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The effect of water and nitrogen availability during grain filling on the timing of dormancy release in malting barley crops

Nicolás A. Gualano · Roberto L. Benech-Arnold

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Abstract Pre-harvest sprouting (PHS) causes immediate loss of seed viability, making barley (*Hordeum vulgare* L.) grains worthless for malting purposes. Grain dormancy release rate in barley crops is genetically and environmentally controlled. A 2 year experiment was conducted to evaluate the effect of soil nitrogen and water availability during grain filling on the dormancy release pattern (and then on the PHS susceptibility) for five malting barley commercial cultivars. Drought and well-irrigated control treatments were imposed from anthesis onwards, and contrast nitrogen fertilization treatments were applied at tillering. Nitrogen availability showed no effects on dormancy release. Drought during grain filling accelerated dormancy release with respect to well-irrigated control in 2004, but not in 2005 year. Mean temperatures during the last stages of grain filling were much higher (ca. 6°C) in 2005 than in 2004, indicating that high-dormancy loss promoting temperatures had masked drought effects on dormancy release.

N. A. Gualano
Cátedra de Cerealicultura, Facultad de Agronomía, Universidad de Buenos Aires/CONICET, Av. San Martín 4453, C1417DSE Buenos Aires, Argentina

R. L. Benech-Arnold (✉)
IFEVA-Cátedra de Cultivos Industriales, Facultad de Agronomía, Universidad de Buenos Aires/CONICET, Av. San Martín 4453, C1417DSE Buenos Aires, Argentina
e-mail: benech@ifeva.edu.ar

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Introduction

Dormancy is an internal trait of the seed that impedes its germination under otherwise adequate temperature, hydric, and gaseous conditions (Benech-Arnold et al. 2000). 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 days 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 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). Malting process requires grain germination; hence, 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). 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. 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 toward a point of no return, beyond which the embryo looses 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. Economic losses by this adversity often occur in many cereal producing regions of the world including Argentina, Brazil, Australia, Europe, Central Asia, Canada, USA and South Africa (Derera 1989).

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 (Fenner 1991; Hillhorst 1995; Sharif-Zadeh and Murdoch 2000; Benech-Arnold 2004). 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).

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). Since 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 seed lot in storage for a long time until dormancy is terminated) to satisfy the requirements of the malting industry, new approaches to reduce the incidence of this adversity were explored. Crop management tools such as simple models that predict the PHS susceptibility of a barley crop from easy-to-gather data were developed in the last years (Rodriguez et al. 2001; Gualano and Benech-Arnold under review). These studies indicated that seed dormancy level between PM and HM was highly and negatively related with mean air temperature within a narrow time window located at last stages of the grain filling period. Rodriguez et al. (2001) established a relationship of this kind working with the barley cultivar Quilmes Palomar. Recently, Gualano and Benech-Arnold (under review) found similar relationships for a wide range of malting barley cultivars commonly grown in Argentina. Hence, the PHS susceptibility prediction generated, together with the weather forecast for the period close to harvest, would allow the estimation of the sprouting risk of the barley crop. If this is high, the growers can take management decisions in consequence such as to anticipate harvest. However, validations of these predictive models against independent field data showed a displacement of the whole relationship with temperature thus suggesting that temperature explains only one dimension of the variability in sprouting susceptibility (Rodriguez et al. 2001; Gualano and Benech-Arnold under review). These findings suggest the role of environmental factors other than temperature on the determination of the dormancy loss rate in a barley crop. Environmental conditions for crop development and growth such as soil properties and water availability were different between experimental and

validation sites, in both studies. For example, experimental and validation plots were irrigated and rainfed, respectively, which could lead to a water and soil N availability lower in validation plots than in experimental plots. Drought during seed development is generally associated with lower dormancy. This effect was reported in *Avena fatua* L. (Sawhney and Naylor 1982) and *Sorghum bicolor* L. (Benech-Arnold et al. 1991). A drought-promoting effect on dormancy release of this kind could be behind the barley crop PHS susceptibility underestimation showed during model validations in Gualano and Benech-Arnold (under review) work. In this study validation plots might have suffered water stress during grain filling and then exhibited a dormancy level lower than expected. In contrast, Aspinall (1965) found that drought imposed during grain filling enhanced dormancy in barley seeds. These findings could explain the PHS susceptibility overestimation from models developed in Rodriguez et al. (2001) experiments. Water stress during grain filling at validation plots might have induced a dormancy level higher than expected. Other factor that could explain the GI-temperature relationships displacements may be soil N availability. High levels of nitrate promoted dormancy release in tomato (*Lycopersicum esculentum* L.; Varis and George 1985), tobacco (*Nicotiana tabacum* L.; Thomas and Raper 1979), tall fescue [*Lolium arundinaceum* (Shreb.) Darbysh.] (Watson and Watson 1982) and *Chenopodium album* L. (Fawcett and Slife 1978). This fact also could explain the downwards GI-temperature relationship displacement (i.e., PHS susceptibility overestimation) found in Rodriguez et al. (2001), but cannot be used to explain the upwards displacement encountered in Gualano and Benech-Arnold (under review) work.

