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# Predicting pre-harvest sprouting susceptibility in barley: Looking for "sensitivity windows" to temperature throughout grain filling in various commercial cultivars

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ABSTRACT

Pre-harvest sprouting (PHS) is common in cereals that lack grain dormancy if maturing grain is exposed to rain. This phenomenon leads to immediate loss of seed viability, and since the malting process requires germination, its occurrence is highly undesirable in malting barley crops. Dormancy release rate is genetically and environmentally controlled. We evaluated the effect of temperature during grain filling on the dormancy release pattern (and then on the PHS susceptibility) of grains from five malting barley (*Hordeum vulgare* L.) cultivars widely sown in Argentina, with the aim of predicting PHS susceptibility of a barley crop from easy-to-gather data. Barley cultivars (Quilmes Ayelén, Q. Palomar, Q. Painé, B1215 and Scarlett) were sown on different dates over a 3-year period for generating variability in the thermal environment during grain filling. The period from pollination to physiological maturity (PM) was adjusted to a thermal time (TT) scale, which was then arbitrarily divided into 50 °C d intervals. Mean air temperature within each interval and for the whole filling period was calculated for the different sowing dates. Dormancy release pattern was followed by determining a weighed germination index (GI) throughout grain filling and maturation. We sought a linear relationship between temperature during grain filling and GI at some moment after PM. For all barley cultivars, except B1215, a significant ($p < 0.001$) and positive correlation was found between the GI of grains with 10–20% moisture content (fresh basis) and mean temperature within TT intervals located at the last stages of seed development. Then, simply temperature-based models for predicting crop PHS susceptibility were generated for each barley cultivar. Moreover, we intended a single, universal prediction model constructed with data from all cultivars. Two general forms were proposed, but the relationships were slightly less tight when each barley cultivar model was used. A preliminary validation for each cultivar model was done for three genotypes with independent data from four sites of the major barley production area in Argentina. When comparing experimental and field data regressions we did not find significant differences in slope for any cultivar ($p > 0.25$). However, most of the observed GIs were higher than predicted. This upwards displacement of GI–temperature relationship suggests the role of other environmental factors (i.e. water and soil N availability, day length), differing among tested locations. We are currently evaluating and quantifying the effect of these factors with the aim of improving PHS susceptibility prediction in malting barley crops.



## 1. Introduction

Dormancy is an internal characteristic of the seed that impedes its germination under otherwise adequate temperature, hydric, and gaseous conditions (Benech-Arnold et al., 2000b). As in most cereals, dormancy in the barley grain is coat-imposed, but presents a distinctive characteristic: the glumellae (hull, lemma and palea) adhering to the caryopsis represents a further constraint for embryo germination in addition to that already imposed by endosperm plus pericarp (Corbineau and Côme, 1980; Benech-Arnold et al., 1999). The inception of dormancy occurs very early in barley (Benech-Arnold, 2001). Embryos are usually fully germinable from early stages of development [i.e. 15–20 d after pollination (DAP)] if isolated from the whole grain and incubated in water (Benech-Arnold et al., 1999); the whole grain, however, reaches full capacity to germinate well after it has been acquired by the embryo. Dormancy release of barley grains rarely starts before the crop reaches physiological maturity (PM). Genotypic

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variability exists in the dormancy release pattern of barley crops: some cultivars are released abruptly from dormancy (i.e. within days), others more gradually (i.e. within weeks), while others remain dormant for several months (Benech-Arnold, 2001). The malting process requires grain germination; hence, a low dormancy level at harvest is a desirable characteristic since the grain can be malted immediately after crop harvest; thus, avoiding costs and deterioration resulting from grain storage until dormancy is terminated (Benech-Arnold, 2001). However, selection pressure against dormancy has gone too far and led to development of genotypes whose grains are fully germinable (i.e. very low dormancy) even prior to crop harvest (Benech-Arnold, 2001). When grain dormancy level in the period from PM to harvest maturity (HM) is low, a short exposure (<24 h) to rain water in the field may trigger embryo growth, and thus lead to pre-germination or pre-harvest sprouting (Benech-Arnold, 2001). Pre-germination takes place when embryo growth begins but the process is interrupted by desiccation before radicle emergence occurs. In this case, grains maintain their viability but seed longevity is reduced dramatically (Del Fueyo et al., 1999). If damp conditions in the field persist longer, the germination process may proceed towards a point of no return beyond which the embryo loses desiccation tolerance (Schoper et al., 1979). This phenomenon is known as pre-harvest sprouting (PHS) and implies immediate loss of seed viability; as a result, grains become useless for malting purposes. The malting industry has high quality standards for the seed lots they buy, and a lot with pre-germinated or sprouted grains can be docked or even rejected (Brooks, 1980; Bason et al., 1992).

Depending on the rate of dormancy loss after PM, barley genotypes can be highly resistant to PHS (i.e. low rate), present an intermediate behavior (i.e. medium rate), or be highly susceptible (i.e. high rate). Sprouting susceptibility is determined mainly by the genotype. However, dormancy can be also influenced by the environment experienced by the mother plant (Kahn and Laude, 1969; Reiner and Loch, 1976; Nicholls, 1982; Schuurink et al., 1992; Cochrane, 1993; Hillhorst, 1995; Biddulph et al., 2007). Some well-defined patterns occur with several environmental factors tending to have similar effects in different species. Lower dormancy is generally associated with high temperatures, short days, light having a high red/far-red ratio, drought, and high N levels during seed development (Fenner, 1991). Among the different factors acting on the mother plant, temperature appears to be the primary determinant of year-to-year variation in grain dormancy in barley (Kivi, 1966; Reiner and Loch, 1976; Nicholls, 1982; Buraas and Skinnes, 1985; Cochrane, 1993). Nevertheless, evidence suggests that temperature might be critical only within a sensitivity period during grain filling (Reiner and Loch, 1976; Buraas and Skinnes, 1985; Rodríguez et al., 2001).

In barley cultivars with fast dormancy release after PM, or in those with long-lasting dormancy, environmental factors might not affect their sprouting behavior; the former will always behave as sprouting-susceptible, while the latter will always be sprouting-resistant. However, in cultivars with intermediate behavior, changes in the speed of dormancy release after PM (as affected by the environment during grain filling) may result in these cultivars behaving as sprouting-resistant in some years and as sprouting-susceptible in other years (Benech-Arnold, 2001). Although PHS could be prevented by using genotypes that lose their dormancy a few weeks after crop harvest, on the basis of the present knowledge, it is very difficult to adjust the timing of dormancy loss to a precise and narrow "time window" (i.e. neither as early as to expose the crop to the risk of PHS, nor as late as to maintain the seed lot in storage for a long time until dormancy is terminated). Therefore, it becomes necessary to develop crop management tools that help to reduce the incidence of this adversity. These tools should include simple models that predict the susceptibility of a barley crop to suffer sprouting damage.

