Predicting Preharvest Sprouting Susceptibility in Barley: A Model Based on Temperature during Grain Filling

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ABSTRACT

Preharvest sprouting (PHS) susceptibility in cereals is a consequence of low grain dormancy before harvest. Dormancy loss rate depends on genotype and may also be affected by environmental conditions during seed formation. To establish a quantitative relationship between temperature and PHS susceptibility, a malting barley (*Hordeum vulgare* L.) cultivar, 'Quilmes Palomar', was sown on different dates over a 3-yr period to obtain a range of thermal conditions during grain filling (soil type: Aeric Argiudoll). The period from pollination to physiological maturity (PM) was adjusted to a thermal time (TT) scale, which was then divided into 50°C-day intervals. Mean temperature within each interval was calculated for the different sowing dates. Grain dormancy was monitored using a germination index (GI). We sought a linear relationship between temperature during grain filling and GI at some moment after PM. The strongest correlation ($P < 0.0001$) was obtained between mean temperature values within the TT interval ranging from 300 to 350°C-day ($T_{m300\text{-}350}$) and GI values 12 d after PM (GI_{12DAPM}). This indicates that temperature during this *sensitivity window* explains variability in dormancy level among years and locations for this cultivar, and may therefore explain differences in PHS susceptibility. A regression model ($GI_{12DAPM} = 7.14 \times (T_{m300\text{-}350}) - 99$; $r^2 = 0.95$, $n = 9$) was generated for predicting GI values 12 d after PM, and tested on commercial plots. The linear relationship between temperature and GI after PM was confirmed, though the effect of one or more undescribed, environmental factors differing among tested locations was revealed.

Dormancy is an internal characteristic of the seed that impedes its germination under otherwise adequate temperature, hydric, and gaseous conditions (Benech-Arnold et al., 2000). 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 days after pollination [DAP]) if isolated from the entire grain and incubated in water (Benech-Arnold et al., 1999); the entire grain, however, reaches full capacity to germinate well after it has been acquired by the embryo. This coat- (endosperm plus pericarp plus glumellae) imposed dormancy is the barrier preventing untimely germination (Corbineau and Côme, 1980; Lenoir et al., 1986). Dormancy release of barley grains rarely started before the crop reached physiological maturity (PM). But once this stage has been reached, some cultivars are released abruptly from dormancy (i.e., within a few days), others more gradually (i.e., within weeks) while others remain dormant for several months (Benech-Arnold, 2001). In malting barley, a low dormancy level at harvest is a desirable characteristic so 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). Selection pressure in this direction has led to development of genotypes whose dormancy is terminated well before harvest maturity. When grain dormancy level in the period from PM to harvest maturity is low (i.e., germinability is high), a short exposure (<24 h) to rain water in the field may trigger embryo growth, and thus lead to pregermination or preharvest sprouting (Benech-Arnold, 2001). Both processes, pregermination and preharvest sprouting, have different adverse consequences on the malting quality of grains. Pregermination takes place when growth of the embryo begins but the process is interrupted by desiccation before radicle emergence occurs. No visible signs can be detected in this case and seeds will be able to germinate again later. However, seed storability is reduced dramatically (Del Fueyo et al., 1999). If damp conditions in the field persist longer, the germination process may proceed toward a *point of no return*, beyond which the embryo looses desiccation tolerance (Schopfer et al., 1979). This process is known as *preharvest sprouting* and implies that the embryo will not survive further desiccation, thus becoming useless for malting purposes. In addition, both pregermination and PHS trigger the synthesis of endosperm degrading enzymes (Bewley and Black, 1994). Malting quality parameters are particularly sensitive to these processes, and affected seed lots can be docked or even rejected at market.

The physiological, genetic, and environmental basis of PHS susceptibility in barley have been a subject of intensive research during the past three decades (for recent reviews see Auranen, 1995; Benech-Arnold, 2001). Sprouting susceptibility is determined mainly by the genotype. According to the rate of dormancy loss after PM, different barley genotypes may vary widely in their sprouting behavior. Some genotypes are highly resistant as a result of a deep and long-lasting dormancy while others are highly susceptible. A third group can be defined to include those genotypes with an intermediate rate of dormancy loss.

Grain dormancy in barley, as in other species, can also be influenced by the environment experienced by

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Abbreviations: A, anthesis; A-PM, anthesis to physiological maturity; DAP, days after pollination; DAPM, days after physiological maturity; DI, dormancy index; FAUBA, Facultad de Agronomía de la Universidad de Buenos Aires; PHS, preharvest sprouting; PM, physiological maturity; TT, thermal time.

the maternal parent (Cochrane, 1993; Hillhorst, 1995; Kahn and Laude, 1969; Nicholls, 1982; Reiner and Loch, 1976; Schuurink et al., 1992). In 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 behave as sprouting-resistant in some years and as sprouting-susceptible in other years (Benech-Arnold, 2001). Since there is no way to predict when the crop will behave as resistant or susceptible, crop management decisions are difficult.

