



Temperature-Dependent Effects of *Beauveria bassiana* on Germination and Early Growth of *Allium cepa* Seedlings

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Abstract

The entomopathogenic fungus *Beauveria bassiana* can associate with plants and promote growth, but these effects may vary with temperature. This study evaluated the effects of *B. bassiana* on germination and early growth of red onion (*Allium cepa* L.) at 22, 28, and 34 °C. Bulbs were soaked for 3 h in 10⁸ conidia/mL or sterile water before planting. Fungal treatments were reinforced by soil drenching at 3, 6, and 9 days after planting (DAP) and foliar spraying at 6, 9, and 12 DAP. Germination, plant height, and leaf number were monitored for 12 days. Temperature significantly affected mean germination time ($F_{2,10} = 51.49$, $p < 0.001$), increasing from 2.98 days at 22 °C to 3.43 days at 28 °C and 4.58 days at 34 °C, whereas *B. bassiana* had no significant effect ($p = 0.339$). At 12 DAP, *B. bassiana*-treated seedlings were significantly taller than controls (18.73 vs. 18.16 cm; $F_{1,10} = 11.75$, $p = 0.006$). Temperature, *B. bassiana*, and their interaction significantly affected area under the plant-height growth curve ($F_{2,10} = 4.99$, $p = 0.031$). Growth promotion occurred at 22 and 28 °C but was negligible at 34 °C. Leaf number was markedly reduced at 34 °C, while *B. bassiana* had no significant overall effect. Thus, the early growth-promoting effect of *B. bassiana* was temperature-dependent and substantially attenuated under continuous high temperature.

Keywords: *Allium Cepa*, *Entomopathogenic Fungus*, *Heat Stress*, *Plant Growth Promotion*, *Seedling Establishment*

INTRODUCTION

Red onion (*Allium cepa* L.) establishment depends on rapid sprouting and early vegetative growth, both of which are strongly influenced by temperature. Supra-optimal temperature can disturb respiration, water relations, and leaf development, reducing seedling vigor even when final germination remains high.

Beauveria bassiana is widely used as an entomopathogenic fungus, but it can also associate with plants as a rhizosphere or endophytic microorganism. These associations may improve plant growth, nutrient acquisition, metabolism, and stress tolerance. Growth promotion following *B. bassiana* inoculation has been reported in several crops (Sui et al., 2023).

This plant-associated role is relevant to *Allium cepa*. Gana et al. (2022) found that *B. bassiana*-inoculated onion plants showed improved growth and altered nutrient and biochemical responses under different water-deficit regimes, suggesting that environmental conditions influence the benefits of fungal association.

Temperature can affect both the host and the fungus. *Beauveria bassiana* generally germinates and grows best at moderate temperatures, whereas temperatures near 34–35 °C may reduce conidial germination and vegetative growth (Mwamburi et al., 2015). High temperatures may therefore stress the plant while simultaneously limiting fungal establishment or activity.

Information on temperature-dependent effects of *B. bassiana* during early onion establishment remains limited, although this interaction is important for tropical and subtropical production systems exposed to substantial thermal variation.

This study evaluated the effects of *B. bassiana* on bulb germination and early seedling growth

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at 22, 28, and 34 °C. We hypothesized that high temperature would delay germination and early development, while *B. bassiana* would promote growth at moderate temperatures but provide less benefit at 34 °C.

LITERATURE REVIEW

Beauveria bassiana is increasingly recognized not only as an entomopathogenic fungus but also as a multifunctional plant-associated microorganism capable of endophytic colonization. Colonization efficiency varies with fungal isolate, host species, inoculation method, application rate, plant developmental stage, and environmental conditions (Yerukala et al., 2022).

Endophytic entomopathogenic fungi may promote plant growth by improving nutrient acquisition, altering metabolism and phytohormonal processes, and enhancing tolerance to biotic and abiotic stresses (Fite et al., 2023; Ahsan et al., 2024).

Several studies have reported growth-promoting effects of *B. bassiana* in crops. In maize, systemic colonization increased plant height, root length, and biomass (Liu et al., 2022), while in rice it improved growth and reduced sheath-blight severity (Deb et al., 2022). Similar benefits have been observed in melon, strawberry, and tomato (Mantzoukas et al., 2022; Sui et al., 2023).