In this paper we explore the effects of the soil N and water availability during grain filling on the timing of dormancy release in a wide range of malting barley cultivars commonly grown in Argentina.

Materials and methods

Plant material

Five two-row malting barley cultivars (Quilmes Ayelén, Quimes Palomar, Quilmes Painé, B1215 and Scarlett) widely grown 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.

Experimental design

A 2 year experiment (2004 and 2005) was conducted at the experimental field of the Facultad de Agronomía of the Universidad de Buenos Aires (FAUBA), located at Buenos Aires city, Argentina (34°25′S, 58°25′W). To evaluate the effect of soil nitrogen (N) and water availability on dormancy release well-watered (control) and high and low (and their combinations) offer of these crop resources treatments were done. Control plots were well watered during the entire crop cycle and fertilizer was applied to achieve a soil N availability of 100 kg N ha^{-1}. High and low soil N availability was imposed through fertilization with urea to obtain total soil content (for the upper 60 cm of the profile) of 180 kg N ha^{-1} (N_{180}) and 40 kg N ha^{-1} (N_{40}), respectively. Fertilization was done at approximately two-leaf stage by incorporating the fertilizer into the soil close to the sowing line. High water availability plots were well-watered throughout the crop cycle, while in the low water treatment a terminal-drought was imposed from few days before anthesis to HM. Drought was imposed by reducing water into the main plots by covering them with a removable polyethylene structure on rainy days. Sub-superficial water flow into the plots was impeded with polyethylene walls that were installed vertically into the soil (80 cm depth) around main plot perimeter. In 2004 all combinations of crop resources offer (soil N and water) were performed, whereas in 2005 the drought-low N availability treatment was replaced by another where drought was imposed from anthesis as well, but when the crop reached the temperature-sensitive window for dormancy release (defined in thermal time and located on the last stages of grain development; Gualano and Benech-Arnold under review) it was irrigated. In this case the N availability was set at high level (N_{180}). This was done to explore the possibility of dormancy release sensitivity to environmental factors other than temperature (in this case to soil water availability) during this window.

Plots of 2.7 m^{-2} were used and their arrangement was done following a split plot design (main plot: soil

N and water availability treatment; subplot: genotype), with three replicates. Sowing date was on 19 July in 2004 and on 4 August in 2005. Distance between rows was 0.15 m, and seeding density was that for obtaining a stand of 250 plants m^{-2}. The weeds in plots were controlled manually. Insects and fungal diseases were controlled with dimetoato (290 g a.i. ha^{-1}, as Galgofos®, Chemotecnica S.A., Argentina) and tebuconazole (150 g a.i. ha^{-1}, as Folicur 25 EW®, Bayer S.A., Argentina), respectively.

Duration of grain filling period

Thermal time (TT) accumulation during the period from anthesis to PM for each barley cultivar and their respective base temperature values (T_b) were calculated in a previous work (Gualano and Benech-Arnold under review; Table 1). Anthesis time was established when 50% of the plants in the plot had reached flowering. The mean daily temperature values used for TT accumulation were obtained from a meteorological station within the experimental field.

Assessment of grain dormancy release

Germination tests were conducted for each treatment, in both experimental years. Spike sampling for germination tests began 22 days after pollination/anthesis (DAP) and was repeated every 5–4 days until harvest maturity. Anthesis date of each plot was defined as the date when 50% of the plants had released pollen. 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.

Table 1 Grain filling duration and base temperature for grain filling period for each barley cultivar (Gualano and Benech-Arnold under review)

Barley cultivar	Grain filling duration (°Cd)	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

On each germination assay, 25 grains from each sample (one per plot) were placed in plastic Petri-dishes (90 mm diameter, with 2 layers of Whatman No. 5 filter paper, and 6 ml of distilled water) and incubated at 20°C for 12 days. The number of germinated grains (radicle protruding >1 mm) was recorded daily and used to calculate a germination index (GI), as done in previous studies (Steinbach et al. 1995; Benech-Arnold et al. 1999). GI values obtained for the three replicates were averaged into a single observation ± standard error.