The effects of the environment encountered by the maternal parent during seed development on the germinability or dormancy level of seeds have been reported for a wide range of species (Fenner, 1991; Wulff, 1995). Some well-defined patterns occur with several environmental factors tending to have similar effects in different species. Lower dormancy, i.e., high germinability, is generally associated with high temperatures, short days, high red/far-red ratio of light, 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 determinate of year-to-year variation in grain dormancy in barley (Buraas and Skinnes, 1985; Cochrane, 1993; Kivi, 1966; Nicholls, 1982; Reiner and Loch, 1976). Evidence suggests that temperature might be critical only within a *sensitivity* period during grain filling (Buraas and Skinnes, 1985; Reiner and Loch, 1976). For example, Reiner and Loch (1976) determined that low temperatures during the first half of grain filling, combined with high temperatures during the second half, were associated with a lower dormancy level of malting barley grains. These authors established a linear relationship between the ratio of the temperatures prevailing at both halves of the filling period and the dormancy level of the grains 3 wk after harvest. This model has since been used by the German malting industry to predict the dormancy level for lots of malting barley 3 wk after harvest. Though very valuable, the model has a series of problems. First, it does not define the temperature-sensitive *time window* in thermal time units and consequently is subjected to displacement between years or locations. As in other cereal crops, the length of the period (measured in days) between anthesis and PM depends on temperature (Wiegand and Cuellar, 1981) and use of a TT scale has been proposed to overcome this effect when comparing experiments conducted under a variety of thermal conditions (Russelle et al., 1984). Second, it predicts grain dormancy level 3 wk after crop harvest and not when the grain is still in the field. Third, to the best of our knowledge, it has not been validated against independent field data.

We hypothesized that knowledge of how temperature during grain development modulates dormancy level before harvest may help predict sprouting susceptibility in cultivars with intermediate sprouting behavior. This, together with meteorological data from the period before harvest, may provide an estimate of sprouting risk. In this work we sought a simple mathematical relationship between air temperature during grain filling and some measure of dormancy level that we assumed to be closely related to PHS susceptibility.

MATERIALS AND METHODS

Plant Material

'Quilmes Palomar', a two-row malting barley cultivar released in 1994 and in high demand in Argentina, was used for the experiments. Seed was provided by Maltería Pampa S.A. Sprouting behavior of this cultivar had been observed to vary dramatically depending on year and location. Quilmes Palomar is generally regarded as moderately sprouting-resistant under normal climatic conditions for its area of adaptation, but PHS was observed for this cultivar in 1996, when rainy conditions occurred before crop harvest.

Experimental Design

Experiments were conducted in the experimental field of the Facultad de Agronomía of the University of Buenos Aires (FAUBA), Argentina (34°25′ S, 58°25′ W). Soil type was an Aeric Argiudoll (sandy loam texture, pH 5.2, 2.4% organic matter, and an original C/N ratio of 9.3). To obtain a range of temperature conditions during grain filling, Q. Palomar was sown on different dates during winter and spring in 1996, 1997, and 1998 (Table 1). Germination data of the 1996 experiment was previously shown in Benech-Arnold et al. (1999). Quilmes Palomar was also sown on six different dates between July and October in 1995 in the experimental field of the FAUBA. On each sowing date a 64-m^2 plot was located arbitrarily within the experimental field. Each plot included three subplots of 1.5 m^2 in the 1995 and 1996 experiments, and 2.7 m^2 in the 1997 and 1998 experiments. Distance between rows was 0.15 m, and seeding density ranged from 330 to 550 plants m^{-2}, as sowing date was delayed within the growing season to compensate the shortening of tillering phase.

All plots were fertilized at sowing with urea to obtain a total soil N content of 120 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 production schedules typical for the region. Supplementary water was regularly provided with a hose whenever soil surface appeared dry for 2 to 3 d.

Duration of Grain-Filling Period

Thermal time accumulation during the period from anthesis to PM was calculated as the sum of mean daily temperature values (T_{md}) above a base temperature (T_b), which had not yet been determined for this cultivar (Eq. [1]; Pararajasingham and Hunt, 1991; Wiegand and Cuellar, 1981). Whenever T_{md} values were less than *Tb*, zero was included in the sum.

$$TT_{A\text{-}PM} = \sum_{d=A}^{PM} (T_{md} - T_b)_d \qquad [1]$$

where d is any day in the interval starting at anthesis until physiological maturity. If $(T_{md} - T_b) < 0$, then $(T_{md} - T_b) = 0$.

Accumulated thermal time at PM was assessed as the TT

accumulated between anthesis and the moment when grain growth ended (i.e., GDW reached a stable value) and was estimated using a linear model subjected to boundary conditions (i.e., grain mass is described by two equations with one boundary, c). Since grains that developed at lower temperatures accumulate more dry matter throughout the filling period, GDW data was first expressed relative to maximum weight (GDW_r) achieved in each case. To fit the GDW_r data over time, the following equations were used (Miralles et al., 1996):

$$GDW_r = a + b \times x \quad \text{if } x \leq c \qquad [2]$$

$$GDW_r = a + b \times c \quad \text{if } x > c \qquad [3]$$

In this function a stands for intercept (kg kg^{-1}), b for rate of GDW_r increase (kg kg^{-1} °C-day^{-1}) during period of linear dry matter accumulation, c for TT (°C-day) at which the filling phase ended (i.e., PM), and x for accumulated TT (°C-day) 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 (Jandell, 1991). Estimates of these parameters were derived from a fitted model (Miralles et al., 1996). Optimization routine was repeated for different T_b values. The T_b value that maximized overall fit, as measured by the r^2, was used in all TT calculations in this work.

The accumulated TT between anthesis and PM ($TT_{A\text{-}PM}$) for Q. Palomar was calculated using T_{md} values obtained from Villa Ortúzar meteorological station (200 m from the experimental field). Grain dry weight values for this analysis were obtained from the experiments conducted in 1995, 1996, and 1997. In the 1995 and 1996 experiments, between 10 and 30 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 dry weight determinations. In the 1997 experiments, two central grains were taken from 5 to 10 randomly selected spikes from each subplot and dried at 80°C for 48 h. All dry weight determinations were done with a precision balance (Sartorius, Germany; 0.1 mg resolution). Values from subplots were always averaged into a single observation for each sampling date.

