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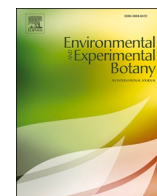
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Research paper

The recovery phase duration shapes plant responses to recurring heat stresses in winter oilseed rape (*Brassica napus* L.)L. Kougiteas^{a,*}, B. Julien^a, B. Bernay^b, Q. Dupas^a, N. Elie^{c,d}, M. Le Guedard^{e,f}, JC Avice^a, S. Brunel-Muguet^{a,*}^a Normandie Université, UNICAEN, INRAE, UMR 950 Ecophysiologie Végétale, Agronomie et Nutritions N, C, S, SFR Normandie Végétal (FED 4277), Esplanade de la Paix, CS14032, Caen Cedex 5, 14032, France^b Université de Caen Normandie, US EMERode, Plateforme Proteogen, Caen F-14000, France^c Normandie Univ, UNICAEN, Federative Structure 4207 "Normandie Oncologie", Service Unit PLATON, Virtual'His platform, Caen, France^d Normandie Univ, UNICAEN, Service Unit EMERODE, Centre de Microscopie Appliquée à la Biologie, CMABio3, Caen, France^e Univ. Bordeaux, CNRS, UMR 5200 Laboratoire de Biogenèse Membranaire (LBM), 71, Avenue Edouard Bourlaux, Villenave d'Ornon, Cedex 33883, France^f LEB Aquitaine Transfert-ADERA, 71, Avenue Edouard, Villenave d'Ornon, Bourlaux 33883, France

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ABSTRACT

The accelerating pace of climate change increases heatwave frequency, challenging crop acclimation. A greenhouse experiment in oilseed rape investigated how prior heat exposure influences seed yield and quality after an intense heat stress (HS). Three sequences of two heat events were tested, differing in recovery duration. We hypothesized that the interval between stresses would determine the priming effect of an initial mild stress (early, intermediate, late) on subsequent HS. Results showed that yield components were not much affected by the heat modalities reflecting the high plasticity of oilseed rape. However, HS-containing sequences significantly reduced seed biomass, with the extent of reduction depending on the timing of the first mild stress. Seed concentration of fatty acids and the seed storage capacity were impacted by the cumulated duration of heat days but the sequence with the intermediate recovery duration (ca. 45°Cd before the intense heat) led to mitigate HS-induced negative effects. Dynamic measurements of fluorescence-based chlorophyll parameters were shown to be able to catch the specificities of the heat sequences and to reflect the differences in final seed biomass accumulation. Overall, our study highlights the critical role of the time interval between stress events in sustaining priming effects induced by the initial stress. More broadly, this work demonstrates the fine tuning of stress priming and advances our understanding of this often-overlooked aspect of stress memory by uncovering the climate-related determinants that shape crop acclimation strategies.

1. Introduction

Heat waves negatively impact the reproductive phase of seed crops, disrupting processes such as pollen formation (Rosenberger et al., 2024), fertilization, seed filling, and maturation (Morrison and Stewart, 2002; Young et al., 2004). These disruptions reduce seed number and/or accelerate phenology, and ultimately lead to yield losses and lower seed quality (Ahmad et al., 2021; Dhaliwal and Williams, 2022; Zhao et al., 2022). Plant responses to heat stress vary depending not only on interactions with concomitant stresses such as drought thereby raising the need for a better understanding of stress interactions (Habibi et al., 2024; Sato et al., 2024; Prado et al., 2025) but also on the intensity,

duration, and timing of the heat event in relation to sensitive growth stages (Hatfield and Prueger, 2015; Wahid et al., 2007). In addition, the increasing frequency of heat waves observed in recent decades (Christidis et al., 2015; Bador et al., 2017; IPCC, 2023) is an additional feature that poses a significant threat to global food security, as crops may face repeated stress events during critical growth phases, compounding the negative effects on productivity and grain quality (Battisti and Naylor, 2009; Deryng et al., 2014; Pullens et al., 2019; Semenov and Shewry, 2011).

Oilseed rape is the second most produced oleaginous crop worldwide, with 87.44 million tons after soybean (US Department of Agriculture, 2024). Seed quality must meet standards for human

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consumption, livestock feed, and bio-products such as biofuel (Lu et al., 2011; Zheng and Liu, 2022). It includes nutritional (fatty acids (FA), protein contents and compositions) and physiological traits (germination, storage), which depend strongly on environmental conditions of the mother plants. In most heat stress-related studies, seed oil content was shown to be negatively affected by increased temperatures during seed development (Canvin, 1965), with more sudden increases having stronger negative effects (Aksouh et al., 2001). However, some studies found higher seed oil concentration when temperature rose later in the reproductive stage (Brunel-Muguet et al., 2015) or when the rise was gradual (Aksouh-Harradj et al., 2006). Conversely, FA composition was consistently altered, showing more unsaturated FAs and fewer polyunsaturated FAs regardless of heat intensity or duration (Aksouh et al., 2001; Aksouh-Harradj et al., 2006; Baux et al., 2013; Canvin, 1965; Deng and Scarth, 1998; Schulte et al., 2013), due to impaired desaturases (Cerone and Smith, 2022; Matsuda et al., 2005). Because of inverse correlation between protein and oil concentrations, high temperatures are more likely to increase protein concentration in seeds of oilseed species (Brunel-Muguet et al., 2015; Jasinski et al., 2018; Kambhampati et al., 2019; Peltonen-Sainio et al., 2011). Finally, high temperatures reduce seed storage quality, lowering desiccation tolerance, breaking dormancy, and causing pre-harvest sprouting and faster germination (Brunel-Muguet et al., 2015; Dürr et al., 2018; Malek et al., 2022; Shu et al., 2015).

Nonetheless, few studies have addressed the effects of successive heat events throughout the crop season, although plants show distinct behaviors under repeated stress compared to a single, isolated episode (Berger et al., 2025). These responses demonstrate that initial stress exposure has lasting impacts, modulating how plants handle later stresses. This illustrates stress memory, that is, when prior stress experiences influence future responses to similar or different stresses (Crisp et al., 2016; Gessler et al., 2020; Hilker et al., 2016). Advances over recent decades have deepened understanding of the molecular and physiological mechanisms behind stress memory (Charnig et al., 2023; Crisp et al., 2016; Liu et al., 2022; M. Sharma et al., 2022). These mechanisms involve specific hormonal and metabolic signatures, primed protein conformations maintained after stress (Pastor et al., 2014), and epigenetic regulations such as DNA methylation, histone modifications, and small RNAs (Auge et al., 2023; Charnig et al., 2023; Kakoulidou et al., 2021; Lämke and Bäurle, 2017; Sharma et al., 2022). Stress memory affects plant responses in various ways: negative memory amplifies adverse effects due to incomplete recovery from initial stress, while positive memory relies on priming, where the first stimulus enhances resilience to subsequent exposures, supporting acclimation to recurring stress (Liu et al., 2022). Here, the first stimulus is termed 'priming', and later ones are 'triggering' stimuli, which may differ in nature and intensity (Charnig et al., 2023). Typically, priming and triggering are separated by a recovery phase, though acclimation can also occur if the priming event gradually intensifies to match the triggering stress (Delamare et al., 2025; Mareri and Cai, 2022). Pioneering studies on systemic acquired resistance against pathogens consistently refer to priming, even when the initial infection persists as the second starts (Conrath et al., 2015). Such cases highlight the diversity of priming scenarios and the need for detailed characterization of recurring stress sequences to identify traits for priming-based plant acclimation.

Little is known about the key characteristics of the expected priming sequences so far, especially in terms of duration between the priming and the triggering events. Thermomemory is complex as it relies on multiple interconnected pathways (Balazadeh, 2022; Kourani et al., 2022), and results from a trade-off between energy-cost-effective processes to maintain thermotolerance and their reset (Bäurle, 2018; Crisp et al., 2016). Mounting evidence for heat stress memory effects throughout the plant cycle has been observed in crop species (Wang et al., 2020). Thermoprimering effects were reported in many crops such as wheat (Fan et al., 2018; Khanzada et al., 2024; Wang et al., 2014), peanut (Selvaraj et al., 2011), maize (Sinsawat et al., 2004), tomato

(Zhou et al., 2020), rice (Jagadish et al., 2010; Kushawaha et al., 2021; Shi et al., 2016). The alleviating effects of the pre-acclimation sequence were mainly observed on photosynthesis, antioxidant activities, membrane stability and when investigated, on flower/spikelet fertility and yield. In these studies, the priming stress ranged from a short (hours) to several days of mild heat stress prior to more intense heat, with or without any recovery phase and mostly at the onset of the reproductive stage, thus illustrating again multifaceted and specific thermoprimering schemes (Liu et al., 2022; Sharma et al., 2022).

