〔韓作誌(Korean J. Crop Sci.) 38(5) : 449~457(1993)〕

Effects of Temperature on Leaf Emergence Rates and Phyllochron of Naked and Malting Barley

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温度가 쌀보리와 맥주보리의 出葉速度와 出葉間隔에 미치는 影響

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ABSTRACT : Three naked and three malting barley cultivars were grown at constant temperatures of 4, 8, 12, 16, 20, 24 and 28℃, and day/night temperatures of 6/2, 10/6, 14/10, 18/14, 22/18, 26/22 and 30/26℃ through the fourth leaf stage in growth chambers to determine the effects of the temperature on leaf emergence rate and phyllochron in naked and malting barley seedlings. The number of leaves per main stem was recorded daily from the first leaf stage to the fourth.

At a given temperature, the emergence of new leaves was a linear function of time for all cultivars. There were no great differences in leaf emergence rate and phyllochron between constant and variable day/night temperature regimes except at 28℃. Leaf emergence rate and phyllochron significantly differed among cultivars and among mean temperatures within cultivars. For all cultivars, leaf emergence rate per day increased parabolically with increasing mean air temperature until an optimum temperature was reached and then declined. There were no differences in the optimum temperatures for the leaf emergence rate per day among six cultivars, which ranged 20.1 to 21.5℃. The leaf emergence rates at the optimum temperatures ranged 0.202 to 0.226 leaves/day for naked barley cultivars and 0.231 to 0.241 leaves/day for malting barley cultivars. As temperature increased, leaf emergence rate per GDD decreased exponentially and the phyllochron (GDD/leaf) increased exponentially. The mean of the phyllochron for six cultivars was 46.2 GDD at 4℃ and 129.3 GDD at 28℃. These results suggest that the temperature and cultivar effects must be considered for prediction of leaf development in barley.

Key word : Temperature, Barley, Leaf emergence rate, Phyllochron

Crop canopy photosynthesis, evapotranspiration, dry matter production and final yields are all influenced by light interception through the leaf area within a crop canopy. In many areas of agronomy research including crop simulation modeling, it is necessary to

This paper was supported by NON DIRECTED RESEARCH FUND, Korea Research Foundation, 1992.
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predict leaf area development. Leaf emergence and tillering are important mechanisms for leaf area of winter cereals including barley.

The concept of growing degree-days (GDD) has been widely used to describe the process of summation of temperature to predict crop development[15]. Some investigators have reported a highly significant linear relationship between the leaf number on the main stem of winter cereals and the accumulated GDD after seedling emergence within a sowing either before or after the double ridge stage[1,3,4,5,6,7]. However, in some experiments, the number of leaves increased as a linear function of the accumulated GDD regardless of the growth stages[8,10,11,12].

The slope of the regression of leaf number on the main stem against the accumulated GDD is the leaf emergence rate per GDD. Cao and Moss[4,5] reported that leaf emergence rate per GDD in wheat and barely decreased either with increasing temperature or with decreasing daylength.

The reciprocal of leaf emergence rate is termed the phyllochron or phyllochron interval. For simulating the vegetative development of the wheat, a value for phyllochron is necessary[14]. In constant environments, Cao and Moss[4,5,6] found that phyllochron was constant for a given environment through the fourth leaf stage of both winter wheat and spring barley, but was larger in higher temperature or shorter photoperiod.

In outdoor plantings of wheat and barley, phyllochron has been shown to vary with growth stages, cultivars, and enivronments. Several researchers reported that phyllochron of barley and wheat was much shorter for leaves formed prior to double ridge formation than those formed latter[1,3,7,17]. In some studies, the phyllochron in wheat and barley was found to be constant during the life of a cultivar planted on a particular date[8,10,11,12]. Cao and Moss[7] proposed that there are at least two periods when phyllochron is sensitive to the environment, one at seedling emergence and another at about the time of the double ridge formation, and the second period of sensitivity does not always occur.

Differences in phyllochron were found among both barley and wheat cultivars[1,2,3,10,12,17]. Bauer et al[2]. found that soil water level and fertilizer nitrogen rate had no effect on phyllochron of spring wheat. However, Baker et al[1]. reported that the phyllochron was shorter for nonirrigated than irrigated winter wheat leaves. They thought that this reduction in phyllochron was caused by the nonirrigated plants being warmer relative to the irrigated plants. Longnecker et al[13]. also reported that nitrogen deficiency reduced leaf emergence rate.

