European Journal of Agronomy 168 (2025) 127623

Contents lists available at ScienceDirect

European Journal of Agronomy

journal homepage: www.elsevier.com/locate/eja

A new dataset to elucidate inaccurate temperature thresholds masking a hidden source of risk uncertainties in common wheat

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ARTICLE INFO

Keywords:
Wheat
Thermal stress threshold
Phenology
Impact uncertainty
Agroclimatic risks

ABSTRACT

Temperatures outside the optimum range for each phenological phase may wreak cereal yield losses. However, there is no consensus on temperature thresholds for assessing thermal stress in wheat. The wide spread use of these thresholds in the scientific literature is hardly ever considered in climate risk assessments. Our review updates the seminal work of Porter and Gawith (1999) by revising thermal stress thresholds, according to the geographical localisation, wheat type, phenological phases and processes involved. A group of 122 publications on the impact of temperature on wheat crops reveals high variability and inconsistencies in the thresholds. We disentangle some of the factors generating this variability and show that when the sample is filtered by geographical localisation, type of common wheat (winter or spring), and biological process (growth or development), the variability decreases within a range of 35–65 % depending on the stress indicator. This variability leads to considerable uncertainty in the estimation of agroclimatic risks to wheat crops. Indeed, a 2°C difference in the stress threshold (25°C vs. 27°C) for the grain-filling phase reduced the heat stress risk (number of days above the threshold) by up to 45 % on average over a 30-year period in France. These results help interpret previous studies by considering how the chosen threshold position within the range of possible values may lead to under or overestimation. We provide the full database from this review, including metadata defining the validity range of each study's threshold. We recommend that future studies avoid deterministic thresholds and instead use a range of values to capture uncertainty and minimize conflicting conclusions.

Introduction

The Food and Agriculture Organization of the United Nations recognised that the Sustainable Development Goal "Zero Hunger" by 2030 is off course (FAO, 2022a). Food production is experiencing instability in crop yields, protein and mineral quality due to climate change (Masson-Delmotte et al., 2021), threatening humanity's food security (Fanzo et al., 2018; Myers et al., 2017; Owino et al., 2022).

Common wheat (*Triticum aestivum* L.) is one of the most important cereal crops in the world (FAO, 2022b), providing nearly one-fifth of the calories and protein in the human diet, with some countries more dependent than others (Shewry and Hey, 2015; Shiferaw et al., 2013). Although wheat yields have increased worldwide since the 1950s, thanks to genetic progress and improved cultivation practices, they stagnated since the 1990s (Helman and Bonfil, 2022), especially in Europe (Bönecke et al., 2020; Le Gouis et al., 2020), due to more frequent and intense droughts and heat stress (Gudmundsson and Seneviratne, 2016; Teuling, 2018).

Climate extremes such as high temperatures, droughts and floods are likely to become more frequent, intense and prolonged threatening to decrease yields (Ben-Ari et al., 2018; Mäkinen et al., 2018; Vogel et al., 2019; Zampieri et al., 2017). Wheat's sensitivity to temperature, varies throughout its development cycle and differs among varieties (Barlow et al., 2015; Farooq et al., 2011; Porter and Gawith, 1999; Wollenweber et al., 2003). Accurately assessing threshold temperatures is crucial to estimate the growth (e.g. ecophysiological processes) and development (e.g. cycle length) of wheat (Gate, 1995; Ritchie, 1991), for feeding agroclimatic indicators and crop growth models.

Growth and development slow or stop, outside a plant's thermal optimum, but damages occur only beyond stress thresholds. Potential damage to the plant and crop yield, depends on the intensity and duration of the stress, and may be compensated if the temperature

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https://doi.org/10.1016/j.eja.2025.127623
Received 24 September 2024; Received in revised form 19 March 2025; Accepted 22 March 2025
Available online 31 March 2025
1161-0301/

returns to the optimal range soon enough (Wu et al., 2014). The complexity of setting thresholds arises from the interplay between stress intensity and duration, ranging from brief freezing exposure to prolonged stress (Fuller et al., 2007) to several days of exposure to heat stress (Yang et al., 2017) for example. This also makes it challenging to compare the methods used to identify thresholds (Huang et al., 2022). Many studies have examined uncertainty in projected yield associated with crop models and/or climate models and/or climate scenarios (Liu et al., 2022; Wang et al., 2020, 2017). Wang et al. (2020) demonstrated that improving the temperature response functions of crop models could reduce the error in grain yield simulations by 19–50 % across various sites worldwide. To our knowledge, no study in the literature has explored how threshold temperatures vary within a crop species as a source of uncertainty. Additionally, no research has proposed a method for selecting stress thresholds, for crop models or for risk indicators.

This review aims to (1) highlight the wide variability in the thresholds used in the literature over the past 30 years and provide a comprehensive database as an update of Porter and Gawith's work, (2) identify key factors for subdividing data within groups with lower variability, (3) demonstrate how varying stress threshold affects a related risk indicators and, (4) offer recommendations for their use based on these findings.

Threshold temperatures for thermal stress from the literature

Porter and Gawith's (Porter and Gawith, 1999) review based on 65 papers (51 retained) derived thermal stress thresholds for wheat and became the reference for the following decades. Here, we added 83 papers published since then, constituting an ensemble of 122 papers. We identified papers based on citations and key words like wheat, adverse events, agro-climate risk and climate change. We selected articles that define thresholds for specific phenophases rather than fixed calendar periods. Although this approach reduces the number of available articles, it ensures greater coherence in the context of phenology acceleration under climate change (Beauvais et al., 2025; Caubel et al., 2015). Each "phenophase" refers to the following nine phases: sowing, germination (BBCH 0, 00–09), seedling growth (BBCH 1, 10–19) and tillering (BBCH 2, 20–29) for the vegetative phase; stem elongation (BBCH 3, 30–39), booting (BBCH 4, 40–49), ear emergence (BBCH 5, 50–59) and flowering (BBCH 6, 60–69) for the reproductive phase; and grain-filling (BBCH 7 and 8, 70–89) for the filling phase.

When a single threshold was applied for several phases or the entire growing season, the threshold value was repeated for each phase. Based on the methods used (S1), we classified the 1135 thresholds identified into six types: maximum (Tx), minimum (Tn) and high night temperatures (HNT), which are harmful but not lethal to the wheat crop; optimum temperature for growth and development (Topt); minimum lethal temperature (LTn) and maximum lethal temperature (LTx). See supplementary information (Fig. S2) for more information about thermal stress impact on common wheat. The review thus summarises the thermal optimum for common wheat and the thresholds that are considered detrimental (Fig. 2).

Tx thresholds were similar among the phenophases (Fig. 2), although some phases are known to be much more sensitive than others, especially meiosis (i.e. BBCH 39), flowering and grain-filling (Barber et al., 2017; Mishra et al., 2015). Although the thresholds ranges were similar among the phenophases, the mean Tn thresholds in this sample did differ significantly among them (Fig. S5).

