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Cent. Eur. J. Biol. • 9(11) • 2014 • 1108-1116
DOI: 10.2478/s11535-014-0338-6

Central European Journal of **Biology**

Effects of smoke water and karrikin on seed germination of 13 species growing in China

Research Article

Junfang Zhou[1, 2], Jaime A. Teixeira da Silva[3], Guohua Ma[1*]

[1]*Key Laboratory of Plant Resources Conservation and Sustainable Utilization, South China Botanical Garden, the Chinese Academy of Sciences, Guangzhou, 510650, P. R. China*

[2]*University of Chinese Academy of Sciences, Beijing 100049, P. R. China*

[3]*P. O. Box 7, Miki-cho post office, Ikenobe 3011-2, Kagawa-ken, 761-0799, Japan*

Received 13 November 2013; Accepted 12 January 2014

Abstract: Plant-derived smoke water (SW), derived from combusted plant material, has been shown to stimulate seed germination and improve seedling vigor of a number of plant species from fire-dependent Mediterranean-type climate areas. The effects of SW on seed germination of 13 plant species from southern tropical and subtropical monsoon climate regions of South China are reported for the first time in this study using laboratory and pot trials. Among the 13 species tested, only *Aristolochia debilis* showed a significant positive response to commercial SW when diluted 1:10. Seed germination of *A. debilis* was also stimulated by 1–100 nM 3-methyl-2H-furo [2, 3-c] pyran-2-one (karrikin 1 or KAR_1) and by 10–1000 μM gibberellic acid (GA_3). GA_3 stimulated seed germination of *Santalum album* and significantly elongated the radicles of *A. debilis* while SW could not. The functions and/or metabolic pathways of Kar_1 and GA_3 are likely to be separate and/or distinct.

Keywords: *Aristolochia debilis* • *Chinese growing species* • *Gibberellic acid* • *Karrikin* • *Light* • *Santalum album* • *Seed germination* • *Smoke water*

Abbreviations:

Kar_1 - karrikin 1;
GA_3 - gibberellic acid;
SW - smoke water

1. Introduction

The stimulation of seed germination by smoke and aqueous smoke extracts from burning plant materials has received much attention in fire-prone areas, primarily areas of Mediterranean climate, such as the Californian chaparral [1,2], the Cape region of South Africa [3-15] and Western Australia [16-21] over the past 20 years. Consequently, plant-derived smoke or aqueous extracts derived from smoke or smoke water (SW) may have broad applications as tools in natural agriculture or ecological restoration, or for enhancing the conservation of threatened or rare species [22-25].

One active compound in smoke which promoted seed germination was identified and named butenolide (3-methyl-2H-furo [2, 3-c] pyran-2-one) [24,26]. It is a heat-stable, long-lasting and water-soluble compound that can stimulate seed germination and seedling growth at very low concentrations (1–100 nM) [25,27-30]. At present, butenolide can be artificially synthesized and has wide applicability as a germination and growth stimulant with potential implications for both weed management and improving crop seedling growth [31-33]. Butenolide was fairly recently reclassified and designated as karrikinolide or karrikins (KAR) [34-39]. The chemical 3-methyl-2H-furo [2, 3-c] pyran-2-one is the first found seed germination stimulant in smoke and was named KAR_1.

* *E-mail: magh@scib.ac.cn*

China has an abundance of plant resources and a vast agricultural economy. Since fire is not that frequent in South China, scant attention has been paid to the effects of smoke and fire-associated byproducts on plant ecology and physiology. Previous studies on SW-stimulated seed germination and SW-enhanced seedling vigor were almost exclusively reported from fire-prone areas but to date no study has examined its effect on seed germination or responses of plants from tropical and subtropical monsoon climate regions such as South China.