However, responses are inconsistent across systems, as colonization does not always promote growth and may depend on application method and fungal genotype (Altaf et al., 2023; Kropf & Gassmann, 2026; Rivera-Núñez et al., 2026).

Evidence in *Allium cepa* is particularly relevant. Gana et al. (2022) showed that *B. bassiana* influenced onion growth, nutrient uptake, secondary metabolites, and antioxidant responses under different watering regimes, indicating strong environmental dependence. Temperature is a likely key regulator because it affects both onion establishment and fungal physiology.

Onion germination is highly temperature-sensitive (Moradi-Shakoorian et al., 2023), while *B. bassiana* isolates differ markedly in thermal tolerance, conidial germination, vegetative growth, and stress response (Mseddi et al., 2022; Guan et al., 2024; Udompaisarn et al., 2025; Mwikali et al., 2026).

Thus, direct evidence linking temperature, *B. bassiana* application, bulb sprouting, and early *A. cepa* growth remains limited. This gap provides a clear rationale for evaluating *B. bassiana* performance across contrasting temperatures.

RESEARCH METHOD

Plant Material and Experimental Conditions

Uniform red onion (*Allium cepa* L.) bulbs of cultivar Bima were obtained from Brebes, Central Java. Healthy bulbs of similar size were selected and planted in germination trays containing sterile soil. Each experimental unit contained ten bulbs and was replicated in three blocks.

Trays were maintained in controlled-environment chambers at constant temperatures of 22, 28, or 34 °C, with three independent chamber replicates. Relative humidity was maintained at 60% under a 12 h light:12 h dark photoperiod and a light intensity of 2560 lux.

Beauveria Bassiana Inoculum

The *B. bassiana* Cangkringan isolate, originally obtained from *Hypothenemus hampei*, was cultured on potato dextrose agar at 26 °C for 14 days. Conidia were harvested in sterile water containing 0.01% Tween 80 and adjusted to 1×10^8 conidia/mL with a hemocytometer. A germination assay assessed conidial viability before inoculation, and suspensions were used only when viability was at least 95% (Johnson et al., 2020).

Fungal Inoculation and Treatments

The experiment followed a 3×2 factorial arrangement: three temperatures (22, 28, and 34 °C) and two inoculation treatments (*B. bassiana* and sterile water), with three replicates. Treatments were T1: *B. bassiana*, 22 °C; T2: water control, 22 °C; T3: *B. bassiana*, 28 °C; T4: water control, 28 °C; T5: *B. bassiana*, 34 °C; and T6: water control, 34 °C.

Before planting, fungal-treated bulbs were submerged in 1×10^8 *B. bassiana* conidia/mL for 3 h; controls were submerged in sterile water. The fungal suspension was subsequently applied as a soil drench at 3, 6, and 9 DAP and as a foliar spray at 6, 9, and 12 DAP. Controls received sterile water on the same schedule. Each drench and foliar application used 5 mL/plant.

Germination and Seedling Growth Measurements

Germination capacity, plant height, and leaf number were recorded daily from 1 to 12 DAP. Germination was expressed as the percentage of bulbs producing visible shoots. Plant height was measured from the substrate surface to the tip of the longest fully extended leaf. The area under the plant-height growth curve (AUPHC) was calculated by trapezoidal integration of observations from 1 to 12 DAP and expressed as cm-day.

Mean germination time (MGT) was calculated from daily cumulative germination using:

$$\text{MGT} = \Sigma(n_i t_i) / \Sigma n_i$$

where n_i represents the proportion of newly germinated bulbs on observation day i and t_i represents time in days.

Because all treatments reached 100% final germination, MGT was used to compare germination dynamics among treatments. MGT is widely used to distinguish treatment effects on germination speed when final germination percentage alone does not adequately describe germination dynamics (Fedeli et al., 2023).

Statistical Analysis

Mean germination time, plant height and leaf number at 12 DAP, and AUPHC were analyzed by factorial ANOVA with temperature, inoculation, and their interaction as fixed effects, and block included in the model. Significant means were compared using Tukey's HSD at $\alpha = 0.05$ after checking residual normality and homogeneity of variance. Analyses were performed in IBM SPSS Statistics 29.0.

