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Research Article

The effects of gibberellic acid and kinetin on overcoming the effects of juglone stress on seed germination and seedling growth

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Abstract: Juglone (5-hydroxy-1,4-naphthoquinone) is an allelochemical responsible for walnut allelopathy. The effects of gibberellic acid (GA_3) and kinetin (KIN) on overcoming the effects of juglone stress on seed germination and seedling growth were investigated in barley, wheat, cucumber, alfalfa, and tomato. Seeds pre-treated with plant growth regulators were used to test their effects on the alleviation of juglone stress. It was observed that seed germination in tomato and wheat was inhibited by juglone and that the plant growth regulators alleviated it significantly. Elongation and dry weight of the seedlings of all the species used in the study were reduced significantly by juglone, and the plant growth regulators alleviated them. The most effective treatment was the GA_3+KIN combination, which was best on seedling growth in tomato and wheat.

Key words: Juglone stress, alleviation, gibberellic acid, kinetin, seed germination, seedling growth

Tohum çimlenmesi ve fide büyümesi üzerindeki juglon stresi etkisinin yenilmesinde giberellik asit ve kinetin etkisi

Özet: Juglon (5-hidroksi–1,4-naftokinon) ceviz allelopatisinden sorumlu bir allelokimyasaldır. Giberellik asit (GA_3) ve kinetin (KIN)'in tohum çimlenmesi ve fide büyümesi üzerindeki juglon stresi etkisinin yenilmesindeki etkinlikleri arpa, buğday, hıyar, yonca ve domateste araştırıldı. Bitki büyüme düzenleyicileri ile ön muamele gören tohumlar juglon stresi sonrasında, etkisini büyüme düzenleyicilerinin ne kadar hafiflettiklerini test etmek için kullanıldı. Buğday ve domateste tohum çimlenmesinin juglon tarafından engellendiği, ancak bunun bitki büyüme düzenleyicileri kullanılarak önemli ölçüde azaltıldığı belirlenmiştir. Çalışmada kullanılan bütün türlerin fide uzunluğu ve kuru ağırlıkları da juglon tarafından önemli ölçüde azaltılmış, fakat bu bitki büyütme düzenleyicilerince iyileştirilmiştir. Bu hususta GA_3+KIN kombinasyonu en etkili muamele olmuş, ve fide büyümesi üzerinde en yüksek etki de domates ve buğdayda kaydedilmiştir.

Anahtar sözcükler: Juglon stresi, iyileştirme, giberellik asit, kinetin, tohum çimlenmesi, fide büyümesi

Introduction

The chemical interactions that occur among plants are known as allelopathy, and organic compounds that play a role in allelopathy are known as allelochemicals, and they become stressful when they are toxic and inhibit growth (Kocaçalışkan, 2006). Juglone (5-hydroxy-1,4-naphthoquinone) is an allelochemical responsible for walnut allelopathy, and the inhibitory effect of black walnut (*Juglans nigra*) on associated plant species is one of the oldest examples of allelopathy (Davis, 1928; Rice, 1984; Rizvi & Rizvi, 1992). Juglone has been isolated from many species

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in the walnut family (*Juglandaceae*), including *J. nigra* L., *J. regia* L., and some others (Daglish, 1950; Prataviera et al., 1983). Hydrojuglone, a colourless, non-toxic reduced form of juglone, is abundant, especially in the leaves, fruit hulls, and roots of walnut. When exposed to air or some other oxidising substances, hydrojuglone is oxidised to its toxic form, juglone (Lee & Campbell, 1969; Segura-Aguilar et al., 1992). Rain disolves and washes juglone from the leaves and transfers it into the soil, where this toxic substance affects neighbouring herbaceous and woody plants that absorb it into their roots (Funk et al., 1979; Rietveld, 1983).

Walnut intercropping is a commonly used system in several regions of Turkey, as in several countries, although the agronomic yield of some species can be significantly reduced by the deleterious effects of walnut on associated juglone-sensitive species (Eriş & Barut, 1989; Jose & Gillespie, 1998a). Although the concentration of juglone decreases with distance from walnut trees, moderate levels of juglone have been detected at a distance of 4.25 m. Juglone has been known to be toxic for a long time and the solution to this problem remains unknown. Installation of polyethylene root barriers has been suggested as a way to prevent juglone from entering the alley where associated crop species are planted (Jose & Gillespie, 1998a). We think this method can only prevent the effect of juglone exuded from walnut roots, but cannot prevent the effect of juglone washed from the leaves.

