植物科学学报 2011，29(3)：352～361
Plant Science Journal

DOI：10.3724/SP.J.1142.2011.30352

野生二棱大麦种子休眠型态与农艺性状及生态地理因素相关性研究

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摘 要：对来自以色列不同地区 16 个生态型野生二棱大麦种子的休眠型态与其农艺性状及起源地生态地里因素的相关性进行了研究。结果表明：高温（40℃）储藏可以打破种子的休眠；16 个生态型种子在高温处理下的萌发率表现出显著差异，其休眠打破过程显示出不同型态的对数生长曲线：8 个旱生生态型为 S 型，而 8 个湿生生态型为倒 L 型。休眠深度用实际达到最大萌发率的时间度量，最低休眠深度（15.6 d）是来自湿润地区“进化峡谷”的生态型 37-N，而最深休眠深度（103.1 d）是来自干旱地区 Ein-Zukim（死海附近）的生态型 32-6。此外，对 11 个物候及农艺性状指标与休眠深度做斯皮尔曼秩相关分析，结果有 9 个显示出显著相关，尤其是粒重与休眠深度有极显著相关性。同时，休眠深度与起源地 15 个生态地理因素中的 9 个有显著相关，种子休眠主要受其起源地的地理位置、温度和水分条件等影响。可见，野生二棱大麦自然选择进化了休眠特性去应对干热环境而繁衍生息。本研究结果可用于进一步遗传研究和现代栽培大麦品种的改良。

关键词：休眠深度；萌发率；生长曲线；野生二棱大麦

中图分类号：Q945.6⁺5；S512.3　　**文献标识码：**A　　**文章编号：**2095-0837(2011)03-0352-10

Caryopsis Dormancy Patterns of Wild Barley (*Hordeum spontaneum*) and Its Association with Agronomic Traits and Ecogeographical Parameters

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Abstract: Patterns in caryopsis dormancy and its agronomic and ecogeographical associations were investigated in 16 wild barley (*Hordeum spontaneum*) ecotypes from different habitats in Israel. The results showed that heat treatment (40℃) could break dormancy of caryopses. Germination percentages under breaking dormancy treatments were significantly different among the 16 ecotypes. Dormancy-break patterns were fitted by logistic growth curves: all eight xeric ecotypes showed an S-shaped curve, whereas all eight mesic ecotypes displayed a reverse L-shaped curve. For depth of dormancy, as reflected by the time to maximum germination percentage, the lowest (15.6 days) was for the ecotype 37-N from the north slop of Evolution Canyon (mesic), whereas it was the highest (103.1 days) for 32-6 from Ein-Zukim (near Dead Sea) (xeric). In addition, nine of 11 Spearman's Rho Correlations between dormancy depth and agronomic traits of 16 *H. spontaneum* ecotypes were significant. Dormancy depth showed closest correlation with kernel weight. Nine of 15 correlations between dormancy depth and ecogeographical factors were significant. Caryopses dormancy was mainly influenced

Received date: 2010-09-13, Accepted date: 2010-12-11.

Foundation item: Bona Terra Foundation in Israel; Hatchery Programme Foundation for the Youth Talents in Science and Technology by Guizhou Province in China (2006－2010).

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by their original location, as well as temperature and local water conditions. Therefore, natural selection adapted wild barley to a dry and warm environment by increasing dormancy. The results of dormancy in wild barley will be subjected to genetic analyses and should be helpful for improving modern barley cultivars.

Key words: Dormancy depth; Germination percentage; Growth curve; *Hordeum spontaneum*

Barley, *Hordeum vulgare*, is a principal cereal crops and among the five most important crop plants in the world, including wheat, rice and corn[1]. As the progenitor of cultivated barley, wild barley, *Hordeum spontaneum* C. Koch is widespread in the Near East Fertile Crescent[2]. In Israel, wild barley is distributed from mesic Mediterranean areas to xeric northern and central areas of the Negev desert[3]. *H. spontaneum* is known to contain diverse resistances to powdery mildew[4], leaf rust[5], aphids[6], and scald[7], and their populations show large genetic variation in their tolerance to drought and salinity[8,9]. Due to its rich adaptive diversity, *H. spontaneum* has proven to be an important genetic resource for crop improvement[10,11].