Warrington and Kanemasu[16] reported that where temperature regimes had lower than 20℃, leaf emergence rate per day in maize was higher with differential temperature treatments than with constant temperature conditions with the same daily mean, but at mean temperature above 20℃, the relationship was reversed. Since day temperatures are almost higher than night temperatures in a natural environment, phyllochron determined at variable day/night temperature would be more appropriate for prediction of leaf number in barley grown in a field. However, no research has been reported that assesses differential effects between constant and variable day/night temperatures on leaf emergence rate of winter cereals grown in controlled environment. The objectives of this research were to determine the responses of leaf emergence rate and phyllochron for naked and malting barley cultivars to constant and alternating day/night temperatures.

MATERIALS AND METHODS

Fourteen separate experiments were conducted in two identical growth chambers (interior size: 113×57×110cm) using three naked barley (winter six-rowed type) cultivars: Nulssalbori, Saessalbori, Hyangcheongwa 1; and three malting barley (spring two-rowed type) cultivars: Doosan 8, Sacheon 6, Jinkwangbori.

The plants were grown in plastic boxes [1380cm^2 (46×30cm, 10cm deep)]. The soil used was a 3:1 mixture (by volume) of sandy loam soil and compost. Before sowing, ground limestone, N, P_2O_5 and K_2O were thoroughly mixed with the soil at rates of 200, 4, 9, and 4g m^{-2}, respectively. Each box consisted of six rows at a 7cm spacing. About 30 seeds were planted in each row for a cultivar. The seedlings were thinned to five per row at the first leaf stage.

Constant temperatures of 4, 8, 12, 16, 20, 24 and 28℃, and day/night temperatures of 6/2, 10/6, 14/10, 18/14, 22/18, 26/22 and 30/26℃ were imposed from planting. All temperatures were maintained within ±0.5℃ of the treatment set temperature. The daylength for all temperature treatments was 12 hours. Photosynthetic photon flux density measured at soil surface, 55cm below the thermal barrier with a LiCor LI-190S quantum sensor (Li-Cor, Inc., Lincoln, NE) was about 340μmol m^{-2} s^{-1}. The boxes were checked daily and irrigated whenever necessary as judged from the appearance and feel of the surface soil.

The experimental design was a randomized complete block with six treatments (cultivars) and three replicates (boxes) for each separate temperature treatment.

Observations were made daily between 8 and 9 a.m. on the number of leaves until the fourth leaf stage, recording the results in the Haun scale[9]. Haun scale stage was regressed with the number of days after seedling emergence for each replication. Daily growing degree-days (GDD) were calculated as: GDD = $T_m - T_b$, where T_m are daily mean air temperatures and T_b is a constant base temperature. For variable day/night temperature treatments, daily mean air temperature was calculated by averaging the day and night temperatures, since the daylength was 12 hours. We used 0℃ as the base temperature[1,4].

Variables were analyzed with randomized complete block analysis of variance techiques on each temperature's data separately and then merged together in a combined analysis across temperature types and mean air temperatures.

RESULTS AND DISCUSSION

An example of the linear response of leaf number over days after seedling emergence is shown in Fig. 1 for 'Nulssalbori' naked barley at two constant day/night temperatures, 12 and 20℃. These responses were typical of the responses of all the cultivars at all temperature treatments. The linear regressions for leaf number vs. time were highly significant ($p<0.001$) for all cultivars at all temperatures. Cao and Moss[4,5,6] also found the linear relationship between leaf number and time for winter wheat and spring barley grown under constant temperatures. Since these experiments were conducted under constant daily