In previous studies (Kocaçalışkan & Terzi, 2001; Kocaçalışkan et al., 2009; Terzi, 2009) juglone was reported to inhibit both seed germination and seedling growth in tomato, cucumber, alfalfa, radish, garden cress, and watermelon, whereas only inhibited seedling growth was reported in wheat, barley, corn, radish, and bean following the treatment. To the best of our knowledge the literature does not contain any reports of a method for avoiding the growth-inhibiting effect of juglone; therefore, in the present study dicotyledonous tomato, cucumber, and alfalfa, and monocotyledonous wheat and barley were tested to determine if pre-treatment of the seeds with gibberellic acid (GA_3) and kinetin (KIN) could overcome juglone-induced inhibition.

Materials and methods

Seeds of tomato (*Lycopersicon esculentum* Mill. cv. SCI 2121), cucumber (*Cucumis sativus* L. cv. Beith Alpha), alfalfa (*Medicago sativa* L. cv. Kayseri), wheat (*Triticum vulgare* L. cv. Hatay), and barley (*Hordeum vulgare* L. cv. Tokak) were obtained from the suppliers BETA and AGROMAR, Bursa, Turkey.

Juglone solution (1 mM) was prepared by dissolving in distilled water with stirring at 40 °C for 24 h. We used 1 mM juglone because it is generally found in the soil of walnut plantations at concentrations less than 0.1 mM. Its level varies according to species, season, and distance from the trunks of walnut trees, but reaching a concentration of 1 mM was considered a weak possibility (Rietveld, 1983; Jose & Gillespie, 1998a). As such, 1 mM was selected as the maximum possible concentration of juglone to determine stress—the reductive effects of plant growth regulators (PGRs). Juglone was purchased from Sigma Company. We prepared 1 mM GA_3, 0.5 mM KIN, and a combination of both substances. Seeds were surface sterilised with 1% sodium hypochloride. Some of the seeds were pre-soaked in solutions of the PGRs or in distilled water for 2 h at room temperature as pre-treatment. This duration was determined with pre-experiments. Thereafter, the solutions were decanted off and the seeds were dried for 1 h. At least 20 seeds treated with PGRs were sown in a 12-cm petri dish furnished with sheets of filter paper moistened with distilled water or with 8-12 mL of juglone solution, depending on seed size. The seeds not treated with PGRs were also sown in distilled water or juglone solution as controls. Then the dishes were left in an incubator at 25 °C in continuous darkness. After 5 days the percentage of germination and post-germinative growth of the seedlings were determined by measuring the length and dry weight of the roots and shoots of the seedlings. Protrusion of the radicle from the seed coat was considered the germination criterion.

The experiments were conducted using a completely randomised design with 3 replicates. Dunnett's test was used to compare the mean values of the PGR treatments in order to control the values obtained in the distilled water or juglone samples for seed germination rates, and length and dry weight of the roots and shoots of the seedlings (Kocaçalışkan & Bingöl, 2008).

Results

Seed Germination

Seed germination in barley, wheat, and cucumber was not inhibited by juglone in the control, but was inhibited by about 60% and 70% in alfalfa and tomato, respectively (Table 1). These inhibitions were alleviated significantly by PGRs. The most effective treatments in overcoming juglone inhibition were the GA_3+KIN combination, with a 183% alleviation rate in tomato and GA_3, with a 175% rate with in alfalfa seeds (Table 1, Figure).

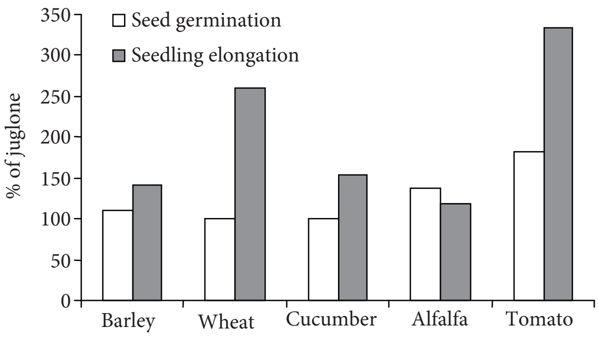

Figure. Effect of GA+KIN on relative seed germination and relative seedling elongation (juglone values = 100%).

