absiscic acid, Exogenous hormones, GA - Gibberellic acid, Germination, Phytohormones, Recalcitrant seeds.

INTRODUCTION

Vateria indica L. is a vulnerable and endemic tree species in South-Western Ghats of India, commercially exploited for its valuable resins. Seed recalcitrance is a major problem associated with this plant, limiting its natural regeneration. Such seeds cannot tolerate desiccation and will not germinate when its moisture content falls below a critical level. The acquisition of desiccation tolerance in orthodox seeds and its absence in desiccation sensitive seeds can be attributed to the consequence of a changed balance between the phytohormones, especially GA and ABA (Bewley *et al*. 2013). The GA-ABA antagonism not only dominates seed development, dormancy and germination, but also contributes to other developmental processes (Liu *et al*. 2018). GA levels normally decrease and ABA increases during later stages of orthodox seed maturation. Results of well-organized research work on these lines in recalcitrant seeds are not much available and hence, the present study will show whether GA/ABA antagonism in recalcitrant seeds is like that of orthodox seeds. The most important plant hormones for seed germination are ABA and gibberellins, which have inhibitory and stimulatory effects on seed germination, respectively. According to Vishal *et al*. (2018), it is essential to maintain an optimal balance between the endogenous levels of ABA and GA for plant development. Numerous studies have focused on the effects of exogenous application of hormones on seed germination. Studies on exogenous hormones pre-treatment have been reported to influence seed germination (Nonogaki *et al*. 2010). In this work, the effect of the exogenous pre-soaking application of phytohormones *viz.* GA_3 and ABA individually, as well as their combinations on seed germination and growth of *Vateria indica* L., were carried out. When different concentrations of each phytohormone were externally given to the seeds, ABA was found to reduce the germination and growth in almost all the concentrations. But GA_3 was found

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to give better results. When combinations of GA_3 and ABA were used, germination was severely hindered in the sample where ABA was more than GA but in samples with same concentrations of both the hormones and with more GA gave better results. This clearly showed that GA_3 when given externally along with ABA, in the same quantity or more, have affected the endogenous ABA in this recalcitrant seed and suppressed its retarding effect. In many studies, it has been shown that GA when given singly or in combination with ABA can overcome the retardation caused by ABA during seed germination (Toyomasu *et al*. 1994). Since the area of the role of phytohormones in the germination of recalcitrant seeds is a less investigated one, this work can surely form a base for further such studies.

MATERIALS AND METHODS

Vateria indica L. trees were identified in their natural stands in South-Western-Ghats (latitude of 8′ 18′-12′ 48′N and longitude of 74′ 52′-77′ 52′E). Recently the species has been categorised as vulnerable since the population is fragmented and rapidly declining (Dhyani *et al*. 2020). The seeds were collected from April to July 2018 and the experiment was designed at Post Graduate and Research Department of Botany, Government College for Women, Thiruvananthapuram. The fruits were cleaned, surface sterilized with 2.5% sodium hypochlorite and fruit wall was removed manually using a secateur. Twenty seeds with uniform size were selected randomly from the lot and immersed in the different concentrations of GA_3 and ABA for 48 hours. Six different concentrations (5 mg/L, 10 mg/L, 25 mg/L, 50 mg/L, 100 mg/L and 125 mg/L) each of GA_3 and ABA were tried, to compare the effect of these hormones on germination as well as to find out the concentration much suitable for germination. Treatments were arranged with five replicates. The seeds, externally treated with different concentrations of phytohormones, were rinsed with distilled water and placed in trays with moist sterilized coir pith for germination. The incubation temperature was set at 28°C.

The combined effect of GA_3 and ABA was studied against a control (C - distilled water), where three different combinations of GA_3 and ABA were tried. In sample 1 (S1), the concentrations of GA_3 and ABA were same (both 10 mg/L), in sample 2 (S2) the concentration of GA_3 was more than that of ABA (10 mg/L GA_3 and 5 mg/L ABA) and in sample 3 (S3) the concentration of GA_3 was less than that of ABA (5 mg/L GA_3 and 10 mg/L ABA). Rate of germination was observed from the beginning when the seed coat split to expose the radicle. In this study, 10 mg/L of GA_3 was taken as an optimum concentration as it gave a better rate of germination when given alone. Growth was analysed by measuring growth parameters like length of the radicle, length of plumule, the number of leaves emerged and the length and width of the leaves. Growth parameters were analysed from 9 days after sowing, as the radicle and plumule developed to a measurable length only after a week.