While the impacts of high temperatures are visibly identified by the severity of organ damage and/or yield, low temperatures have more subtill impact, slowing down growth and development. However, the cold stress literature is more extensive and better documented. This greater amount of information is reflected in the amount of data on cold stress thresholds (n = 452) vs. heat stress thresholds (n = 299) and improves the measure of standard deviation, which gives a better mean standard deviation per phenophase (for all thresholds except

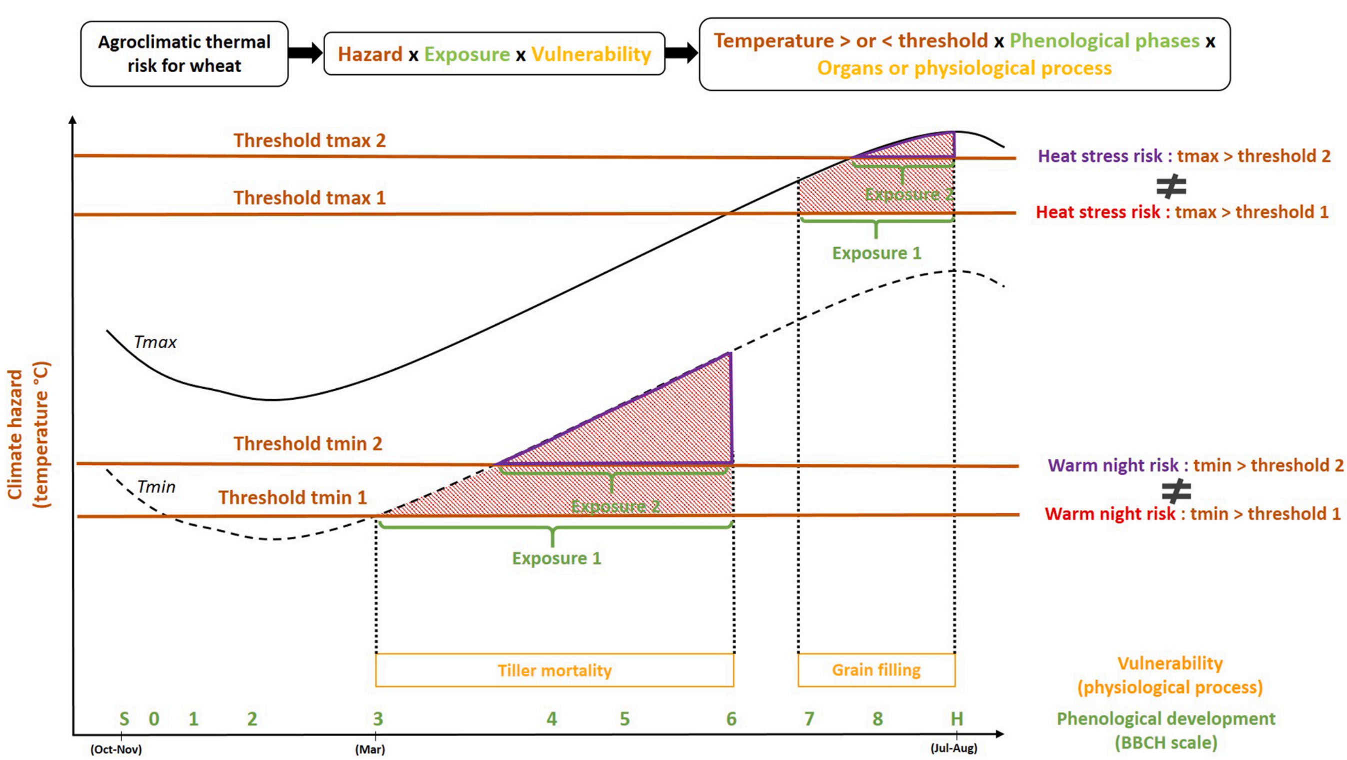

Fig. 1. Conceptual diagram depicting the impact of selected threshold temperatures on estimated agroclimatic risks for common wheat during different main phenological phases (green, indicated by the BBCH scale (Meier, 2018), including Sowing (S) and Harvest (H)). i) Risk of high nights temperature (represented by red and violet areas for thresholds tmin 1 and 2) due to high minimum temperatures leading to increased tiller mortality, and ii) Risk of heat stress (represented by red and violet areas for thresholds tmax 1 and 2) due to high maximum temperatures affecting grain-filling.

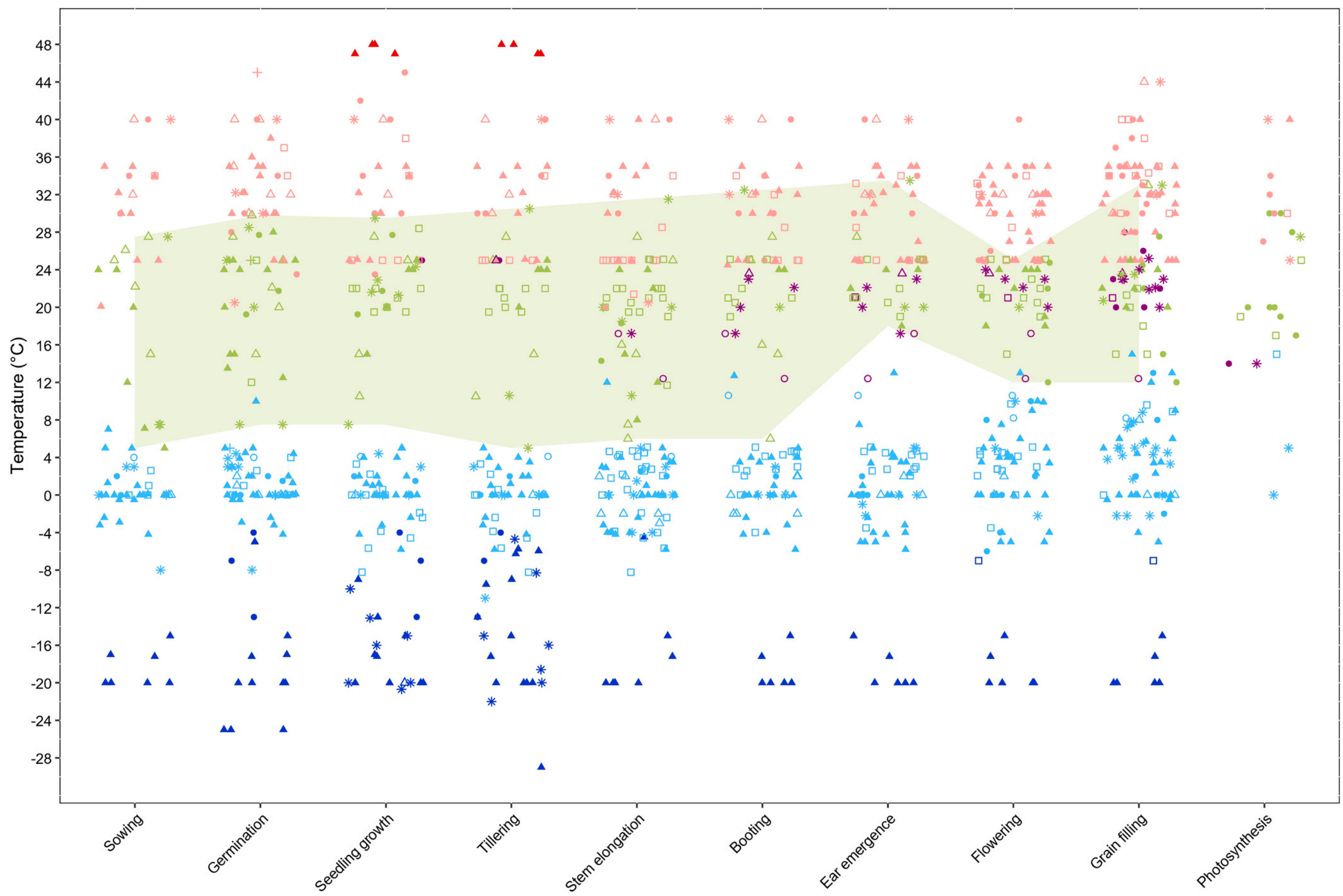

Fig. 2. Distribution of 1135 thermal stress and thermal optimum threshold values from 122 scientific articles on wheat for different phenophases and photosynthesis. Thermal optimum (Topt; green zone: range of extreme values for Topt) and thermal stress thresholds (lethal maximum temperature (dark red), maximum temperature (light red), high night temperature (purple), minimum temperature (light blue) and lethal minimum temperature (dark blue)) by phenophase, and for photosynthesis. The corresponding BBCH interval is shown in brackets. Symbols specify the geographic location (•: Multi-locations, +: Africa, □: Oceania, ✳: North America, Δ: Asia and ▲: Europe).

photosynthesis) for cold stress (3.5) than for heat stress (5.2) (Tables S4.1 and S4.2).