The exact mechanism by which fire and smoke affect seed germination and the chemical and physical nature of burned products that may benefit plant growth have been examined. The action of SW has been paralleled to that of gibberellic acid (GA_3) [40,41]. Butenolide could act in a similar fashion as GA_3 and stimulate seed germination of light-sensitive species (*Angianthus tomentosus*, *Myriocephalus guerinae* and *Podolepis canescens*), providing evidence that butenolide can promote seed germination of light-sensitive seeds [42]. Analysis of germination of a phytohormone mutant revealed that suppression of butenolide's responses by abscisic acid (ABA) is a requirement for gibberellin (GA) synthesis and the reduced germination of *sleepy1* mutants could be partially recovered by KAR_1, suggesting that enhanced germination by karrikin is only partly dependent on DELLA [35]. In their study, KAR_1 had little effect on the sensitivity of germination to exogenous GA; rather, it enhanced the expression of two GA biosynthetic genes (*GA3ox1* and *GA3ox2*) during seed imbibition. Even though there were differences in the outcome of germination, neither ABA nor GA levels in seed were affected by KAR_1 treatment prior to radicle emergence. Nelson *et al*. [35] further showed that KAR_1 stimulation of *Arabidopsis* germination was light-dependent and reversible by exposure to far-red light, although limited induction of *GA3ox1* occurred in the dark. Their observed requirements for light and GA biosynthesis provided the first insight into karrikin's mode of action. Consequently, an understanding of the relationship between GA and karrikin (or SW) remains incomplete.

The aim of the present study was to study the effects of SW on seed germination of Southern Chinese plant species as a new way to break dormancy. Secondly, we also wished to test how seeds from a southern tropical and subtropical monsoon climate region would respond to SW or Kar_1 since, to date, only the responses of plants from Mediterranean-type climates have been tested. Finally, we also compared the efficacy of SW or KAR_1 and GA_3 on seed germination under a light/dark photoperiod or in the dark and explored the primary mechanism of KAR_1 on seed germination by investigating the relationship between KAR_1 and GA_3.

2. Materials and Methods

2.1 Smoke water

A commercial "Seed Starter, Australian Smoky Water" (hereafter SW) was received from Kings Park and Botanic Garden. Karrikin 1 (Kar_1) was kindly supplied from the University of Western Australia, Perth, Western Australia. The concentration used (*i.e*., 1:10 dilution) was based on the instructions for use and on previous studies [17,20,26,31,43]. Solutions of GA_3 at 1000 μM were made by Shanghai Biological Life Science & Technology Co. Ltd. All solutions for all experiments were sterilized with a 1‰ carbendazim (Shanghai Agro China International Co., Ltd.) solution to prevent the growth of microorganisms during seed germination.

2.2 Plant material

The tested plant species were: *Acacia auriculiformis* A. Cunn. ex Benth., *Aristolochia debilis* Sieb. et Zucc., *Bixa orellana* Linn., *Cassia surattensis* Burm. f., *Cassia bicapsularis* Linn., *Gymnema sylvestre* Schult, *Hibiscus mutabilis* Linn., *Lagerstroemia indica* Linn., *Pinus massoniana* Lamb., *Santalum album* Linn., *Stenolobium stans* (L.) Seem, *Tigridiopalma magnifica* C. Chen and *Urena lobata* Linn. All seeds for germination experiments were freshly collected from the South China Botanical Garden, Guangzhou in January, 2007 and preserved in a 4°C refrigerator until use.

2.3 Effect of SW on seed germination of 13 species

Seed germination tests were performed in March, 2007. For germination trials, 25 collected seeds of each of the 13 species were placed in separate 90-mm Petri dishes on two layers of Whatman® No. 1 filter paper moistened with 2.0 ml of evenly distributed distilled water (DW; control) or SW. The Petri dishes were placed in a culture room at 25 ± 2°C under a 16-h photoperiod at a photosynthetic photon flux density (PPFD) of 50 μmol m^{-2} s^{-1} or in the dark. Every treatment was repeated in four Petri dishes. Filter paper was moistened with DW when and if required during the course of the experiment. Seeds from which a radicle ≥ 2 mm long emerged were considered to be germinated. The percentage seed germination after culture for 24 days was calculated. In addition, we selected *S. album*, which is sensitive to GA_3 [44,45] and another species *A. debilis*, which initially responded positively to SW, for subsequent trials. 50 seeds of each species were immersed in SW (1:10 solution), DW or GA_3 (1000 μM) for 24 h at room temperature, and then sown in clay pots (20 cm high and diameter, two per treatment) with wet river sand to a depth of 3–5 mm in a greenhouse at the