Daily observations of germination, plant height, and leaf number were used to visualize developmental trajectories and were not treated as statistically independent replicates. This distinction between repeated observational measurements and independent experimental units avoids inflating sample size and pseudoreplication (Lazic et al., 2018).

FINDINGS AND DISCUSSION

Temperature Delayed Germination, But *B. Bassiana* Did Not Affect Final Germination

All treatments reached 100% germination by 6 DAP, showing that temperature influenced the rate of bulb sprouting rather than final sprouting capacity. Germination became progressively slower as temperature increased. At 22 °C, approximately 82% of bulbs had germinated by 3 DAP, whereas no germination occurred at 34 °C during the first three days. Accordingly, mean germination time (MGT) increased significantly from 2.98 days at 22 °C to 3.43 days at 28 °C and 4.58 days at 34 °C ($F_{2,10} = 51.49$, $p < 0.001$) (Table 1-2, Figure 1).

This response is consistent with the temperature sensitivity of *Allium cepa* establishment. Moradi-Shakoorian et al. (2023) showed that onion germination has cultivar-dependent optimum

temperature ranges and becomes progressively restricted above the optimum. Although their study examined true onion seed rather than bulb sprouting, the same general pattern supports the delayed emergence observed at 34 °C.

In contrast, *B. bassiana* did not significantly affect MGT ($F_{1,10} = 1.01$, $p = 0.339$), and the temperature $\times$ inoculation interaction was not significant. Thus, fungal application neither accelerated nor inhibited bulb sprouting. This suggests that the subsequent growth response to *B. bassiana* occurred mainly after emergence rather than through earlier germination.

Beauveria Bassiana Increased Early Seedling Height

At 12 DAP, *B. bassiana*-treated seedlings averaged 18.73 cm compared with 18.16 cm in controls, representing an overall increase of about 3.2%. The fungal effect was significant ($F_{1,10} = 11.75$, $p = 0.006$). The strongest numerical responses occurred at 22 °C (+5.0%) and 28 °C (+3.7%), whereas little difference was observed at 34 °C (Table 1-2, Figure 2).

This result agrees with previous evidence of *B. bassiana*-associated plant growth promotion. In onion, [Gana et al. \(2022\)](#) reported increased leaf growth and changes in biomass, nutrient uptake, and biochemical responses following endophytic inoculation.

Similarly, [Liu et al. \(2022\)](#) observed increased maize growth, while [Sui et al. \(2023\)](#) reported greater tomato root length and plant height after successful *B. bassiana* colonization. Field studies in melon and strawberry have also demonstrated its potential as both a biocontrol agent and plant biostimulant ([Mantzoukas et al., 2022](#)).

However, such effects are not universal. [Kropf and Gassmann \(2026\)](#) found successful endophytic colonization of maize without significant growth promotion. This indicates that fungal strain, host species, inoculation method, and environmental conditions determine the magnitude of the response. The modest but significant height increase observed here therefore fits the broader view that *B. bassiana*-plant interactions are context-dependent.

The Cumulative Growth-Promoting Effect of B. Bassiana Depended On Temperature

The clearest evidence of temperature dependence was obtained from AUPHC. Temperature ($F_{2,10} = 101.78$, $p < 0.001$), *B. bassiana* inoculation ($F_{1,10} = 23.88$, $p < 0.001$), and their interaction ($F_{2,10} = 4.99$, $p = 0.031$) were all significant. *B. bassiana* increased AUPHC by 4.9% at 22 °C and 6.5% at 28 °C, but produced virtually no advantage at 34 °C (Table 1-2).

This pattern is consistent with previous studies showing that abiotic conditions modify the plant response to *B. bassiana*. [Gana et al. \(2022\)](#) found that water availability influenced fungal effects on onion growth and physiology, while [Guo et al. \(2024\)](#) showed that endophytic *B. bassiana* altered growth, water relations, and antioxidant responses in drought-stressed tomato.

The weaker response at 34 °C is also biologically consistent with the thermal sensitivity of *B. bassiana*. [Mseddi et al. \(2022\)](#) demonstrated substantial differences among isolates in heat tolerance, conidial germination, and mycelial growth. [Mwikali et al. \(2026\)](#) reported that vegetative growth and sporulation were generally greatest at 25–30 °C and declined near 35 °C, while [Udompaisarn et al. \(2025\)](#) showed that heat exposure alters fungal germination, growth, metabolism, and virulence. Continuous exposure to 34 °C may therefore have reduced fungal establishment or physiological activity, weakening its growth-promoting effect.