Statistical analysis

Results were subjected to analysis of variance (ANOVA) to evaluate the effects of treatments and their interaction on measured variables.

Results

Dormancy release in control plots

Dormancy release pattern was seen as the evolution of the germination index of grains throughout seed development and maturation. Averaging across all barley genotypes analyzed, GI evolution at control plots during 2004 followed a sigmoid pattern, with values remaining lower than 20 until 36 DAP (approximately when PM was attained), indicating that virtually no sprouting risk exists before PM (Fig. 1a). Thereafter, GI began a rapid increase reaching values close to 70 at 52 DAP (near HM; Fig. 1a). In 2005, mean (averaging across all varieties) dormancy release rate was much higher than in 2004, with GI evolution adopting an asymptotic pattern in which GI values close to 60 were reached at PM, and a plateau with a GI around 80 was attained at HM stage (48–52 DAP; Fig. 1b).

In both experimental years, there were not great differences between barley cultivars in the GI evolution pattern at control plots, with the only exception of genotype B1215 in 2004 (Fig. 2). The genotype B1215 is a highly PHS-susceptible barley cultivar, and therefore generally shows a rate of dormancy loss that is much higher (particularly from PM onwards) than those of cultivars with intermediate PHS resistance. Surprisingly, this differential PHS behaviour was not shown in 2005, in which all barley cultivars

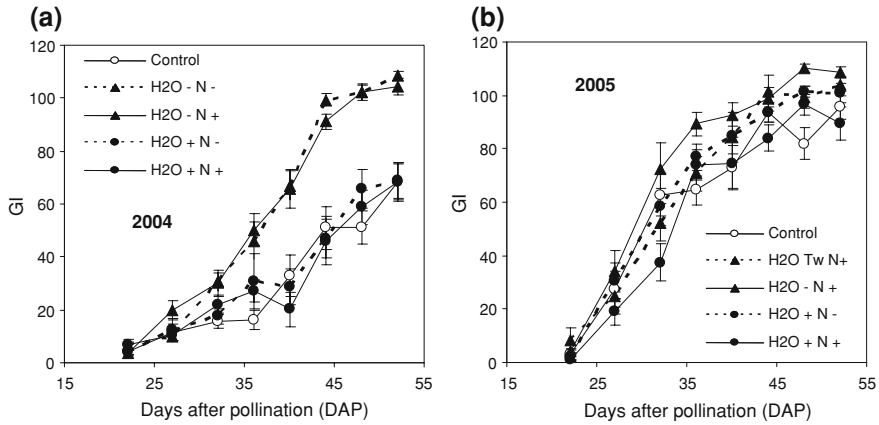

Fig. 1 Mean germination index (GI) evolution along time for grains harvested from plots under different treatments during grain filling, in 2004 (**a**) and 2005 (**b**) experimental years. Treatments were: control plots, and low (−) or high (+) water and soil N availabilities (and their combinations). In 2005 the H_2O-N− treatment was replaced by another (H_2O_{Tw} N+) where drought was imposed from anthesis as well, but irrigated during the temperature-sensitive window sensu Gualano and Benech-Arnold (under review). Each value is the average of three replicates. *Vertical bars* are mean SE when larger than the symbol

analyzed showed a high rate of dormancy loss at control plots (Fig. 3).

Dormancy release as affected by soil N availability

In both experimental years, dormancy release was not affected by soil N availability since mean pattern (averaged across all barley genotypes analyzed) for N_{180} and N_{40} treatments did not differ significantly, for any water availability treatment (Fig. 1a, b). Moreover, N availability effects were not found either when each barley cultivar was considered individually (Figs. 2, 3).

