Lamont et al. Fire Ecology (2024) 20:20
https://doi.org/10.1186/s42408-024-00251-5

Fire Ecology

Association for Fire Ecology

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Fire-type heat increases the germination of Cistaceae seeds in contrast to summer heat

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Abstract

Our analyses of data in Luna et al. (Fire Ecology 19:52, 2023) do not support the proposal that dormancy release of the hard seeds in 12 species of Cistaceae is a "two-step process" involving high summer temperatures followed by fire-type heat. The reverse is true: subjection to a month of daily alternating temperatures of 50/20 °C (summer heat) is more likely to induce dormancy among initially soft seeds or secondary dormancy among those softened by fire heat or reduce the ability of fire heat to soften the seeds. The need to inspect seeds for the presence of an open "water gap" following various heat treatments, and using more realistic summer temperatures in future studies, is clear.

Resumen

Nuestros análisis de datos de Luna et al. (Fire Ecology 19:52, 2023), no apoyan la propuesta de que la liberación de la dormancia de las semillas duras de 12 especies de Cistáceas es un proceso de dos pasos, que involucran temperaturas altas durante el verano seguido de un tipo de calor producido por fuego. Lo contrario es cierto: la exposición a un mes de temperaturas diarias alternas de 50/20 °C (calor de verano) es más probable que induzca dormancia entre semillas inicialmente blandas o dormancia secundaria entre aquellas ablandadas o suavizadas por el calor del fuego, o reducir la habilidad del calor del fuego para ablandar esas semillas. Resulta entonces clara la necesidad de inspeccionar las semillas para verificar la presencia de una "apertura de agua" luego de varios tratamientos de calor, y usar temperaturas de verano más realistas en estudios futuros.

Introduction

Luna and colleagues have twice examined the possibility of an interactive effect between high summer temperatures and fire on eight *Cistus* species and four *Halimium* species (Luna 2020; Luna et al. 2023). They exposed these species to 1–2 months of 12-h cycles at 50/20 °C and compared the results against dry heat at 100 °C for 10 min. All pretreatments were followed by incubation at 20 °C. In addition, Luna alternated the "summer" and fire pretreatments to see if this had any differential effect. Each time, they concluded that high summer temperatures primed ("sensitized") the seeds for maximum germination in the presence of fire in a two-step process (summer and fire heat "work together") to break physical dormancy. Here, we show that the new data are no more supportive of this proposal than the previous results: fire heat by itself is sufficient, and we comment on other limitations of the study.

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Methods

As the statistical analyses of Luna et al. (2023) did not directly assess the hypotheses that they proposed (comparisons were only made within the presence/absence of summer treatments), we graphically evaluated whether there are any differences between the presence/absence of summer treatments. Mean values and standard errors (SEs) given in Figs. 2 and 3 of Luna et al. (2023) were extracted with the help of calipers (12 species × 4 ± heat treatments × 2 ± summer treatments). The data were graphed with the control (lab conditions, i.e., 20 °C continuously, with no summer heat) on the abscissa (*X*) axis and treatment (applying summer heat, 50/20 °C) on the ordinate (*Y*) axis for each fire-heat treatment: no fire heat (H-), fire heat before summer heat (HB), fire heat treatment after summer heart (HA), and fire heat then summer then fire heat again (HBA). A diagonal placed at equal values along the axes indicates a positive summer heat effect on the upper triangle, and a negative effect on the lower triangle, and no effect along the diagonal (SEs overlapped it). We added the expected outcome from the two-step hypothesis of Luna et al. (2023) to the figures: no difference in the case of H- (as summer by itself is expected to be ineffective), enhanced germination in HA (as this is the correct sequence for operation of the two-step process: summer heat followed by fire heat), germination unaffected in HB (as the order is the reverse of that "required"), and enhanced germination in HBA (as the final treatment is in the "right" order). The same was done with the time to first (T_0) and 50% (T_{50}) germination, except that the actual means and SEs were already provided (Table 2 in Luna et al. 2023). Here, the appropriate hypotheses are that there is no time difference for H-, shorter with HA, no difference with HB, and shorter with HBA.

