Korean J. Crop Sci. 46(4): 296~302(2001)

Genetic Analysis of Photoinhibition in Barley

Jong Un Chun*†

**School of Plant Production Science, Sunchon National University, Sunchon, 540-742, Korea*

ABSTRACT : Winter cereals are acclimated during wintering, and thereafter their freezing resistance is increased. In order to analyze inheritance and heritabilities for photoinhibition of photosynthesis by high light intensity under low temperature, and to evaluate the relationship between low temperature-induced photoinhibition and winter survival, 4 parental half diallel crosses were used. The detached leaves of 7~8 cm long from plants grown for 35 and 55 days were placed on wet filter paper and placed in trays at 5°C cold room with 1,200 μmol $m^{-2}s^{-1}$ PPFD. Chlorophyll fluorescence was measured with a chlorophyll fluorescence system after dark adaptation for 30 min. The Fv/Fm of 35-day old plants was reduced from 0.714 in the control leaves to 0.409 and 0.368 following photoinhibitory treatment of 6h and 8h and the CVs were increased from 0.8% to 22.2~22.3%. The Fv/Fm of 55-day old plants was reduced from 0.775 in the control leaves to 0.485 and 0.439 following photoinhibitory treatment of 10h and 12h, respectively. According to half diallel cross analysis, Reno and Dongbori 1 (highly resistant to photoinhibition) was dominant, but Oweolbori (susceptible to photoinhibition) was recessive, and photoinhibition showed partial dominance with highly additive gene action. Dongbori 1 showed the greatest GCA effects for photoinhibition, and GCA/SCA ratios (8.7~22.3 times) indicated that the additive variance for the character was more important. Winter survival in barley crosses was positively correlated with resistance to photoinhibition and significantly fitted by linear regression (R^2=0.751~0.779**). The chlorophyll fluorescence measured by Fv/Fm has been found to be highly inheritable and very useful in evaluating relative levels of freezing resistance in barley.**

Keywords **:** genetic analysis, photoinhibition, chlorophyll fluorescence, Fv/Fm, freezing resistance, barley

Cold-resistant cereals such as winter wheat, rye and barley and wintering forage crops acquire maximum freezing resistance following cold acclimation (Levitt, 1980). Growth at low temperature not only induces freezing resistance of winter cereals, but also induces an increased resistance to low-temperature-induced photoinhibition of photosynthesis. However, spring cereals exhibit limited ability to obtain an increased resistance to photoinhibition during growth at low, nonfreezing temperatures (Öquist & Huner, 1991; Hurry & Huner, 1992). Winter rye acquires the increased resistance to photoinhibition of photosynthesis during cold-acclimation due to an increased capacity to maintain a greater fraction of the PSII reaction centers in an open configuration under given light and temperature conditions (Öquist & Huner, 1991).

Adequate photosynthesis is a requirement for the expression of freezing resistance in cold-resistant cereals. However, photosynthesis is one of the first processes adversely affected by exposure to low temperature. Damage to the photosynthetic apparatus (photoinhibition) is aggravated when high irradiance accompanies the low temperature exposure (Powles, 1984). According to Greer *et al.* (1991), the susceptibility of barley to low-temperature-induced photoinhibition is due to an imbalance between rates of damage and repair of PSII reaction center polypeptides through *de novo* chloroplastic protein synthesis. However, winter rye (Öquist & Huner, 1991) exhibit reduced sensitivity to low-temperature-induced photoinhibition when acclimated to low temperature. Overwintering plants are exposed to low temperature and high irradiance in the field. The relative resistance of plants to photoinhibition may contribute to their ability to cold-acclimation and freezing resistance. The cold-acclimated wheat plants were less susceptible to photoinhibition at 5°C than nonacclimated plants, and the winter cultivars were less susceptible than the spring cultivars (Hurry & Huner, 1992; Chun *et al.*, 1997). Chlorophyll fluorescence has been used to estimate the effects of environmental stresses, including freezing damage, chilling injury, drought etc. The quantum yield estimated with variable fluorescence attribute Fv/Fm has been found to be very useful for detecting freezing damage (Chun *et al.*, 1997; Binder & Fielder, 1996). Objectives of this study were to analyze inheritance, heritability, combining ability effects for photoinhibition as measured by Fv/Fm and relationship with freezing resistance.