Assessment of Grain Dormancy Release

Germination tests were conducted in the 1996, 1997, and 1998 experiments. Spike sampling for germination tests began 15 d after anthesis (anthesis date for the whole plot was estimated as 40°C-day, i.e., 2 to 4 d, before heading occurred in 50% of the plants) or later and was repeated every 5 to 8 d until harvest maturity. On each sampling date, 10 to 12 spikes were randomly collected from the inner area of each subplot and represented a subsample. Grains from the central third of the spikes were pooled and immediately used for germination assays.

On each germination assay, 25 grains from each subsample (one per subplot) were placed in plastic Petri-dishes (10 cm diam. with 2 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 more than 5 mm) was recorded daily and used to calculate a germination index (GI, Eq. [4]), as done in previous studies (Benech-Arnold et al., 1999; Steinbach et al., 1995, 1997). In this index maximum weight is given to grains that germinated first and less weight to those that germinated later.

$$GI = \left\{\sum_{i=1}^{12}[12 - (i - 1)] \times n_i\right\}/2.5 \qquad [4]$$

Table 1. Sowing date, planting density, anthesis date, and number of days from anthesis to physiological maturity for Q. Palomar sown on 1996, 1997, and 1998.

Year	Sowing date	Anthesis date	Days from anthesis to PM†	Planting density
			days	Plants m^{-2}
1996	20 July	6 Oct.	32	330
1997	22 July	7 Oct.	34	330
	22 Aug.	24 Oct.	31	400
	22 Sept.	12 Nov.	29	400
	22 Oct.	2 Dec.	27	550
1998	16 July	12 Oct.	31	330
	15 Aug.	22 Oct.	29	400
	14 Sept.	7 Nov.	27	400
	21 Oct.	8 Dec.	26	550

† PM = physiological maturity.

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 subplots were averaged into a single observation.

Dormancy in winter cereals is virtually not expressed at low temperatures (i.e., 10°C or below) but it increases as the temperature rises (Black et al., 1987; Corbineau and Côme, 1980). In the 1997 experiments, germination assays were also conducted at 10 and 25°C to evaluate germination increase from higher to lower temperatures as a result of dormancy release. Subsamples (one per subplot) of 25 grains each were incubated in plastic Petri-dishes at 10 and 25°C, and the final germination percentage was recorded after a 15- and 12-d incubation period, respectively. These values were used to calculate a dormancy index (DI) that related the final germination percentage obtained at 10°C with that obtained at 25°C. This index, as proposed by Gate (1995), was calculated as follows:

$$DI = \frac{\%\ \text{Germinated at } 10°C - \%\ \text{Germinated at } 25°C}{\%\ \text{Germinated at } 10°C} \qquad [5]$$

Whenever dormancy is expressed stronger at 25°C than 10°C or equally, this index will adopt values between zero (i.e., when germination percentages at 10 and 25°C are equal because of a low dormancy level) to one (i.e., grains germinate at 10°C but not at 25°C, indicating a high dormancy level). Otherwise, this index will adopt negative values if, by some reason other than dormancy, germination is higher at 25°C than at 10°C.

Generation of the Model

Our objective was to establish a relationship between temperature experienced by the crop during grain filling (or during a particular stage within grain filling) and some measure of the rate with which grains are released from dormancy after PM. We assumed that GI of grains harvested some time after PM (about half way between PM and harvest maturity) should be a good estimate of the rate with which grains are released from dormancy and, consequently, of the crop's susceptibility to PHS (Benech-Arnold et al., 1999). Therefore, we carried out the following procedure:

1. Mean temperature between anthesis and PM was calculated for each sowing date and correlated with GI values for grains harvested 12 d after PM (GI_{12DAPM}) for that sowing date.
2. The TT from anthesis to PM was arbitrarily divided into

50°C-day intervals, where *dt* is the date at which a TT interval begins and *dT* the date at which the TT interval ends for each sowing date.

3. Average temperature within each TT interval was calculated as:

$$T_{m_{TT}} = \left[\sum_{d=dt}^{dT} (T_{md})_d\right] / \text{No. of days within the interval } dt - dT \quad [6]$$

for each one of the nine sowing dates, thus giving a total of nine mean temperature values per TT interval.

4. For each TT interval, a set of nine mean temperature values (T_{mTT}) was then correlated with GI_{12DAPM}.

An interval within grain filling with sensitivity to temperature for the determining of the rate of dormancy release would be that showing a significant correlation between mean temperature (T_{mTT}) for the interval and GI_{12DAPM} values. For simplicity, we expected this association to be linear. The general expression for the model was:

$$GI_{12DAPM} = b \times (T_{mTT}) + a \quad [7]$$

Field Validation of the Model

To test the model on a production system, irrigated-commercial plots sown with Q. Palomar at Coronel Suárez (37°30′ S, 61°57′ W, Buenos Aires) and Puán (37°32′ S, 62°45′ W, Buenos Aires) were evaluated. Both localities are 370 and 450 km away from the experimental field of the FAUBA, respectively. Several plots were sown on each of six sowing dates for C. Suárez and four for Puán (total no. of plots = 20) between July and September of 1998. Plots belonged to Maltería Pampa, and were followed until the exact date of heading was determined (and anthesis date estimated as described above). Soil characteristics were similar at both sites and were described as Entic Hapludoll with soil-available N ranging from 60 to 64 kg N ha^{-1} within the upper 60 cm of the profile.