South China Botanical Garden. Pots were incubated at 23 ± 3°C and sand was kept moist with tap water in the greenhouse. Germination frequency was monitored for 44 days.

2.4 Effect of SW and GA_3 on *A. debilis* seed germination and radicle elongation

The tests were performed in May 2009. Twenty five fresh seeds of *A. debilis* were placed in 90-mm Petri dishes on two layers of Whatman® No. 1 filter paper moistened with 2.0 ml DW, SW or GA_3 (1000 μM). The Petri dishes were placed in a culture room at 25 ± 2°C under a 16-h photoperiod at a PPFD of 50 μmol m^{-2} s^{-1} or in the dark. They were moistened with DW if and when required during the course of the experiment. Seeds with a radicle ≥ 2 mm long were considered to be germinated. Four Petri dishes were used for every treatment. Seed germination and radicle growth at different times (12-16 days, respectively) were investigated.

2.5 Effect of KAR_1, GA_3 and light on seed germination of *A. debilis* in Petri dishes

The tests were performed in September 2009. Twenty five fresh *A. debilis* seeds were placed in 90-mm Petri dishes on two layers of Whatman® No. 1 filter paper moistened with 2.0 ml DW, or different concentrations of Kar_1 (1, 10, 100 nM) and GA_3 (1, 10, 100, 1000 μM). The Petri dishes were placed in a culture room at 25 ± 2°C under a 16-h photoperiod at a PPFD of 50 μmol m^{-2} s^{-1} or in darkness. They were moistened with DW if and when required during the course of the experiment. Seeds with a radicle ≥ 2 mm long were considered as germinated. Four Petri dishes were used for every treatment and the percentage seed germination at different times (12-16 days, respectively) was investigated.

2.6 Statistical analysis

All experimental treatments were repeated at least twice within one month and seed germination data was analyzed by one-way AVOVA with a *post-hoc* test (PLSD) used to separate treatment means ($P \leq 0.05$). Percentage data were arcsine transformed prior to statistical analysis.

3. Results

3.1 Effect of SW on seed germination of 13 species growing in Petri dishes and sandy pots

The time required for different plant species to begin germination varied substantially. Seeds of *U. lobata*, *T. magnifica*, *C. surattensis*, *B. orellana*, *G. sylvestre*, *A. auriculiformis*, *C. bicapsularis*, *H. mutabilis* and *S. stans* began to germinate within 3–7 days but within 11–19 days for *A. debilis*, *P. massoniana* and *L. indica*. The speed of seed germination after 24 days differed among species depending on whether seeds were treated with SW or DW (Figure 1). *S. album* seed needed at fewest (32) days to germinate. *A. auriculiformis*, *G. sylvestre* and *A. debilis* had a high seed germination