MATERIALS AND METHODS

This study was done from 1999 to 2001 at the experimental field and physiology lab. of Sunchon National Univer-

†Corresponding author: (Phone) +82-61-750-3216 (E-mail) Chunju@sunchon.ac.kr <Received July 29, 2001>

sity. Four cultivars of barley (*Hordeum vulgare* L., cvs Sacheon 6, Oweolbori, Dongbori 1 and Reno) were grown and made 6 crosscombinations in an half diallel design. On 25 October in 2000, seeds of 4 parents and 6 F_1 hybrids were planted with row length of 20 cm and plant space of 3 cm in a row. The experimental design was a randomized complete block design with two replications. Fully expanded, third and fourth leaves developed in field were sampled on December 5 and 26 (35- and 55-day old). The detached leaf segments of 7 to 8 cm long were placed on wet filter paper and placed in trays at 5°C cold room with light intensity of 1,200 μmol $m^{-2}s^{-1}$ (high pressure sodium lamp, Son-T AGRO 400, Philips) for 3 to 12 hours. To prevent desiccation of leaves, the filter paper was moistened with distilled water and the cut ends of the leaf segments were also covered with moistened filter paper. Chlorophyll fluorescence was measured with Chlorophyll Fluorometer (PAM-2000, Heinz Walz, Germany) after dark adaptation for 30 minutes at room temperature. According to experimental protocols of Chun *et al.* (1997, 2000a) and Hurry and Huner (1991), instantaneous Fo (initial fluorescence), Fv (variable fluorescence), and Fm (maximal fluorescence) were determined and the ratio of variable to maximum fluorescence (Fv/Fm) was calculated, reflecting the maximum photochemical yield of PSII. The change in the Fv/Fm ratio relative to control was used to quantify the degree of photoinhibition.

The freezing resistance was tested by reduction of 2, 3, 5-tripenyl tetrazolium chloride (TTC) to a water-insoluble red formazan followed by the modified methods described by Chun *et al.* (2000b) or Steponkus & Lanphear (1967) with slight modification.

RESULTS AND DISCUSSION

Comparison of photoinhibition in parents and F_1 hybrids

Chlorophyll fluorescence (CF) is used to measure the efficiency of the light-absorbing portion of a plant photosynthetic system. The change of chlorophyll fluorescence can be used to estimate the effects of environmental stresses, including freezing on photosynthesis (Binder & Fielder, 1996).

The Fv/Fm ratios in 4 parental diallel crosses were shown in Table 1. The mean of Fv/Fm was reduced from 0.714 for the control of 35-day old plants to 0.409 and 0.368 following photoinhibitory treatments of 6 and 8 hours, and the coefficients of variation (CVs) were increased to 22.2~22.3%, respectively. Fv/Fm for 55-day old plants was reduced from 0.775 to 0.485 and 0.439 with photoinhibitory treatments of 10 and 12 hours, respectively, and the CVs became 13.6% and 12.5%. As photoinhibitory duration was extended, the values of Fv/Fm were reduced linearly. The resistance to photoinhibition in completely cold-acclimated plants (55-day old) was increased much more as compared with incompletely cold-acclimated plants (35-day old). Reno showed

Table 1. The Fv/Fm values and relative ratios to control treated with different durations of photoinhibition in 4 parental diallel cross grown in field.

Cross	Fv/Fm						Relative Fv/Fm to control			
	FNA†			FCA‡			FNA		FCA	
	Cont	H-6h	H-8h	Cont	L-10h	L-12h	H-6h	H-8h	L-10h	L-12h
S6 × S6	0.708	0.283	0.257	0.776	0.378	0.350	40.0	36.4	48.7	44.1
S6 × OW	0.715	0.307	0.276	0.775	0.459	0.418	43.0	38.6	59.3	54.0
S6 × D1	0.721	0.403	0.365	0.770	0.471	0.427	56.0	50.7	61.3	55.7
S6 × R	0.712	0.432	0.389	0.768	0.549	0.488	60.5	54.6	71.6	65.1
OW × OW	0.717	0.283	0.254	0.769	0.405	0.379	39.5	35.6	54.4	49.4
OW × D1	0.719	0.426	0.377	0.787	0.455	0.410	59.4	52.5	57.9	52.1
OW × R	0.716	0.486	0.438	0.766	0.522	0.460	68.0	61.1	68.2	62.3
D1 × D1	0.718	0.424	0.382	0.781	0.473	0.431	59.2	53.3	60.7	55.3
D1 × R	0.703	0.501	0.450	0.786	0.557	0.503	71.3	64.0	70.9	64.0
R × R	0.710	0.541	0.487	0.776	0.576	0.522	76.3	68.7	74.2	67.3
Mean	0.714	0.409	0.368	0.775	0.485	0.439	57.3	51.6	62.7	56.9
SD	0.006	0.091	0.082	0.007	0.066	0.055	12.9	11.6	8.3	7.5
CV(%)	0.8	22.2	22.3	0.9	13.6	12.5	22.6	22.5	13.2	13.2