Dormancy is defined as the inability of a viable seed to germinate (or poor germination) under environmental conditions favorable for germination[12,13]. Dormancy plays a major role in the ecological adaptation of wild plant species[13]. In areas with long, hot and dry summers following the season with rain and mild temperatures, many plants have developed seeds with primary dormancy. These include *Plantago coronopus L.* subsp. *commutata* (Guss.) Pilger (Plantaginaceae)[14], *Schismus arabicus* Nees, *Ammochloa palaestina* Boiss., *Stipa capensis* (Thunb.)[15], *Haloxylon ammodendron* (C. A. Mey) Bunge (chenopodiaceae)[16], *Brochypodium distachyon* (L.) Beauv[17], *Triticum turgidum* ssp. *dicoccoides* (Korn.) Thell[15,18] and *Hordeum spontaneum* C. Koch[19-21]. The various levels of seed dormancy in wild barley are adequate as a safeguard against natural hazards[14,15,22,23] and an important survival strategy given the unpredictable small amounts and distribution of winter rain in the areas[14,19,22]. For cultivated barley, the balance between a limited level of dormancy at grain maturity and rapid germination after seed harvest is highly warranted[24]. A lack of or low seed dormancy may lead to pre-harvest sprouting and low malting quality. On the other hand, high seed dormancy results in non-uniform seed germination, causing problems in the establishment of field stands and low yields of malt extract[25]. In agricultural production, a better understanding of the relevant mechanisms of dormancy, and the relationship between seed dormancy and environmental conditions, will help geneticists and breeders control dormancy level or dormancy release at proper time and proper percentages as required[26].

The objective of the present study is to investigate the patterns of *H. spontaneum* caryopsis dormancy, using 16 ecotypes from six different locations in Israel, and the relationships between caryopses dormancy and the ecogeographical conditions of their collection sites.

1 Materials and methods

1.1 Plant materials and seed propagation

Caryopses of wild barley (*H. spontaneum*) were collected by the Institute of Evolution, University of Haifa from six geographical populations in Israel. The populations are listed in Table 1 along with their geographical origin and climatic conditions. Sixteen ecotypes derived from six populations were selected: eight of them originated from mesic habitats (mean annual rainfall > 600 mm) in the north of Israel, including Mt. Hermon (Site 1), Maalot (10), and "Evolution Canyon" (37), and the other eight were from xeric habitats (mean annual rainfall < 300 mm) in central and southern regions of Israel, such as Mehola (22), Ein-Zukim (near Dead Sea) (32) and Sede Boker (20) (Table 1).

In total, 512 (32 × 16) germinating seeds were sown in elevated beds of loess soil with the addition of compost and irrigated by a dripping system in the experimental station, Sede Boker Campus, Ben-Gurion University of the Negev. Approximately 40000 caryopses of *H. spontaneum* were obtained, and freshly harvested caryopses were stored separately in brown paper bags at 5℃ until being used in the experiment.

1.2 Heat-treatment of caryopses and dormancy break

The caryopses of the 16 *H. spontaneum* ecotypes were stored at 5℃ for six months after harvest. They were then incubated at 40℃ for periods of 0, 14, 28, 42, 56, 70, 84, 100 and 114 days. Six replicates of 40 caryopses from each of the heat-treated caryopsis groups were wetted with 4 mL of distilled water in a 90 mm Petri dish on one piece of Whatman No. 1 filter paper, and kept at 15℃ in the dark for 7 days. Dormancy break (measured as germination percentage) was checked three times, on days 2, 4 and 7 of the incubation[17].

1.3 Definition of dormancy depth and statistical analysis

The following growth curve was used to describe germination characteristics[17].

$$G_t = K/(1 + ae^{-rt}) \quad (1)$$

Where G_t is the germination percentage (%); t is the dormancy-break treatment time (days); K (usually less than 100) is the maximum germination percentage (%), and r is the slope representing the relative growth rate.