The mean Tn threshold for flowering and grain-filling are significantly higher than that for sowing, germination, seedling growth and tillering (which is the most resistant phase). These differences are explained by the fact that the reproductive stage is more sensitive to cold stress than the vegetative stage (Manasa et al., 2022).

The mean Tx threshold does not differ significantly among phenophases, although its mean was lower for flowering than for grain-filling, also noted by Rezaei et al. ((2015). Some temperatures being used as stress thresholds lay in the thermal optimum in other studies (Fig. 2). Thus, we subsequently aimed to identify reasons for this high variability and inconsistency in thermal stress thresholds within our sample.

Variability and inconsistency in threshold temperatures

We categorised the data by geographic location (i.e. Africa, Asia, Europe, Oceania, North America, South America or multi-locations), type of wheat (i.e. winter, spring or not specified (NS)) and type of biological process for which the threshold was studied (i.e. growth (G), development (D), growth and development combined (G&D), lethal (LT) or damaging to wheat (WD) (i.e. detrimental to the wheat crop in general, without a specific organ or process) (Fig. 3). Supplementary information (S1, S3 and S4) provides information on the method, the number of threshold temperatures by category, a summary of all stress threshold values by thermal stress indicator and phenophase, and a summary of the 90 % interval for each category tested respectively.

As expected, winter wheat is more resistant than spring wheat to minimum and lethal temperatures (Fig. 3B). Thus, continents that grow mainly winter wheat (e.g. Europe) were likely to have lower Tn and LTn thresholds than countries that grow spring wheat (e.g. North America). Developmental (D) processes are more sensitive to low temperatures than growth (G) processes, because even though the basal temperature for wheat development is set at 0°C, certain growth processes of wheat can tolerate lower temperatures (Fuller et al., 2007).

Geographic location

The LTn thresholds from Europe and North America (mean of −17.5°C (± 0.6°C) and −15.7°C (± 1.4°C), respectively) did not differ significantly (Fig. 3A). However, the mean LTn threshold of the multi-location group was much higher (-8.0°C (± 1.3°C)). This result shows that when generalist articles (reviews or multisite studies) use thresholds, they tend to choose values in the moderate range rather than extremes (Table S4.2), which are more typical of a specific context. But the few thresholds from Oceania (n = 2) made the analysis unbalanced (Figs. S3.1 and S3.2).

Among the non-lethal thresholds, only the mean Tn threshold from South America (mean of 6.6°C (± 0.9°C)) differed significantly from those of other regions, which ranged from 0.2°C (± 0.3°C) for Asia to 1.6°C (± 0.5°C) for North America, indicating a particular sensitivity of wheat in this region, consistent with the absence of negative values in the 90 % interval (Table S4.2). However, the climate of South America (represented only by Argentina in the present study) oscillates between

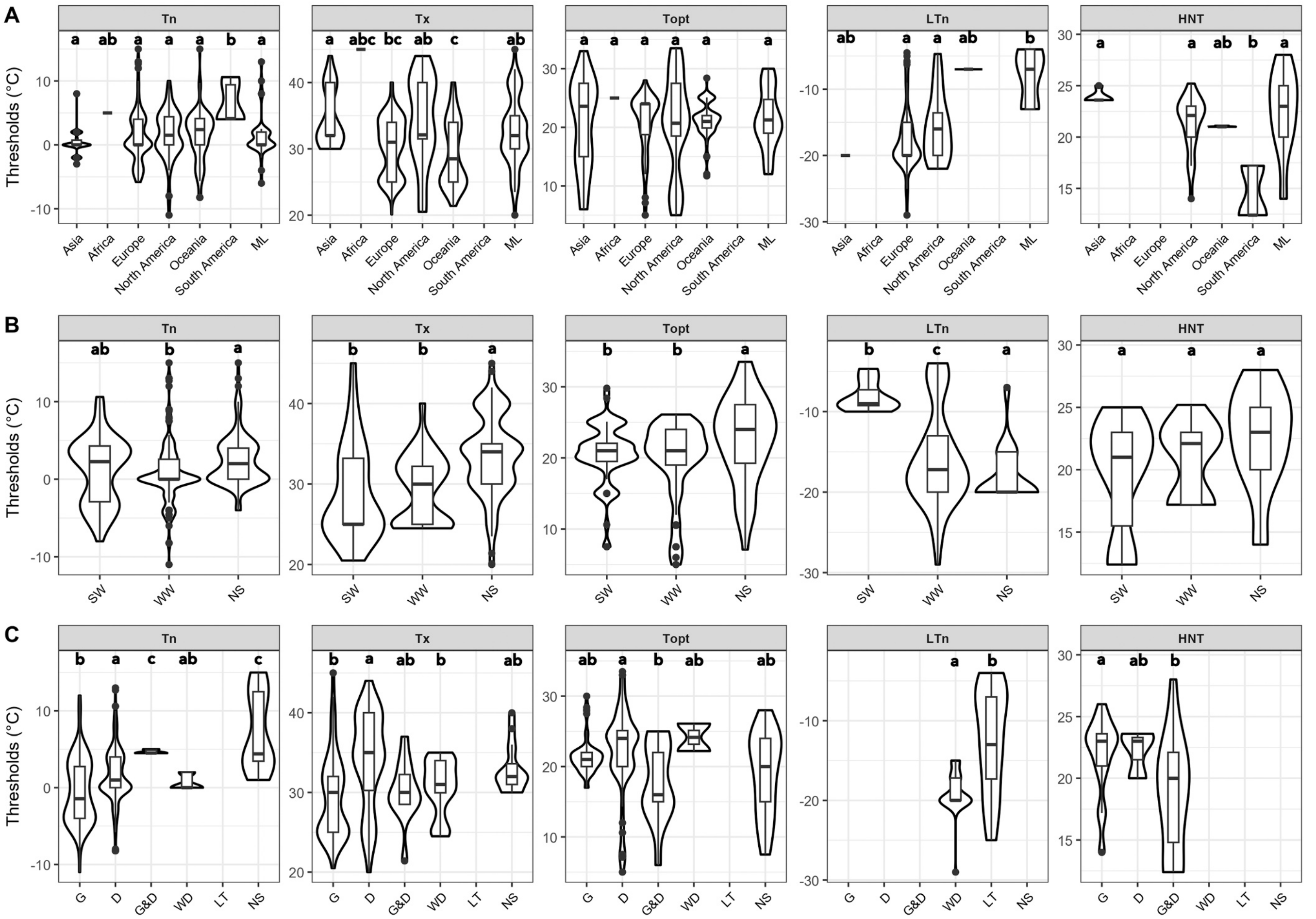

Fig. 3. Violin plots and boxplots of thermal stress thresholds (minimum (Tn), maximum (Tx), optimum (Topt), minimum lethal (LTn) and maximum night (HNT)) for all phenophases as a function of (A) geographic location (including multi-locations (ML)), (B) type of wheat (spring (SW), winter (WW) or not specified (NS)) or (C) type of process studied (growth (G), development (D), growth and development combined (G&D), lethal temperature (LT), damaging to wheat (WD) or NS)). Whiskers represent 1.5 times the interquartile range. Different letters indicate significant differences based on Dunn's alpha 5 % test and the Holm adjustment method.