Temperature data was collected from nearby meteorological stations (within 2 km from field plots). In this way, time of PM was identified when the accumulated TT after anthesis reached the estimated value for this cultivar. Twelve days after PM, 20 to 30 spikes were randomly collected from each of 3 to 4 sampling sites (subsamples) separated by at least 5 m within each plot. Germination assays began within 48 h after harvest at 20°C as described above. Grains were also incubated at 6°C, i.e., a temperature at which we expected dormancy to be expressed weakly. Daily germination values were used to calculate GI_{12DAPM} at 20 and 6°C.

Statistical Analysis

The GI_{12DAPM} values (average of three subsamples) obtained for different sowing dates were considered as independent observations. The relationship between GI_{12DAPM} and mean temperature values (Eq. [6]) was assessed with correlation analysis, and correlation coefficients (r) tested for significance (df = $n - 2$). Significant relationships were then described with a simple linear regression model. Regression equations were tested for parallelism with the following formula (Mead and Curnow, 1983; Sokal and Rohlf, 1969). Slopes b_1 and b_2 were considered not to differ significantly if $P > 0.20$:

$$F = [(b_1 - b_2)^2 \times (SSxx)_1 \times (SSxx)_2] / (SSxx_1 + SSxx_2) \times S^2$$
$$S^2 = [(SS\ residual)_1 + (SS\ residual)_2] / (n_1 + n_2 - 1) \quad [8]$$

where SSxx is the sum of squares for independent variable x values (e.g., $T_{m300\text{-}350}$ values) and SS residual is the residual sum of squares of the regression's ANOVA. The obtained F value was compared with F (1; q), with $q = n_1 + n_2 - 4$, where n is the number of observations for each sample.

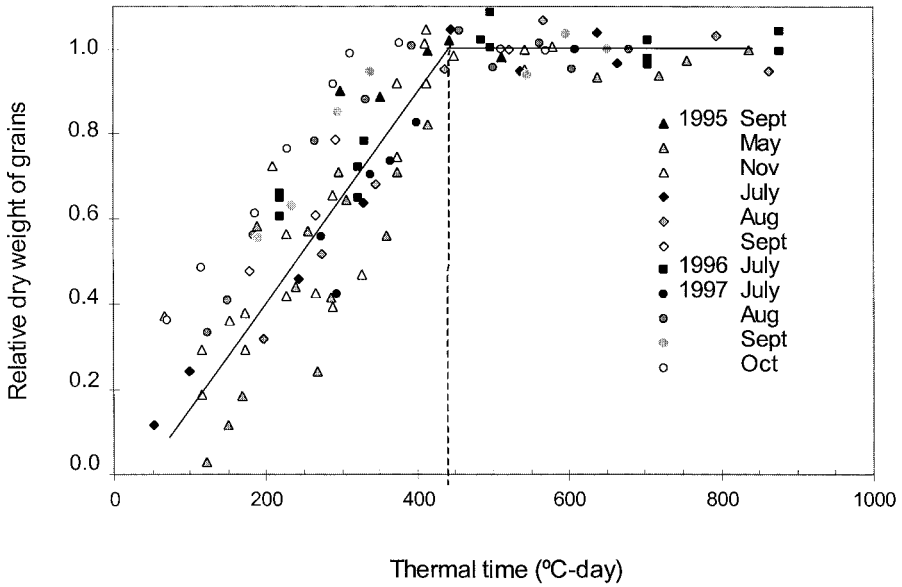

Fig. 1. Evolution of relative grain dry weight on a thermal time scale for Q. Palomar cultivar from different experiments done at the Facultad de Agronomía de la Universidad de Buenos Aires (six in 1995, one in 1996, and four in 1997). Data was fitted to a model with two linear equations (r^2 = 0.81, n = 108). Physiological maturity occurred at the interception of both lines, i.e., 440°C-day (SE = 16.2°C-day). Base temperature that maximized r^2 was T_b = 5.5°C.

RESULTS AND DISCUSSION

Grain-Filling Period and Physiological Maturity for Quilmes Palomar

The accumulated TT between anthesis and PM obtained by regression analysis for Q. Palomar was TT = 440°C-day (SE = 16.2°C-day; r^2 = 0.81; n = 108) (Fig. 1). Base temperature value that maximized data fitness to the regression model was T_b = 5.5°C. This value is similar to T_b values reported for other barley cultivars (Goyne et al., 1996).

A TT scale was necessary not only to synchronize periods of grain filling obtained under a variety of temperature environments but also to identify PM easily (i.e., without depending on GDW measurements). After PM, no clear association between dormancy release and temperature experienced by the grains in the field had been described in barley nor was found in this work for this cultivar. Therefore, GI and DI values after PM were plotted using a daily scale (days after PM, DAPM). This scale proved adequate for describing dormancy release after PM.

Dormancy Release in Quilmes Palomar

A germination index was calculated for grains harvested at different times and incubated at 20°C. Germination index remained close to zero until PM (Fig. 2), indicating that no sprouting risk existed before PM. After PM, an unexpected general pattern was observed for dormancy release. The GI began to increase after PM but it did not follow a sigmoid nor a linear pattern.