The results are presented as mean±standard errors obtained from at least five replicates. Significant differences were determined using ANOVA. Statistical analysis was conducted using the statistical software package SPSS13.0 for Windows.

RESULTS AND DISCUSSION

The individual effect of external application of GA_3 and ABA on seed germination

The seeds were externally treated with six different concentrations each of GA_3 and ABA ranging from 5 mg/L to 125 mg/L. All the seeds treated with ABA showed a poor percentage of germination. But the seeds treated with GA_3 showed a better rate of germination. Paired t-test showed that the percentage of germination is significantly higher in GA than ABA at 1% level of significance (Table 1). At 10 mg/L GA_3 concentration more than 90 of the seeds germinated. But at higher concentrations, the rate of germination began to decline.

In this work, when ABA and GA were externally given, separately, all the ABA treated seeds showed a poor percentage of germination while the seeds treated with GA_3 showed a better rate of germination, especially at 10 mg/L GA_3 concentration. Mukherjee (2016) reported better seed germination rate in Swertia seeds pre-soaked with GA_3. Increased rate of germination of Guava seeds was also reported by the exogenous treatment with GA_3 and this has been attributed to the fact that either GA_3 might have involved in the activation of cytological enzymes which stimulate seed germination of an amylase enzyme for converting insoluble starch into soluble sugars or might have antagonized the effect of inhibitors present in seeds (Kalyani *et al*. 2014). It has been reported by Copeland and Mc Donald (1995) that GA induces *de novo* synthesis of proteolytic enzymes like Amylase and ribonuclease. Amylases hydrolysing starch and providing essential sugars for growth initiation processes and liberating chemical energy which is used in the activation of the embryo as well as suppression of inhibition. But at higher concentrations of GA, the rate of germination began to decline. This can be due to GA toxicity at higher levels. According to Chetouani *et al*. (2017), a surplus of GA used has been considered as an onset of toxicity.

The combined effect of different concentrations of GA_3 and ABA on seed germination

No seed germinated in sample 3 and hence it is not considered for the analysis of significance in the difference in the percentage of germination. Analysis of variance of repeated measures is administrated to compare the significance of differences in the germination of seeds among control, S1 and S2 and among days. There is a significant difference in the mean percentage of germination among samples (F=180.942, p-value <.01) at 1% level of significance. Also, there is a significant difference in the mean percentage of germination among days (F=76.94, p-value <.01) at 1% level of significance. The estimated

Table 1: Paired t-test shows the percentage germination is significantly higher in GA than ABA at 1% level of significance.

Concen. mg/L	Fresh seed (%)		Mean±SD (%)		t-value
	GA	ABA	GA	ABA	(p-value)
0	54	54	65.56±16.51	9.91±19.62	5.21(<.01)
5	69	5.67			
10	90.3	6			
25	78	3.67			
50	65.3	0			
100	54.3	0			
125	41	0			

Table 2: Combined effect of different concentrations of GA_3 and ABA on seed germination.

Sample	Percentage of seeds germinated (Mean±SD)							F-value
	Day 3	Day 5	Day 7	Day 9	Day 11	Day 13	Day 15	(p-value)
Control	41.0^{a}±8.9	42.0^{b}±9.1	52.0^{a}±5.7	53.0^{a}±4.5	60.0^{a}±0.0	58.0^{a}±2.7	60.0^{a}±0.0	180.942(<.01)
S1	31.0^{a}±8.2	31.0^{a}±8.2	53.0^{a}±5.7	60.0^{a}±7.9	71.0^{b}±4.2	71.0^{b}±2.2	70.0^{b}±0.0	
S2	76.0b±4.2	77.0^{c}±2.7	78.0^{b}±2.7	80.0^{b}±5.0	87.0^{c}±2.7	89.0^{c}±2.2	90.0^{c}±0.0	
Total	49.3±21.1	50.0±21.4	61.0±13.3	9.6±6.1	72.7±11.8	72.7±13.3	73.3±12.9	

F-value (p-value) 76.494 (<.01).

a.b.c are homogeneous subsets: Duncan's post hoc multiple comparison test (One way ANOVA).

mean germination in control is 52.29%, in S1 is 55.29% and in S2 is 82.43% and Duncan's post hoc multiple comparison test shows that there is no significant difference in germination in between control and S1 but the number of germinations is significantly higher in S2 than control and S1 at 5% level of significance. The one-way ANOVA showed that there is a significant difference in the percentage of germination on all days among various treatments (control, S1, S2) at a 1% level of significance (Table 2).