Rodríguez et al. (2001) found a close relationship between mean temperature during a narrow thermal time window within the grain-filling period (i.e. 300–350 °C d after anthesis), and grain dormancy level at half-way between PM and harvest maturity (HM) (estimated through a germination index 12 d after PM) in cultivar Quilmes Palomar. This resulted in the development of a mathematical linear model that permits, on the basis of easy-to-gather data (i.e. anthesis date and mean daily temperature during grain filling), the prediction of the susceptibility of a barley crop to suffer sprouting damage. This prediction, together with the weather forecast for a moment close to harvest, should allow one to make crop management decisions as, for example, anticipating harvest if the risk is high (Mares, 1984; Paulsen and Auld, 2004).

In order to generalize this model, it is necessary to explore the existence of similar sensitivity windows in a wide range of cultivars. Moreover, if these sensitivity windows have a similar relative location within the grain-filling period in all cultivars, it could be indicating that a major physiological process determining the timing of dormancy release is taking place during that period. Clearly, this would constitute a step forward towards the manipulation of the timing of exit from dormancy in this crop.

In this work we studied the dynamics of grain dormancy release in five commercial barley cultivars growing under different thermal environments (i.e. several sowing dates in three different years). We sought simple mathematical relationships between air temperature during a narrow window of the grain-filling period and some measure of grain dormancy level in the PM–HM period that we assumed to be closely related to PHS susceptibility. The validity of the obtained relationships was tested against independent data from crops growing in commercial plots.

## 2. Materials and methods

### 2.1. Plant material

Five two-row malting barley cultivars (Quilmes Ayelén, Quimes Palomar, Quilmes Painé, B1215 and Scarlett) widely sown in Argentina were used for the experiments. Seed was provided by Maltería Pampa S.A and Cervecería y Maltería Quilmes S.A.I.C.AyG.

### 2.2. Experimental design

Experiments were conducted in the experimental field of the Facultad de Agronomía of the Universidad de Buenos Aires (FAUBA), placed in Buenos Aires city, Argentina (34°25′S, 58°25′W). To obtain a range of temperature conditions during grain filling, all barley genotypes were sown on four different dates in 2004 (between July and October) and 2005 (between June and September), and on three dates in 2006 (between July and September). On each sowing date and for each barley cultivar, 2.7 $m^2$ plots were located within the experimental field following a randomized complete block design, with three replicates. Distance between rows was 0.15 m, and seeding density was that for obtaining a stand of 250 plants $m^{-2}$. All plots were fertilized at approximately two leaves appearance with urea to obtain a total soil content of 100 kg N $ha^{-1}$ for the upper 60 cm of the profile. Amount of urea applied at each sowing date varied to compensate for residue soil nitrate content (determined from soil samples collected at each date). Weeds were removed manually. Insects and diseases were controlled following the typical schedule used under production conditions. Supplementary water was provided when necessary to avoid water stress.

### 2.3. Duration of grain-filling period

Thermal time (TT) accumulation during the period from anthesis to PM was calculated for each barley cultivar following the methodology used by Rodríguez et al. (2001). Base temperatures ($T_b$) values for the grain-filling period were unknown for these cultivars, except for Quilmes Palomar, which was determined to be 5.5 °C by Rodríguez et al. (2001). Briefly, for each cultivar, the relative grain dry weight (GDWr) (i.e. grain dry weight at each sample date was related to its maximum value) throughout grain filling was plotted against TT accumulated from anthesis onwards using a bilinear model subjected to boundary conditions [i.e. grain mass is described by two equations with one boundary, $c$ (Miralles et al., 1996)]:

$$\text{GDWr} = a + b \times x \quad \text{if } x \leq c \tag{1}$$

$$\text{GDWr} = a + b \times c \quad \text{if } x > c \tag{2}$$

In this function $a$ stands for intercept (kg kg$^{-1}$), $b$ for rate of GDWr increase (kg kg$^{-1}$ °C d$^{-1}$) during period of linear dry matter accumulation, $c$ for TT (°C d) at which the filling phase ended (i.e. PM), and $x$ for accumulated TT (°C d) after anthesis. Parameters $a$, $b$ and $c$ were iteratively calculated by fitting least squares until no improvement in $r^2$ was obtained with further iterations using the optimization routine of Table Curve software (Jandell, 1991). Optimization routine was repeated in each barley cultivar for different $T_b$ values. The $T_b$ value that maximized overall fit in each case, as measured by the $r^2$, was chosen as the grain filling $T_b$ value for that cultivar.

The mean daily temperature values ($T_{md}$) used for TT accumulation were obtained from a meteorological station located in the experimental field. In all experimental years and for each cultivar, 4–5 spikes were randomly collected on each of several sampling times over the grain-filling period, and grains from the central third of spikes were separated and dried at 80 °C for 48 h for grain dry weight (GDW) and relative (fresh weight basis) grain moisture content (%GMC) determinations. All dry weight determinations were done with a precision balance (Mettler Toledo AB204, Switzerland; 0.1 mg resolution).

### 2.4. Assessment of grain dormancy release

Germination tests were conducted in the three experimental years. Spike sampling for germination tests began 22 d after anthesis and was repeated every 5–4 d until harvest maturity. On each sampling date, 6–7 spikes were randomly collected from the inner area of each plot. Grains from the central third of the spikes were pooled and immediately used for germination assays.

On each germination assay, 25 grains from each sample (one per plot) were placed in plastic Petri-dishes (90 mm diameter, with two layers of Whatman no. 5 filter paper, and 6 mL of distilled water) and incubated at 20 °C for 12 d. The number of germinated grains (radicle protruding > 1 mm) was recorded daily and used to calculate a weighed germination index (GI, Eq. (3)), as done in previous studies (Steinbach et al., 1995; Benech-Arnold et al., 1999). In this index maximum weight is given to grains that germinated first and less weight to those that germinated later:

$$\text{GI} = \frac{\{\sum_{i=1}^{12}[12 - (i-1)] \times n_i\}}{2.5} \tag{3}$$

where $n_i$ is the number of seeds germinated within day $i$ (and not the accumulated number of germinated seeds) for a 12-d incubation period. This index ranges from 0 (no germination within the 12-d period) to 120 (25 seeds germinated on the first day). On each sampling date GI values obtained for the three replicates of each cultivar were averaged into a single observation.

### 2.5. Generation of the models

We followed the methodology used by Rodríguez et al. (2001), with modifications. Seed water status is a good indicator of grain's stage of development and maturation (Bradford, 1994; Saini and Westgate, 2000). Grain drying dynamics has been reported to have an impact on the pattern of dormancy release of many seeds (Nicholls, 1979; Sawhney and Naylor, 1982; Bewley et al., 1989; Oishi and Bewley, 1992). Rodríguez et al. (2001) assessed grain dormancy 12 d after PM, considering that this stage was representative enough of the dormancy status of the grain during the time window going from PM to HM, and hence, indicative of crop's PHS susceptibility. In this case we measured dormancy when the grain had reached a particular water content (instead of measuring it after certain amount of days after PM), thus allowing us to compare dormancy levels of grains coming from crops with different grain drying rates (resulting from the different environmental conditions during the drying period among sowing dates).