high and cool temperatures, like those of North America, Asia and Oceania (Sayre et al., 2019). Consequently, the significant differences we observed may have been due to the high variability in the thresholds among regions (Fig. S3.2). For the mean Tx threshold, the climates of the regions could not explain the significant differences among Oceania (29.3 ± 0.6°C), Asia (34.6 ± 0.8°C), North America (34.1 ± 1.5°C) and the multi-location group (32.6 ± 0.7°C). The mean Tx threshold also differed significantly between Asia and Europe (30.4 ± 0.4°C), whereas that for the multi-location group lay between those of Asia and Oceania.

However, it is difficult to separate the geographical (or environmental) effect, which highlights the impact of local pedoclimatic conditions, from the cultivar effect, which reflects the selection and/or adaptation of cultivar (the cultivar effect may be stronger than the geographical effect). In addition, the geographical origin of our data sample is unbalanced (Figs. S3.1 and S3.2), with the majority of publications coming from Europe and North America.

Spring or winter wheat

Fuller et al. (2007) described how winter wheat resists low temperatures better than spring wheat. Because winter wheat is sown in autumn, it spends part of its cycle in winter, when temperatures are lowest, and has thus developed more resistance, which is enhanced by vernalisation, a process that does not occur in spring wheat. Analysing the thresholds by type of wheat (Fig. 3B) indicated that the mean LTn and Tn thresholds of winter wheat (-15.9 ± 0.8°C and 0.8 ± 0.2°C, respectively) are lower for Tn and significantly lower for LTn compared to spring wheat (-8.1 ± 0.7°C and 1.1 ± 0.4°C, respectively) (Fig. 3B), which confirmed their differing sensitivity particularly evident in the 90 % interval analysis for LTn (Table S4.2). Spring and winter wheat had the same sensitivity to heat stress, however, as their mean Tx thresholds did not differ significantly (28.7 ± 1.1°C vs 29.5 ± 0.4°C, respectively).

Overall, 37 % of the stress thresholds came from studies that did not specify the type of wheat (compared to 42 % and 21 % for winter and spring wheat, respectively). Most mean thresholds of the NS group (i.e. Tn: 2.4 ± 0.3°C, Tx: 33.5 ± 0.4°C, Topt: 22.6 ± 0.8°C and LTn: −18.1 ± 0.5°C) were significantly different than those of winter and spring wheat, likely because when the type of wheat was not specified, a wider range of thresholds was selected to represent both types. As the mean LTn threshold was closer to that of winter wheat (i.e. −15.9 ± 0.8°C), the NS group may have consisted mainly of winter wheat. Although many studies do not distinguish winter and spring wheat (Akter and Rafiqul Islam, 2017; Asseng et al., 2015, 2004; Bogard et al., 2021), it is important to do so for selecting LTn and Tn thresholds, especially because winter wheat is more tolerant to low temperatures than spring wheat.

Growth and development process

In characterising climatic risks to wheat crops, it is important to distinguish between development and growth. Indeed, development refers to all qualitative changes associated with the appearance of new plant organs and is directly related to phenology. Growth, on the other hand, refers to the quantitative increase in all plant dimensions and is directly related to biomass. While growth parameters are primarily studied due to their direct link to yield components, developmental parameters (associated with phenology) also play a crucial role. Indeed, they interact closely with the processes of growth and yield formation, decisively influencing the allocation of resources essential for plant development.

In our case study, mean HNT thresholds were similar between growth (G) processes (21.8 ± 0.6°C) and development (D) (22.2 ± 1.1°C) processes but significantly higher than that for the two combined (G&D) (18.5 ± 1.1°C) (Fig. 3C). The imbalance in the distribution of threshold samples by category (Figs. S3.1 and S3.2) has complicated the interpretation of the results. The observed significant difference can be attributed to a high number (26 %) of low thresholds (12°C), which originate from the same study (Giménez et al., 2021) conducted under field conditions.

For the LTn threshold, studies on the general effect of low temperatures on wheat (WD) selected more extreme thresholds than those that focused on LTn thresholds for wheat (Fig. 3C). Mean LTn and WD thresholds differed by ca. −6°C (-12.3°C (± 1.1°C) and −18.8°C (± 0.3°C), respectively). Impact studies on wheat (especially those on yield and/or adverse events) support these thresholds, as certain varieties in Canada and northern Europe can survive temperatures as low as −20°C.

For the Tn threshold, development (D) processes (1.7 ± 0.2°C) were more sensitive than growth (G) processes (-0.5 ± 0.4°C) (Fig. 3C). Although phenology can influence yield strongly, damage to wheat growth ultimately has the most direct influence on yield. Thus, studies that focused on wheat yield and/or feasibility (WD) had a mean Tn threshold (0.7 ± 0.1°C) between those of growth or development, perhaps in part because impact studies used lower extreme (except for LTn) and more general thresholds to ensure that they estimated risk accurately. The mean Tn thresholds reviewed did not differ among phenophases. However, some phenophases, such as tillering, are more resistant to low temperatures than others and can compensate for damage, whereas others, such as meiosis or flowering, are more sensitive and can experience irreversible damage (Gate et al., 2008).

Conversely, for the Tx threshold, growth (G) processes were more sensitive (29.4 ± 0.5°C) than development (D) processes (34 ± 0.7°C) (Fig. 3C). Although 29.4°C is the average threshold temperature that characterises thermal stress for growth (without distinction on wheat type, geographical location), several studies have used lower thresholds, for example 25°C for winter wheat type in France (Brisson et al., 2010); 25 °C for both spring and winter wheat type in western Europe (Le Gouis et al., 2020) or 27°C for winter wheat in Germany (Bönecke et al., 2020;