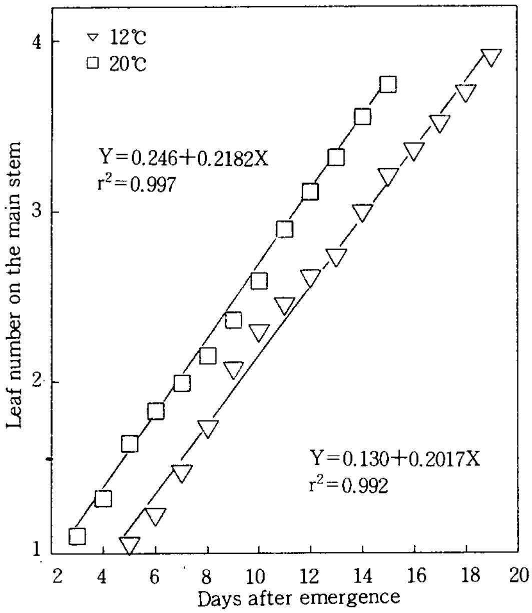

Fig. 1. Leaf number on then stem(Haun growth units) vs. the number of days after seedling emergence for 'Nulssalbori' at two constant temperatures, 12 and 20℃.

mean temperatures, the accumulated GDD after seedling emergence are a constant multiple of time for each temperature. Therefore, the time responses of leaf number have the same shape and correlation coefficients in units of accumulated GDD or of time. Thus, our results are also consistent with the linear relationship between leaf number and accumulated GDD before double ridge formation reported by some researchers for wheat and barley grown in the field[1,3,7].

Mean squares from the analysis of variance for leaf emergence rate per day and phyllochron (GDD/leaf) are presented in Table 1. The temperature and cultivar effects greatly contributed to total variability in these variables. Although temperature type and cultivar×temperature×temperature type interaction effects are significant in the leaf emergence rate per day and the phyllochron, their effects are relatively small and temperature×temperature type effects are not significant. Thus, for each cultivar a regression equation was fitted to describe the relationship between these variables and temperature regardless of temperature types.

Table 1. Mean squares for leaf appearance rate per day and phyllochron(GDD/leaf) of six barley cultivars across two temperature types and seven mean air temperatures

Source	df	Leaf appearance rate$^+$	Phyllochron
Temperature type (Tt)	1	250.38**	555.68*
Temperature (T)	6	8498.14**	41200.03**
T×Tt	6	28.94	93.04
Blocks/T×Tt	28	33.29	80.42
Cultivar (C)	5	468.90**	1068.91**
C×Tt	5	2.40	6.40
C×T	30	24.71**	69.57**
C×T×Tt	30	5.71*	15.82**
Pooled error	140	3.52	8.15

$^+$ Table values must be divided by 10^5.
*, ** Significant at the 0.05 and 0.01 levels, respectively.

The slopes of the regression lines of leaf number vs. time are the leaf emergence rates per day. There were no great differnces in leaf emergence rate per day between constant and variable day/night temperatures except at daily mean temperature of 28℃, at which leaf emergence rate was higher at constant temperaure than at variable day/night temperature for all cultivars. However, Warrington and Kanemasu[16] reported that leaf emergence rate per day in maize was higher with variable day/night temperature treatments than with constant temperature where temperature regimes had lower than 20℃, but at mean temperatures above 20℃, although the relative differences were small, the relationship was reversed.

For all cultivars, the leaf emergence rate per day increased with increasing temperature until an optimum temperature was reached