Rearranging Eq. (1), and converting into logarithmic form, gives:

$$\ln\left(\frac{K - G_t}{G_t}\right) = \ln a - rt \quad (2)$$

The value of K can be calculated according to Eq. (3)[27] by using three pairs of observed values: (G_1, t_1), (G_2, t_2) and (G_3, t_3): here, the time intervals between t_1, t_2 and t_3 have to be equal, namely $(t_1 - t_2)/(t_2 - t_3) = 1$:

$$K = \frac{G_2^{\ 2}(G_1 + G_3) - 2G_1G_2G_3}{G_2^{\ 2} - G_1G_3} \quad (3)$$

a and r can then be obtained by fitting into the linear Eq. (2).

Theoretically, the time at which G_t reaches K indicates dormancy depth. However, K is the asymptotic value of G_t at $t \rightarrow \infty$. Thus, in practice, a critical time of t_c at which G_t reaches 95% of the K value is used to represent dormancy depth.

The JMP® ver. 6.0 statistical package (SAS Institute) was used for ANOVA and Spearman's Rho Correlation analyses.

Table 1 Ecogeographical data of the growing sites of six *H. spontaneum* populations residing in Israel

Code*	Pop	Lon	Lat	Alt	Tm	Ta	Tj	Td	Tdd	Ev	Rn	Rd	Hu14	Huan	Dwsm	So
1	Mt. Hermon	35.75	33.28	1530	11	20	1	19	6	160	1400	70	52	58	60	1
10	Maalot	35.27	33.00	500	17	23	8	15	10	150	785	55	50	64	55	4
20	Sede Boqer	34.78	30.87	450	19	26	9	15	13	168	91	15	36	53	70	3
22	Mehola	35.48	32.13	-150	22	30	13	17	13	180	270	39	34	53	22	1
37	Evolution Canyon	34.58	32.43	90	22.5	28	13	15	-	142	600	-	-	67	-	2
32	Ein-Zukim	35.44	31.74	-200	24	31	15	16	12	210	100	20	35	52	8	3

* Population IDs and selected environmental data are based on reference [3] and [28]; Ein-Zukim data is based on reference [29]. Symbols of variables: Pop - Population. Geographical variables: Lon - longitude (decimals); Lat - latitude (decimals); Alt - altitude (m). Temperature variables: Tm - mean annual temperature (℃); Ta - mean August temperature (℃); Tj - mean January temperature (℃); Td - mean seasonal temperature difference (℃); Tdd - mean daily temperature difference (℃); Ev - mean annual evaporation. Water variables: Rn - mean annual rainfall (mm); Rd - mean number of rainy days; Hu14 - mean humidity at 1400 (%); Huan - mean annual humidity (%); Dwsm - mean number of dewy nights in summer (mm). Dummy soil variables: So - soil types; 1 Rendzina; 2 Terra Rossa; 3 Loess; 4 Alluvium. Soil types are in ascending order from light to heavy.

2 Results and discussion

2.1 Patterns of caryopsis dormancy in 16 *H. spontaneum* ecotypes

Caryopsis germination percentages under the breaking dormancy treatments in 16 *H. spontaneum* ecotypes from different habitats in Israel are shown in Fig. 1 (data cited from reference [17]). Germination percentages were significantly different ($p = 10^{-8}$ by ANOVA) among the ecotypes. The fitted logistic growth curve of germination rate for each of the 16 ecotypes was plotted in Fig. 2. Based on the number of days needed to reach 95% of K, the 16 ecotypes were clearly classified into two types: mesic (ecotypes 37-B, 37-S, 37-N, 1-6, 1-12, 10-1, 10-20 and 10-50) and xeric (ecotypes 20-A, 20-B, 20-C, 22-15, 22-42, 22-55, 32-6 and 32-20), coupled with the environments from which they were collected. As a reflection of dormancy break, all eight xeric ecotypes showed a normal S-shaped growth curve, while all eight mesic ecotypes displayed a reverse L-shaped growth curve (Fig. 2). Except for two types of curves, each of the two types can be subdivided into subgroups. At least three subgroups were characterized by their curves: Ⅰ) including ecotypes 20-A, 20-B, and 22-55; Ⅱ) 20-C, 22-15, and 22-42; and Ⅲ) 32-6 and 32-20. In reversed L groups, there were obvious differences between two subgroups: ecotypes 37-B, 37-S, 10-1, 1-6 and 1-12, 37-N, 10-20, 10-50.