†FNA; nonacclimated in field (35-day old plants), ‡FCA; cold-acclimated in field (55-day old plants), Cont; control, H-6h and H-8h; 6 and 8 hour photoinhibitions in plants grown for 35 days in field. L-10h and L-12h; 10 and 12 hour photoinhibitions in plants grown for 55 days in field. S6; Sacheon 6, OW; Oweolbori, D1; Dongbori 1, R; Reno

the greatest value of Fv/Fm among parents followed by Dongbori 1>Oweolbori>Sacheon 6, showing the similar tendency to degree of freezing resistance. The cross combination of Dongbori 1 × Reno showed the greatest Fv/Fm among F_1 hybrids. As the values of Fv/Fm for the control were different in the different treatments, the relative Fv/Fm ratio to control was calculated. The relative Fv/Fm ratio and CV were 57.3% and 22.6% at the 6h photoinhibitory plot in 35-day old plants. Also, the Fv/Fm ratio was 62.7% with CV of 13.2% at the 10h photoinhibitory plot, and 56.9% with CV of 13.2% at the 12h photoinhibitory plot in 55-day old plants. The values of Fv/Fm in the control and photoinhibitory plots were the same as the relative Fv/Fm ratios to control, and relative Fv/Fm ratios were used as for genetic analysis and estimate of combining ability effects.

When the leaves were in the dark-adapted state, the ratio of variable to maximal fluorescence (Fv/Fm) attained during the fast induction of CF is a measure of the potential or maximal quantum yield of PSII. Thus, Fv/Fm typically in the range of 0.75~0.85 for nonstressed plants (Bolhar-Nordenkampf *et al.*, 1989) is closely correlated with the quantum yield of net photosynthesis of intact leaves, but the values of Fv/Fm in the range of 0.703~0.786 measured here were smaller than those expected values for nonstressed plants. According to Chun *et al.* (1997), the values of Fv/Fm for the control of wheat were decreased from 0.81 to 0.33 with 8h photoinhibition in cold-acclimated plants and from 0.82 to 0.39 with 6h photoinhibition in nonacclimated plants. Those studies showed that the Fv/Fm values were decreased with increasing duration of photoinhibition, and completely cold-acclimated plants showed greater resistance to photoinhibition than the incompletely cold-acclimated plants did. The cold-acclimation increased the resistance to photoinhibition imposed under low temperature (5°C) and high light intensity (Hurry & Huner, 1992).

Genetic analysis of photoinhibition

The Wr-Vr for photoinhibition among parents were analysed to estimate genetic parameters (Table 2). The Wr-Vr for photoinhibition were not significant among the all treatments (H-6h, H-8h, L-10h and L-12h), which fitted to additive-dominance model applicable in case of no interaction among non-allelic genes. The Vr · Wr graphs for photoinhibition of photosynthesis were shown in Fig. 1 and 2. The linear regression coefficients of Wr on Vr for photoinhibition with 0.95~0.96 for all photoinhibitory treatments (35-and 55-day old plants) were not different from 1 by t-test (b=1), and linear regression lines passed above original point (0, 0),

Table 2. Mean squares for Wr-Vr of photoinhibition ratios (Fv/Fm) to control in 4 parental diallel cross grown in field.

Source	DF	Mean square			
		H-6h†	H-8h	L-10h‡	L-12h
Replications	2	1768.2	281.1	71.3	42.3
Arrays	3	245.5^{ns}	106.9^{ns}	62.6^{ns}	45.7^{ns}
Error	6	109.2	38.1	20.1	26.8

ns; not significant. †H-6h and H-8h; 6 and 8 hour photoinhibitions in plants grown for 35 days. ‡L-10h and L-12h; 10 and 12 hour photoinhibitions in plants grown for 55 days.