For each barley cultivar we related the temperature experienced by the crop during grain filling with the GI of grains harvested with 10–20% (fresh basis) moisture content (approximately 15 d after PM). This should give us a close idea of the rate with which grains are being released from dormancy, and, consequently, of the crop's susceptibility to suffer PHS (Benech-Arnold et al., 1999).

The procedure carried out to generate the models was as follows:

1. Mean temperature between anthesis and PM was calculated for each sowing date and genotype and correlated with GI values for grains harvested with 10–20% (fresh basis) moisture content ($GI_{10–20\%GMC}$) for that sowing date and genotype.
2. The TT from anthesis to PM was arbitrarily divided into 50 °C d intervals.
3. Average temperature within each TT interval ($T_{mTT}$) was calculated from averaging mean daily temperature in the interval. Mean daily temperature was calculated as: [$T_{max}$ (maximum daily temperature) + $T_{min}$ (minimum daily temperature)]/2
4. For each genotype, and for each TT interval, the mean temperature values for each sowing date were then correlated with $GI_{10–20\%GMC}$ for that sowing date.

An interval within grain filling with sensitivity to temperature for the determination of the rate of dormancy release would be that showing a significant correlation between mean temperature for the interval and GI values. For simplicity, and on the basis of previous knowledge (Rodríguez et al., 2001), we expected this association to be linear.

### 2.6. Field validation of the models

We tested the models generated for three cultivars (Q. Ayelén, Q. Painé and Scarlett) using seed from experimental plots located at four sites of the SE [Barrow (38°20′S, 60°13′W) and Tres Arroyos (38°23′S, 60°17′W)] and SW [Coronel Suárez (37°28′S, 61°56′W) and Bordenave (37°46′S, 63°04′W)] of Buenos Aires province, the major region for barley production in Argentina. Plots belonged to experimental fields of commercial malthouses (Cervecería y Maltería Quilmes and Maltería Pampa) and to the INTA (National Agriculture Research Institute of Argentina). Several sowing dates were used for each cultivar and location (total no. of plots = 115). All plots were rainfed and N fertilized with agronomic rates (i.e. 40–100 kg N ha$^{-1}$). Anthesis date was estimated from heading date (40 °C d before heading occurred in 50% of the plants).

Temperature data were collected from the nearby meteorological stations (inside the experimental field in some locations). Time of PM for each plot was identified when the accumulated TT after anthesis reached the previously estimated value for each cultivar. Between 5 and 15 d after PM, 15–20 spikes were randomly collected from each plot. The samples were stored at −20 °C until germination assays began (as described above).

### 2.7. Statistical analysis

The $GI_{10-20\%GMC}$ values (average of three subsamples) obtained for different sowing dates and barley cultivars were considered as independent observations. The relationships between $GI_{10-20\%GMC}$ and mean temperature values were assessed with correlation analyses, and correlation coefficients ($r$) tested for significance. Significant relationships were then described with a simple linear regression model. Significance of differences between the parameters of linear models was evaluated using the $F$-test (Statistix v7.0, 2000). Correlation and $F$ tests were considered significant at $p < 0.05$.

**Table 1**
Grain filling duration and base temperature for grain-filling period for each barley cultivar.

| Barley cultivar | Grain filling duration (°C d) | Base temperature (°C) |
|---|---|---|
| Quilmes Ayelén | 377 | 5.0 |
| B1215 | 393 | 4.5 |
| Quilmes Palomar | 347 | 5.5 |
| Quilmes Painé | 345 | 5.0 |
| Scarlett | 358 | 7.5 |

## 3. Results

### 3.1. Grain-filling period and physiological maturity

For each barley cultivar, the accumulated TT between anthesis and PM obtained by a bilinear regression analysis and the base temperature value that maximized data fitness to the regression model are presented in Table 1. Grain filling duration for all cultivars was between 345 and 393 °C d; with Quilmes Painé