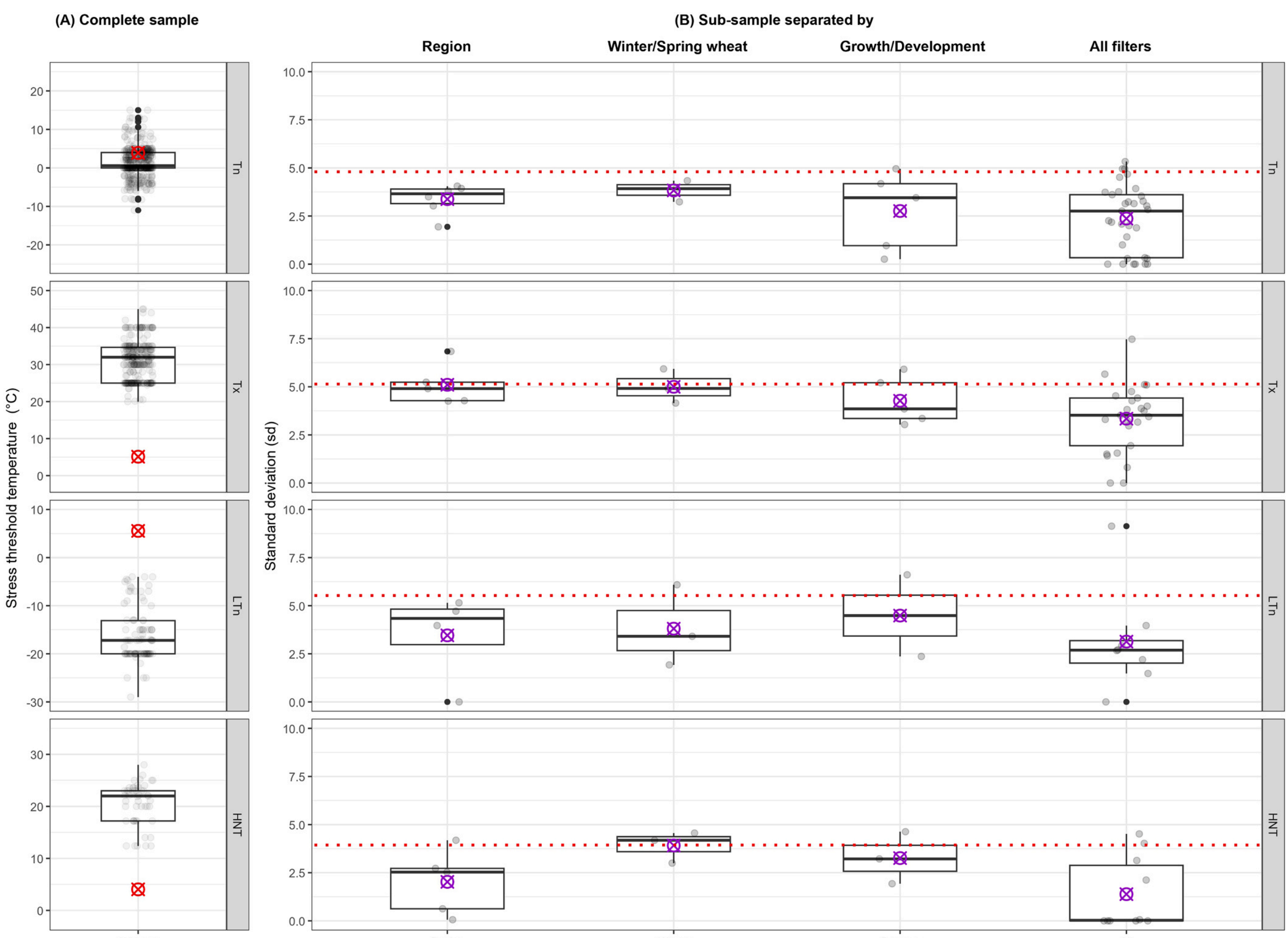

Fig. 4. (A) Boxplots of thermal stress thresholds (Tn: minimum, Tx: maximum, LTn: lethal minimum and HNT: maximum night) without categorisation (i.e. all data). The red symbol is the corresponding standard deviation (sd; i.e. dashed red line in B). (B) Boxplots of the SD by category (Region: geographic location, Wheat: type of wheat, Process: type of process targeted, and All: all three categories). Each point in the boxplot is the SD of a value of the category (e.g. for wheat: spring, winter or not specified). The purple symbols are the mean of the SDs in the boxplot, which can be compared to the SD without categorisation (dashed red line, i.e. red symbol in A). Whiskers represent 1.5 times the interquartile range.

Rezaei et al., 2018), to characterised impact of maximal temperature on some growth parameters involved in the development of yield components. The use of these lower thresholds can be justified as they are used in a specific pedoclimatic context and for specific types of wheat.

Influence of categorisation on thresholds variability

The standard deviation (SD) measures the dispersion(Altman and Bland, 2005) of the thresholds within the sub-samples of each category. The SD distribution of each stress threshold indicates that simultaneously categorising thresholds by the geographic location, type of wheat and process targeted simultaneously (Fig. 4B- all filters) decreased the SD compared to the SD of the complete sample (i.e. without categorisation) (Fig. 4 A).

To reduce the average variability of thresholds (ranging from 35 % to 66 % depending on the threshold type, Table 1), it is essential to simultaneously consider three categories: the geographical location, the type of wheat (winter or spring), and the process targeted (growth or development) (Fig. 4 B). This approach facilitates the selection of more consistent thermal stress thresholds that are better adapted to the specific characteristics of the system under study.

The consistency of the Tn threshold was improved most by categorising by the process targeted, as development processes are much more sensitive to high temperatures than growth processes. The consistency of the Tx threshold was also improved most by categorising by the process targeted, as growth processes are much more sensitive to high temperatures than development processes. The consistency of the LTn threshold was improved most by categorising by wheat type, as winter wheat is less sensitive to low temperatures than spring wheat. Choosing a subsample of threshold values used in the same geographical location can increase the precision, but it can also be too restrictive for regions with fewer information. On the other hand, for locations with abundant data, it can be possible to reach higher precision by selecting smaller geographical sub-samples.

Influence of threshold uncertainty on ecoclimatic risks

The following example highlights the potential mismatch of agroclimatic risk when using threshold values within the ranges identified in our sample. We picked the number of days that maximum temperatures exceeded Tx thresholds, or that minimum temperatures fell below Tn thresholds (Figs S6.1 and S6.2). We calculated these indicators for a common wheat variety (cv. Talent) grown in France. These indicators were calculated over phenological stages (ecoclimatic) rather than fixed calendar period (agro-climatic)(Beauvais et al., 2025; Caubel et al., 2015; Le Roux et al., 2024).

The climatological time-series is composed by 30-year period (1992–2022) from the SAFRAN reanalysis weather data interpolated in an 8 × 8 km grid in France (Météo-France) (Vidal et al., 2010). Based on our data sample, six Tx thresholds were selected for the grain-filling stage (BBCH 70–89) (Figs. 5–6), which is sensitive to high temperatures, and six Tn thresholds were selected for the stem-elongation phase (BBCH 30–39), which is particularly sensitive to low temperatures (Tn < 4°C) due to crucial processes such as meiosis (de los Campos et al., 2020; Draeger et al., 2023) (Figs S6.1 and S6.2). The Tx threshold ranged from 25°C (10th percentile) to 38°C (90th percentile), with increments of 2°C. In this way, we accurately represent the variability identified in our studies. As too few days exceed 38°C in the dataset, this threshold was excluded (Fig. 5). Over the 30-year period, mean daily maximum temperatures in France ranged from 25 to 29°C, which lay within the range for Europe. In North America, the range was much wider (Fig. 3). Maximum temperatures in France exceed 33 °C less than one day during the grain-filling phase.

We also observed large spatial differences between the regions of Normandy and Provence-Alpes-Côtes d'Azur (PACA), which have similar surface area but contrasting climates (oceanic vs. Mediterranean and mountainous, respectively) (Fig. 6). The number of days above 25°C threshold in PACA region is around 15 days and 7 days above 27°C. The climate varied more in PACA than in Normandy. Selecting a threshold of 27°C or 29°C for the grain-filling phase instead of 25°C decreased the risk of heat stress on grain during grain-filling by 45 % and 75 %, respectively. The weight loss of 1000 grains was best represented by the number of days with temperature above 25°C, for which each additional day resulted in a loss of 0.14 t/ha (Brisson et al., 2010; Brisson and Levrault, 2010; Gate and Gouache, 2010). Results were similar for the stem-elongation phase, with a decrease in the number of damaging days of about 59 % when selecting a threshold of 1°C instead of 3°C (Figs S6.1 and S6.2).