In oilseed rape, pioneering studies on the effects of repeated heat stresses on seed yield and quality highlighted that most quality criteria were subjected to the specificity of the recurring stresses scenarios (Delamare et al., 2025; Magno Massuia De Almeida et al., 2021, 2023). Indeed, a prior exposure to 5-day mild heat followed by 5-day recovery did not alleviate the negative impact of 5-day heat peaks (i.e. recovery scenario (Magno Massuia De Almeida et al., 2021, 2023) on seed yield, FAs concentrations and proportions, nor on the seed storage capacity using the Abscicic Acid (ABA): Gibberellic Acid (GA) ratio as a proxy for seed dormancy (Magno Massuia De Almeida et al., 2021). Because worst effects were observed under the recurring heat stress sequence than under the heat peaks alone for most variables, the early mild stress was not priming but it had rather negative impacts on the response to the later heat peaks, which illustrates negative memory. Contrastingly, a gradual increase in temperature prior to 5-day heat peaks (gradual increase scenario, Delamare et al., 2025) was shown to reduce the negative effects of the late heat peaks on seed yield, seed oil concentration and the proportion of unsaturated FAs as well as on the ABA: GA ratio (Delamare et al., 2025). The prior gradual increase in temperature had a significant priming effect, thereby reducing the negative impacts of the late heat peaks. These observations raised the question of the duration of the recovery phase as key in the maintenance or resetting of priming effect induced by the early mild stress. Furthermore, these effects described at the whole plant scale were mainly due to specific cohorts of seeds i.e. filling seeds during or maturing seeds during the heat sequence for the recovery (Magno Massuia De Almeida et al., 2021, 2023) or gradual increase protocol (Delamare et al., 2025) respectively, which also pointed out an additional layer of complexity for the analyses of recurring stresses in crop species with indeterminate growth and as a result, the need to examine the observed effects in relation with seed age when exposed to the stress.

Altogether, these exploring studies allow recurring heat stress sequences to be refined in the perspective to better identify and possibly set up thresholds in terms of heat stress memory duration in oilseed rape. Following these observations, we designed an experiment to test the effects of the duration of the recovery phase in between the expected 'priming' stimulus and 'triggering' stimulus. We quantified their effects on seed yield components, seed nutritional and physiological quality criteria at the whole plant and the cohort levels in order to analyze these effects according to the age of seeds. Our leading questions were the following: (i) Are the effects of single and recurring stress sequences similar on the different seed quality criteria? (ii) To what extent does the duration of the recovery phase between the two heat events determine the effects of the second (intense) heat event? (iii) Are photosynthesis-related parameters impacted throughout the different heat stress sequences and can they explain final performances? We expected to provide forward thinking knowledge to assist growers and breeders in the identification of thermo-sensitization protocols.

2. Material and methods

2.1. Plant cultivation conditions and recurring heat stress modalities

The experiment was conducted in the greenhouse of the University of Caen (49.18, −0.35). On the 13th October 2023 seeds of *Brassica napus*, cv. Aviso, were sown in vermiculite in a 24-cell seed tray, and placed into dark for 5 days. Afterwards, seedlings were exposed to 16 h day

($19.9 \pm 2.3^\circ\text{C}$) and 8 h night ($15.3 \pm 1.2^\circ\text{C}$) provided with 25 % Hoagland solution. After one month, seedlings were transplanted into a mix of perlite and vermiculite (2:1 v/v) in 2 L pots while irrigated with 25 % Hoagland solution [$1.25 \text{ mM Ca}(\text{NO}_3)_2 \cdot 4 \text{ H}_2\text{O}$, 1.25 mM KNO_3 , $0.25 \text{ mM KH}_2\text{PO}_4$, 0.5 mM MgSO_4 , $0.2 \text{ mM Fe-Na EDTA}$, $14 \text{ }\mu\text{M H}_3\text{BO}_3$, $5 \text{ }\mu\text{M MnSO}_4$, $3 \text{ }\mu\text{M ZnSO}_4$, $0.7 \text{ }\mu\text{M CuSO}_4$, $0.7 \text{ }\mu\text{M (NH}_4)_6\text{Mo}_7\text{O}_{24}$, $0.1 \text{ }\mu\text{M CoCl}_2$]. At 56 days after sowing, plants were vernalized for 12 weeks ($5.97 \pm 1.06^\circ\text{C}$) in a cold chamber (standard model, Froid & Mesures, Beaucoz , France), under artificial light (10 h day/ 14 h night, average density flux photosynthetic photon (DFPP) $96.7 \pm 1.8 \mu\text{mol/m}^2\text{s}$) and they were supplied with 25 % Hoagland deficient in nitrogen (N) and sulphur (S) [$0.25 \text{ mM KH}_2\text{PO}_4$, 1.25 mM CaCO_3 , 1.25 mM KCl , $0.5 \text{ mM MgCl}_2 \cdot 6 \text{ H}_2\text{O}$, $0.2 \text{ mM Fe-Na EDTA}$, $4 \times 10^{-4} \text{ mM NiCl}_2 \cdot 6 \text{ H}_2\text{O}$, $14 \text{ }\mu\text{M H}_3\text{BO}_3$, $5 \text{ }\mu\text{M MnSO}_4 \cdot \text{H}_2\text{O}$, $3 \text{ }\mu\text{M ZnSO}_4 \cdot 7 \text{ H}_2\text{O}$, $0.7 \text{ }\mu\text{M CuSO}_4 \cdot 5 \text{ H}_2\text{O}$, $0.7 \text{ }\mu\text{M (NH}_4)_6\text{Mo}_7\text{O}_{24}$, $0.1 \text{ }\mu\text{M CoCl}_2$], the latter was provided to the plants until the end of cultivation. Subsequently, the plants were

conveyed back to the greenhouse-without additional light-at $18.4 \pm 2.8^\circ\text{C}$ (day) and $15.6 \pm 0.7^\circ\text{C}$ (night). The plants were manually supplied with N, twice at the end of vernalization and stem elongation (at rates 100 kg N/ha and 50 kg N/ha respectively) and S, once at the end of the vernalization (at rate of $75 \text{ kg SO}_3/\text{ha}$) to follow the conventional recommendations for field-grown oilseed rape plants. In addition, *Brassica napus* is a species which presents a peculiar indeterminate flowering meaning; flowers, filling and maturing pods co-occur during the reproductive phase. Therefore, the day before applying the heat modalities, three cohorts (lower, intermediate, and upper) of reproductive organs were identified and labelled on each plant in order to consider their respective age at stress exposure. The lowest cohort contained fully developed pods (Pods $_{\geq 5 \text{ cm}}$, with seeds that were maturing), the intermediate contained shorter pods (Pods $_{< 5 \text{ cm}}$ with seeds that were filling), and the upper cohort contained flowers (Pods $_{\text{flowers}}$).

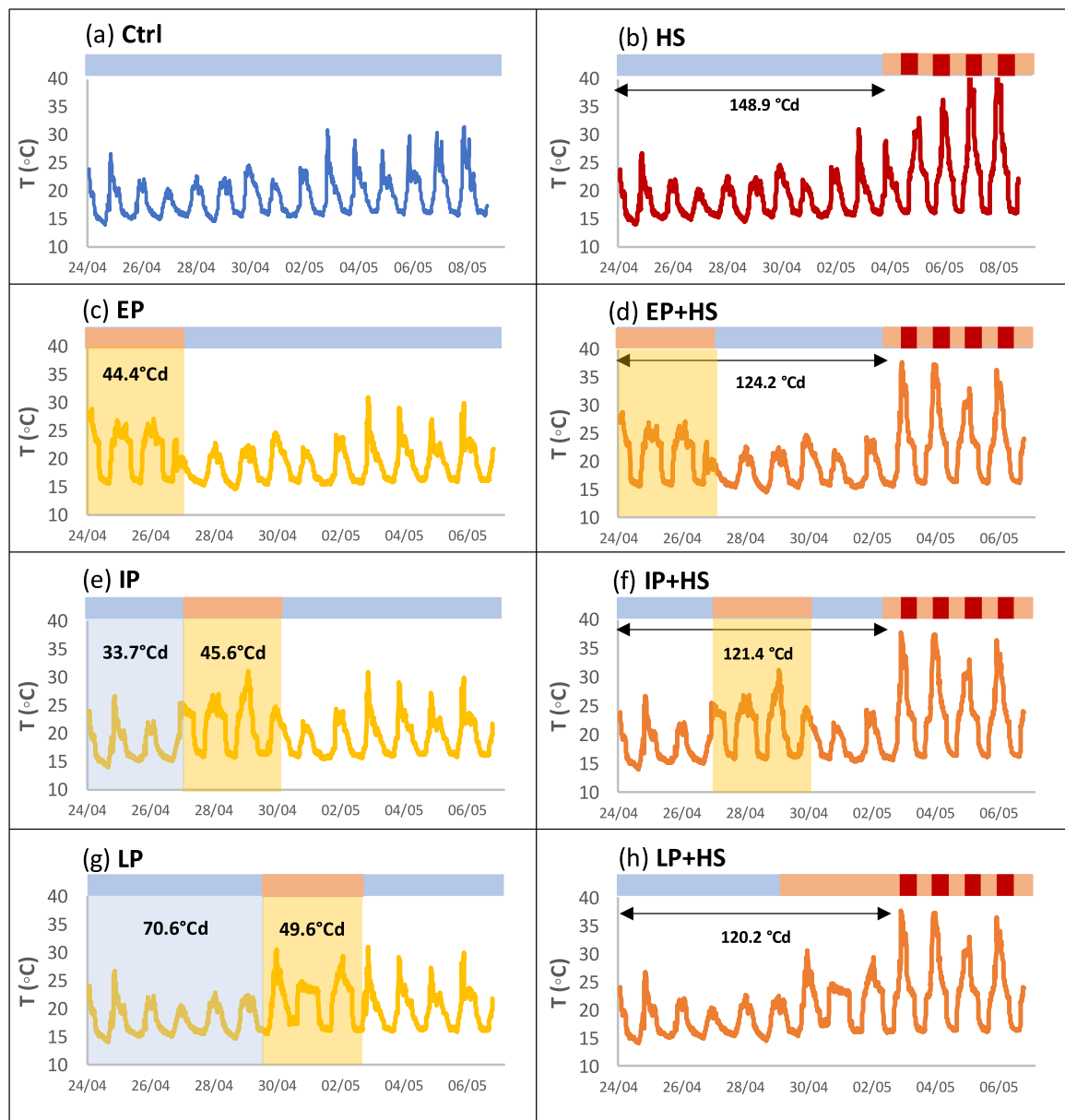


Fig. 1. Temperature recordings of the eight temperature modalities (including Control) over 15 full days (from 24th April at 4 pm until 9th May at 8 pm). The duration of the pre-stress sequences (period prior to the intense heat stress from the start of the heat treatment) lasted 124.2°Cd , 121.4°Cd and 120.2°Cd for EP+HS, IP+HS and LP+HS, respectively. Each mild heat event lasted 44.4°Cd , 45.6°Cd and 49.6°Cd for EP, IP and LP respectively. The recovery period between the mild warming and the intense heat stress lasted 79.7°Cd and 42.1°Cd for EP+HS and IP+HS respectively.