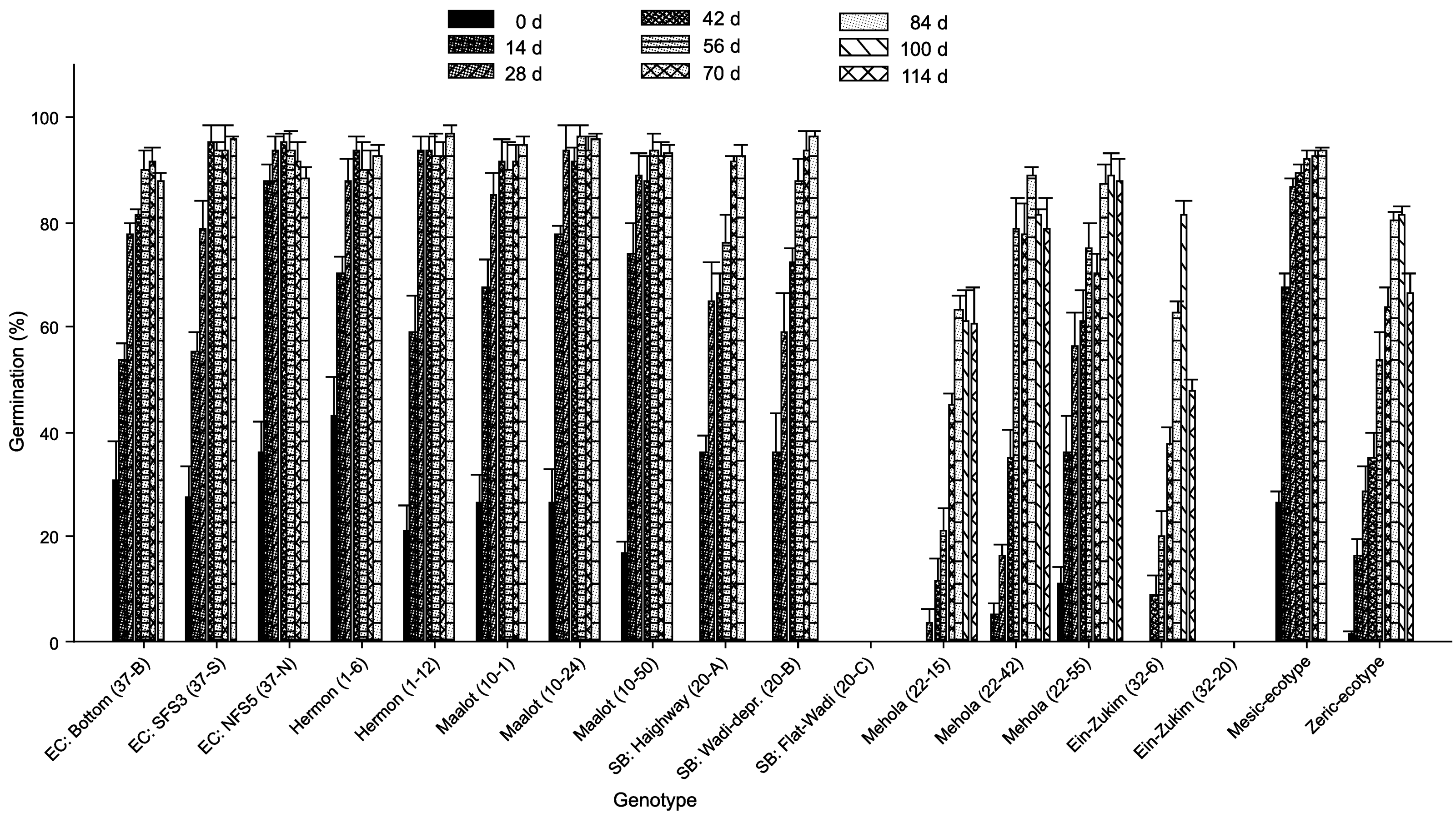
In present study, dormancy depth [the critical time (t_c) (day) at which germination percentage reaches a plateau] was significantly greater for xeric ecotype (mean = 83 days) than mesic ecotypes (mean = 40 days) ($p = 10^{-8}$) (Table 2). The time to reach a plateau progressively increased from mesic ecotype 37-N, 10-20, 1-12, 10-50, 37-B, 10-1, and 1-6, to xeric ecotype 22-42, 20-B, 20-A, 22-55, 22-15, 20-C, 32-20, and 32-6 (Table 2, Fig. 2). Dormancy depth was the lowest (15.62 days) for ecotype 37-N from the north slop of Evolution Canyon (mesic), whereas the highest (103.1 days) was for 32-6 from Ein-Zukim (near the Dead Sea, xeric). In addition to critical time, the minimum value of germination percentage (without heat treatment) in the xeric ecotypes was significantly lower (2.89%) than that in the mesic ecotypes (36.44%) ($p = 0.00052$). Ecotype 32-20 from Ein-Zukim had the lowest value (0.02%) and ecotype 1-6 from Mt. Hermon had the highest (41.16%). The maximum germination-percentage values for xeric (82.54%) and mesic (93.59%) ecotypes were not significantly different ($p = 0.065$) (Table 2).