Table 1
Standard deviation of thermal stress thresholds for all phenophases when using no categories or using all three categories, and the main category that decreased it.

Threshold type	Using no categories	Using all 3 categories	Decrease	Main category
Maximum night (HNT)	4.1	1.4	66 %	Region
Minimum lethal (LTn)	5.5	3.1	44 %	Wheat type
Minimum (Tn)	3.9	2.4	38 %	Process targeted
Maximum (Tx)	5.1	3.3	35 %	Process targeted

Discussion

Our review updates the seminal work of Porter and Gawith (Porter and Gawith, 1999) by revising thermal stress thresholds according to the phenological phases and processes involved. We examined the variability of thermal stress thresholds used in an ensemble of 122 studies on common wheat and showed that filtering by geographic location, type of wheat and type of process targeted can increase the precision when selecting thresholds. It is therefore important to identify these characteristics and understand how they can influence the determination of stress thresholds.

Influence of selecting thresholds by category

Understanding the type of process targeted by the thresholds (development or growth) and the methods used in each study to define them may partly explain why the stress thresholds applied to the same process and phenological phase differed significantly. For example, thresholds estimated for wheat development were less sensitive to high temperatures but were more sensitive to low temperatures than those for growth. Some studies have combined thresholds from multiple sources before averaging and using them (Farooq et al., 2011; Khan et al., 2021; Porter and Gawith, 1999). Similarly, wheat yield and/or crop feasibility studies have sometimes averaged or overestimated thresholds to capture the variability observed in the literature (Bönecke et al., 2020; Trnka et al., 2015, 2014, 2011).

The developmental thresholds often used in phenological models of wheat are derived from cardinal temperatures obtained from temperature-response curves. These are usually mean temperatures that reflect developmental thresholds rather than growth stress thresholds (Wang et al., 2017). Similarly, assuming that wheat develops linearly as a function of temperature, which determines the basal temperature (i.e. the "apparent thermal threshold"), can lead to inaccurate estimates of the minimum and maximum development temperatures (i.e. true thermal thresholds) (Wang and Engel, 1998; Yin, 1995). Therefore, 0°C is often used as the reference Tn threshold for wheat. This indicates that cardinal temperature thresholds for development need to be distinguished from the stress thresholds for growth, which have significant

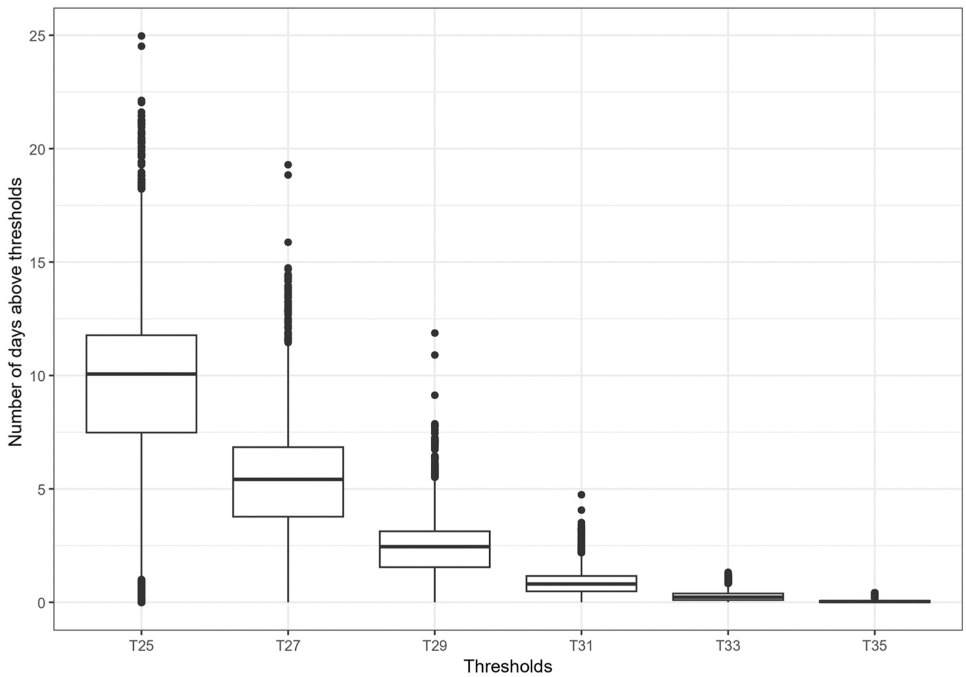

Fig. 5. Influence of the threshold temperature selected (from 25 to 35°C) on the number of days above the given temperature during the grain-filling phase (BBCH 70–89) of wheat (cv Talent), averaged over 1992–2022 for all Safran grid points (8 × 8 km) in France. Each boxplot represents the mean number of days above the threshold for each grid point. Whiskers represent 1.5 times the interquartile range.

negative effects, particularly on grain yield. Identifying the timescale of climate variables associated with a thermal stress threshold can be challenging. Sometimes, we could not tell if the article used daily or hourly mean temperature or even instantaneously measured temperatures to infer the maximum or minimum values due to lack of metadata. This is probably the reason why several Tx and Tn thresholds lie in the thermal optimum zone (Fig. 2). For example, some studies recommend a maximum of 15.7°C (Porter and Gawith, 1999) for vernalisation, while others recommend 30°C (Evans et al., 1975; Weir et al., 1984). Some studies use a Tn threshold specific to a particular phenophase, but others use the same value instead of the entire growing season, often lethal temperatures between −15°C and −20°C and a last-frost-day index, with thresholds of around −2°C (Ben-Ari et al., 2016; Di Paola et al., 2018; Harkness et al., 2020; Mäkinen et al., 2018; Trnka et al., 2015, 2014, 2011).

The type of wheat (winter or spring) should also influence the selection of thresholds, particularly for LTn and Tn, mainly because of the hardening process and vernalisation of winter wheat. Although the two wheat types had similar Tx thresholds, a higher mean Tx threshold was observed for winter wheat (Fig. 3B), which is reflected in its higher resistance to high temperatures (Zhang et al., 2022). Consequently, some studies (He et al., 2020; Zhang et al., 2022) predicted greater yield losses for spring wheat than winter wheat in the future. Breeding new varieties that are significantly more resistant to frost and high temperatures also shifts these thresholds. Numerous studies have demonstrated that the tolerance of various cultivars can be improved by introducing the specific genes responsible for this trait (Ma et al., 2024). Notably, Fowler and Limin (2004) reported a shift in sensitivity thresholds of up to −5°C (depending on the acclimation period) between a spring wheat cultivar and the same cultivar genetically modified to improve frost tolerance as a winter wheat type. Furthermore, although Zhang et al. (2022) did not directly measure differences in thermal thresholds, their study showed that, in winter wheat, a 1°C increase in temperature had a lesser impact on yield estimates for newly developed varieties—selected for greater resilience to extreme conditions (above the optimal growth temperature or below the frost threshold)—than for an older control variety. These examples illustrate the extent to which varietal improvement can profoundly alter the wheat resistance thresholds to thermal stress.