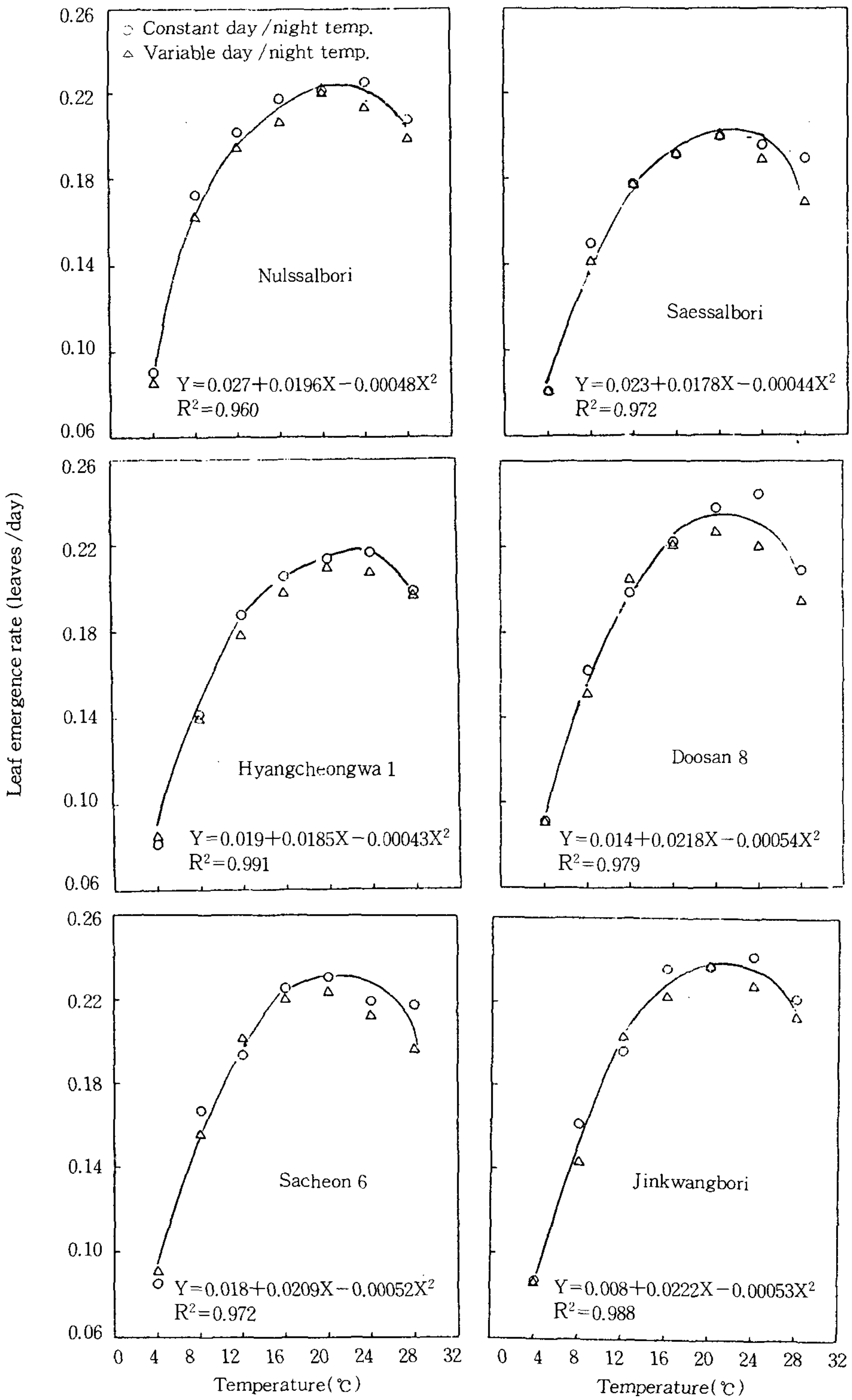

Fig. 2. Response of leaf emergence rate per day to daily mean air temperature for six barley cultivars.

reached and then declined with further increases in temperature (Fig. 2). These optimum type response curves fit well to quadratic polynomials(parabolic curves). The R^2 values for the polynomial fittings of the leaf emergence rates to temperature for all the cultivars were greater than 0.96 (Fig. 2). This is similar to the response of leaf emergence rate per day to temperature in winter wheat and spring barley reported by Cao and Moss[4]. Baker et al[1]., however, found a linear relationship between leaf emergence rate per day and mean air temperature below 20℃ in winter wheat grown in the field.

At all temperature treatments, particularly at higer temperatures, leaves emerged more slowly in naked barley cultivars, especially in 'Saessalbori' and 'Hyangcheongwa 1' than in malting barley cultivars. Shown in Table 2 are the optimum temperatures and maximum rates of leaf emergence for six cultivars calculated using the equations in Fig. 2. There were no marked differences in the optimum temperatures for leaf emergence rate per day among cultivars. However, Cao and Moss[4] found that spring barley had a lower optimum temperature than winter wheat for leaf emergence rate per day. The leaf emergence rates at the optimum temperature ranged 0.202 to 0.226 leaves/day for winter naked barley and 0.231 to 0.241 leaves/day for spring malting barley. This is similiar to the previous study that spring barley appeared to have a little higher maximum leaf emergence rate per day than winter wheat[4].