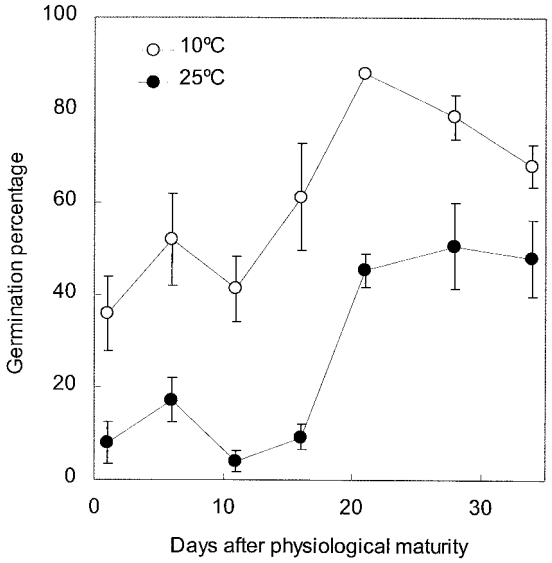

Fig. 3. Final germination percentage of grains harvested at different times after PM and incubated at 10 and 25°C for Q. Palomar sown on July 1997. Each value is the average of three subplots. Vertical bars indicate SE.

In most cases GI increased until it became stable or even decreased temporarily between 10 and 15 DAPM (Fig. 2). Afterward, GI continued to increase until maximum values were reached at about 30 DAPM or later. A similar pattern was also observed for final germination percentage at other incubation temperatures (Fig. 3). Contrasting GI values among sowing dates were evident after PM (Fig. 2). Significant differences among sowing

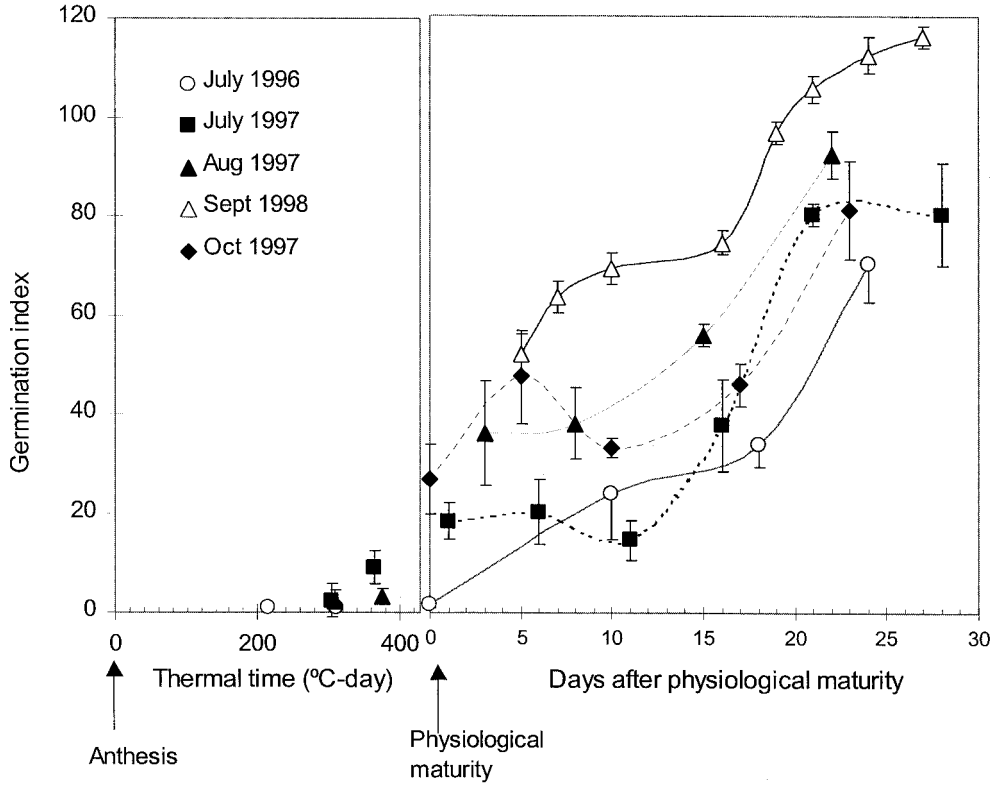

Fig. 2. Germination index for grains harvested before (thermal time scale) and after PM (days after PM scale) for Quilmes Palomar cultivar sown on different dates during 1996, 1997, and 1998. Each value is the average of three subplots. Vertical bars indicate SE.

Table 2. Day-to-day evolution of cumulative germination percentage for grains with four different GI values (i.e., dormancy levels) incubated at 20°C. Values are the average of three independent germination trials with the same GI.

	Sample			
Day	A	B	C	D
	% germination			
1	0	2	11	57
2	1	7	36	68
3	11	16	47	76
	Germination index (GI)†			
	18	30	45	80

† GI is calculated upon daily germination records along a 12-d incubation period as

$$GI = \left\{\sum_{i=1}^{12}[12 - (i - 1)]*n_i\right\}/2.5$$

where n_i is the number of germinated seeds within incubation day i.

dates occurred between 5 and 25 DAPM, and greatest variability was observed between 9 and 13 DAPM, with GI values ranging from 14 to 70 (July 1997 and September 1998 sowing dates, respectively). These differences in GI values presumably reflect differences in sprouting susceptibility. Indeed, a GI of 18 means 1% germination after a 48-h imbibition period at 20°C, while a GI of 80 represents 68% germination after the same period (Table 2).