Dormancy release as affected by water availability during grain filling

In 2004 experimental year, drought imposed during grain filling had a significant ($P < 0.05$) positive effect on dormancy release; regardless of soil nitrogen availability and barley cultivar (highly PHS-susceptible cv. B1215 was the only exception; Figs. 1a, 2). In contrast, this drought-promoting effect on dormancy release was not shown in 2005 since grains from both drought and irrigated plots had similar GI values (Figs. 1b, 3). In both experimental years, the mean dormancy release pattern at drought plots was similar (Fig. 1a, b: mean across all barley cultivars; Fig. 4: excluding cultivar B1215), showing a high rate of exit from dormancy; however, significant differences between years were found in control and irrigated plots (Figs. 1a, b, 4). In 2005, grains from the irrigated plots showed a dormancy loss rate that was unexpectedly high (similar to that of drought plots), while in 2004 GI values in grains from these plots were ca. 40 points lower than in grains from drought ones from PM onwards (Figs. 1a, b, 4). The mean effect of drought on dormancy release can be easily seen by relating the GI (mean across all varieties analyzed, except cv. B1215) of grains from drought plots with that of grains from irrigated ones (i.e., drought/irrigated GI ratio), for each sampling date and experimental year (Fig. 5). When the value of this ratio is close to one it means that the GI values of grains from drought and irrigated plots do not differ significantly (i.e., there was not a drought effect on dormancy release); if the ratio is <1 it indicates that drought lowers GI in comparison with an adequate water supply condition (i.e., drought had a negative effect on dormancy loss rate); and when the ratio is >1 it means that a promoting effect of drought exists on dormancy release. When we compared the mean drought/irrigated GI ratio throughout seed development and maturation for both experimental years we found, until PM, a higher ratio in 2005 than in 2004 (with >1 values; Fig. 5). Conversely, from PM

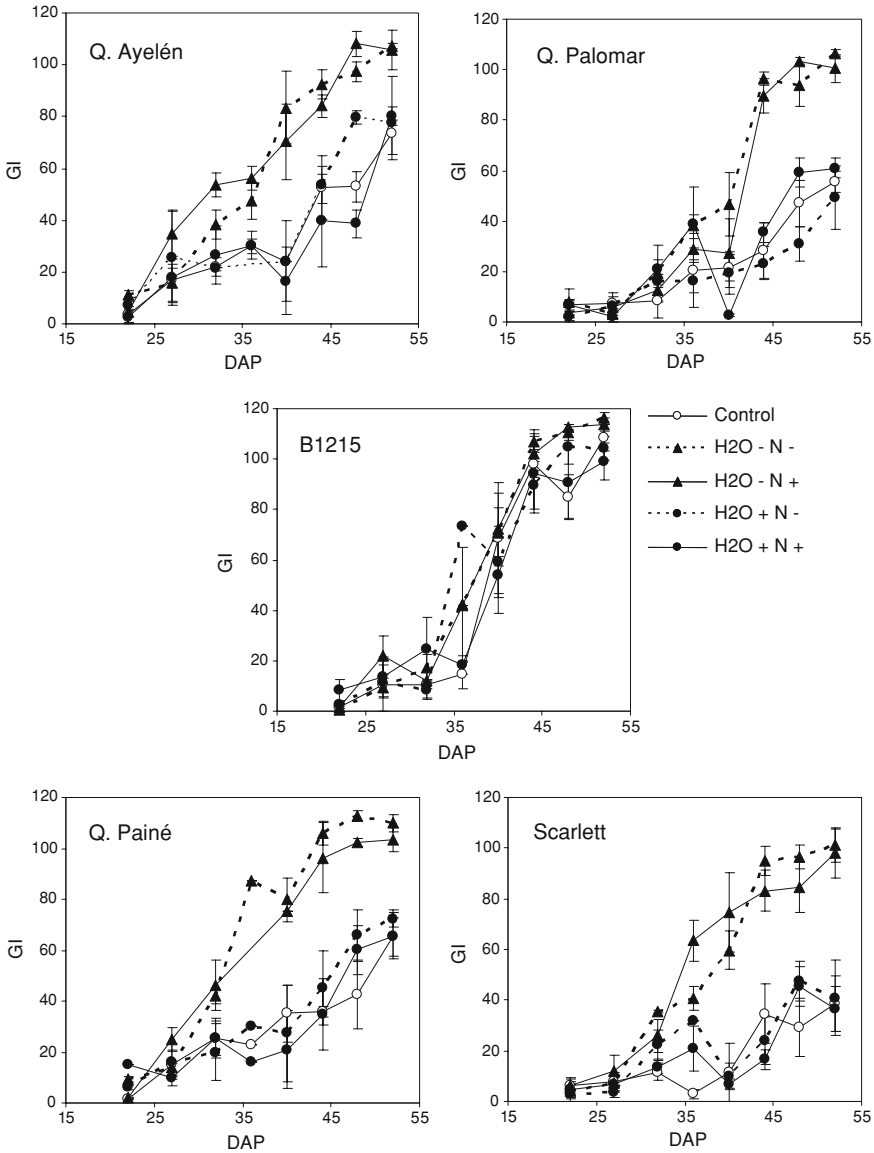

Fig. 2 Germination index (GI) evolution along time for grains of each barley cultivar in 2004 experimental year. Treatments were as in Fig. 1. Each value is the average of three replicates. *Vertical bars* are mean SE when larger than the symbol

onwards, in 2005 this ratio remained close to one while in 2004 the GI at drought plots was up to fivefold higher than at irrigated ones (Fig. 5).