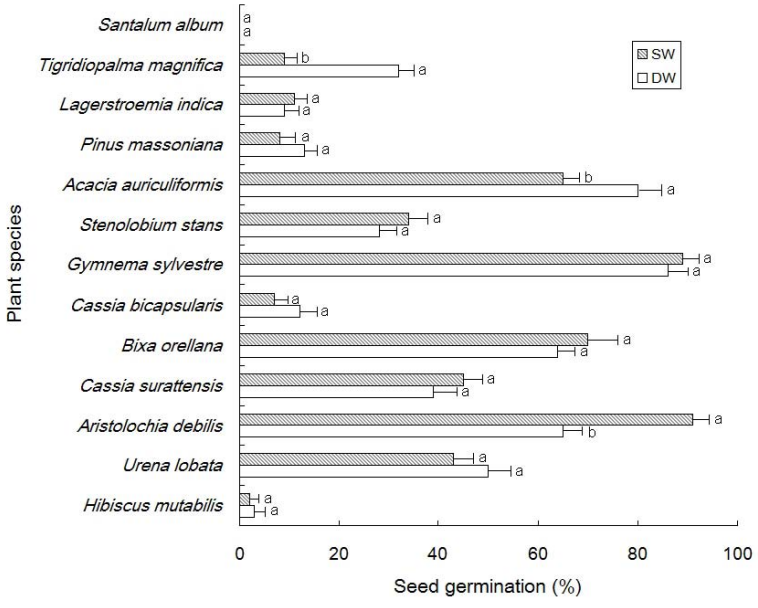

Figure 1. Effect of SW on seed germination of 13 Chinese plant species after cultured for 24 days in light. The same letter in the same species indicates no significant differences according to the PLSD test ($P = 0.05$) ($n = 25 \times 4$).

percentage (> 80%) while *C. bicapsularis*, *P. massoniana* and *L. indica* had a lower seed germination percentage (< 20%).

SW significantly decreased the germination of *T. magnifica* and *A. auriculiformis* seeds compared to DW under a 16-h photoperiod (Figure 1). *T. magnifica* seeds could, however, not germinate in the dark, indicating that *T. magnifica* is a light-sensitive species.

SW resulted in higher germination of *A. debilis* seed than control treatments, peaking at 91% after exposure to a 16-h photoperiod within 24 days (Figure 1, 2). Even in this condition with DW, 64% of seed germinated within 24 days (Figure 1, 2). However, in the dark, *A. debilis* seed treated only with DW could not germinate (Figure 2, 3A). Even in sand pots, *A. debilis* seedlings treated with SW (Figure 3C) were visible earlier than

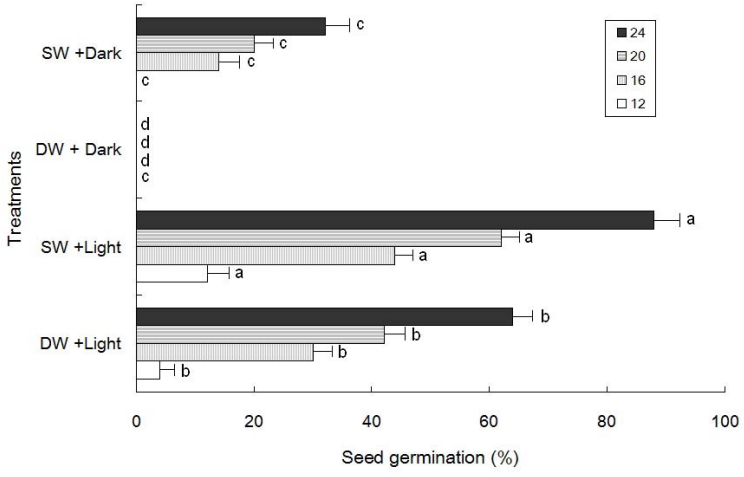

Figure 2. Effect of SW and light on seed germination of *Aristolochia debilis*. The same letters for the same periods (12, 16, 20, 24 h) are not significantly different according to the PLSD test ($P = 0.05$) (n = 25×4).