When the combined effect of GA_3 and ABA on germination and growth, was studied against a control (distilled water), sample 3 (S3) showed almost no response as it had a greater concentration of ABA. Sample 1 and 2 (S1 and S2) showed a better response when compared to Control (C) that is, distilled water, where S2 showed the best response with respect to C and S1. It can be seen that GA when present in same or more level, than ABA, suppressed the physiological inhibition caused by ABA. Similar results were obtained in the seeds of *Phellodendron amurense var. wilsonii*, where exogenous ABA inhibited germination, but the addition of GA_3 balanced the ABA effect and promoted germination (Chen *et al*. 2009). The inhibitory effects of ABA on seed germination are through delaying the radicle expansion and weakening of endosperm, as well as the enhanced expression of transcription factors, which may adversely affect the process of seed germination (Graeber *et al*. 2010). Application of certain exogenous hormones may correct a deficiency in the endogenous level of that hormone or change the balance of hormones in the seed. Toyomasu *et al*. (1994), showed that the endogenous ABA contents were reduced by GA_3 treatment in lettuce seeds. There are studies revealing the antagonistic effects of GA on the expression of ABA-inducible genes in dormant beechnut seeds (Nicolas *et al*. 1997; Lorenzo *et al*. 2001).

The combined effect of different concentrations of GA_3 and ABA on seedling growth

Growth parameters like length of the radicle, length of the plumule, number of leaves emerged as well as the length and width of the leaves were analysed to study the combined effect of GA_3 and ABA on growth.

Length of the plumule

Analysis of variance of repeated measures was administrated to compare the significance of differences in the mean Plumule length among control, S1 and S2 and days (Table 3). There was a significant difference in mean plumule length among days and among samples at 1% level of significance. The estimated mean plumule length in control was 2.392 cm, in S1 was 3.955 cm and in S2 was 6.29 cm and Duncan's post hoc multiple comparison test showed there is a significant difference in mean plumule length in S2 than control and S1 at 5% level of significance. There was a significant difference in the mean plumule length on days 9,10,11,13,16 and 19 among various treatments (control, S1, S2) at 1% level of significance, as shown by one-way ANOVA.

Length of the radicle

A significant difference in mean radicle length among days (F=64.477) and among samples (F=18.983) at 1% level of significance can be found. The estimated mean radicle length in control was 3.6 cm, in S1 was 6.22 cm and in S2 was 7.97 cm and Duncan's post hoc multiple comparison tests showed a significant difference in mean radicle length at 5% level of significance along with all the three pairs (Table 3). The one-way ANOVA showed that there was a significant difference in the mean radicle length on days 9,10,11,12,16 and 19 among various treatments (control, S1, S2) at a 1% level of significance. On day 13 and 15, it was significant at 5% level of significance.

Number of leaves

There was a significant difference in the mean number of leaves among days (F=57.569) and among samples (F=14.396) at 1% level of significance. The estimated mean number of leaves in control was 2.4, in S1 was 3.633 and in S2 was 4.267 and Duncan's post hoc multiple comparison test showed a significant difference in the mean number of leaves in S1 and S2 and significantly more than control at 5% level of significance (Table 3). There was a significant difference in the mean number of leaves on days 12 among various treatments (control, S1, S2) at 5% level of significance as shown by one-way ANOVA. On day 16, it was significant at 5% level of significance.

Length of leaves

The difference in mean leaf length among days (F=40.717) was significant at 1% level of significance and among samples (F=4.662) significant at 5% level of significance. The estimated mean leaf length in control was 1.863 cm, in S1 was 2.217 cm and in S2 was 3.930 cm and Duncan's post hoc multiple comparison tests showed a significant difference in mean leaf length in S2 than control and S1 at 5% level of significance. The one-way ANOVA showed that there was a significant difference in the mean leaf length on days 11,12 and 15 among various treatments (control, S1, S2) at a 1% level of significance. On day 13, it was significant at 5% level of significance and on the day 15 at 10% level of significance (Table 3).