Seedling Growth

Both root and shoot elongation decreased with juglone in all of the species studied. Growth inhibition due to juglone was not very different in the roots and shoots of the samples studied (Table 2). Juglone had the highest inhibitory effect on both root and shoot elongation in tomato; however, juglone inhibition on root and shoot elongation in all the species was alleviated by all of the PGR treatments studied. The alleviation effects of the treatments were higher in tomato and wheat than in the other species, and the most effective treatment was GA_3+KIN. Alleviation by GA_3+KIN was 350% and 300% on tomato root and shoot elongation, respectively, versus 260% on root and 261% on shoot elongation in wheat. On the other hand, generally, PGR alleviation of juglone stress was higher on root elongation than on shoot elongation (Table 2).

Seedling (root and shoot) elongation was also reduced by juglone, but it was alleviated by the PGRs and the most effective treatment was GA_3+KIN. The greatest alleviation was achieved with this combination—333% in tomato and 260% in wheat seedling elongation. The weakest alleviation effect of the treatment was observed on alfalfa seedling elongation (118% alleviation) (Figure).

Table 1. The effects of PGRs on the percentage of germination in seeds under juglone stress.

		Control	GA_3	[%]	KIN	[%]	GA_3+KIN	[%]
Barley	D. water	100 ± 0.0	100 ± 0.0	100	100 ± 0.0	100	100 ± 0.0	100
	Juglone	90 ± 5.0	100 ± 0.0	111	100 ± 0.0	111	100 ± 0.0	111
Wheat	D. water	100 ± 0.0	100 ± 0.0	100	100 ± 0.0	100	100 ± 0.0	100
	Juglone	100 ± 0.0	100 ± 0.0	100	100 ± 0.0	100	100 ± 0.0	100
Cucumber	D. water	100 ± 0.0	100 ± 0.0	100	90 ± 5.0	90	100 ± 0.0	100
	Juglone	90 ± 2.9	80 ± 5.8	89	80 ± 6.0	89	90 ± 6.0	100
Alfalfa	D. water	95 ± 7.6	95 ± 4.4	100	90 ± 5.8	95	95 ± 4.4	100
	Juglone	40 ± 6.5	70 ± 8.9**	175	65 ± 8.3**	163	55 ± 8.9*	137
Tomato	D. water	90 ± 5.7	90 ± 6.5	100	90 ± 7.2	100	95 ± 5.0	105
	Juglone	30 ± 3.8	50 ± 4.4**	167	45 ± 5.3**	150	55 ± 4.1**	183

**($P < 0.01$), *($P < 0.05$). Treatments differ significantly from the control (Dunnett's) ± SE.
[%] Relative germination with respect to the control (D. water or juglone).

Table 2. The effects of PGRs on root and shoot elongation (cm) under juglone stress.