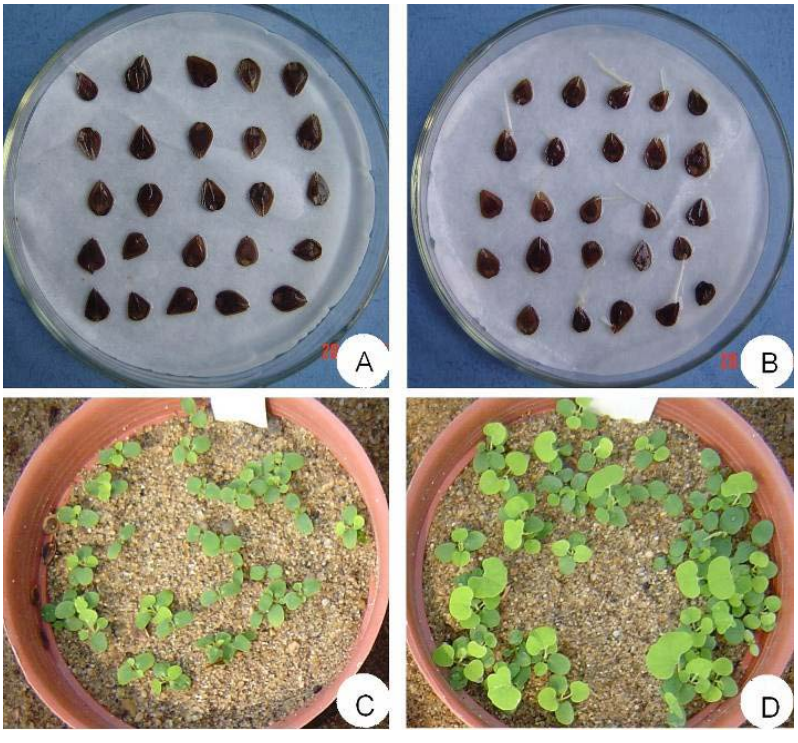

Figure 3. Effect of SW on seed germination and seedling growth of *Aristolochia debilis.* A and C: Treated with DW; B and D: Treated with SW; A and B: Petri dish cultured in dark culture for 26 days (n=25×4); C and D cultured in natural light, in sandy pots, in a greenhouse for 44 days (n=50×2).

seedlings treated with DW (Figure 3D). Highly significant differences were observed.

Germination percentage of *S. album* seeds treated with SW or DW was very low (<5%) (with no significant differences) after 44 days in sandy pots (Figure 4A). However, *S. album* seeds showed a 72% germination peak when treated with 1000 μM GA_3 in the same period (Figure 4B).

3.2 Effect of SW, GA_3 and light on radicle elongation of *A. debilis*

A. debilis seeds from all three treatments (SW, GA_3 and DW) began to germinate after 11–12 days in the light. Among them, seeds treated with SW germinated earliest at 11 days and those treated with GA_3 germinated at 12 days. However, as culture period was prolonged, the post-germinative growth of *A. debilis* radicles treated with GA_3 was significantly more enhanced than the control and SW. Emergence of the radicle was accelerated in seeds treated with GA_3 for 12–16 days, indicating some obvious differences between SW and GA_3 (Figure 5).

3.3 Effect of KAR_1, GA_3 and light on growth of *A. debilis* seedlings

In the dark, *A. debilis* seeds treated with DW did not germinate; even treatment with KAR_1 (1–100 nM) stimulated a low level of germination (about 40%) after culture for 16 days. When cultured for 24 days, the percentage only increased to 46% (Figure 6). Different concentrations of KAR_1 showed no significant

Figure 4. Effect of SW (A) and GA_3 (B) on seed germination of *Santalum album* in sandy pots in a greenhouse after 44 days (n=50×2).