Table 2. Optimum tepmeratures (T_{opt}) and maximum rates (R_{max}) of leaf emergence for naked and malting barley cultivars

Type	Cultivar	T_{opt} (℃)	R_{max}(leaves/day)
Naked barley	Nulssalbori	20.4	0.226
	Saessalbori	20.1	0.202
	Hyangcheongwa 1	21.3	0.215
Malting barley	Doosan 8	20.3	0.235
	Sacheon 6	20.3	0.231
	Jinkwangbori	21.5	0.241

An example of the exponential response of leaf emergence rate per GDD to the temperature is shown in Fig. 3. The leaf emergence rate per GDD for 'Nulssalbori' decreased exponentially as temperature increased. The other cultivars showed similar resonses of leaf emergence rate per GDD to temperature, which are calculated as the reciprocal of the phyllochron (GDD/leaf) (data are not shown).

The phyllochron increased exponentially with increasing temperature for all six cultivars used in these experiments because leaf emergence rate per GDD decreased exponentially as temperature increased (Fig. 4).

The mean of the phyllochron of the cultivars was 46.2 GDD at 4℃ and 129.3 GDD at 28℃. The relationships between phyllochron

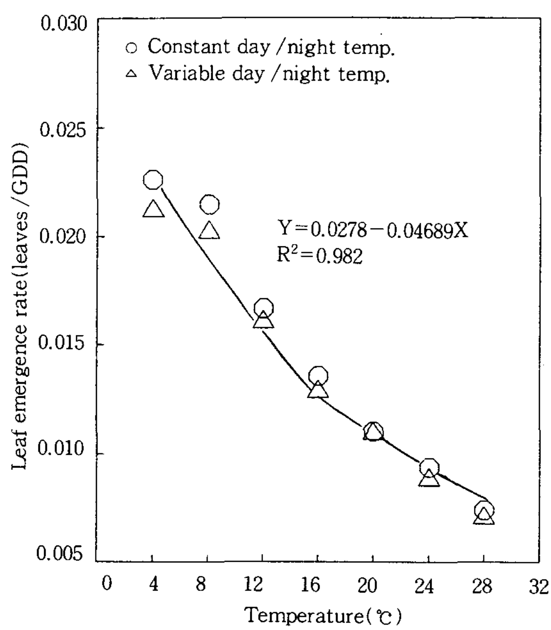

Fig. 3. Response of leaf emergence rate per GDD to daily mean air temperature for 'Nulssalbori'.