Width of leaves

The estimated mean leaf width in control was 1.02 cm, in S1 was 1.065 cm and in S2 was 2.12 cm and Duncan's post hoc multiple comparison tests showed a significant difference in mean leaf width in S2 than control and S1 at 5% level of significance. A significant difference in mean leaf width among days (F=13.338) significant at 1% level of significance and among samples (F=8.121) significant at 1% level of significance can be found. The one-way ANOVA showed that there was significant difference in the mean leaf width on days 13 and 15 among various treatments (control, S1, S2) at a 1% level of significance. On day 16, it was significant at 10% level of significance (Table 3).

GAs and ABA are plant growth regulators, that act in an antagonistic manner to control plant developmental processes, like root and stem elongation, floral induction, anther development and seed germination (Yamaguchi 2008). It has been reported by Philosoph-Hadas *et al.* 2005 and Kucera *et al.* 2005, that germination is regulated by a balance between the relative amounts of endogenous GA_3 and ABA in seeds. GA levels normally decrease and ABA

Table 3: Combined effect of different concentrations of GA_3 and ABA on seedling growth.

Parameter	Samples	Day 9	Day 10	Day 11	Day 12	Day 13	Day 15	Day 16	Day 19	F (p-value)
Radicle length (cm)	Control	0^{a}	$2.50^{a}\pm1.06$	$3.40^{a}\pm0.96$	$4.16^{a}\pm1.26$	$4.20^{a}\pm1.81$	$4.76^{a}\pm1.78$	$4.80^{a}\pm1.76$	$4.98^{a}\pm2.28$	18.983 (<.01)
	S1	$3.00^{b}\pm0.76$	$3.58^{a}\pm1.41$	$3.88^{a}\pm1.87$	$5.00^{a}\pm1.58$	$5.64^{a}\pm2.02$	$8.20^{b}\pm1.79$	9.24±1.85	$11.20^{b}\pm2.39$	
	S2	$3.88^{b}\pm0.81$	$5.96^{b}\pm0.76$	$6.90^{b}\pm0.59$	$7.64^{b}\pm0.43$	$8.20^{b}\pm2.06$	$8.80^{b}\pm1.92$	$10.20^{b}\pm1.62$	$12.20^{b}\pm1.92$	
Plumule length (cm)	Control	0^{a}	$0.72^{a}\pm0.23$	$1.22^{a}\pm0.23$	$2.18^{a}\pm0.25$	$1.72^{a}\pm0.61$	$2.64^{a}\pm0.99$	$5.20^{a}\pm1.87$	$5.46^{a}\pm2.97$	12.257 (<.01)
	S1	0^{a}	$1.22^{b}\pm0.18$	$1.60^{a}\pm0.38$	$2.60^{a,b}\pm0.42$	$2.60^{a}\pm0.44$	$6.40^{a,b}\pm3.44$	$8.16^{a}\pm3.42$	$9.06^{a}\pm4.01$	
	S2	$0.74^{b}\pm0.28$	$1.86^{c}\pm0.30$	$2.20^{b}\pm0.21$	$3.40^{b}\pm0.96$	$4.12^{b}\pm1.18$	$7.40^{b}\pm4.04$	$12.40^{b}\pm3.13$	$18.20^{b}\pm4.32$	
No. of leaves	Control	0	0	0	0^{a}	2.40±0.89	3.20±1.10	$4.00^{a}\pm0.00$	4.80±1.10	14.396 (<.01)
	S1	0	0	2.0±0.0	$2.60^{b}\pm0.55$	3.00±1.00	3.80±0.84	$5.20^{a,b}\pm1.10$	5.20±1.79	
	S2	0	0	2. 0±0.0	$3.20^{b}\pm0.84$	3.60±0.55	4.00±0.71	$6.40^{b}\pm1.67$	6.40±1.67	
Leaf length (cm)	Control	0	0	0^{a}	0^{a}	$0.82^{a}\pm0.43$	$2.10^{a}\pm0.85$	3.06±0.78	5.20±1.92	4.662 (<.05)
	S1	0	0	$0.40^{b}\pm0.07$	$1.12^{b}\pm0.53$	$1.52^{a,b}\pm0.64$	$3.20^{b}\pm0.42$	3.40±1.16	3.66±1.14	
	S2	0	0	$0.66^{c}\pm0.15$	$1.34^{b}\pm0.59$	$2.50^{b}\pm1.00$	$5.28^{c}\pm1.56$	6.40±3.85	7.40±4.34	
Leaf width (cm)	Control	0	0	0	0	0^{a}	$0.72^{a}\pm0.40$	$1.16^{a}\pm0.61$	2.20±1.53	8.121 (<.01)
	S1	0	0	0	0	0^{a}	$1.14^{a}\pm0.42$	$1.36^{a,b}\pm0.50$	1.76±0.48	
	S2	0	0	0	0	$0.96^{b}\pm0.36$	$1.76^{b}\pm0.48$	$2.40^{b}\pm1.14$	3.36±2.36	