Plant phenology should also be considered because the sensitivity of meiosis, flowering, and grain-filling to low and high temperatures is relevant when selecting thresholds. These phenophases play crucial roles in the development of yield components (Brisson and Levrault, 2010). Unlike vegetative development, which can be compensated for through tillering, there are no effective compensation strategies for these sensitive phenophases. However, particularly between stem elongation and booting, acclimatisation phenomena can occur, significantly mitigating the reduction in grain yield caused by heat stress during grain-filling (Fan et al., 2022, 2018)

As the response of varieties to growing conditions depends on the interactions between genotypes and the environment, each wheat variety has an optimal production zone and characteristics that can influence thresholds (Barkley and Peterson, 2008). Thus, must be selected from a consistent set. The geographic location of the study area is important when selecting thresholds, particularly for minimum lethal temperatures. In the geographical study (Fig. 3), the significant differences observed among thresholds were due to a lack of representativeness of certain regions, and thus their thresholds were influenced more by the methods of the studies than by the climate of the regions. Moreover, our dataset lacks a substantial representation of hotter and drier regions, such as parts of Africa, where yield potential is lower. This gap arises from the limited availability of studies conducted in these environments. Therefore, the thresholds defined in this study, which primarily reflect high-yielding production areas without irrigation, may not be directly applicable to such conditions. Therefore, their use should be approached with caution, as they may not accurately capture the dynamics of heat stress in these environments. For example, Shew et al. (2020) identified a threshold of 30°C as a relevant indicator of wheat yield loss in South Africa.

Therefore, it is crucial to disentangle the characteristics that introduce uncertainty in the determination of stress thresholds: was the threshold assessment made for growth or developmental processes in winter or spring wheat, and for what spatial scale? Furthermore, the experimental conditions vary among studies and have a direct impact on

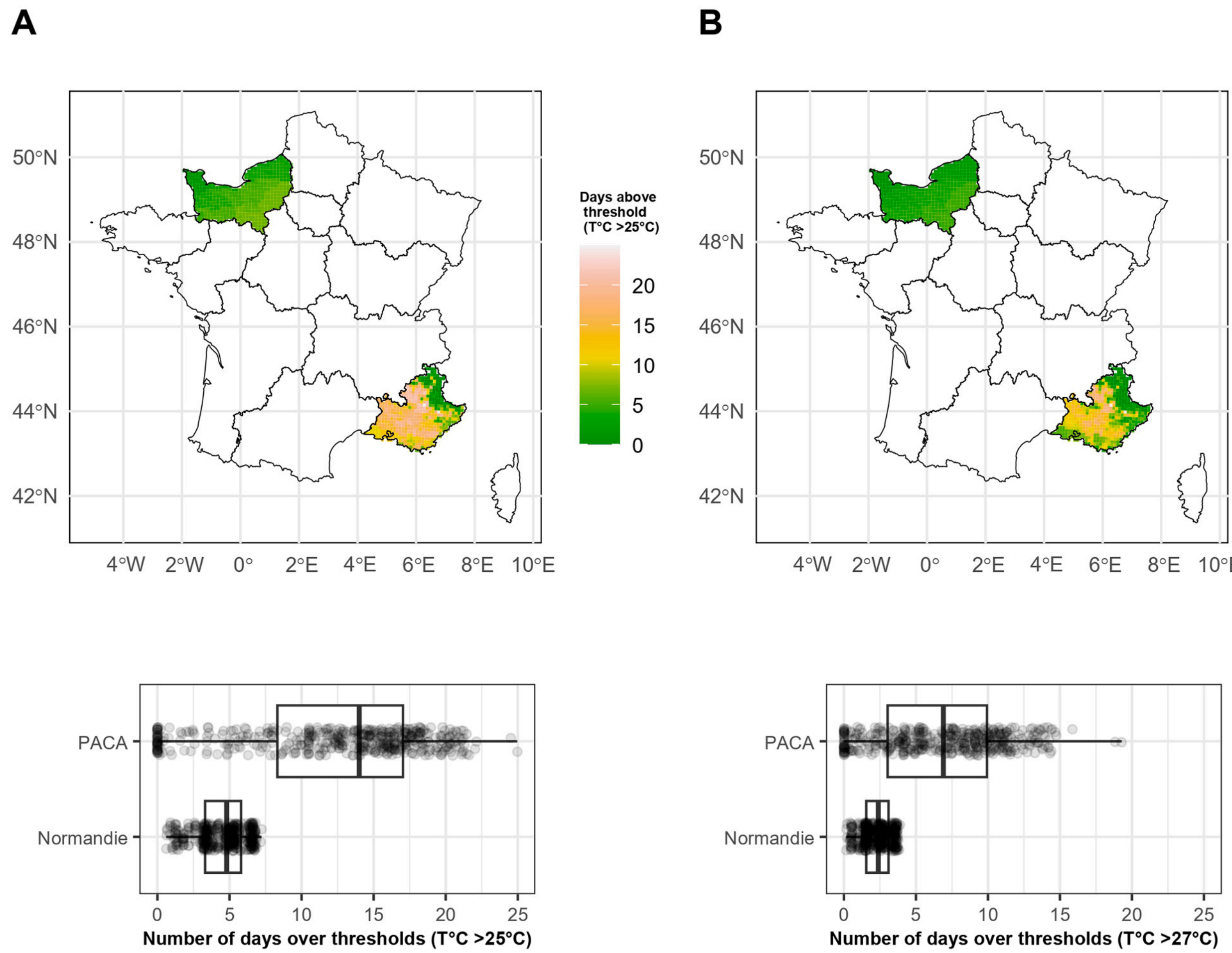

Fig. 6. Spatial variability in the number of days above a given temperature for the grain-filling phase (BBCH 70–89) for wheat (cv Talent), averaged over 1992–2022 for each Safran grid point (8 × 8 km) in Normandy (left) and Provence-Alpes-Côtes d'Azur (PACA) (right). Spatial distribution (top) and boxplots (bottom) of the number of days above (A) 25°C or (B) 27°C. Each point represents each Safran grid point in the region. Whiskers represent 1.5 times the interquartile range.

the measured thresholds. For example, is the stress threshold determined under controlled conditions or in a field where the canopy temperature can differ depending on agricultural practices (Birthal et al., 2021) ? Is stress treatment applied continuously or over a specific time? Similarly, is stress induced gradually or suddenly? In addition, the availability of water, nitrogen, or light may also modulate the observed effects, but the lack of metadata in the articles prevents us from including them in our classification to analyse the influence of such parameters on thresholds. The stress thresholds were lower for the field experiments than for those conducted in a controlled environment, particularly for HNT, Tn, and LTn (Fig. S7). These results were consistent with those of a large study by Wolkovich et al. (2012). They showed that warming experiments strongly underestimated the phenological sensitivity of plants to temperature compared with observations because of experimental artefacts. This initial finding highlights the need for a more detailed experimental setup for thresholds assessment.

Rezaei et al.(2018) addressed this issue by showing that the uncertainty of the thermal stress at anthesis (temperatures above 31 °C) on yield could be attributed to differences in experimental methodology, particularly the additional effect of drought depending on the substrate used. Furthermore, Wardlaw et al. (2002) showed that at maturity, chronic heat stress (24/19 °C) applied during the grain-filling period was more detrimental in terms of kernel dry weight than heat shock exposures of 7 days at 27 °C or 6 days at 30 °C during the same period.