At stage GS72 (i.e. when 20 % of the pods were fully developed, (Lancashire et al., 1991)), the plants ($n = 4$) were exposed to different thermal schemes designed to test the effects of different recovery period (RP) duration between one mild warming event (EP, IP or LP) and one intense heat stress (HS). In order to avoid any plant age effects when exposed to HS, the pre-stress sequence (mild warming event followed by the recovery phase) was designed in a way that the duration - prior to HS from the start of the heat experiment at GS72 - calculated in thermal time (base temperature 5°C (Morrison et al., 1989)) was the same for each modality (Fig. 1). These durations ranged from 120.2 to 124.2°Cd according to the two heat-event modalities (i.e. EP+HS, IP+HS and LP+HS) because of the temperature variability under the natural conditions (Fig. 1). Therefore, eight thermal schemes were tested with the following characteristics: (i) the control modality (Fig. 1a) consisted in the natural thermoperiod for 10 days at 20.20°C/16.29°C (d/n), (ii) the intense heat stress (HS, Fig. 1b) consisted of four days at 26.04°C/17.96°C (d/n) with daily heat peaks at 32.41°C from 11 am to 4 pm, (iii) three modalities of moderate warming (ca. 50°Cd) without later intense stress (i.e. single heat event-modalities): early priming (EP, Fig. 1c) for 44°Cd at 23.16°C/ 17.68°C (day/night), intermediate priming (IP, Fig. 1e) for 45°Cd at 23.34°C/ 17.65°C (day/night) and late priming (LP, Fig. 1g) 49°Cd at 23.42°C/17.47°C (day/night) and (iv) three sequences of moderate warming followed by an intense stress: early priming and heat stress (EP+HS, Fig. 1d) [EP for 44°Cd at 23.16°C/17.68°C (day/night) followed by RP for 79.7°Cd at 19.34°C/16.23°C (day/night)], intermediate priming and heat stress (IP+HS, Fig. 1f) [natural thermoperiod for 44°Cd at 18.78°C/15.42°C (d/n), IP for 45°Cd at 23.34°C/17.65°C (day/night), RP for 42°Cd at 19.74°C/16.34°C (day/night)], and late priming and heat stress (LP+HS, Fig. 1h) [natural thermoperiod for 71°Cd at 18.81°C/15.79°C (day/night), LP for 49.6°Cd at 23.42°C/17.47°C (day/night)]. Both pre-stress sequences and intense heat stress were applied in the greenhouse, in a separate unit from the natural condition (control plants). Sentence about adjustment of water to avoid water stress in the heat unit. Temperature and photosynthetically active radiation (PARI) (Table SD1) were recorded every ten minutes using the aramet4 sensor and Aranet PAR sensor respectively (SAF Tehnika JSC, Latvia). Moreover, the plants in the natural condition unit were rotated regularly in order to avoid any differences due to radiation gradient. From the day of sowing until the final harvest of the cultivation, the relative humidity in the greenhouse, in both control and heat units, ranged from 48 % to 60 %.

2.2. Characterization of seed yield and its components

At the final harvest when the plants ($n = 4$) reached the full maturity stage, the seeds from each cohort were weighed in order to estimate the seed yield at the cohort, and whole plant levels. Afterwards, for each cohort, the seeds were pictured to be scored using image analyses (ImageJ, (Schindelin et al., 2012)) in order to estimate the seed number and the thousand seeds weight (TSW) at both the cohort and whole plant levels.

2.3. Analyses of seed storage compounds in mature seeds

For each plant ($n = 3$), seeds from each cohort were oven-dried at 50°C and ground with the use of mortar and pestle. Afterwards, their concentrations in FAs, soluble sugars (SS), polyphenols, as well as in nitrogen (N), and carbon (C) were analyzed at the cohort level.

2.3.1. Seed fatty acids concentrations

Oil content and FA profiles (C16:0, C16:1, C17:0, C18:0, C18:1, C18:2, C18:3, C20:0, C20:1, C22:0, C22:1) were quantified as described in Delamare et al. (2025). Approximately 15 mg of ground seeds-per plant and per cohort- was suspended in 1 mL of methanol/toluene/H₂SO₄ solution (100:20:2.5; v/v) containing C17:0 as

internal standard (25 µg mL⁻¹), remaining 1 h at 80°C for trans-methylation. After cooling, 750 µL of hexane and 1.5 mL of water were added, and the hexane phase containing the resulting fatty acid methyl esters (FAMES) was recovered for gas chromatography analysis combined with flame ionization detection (GC-FID). The FAMES (1 µL) were injected into an Agilent 7890 A gas chromatograph equipped with a DB-WAX column (15 m x 1 µm, 0.53 mm, Agilent). FAMES were identified by comparing their retention times with those of commercial standards (Sigma, St. Louis, MO, USA), and the amount of each fatty acid was calculated from the peak area quantified using ChemStation (Agilent).

2.3.2. Soluble sugars concentrations

About 25 mg ground seeds were used for the extraction of soluble sugars. After adding 500 µL of ultrapure water, the samples were vortexed, water-bathed at 80°C for 15 min and then centrifuged at 13000 rpm for 3 min. For each sample, the supernatant was collected into a 15 mL Falcon polypropylene tube. The latter process was repeated twice, with a bath water at 60°C. Each time, the supernatant was collected and pooled with the previous one(s) in the 15 mL Falcon. Then, the pooled supernatants were lyophilized with an initial volume of 1.5 mL of ultrapure water, and re-concentrated at 500 µL. The purification of the samples was performed with the use of a Mobicol mini-column (Mobitec, Göttingen, Germany) with glass cotton. Subsequently, 250 µL of a cation exchange resin (Dowex 50 W X8-400, ref 217514, Sigma, Saint-Louis, MO, USA) in the form of H⁺, 80 µL of PVPP (polyvinylpyrrolidone, ref. 77627, Sigma), and 150 µL of an anion exchange resin (Dowex 1 x8, ref. 44340, Sigma) in highly basic form were added successively. Three successive centrifugations at 300 rpm for 1 min, 1000 rpm for 1 min and 10000 rpm for 2 min were performed with the sample on the mini-column. Glucose, fructose, sucrose, raffinose, and stachyose were then quantified as described in (Magno Mas-suia De Almeida et al., 2021).

2.3.3. Phenolic compounds concentrations

For the determination of phenolic concentrations, the same extracts following soluble sugars extractions were used. The quantification was performed by spectrophotometry with the Folin-Ciocalteu method, as described by (Moreira et al., 2020).

2.3.4. Nitrogen and Carbon concentrations in matured seeds

Nitrogen (N) and Carbon (C) contents were quantified in seeds of individual plants ($n = 3$). About 2.5 mg to 6 mg of ground material (according to the plant tissue) were weighted and placed into tin micro-capsules for spectrometry analysis. The analyses were performed using an Isoprime precisiON (Elementar, Germany) coupled to a vario ISO TOPE select (Elementar, Germany).

2.4. Pre-harvest sprouted seeds

Pre-harvest sprouted seeds were scored after heat peak (Fig. 1) on four plants ($n = 4$) per modality. The seeds were manually separated from the pods to score the number of preharvest sprouted seeds. The procedure was performed only on Pods_{≥5 cm} and Pods_{<5 cm} as the seeds from Pods_{Flowers} were too small to detect any radicle with confidence. Statistical analyses have been performed at the cohort (Supplementary Table SD3) and whole plant levels (Table 3).