The graphical presentations were backed up by two formal statistical analyses: (a) species responses to the treatment were placed into three categories compared with the mean control: increase, decrease, no effect (overlapping of SEs with the diagonal) and the numbers of species in each expected from the two-step hypothesis, and the totals compared by Fisher's goodness-of-fit test to derive their *P* level, as available in http://Vassarstats.net®; (b) means were collated and submitted to a paired *t*-test and overall mean, 95% confidence interval (CI), and *P* level calculated per treatment with the same program.

Results and discussion

All 12 species showed germination up to 50% among the controls (mean ± CI = 21.6 ± 9.9%) that was reduced to < 10%, except in one species (6.7 ± 6.9%, $P = 0.0076$, Table S1), when submitted to the summer treatment (Fig. 1a). We interpret this as already soft seeds becoming hard in the presence of a month of hot, dry air (although not losing viability as now shown with the new Luna data). There are records for two Cistaceae species going from soft to hard (failing to germinate under optimal conditions) when stored under cool, dry conditions, unlike the controls left in the laboratory (Castro and Romero-García 1999; Sánchez et al. 2014). We showed earlier (Lamont et al. 2022) how summer heat implies a marked drop in relative humidity in the cabinet when there is no humidity control, as here.

The HA control with fire heat only resulted in all species germinating at > 50% (mean ± CI = 83.6 ± 8.2%), compared with one species exceeding the control, SEs of three species overlapping the diagonal, and eight species germinating less in the presence of summer heat (Fig. 1b, $P < 0.0001$ by Fisher's test, Table S2). Thus, fire heat promotes germination of all species (compared with Fig. 1a), but summer heat is highly likely to result in a reduction of the beneficial fire treatment (72.0 ± 10.4%, $P = 0.0125$, Table S1). Had summer heat been required to "sensitize" the seeds to respond to fire heat, then germination of all species should have been higher than when receiving fire heat only. We interpret the small drop in germination to some seeds becoming harder in the presence of the pretreatment and not responding to the fire-heat treatment since it was not due to viability loss (Luna et al. 2023).

Neither summer heat nor fire heat resulted in faster initial (T_0) or 50% (T_{50}) germination, as might be consistent with the hypothesis, as it was either longer or not significantly different, except for a few species among the four treatments (Fig. 2).

When the summer fire treatments were reversed (HB), germination of the controls tended to drop 10–20%, except for three species (mean ± CI = 74.9 ± 11.1%), but the fall for summer heat was greater at 20–60%, except for four species (Fig. 1c, 30.8 ± 21.8%, $P = 0.0002$, Table S1). The data used in the Fisher exact test ($P < 0.0001$) are given in Table S2. The hypothesis of no difference expected (as the sequence was the reverse of that "required") therefore was not only not supported, but summer heat also had a strong retarding effect on germination. Luna et al. (2023) provided viability details that confirm viability loss did not cause the decline. We wonder how leaving the seeds in the laboratory after fire heat could lead to softening, but giving them summer heat after fire heat not do so, as the HA experiment showed that most softened without a summer pretreatment. This supports our earlier interpretation (Lamont et al. 2022) that the seeds which did not germinate subsequent to the summer treatment had returned to dormancy (hard-seededness) rather than failed to soften as in the Luna hypothesis. There is little value in continuing to claim that such secondary dormancy is