The same study addressed the concept of exposure duration, which was not evaluated in this study. Indeed, the results indicate that exposure to heat shock at 27 °C for 7–8 days appears to be less harmful than exposure at 33 °C for 5–6 days, highlighting the inverse correlation between duration and intensity of stress. In general, the stress duration in threshold characterisation studies is often expressed in hours per day over variable periods ranging from a few days to several weeks. In addition, exposure conditions may vary considerably, whether continuous, intermittent, abrupt, or gradual, making the analysis of the duration more complex. Given the scale mismatch between data from threshold characterisation studies (hourly scale) and climatic data used in impact studies (mostly on a daily scale), it is common practice to consider the day as the reference unit for discussing stress. We chose not to consider duration and focused on the intensity thresholds above which there is a risk to the plant, rather than the potential damage to the plant caused by the combination of stress intensity and duration.

The question of the dependence of thresholds on the environmental conditions in which they are established is more broadly linked to the need to better characterise the laws governing the response of ecophysiological processes to extreme temperature ranges. The duration, variability, continuity or discontinuity, and gradual or abrupt establishment of extreme temperature conditions need to be studied at finer scales to better understand their interaction with plant sensitivity.

The database provided in with article offers access to all relevant information and enables the selection of stress values tailored to the specific requirements of the intended application of the data. (https://entrepot.recherche.data.gouv.fr/privateurl.xhtml?token=3e1e8f0c-e8c2-44c6-94d6-15e83253bb17).

Relevant details of the method used

Although some articles are likely to have been omitted, the ensemble we sorted is more than twice as large as the seminal paper of Porter and Gawith (1999) (reference database) and allows statistically significant results to be drawn. We have highlighted the magnitude of uncertainty from stress thresholds in the estimation of agro-climatic risks for wheat, and consequently, on yields. This has rarely been explored in studies on impacts of climate on wheat. The number of articles differed among categories (region, wheat, and process) and thermal stress thresholds. For example, some conclusions can be drawn about the HNT threshold (high night temperatures), although there seems to be a convergence around 23°C, which appears to be particularly detrimental to wheat yield (i.e. reduced spikelet fertility, grains per spike, and grain size) before flowering and during the grain-filling phase (García et al., 2015; Impa et al., 2021; Parveen et al., 2022; Prasad et al., 2008). These results show a lack of information and diverse studies on this phenomenon, which were not taken into account in the previous review by Porter and Gawith (1999). This is a relatively new phenomenon, which remains to be understood and proves to be very important as global nighttime minimum temperatures are rising faster than daytime maximum temperatures (Cox et al., 2020; Impa et al., 2021).

In addition, threshold ranges were provided for each phenophase (S1). When a study used a threshold for several phases (e.g. booting to flowering) or the entire growing season, the latter was repeated for each phase. Consequently, mean LTn, Topt, HNT, and Tx thresholds did not differ significantly (Fig. S5). Measurement conditions (i.e. in a controlled environment or the field) can also influence results greatly (Langstroff et al., 2022). Similarly, a change in scale (i.e. fine-scale processes of individual organs or plants vs longer-term processes over multiple phenophases at the field scale) can cause results to differ (Poorter et al., 2016). Consequently, the literature does not agree on threshold temperatures. The hourly or daily duration of stress was not considered, which is important information that can be obtained by comparing phenotyping in a controlled environment or the field.

Importance of a systemic approach

The thresholds used to estimate climate risks for wheat crops and other hazards play a crucial role. Focusing only on thermal stress thresholds does not fully capture the overall risk or future of the wheat production sector. For example, rising atmospheric CO2 levels (Zhu et al., 2023) and their interactions with temperature must be considered. Water deficits also interact with these factors and alter the canopy microclimate. (Bazzaz et al., 2015). This may ultimately help explain the conflicting results of studies on yields in the context of climate change, with some predicting an increase in yield (Asseng et al., 2019; Bouras et al., 2019; Challinor et al., 2014), and others predicting a decrease (Anwar et al., 2007; Asseng et al., 2015; Geng et al., 2019). The effects of increased $CO_{2,}$ such as increased photosynthetic efficiency and water use, also contribute to these inconsistencies and uncertainties (Asseng et al., 2019; Kimball, 2016). Other adverse events, such as droughts and floods, are also relevant when determining yields (Ben-Ari et al., 2016; Lesk et al., 2016; Trnka et al., 2015; Zhu et al., 2021). Interactions between and combinations of climate hazards can have more damaging effects than individual hazards (El Habti et al., 2020). Diseases (Bajwa et al., 2020; Chaloner et al., 2021; Juroszek and von Tiedemann, 2013) and storms (Elahi et al., 2022) can add to these hazards and further damage crops. Nevertheless, when considered, these interactions between different stress and management factors, are included downstream the analysis chain, which usually begins with the choice of stress threshold values. An additional issue is the impact of rising temperatures on the length of the wheat cycle and associated adaptation strategies that need to be developed to address climate change (Bönecke et al., 2020; Dížková et al., 2022; Hu et al., 2005; Le Gouis et al., 2020; Xiao et al., 2013; Zhang et al., 2021).

Conclusion

This review complemented Porter and Gawith's (1999) seminal work, highlighting the high variability of thermal stress thresholds for common wheat in literature and resulting inconsistencies. Consistent threshold temperatures require consideration of contextual framework, location, target process, and phenological phase. We analysed the main categories of geographic location, type of wheat, and targeted biological processes. Considering all three categories improved threshold precision by a mean of 46 % (from 35 % to 65 %, depending on the threshold type). Awareness of threshold value uncertainty is crucial for impact studies. For example, selecting a Tx threshold that is 2°C higher (27°C vs. 25°C) decreased estimated f heat stress risk on grains during grain-filling in wheat in France by 45 %. We provide a complete database from this review, including thresholds from 122 articles and associated metadata. These metadata make it possible to characterise the validity range of these thresholds according studied region, the type of wheat (winter or spring), and the process and phenological stage involved. This database allows the user to select the most relevant sources to define thresholds and their uncertainties. This selection is based on the agroclimatic indicator to be constructed or the model to be parameterised, and its application domain. We argue that threshold uncertainties should be included in impact assessments to better understand the agro-climatic risks for crops in the context of climate change. These risk analyses can help interpret decreases in production and promote the development of new varieties more resistant to climatic hazards, including thermal and water stress (Gabay et al., 2023). Structural changes in climate hazards (Amouzay et al., 2023; Mbow et al., 2022) challenge current thresholds used to calculate climate risks. This requires the development of new stress thresholds to reflect phenological shifts in the crop cycle, which, in turn, changes the balance between the exposure and vulnerability of phenophases owing to increases in climate extremes.

Our results provide a context for interpreting previous studies depending on the position of the thresholds used (Figs. 2 and 3) within the ensemble of possible values, and thus to estimate the potential under/over estimation. We recommend avoiding deterministic thermal thresholds in future studies, but rather a range of values (Fig. 6), to incorporate the uncertainty of this probabilistic parameter and avoid one of the many potential sources of contradictory conclusions, along with interactions with other environmental conditions and differences in the experimental protocols.

CRediT authorship contribution statement

Aubry Mael François Joseph: Writing – original draft, Methodology, Investigation, Conceptualization. **Furusho-Percot Carina:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **García de Cortázar-Atauri Iñaki:** Writing – review & editing, Validation. **Launay Marie:** Writing – review & editing, Methodology, Conceptualization. **Le Roux Renan:** Writing – review & editing, Methodology, 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.

Acknowledgements

We thank Marie-Odile Bancal and Elizabeth Wolkovich for their proofreading and invaluable feedback on the draft of this paper. We thank Arvalis for co-funding the phd project. Finally, we thank Météo-France for providing the climate data (SAFRAN).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.eja.2025.127623.

Data availability

I have included the database link in my manuscript

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