2.5. Dynamic measurements of photosynthetic performances

Non-invasive chlorophyll fluorescence-based sensor (Pocket PEA (Plant Efficiency Analyzer), Hansatech Instruments LTD) was used to measure the dynamics of parameters that reflect the efficiency of photosynthesis performance under the heat modalities. In order to follow the dynamics on the same plants, these measurements were performed on another set of plants that were grown in the same units

and underwent similar thermo-photoperiods and nutritional conditions as the ones used for the destructive measurements. The parameters of photosynthesis performance derive from the fast induction of chlorophyll fluorescence after a dark period adaptation of leaf (JIP-test; [Stirbet and Govindjee, 2011](#); [Strasser and Strasser, 1995](#)), and were shown to distinguish genotypic differences, phenological stage effects, and differences in stress event intensity and recurrence in several species ([Ripoll et al., 2016](#), [Zhou et al., 2015](#), [Sharma et al., 2015](#); [Medyouni et al., 2021](#)). Different tests were carried out in order to obtain accurate and reproducible measurements of chlorophyll fluorescence parameters related to photosynthesis performance of oilseed rape leaves. Thus, the optimal duration of dark adaptation was determined after several tests (at 10, 15, 20 and 25 min) and the optimal light intensity was fixed after measurements of chlorophyll fluorescence with various levels of light intensity (between 1000 and 3500 μmol photosynthetically active radiation $\text{m}^{-2} \text{s}^{-1}$). Based on this calibration, chlorophyll fluorescence parameters were measured after 15 min of dark adaptation with the leaf-clip portable Pocket PEA and the fluorescence signal has been collected in red actinic light (peak wavelength of 627 nm) after exposure for 1 s at the maximum light intensity of 3500 μmol photosynthetically active radiation $\text{m}^{-2} \text{s}^{-1}$. Based on the fluorescence values observed for F0 (initial chlorophyll fluorescence), Fm (maximal chlorophyll fluorescence) and Fv (variable fluorescence ($F_v = F_m - F_0$)), the photosynthetic activity was followed using (i) the ratio F_v/F_0 , corresponding to maximum quantum yield of primary photochemistry (ii) the ratio F_v/F_m , corresponding to the maximum photochemical efficiency of photosystem II (PSII) that is widely considered to be a sensitive indicator of plant photosynthetic performance; and (iii) Sm, normalized Area (above the fluorescence rise between F0 and Fm) which measures the energy needed to close all reaction centers of PSII. Each measurement ($n = 4$ plants) was carried out on the lowest mature leaf (oldest one) that showed no injury and/or no sign of senescence.

2.6. Statistical analyses

All statistical analyses were performed using R software (version 4.4.1, [R Core Team \(2024\)](#)). Residuals were tested for their normality

(Shapiro-Wilk test), and all the data for their homogeneity (Bartlett test, and Brown-Forsythe test). For all variables that meet the assumption of normality and homogeneity standard ANOVA was performed in order to assess the temperature effect. Afterwards, the post-hoc test of least significant difference (LSD test) was performed to compare the different treatments. If the assumption of normality was violated, Welch's ANOVA was performed to evaluate the temperature effect, followed by Games-Howell nonparametric post hoc test. In case both assumptions, normality and homogeneity, were violated, Kruskal-Wallis test was performed to examine the temperature effect, followed by Dunn's nonparametric post hoc test. All the variables are presented as the mean and standard deviation values for each heat modality.

3. Results

The results below described the values acquired at the whole plant and at cohort levels ($\text{Pods}_{\geq 5 \text{ cm}}$, $\text{Pods}_{< 5 \text{ cm}}$, $\text{Pods}_{\text{flowers}}$). The latter are displayed in Tables of the [Supplemental Data \(SD\)](#).

3.1. Seed yield components

Seed yield and its components were measured at the whole plant (total) and cohort levels ([Table 1](#)). At the whole plant scale, the total yield ranged from 4.6 to 6.2 g. plant^{-1} (EP+HS and EP respectively) while the TSW varied from 2.4 to 3 g (HS and EP, LP respectively). The total number of seeds per plant was estimated from 1762 (Control) up to 2170 (HS). No significant global effect of the heat modality was observed on any of the aforementioned yield components. However, there were different rankings among the modalities for TSW which tended to indicate that HS was significantly negative (2.4 g vs 2.8 g for Control), and that the one event-modalities (EP, LP) were slightly positive compared to the two-event modalities (EP+HS, LP+HS) and HS treatment ([Table 1](#)).

At the cohort level, no significant effect of the heat modalities was observed for any of the seed yield components except for the yield of $\text{Pods}_{\text{flowers}}$ although different rankings among modalities were observed according to the variable and the cohort ([Table 1](#)). For the highest cohort

Table 1

Mean values ($\pm$ SD, $n = 4$) of seed yield, seed number (Seed nb) and TSW at the whole plant scale and for the three cohorts ($\text{Pods}_{\text{flowers}}$, $\text{Pods}_{< 5 \text{ cm}}$ and $\text{Pods}_{\geq 5 \text{ cm}}$) for each heat modality.

Heat modality	Seeds from the whole plant			Seeds from $\text{Pods}_{\text{flowers}}$			Seeds from $\text{Pods}_{< 5 \text{ cm}}$			Seeds from $\text{Pods}_{\geq 5 \text{ cm}}$		
	Yield (g. plant^{-1})	Seed nb (plant $^{-1}$)	TSW (g)	Yield (g. plant^{-1})	Seed nb (plant $^{-1}$)	TSW (g)	Yield (g. plant^{-1})	Seed nb (plant $^{-1}$)	TSW (g)	Yield (g. plant^{-1})	Seed nb (plant $^{-1}$)	TSW (g)
Control	4.9 ± 1.1 ns	1762 ± 305 ns	2.8 $\pm 0.2^{ab}$	0.2 $\pm 0.2^c$	72 $\pm$ 81 ^b	2.8 ± 0.6 ns	3.0 ± 0.8 ns	1122 ± 282 ns	2.7 $\pm 0.2^{abc}$	1.7 ± 0.6 ns	568 ± 140 ns	3.0 ± 0.4 ns
EP	6.2 ± 0.4 ns	2109 ± 144 ns	3.0 $\pm 0.1^a$	0.4 $\pm 0.4^{bc}$	169 $\pm 151^{ab}$	2.5 ± 0.5 ns	3.7 ± 0.6 ns	1257 ± 263 ns	3.0 $\pm 0.1^{ab}$	2.1 ± 0.7 ns	683 ± 234 ns	3.1 ± 0.2 ns
IP	5.2 ± 1.5 ns	1851 ± 290 ns	2.8 $\pm 0.5^{ab}$	0.8 $\pm 0.5^{ab}$	343 $\pm$ 248 ^a	2.6 ± 0.4 ns	3.1 ± 1.6 ns	1086 ± 413 ns	2.8 $\pm 0.5^{abc}$	1.3 ± 0.2 ns	421 ± 48 ns	3.0 ± 0.3 ns
LP	5.2 ± 1.0 ns	1773 ± 245 ns	3.0 $\pm 0.4^a$	1.1 $\pm 0.5^a$	409 $\pm$ 162 ^a	2.6 ± 0.3 ns	2.9 ± 0.7 ns	964 ± 305 ns	3.1 $\pm 0.4^a$	1.2 ± 0.4 ns	400 ± 94 ns	3.1 ± 0.4 ns
EP+HS	4.6 ± 1.1 ns	1781 ± 252 ns	2.6 $\pm 0.4^{ab}$	0.2 $\pm 0.2^c$	92 $\pm$ 81 ^b	1.9 ± 1.3 ns	2.9 ± 0.4 ns	1163 ± 81 ns	2.5 $\pm 0.4^{bc}$	1.5 ± 0.7 ns	525 ± 234 ns	2.7 ± 0.4 ns
IP+HS	5.3 ± 1.6 ns	1840 ± 333 ns	2.8 $\pm 0.4^{ab}$	0.1 $\pm 0.1^c$	45 $\pm$ 34 ^b	2.8 ± 0.3 ns	3.4 ± 1.0 ns	1201 ± 190 ns	2.8 $\pm 0.4^{abc}$	1.8 ± 1.0 ns	594 ± 321 ns	3.0 ± 0.3 ns
LP+HS	5.0 ± 0.1 ns	1856 ± 129 ns	2.7 $\pm 0.2^{ab}$	0.7 $\pm 0.6^{abc}$	246 $\pm 214^{ab}$	2.6 ± 0.2 ns	3.5 ± 0.6 ns	1280 ± 338 ns	2.8 $\pm 0.3^{abc}$	1.1 ± 0.1 ns	382 $\pm$ 3 ^{ns}	2.7 ± 0.1 ns
HS	5.2 ± 2.0 ns	2170 ± 555 ns	2.4 $\pm 0.4^b$	0.5 $\pm 0.4^{abc}$	236 $\pm 233^{ab}$	2.6 ± 1.0 ns	3.2 ± 1.2 ns	1389 ± 409 ns	2.3 $\pm 0.3^c$	1.5 ± 1.0 ns	545 ± 275 ns	2.7 ± 0.4 ns
Temperature Effect	0.762 ns	0.448 ns	0.372 ns	0.0356*	0.0589 ns	0.637 ns	0.922 ns	0.697 ns	0.187 ns	0.34 ns	0.285 ns	0.703 ns

The heat modalities were: Control, Early Priming (EP), Intermediate Priming (IP), Late Priming (LP), Early Priming and Heat Stress (EP+HS), Intermediate Priming and Heat Stress (IP+HS), Late Priming and Heat Stress (LP+HS), single Heat Stress (HS).