The dormancy index remained high (i.e., close to 0.7) during the first 10 DAPM, and did not differ significantly among sowing dates in the 1997 experiments (Fig. 4). The DI decreased gradually between 10 and 25 DAPM. Final germination percentage increased rapidly after PM when seeds were incubated at 10°C but germination at 25°C remained low for longer, as shown for the July 1997 sowing date (Fig. 3). Afterward, lower DI values were attained as germination percentage at 25°C approached that obtained at 10°C.

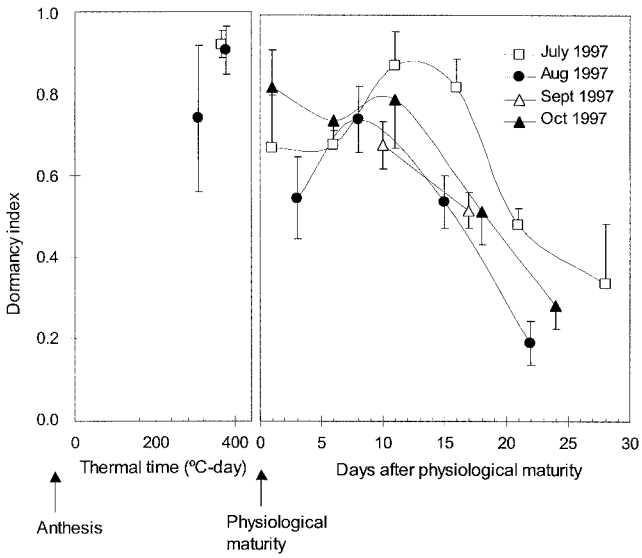

Fig. 4. Dormancy index of grains harvested at different times after PM and incubated at 10 and 25°C for Quilmes Palomar cultivar sown on four different dates during 1997. Each observation is the average of three subplots. Vertical bars indicate SE.

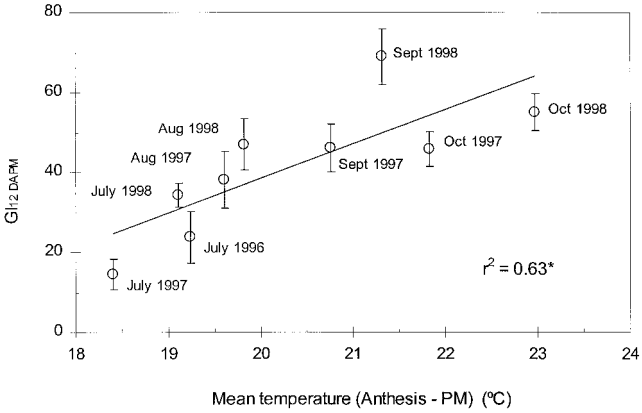

Fig. 5. Linear relationship between GI of grains harvested 12 d after physiological maturity (GI_{12DAPM}) and incubated at 20°C, and mean air temperature occurred between anthesis and PM for Quilmes Palomar cultivar sown on nine dates in 1996, 1997, and 1998. Regression equation: $GI_{12DAPM} = 8.7 \times T_{mA\text{-}PM} - 135.2$ ($r^2 = 0.63$, $P < 0.05$, $n = 9$). Vertical bars indicate SE.

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 (see Introduction), we chose this variable to explain the high degree of variability in the rate of dormancy release after PM.

When GI after PM was plotted as a function of time (days after PM, DAPM) we identified a time, about 12 DAPM, which is half-way between PM and the time where GI approaches its maximum and also harvest maturity is attained (about 25 DAPM). At this time GI appeared to have reached a temporary plateau (Fig. 2), though at different GI values among sowing dates. Hence, we assumed that GI measured on grains harvested at this stage was a good estimate of the rate of dormancy loss for Q. Palomar and, consequently, explained differences in the crop's susceptibility to PHS among sowing dates.

A significant correlation ($r = 0.79$, $P < 0.05$, df = 7) was obtained between GI_{12DAPM} values and mean temperature between anthesis and PM ($T_{mA\text{-}PM}$) (Fig. 5). This means that grains that developed under warmer conditions were less dormant 12 DAPM than grains that developed under cooler conditions. In spite of these results, sensitivity to temperature should be limited to a particular stage within seed development rather than to the whole filling period. Therefore, the grain-filling period was divided into intervals of 50°C-day each, and correlation analysis was done between temperature experienced at each TT interval and GI_{12DAPM} (Fig. 6). A significant correlation ($r = 0.97$, $P < 0.0001$, df = 7) was obtained between mean temperature for the 300 to 350°C-day period ($T_{m300\text{-}350}$) and GI_{12DAPM} (Fig. 6 and 7). Mean temperature for other TT intervals was not significantly correlated with GI_{12DAPM} ($P > 0.05$, Fig. 6). The relationship between $T_{m300\text{-}350}$ and GI_{12DAPM} was described with a regression model ($r^2 = 0.95$, $n = 9$) (Fig. 7):