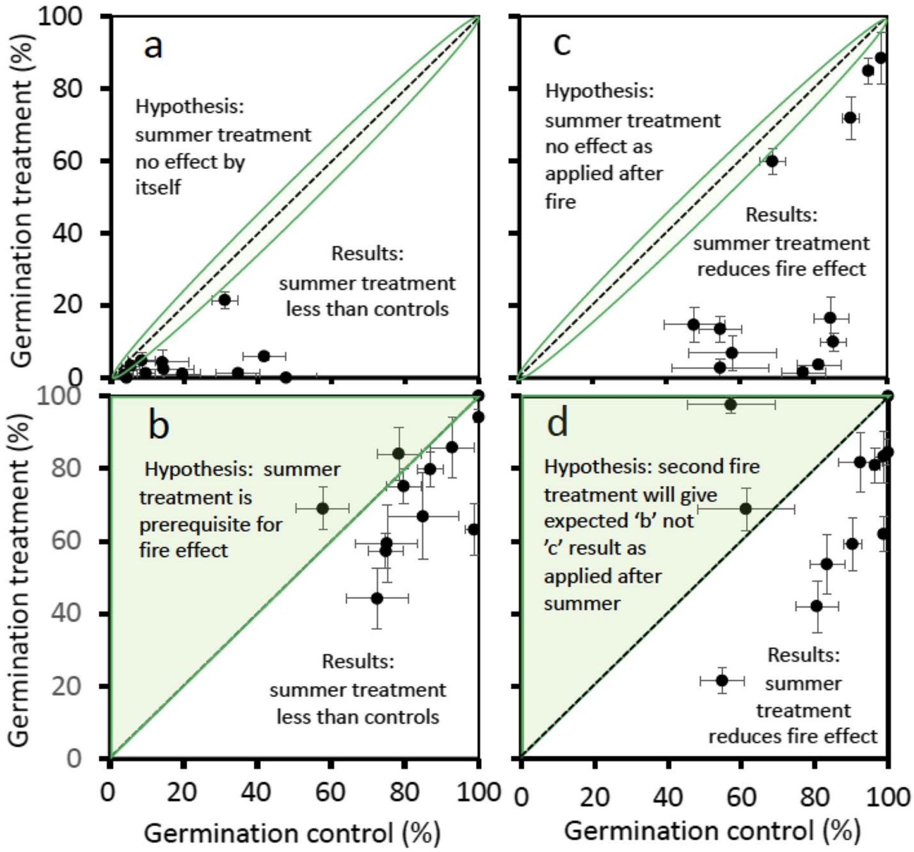

Fig. 1 Means and SEs for summer/fire-type heat treatments on 12 Cistaceae species (*Y*-axis) versus corresponding controls (*X*-axis) collated from Luna et al. (2023). **a** Summer heat treatment (H-) vs lab conditions control, **b** summer heat applied before fire heat vs lab conditions before fire heat (HA = fire heat after), **c** summer heat applied after fire heat vs after lab (HB = fire heat before), **d** fire heat applied before summer heat and again after summer treatment vs lab conditions in between (HBA). Shaded areas represent hypotheses as in Luna et al. (2023)—see the "Methods" section

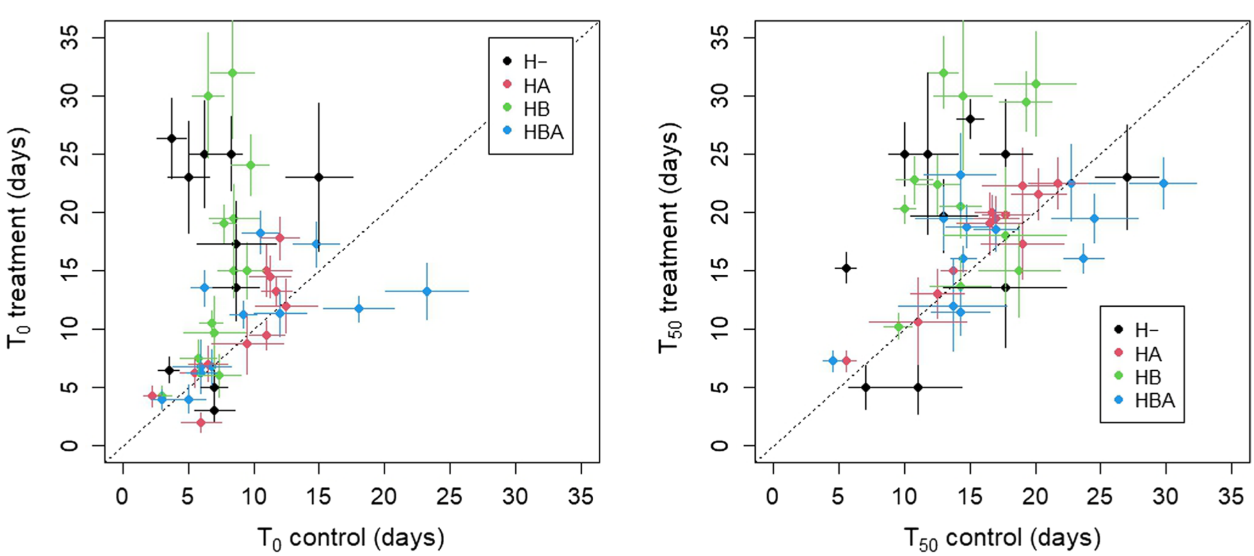

Fig. 2 Means and SEs for summer/fire-type treatments on 12 Cistaceae species (*Y*-axis) versus corresponding controls (*X*-axis). Left: number of days for first seed to germinate (T0). Right: number of days to reach 50% of final germination (T50). See Fig. 1 for meaning of acronyms