For a given variable, the effects of the modalities were tested with a one-way ANOVA. Letters or ns when not significant indicate the ranking among the heat modalities following a mean comparison test (LSD multiple comparisons test). *P*-value and level of significance are given for modality effects. Levels of significance: ns non-significant, $p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$. *P*-value = 0.05.

of pods ($\text{Pods}_{\text{flowers}}$), significant effects were observed on yield ($p < 0.05$, Table 1). All the modalities displayed higher values than the Control (up to ca. 5.5 times higher for LP), except for the two-event modalities with recovery (EP+HS and IP+HS) (Table 1). This was explained by the number of seeds which displayed similar rankings to yield. These observations indicated that whether mild (EP, IP and LP) or intense (HS), above-control temperatures had a positive effect when applied early at GS72 (651°Cd , 695°Cd , 740.6°Cd after vernalization for EP, IP and LP respectively) or later (790.2°Cd after vernalization for HS). In addition, the presence of a recovery period between the mild and intense heat events (EP+HS, IP+HS) have led to cancelling the positive effects of both individual events of this cohort. For the intermediate cohort ($\text{Pods}_{<5\text{ cm}}$), only TSW displayed different rankings among the modalities with extreme values observed for EP and HS (Table 1). The negative effect of HS was alleviated in the two-event modalities with (EP+HS, IP+HS) or without recovery (LP+HS) as a consequence of the positive effects of the mild stress alone (EP, IP and LP). Eventually, for the lowest cohort of pods ($\text{Pods}_{>5\text{ cm}}$), no rankings were observed as expected because the number of seeds and their weight were already set prior to the heat sequences (i.e. the $\text{Pods}_{>5\text{ cm}}$ belonged to the 20 % of pods that reached their final size at GS72). Overall, the effects of the heat modalities were rather positive - except under the late intense heat peaks (HS) on seed yield components at the cohort levels and thus at the whole plant scale. However, these positive effects tended to be tempered in the two-event modalities which displayed a recovery phase as observed in the $\text{Pods}_{\text{flowers}}$ and $\text{Pods}_{<5\text{ cm}}$ cohorts.

3.2. Nutritional seed quality criteria

3.2.1. Carbon and Nitrogen concentrations

At the whole plant scale, seed C concentrations ranged from 54.2 % to 57.7 % for EP+HS and EP respectively. The heat modality effects were significant ($p < 0.01$, Table 2) with slightly higher values in seeds from mild single-event modalities (+3 %, +0.5 % and +0.9 % for EP, IP, and LP compared to the Control) and slight lower values in seeds from the two event-modalities (-3.2 %, -1.8 % and -1.25 % for EP+HS, IP+HS and LP+HS compared to the Control). By contrast, no effect of HS was observed. At the cohort level, the heat modality effect was significant only in seeds from $\text{Pods}_{<5\text{ cm}}$ ($p < 0.01$, Table SD2) with increased C concentrations under the mild single-events and decreased C concentrations under the two-events modalities. Despite non-significant heat modality effects, similar rankings were observed for $\text{Pods}_{>5\text{ cm}}$ with higher values under EP, IP and LP, lower values under the two-event modalities. These rankings were also observed in the intermediate cohort but to a lower extent. Altogether, these observations tended to indicate that the duration of heat -whether mild or intense - accounted for the negative effects of C concentrations in the two event-modalities

with no benefits of the prior mild exposure (EP, IP and LP).

Considering the seed N concentration, no heat modalities effects were observed at the whole plant scale, but slight differences amongst the modalities as revealed by the multiple comparison tests (Table 2). While the N concentration tended to decrease under the mild single-events (EP, IP and LP), it increased under the modalities with HS, except for IP+HS. Interestingly, for EP+HS and LP+HS, the negative effects of EP and LP were likely to offset the positive effects of HS alone whereas this is not observed under the IP+HS modality for which the value was similar to the Control. At the cohort level, the heat modality effect was not significant but different modality rankings were observed in the lowest cohorts of pods ($\text{Pods}_{<5\text{ cm}}$ and $\text{Pods}_{>5\text{ cm}}$, Table SD2). These rankings reflect the observations at the whole plant scale with lower values under the mild single-events (EP, IP and LP) and higher values under HS and to some extent under the two-event modalities. Overall, the late intense stress induced higher seed N concentration by contrast with mild prior exposures (EP, IP and LP). The timing of the mild stress mattered since there were no differences to the Control under IP or IP+HS by contrast with the two other event-combinations.

3.2.2. Fatty acids concentrations

The concentrations of the fatty acids (FAs), saturated fatty acids (SFAs), mono- (MUFAs) and poly-unsaturated fatty acids (PUFAs), and the $\omega 6:\omega 3$ ratio were displayed at the whole plant (Table 2), and cohort levels (Table SD2). Heat modalities resulted in a significant effect on the FAs concentration ($p < 0.05$) as a consequence of changes in the unsaturated FAs (especially PUFAs) concentration only. The concentration of FAs ranged from 25.9 % for EP+HS to 34.8 % for EP (compared to 30.7 % for the Control), which also displayed the extreme values for the concentrations of MUFA and PUFAs (Table 2). Interestingly, EP and LP alone had a slight positive effect of FAs, MUFAs and PUFAs compared to the control (+13.4, +15.2, +10.6 % respectively, for EP and +10.1, +9.6 and +10.6 % respectively, for LP) whereas IP led to reduced concentrations of FAs, MUFAs and PUFAs compared to the control (-5.2, -3.9, -6.7 % respectively). The HS condition also reduced the concentrations of FAs, MUFAs and PUFAs (-7.2, -9.0, -5.8 % respectively, compared to the control). When combined with HS, EP and LP allowed the negative effects of HS on FAs, MUFAs and PUFAs concentrations to be reduced as a consequence of their own individual positive effects (-15.6 %, -18.1 % and -13.4 % respectively under EP+HS and -11.7 %, -10.7 % and -10.6 % respectively under LP+HS). In addition, prior exposure to IP tended to reduce the negative effects of HS despite its own individual negative effect (-5.5 % (FAs), -3.4 % (MUFAs) and -9.6 % (PUFAs) respectively under IP+HS, compared to the control). This could reflect an IP-induced priming effect.

As shown in Table SD2, the effects observed at the whole plant scale were mainly explained by those in the seeds from the lowest cohorts of

Table 2

Mean values ($\pm$ SD, $n = 3$) of total FA, saturated FA (SFA), unsaturated FA (UFA), monounsaturated FA (MUFA) concentrations (%DW), the $\omega 6:\omega 3$ ratio, and of C and N concentrations in the seeds produced under heat modalities at the whole plant scale. The heat modalities were: Control, Early Priming (EP), Intermediate Priming (IP), Late Priming (LP), Early Priming and Heat Stress (EP+HS), Intermediate Priming and Heat Stress (IP+HS), Late Priming and Heat Stress (LP+HS), single Heat Stress (HS).

Heat modality	FA (%DW)	SFA (%DW)	UFA (%DW)	MUFA (%DW)	PUFA (%DW)	$\omega 6:\omega 3$	C (%DW)	N (%DW)
Control	30.7 $\pm$ 3.0 ^{abc}	2.6 $\pm$ 0.2 ^{abc}	28.1 $\pm$ 2.8 ^{abc}	17.7 $\pm$ 1.9 ^{abc}	10.4 $\pm$ 0.9 ^{abc}	1.9 $\pm$ 0.1 ^{ab}	56.0 $\pm$ 0.5 ^{bc}	3.6 $\pm$ 0.2 ^{ab}
EP	34.8 $\pm$ 1.2 ^a	2.8 $\pm$ 0.1 ^a	32.0 $\pm$ 1.2 ^a	20.4 $\pm$ 1.0 ^a	11.5 $\pm$ 0.3 ^a	1.9 $\pm$ 0.1 ^{ab}	57.7 $\pm$ 0.4 ^a	3.3 $\pm$ 0.2 ^b
IP	29.1 $\pm$ 3.1 ^{bc}	2.4 $\pm$ 0.1 ^{abc}	26.7 $\pm$ 2.9 ^{bc}	17.0 $\pm$ 1.8 ^{abc}	9.7 $\pm$ 1.2 ^c	2.0 $\pm$ 0.1 ^{ab}	56.3 $\pm$ 0.7 ^{abc}	3.5 $\pm$ 0.3 ^{ab}
LP	33.8 $\pm$ 1.8 ^{ab}	2.7 $\pm$ 0.2 ^{ab}	31.0 $\pm$ 1.6 ^{ab}	19.6 $\pm$ 1.4 ^{ab}	11.5 $\pm$ 0.2 ^{ab}	1.8 $\pm$ 0.2 ^b	56.5 $\pm$ 0.6 ^{ab}	3.5 $\pm$ 0.4 ^{ab}
EP+HS	25.9 $\pm$ 0.4 ^c	2.4 $\pm$ 0.1 ^{bc}	23.5 $\pm$ 0.4 ^c	14.5 $\pm$ 0.7 ^c	9.0 $\pm$ 0.4 ^c	2.0 $\pm$ 0.1 ^a	54.2 $\pm$ 0.6 ^d	3.8 $\pm$ 0.1 ^a
IP+HS	29.0 $\pm$ 5.2 ^{bc}	2.5 $\pm$ 0.2 ^{abc}	26.5 $\pm$ 5.0 ^{bc}	17.1 $\pm$ 3.7 ^{abc}	9.4 $\pm$ 1.3 ^c	2.0 $\pm$ 0.1 ^a	55.0 $\pm$ 1.1 ^{cd}	3.6 $\pm$ 0.2 ^{ab}
LP+HS	27.3 $\pm$ 4.5 ^c	2.3 $\pm$ 0.5 ^c	25.0 $\pm$ 4.0 ^c	15.8 $\pm$ 3.0 ^c	9.3 $\pm$ 1.1 ^c	1.9 $\pm$ 0.1 ^{ab}	55.3 $\pm$ 1.4 ^{bcd}	3.7 $\pm$ 0.1 ^{ab}
HS	28.5 $\pm$ 2.3 ^{bc}	2.5 $\pm$ 0.2 ^{abc}	26.0 $\pm$ 2.2 ^c	16.1 $\pm$ 1.2 ^{bc}	9.8 $\pm$ 1.3 ^{bc}	2.1 $\pm$ 0.1 ^a	56.0 $\pm$ 1.3 ^{bc}	3.8 $\pm$ 0.3 ^a
Temperature Effect	0.034*	0.165 ns	0.0311*	0.0504 ns	0.0234*	0.137 ns	0.00434**	0.2807 ns

For a given variable, the effects of the modalities were tested with a one-way ANOVA. Letters or ns when not significant indicate the ranking among the heat modalities following a mean comparison test (LSD multiple comparisons test). *P*-value and level of significance are given for modality effects. Levels of significance: ns non-significant, $p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$. *P*-value = 0.05.