$$GI_{12DAPM} = 7.14 \times (T_{m300\text{-}350}) - 98.9 \qquad [9]$$

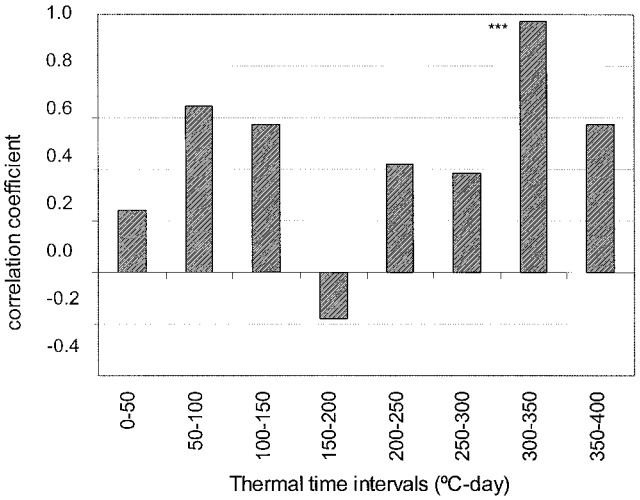

Fig. 6. Correlation coefficient (r) obtained between GI_{12DAPM} and mean air temperature occurred within 50°C-day intervals at different thermal time (TT) values between anthesis and PM (TT to PM = 440°C-day). Data belong to Q. Palomar cultivar sown on nine dates between 1996 and 1998. Each correlation included nine observations (df = 7). The only significant correlation was that obtained for the 300 to 350°C-day interval ($P < 0.0001$).

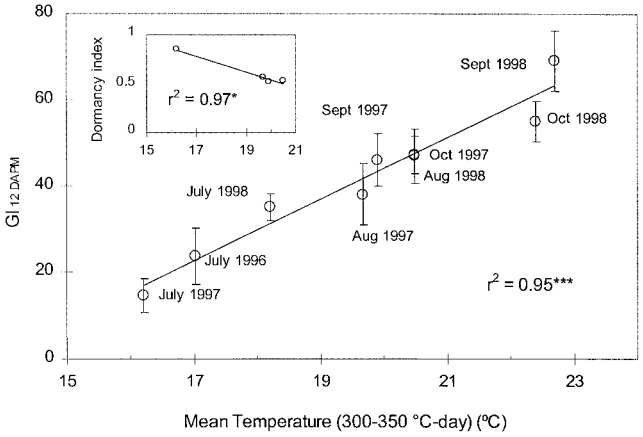

Fig. 7. Linear regression between GI of grains harvested 12 d after PM and incubated at 20°C, and mean air temperature occurred within the 300 to 350°C-day interval after anthesis (T_b = 5.5°C) for Q. Palomar cultivar sown on nine dates between 1996 and 1998. Regression equation: $GI_{12DAPM} = 7.14 \times T_{m300\text{-}350} - 98.8$ ($r^2 = 0.95$, $P < 0.0001$, $n = 9$; SE of estimate: 4.03; regression sum of squares = 2010.5; mean value of independent variable = 19.67). Inset shows association between DI and mean air temperature for the 300 to 350°C-day interval for 1997 experiments ($P < 0.05$). Vertical bars indicate SE.

Temperature during this period explained, better than any other, the variability observed for GI_{12DAPM} values calculated over several years and sowing dates. The significant, though weaker, correlation between GI_{12DAPM} and mean temperature within the entire A–PM period was probably due to some degree of correlation between both temperature variables, i.e., $T_{mA\text{-}PM}$ and $T_{m300\text{-}350}$. Nevertheless, since sensitivity to temperature throughout the whole filling period could not be ruled out, this hypothesis was also tested with field validation experiments.

The DI also showed a significant ($r = -0.985$, $P < 0.05$, df = 2) but negative association with $T_{m300\text{-}350}$ (Fig. 7, *inset*). These results suggest that temperature experienced in the sensitivity window explains variability in more than one aspect related to dormancy: germination rate at 20°C as estimated by GI, and capacity to germinate at warmer temperatures as assessed by DI.

The above results allowed us to propose a method for predicting dormancy level of grains for Q. Palomar, following the procedure below:

1. Thermal time is accumulated from anthesis until 440°C-day are reached (i.e., time of PM) using Eq. [1] with T_b = 5.5°C. The dates at which 300 and 350°C-day have accumulated (dt and dT, respectively) are identified.
2. Mean temperature for the TT interval 300 and 350°C-day ($T_{m300\text{-}350}$) is obtained as the average of T_{md} values for this interval (Eq. [6]).
3. The obtained mean temperature value ($T_{m300\text{-}350}$) is entered into Eq. [9] to estimate an expected GI_{12DAPM} value, which should be an indicator of the crop's susceptibility to PHS.

If high temperatures are experienced during the sensitivity window, and therefore a high sprouting susceptibility is predicted (i.e., GI ≥ 30), a risk situation can be envisioned if rainy conditions are forecasted before crop harvest. Under such circumstances the farmer can decide to harvest early, and thus avoid taking any risk.

Field Validation of the Model

Temperature experienced by the crop during the whole filling period was not correlated with GI_{12DAPM} ($r = 0.34$, $P > 0.05$, df = 18), allowing us to discard this variable as relevant to modulation of dormancy. On the other hand, GI_{12DAPM} was significantly correlated ($r = 0.88$, $P < 0.01$, df = 18) with mean temperature recorded during the 300 to 350°C-day interval (Fig. 8a). The equation describing such association was ($r^2 = 0.77$, $P < 0.01$, $n = 20$):

$$GI_{12DAPM} = 8.14 \times T_{m300\text{-}350} - 143.0 \qquad [10]$$

When compared with the model's regression line, two important conclusions were drawn. First, regression slope for the new data set did not differ significantly from that of the model (null hypothesis stating no difference among slopes was accepted with $P > 0.22$, Eq. [8]), confirming GI's dependence on temperature during the 300 to 350°C-day interval. Second, most observed GI values were found to be significantly lower than predicted, and the whole relationship with temperature was displaced as is evidenced by a lower intercept for Eq. [10] compared with Eq. [9]. These results show that temperature experienced by the crop in 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 higher dormancy levels in seeds from the C. Suárez and Puán plots than those expected from the experimental model. When grains were incubated at 6°C, the GI values obtained were very similar to those predicted by