For all barley varieties analyzed (except B1215), the largest effect of drought during the entire grain filling period on dormancy release was evidenced around 40 DAP (a few days after PM), as indicated by the highest drought/irrigated GI ratio at this stage (Fig. 6). In this moment the grain is still in the field (i.e., seed drying stage) and, under drought conditions during grain filling, the dormancy level developed in the seeds is low enough for sprouting damage to occur if rainy, increased moisture conditions take place. There were significant ($P < 0.05$) differences between cultivars in the GI response to drought at this developmental stage. The most sensitive cultivar to drought was Scarlett, followed by Q. Palomar, Q. Ayelén, Q. Painé and B1215, in decreasing order (Fig. 6). Regardless of these differences, the PHS susceptibility genotype ranking was practically not changed under drought (Fig. 7). Genotypes with high PHS susceptibility were those with a high dormancy release rate. As expected, the most PHS susceptible cultivar was B1215, followed by

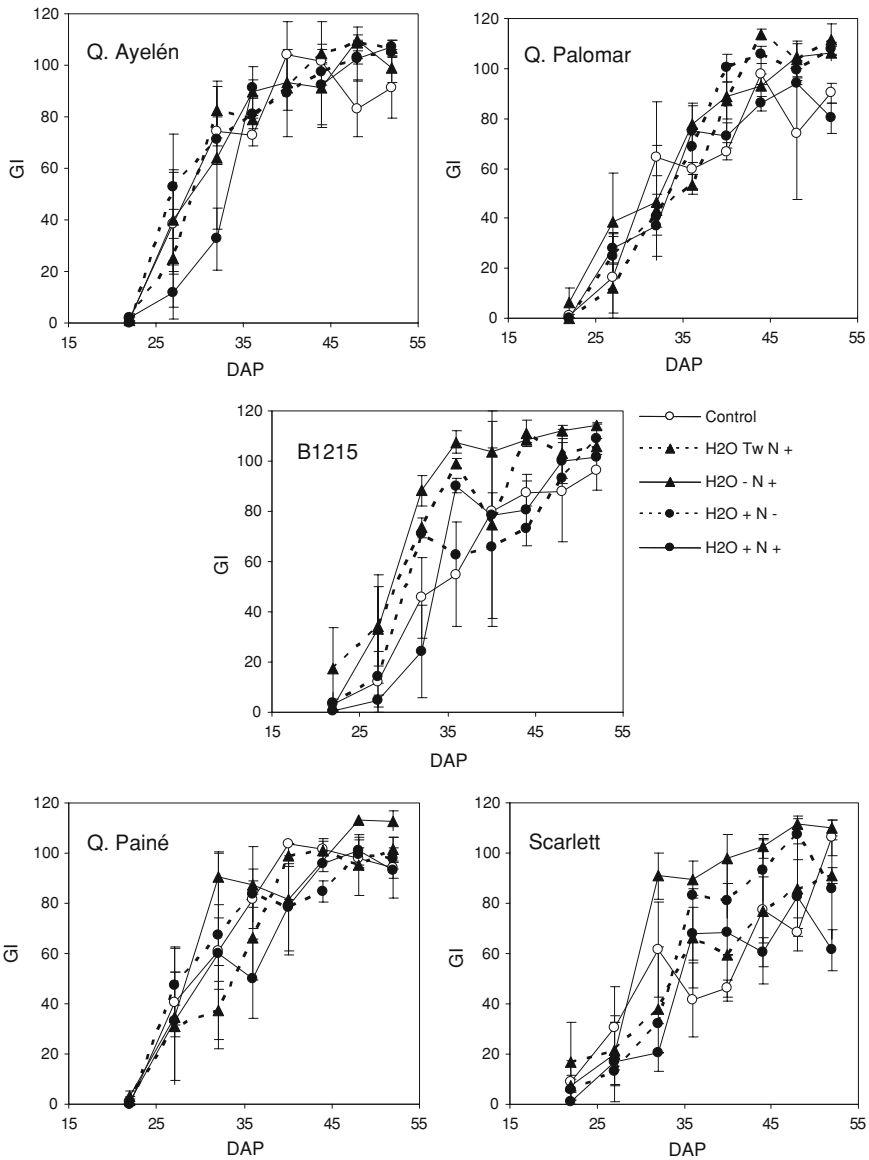

Fig. 3 Germination index (GI) evolution along time for grains of each barley cultivar in 2005 experimental year. Treatments were as in Fig. 1. Each value is the average of three replicates. *Vertical bars* are mean SE when larger than the symbol

Q. Ayelén, Q. Painé, Q. Palomar and Scarlett, in decreasing PHS susceptibility order (Fig. 7a). Under drought, there was some change in the genotype ranking: Scarlett seemed to exhibit a higher dormancy release rate than Q. Palomar (Fig. 7b).