Because we did not directly quantify fungal colonization, this interpretation remains hypothetical. Future studies should confirm colonization at each temperature by re-isolation, microscopy, or qPCR. Potential mechanisms for beneficial endophytic fungi include improved nutrient acquisition, phytohormonal modulation, and changes in plant metabolism ([Fite et al., 2023](#)). However, the present study did not measure them.

High Temperature Reduced Leaf Development Irrespective of Fungal Treatment

Leaf number was strongly reduced at 34 °C. Seedlings produced 10.53 and 10.85 leaves at 22 and 28 °C, respectively, but only 7.63 leaves at 34 °C, approximately 28–30% fewer. Temperature had a significant effect ($F_{2,10} = 30.42$, $p < 0.001$), whereas *B. bassiana* and the interaction were not significant (Table 1-2).

This agrees with studies showing that high temperature can reduce leaf initiation and vegetative development in onion (Moradi-Shakoorian et al., 2023). Interestingly, plants at 34 °C eventually approached the height of those at moderate temperatures but produced substantially fewer leaves. This suggests that leaf elongation and leaf initiation responded differently to heat stress. Overall, *B. bassiana* promoted cumulative height growth under moderate temperatures but did not alleviate the inhibitory effect of 34 °C on leaf production (Figure 3).

Table 1. Germination and Growth Responses of Red Onion Seedlings Treated with *Beauveria bassiana* or Sterile Water at Three Temperatures

Treatment	Germination time (days)	Plant height at 12 DAP (cm)	Number of Leaves at 12 DAP	AUPHC (cm·day)
Temperature				
22 °C	2.99±0.12 c	18.24±1.66 a	10.53±0.20 a	52.41±1.95 b
28 °C	3.44±0.04 b	18.77±4.45 a	10.85±0.22 a	55.79±2.54 a
34 °C	4.58±0.05 a	22.30±7.80 a	7.63±0.23 b	52.74±0.18 b
Inoculation				
<i>B. bassiana</i>	3.73±0.46 p	18.73±0.21	9.76±0.97 p	79.20±3.91 p
Sterile water	3.60±0.49 p	20.81±2.70	9.56±1.09 p	76.18±2.53 q
Interaction	-	-	-	-

Values are mean ± SE, n = 3 blocks

Table 2. Factorial ANOVA for Germination and Seedling Growth Parameters

Response Variable	Effect	F	p-value	Partial η^2
Mean germination time	Temperature	51.49.00	<0.001	0,632638889
	<i>B. bassiana</i>	01.01	0,235416667	0.092
	Temperature × <i>B. bassiana</i>	00.15	0,600694444	0.029
Height at 12 DAP	Temperature	0,180555556	0.059	0,3
	<i>B. bassiana</i>	0,510416667	0.006	0,375
	Temperature × <i>B. bassiana</i>	0,091666667	0,159027778	0,177777778
Leaves at 12 DAP	Temperature	30.42.00	<0.001	0,596527778
	<i>B. bassiana</i>	00.20	0,460416667	0.020
	Temperature × <i>B. bassiana</i>	00.58	0,4	0,072222222
Plant-height AUC	Temperature	101.78	<0.001	0,661805556
	<i>B. bassiana</i>	1,019444444	<0.001	0,489583333