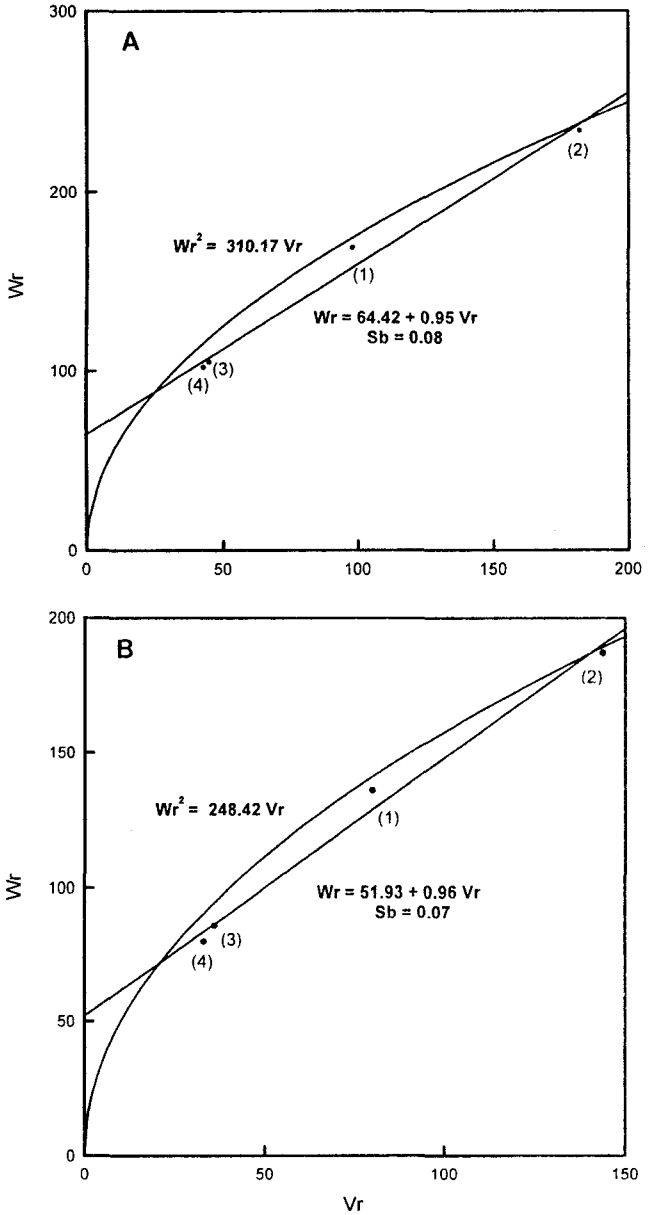

Fig. 1. Vr · Wr graphs for photoinhibition of photosynthesis in 4 parental diallel cross grown for 35 days. A; 6 hour photoinhibition, B; 8 hour photoinhibition. The parents are; (1) Sacheon 6, (2) Oweolbori, (3) Dongbori 1, (4) Reno.