In 2005, the treatment with drought from anthesis onwards, but irrigated during the temperature-sensitive window for grain dormancy (Gualano and Benech-Arnold under review) did not produce significant differences in the dormancy release pattern with respect to that produced by the drought treatment imposed during the entire grain filling period (Fig. 1b).

Thermal environment during grain filling

In 2004, mean air temperature during the grain filling period took values, depending on barley cultivar, between 18.3 and 18.7°C. These values were slightly higher in 2005, between 18.7 and 20.4°C (data not shown). Hence, there were little differences between years in mean temperature during the whole grain filling for each barley cultivar (Table 2). However, great significant ($P < 0.01$) differences between experimental years were found in the temperature during the sensitivity window for dormancy release defined for each cultivar in a previous work (Gualano

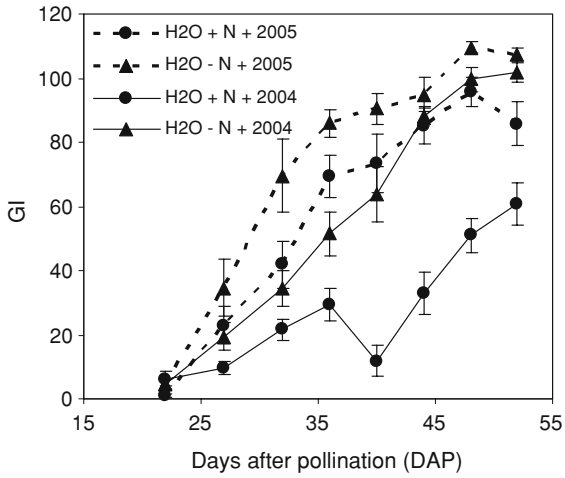

Fig. 4 Mean (except B1215) germination index (GI) evolution along time for grains harvested from plots subjected to (−) or (+) water and (+) soil N availability during grain filling, in both 2004 and 2005 experimental years. Each value is the average of three replicates. *Vertical bars* are mean SE when larger than the symbol

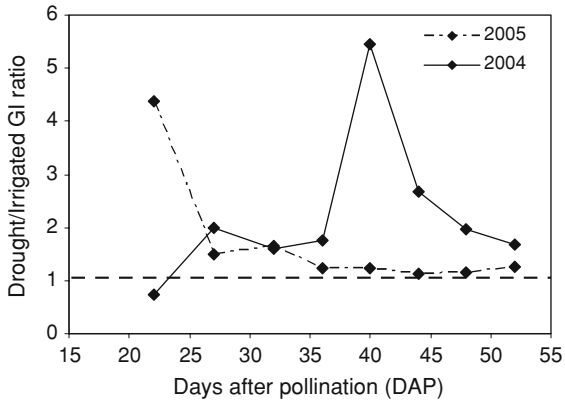

Fig. 5 Ratio between mean (except B1215) germination index (GI) in drought and irrigated plots (high soil N availability treatment) for grains harvested at different days after pollination, in both 2004 and 2005 experimental years. Dashed line indicates a drought/irrigated GI ratio equal to one, meaning no effect of drought on dormancy release

and Benech-Arnold under review; Table 2). For all barley cultivars, mean air temperature during this window was much higher (6°C average) in 2005 than in 2004 (Table 2). Since this temperature is directly related with dormancy loss rate (Gualano and Benech-Arnold under review), this implicated that GI of grains at about half way between PM and HM from irrigated plots were much higher (160% average) in 2005 than in 2004 (Table 2).