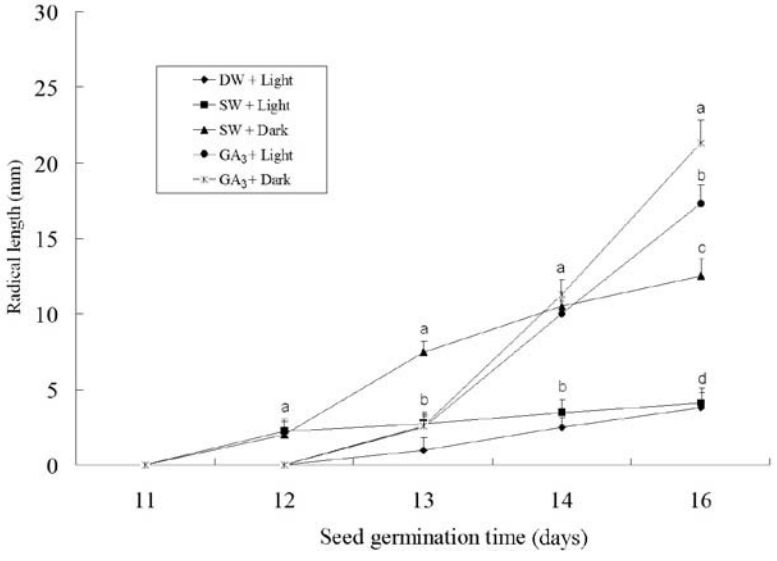

Figure 5. Effects of SW, GA_3 (1000 μM) and light on radicle growth of *Aristolochia debilis*. The same letters are not significantly different at same culture time (12-16 days, respectively) by the PLSD test (P = 0.05) (n = 25×4).

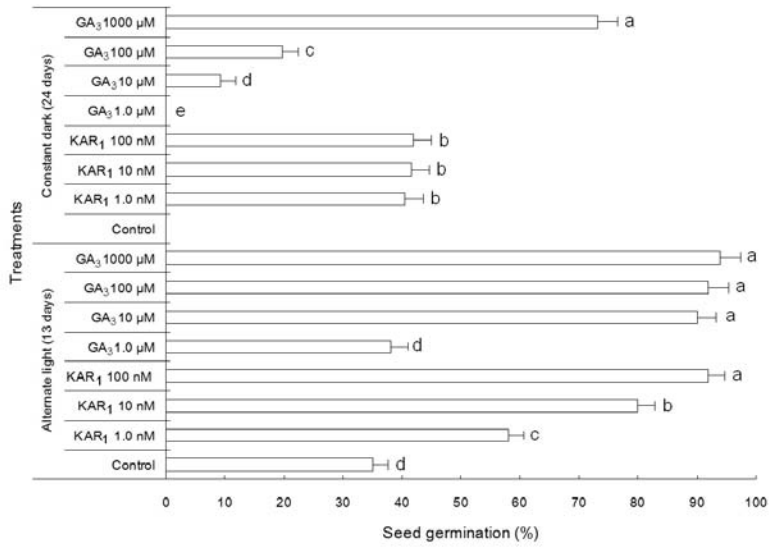

Figure 6. Effect of different concentrations of KAR_1 and GA_3 on seed germination of *Aristolochia debilis* in different culture conditions. The same letters in the same culture condition showed no significant differences according to the PLSD test ($P = 0.05$) ($n = 25 \times 4$).

differences in the dark (Figure 6). As seeds were exposed to light, the shortest time for seed germination was also 12 days (the same as the SW treatment). The percentage seed germination increased to over 80% within 24 days (Figure 6) indicating that both Kar_1 and light play a positive role in seed germination of *A. debilis*.

In the dark, A low concentration of GA_3 (1.0 μM) could not stimulate seed germination but 10–1000 μM GA_3 could. As the concentration increased, the percentage seed germination increased to 40% (Figure 6) showing some positive effect on germination of *A. debilis* seed. In the light, a low concentration of GA_3 (1.0 μM) could stimulate seed germination, reaching 40%. However, 10–1000 μM L^{-1} GA_3 could stimulate seed germination to levels that exceeded 90%.