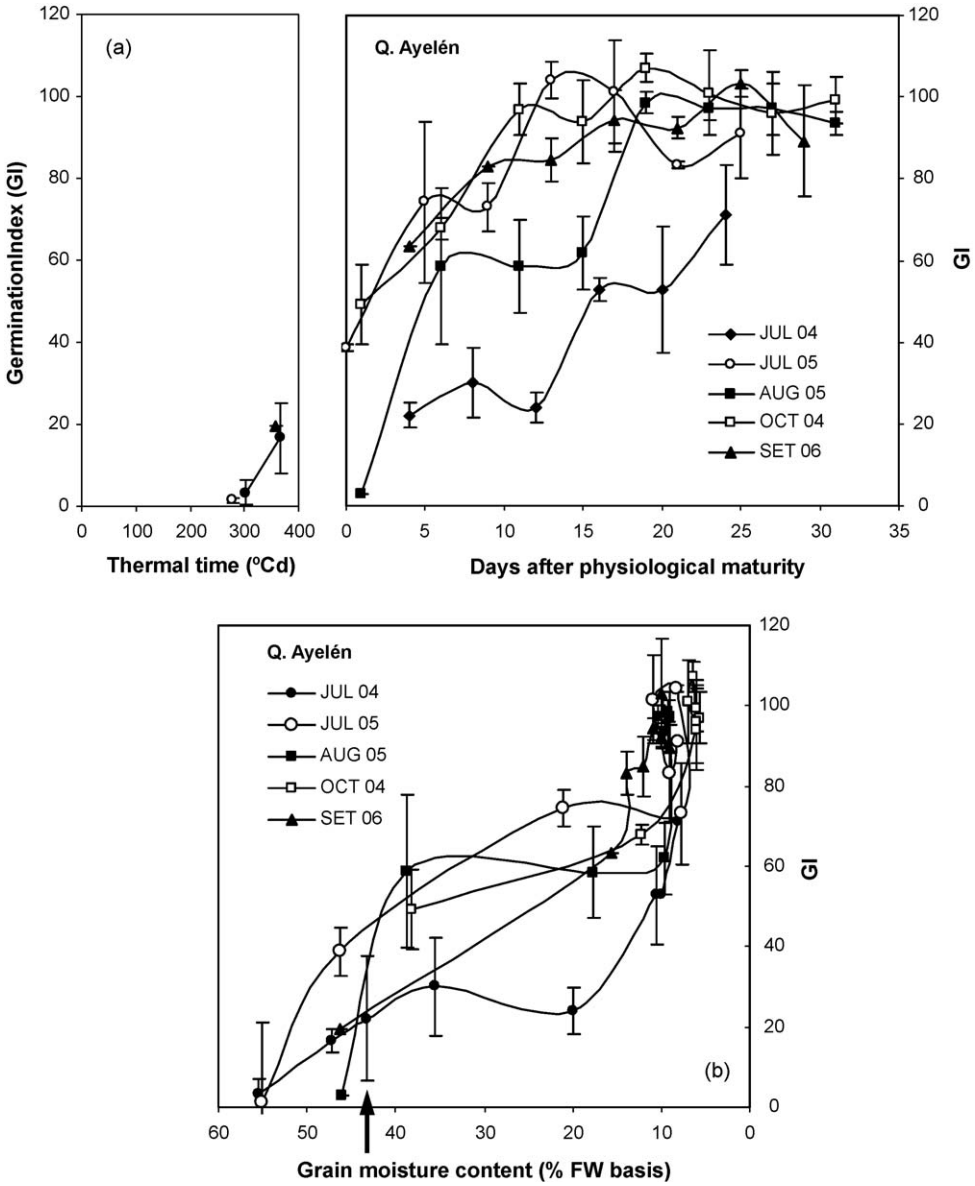


**Fig. 1.** (a) Germination index for grains harvested at different times before (thermal time scale) and after physiological maturity (PM) (days after PM scale) for Quilmes Ayelén cultivar sown on different dates during 2004–2006 years. Each value is the average of three replicates. (b) The same GI evolution pattern plotted against a relative grain moisture content scale. Vertical arrow indicates PM. Vertical bars are mean SE when larger than the symbol.

exhibiting the shortest duration (345 °C d) and B1215 the longest one (393 °C d). Base temperature ($T_b$) for this period was similar for all cultivars (ca. 5.0 °C), except for Scarlett that exhibited a markedly higher value (7.5 °C). The $T_b$ value for Q. Palomar coincided with that found by Rodríguez et al. (2001), and the $T_b$ values for the other genotypes analyzed in this paper were similar to those reported for other barley cultivars (Goyne et al., 1996). Grain filling duration for Q. Palomar found by Rodríguez et al. (2001) was longer (440 °C d) with respect to the value found in our experiments (347 °C d).

### 3.2. Dormancy release

The dormancy release pattern of each barley cultivar was seen as the evolution of the GI of grains throughout seed development and maturation. The GI evolution pattern of grains from cv. Quilmes Ayelén, in days after physiological maturity (DAPM) and relative grain moisture content (%GMC) scales is shown as an example (Fig. 1a and b). For all barley cultivars GI remained close to zero until PM (data not shown), indicating that virtually no sprouting risk exists before PM. The GI began to increase after PM but it did not follow a sigmoid or a linear pattern. For some sowing dates and cultivars (data shown only for cv. Q. Ayelén) the GI evolution showed a bilinear pattern, with a plateau (Fig. 1a). Others dates exhibited an increase of GI from PM until it became stable or even decreased temporarily between 5 and 15 DAPM (Fig. 1a). Afterward, GI continued to increase until maximum values were reached at about 30 DAPM or later (Fig. 1a). All barley cultivars presented these two types of GI evolution pattern, with B1215 showing the more rapid GI increase throughout maturation in agreement with its high PHS susceptibility (data not shown). Contrasting GI values among sowing dates were evident after PM, for all the cultivars tested. Significant differences among sowing dates occurred between 5 and 25 DAPM, and greatest variability was observed between 8 and 13 DAPM, with GI values ranging from 11 to 100 (data not shown). These differences in GI values presumably reflect differences in sprouting susceptibility. Indeed, a GI of 27 indicates 2% germination after a 48-h imbibition period at 20 °C, while a GI of 111 represents 87% germination after the same period (Table 2).

**Table 2**
Day-to-day evolution of cumulative germination percentage for grain samples (cv. Quilmes Ayelén) with five different germination index (GI) values incubated at 20 °C. Values are the average of three independent germination trials with the same GI.

| GI | % Germination | | | |
|---|---|---|---|---|
| | Day of incubation | | | |
| | 1 | 2 | 3 | 4 |
| 6 | 0 | 0 | 0 | 1 |
| 27 | 0 | 2 | 6 | 10 |
| 44 | 2 | 11 | 21 | 34 |
| 82 | 18 | 39 | 62 | 70 |
| 111 | 53 | 87 | 96 | 97 |

When GI was plotted against relative grain moisture content (%GMC) a particular pattern emerged for most cultivars and sowing dates (data shown only for cv. Q. Ayelén). GI began to increase when the barley grain had reached a moisture content of 55–45%, immediately before PM was attained (around 45–40% GMC) (Fig. 1b). Then, GI became stable between 40 and 15% GMC, for most sowing dates. Afterward, GI continued to increase rapidly until maximum values were reached at around 12–8% GMC (Fig. 1b). Using this moisture scale we identified a range of water content (i.e. 10–20% GMC, around 15 DAPM for most sowing dates) within which maximum differences in GI between sowing dates