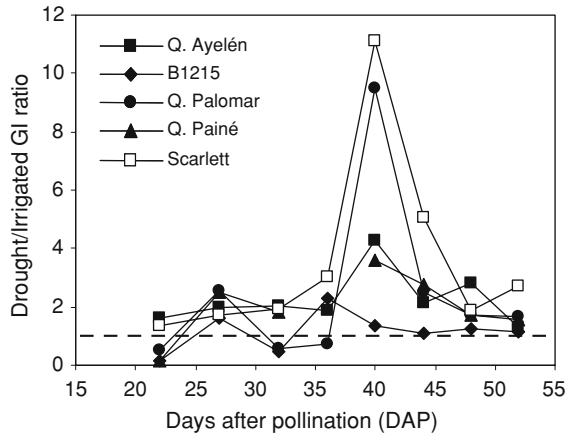

Fig. 6 Ratio between germination index (GI) in drought and irrigated plots (high soil N availability treatment) for grains of each barley cultivar analyzed harvested at different days after pollination, in both 2004 and 2005 experimental years. Dashed line indicates a drought/irrigated GI ratio equal to one, meaning no effect of drought exists on dormancy release

Discussion

Drought during grain filling largely ($P < 0.05$) increased the rate of dormancy loss from physiological maturity onwards in a wide range of malting barley cultivars with intermediate PHS resistance. Similar drought effects were reported in *Avena fatua* L. (Sawhney and Naylor 1982) and *Sorghum bicolor* L. (Benech-Arnold et al. 1991). In years with an unusual low rainfall during the grain filling period, or in terminal drought environments, this fact could do that a moderately PHS resistant barley cultivar behaves as a susceptible one, exposing the crop to a high risk of pre-germination/sprouting damage if some rainfall event occurs (Benech-Arnold 2001). In contrast to our results, Aspinall (1965) found that drought imposed during grain filling enhanced dormancy in barley seeds.

Although N supply effects on dormancy were reported in grasses (Watson and Watson 1982) and other species (Fawcett and Slife 1978; Thomas and Raper 1979; Varis and George 1985), in this study soil nitrogen availability did not affect dormancy release, in any soil water condition during grain filling.

In a recent work (Gualano and Benech-Arnold under review), and with the aim of improving crop management, we developed models that predict the PHS susceptibility of a malting barley crop from

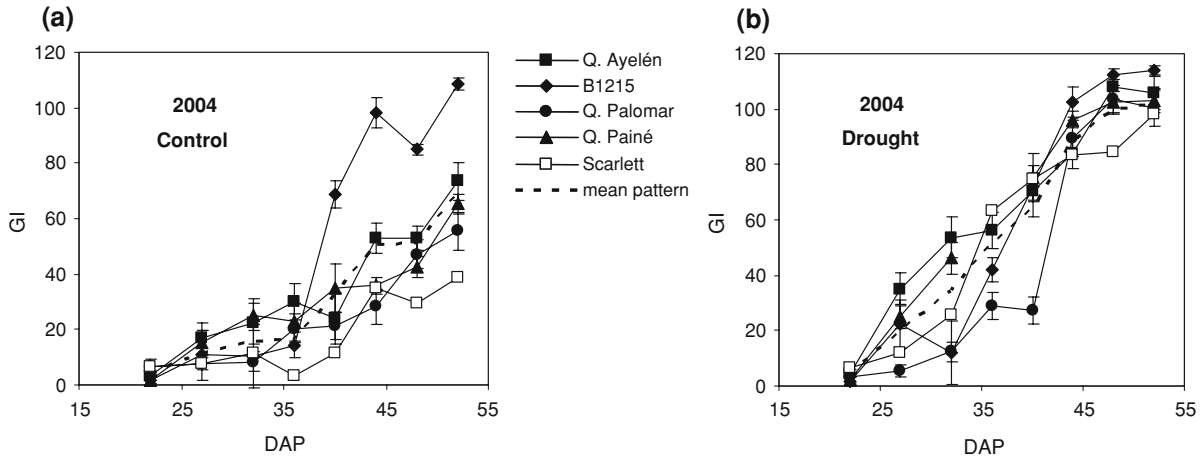

Fig. 7 Germination index (GI) evolution along time for grains of each barley cultivar harvested from control (**a**) and drought (**b**) plots, in 2004 year. *Dashed line* represents the mean dormancy release pattern for each situation, averaged across all barley genotypes analyzed. Each value is the average of three replicates. *Vertical bars* are mean SE when larger than the symbol

Table 2 Grain filling temperature-sensitive window (sensu Gualano and Benech-Arnold under review) defined in thermal time from anthesis; mean air temperature during this window (both soil N availability irrigated treatments average) and GI of grains at half way between PM and HM predicted from models developed previously (Gualano and Benech-Arnold under review), for both 2004 and 2005 experimental years. Difference between years in mean temperature during the sensitivity window and whole grain filling for each barley cultivar tested are presented