4. Discussion

In this study, the effects of SW on seed germination of 13 plant species from South China, which falls within a southern tropical and subtropical monsoon climate region, were documented for the first time. SW could stimulate seed germination of only one species, *A. debilis*, but had negative effects on seed germination of some species (compared to control treatments), including *T. magnifica* and *A. auriculiformis*, indicating that not all species responded positively to SW treatment. Thus, SW was not equally effective in promoting seed germination among species in this study. Similarly, SW derived from five grass species inhibited the *in vitro* growth of *Cymbidium*, most likely because this species is not exposed to nor does it require SW or fire for seed germination of other growth-related processes [46]. In a previous study of taxa in the Cape Ericaceae, of the 40 *Erica* species tested, seed of 25 species showed a significant improvement in germination following treatment with smoke [8]. In the first comprehensive study of germination in the Restionaceae, [47] showed that 25 of the 32 species studied also responded positively to smoke treatment. These findings were particularly significant as many of the restio species responding to smoke had previously been difficult or impossible to germinate. The latest available data for fynbos seeds tested 215 species, 101 of which responded positively to smoke [5]. Dixon *et al*. [18] showed that smoke had a positive influence on germination of 45 out of 94 species of native Western Australian plants. A group of 23 species which responded positively had previously been recorded as extremely difficult or impossible to germinate using conventional techniques. These included members of the genera *Geleznowia* (Rutaceae), *Hibbertia* (Dilleniaceae), *Stirlingia* (Proteaceae), *Verticordia* (Myrtaceae), *Actinostrobus* (Cupressaceae) and *Pimellia* (Thymelaeaceae). The promotive effect of smoke may have been independent of seed size, shape and plant life form, namely, whether an annual, perennial, herbaceous, seeder (fire sensitive) or resprouter (fire tolerant) [19]. The main reason for this negative result is likely to be the complex nature of SW, with some constituents likely to inhibit seed germination. Our study indicates that SW is able to stimulate seed germination over broad

geographic areas, but with limited success (only one out of 13 species) on plants growing in tropical and subtropical monsoon climates, which dominate South China.

When *A. debilis* seeds were treated with SW (1:10 solution), no germination was observed in the dark while as many as 40% of seeds treated with KAR_1 (1-100 nM) germinated in the dark. This shows some differences between SW and KAR_1. One reason may be that SW and KAR_1 are chemically different: SW is a complex compound while KAR_1 is a single chemical, thus their functional effects would not be the same. Soós *et al*. [12] showed that although treatment of maize (*Zea mays* L.) kernels with SW and KAR_1 resulted in a similar physiological response, the gene expression and protein ubiquitination patterns were quite different.

GA_3, SW and KAR_1 could stimulate *A. debilis* seed germination and GA_3 could stimulate *S. album* seed germination. However, SW could not stimulate *S. album* seed germination. Previous studies indicated that plant-derived smoke-treated seeds grew vigorously [8]. However, GA_3 characteristically causes hypocotyl and stem elongation [48]. As expected, our study found that the radicles of *A. debilis* from GA_3-treated seeds grew longer than those treated with SW and DW, proving that SW differs from GA_3 with regard to its growth-stimulating ability, namely radicle elongation. The efficient concentrations of GA_3 and KAR_1 were considerably different: for the former, it was at least 10–1000 μM while for the latter it was usually 1–100 nM, indicating an at least 1000-fold difference. All these differences suggest that GA_3 and SW (KAR_1) may not function directly but may have an indirect metabolic pathway or relationship although physiological activity and metabolism need to be studied in detail to clarify the exact mechanism and relationship, if any, between the two compounds. In this study, KAR_1 and GA_3 could both enhance seed germination but KAR_1 might play different roles or functions in an indirect way in seedling establishment because it could not enhance seedling growth while GA_3 is able to stimulate the elongation of hypocotyls and radicles [9,49].

Acknowledgements

We thank Kings Park and Botanic Garden and University of Western Australia for kindly supplying SW and KAR_1. We also thank Ms. Caixia Peng and Dr. Jinsong Zhou for collecting plant seeds. The program supported by the National Natural Science Foundation of China (Grant Nos. 31100498, 31270720 and 30972295) is great acknowledged.

Conflicts of interest

The authors declare no conflicts of interest.

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