Mean±SD and ANOVA (Repeated measures and One way). Comparison among days: Significant all parameters at 1% level of significance (p-value<.01).

^{a,b,c}Are homogeneous subsets : Duncan's post hoc multiple comparison test (One way ANOVA among samples on all days).

increase during later stages of orthodox seed maturation and very high levels of GA causes precocious germination (White *et al*. 2000). The GA and ABA antagonistic crosstalk comprises two main aspects, one is the metabolic homeostasis of ABA and GA, which are controlled by distinct regulators in response to specific endogenous and environmental signals, leading to opposite patterns of ABA and GA accumulation and the other one is the direct molecular interaction between core ABA and GA- signaling components, which orchestrates a rapid and efficient response to developmental changes and external challenges by quickly mediating the antagonistic interaction of ABA and GA (Vishal *et al*. 2018). It is well known that GA_3 and ABA are antagonistic in action especially in physiological processes like seed germination and growth, GA_3 promoting it and ABA retarding the same process (Kermode, 2005). Phytohormones and plant growth regulators have been used as pre-sowing seed treatment agents (Nascimento 2003, Tiwari *et al*. 2011). According to Shu *et al*. (2016), the interactions of diverse hormonal signals in seed dormancy and germination maybe by the ABA: GA balance.

In the present study, all growth processes like seed germination and development, stimulation of stem and root growth, increase in the number and size of leaves, increase of seed germination rate, all are found to be better in a combination where GA is more than or equal to ABA level when compared to control. Exogenous GA application and enhanced seedling growth were also reported in other experiments (Khan *et al*. 2003, Tiwari *et al*. 2011, Khodadadi *et al*. 2018). Exogenous application of GA_3 was reported to be highly effective for plumule growth in *Withania somnifera* (Kumar *et al*. 2012). It can be assumed that the exogenous GA enhances the ABA catabolism. Schmitz *et al.* (2002) suggested that dormancy-breaking treatments including GA_3 applications enhance ABA degradation in yellow-cedar seeds. Keeping a low level of ABA in the embryo is a strategy shown by many recalcitrant and viviparous seeds to facilitate faster germination without dormancy (Prajith *et al*. 2017). According to White *et al*. (2000), high levels of GA have been associated with vivipary and desiccation sensitivity in the case of recalcitrant seeds. During later stages of orthodox seed maturation, GA levels are normally decreased and those of ABA increased. At seed maturation, ABA is responsible for the acquisition of desiccation tolerance in orthodox seeds (Gutierrez *et al*. 2007). However, this cannot be seen in recalcitrant seeds like *Vateria indica* L. Recalcitrant seeds do not have any mechanisms that facilitate the acquisition and maintenance of desiccation tolerance as orthodox seeds (Berjak and Pammenter, 2013).

CONCLUSION

From the study, it can be concluded that in the recalcitrant seeds of *Vateria indica* L., we can visualise the same pattern of GA/ABA antagonism, during seed germination and growth, as in orthodox seeds. However, their lack of desiccation tolerance, as shown by orthodox seeds, may due to less amount of ABA and high amount of GA at the time of seed maturation. The role of phytohormones in the germination of recalcitrant seeds is a poorly investigated area and this work can contribute a lot more to this particular area.

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