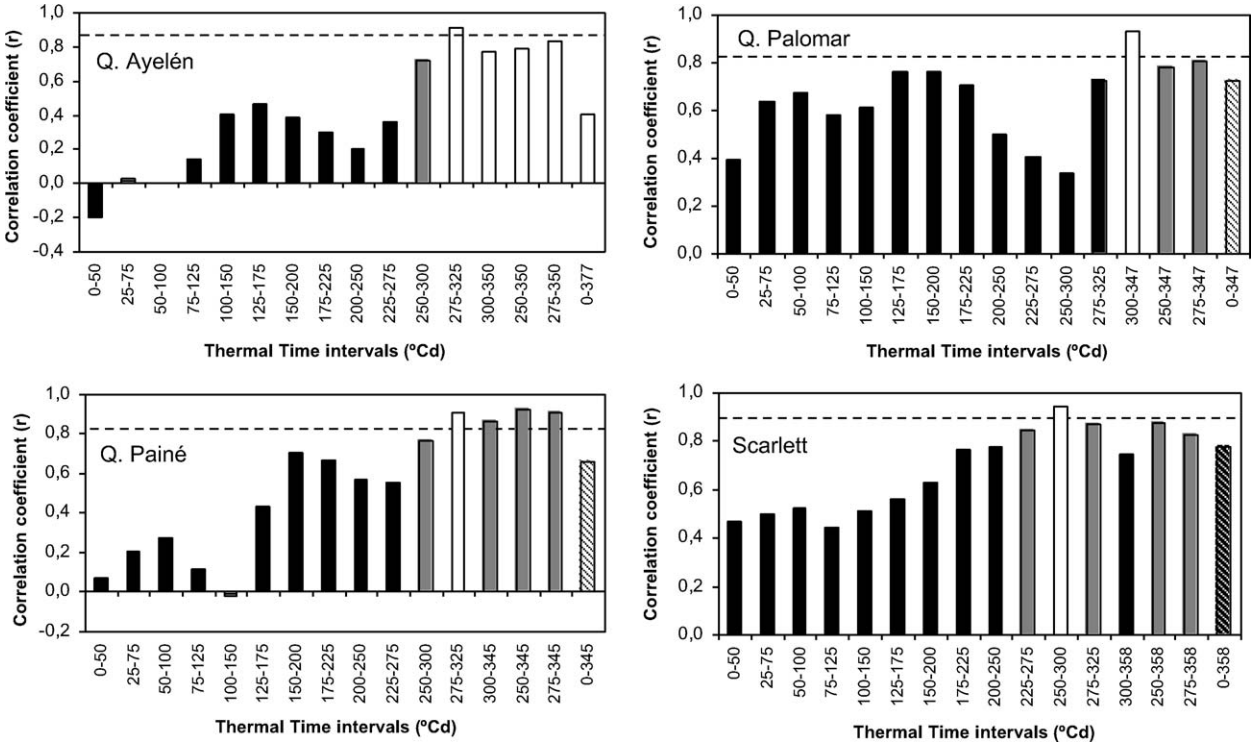


**Fig. 2.** Correlation coefficients ($r$) obtained between GI of grains harvested with 10–20% moisture content ($GI_{10-20\%GMC}$) and mean air temperature occurred within different 50 °Cd intervals throughout grain-filling period, for four barley cultivars (Quilmes Ayelén, Q. Palomar, Q. Painé and Scarlett). Empty bars indicate the TT interval significant at $p < 0.001$ (dotted bars include or overlap this TT interval); dashed bars indicate the correlation for the mean air temperature during the whole grain-filling period. Horizontal dashed line indicates statistical significance at $p < 0.001$. Each correlation included eleven observations, except for Scarlett (10 observations).

were found for all cultivars (near PM and close to HM all sowing dates showed similar values of GI), possibly associated with differences in the crop's PHS susceptibility among sowing dates.

Since grain drying dynamics can modify the dormancy release pattern, the use of a relative grain moisture content scale for plotting GI allows comparing dormancy level of grains coming from crops with different grain drying rates. In this way, differences found in GI would be given by different environmental conditions (e.g. thermal conditions) explored by the crop during grain filling rather than by differences in grain moisture content at harvest time (Figs. 1a and b).

### 3.3. Dormancy release as affected by temperature during grain filling

Since temperature during grain filling had been previously identified as a main factor modulating grain dormancy in barley and other species, we chose this variable to explain the high degree of variability in the rate of dormancy release after PM, in a wide range of barley cultivars.

When $GI_{10-20\%GMC}$ values were related to mean temperature during the whole grain-filling period (i.e. from anthesis to PM) ($T_{mA\text{-}PM}$), no significant correlations ($p < 0.001$) were found for any barley cultivar (Fig. 2). Therefore, we looked for relationships between these values and the mean temperature experienced during narrow "time windows" within the grain-filling period (TT intervals) (Fig. 2). Significant positive correlations ($p < 0.001$) between the $GI_{10-20\%GMC}$ and mean temperature during particular TT intervals were obtained for all barley cultivars, except for B1215 (Figs. 2 and 3, Table 3). The relative location within grain filling of these temperature-sensitive time windows was very similar among barley cultivars (Fig. 4). All of them were located on the last stages of grain filling: 275–325 °C d from anthesis for Q. Ayelén and Q. Painé; 300–350 °C d for Q. Palomar; and 250–300 °C d for Scarlett (Table 3). In this way, those grains that experienced warmer conditions during the last phases of their development were less dormant (at least at the 10–20%GMC stage) than those that developed under cooler conditions. Mean temperature for other TT intervals were also significantly correlated with $GI_{10-20\%GMC}$ ($p < 0.05$) (Fig. 2), but the highest correlation was obtained for only a particular TT interval of each barley cultivar (Table 3).

**Table 3**
TT intervals significant ($p < 0.001$) for the $GI_{10-20\%GMC}$–$T_{mTT}$ relationship; adjusted coefficients of determination ($r^2$) values for the relationship between $GI_{10-20\%GMC}$ and mean temperature into: (1) the whole grain-filling period and (2) these TT intervals; for each barley cultivar.

| Barley cultivar | TT interval (°C d) | Coefficient of determination ($r^2$) | |
|---|---|---|---|
| | | Whole grain filling | TT interval |
| Q. Ayelén | 275–325 | 0.0706 | 0.8215*** |
| B1215 | 325–375 | 0.0124 | 0.0538 |
| Q. Palomar | 300–350 | 0.4750* | 0.8516*** |
| Q. Painé | 275–325 | 0.3696* | 0.8110*** |
| Scarlett | 250–300 | 0.5604** | 0.8715*** |

* Significance at $p < 0.05$.
** Significance at $p < 0.01$.
*** Significance at $p < 0.001$.

The relationship between $T_{mTT}$ and $GI_{10-20\%GMC}$ was described with the general linear regression model expression:

$$GI_{10-20\%GMC} = b \times (T_{mTT}) + a$$

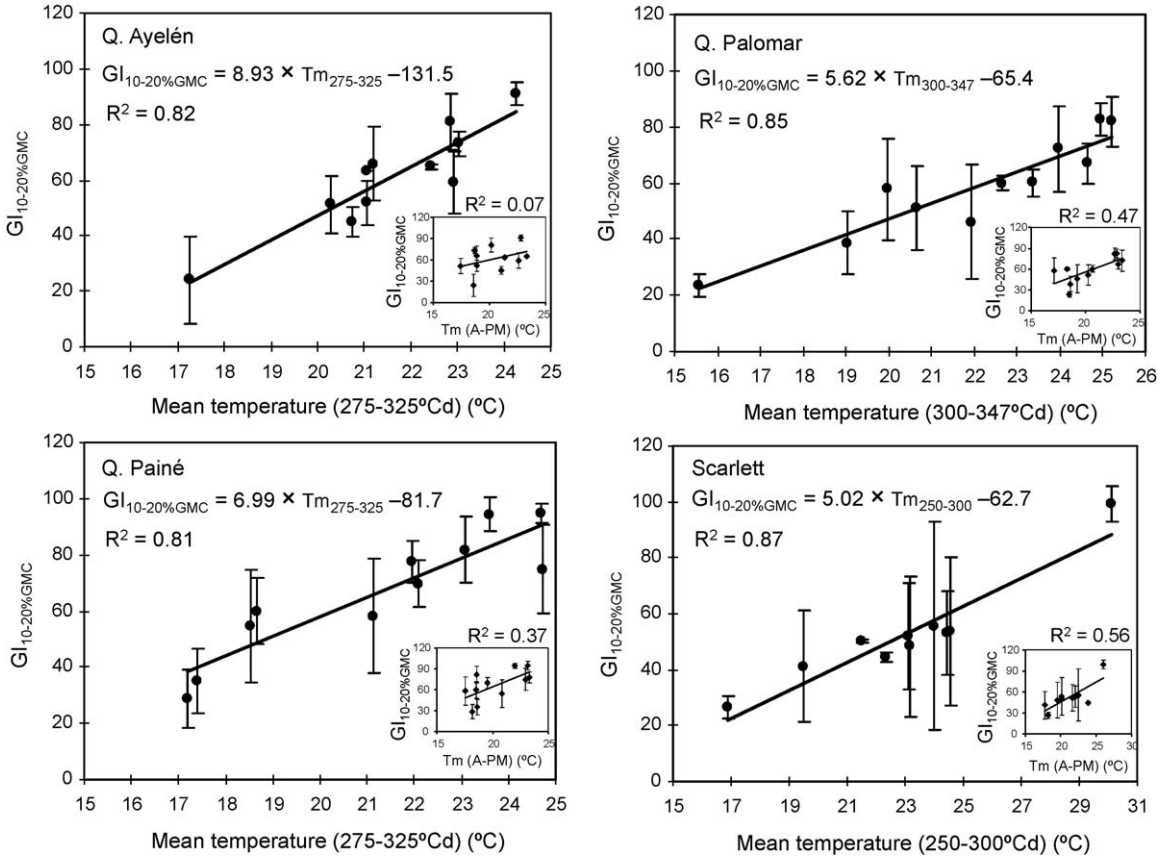


**Fig. 3.** Linear regression between GI of grains harvested with 10–20% moisture content (FW basis) ($GI_{10-20\%GMC}$) and incubated at 20 °C, and mean air temperature occurred within the best fit thermal time interval, for each barley cultivar. Regressions equations are shown inside each graph. Insets show the regressions between $GI_{10-20\%GMC}$ and the mean temperature during the whole grain-filling period ($T_{mA\text{-}PM}$). Vertical bars are mean SE when larger than the symbol.

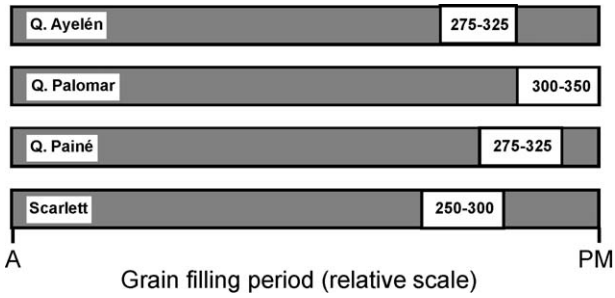


**Fig. 4.** Relative location of the temperature-sensitive window within grain-filling period, for each barley cultivar. Numbers indicate TT intervals.

**Table 4**
Slopes ($b$), $y$-intercepts ($a$) and adjusted coefficients of determination ($r^2$) values of the linear regression between $GI_{10-20\%GMC}$ and the $T_{mTT}$, for each barley cultivar.

| Barley cultivar | Sensitivity window (TT interval) (°C d) | $b$ | $a$ | $r^2$ |
|---|---|---|---|---|
| Q. Ayelén | 275–325 | 8.93 | −131.5 | 0.8215*** |
| B1215 | 325–375 | 2.48 | 25.8 | 0.0538 |
| Q. Palomar | 300–350 | 5.62 | −65.4 | 0.8516*** |
| Q. Painé | 275–325 | 6.99 | −81.7 | 0.8110*** |
| Scarlett | 250–300 | 5.02 | −62.7 | 0.8715*** |

*** Significance at $p < 0.001$.

The values of linear regression parameters (slope and $y$-intercept) for each barley cultivar are presented in Table 4.

For each barley cultivar, temperature during the sensitivity window explained, better than any other temperature, the variability observed for $GI_{10-20\%GMC}$ values calculated over several years and sowing dates.

### 3.4. One cultivar model vs. general model

We considered the possibility of a single linear regression model between $GI_{10-20\%GMC}$ and temperature during sensitivity window for all barley cultivars (except B1215). We compared the parameters (slope and $y$-intercept) of the models for each cultivar against those of a general model that includes data of all barley cultivars analyzed (except B1215). This general model was constructed with temperature data from: (1) best fit sensitivity windows of each cultivar (Table 5); or (2) a single sensitivity window for all barley cultivars (universal form) (Table 6). Using a single window for all cultivars the best fit was obtained for the thermal time window going from 300 to 350 °C d after anthesis. Both ways of producing a general model yielded significant regressions between GI and temperature; however, the best fit was obtained when individual sensitivity windows were maintained for each cultivar (general model 1) (Tables 5 and 6). When parameters of each cultivar model and general model were compared three (Q. Palomar, Q. Painé, Scarlett) or two (Q. Palomar, Scarlett) cultivars out of four did not show significantly different slopes ($p > 0.25$) using general model 1 and 2, respectively (Tables 5 and 6). $y$-Intercepts did not differ significantly ($p > 0.25$) in two (Q. Ayelén, Q. Palomar) of the four barley cultivars, using both general models (Tables 5 and 6).

### 3.5. Preliminary validation of the models

We tested the models generated (Q. Ayelén, Q. Painé and Scarlett) against independent field data from commercial plots located at four sites in the SE and SW of the Buenos Aires province. For each one of these cultivars, we obtained a significant and positive association between the GI around 5–15 d after PM ($GI_{5-15\ DAPM}$) and the mean temperature recorded during the sensitivity window defined in TT previously (Fig. 5, Table 7).

When we compared the regression line of field data with the experimental model we did not find significant differences in slope, for any of the barley cultivars validated (Table 7). However, most observed GI values were found to be significantly higher than predicted, and the whole relationship with temperature was displaced upwards as is evidenced by different $y$-intercept values between field data and experimental model regression lines (Table 7).

Environmental conditions for crop development under which experimental models were generated and at validation sites were different. Water availability during grain filling was markedly lower at all validations sites: experimental models were developed under irrigated conditions while validation was done in natural rainfed plots (and rainfall during the grain-filling period was lower than normal, at all validation sites) (Fig. 6).

**Table 5**
Comparison of the slope ($b$) and $y$-intercept ($a$) from a general model constructed with data of all cultivars (except B1215) vs. those from each barley cultivar model. Temperature data from best fit sensitivity window of each cultivar (general model 1).

| Barley cultivar | $n$ | Adjusted $r^2$ | $b$ | $a$ | MSE | Comparison ($p$-values) | |
|---|---|---|---|---|---|---|---|
| | | | | | | $B$ | $a$ |
| General model 1 | 43 | 0.6127 | 5.38 | −58.1 | 140.7 | – | – |
| Q. Ayelén | 11 | 0.8215 | 8.93 | −131.5 | 58.6 | 0.0828 | 0.4044 |
| Q. Palomar | 11 | 0.8516 | 5.62 | −65.4 | 47.8 | 0.8534 | 0.6173 |
| Q. Painé | 11 | 0.8110 | 6.99 | −81.7 | 88.0 | 0.2674 | 0.0086 |
| Scarlett | 10 | 0.8715 | 5.02 | −62.7 | 43.8 | 0.7720 | 0.0020 |

**Table 6**
Comparison of the slope ($b$) and $y$-intercept ($a$) from a general model constructed with data of all cultivars (except B1215) vs. those from each barley cultivar model. Temperature data from a single sensitivity window ranging 300–350 °C d from anthesis (general model 2).