Temperature $\times$ *B.*
bassiana

0,235416667

0.031

0,346527778

For temperature and interaction, df = 2,10; for *B. bassiana*, df = 1,10

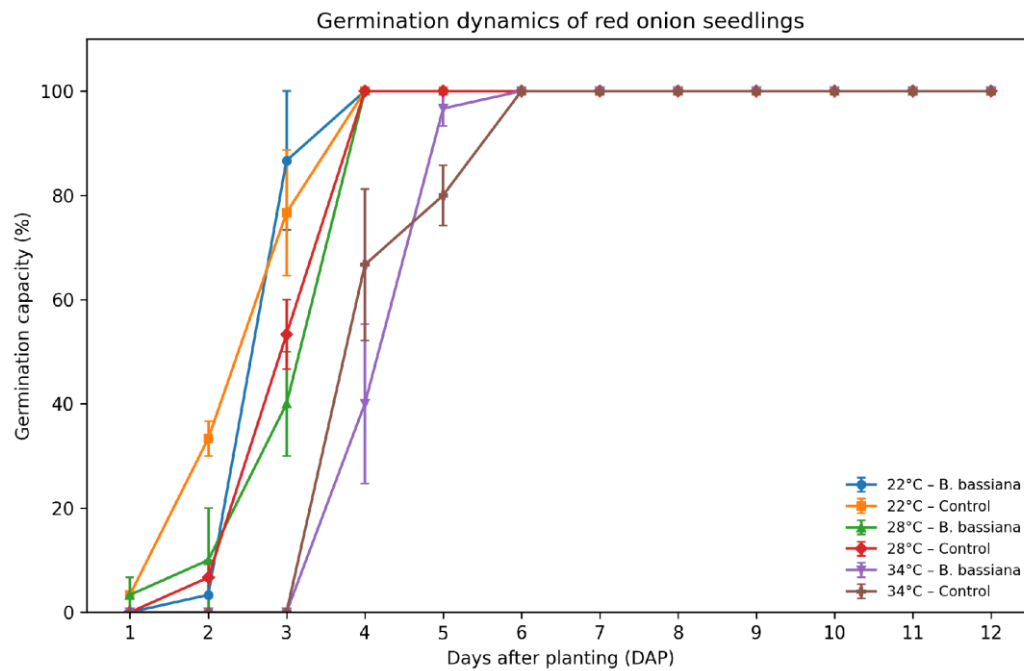


Figure 1. Germination Dynamics of Red Onion Bulbs Treated with *Beauveria Bassiana* or Sterile Water and Maintained at 22, 28, or 34 °C. Values Represent Means $\pm$ SE of three-block replication

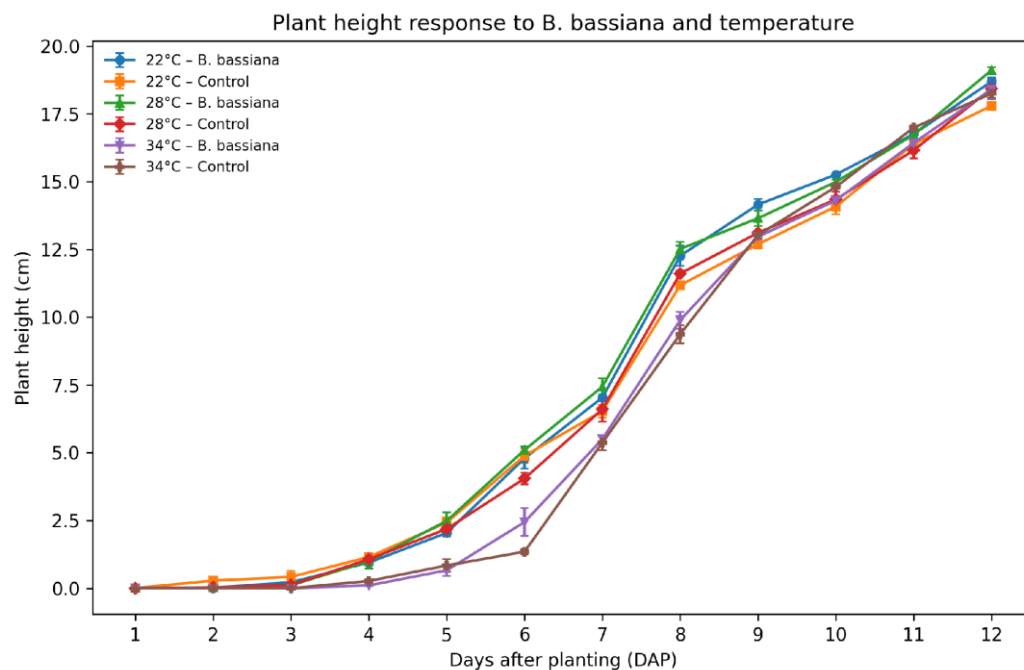


Figure 2. Plant-Height Development of Red Onion Seedlings Treated with *Beauveria Bassiana* Or Sterile Water at 22, 28, and 34 °C During the First 12 Days After Planting. Values Represent Means $\pm$ SE of three-block replication.