Pods_{≥5 cm}). Indeed, FAs, MUFAs and PUFAs concentrations were significantly reduced by two-event modalities (EP+HS, IP+HS and LP+HS) followed by HS and IP. A slight priming effect of IP prior to HS was also observed, thus reducing the extent of the negative effects of HS, mainly on FAs and MUFAs (Table SD2). Overall, the longer the duration of heat days (mild or intense), the more impaired the concentrations of FAs and especially of unsaturated FAs, likely as a consequence of the desaturases' activity. However, a prior exposure to a mild stress can reduce the negative impacts of late intense heat (HS), either as a result of an individual positive effect (EP, LP) or a priming effect (IP) of the mild heat according to the duration of the recovery phase in between.

Globally, no significant difference on the ω6:ω3 ratio was observed but the multiple comparison test indicated negative effects of EP+HS, IP+HS and HS (highest values) and positive effects of LP (Table 2). As observed at the whole plant level (Table 2), HS treatment increased the ω6:ω3 ratio in seeds from cohorts of Pods_{flowers} and Pods_{<5 cm} compared to Control condition (Table SD2). In the seeds from the lowest cohorts of pods (Pods_{≥5 cm}), a significant increase of ω6:ω3 ratio was also observed in LP+HS when compared to HS and Control (Table SD2).

3.3. Physiological seed quality-related criteria

3.3.1. Soluble sugars

Table 3 summarizes the concentration of soluble sugars (i.e. stachyose, raffinose, and sucrose) in the seeds, and the [Stachyose + Raffinose]: Sucrose ratio which is a proxy of the seed desiccation tolerance (Bailey et al., 2001). At the whole plant scale, the only significant heat modality effect was observed on the stachyose concentration (Table 3) for which EP and LP+HS displayed the highest (+8.3 %) and lowest (-38.5 %) values respectively. Consequently, slight differences among the heat modalities were observed for the [Stachyose + Raffinose]: Sucrose ratio -which were explained by the changes in the stachyose concentration- in seeds of Pods_{≥5 cm} ($p > 0.05$, Table SD3). The effects were negative as the ratio decreased up to -50 % for LP+HS, compared to the Control. However, the effects of the mild single-event modalities (EP, IP and LP) were almost non-significant while in the two event modalities EP+HS and LP+HS, a strong reduction of the ratio was observed. Interestingly, the timing of the mild stress mattered since IP did not reduce the ratio, nor when combined with HS (Table SD3). For Pods_{<5 cm}, different rankings were also observed on the [Stachyose + Raffinose]: Sucrose ratio although the extent of the modality effects was lower (up to -25 % for IP, compared to the Control). No negative cumulative effects (under EP+HS, IP+HS and LP+HS) were noticed (Table SD3).

3.3.2. Polyphenols

The polyphenol concentration in the seeds at the whole plant scale

ranged from 10.4 µg/mL to 12.7 µg/mL for LP and Control respectively without any significant heat modality effects nor modality ranking (Table 3). However, the three cohorts displayed significant heat modality effects ($p < 0.05$, Table SD3). In seeds from Pods_{flowers}, the polyphenol concentrations under the mild single-event modalities (EP, IP, LP) were lower than under the Control, and significantly for LP (-15.2 %) while it increased under the modalities with HS (alone and combined). Interestingly, the concentrations decreased under EP+HS and LP+HS compared to HS alone, as a consequence of the positive effects (low values) of EP and LP alone. Additionally, the polyphenol concentration under IP+HS was even higher than HS despite the slight IP-induced lower concentration (Table SD3). In seeds from Pods_{<5 cm} and Pods_{≥5 cm}, the polyphenol concentrations were not only reduced under the mild single-event modalities (EP, IP, LP) but also under IP+HS (and EP+HS for Pods_{<5 cm}) while it increased under LP+HS and HS (Table SD3).

3.3.3. Pre-harvest sprouted seeds

Table 3 presents the percentage of pre-harvest sprouted seeds in the two cohorts Pods_{<5 cm} and Pods_{≥5 cm} in proportion to the seed number in these cohorts. The proportion ranges from 0.98 % for LP to 3.51 % for IP+HS, which displayed significant extreme rankings. No significant differences were observed amongst the other modalities. At the cohort level, different rankings were observed only for Pods_{≥5 cm} with lowest and highest proportions under LP and EP, respectively and no significant effects of the heat duration (Table SD3).

3.4. Chlorophyll fluorescence parameters related to photosynthetic performance in mature leaves

Table 4 displays several chlorophyll fluorescence parameters in relation with photosynthetic performance that were acquired in mature leaves 2 days after beginning of HS (HS_{ini}), at the end of HS (HS_{end}) and 5 days post HS under the heat modalities. Values of the parameters (relative difference from the control) varied according to the timing of measurement and to the heat sequence. At 2 days post HS_{ini}, F₀, F_m and to a lower extent F_v/F₀ and F_v/F_m increased under the heat modalities compared to non-stressed plants (Table 4). At HS_{end} and 5 days after HS_{end}, these parameters tended to decrease compared to the control (negative relative differences), meaning that there is a long-lasting and negative impact of the previous heat exposure(s). The heat modalities induced different magnitude changes in F₀, F_m at the three dates and F_v/F₀ and F_v/F_m at 2 days post HS_{ini} only, due to a high plant variability at HS_{end} and 5 days post HS_{end} (data not shown). At 2 days post HS_{ini}, the highest values of the ratios F_v/F₀ and F_v/F_m were observed under LP+HS (14.3 % and 2.4 % respectively). No significant distinction could be observed among the mild single events (EP, IP, LP) but the late

Table 3

Mean values (± SD) of the seed concentrations in stachyose, raffinose, sucrose and polyphenols (µg/mg), of the [Stachyose+Raffinose]: Sucrose ratio ($n = 3$) and of the percentages of pre-harvest sprouted seeds ($n = 4$) for each heat modality at the whole plant scale. Pre-harvest sprouted seeds were scored at the end of HS. The values represent the proportion of pre-harvest sprouted seeds Pods_{≥5 cm} and Pods_{<5 cm} out of the number of seeds in these two cohorts at the same date.

Heat modality	Stachyose (%DW)	Raffinose (%DW)	Sucrose (%DW)	[Stach+Raff]: Sucrose	Polyphenols (µg/mg DW)	Pre-harvest sprouted seeds (%)
Control	1.2 ± 0.1 ^{ab}	0.19 ± 0.01 ^{ns}	4.7 ± 0.3 ^{ns}	0.30 ± 0.03 ^a	12.7 ± 1.6 ^{ns}	2.70 ± 1.61 ^{ab}
EP	1.3 ± 0.1 ^a	0.20 ± 0.03 ^{ns}	4.9 ± 0.2 ^{ns}	0.31 ± 0.01 ^a	11.5 ± 1.6 ^{ns}	3.02 ± 1.44 ^{ab}
IP	0.9 ± 0.1 ^{bc}	0.18 ± 0.01 ^{ns}	4.8 ± 0.7 ^{ns}	0.24 ± 0.05 ^b	10.5 ± 1.2 ^{ns}	2.64 ± 2.60 ^{ab}
LP	1.2 ± 0.2 ^{ab}	0.21 ± 0.03 ^{ns}	5.0 ± 0.6 ^{ns}	0.29 ± 0.05 ^{ab}	10.4 ± 0.4 ^{ns}	0.98 ± 0.57 ^b
EP+HS	0.9 ± 0.2 ^{bc}	0.29 ± 0.17 ^{ns}	5.1 ± 0.2 ^{ns}	0.24 ± 0.03 ^{ab}	12.0 ± 0.1 ^{ns}	2.39 ± 1.91 ^{ab}
IP+HS	1.0 ± 0.3 ^{bc}	0.25 ± 0.13 ^{ns}	4.4 ± 0.3 ^{ns}	0.28 ± 0.06 ^{ab}	12.0 ± 2.1 ^{ns}	3.51 ± 0.72 ^a
LP+HS	0.8 ± 0.3 ^c	0.20 ± 0.02 ^{ns}	4.3 ± 1.4 ^{ns}	0.23 ± 0.03 ^b	12.5 ± 2.0 ^{ns}	2.14 ± 1.36 ^{ab}
HS	1.3 ± 0.1 ^{ab}	0.20 ± 0.04 ^{ns}	4.9 ± 0.7 ^{ns}	0.30 ± 0.01 ^{ab}	12.5 ± 0.5 ^{ns}	2.21 ± 1.49 ^{ab}
Temperature Effect	0.0328 [*]	0.8775 ^{ns}	0.793 ^{ns}	0.12 ^{ns}	0.336 ^{ns}	0.544 ^{ns}

The heat modalities were: Control, Early Priming (EP), Intermediate Priming (IP), Late Priming (LP), Early Priming and Heat Stress (EP+HS), Intermediate Priming and Heat Stress (IP+HS), Late Priming and Heat Stress (LP+HS), single Heat Stress (HS).