not possible among hard seeds when the contrary has been demonstrated in *Trifolium subterraneum* (Hagon and Ballard 1970). It seems quite possible to us that, as the plug is beneath (not above) the pore among Cistaceae seeds, it could be pushed back easily as the seed shrinks under the drying conditions imposed here. As we noted earlier, this issue will not be resolved until the seeds are examined using SEM (as undertaken by Gama-Arachchige et al. 2013, except that they used boiling water).

Giving two fire-type heat treatments with ambient temperature in between as control and summer heat in between as the treatment (HBA, of course, not possible in nature) should have resulted in greater germination to support the hypothesis, as the final sequence is summer then fire. However, one species germinated better, one species was unaffected, and ten germinated worse than the controls (Fig. 1d; mean ± CI = 84.5 ± 11.0%). Again, summer heat is redundant, if not inhibitory, as in the HA treatment (Fig. 1b; 69.6 ± 14.7%, $P = 0.0443$, Table S1). Therefore, both pairs of treatments confirm their 2020 study that a "two-step process" (summerfire "working together") is not required. As we showed with hard-seeded Acacias (Lamont et al. 2022), heat alone is sufficient to open the water gap and allow water to enter; there is no prior "softening" process—permeability gain is caused by opening of the water gap, and this is caused by fire-type heat (Gama-Arachchige et al. 2013).

Finally, we note the defense by Luna et al. (2023) to imposing 12 h cycles of 50/20 °C for a month as simulating typical summer conditions on Cistaceae seeds. This is literally a constant 50 °C from 7 am to 7 pm every day for 28 days for seeds beneath the soil to at least a depth of 5 mm and probably up to 25 mm from which they can emerge (Dias et al. 2019). Such high temperatures are unlikely to be met except by postfire seeds now lying in mineral soil exposed to the sun (i.e., after, not before, the fire heat treatment). Referencing previous papers that used such high temperatures does not justify using them in the current study when counter evidence exists of more likely milder temperatures (Brits 1986). They did not mention that Moreira and Pausas (2012) used a more realistic temperature regime based on local data for summer (30 days with daily cycles of 3 h at 31 °C, 4 h at 43 °C, 3 h at 33 °C, and 14 h at 18 °C) in their summer vs fire study, which included Cistaceae species. It is tempting to interpret their motives in applying such extreme levels as an attempt to get closer to simulating a fire-type treatment (Lamont and Pausas 2023). Seed burial under different field conditions is required to ensure future studies mimic what actually occurs in nature.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-024-00251-5.

Additional file 1: Table S1. Means for 12 hard-seeded Cistaceae species with controls (fire-type heat only) compared with fire-type heat (H) applied before (B) or after (A) summer heat or before and after (BA). 95% confidence intervals are also given. Expected results from hypotheses in Luna et al. (2023). *P* values refer to paired *t*-test. **Table S2.** Number of predominantly hard-seeded Cistaceae species responding to two treatments in three ways: no significant difference, less than the control, or greater than the control. Based on whether or not standard errors overlapped, as treatments were not previously compared statistically. Expected results from hypotheses in Luna et al. (2023) bracketed. *P* values for Fisher's exact test (2-tailed) also given.

Acknowledgements
None.

Authors' contributions
BBL: initiation, analysis, original drafts, editing and oversight. JGP (analysis) and GEB: further interpretation and editing.

Funding
This research was unfunded.

Availability of data and materials
As in Luna et al. (2023).

Declarations

Ethics approval and consent to participate
Does not apply.

Consent for publication
Does not apply.

Competing interests
We declare no competing interests.

Received: 22 October 2023 Accepted: 2 January 2024
Published online: 13 February 2024

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