Variation in agronomic traits revealed genetic differences resulting from the adaptation of *H. spontaneum* to different eco-environments. This was, because in the current set of experiments, the caryopses were harvested from plants that had been grown in the same location, at the same time, under the same conditions. These rich variations provide the possibility for improving dormancy in cultivated barley. The vast genetic resources of wild barley provide the best, largely unexploited, resource for improving the narrowing genetic base of cultivated barley[3].

2.2 Correlation between caryopsis dormancy and agronomic traits

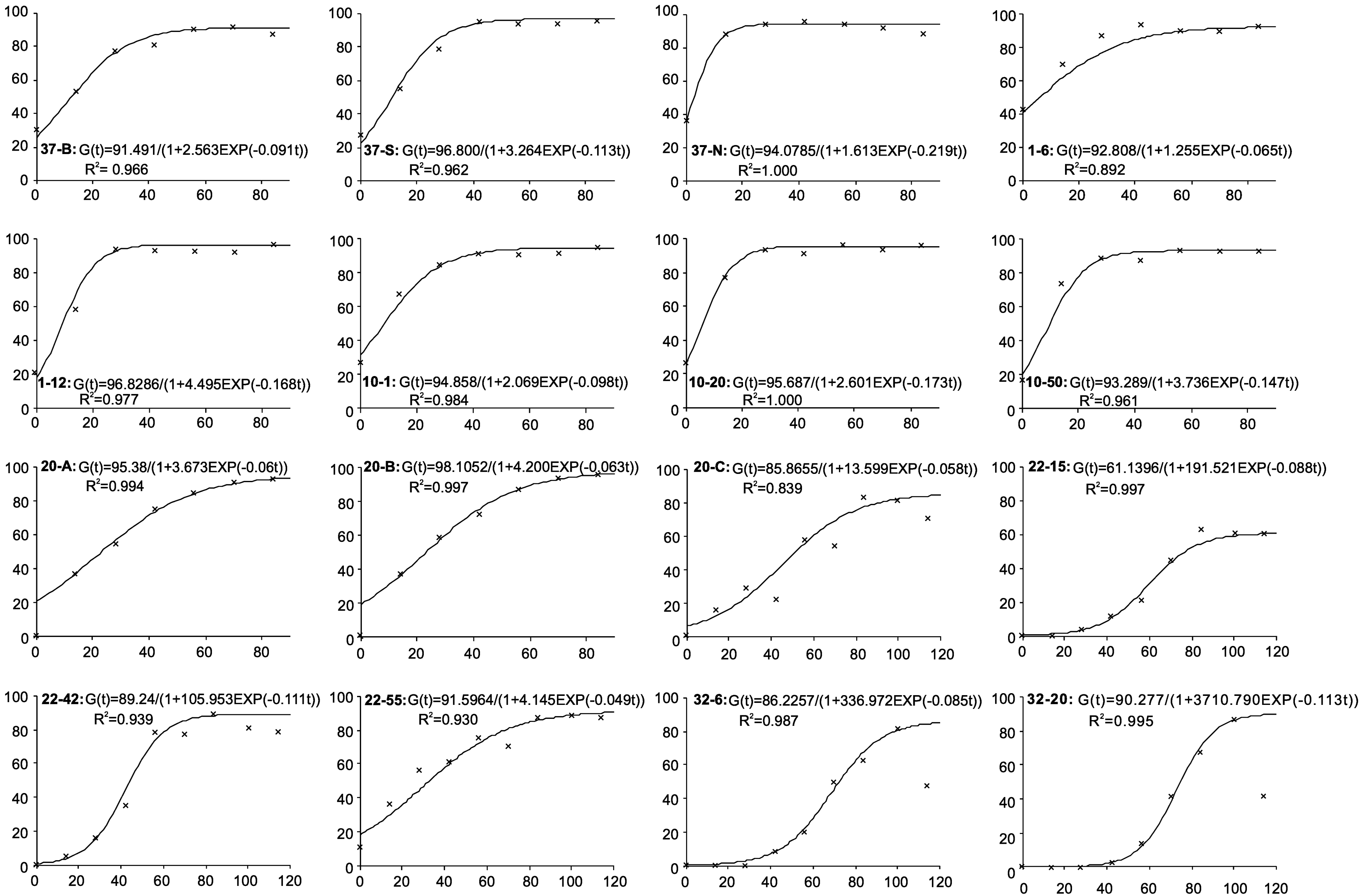
Spearman's Rho Correlations between dormancy depth and 11 agronomic traits of 16 *H. spontaneum* ecotypes are summarized in Fig. 3. Data on the agronomic traits are based on reference[30]. Dormancy depth was significantly correlated with nine of the 11 agronomic traits.

Dormancy depth was correlated negatively with kernel weight, spikelet weight, tillering stage, heading stage, maturity period, plant height, spike length and spike length + awn, and positively correlated with spikelet number per spike. The dormancy depth had the closest correlation with kernel weight among the 11 traits. Figure 4 shows the association between dormancy depth and kernel weight based on Pearson product moment



The 16 ecotypes were stored at 5℃ for six months after harvest,and then transferred to 40℃ storage for either 0,14,28,42, 56,70,84,100 and 114 days.Afterwards the caryopses were geminated for seven days at 15℃ in darkness.

Fig.1 The germination percentage of *H. Spontaneum* caryopses in heating treatment at different periods



Abscissa: Days of storage at 40℃ for breaking caryopsis dormancy; **Ordinate:** Caryopsis germination (%) of an ecotype. The fitted curve represents a characteristic growth curve of an ecotype; the symbol ‘×’ denotes the experimental data.

Fig.2 Variation of the germination percentage for caryopses with treatment period (heat of 40℃) as fitted by logistic growth curve based on 16 *H. spontaneum* ecotypes

Table 2 Calculated values of fitted growth curve of 16 *H. spontaneum* ecotypes in heat treatment for different periods