| Barley cultivar | $n$ | Adjusted $r^2$ | $b$ | $a$ | MSE | Comparison ($p$-values) | |
|---|---|---|---|---|---|---|---|
| | | | | | | $B$ | $a$ |
| General model 2 | 43 | 0.5528 | 4.70 | −43.8 | 162.5 | – | – |
| Q. Ayelén | 11 | 0.8215 | 8.93 | −131.5 | 58.6 | 0.0527 | 0.4073 |
| Q. Palomar | 11 | 0.8516 | 5.62 | −65.4 | 47.8 | 0.5154 | 0.7316 |
| Q. Painé | 11 | 0.8110 | 6.99 | −81.7 | 88.0 | 0.1361 | 0.0139 |
| Scarlett | 10 | 0.8715 | 5.02 | −62.7 | 43.8 | 0.8120 | 0.0069 |

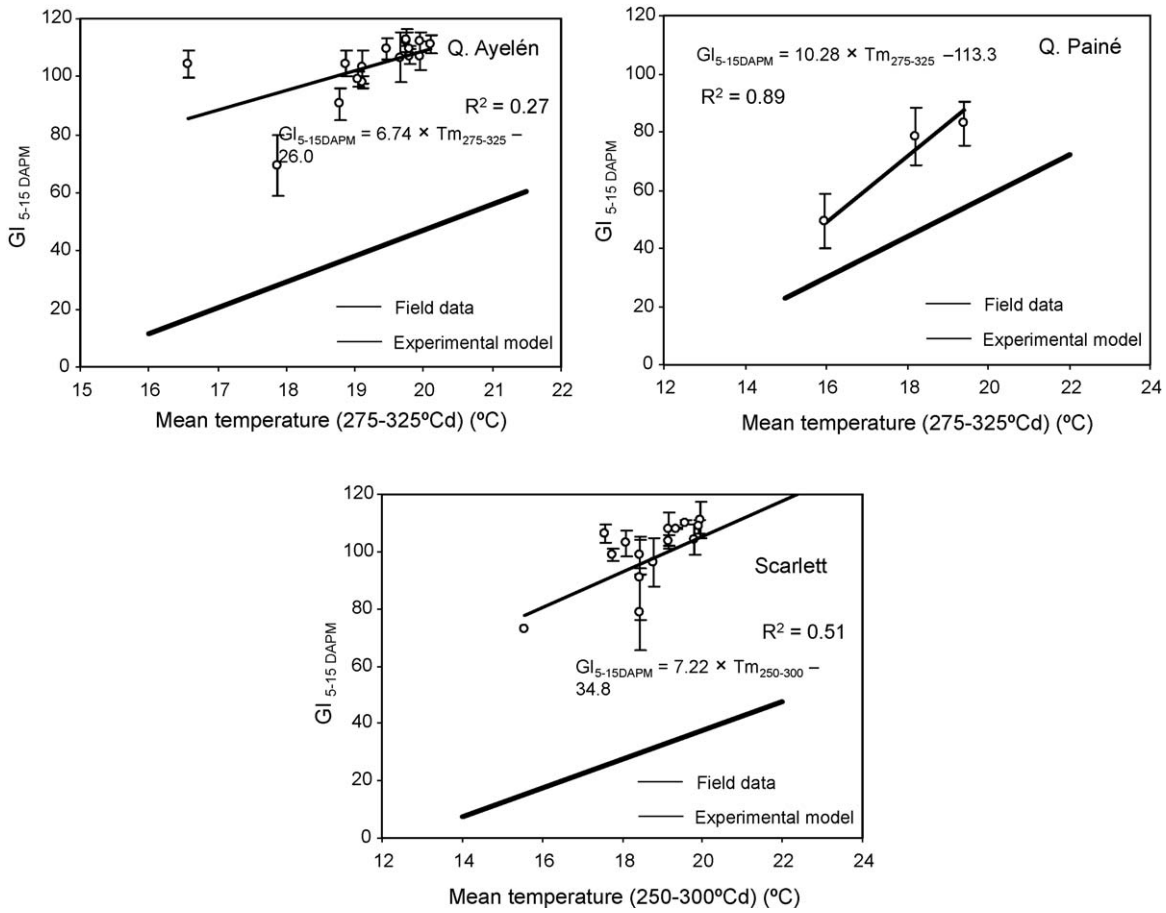


**Fig. 5.** Linear relationship between GI 5–15 d after PM ($GI_{5-15\ DAPM}$) and sensitivity window (as defined previously) mean temperature at validation sites, for three barley cultivars. For each cultivar, the regression line equation and adjusted coefficient of determination ($r^2$) for field data are shown. Thick line indicates experimental model. Note that slopes of both regression lines (field data vs. experimental model) did not differ significantly, for any cultivar ($p > 0.22$). Vertical bars are mean SE when larger than the symbol.

**Table 7**
Slopes ($b$), $y$-intercepts ($a$) and adjusted coefficient of determination ($r^2$) of the linear regression describing the association between $GI_{5-15\ DAPM}$ and the mean temperature in the sensitivity window at the validation sites, for each barley cultivar tested. Parameter comparison between the linear regression of field data and the experimental model generated previously.

| Barley cultivar | $n$ | Adjusted $r^2$ | $p$-Value | Sensitivity window (TT interval) (°C d) | $b$ | $a$ | Comparison ($p$-values) | |
|---|---|---|---|---|---|---|---|---|
| | | | | | | | $b$ | $a$ |
| Q. Ayelén | 16 | 0.2681 | 0.02 | 275–325 | 6.74 | −26.0 | 0.4750 | 0.0000 |
| Q. Painé | 3 | 0.8937 | 0.15 | 275–325 | 10.28 | −113.3 | 0.4065 | 0.0015 |
| Scarlett | 15 | 0.5056 | 0.002 | 250–300 | 7.22 | −34.8 | 0.2258 | 0.0000 |

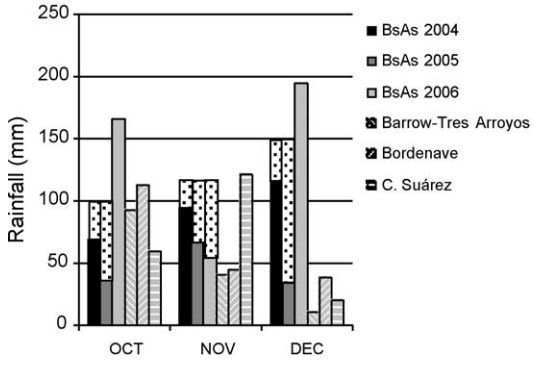


**Fig. 6.** Rainfall (mm) during the grain-filling period at Buenos Aires in 2004–2006 years (data for development of models); and at validation sites (year 2007). Dotted bars above Buenos Aires location indicate supplementary irrigation (when necessary) to reach a month total rainfall of 100 mm in October, 120 mm in September and 150 mm in December.