			Control	GA_3	[%]	KIN	[%]	GA_3+ KIN	[%]
Barley	Root	D. water	10.7 ± 0.21	10.9 ± 0.37	102	8.6 ± 0.23*	80	9.5 ± 0.23	89
		Juglone	5.6 ± 0.23	6.5 ± 0.32*	116	5.3 ± 0.18	95	5.4 ± 0.20	96
	Shoot	D. water	9.0 ± 0.40	12.2 ± 0.26**	136	8.7 ± 0.28	97	10.0 ± 0.30	111
		Juglone	1.7 ± 0.15	4.5 ± 0.24**	265	4.1 ± 0.20**	241	4.2 ± 0.32**	247
Wheat	Root	D. water	10.2 ± 0.29	9.2 ± 0.24	90	5.8 ± 0.25**	57	7.2 ± 0.11**	71
		Juglone	2.2 ± 0.14	4.6 ± 0.17**	209	5.6 ± 0.23**	255	5.7 ± 0.24**	260
	Shoot	D. water	8.2 ± 0.25	8.7 ± 0.15	106	8.6 ± 0.21	105	9.2 ± 0.25*	112
		Juglone	3.1 ± 0.20	5.2 ± 0.20**	168	6.3 ± 0.15**	203	8.1 ± 0.18**	261
Cucumber	Root	D. water	9.1 ± 0.12	9.0 ± 0.20	99	10.5 ± 0.17	115	9.3 ± 0.20	102
		Juglone	4.5 ± 0.11	8.2 ± 0.14**	182	7.4 ± 0.15**	164	7.7 ± 0.11**	171
	Shoot	D. water	5.7 ± 0.20	5.9 ± 0.17	104	5.8 ± 0.12	102	5.7 ± 0.14	100
		Juglone	3.2 ± 0.22	3.7 ± 0.18	116	4.4 ± 0.14*	138	4.1 ± 0.15	111
Alfalfa	Root	D. water	2.1 ± 0.22	2.3 ± 0.21	110	1.5 ± 0.12	71	1.1 ± 0.14**	53
		Juglone	0.6 ± 0.07	0.7 ± 0.08	116	0.8 ± 0.07*	133	0.7 ± 0.08	116
	Shoot	D. water	2.2 ± 0.12	2.7 ± 0.18	123	2.5 ± 0.15	114	2.3 ± 0.17	105
		Juglone	0.5 ± 0.09	0.6 ± 0.09	120	0.6 ± 0.07	120	0.6 ± 0.07	120
Tomato	Root	D. water	2.4 ± 0.24	2.6 ± 0.20	108	2.5 ± 0.17	104	2.6 ± 0.15	108
		Juglone	0.2 ± 0.03	0.6 ± 0.12**	300	0.6 ± 0.09**	300	0.7 ± 0.12**	350
	Shoot	D. water	1.6 ± 0.18	1.8 ± 0.19	113	2.0 ± 0.27**	125	2.1 ± 0.20**	131
		Juglone	0.1 ± 0.00	0.2 ± 0.09**	200	0.3 ± 0.08**	300	0.3 ± 0.07 **	300

**($P < 0.01$), *($P < 0.05$). Treatments differ significantly from the control (Dunnett's) ± SE.
[%] Relative growth as elongation, with respect to the control (D. water or juglone).

Similarly, dry weight of the species was also reduced by juglone and the effect was alleviated by PGRs (Table 3). As seen in Table 3, the alleviation effect of the PGRs was greater on root and shoot dry weight in tomato and wheat than in the other species. In general, the alleviation effects of the PGRs were stronger on shoots than on roots. In addition, the most effective PGR treatment was GA_3+KIN, with an effect of 300% in tomato. The weakest alleviation effect of the PGRs was observed in alfalfa.

Discussion

Previous research has shown that juglone inhibits germination and seedling growth in several plant species, and that seedling growth was much more sensitive to juglone than seed germination (Rietveld, 1983; Tekintaş et al., 1988; Dornbos & Spencer, 1990; Kocaçalışkan & Terzi, 2001; Terzi et al., 2003; Terzi, 2008, 2009). However, to the best of our knowledge the literature does not contain any reports of a method for overcoming the effects of juglone stress on seed germination and seedling growth. It has been indicated that PGRs can overcome some stresses on plants (Hale & Orcutt, 1987). For example, salt (NaCl) stress on seed germination can be overcome by the use of GA_3 and KIN (Kabar, 1990).

The present study shows that PGRs (GA_3 and KIN) overcame the allelochemical stress of juglone on seed germination and seedling growth by affecting root and shoot growth rates in several species. The barley and wheat used in the present study are monocot members of *Gramineae*, and cucumber, alfalfa, and tomato are dicots. When we compared the alleviation effect of GA_3 and KIN on juglone stress in

Table 3. The effects of PGRs on root and shoot dry weight (mg) under juglone stress.