Barley cultivar	Grain filling temperature-sensitive window (°Cd)	Mean temperature during sensitivity window (°C)		Predicted GI at half way between PM and HM		Difference in mean temperature between years 2005 vs. 2004 (°C)	
		2004	2005	2004	2005	Sensitivity window	Whole grain filling
Q. Ayelén	275–325	16.3	23.2	14.06	75.68	+6.8	+0.3
B1215	325–375	18.4	24.1	71.43	85.57	+5.7	+1.1
Q. Palomar	300–350	17.3	23.4	31.83	66.11	+6.1	+0.4
Q. Painé	275–325	17.4	23.1	39.93	79.77	+5.7	0.0
Scarlett	250–300	17.5	24.4	25.15	59.79	+6.9	+2.1

temperature data during grain filling. For various commercial cultivars we established close and positive relationships between the GI of grains at half way between PM and HM and the mean air temperature during a narrow time window defined in thermal time and located at the last stages of grain filling. When a preliminary validation against independent field data for these models were done, it was found that most observed GI values were higher than predicted (models underestimated crop PHS susceptibility). However, the slopes of the GI-temperature relationships were conserved. These results indicated that temperature explains only one dimension of the variability in dormancy, and suggest the role of other environmental factors in the modulation of dormancy release rate in barley crops. Environmental conditions for crop growth and development were different between experimental site and validation locations. Water availability, particularly during grain filling, was much lower at validation plots. N fertilization rate between environments was different also. In the present study no significant effects of soil N availability on dormancy release pattern of a barley crop were found. However, and since the temperatures at validation plots during the sensitivity windows were moderate (see below), the drought-promoting effect

on exit from dormancy revealed in this study could be behind the PHS susceptibility underestimation found during validation of the experimental models developed previously (Gualano and Benech-Arnold under review).

As we found for temperature in that study (Gualano and Benech-Arnold under review), the sensitivity of barley seed dormancy to soil water availability could be limited to a particular stage within seed development rather than to the entire grain filling period. We tested this possibility with plots under drought treatment from anthesis, irrigating them at the end of grain filling [during the temperature-sensitive windows for grain dormancy determined previously (Gualano and Benech-Arnold under review)]: the dormancy release pattern of grains from these plots was not significantly different from that of grains from plots with drought treatment imposed during the whole grain filling period. However, since in the year when these experiments were conducted (2005) there were no significant differences between drought (whole filling period) and irrigated treatments either, the possibility that sensitivity to water availability could be limited to a narrow time window within seed development (as in the case of temperature) rather than to the entire grain filling period cannot be ruled out.

The drought effect on dormancy loss rate seems to be dependent on the year, since drought affected dormancy release in 2004 experimental year but not in 2005 one (Fig. 4). The analysis of environmental conditions in each year indicated significant ($P < 0.01$) differences in temperature regimes during the sensitivity window for dormancy release (sensu Gualano and Benech-Arnold under review) defined for each cultivar. For all barley varieties, mean air temperature during this window was much higher (6°C average) in 2005 than in 2004 (Table 2). According to the models developed previously (Gualano and Benech-Arnold under review), a temperature increase during the sensitivity window of this kind would imply an increase of about 160% (average) in the GI of the grains half way between PM and HM and thus determining a PHS-susceptible behaviour in all cultivars. In other words, these largely higher temperatures may have increased the rate of dormancy loss until to its maximum, masking drought effects and doing the dormancy release insensitive and independent of soil water availability. In fact, in 2005 all barley cultivars, and independently of water availability treatment, exhibited a dormancy release pattern similar to that of B1215 cultivar, which is considered highly PHS-susceptible due to a very rapid exit from dormancy (Fig. 3). Hence, the influence of the thermal environment during grain filling on dormancy release could explain differences in drought effects between years.

We conclude that drought effect on dormancy release depends on the thermal conditions during the temperature-sensitive time window for dormancy located at the last stages of seed development (sensu Gualano and Benech-Arnold under review). Under warmer conditions (temperature above 22°C, e.g., 2005 year) the dormancy release pattern would be mainly determined by temperature during the sensitivity window, being virtually independent of soil water availability; while under cooler conditions (e.g. 2004) both temperature and water availability effects should be considered. Under extreme drought conditions during grain filling (as evaluated in these experiments) dormancy loss rate is high and virtually independent of temperature during sensitivity window. However, moderate water stresses of variable intensity often occur in many barley growing areas of the world (including Argentinean Pampas). Establishing the quantitative relationship between soil water availability during grain filling and dormancy release rate in malting barley crops is required. This information, together with previous studies about the modulation of dormancy release by the grain filling thermal environment, may help in predicting PHS susceptibility of a barley crop more accurately in years/environments with temperate and moderate rainfall climate.

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