Day length at the validation areas was slightly longer (ca. 5 min) than at experimental site.

## 4. Discussion

In order to predict the sprouting susceptibility of a barley crop, we found positive significant relationships between the air temperature experienced by the crop during a narrow time window of grain filling and its PHS susceptibility, for a wide range of malting barley cultivars commonly grown in Argentina. Grain dormancy level, and hence crop's PHS susceptibility, was assessed when barley grain had reached 10–20% (fresh basis) moisture content, instead of measuring it after certain amount of days after PM, as in Rodríguez et al. (2001) experiments. Since grain drying dynamics has been reported to have an impact on the pattern of dormancy release of many seeds (Nicholls, 1979; Sawhney and Naylor, 1982; Bewley et al., 1989; Oishi and Bewley, 1992), this

methodology supposes some advantages: it allows us to compare dormancy levels of grains coming from crops with different grain drying rates (resulting from the different environmental conditions during the drying period among sowing dates).

We have established a linear regression model for predicting crop's PHS susceptibility for each barley genotype, and we explored the possibility of using a single universal model. Although the use of this latter form would make the crop management and decision-making easier for growers, the universal model did not adequately represent the PHS susceptibility response to temperature of all barley cultivars analyzed, and hence its use should be discarded.

These findings could allow barley growers to predict, in a simple way and from easy-to-gather data, the PHS susceptibility of their crops. Anthesis can be inferred from heading date, and mean daily air temperature during grain filling can be obtained with a maximum–minimum thermometer installed on the farm or from the nearest meteorological station. These data allow determination of the accumulated thermal time (over a base temperature defined for each cultivar) from anthesis onwards, identifying the beginning and the end of the sensitivity window. Mean temperature value within this window is entered into the model to estimate an expected $GI_{10-20\%GMC}$ value. Interpretation of results is very simple: a predicted GI $<30$ indicates a low sprouting susceptibility; GI values between 40 and 50 mean moderate susceptibility; and GI values $>70$ indicate high PHS susceptibility. In this case, a 24-h imbibition period may cause $>20\%$ of germinated grains. The PHS susceptibility prediction generated, together with the local weather forecast for the period close to harvest, would allow the estimation of the sprouting risk of the barley crop. If rainy conditions are forecasted for a crop with a high PHS susceptibility (i.e. high PHS risk) the growers can take management decisions in consequence, such as to anticipate harvest (i.e. to harvest with a grain moisture level higher than recommended and dry artificially). Sprouting damage could be more severe than predicted if relatively low temperatures (ca. 10 °C) occur together with rainy weather in the field (Mares, 1984; Bewley and Black, 1994; Benech-Arnold, 2004). Also, these models could be useful for barley grain purchasers, as a tool for identifying those regions where PHS may be problematic.

In a preliminary validation, we compared for three barley cultivars the regression line of field data against that generated from experimental data and found no significant differences in slope, for any of the tested cultivars. This confirms the GI's dependence on temperature during the sensitivity window, and indicates that the PHS susceptibility response to mean temperature was maintained across the three cultivars. However, for all validated cultivars, most observed GI values were found to be significantly higher than predicted (i.e. experimental models underestimated PHS susceptibility, which was much higher than expected), and the whole relationship with temperature was displaced upwards. In agreement with findings reported by Rodríguez et al. (2001), these results show that temperature experienced by the crop during the sensitivity window explains only one dimension of the variability in dormancy. Indeed, this validation suggests the role of other environmental factors that, in this case, induced lower dormancy levels in grains than those expected from the experimental models. Environmental conditions for crop development such as soil properties, water supply and day length were different at both test areas. Water availability during grain filling was markedly lower at all validations sites. Low water availability during grain development often results in lower seed dormancy (Peters, 1982; Sawhney and Naylor, 1982; Benech-Arnold et al., 1991). Hence, the action of this factor might explain the differences between the observed and predicted GI values obtained during validation, and then the upwards displacement of the GI–temperature relationship.

Low N supply is known to increase dormancy in grasses (Watson and Watson, 1982) and other species (Fawcett and Slife, 1978; Thomas and Raper, 1979; Varis and George, 1985); however, N supply was similar at both experimental and validation sites (data not shown). Day length was slightly longer at the validation sites; longer days can promote dormancy in some species (Wurzburger and Koller, 1976), although they can act in the opposite way in some others (Gutterman, 1973; Somody et al., 1984).

The similar location of temperature-sensitive time window within the grain-filling period in four out of five cultivars suggests, that, in *Hordeum vulgare* L., the dormancy release pattern is regulated by environmental sensitive physiological events that take place during the last stages of seed development. Research on the mechanisms of dormancy in the developing seeds of many species suggests a strong involvement of plant growth regulators (Robichaud et al., 1980; Walker-Simmons, 1987; Benech-Arnold et al., 1999, 2000a). Abscisic acid (ABA, germination inhibitor) and gibberellins (GAs, germination promoters) are among the most important. In barley, Benech-Arnold et al. (1999) working with B1215 (sprouting-susceptible) and Quilmes Palomar (sprouting-resistant) cultivars found that differences in sprouting behavior were due to the presence of the hull (lemma + palea) (i.e. dormancy release pattern of nude caryopses was not different between cultivars). This contrasting behavior was mainly explained by differences in embryo ABA content and, to a lesser extent, by different embryo sensitivity to ABA. After physiological maturity, B1215 embryos started to reduce ABA content and to lose sensitivity to ABA well before those from cv. Q. Palomar. It has been suggested that barley hull limits oxygen supply to the embryo by oxygen fixation that results from phenolic compounds oxidation, and this fact modulates dormancy of barley grains (Lenoir et al., 1986; Benech-Arnold et al., 2006). Oxygen concentration might determine the rate with which ABA or other germination inhibitors are catabolized (Neill and Horgan, 1987; Barthe et al., 2000); thus, influencing the embryo ABA content and, possibly, also sensitivity to ABA (Benech-Arnold et al., 2006).

Temperature during grain filling could alter the hormonal metabolism of the embryo and grain dormancy (Fenner, 1991). Therefore, in the present study, high temperatures during the sensitivity window could have reduced the embryo ABA content/sensitivity, and/or increased embryo GAs content/sensitivity, and then lead to weaker dormancy and high PHS susceptibility. These changes might be mediated, at least in part, by modifications of the morphology/physiology of the hull that could diminish the functionality of the hull oxygen "trap". Additionally, the displacement of the GI–temperature relationship in the validation tests could be due to action of other environmental factors (e.g. drought, soil nutrients, day length) that might have caused lower dormancy through alterations in grain hormonal balance. Current efforts are directed towards identifying and quantifying the effects of other environmental factors that modulate dormancy release dynamic in malting barley crops. The quantification of such effects, and the incorporation of the resultant functional relationships to models as those presented in this paper, should allow the improvement of PHS susceptibility predictions.

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