For a given variable, the effects of the modalities were tested with a one-way ANOVA. Letters or ns when not significant indicate the ranking among the heat modalities following a mean comparison test (LSD multiple comparisons test). *P*-value and level of significance are given for modality effects. Levels of significance: ns non-significant, $p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$. *P*-value = 0.05.

Table 4

Measured values (control in italics) and relative differences from the control for the heat modalities for several photosynthetic performance parameters acquired with chlorophyll fluorescence sensor (Pocket Pea, Hansatech Instrument) on dark adapted leaves, 2 days after HS start (2 days post HS_{ini}), at the end of HS (HS_{end}) and 5 days post HS_{end}. The measured values were given for the control. Letters indicate the rankings among modalities (multiple comparison test, LSD). Bold values are extreme. ns non-significant.

Modality	F0	Fm	Fv/F0	Fv/Fm	Sm
2 days post HS_{ini}					
Ctrl	5570 c	29509 d	4.3 c	0.8 c	<i>16.1 a</i>
EP	21.7 a	28.6 a	6.9 abc	1.2 abc	3.3 a
IP	12.2 ab	23.9 ab	12.9 ab	2.2 ab	9.5 a
LP	11.1 b	19.2 bc	9.0 ab	1.6 ab	2.7 a
EP+HS	15.0 ab	23.6 ab	9.4 abc	1.6 ab	-1.5 a
IP+HS	13.3 ab	16.5 bc	3.5 bc	0.6 bc	-3.3 ab
LP+HS	10.9 b	23.5 ab	14.3 a	2.4 a	7.4 a
HS	8.8 bc	11.0 c	3.1 bc	0.5 bc	-15.6 b
HS_{end}					
Ctrl	5816 b	32439 bc	4.6 ns	0.8 ns	17.6 a
EP	16.1 a	6.0 ab	0.4 ns	-2.1 ns	-15.1 ab
IP	10.9 ab	4.0 abc	-7.2 ns	-1.5 ns	-13.3 ab
LP	7.9 ab	1.6 bc	-6.3 ns	-1.3 ns	-8.5 ab
EP+HS	8.7 ab	6.2 ab	-2.6 ns	-0.5 ns	-14.6 ab
IP+HS	7.9 ab	4.2 abc	-3.8 ns	-0.8 ns	-17.0 b
LP+HS	13.8 a	12.7 a	-1.2 ns	-0.2 ns	-11.3 ab
HS	1.2 b	-4.7 c	-7.1 ns	-1.5 ns	-9.1 ab
5 days post HS_{end}					
Ctrl	6339 ns	30346 abc	3.9 ns	0.8 ns	<i>16.1 a</i>
EP	6.8 ns	4.1 ab	-6.1 ns	-0.3 ns	-13.7 bc
IP	5.3 ns	4.3 ab	-4.2 ns	0.3 ns	-9.9 abc
LP	16.1 ns	8.4 a	-9.1 ns	-1.5 ns	-14.3 b
EP+HS	-0.5 ns	-6.2 bc	-9.7 ns	-1.6 ns	-9.9 abc
IP+HS	0.7 ns	-3.2 abc	-8.0 ns	-0.7 ns	-13.7 bc
LP+HS	5.0 ns	6.2 ab	-1.5 ns	0.9 ns	-3.7ab
HS	7.7 ns	-9.6 c	-21.7 ns	-4.4 ns	-24.2 c

Color scale:  -30 0 +30

F0 initial fluorescence (dark adapted); Fm maximum fluorescence (light-saturated); Fv/Fm maximum quantum efficiency of photosystem II; Sm is a parameter of the equations of the JIP-test (Strasser and Tsimilli-Michael 2001) that represents the normalized area above the fluorescence rise between F0 and Fm: it is a function of the number of electrons transported by PSII in the range from 0 to the time to reach Fm. The chlorophyll index is acquired with Multiplex® fluorimeter.

and more intense HS induced the lowest relative increase in Fv/F0 and Fv/Fm (3.1 % and 0.5 % respectively). Relative values of Fv/F0 and Fv/Fm under the combined sequences were slightly higher than under HS, indicating a positive effect of the prior mild stress exposure which was even more pronounced for the LP+HS condition.

Interestingly, Sm, which is the normalized area indicating the vitality of the plants to withstand stress, displayed significant different rankings among the heat modalities at the three dates of measurement. At 2 days post HS_{ini}, while the relative values under single mild heat events were slightly increased, the HS-induced value was much lower. Overall, the mild events helped mitigate the HS-induced effects but while IP alone led to the highest increase (+9.5 %), IP+HS led to the lowest decrease (-3.3 %) among the combined sequences and while LP alone led to the lowest increase (+2.7 %), LP+HS led to the highest increase (7.4 %) among the combined sequences. At HS_{end} and 5 days post HS_{end}, Sm

relative values were negative regardless of the heat modalities with the lowest ones being recorded under HS (-24.2 %).

Overall, variations among the modalities in the fluorescence chlorophyll parameters were observed from 2 days post HS_{ini} meaning that the prior mild stress exposure with or without recovery has a long-lasting impact on HS-induced photosynthesis parameters. They tended to be attenuated (F0, Fv/F0, Fm/Fv) over time or amplified (Fm, Sm) thus exacerbating differences among the heat modalities.

4. Discussion

4.1. Significant heat modality effects at the cohort level reflect a synchrony between the heat event(s) and underlying metabolic processes to the seed storage compounds

The effects of the heat modalities on yield and its components highlight that only the upper cohorts of pods ($\text{Pods}_{<5\text{ cm}}$ and $\text{Pods}_{\text{Flowers}}$) were impacted as a result of the overlap between seed set and/or seed filling with the heat modalities in contrast to the lower cohort ($\text{Pods}_{\geq 5\text{ cm}}$) which gathered maturing seeds when the cohorts were defined at GS72. This was in line with prior studies that demonstrated the drastic effects of heat at flowering on seed yield (Angadi et al., 2000; Morrison and Stewart, 2002). These cohort level effects were mostly positive under the single mild event but negative under either the intense heat alone or when combined to the mild stress events. The solely whole plant scale effects were observed on TSW with LP and HS leading to the highest and lowest values respectively, as a consequence of the seeds in the cohort of $\text{Pods}_{<5\text{ cm}}$ being the most important at GS72. However, because of the indeterminate growth pattern of oilseed rape, yield components can adjust over a stressful period resulting in blurred stress effects at the whole plant scale as already observed in this species (Delamare et al., 2025; Magno Massuia De Almeida et al., 2021, 2022).

The FA-related variables were significantly impacted by the heat modalities in seeds from the lowest cohort ($\text{Pods}_{\geq 5\text{ cm}}$) which resulted in significant differences at the whole plant scale. Again, this was expected because of the longest overlap between the heat sequences and the seed maturing phase (i.e. when FAs synthesis and FAs desaturation occur) (Baud et al., 2002) in this cohort compared to the upper ones. Storage lipids accumulation are spread over several weeks mostly during the second half of seed filling stage and are largely determined by the photosynthetic activity of leaves and pod envelopes that provide the carbon source (Wang et al., 2016). In addition, the lipids maturation - mainly triacylglycerols (TAGs) in oil crops (Voelker and Kinney, 2001) - is governed by a complex transcriptional network, intracellular transporters and modifying enzymes. Among them, FAD2 activity which accounts for by FAs desaturation, was shown to be modulated by temperature as a result of long-term direct effects on the stability of seed-specific isoforms of FAD2 (Martínez-Rivas et al., 2003) or short-term indirect effects on dissolved oxygen levels in seeds which is a co-substrate of FAD2 (Rolletschek et al., 2007). In our experiment, we observed reduced concentrations of polyunsaturated FAs (up to 50 %) in HS-including modalities or in the intermediate pre-stress positioning modality (IP). These HS-including conditions were likely to disadvantage desaturase activities as a result of an above threshold temperature either to maintain structural stability or sufficient oxygen level. Nevertheless, no additional negative effects of HS and IP were observed whereas the negative effect of HS alone was amplified when combined to EP and LP despite individual positive effects. This underlies the specificity of the IP event to induce lasting processes on later responses to heat and, to some extent, to prime the plants prior to intense heat.

The relative concentration of N in seeds of the lowest cohorts were affected in the opposite way to the FAs concentrations (Table SD2). N uptake is generally low after flowering when N remobilization from vegetative organs becomes predominant (Malagoli et al., 2005) meaning that the allocation of N in the seeds is tightly dependent on its transportation, and seed N concentration results from this availability and its dilution in the seed biomass. Our results indicated such effects as the lowest TSW were observed in EP+HS and HS seeds where N concentrations were the highest.

The acquisition of seed desiccation tolerance in orthodox seeds has long been attributed to the role of raffinose family oligosaccharides (RFOs) in cell protection through the prevention from the crystallization of cellular solutes by the formation biological glass and/or the stabilization of cell structures by the maintenance of hydrogen bonds within and between macromolecules (Berjak et al., 2007; Hoekstra, 2000). A

transcriptome analysis of *Medicago truncatula* (Buitink et al., 2006) confirmed that sucrose, and often specific oligosaccharides, stachyose and raffinose being the major ones, commonly accumulate as plants acquire desiccation tolerance. Although sucrose accumulation is also observed in desiccation-sensitive recalcitrant seeds, the soluble oligosaccharides to sucrose ratio is commonly used to qualify the seed storage capacity (Bailly et al., 2001; Buitink et al., 2006; Horbowicz and Obendorf, 1994). Our results indicated that the effects on the ratio were mainly due to heat-induced changes on the stachyose concentration. Therefore, because stachyose results from the transfer of a galactosyl residue from galactinol to raffinose and is catalyzed by stachyose synthase, it can be hypothesized that the heat sequences coincided with the last steps of the RFOs synthesis. Moreover, similar to FAs variables, the effects of the single mild stress events on stachyose concentration and eventually, on the RFOs-to-sucrose ratio allowed the distinction of IP from EP and LP. However, contrastingly, intense heat (HS) increased stachyose concentration while it decreased FAs concentration.