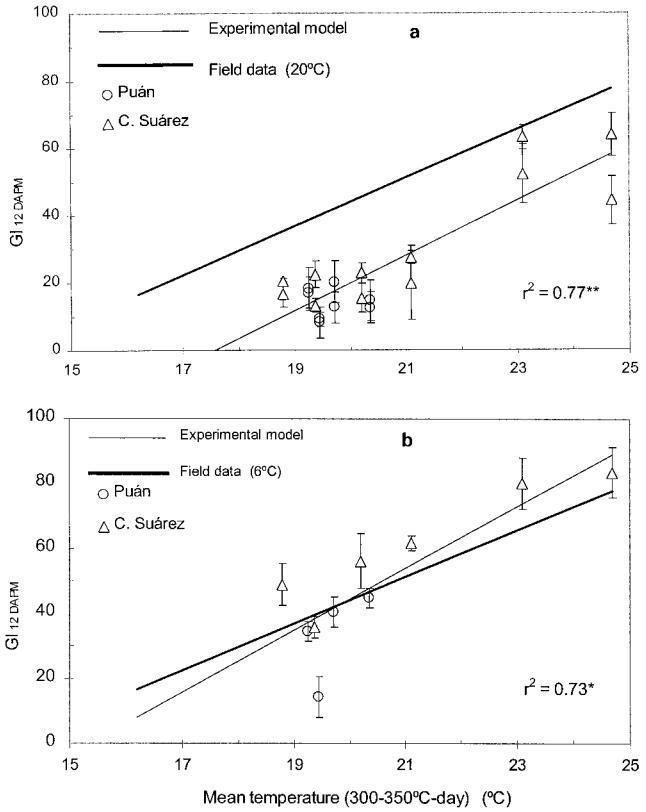

Fig. 8. (a) Linear relationship (r^2 = 0.77, P < 0.01, n = 20) between mean temperature for the 300 to 350°C-day interval and GI obtained for grains harvested 12 d after PM at validation sites (Cnel. Suárez and Puán, 370 and 450 km away from the FAUBA) and incubated at 20°C. Observations belong to plots of Q. Palomar cultivar sown on different dates or sites during 1998 for each location. The experimental model was developed at the Facultad de Agronomía (Universidad de Buenos Aires) with Q. Palomar sown on nine dates between 1996 and 1998. Slopes of both regression lines did not differ significantly (P > 0.20). (b) Linear relationship between GI of grains harvested 12 d after PM at validation sites and incubated at 6°C, and mean temperature for the 300 to 350°C-day interval (r^2 = 0.73, P < 0.05, n = 10). The experimental model predicts GI values for grains incubated at 20°C. Slopes do not differ significantly (P > 0.20). Vertical bars indicate SE.

the model at 20°C (Fig. 8b), supporting the idea that lower germinability was due to a stronger dormancy. It is not known which environmental variables might have acted to increase the dormancy level of grains at the validation sites. Environmental conditions for crop development such as soil properties, day length, and water supply were different at both test areas. For example, both soil N content and water availability were markedly lower at C. Suárez and Puán, whereas day length was slightly longer. A low water availability during grain development often results in weak grain dormancy (Benech-Arnold et al., 1991; Peters, 1982; Sawhney and Naylor, 1982), whereas low N supply is known to strengthen dormancy in grasses (Watson and Watson, 1982) and other species (Fawcett and Strife, 1978; Thomas and Raper, 1979; Varis and George, 1985). Longer days can promote dormancy in some species (Wurzburger and Koller, 1976), although they can do the opposite in some others (Gutterman, 1973; Somody et al., 1984).

FURTHER DISCUSSION

Temperature during a relatively short time window during grain filling can be used to effectively predict sprouting susceptibility in Q. Palomar (as measured by a germination index) under field conditions similar to those in Buenos Aires, Argentina, where experiments and validation tests were done. The relationship between temperature experienced during seed development and seed dormancy has been established for several species (Fenner, 1991). This relationship has been quantified and predictive models have been developed for barley (Reiner and Loch, 1976). However, this is the first case in which a stage with sensitivity to temperature within seed development has been identified using a thermal time scale. This allows identification of the beginning and the end of this sensitivity period, regardless of prevailing thermal conditions during grain filling.

Some advantages can be pointed out from our model. First, information required to run the model is easy to gather. Anthesis can be inferred from heading date, and mean daily temperature during grain filling can be obtained from the nearest meteorological station. Second, interpretation of results is simple; if the estimated GI value is <30, sprouting susceptibility can be considered low (Table 2); GI values between 40 and 50 indicate moderate susceptibility, while GI values over 60 indicate a high susceptibility to sprouting. In this case, a 24-h imbibition period may cause >30% of germinated grains. Lower temperatures (around 10°C) during grain imbibition may increase rate of germination and sprouting damage if low temperatures and rainy conditions occur together in the field. This situation is not common in Buenos Aires province, where climatic conditions at harvest are generally warm and mean temperatures around 20°C can be expected. Nevertheless, sprouting risk assessment should consider both sprouting susceptibility (based on GI_{12DAPM}) and local weather predictions.

Although this model was developed and validated for only one cultivar, the methodology used to generate the model can be the basis for the development of similar models for other barley cultivars. We are currently analyzing other genotypes and expecting to confirm the existence of a similar sensitivity window.

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