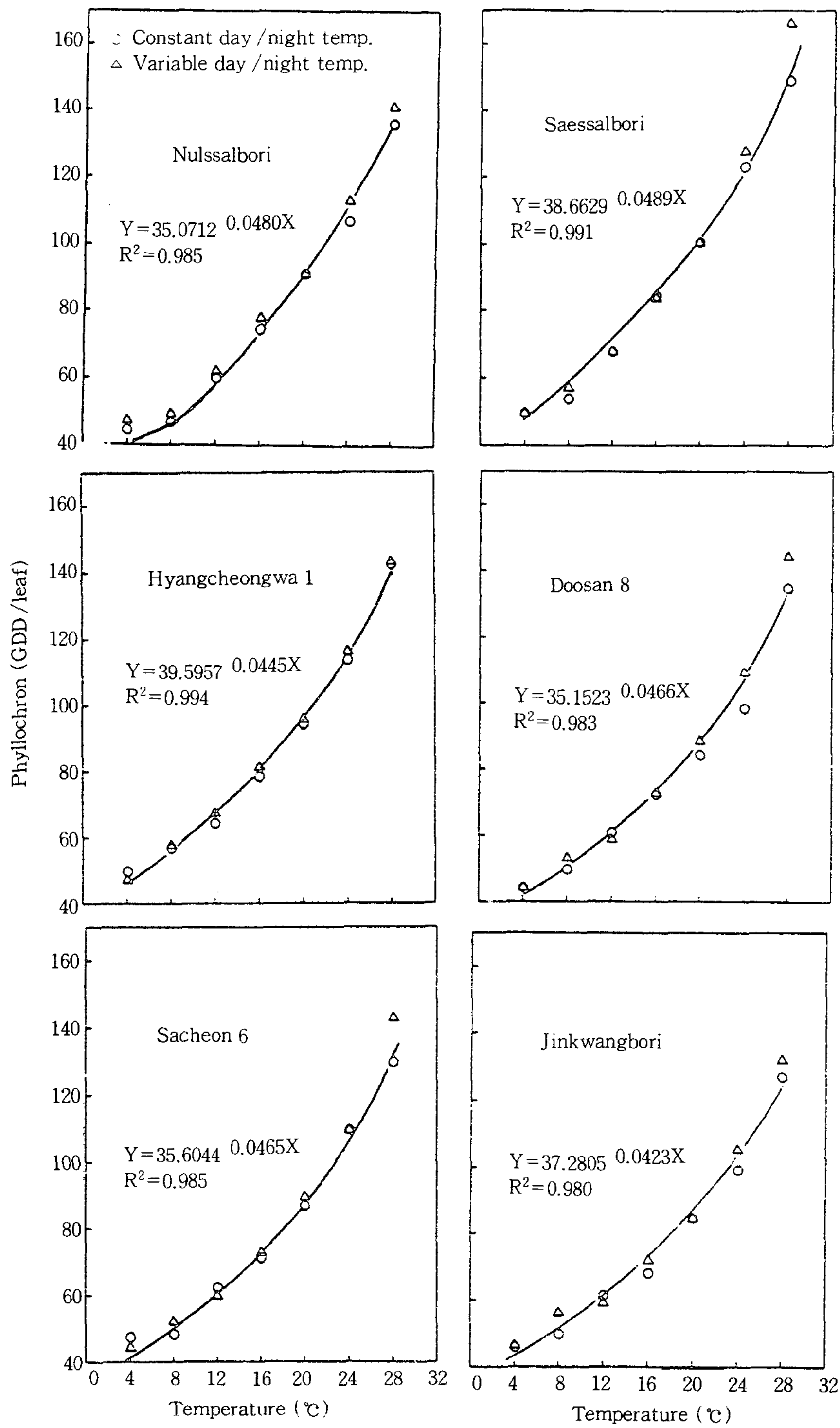

Fig. 4. Respose of leaf phyllochron to daily mean air temperature for six barley cultivars.

and temperature fit exponential equation, with R^2 values for all cultivars being greater than 0.98. This result is consistent with the previous study reported by Cao and Moss[4] for winter wheat and spring barley. This response could be one of the reasons why phyllochron varies with planting dates and latitudes[7,12,14]. The phyllochrons of 'Saessalbori' and 'Hyang-cheongwa 1' are longer than those of the other cultivars used in this study. These results indicate that effects of temperature and cultivar should be considered for estimating leaf development in barley.

摘　要

溫度가 쌀보리와 맥주보리의 出葉速度와 出葉間隔에 미치는 영향을 구명하고자 쌀보리 3품종(늘쌀보리,새쌀보리,향천과 1호)과 맥주보리 3품종(두산 8호,사천 6호, 진광보리)을 恒溫 7수준(4, 8, 12, 16, 20, 24, 28℃)과 變溫 7수준[6/2(明期/暗期), 10/6, 14/10, 18/14, 22/18, 26/22, 30/26℃]으로 유지시킨 생장상에서 4엽기까지 키우면서 매일 主稈葉數를 조사하여 出葉速度 및 出葉間隔를 산출한 결과를 요약하면 다음과 같다.

항온과 변온에 관계없이 공시품종 모두 동일 온도내에 있어서는 出芽後 일수가 증가됨에 따라 主稈 出葉數도 직선적으로 증가되었다. 평균기온 28℃를 제외하고는 出葉速度와 出葉間隔이 恒溫과 變溫間에 현저한 차이를 보이지 않았다. 出葉速度와 出葉間隔은 品種間에 有意한 차이가 있었고 동일 품종내 온도간에도 현저한 차이가 있었다.

평균기온이 증가됨에 따라 日當 出葉速度는 出葉 最適溫度까지 곡선적으로 증가된 다음 감소되었는데, 6품종의 出葉 最適溫度은 20.1~21.5℃로 품종간 현저한 차이는 없었으나 出葉 最適溫度에서의 출엽속도는 쌀보리가 0.202~0.226葉/日, 맥주보리가 0.231~0.241葉/日으로 맥주보리가 큰 경향이었다. 평균이온이 증가됨에 따라 有效積算溫度當 出葉速度는 指數函數的으로 감소되었고, 出葉間隔(一葉當 積算溫度)은 지수함수적인 증가를 보였는데, 6품종의 평균 출엽간격은 4℃에서 46.2 GDD/葉, 28℃에서 129.3 GDD/葉이었다.

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