			Control	GA_3	[%]	KIN	[%]	GA_3+ KIN	[%]
Barley	Root	D. water	0.78 ± 0.0 18	0.80 ± 0.030	103	0.60 ± 0.012**	77	0.71 ± 0.015	91
		Juglone	0.40 ± 0.017	0.47 ± 0.015	118	0.39 ± 0.021	98	0.40 ± 0.017	100
	Shoot	D. water	0.68 ± 0.015	0.92 ± 0.025**	135	0.65 ± 0.015	96	0.76 ± 0.018*	112
		Juglone	0.12 ± 0.014	0.34 ± 0.015**	283	0.30 ± 0.018**	250	0.28 ± 0.019**	233
Wheat	Root	D. water	0.63 ± 0.022	0.62 ± 0.015	98	0.51 ± 0.012*	81	0.69 ± 0.023	110
		Juglone	0.21 ± 0.019	0.45 ± 0.018**	214	0.50 ± 0.022**	238	0.48 ± 0.025**	229
	Shoot	D. water	0.69 ± 0.020	0.73 ± 0.018	106	0.72 ± 0.028	105	0.79 ± 0.024*	108
		Juglone	0.26 ± 0.023	0.40 ± 0.017**	154	0.57 ± 0.017**	219	0.70 ± 0.012**	269
Cucumber	Root	D. water	0.76 ± 0.019	0.74 ± 0.015	97	0.89 ± 0.018**	117	0.78 ± 0.015	103
		Juglone	0.34 ± 0.023	0.68 ± 0.017**	200	0.60 ± 0.023**	176	0.63 ± 0.023**	185
	Shoot	D. water	0.71 ± 0.015	0.69 ± 0.024	97	0.66 ± 0.018	93	0.73 ± 0.015	103
		Juglone	0.24 ± 0.012	0.45 ± 0.022**	189	0.54 ± 0.020**	225	0.51 ± 0.021**	213
Alfalfa	Root	D. water	0.29 ± 0.019	0.32 ± 0.018	110	0.21 ± 0.015**	72	0.16 ± 0.012**	55
		Juglone	0.08 ± 0.009	0.09 ± 0.007	113	0.09 ± 0.008	113	0.09 ± 0.008	113
	Shoot	D. water	0.51 ± 0.021	0.63 ± 0.026	124	0.58 ± 0.018	114	0.54 ± 0.025	106
		Juglone	0.12 ± 0.017	0.16 ± 0.015**	133	0.14 ± 0.012*	117	0.14 ± 0.015*	117
Tomato	Root	D. water	0.34 ± 0.015	0.37 ± 0.021	109	0.35 ± 0.026	103	0.37 ± 0.014	109
		Juglone	0.02 ± 0.000	0.04 ± 0.005*	200	0.05 ± 0.008**	250	0.06 ± 0.007**	300
	Shoot	D. water	0.55 ± 0.022	0.62 ± 0.027	113	0.67 ± 0.025**	129	0.73 ± 0.029**	133
		Juglone	0.04 ± 0.000	0.09 ± 0.007**	225	0.11 ± 0.009**	275	0.12 ± 0.008**	300

**($P < 0.01$), *($P < 0.05$). Treatments differ significantly from the control (Dunnett's) ± SE.
[%] Relative growth as dry weight, with respect to the control (D. water or juglone).

monocot and dicot species, no obvious differences were observed. For example, in barley the alleviation effect of GA_3 was stronger than that of KIN, whereas the alleviation effect of KIN in wheat was stronger than that of GA_3. This indicates that the alleviation effect of GA_3 and KIN on juglone stress may not be class dependent (monocot vs. dicot), but may be species dependent. This result differs from the alleviation of salt stress; Kabar reported that GA_3 was more effective on salt stress alleviation in *Gramineae*, whereas KIN was more effective in dicots. The differences in results may be due to the application of different stress inducers.

The literature on the physiological action of juglone shows that the mechanism of action is not well understood: juglone inhibits plant growth by reducing photosynthesis and respiration (Hejl et al., 1993; Jose & Gillespie, 1998b), increasing oxidative stress (Segura-Aguilar et al., 1992), and blocking protein synthesis in the transcription stage by inhibiting RNA polymerases (Chao et al., 2001). The mechanisms of action of GA_3 and KIN in overcoming juglone stress are unknown at present; however, it is known that during seed germination the most important event is protein synthesis, as it is necessary for embryo growth (Bewley et al., 1983), implying that GA_3 and KIN may protect protein synthesis against juglone's inhibitory effect. Some allelochemicals, such as benzoic acids, lower auxin concentrations in plants by triggering auxin catabolism, so that plant growth is inhibited (Weir et al., 2004). Although there are no reports on the effects of other PGRs in this respect, a similar mechanism may result in juglone's inhibitory effect by decreasing gibberellin and cytokinin concentrations in the seeds during germination. As shown in the present study, exogenous seed supplementation with PGRs may trigger a mechanism that overcomes juglone stress, probably by reversing lowered PGR concentrations.

In conclusion, the present study shows that pre-treatment of seeds with GA_3 and KIN, or their combination, alleviated the inhibitory effect of juglone on seed germination and seedling growth. This may be beneficial to the arrangement of intercropping system(s) of juglone-sensitive species between walnut trees in the same field.

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