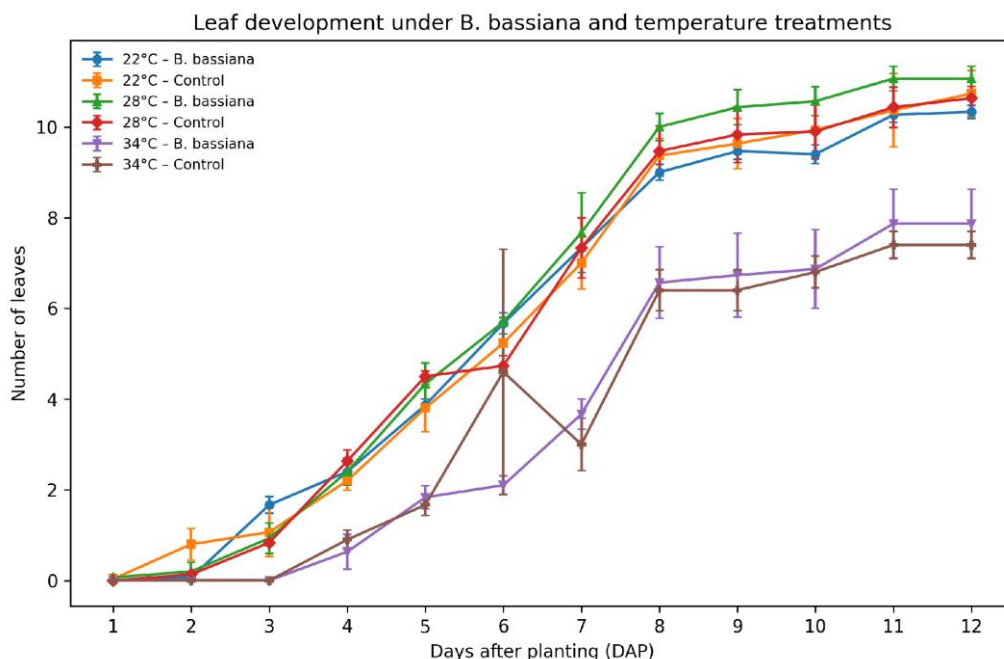


Figure 3. Number of Leaves of Red Onion Seedlings Treated with *Beauveria Bassiana* or Sterile Water at 22, 28, and 34 °C During the First 12 Days After Planting. Values Represent Means $\pm$ SE of a three-block replication

Implications for Biological Control and Climate-Resilient Crop Management

These findings are relevant to using *B. bassiana* as both a biological control agent and a plant-associated growth promoter. Environmental conditions that reduce fungal activity may also reduce plant-mediated benefits.

The loss of growth promotion at 34 °C is especially important for tropical horticulture and warming production environments, where high-temperature episodes increasingly affect crop establishment. Because endophytic and entomopathogenic fungal performance is environmentally dependent (Fite et al., 2023), selection of thermotolerant isolates may improve the reliability of *B. bassiana*-based products under hot conditions.

CONCLUSIONS

Temperature and *B. bassiana* affected different components of early red onion development. Increasing temperature from 22 to 34 °C delayed germination and reduced leaf production, although all treatments ultimately reached 100% germination. *B. bassiana* did not significantly alter germination timing or leaf number.

In contrast, *B. bassiana* promoted seedling height, and its cumulative growth benefit depended on temperature. Growth promotion was evident at 22 and 28 °C but was negligible at 34 °C. Moderate temperatures therefore favored expression of *B. bassiana*-associated growth promotion, whereas continuous high temperature diminished this benefit. Consider thermal adaptation when selecting fungal isolates for crop protection and growth-promotion applications.

LIMITATIONS & FURTHER RESEARCH

The study covered only 12 days and evaluated one *B. bassiana* isolate. Fungal colonization was not verified, so the results demonstrate effects of fungal application rather than confirmed endophytic activity. Future studies should test additional thermotolerant isolates, quantify colonization by re-isolation or molecular methods, and measure root and shoot biomass,

chlorophyll, nutrient status, and stress-related metabolites. Experiments using realistic day/night temperature cycles and longer growth periods are also needed to determine whether early responses persist into bulb development and yield.

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