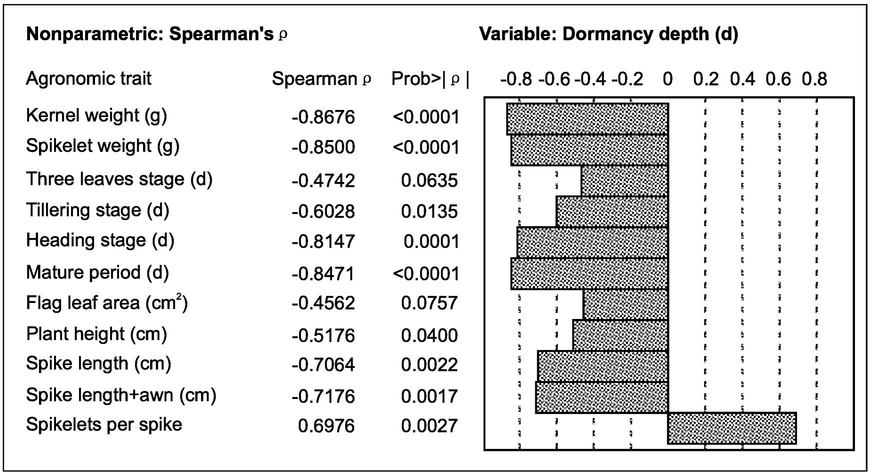
Ecotype	Minimum value(%) $Gt_0 = K/(1+a)$	Maximum value (%) (Plateau) K	Slope of growth r	Days reaching 95% of K t_c
37-B	25.68	91.49	0.091	42.71
37-S	22.70	96.80	0.113	36.53
37-N	36.01	94.08	0.219	15.62
1-6	41.16	92.81	0.065	48.80
1-12	17.62	96.83	0.168	26.48
10-1	30.91	94.86	0.098	37.48
10-20	26.57	95.69	0.173	22.54
10-50	19.70	93.29	0.147	28.99
Mesic	36.44	93.59	0.084	40.40
20-A	20.41	95.38	0.060	70.75
20-B	18.87	98.11	0.063	69.52
20-C	5.88	85.87	0.058	95.77
22-15	0.32	61.14	0.088	93.18
22-42	0.83	89.24	0.111	68.52
22-55	17.80	91.60	0.049	89.13
32-6	0.26	86.23	0.085	103.10
32-20	0.02	90.28	0.113	98.80
Xeric	2.89	82.54	0.075	83.49
ANOVA (Xeric vs. Mesic) (p)	0.00052	0.065		10^{-8}

correlation analysis ($r = -0.929$, $p < 0.000005$). Therefore, the dormancy depth of wild barley caryopsis could be predicted by kernel weight, whereby the lighter the kernel weight, the more depth dormancy of the *H. spontaneum* caryopsis. This result is similar with Chen *et al*[20]. Wild barley originating from mesic areas exhibited caryopses with low dormancy, associated with big seed size (heavy kernel weight).

2.3 Association of caryopsis dormancy with ecogeographical factors

Among the 15 correlations between dormancy depth and ecogeographical factors (Table 1), nine of them were statistically significant (Fig. 5). Dormancy depth was correlated negatively with latitude, altitude, mean annual rainfall, mean number of rainy days, mean humidity at 14:00 hours, and mean annual humidity, and positively with mean August temperature, mean January temperature, and mean annual evaporation, indicating that dormancy depth increased with August and January temperature and annual evaporation, and decreased with latitude, altitude, annual rainfall, number of rainy days, humidity at 14:00 hours and annual humidity, irrespective of longitude, annual temperature, and soil type. Therefore, the caryopses dormancy was mainly influenced by their original location, as well as the local temperature and water conditions.

A large number of studies have demonstrated the variation in germination responses of seeds from different populations of the same species. Depending on the species, germination responses



Dormancy depth was defined as a critical time (day) at which germination percentage reached plateau.