Eventually, a measure of the stress response was given by the polyphenol concentration in the seed. Polyphenols are involved in abiotic stress responses and contribute to scavenge reactive oxygen species (ROS) and free radicals owing to their anti-oxidant activities (Parvin et al., 2022). Accordingly, in our conditions, the highest concentrations were observed under HS-including modalities. However, at the cohort level, the prior exposure to the pre-stress helped mitigate the negative effects of HS, as observed in by Magno Massuia De Almeida et al. (2021), but this effect was specific to its timing.

Altogether, these results suggest that the effects of heat stress on seed storage compounds and stress proxies, should be interpreted in light of the synchrony between the heat event and their respective metabolic processes involved in their sequential biosynthesis (Baud et al., 2002). This is made even more complex in indeterminate growth species.

4.2. The duration of the recovery phase determines the effects of the following intense heat event

Our objective was to assess to what extent the duration of the recovery phase/the positioning of the triggering event (expected to be 'priming'), further determine the plant response to later intense heat exposure (expected to be 'triggering'). As previously discussed, the most significant effects were observed at the cohort level which allows the different seed stages at the time of the stress to be considered. First, our results pointed out specific effects of the single mild event (EP, IP, LP) which highlight the importance of the pre-stress positioning over the seed filling/maturation stages. Secondly, on most seed quality criteria, the effects (magnitude and direction) of the intense stress varied according to the pre-stress sequences which differed from the time lapse in between the two events (79.7°Cd post EP, 42.1°Cd post IP and without under the LP+HS sequence) and consequently from the timing of the pre-stress exposure (at GS72 for EP, ca. 33.7°Cd later for IP and ca. 70.6°Cd later for LP). For instance, while EP and LP led to increase seed FAs, MUFAs and PUFAs concentrations, IP induced slight negative effects. Then, while the EP or LP prior exposure to HS amplified the negative effect of HS alone on these variables, this decrease was attenuated under the prior IP exposure which could reflect an IP-induced priming effect. Overall, although slight, these differences highlight non-random effects that are consistent with our initial assumption that the potential priming effects of a pre-stress sequence are driven by its characteristics, particularly those related to the duration of the recovery phase. Indeed, in previous studies in oilseed rape (Magno Massuia De Almeida et al., 2021, 2023), a prior exposure to 5-day mild heat followed by 5-day recovery did not alleviate the negative impact of 5-day intense heat peaks on seed yield, FAs, PUFAs concentration, nor on the seed storage capacity. Contrastingly, Delamare et al. (2025) showed that a gradual increase in temperature over 5 days, prior to 5-day heat peaks helped reduce their negative effects on seed yield and similar quality criteria. In relation to our experimental design, because the recovery

phase between IP and HS was intermediate between these two above-mentioned thermo-protocols, we expected the effects of IP to differ from those of EP and LP. Our results tended to demonstrate these contrasting effects of IP, although slight which can be accounted for by a lower temperature intensity than in other studies (Magno Massuia De Almeida et al., 2021, 2022; Delamare et al., 2025) where the temperature of the mild stress event was ca. 26°C or the gradual event increased from ca. 19°C to 26°C. To our knowledge, little information is available on the duration of heat stress over the plant life. When documented, it refers to the lasting of specific stress-induced molecular regulations such as epigenetic and post-transcriptional modifications which ranges from a few hours to several days (e.g. Auge et al., 2023; Charnig et al., 2023; Crisp et al., 2016; Kambona et al., 2023; Kashyap et al., 2024; Lamke and Baurle, 2017,) but the links with crop traits are mostly missing.

4.3. Photosynthesis-related proxies can picture specific heat sequence effects on seed biomass

Because heat stress causes impairment in the photosynthetic apparatus in the first line, modification of the PSII functioning can highlight early effects on the stressed plants (Mathur et al., 2011). In this study, the dynamics of fluorescence chlorophyll parameters were followed in the aim to catch the specificities of the heat sequences and to assess their potential to reflect the differences in final yield and seed quality criteria among the heat modalities, thus raising the question of their relevance as proxies of recurrent sequences effects.

The Fv/Fm ratio is commonly used as an indicator of heat stress and has been shown to distinguish heat tolerant from heat sensitive genotypes (Sharma et al., 2015; Zhou et al., 2015) or recurrence heat effects (Berger et al., 2025; Ripoll et al., 2016). Usually, under unstressed conditions, leaf values of Fv/Fm are ca. 0.83 (Murchie and Lawson, 2013) which matched our observations under the control. As expected, in our heat conditions, the ratio Fv/Fm slightly decreased with time, even after the heat stress ceased. However, the ratio could not allow differences among the heat modalities to be caught after HS. Indeed, while negative relative differences from the control were observed, no significant effects of the heat modalities after the heat sequences (5 days post HS_{end}) could be highlighted. As explained in the Material and Methods, because of monocarpic leaf senescence in oilseed rape, leaves continuously fall, regardless of any stress exposure. Therefore, when necessary, the upper leaf of the fallen ones was used to get dynamic measurements. This is likely to introduce a bias since the younger upper leaf may have not witnessed the complete heat modality thus making it a weaker proxy of the full sequence. Nevertheless, interestingly, 2 days post HS_{ini} - when measurements were still made on the initial chosen leaves - the Fv/Fm ratio differed among the heat modalities. Although slight, the differences tended to distinguish IP from EP and LP (increased Fv/Fm ratio under IP). It also pictured the contrasting effect of IP over HS (compared to the effects of EP and LP over HS) as IP+HS led to a reduced Fv/Fm ratio despite the highest positive individual effect of IP among the mild stress events. In contrast to Fv/Fm, Sm which reflects the vitality of the plants subjected to stresses (Oukarroum and Strasser, 2004) displayed significant modalities differences even after the end of HS, with the most reduced relative value observed under HS. Again, IP is distinguished from the other single mild events with the lowest relative decrease and the highest one when combined to HS.

In our protocol, final differences in seed performances among the heat modalities are difficult to picture from the fluorescence chlorophyll measurements as a consequence of inherent issues of phenotyping continuous senescing plants. However, because these parameters indicate PSII functioning and eventually carbohydrate assimilation, it is relevant to correlate modality-specific effects between TSW and measurements of Sm, Fm - which are significant during and after the intense stress - and of Fv/Fm which was significant early after HS. Indeed, altogether, these observations reflect that (i) IP alone led to a specific functioning of PSII compared to EP and LP which turned to impair seed

filling (lower TSW at the whole plant scale, mainly due to seeds from Pods_{<5 cm}) (ii) prior exposure to IP led to opposite effects of HS alone on PSII functioning which led to mitigate the effects of HS on TSW. These observations were in line with results in sorghum (Berger et al., 2025) where a lower reduction of Fv/Fm was observed under heat when the plants had been previously exposed to a similar stress. Consistent with our results, the thousand grain weight was reduced under the recurrent heat modalities.

Further relationships between photosynthesis-related parameters and the quality of storage compounds are very limited since their biosynthesis involves a wide range of metabolic processes that are regulated on a multiscale basis (Balazadeh, 2022; Staacke et al., 2025). In order to provide proxies of the complex effects of heat recurring stresses on seed quality criteria, more integrative parameters must be used such as near infra-red (NIR) spectrum. This approach refers to emerging spectral methodologies to predict endophenotypes which reflect the expression of the transcriptome, proteome or metabolome underlying traits of interest (De Salvio et al., 2024; Mackay et al., 2009; Robert et al., 2022).

5. Conclusion

In this study, we analyzed the effects of several recurring heat stress sequences on seed yield and quality criteria in oilseed rape that differed from the duration between two stresses. Our initial assumption was that the potential priming effect of the first heat event was determined by the duration of the recovery phase, meaning that above or below a given lapse of time, this effect could not be observed. Our experimental design allowed the modality-specific effects on the main nutritional seed quality variables to be caught. More precisely, it allowed the distinction of the intermediate recovery duration from longer recovery and no recovery thermo-protocols to be made, thus confirming the idea that the recovery period is key to maintain stress-induced priming effect. Besides, chlorophyll fluorescence-based parameters measured on mature leaves were reliable proxies of carbon assimilation in seeds and eventually yield components. More broadly, this work demonstrates that a better characterization of the environmental conditions that could induce priming effects would open avenues to acclimate crop to recurring stresses within and over crop seasons. A better understanding of this often-overlooked aspect of memory effects could unlock priming effects and contribute to advances for crop acclimation strategies.

CRedit authorship contribution statement

L. Kougiteas: Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Data curation, Conceptualization. **B. Julien:** Methodology, Formal analysis. **B. Bernay:** Supervision, Methodology, Investigation. **Q. Dupas:** Writing – original draft, Validation, Methodology. **N. Elie:** Methodology. **M. Le Guedard:** Formal analysis, Methodology. **JC Avic:** Writing – review & editing, Validation, Supervision, Methodology, Investigation. **S. Brunel-Muguët:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.envexpbot.2025.106263](https://doi.org/10.1016/j.envexpbot.2025.106263).

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