Fig. 3 Spearman's Rho significant correlations between dormancy depth and agronomic traits of 16 *H. spontaneum* ecotypes

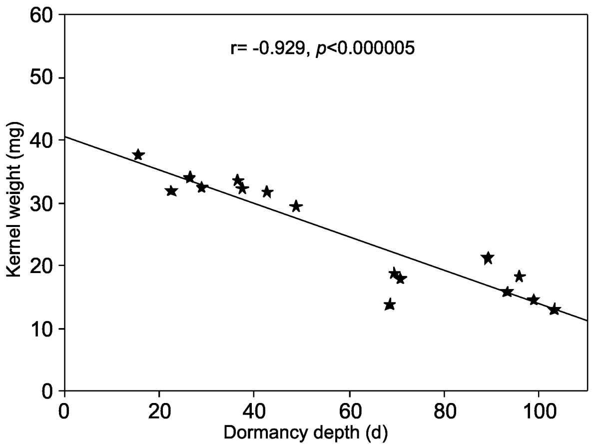


Fig.4　Relationship between caryopsis dormancy depth and kernel weight of 16 *H. spontaneum* ecotypes

vary with latitude, elevation, soil moisture, soil nutrients, temperature, kind and density of plant cover, and degree of habitat disturbance of sites where the seeds matured[12]. *H. spontaneum* occurs in areas that receive winter rains followed by long, dry and hot summer[14,15,22]. The amount and distribution of rainfall in areas where *H. spontaneum* is naturally distributed change and fluctuate greatly from year to year and from season to season[14,15,22,31]. Therefore, wild barley has developed specific strategies to adapt to the conditions featured with unpredictable rainfalls to avoid the risk of germination during out-of-season summer rain[32].

3　Conclusions

(1) Heating treatment (40℃) could break dormancy of caryopses. The dynamic process of the germination rate at designated times could be fitted by a logistic growth curve. These dormancy curves revealed abundant patterns for different genotypes. The xeric ecotypes, which had deeper dormancy, displayed an S-shaped curve, whereas the mesic ecotypes, which had lower dormancy, displayed L-shaped curve.

(2) Caryopses from xeric environments have developed deeper dormancy than that from mesic environments. Caryopsis dormancy was mainly influenced by their original location, as well as the local temperature and water conditions. Therefore, natural selection caused wild barley to adapt to a dry and warm environment by increasing dormancy.

(3) Dormancy depth was correlated with many agronomic traits and had the closest correlation with the kernel weight among 11 traits.

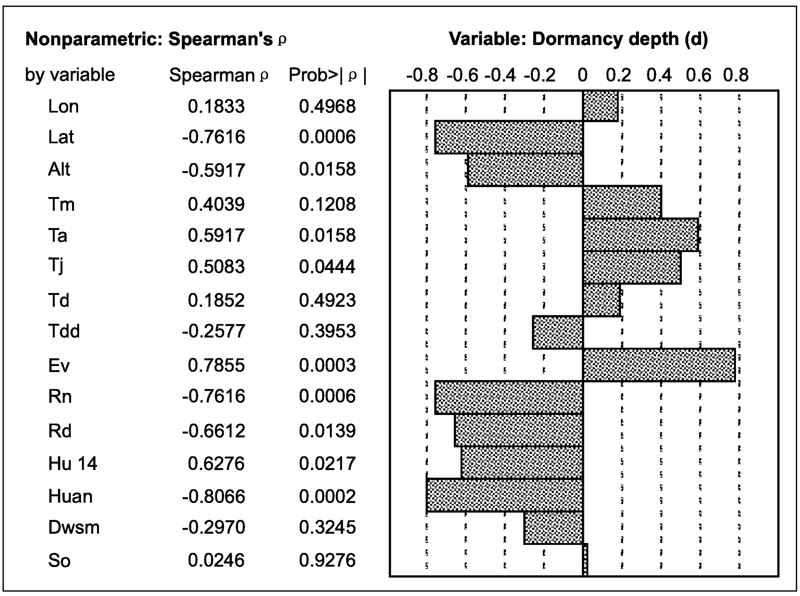


Fig.5　Spearman's Rho significant correlations between dormancy depth and ecogeographical factors (Table 1) of 16 *H. spontaneum* ecotypes

Therefore, dormancy depth of wild barley caryopsis may be indicated by a very simple index, i. e., kernel weight. Thus, seed size might be applied to estimate dormancy depth of *H. spontaneum* caryopsis.

Acknowledgements: This study was funded by the Hatchery Programme Foundation for the Youth Talents in Science and Technology of Guizhou Province in China and the Bona Terra Foundation in Israel.

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