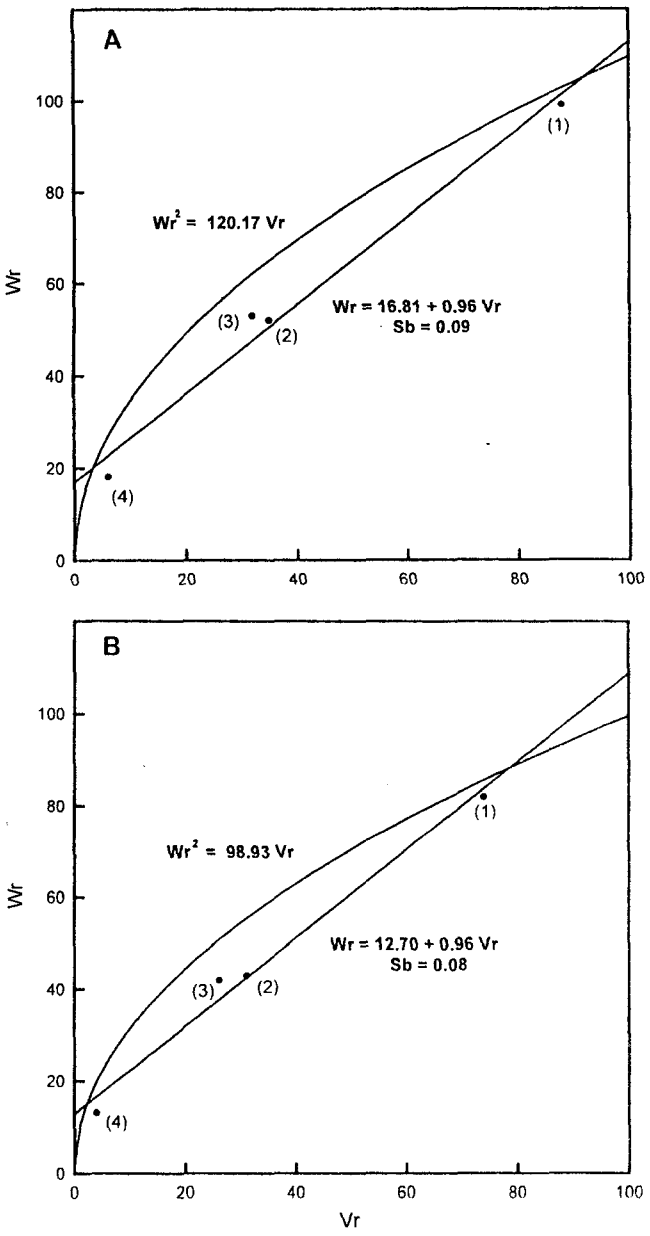

Fig. 2. Vr · Wr graphs for photoinhibition of photosynthesis in 4 parental diallel cross grown for 55 days. A; 10 hour photoinhibition, B; 12 hour photoinhibition. The parents are; (1) Sacheon 6, (2) Oweolbori, (3) Dongbori 1, (4) Reno.

showing that photoinhibition in photosynthesis was partially dominant with non-allelic genes in F_1 hybrids. The parents having dominant, allelic genes have small variance and covariance are placed on near original point of linear regression lines. However, the parents with recessive, allelic genes have large variance and covariance are placed on further original point. The nearer to the point of the origin on the Vr · Wr graph a cultivar is located, the more it has dominant alleles (Hayman, 1954). Reno and Dongbori 1 (greatly resistant to photoinhibition) were dominant, and Oweolbori (susceptible to photoinhibition) was recessive for 35-day old plant (Fig. 1; A, B). However, for 55-day old plants (Fig. 2; A, B), Reno was dominant, and Sacheon 6 was recessive. The degree of dominance was changed with photoinhibitory intensity (Fig. 1 and 2).

Table 3 showed the genetic parameters for the character estimated by Hayman's method (1954). The average degree of dominance $[(H_1/D)^{1/2}]$ in intra-locus gene interaction for photoinhibition were smaller than 1 (0.45~0.72) with $D>H_1$, indicating the partial dominance with great additive gene action. The $H_2/4H_1$ which represents the proportion of genes with positive and negative effects in the parents was 0.22~0.27 with nearly equal frequency of positive and negative alleles for photoinhibition. The K_D/K_R which denotes the proportion of dominant and recessive alleles in the parents ranged from 1.04 to 1.25, indicating that frequency of dominant genes was nearly equal or a little greater than that of recessive genes. The character was controlled by at least 2 major genes. Heritability analysis revealed that chlorophyll fluorescence had high narrow-sense heritabitities (0.79~0.90), which indicated that this character could be selected for freezing resistance in the segregating generation of a barley breeding program.

Combining ability effects for photoinhibition

Analysis of variance of general combining ability (GCA) and specific combining ability (SCA) for photoinhibition in 4 parental diallel crosses were shown in Table 4. All the GCA and SCA effects were significant. The variance of GCA effects were greater than that of SCA effects (8.68~22.28 times), indicating that variance components due to additive effects might be larger than those due to non-additive effects for the character, although both additive and non-additive effects were important. The GCA of parents for photoinhibition was shown in Table 5. GCA effects of Reno was much higher than that of other parental cultivars. The large positive GCA for Fv/Fm indicated that Reno was a desirable parent with high photosynthetic efficiency under photoinhibitory condition. Sacheon 6 and Oweolbori showed negative GCA effect for two plots but Dongbori 1 showed positive or negative GCA effects in the different photoinhibitory treatments.

The crosses of Sacheon 6× Dongbori 1, Oweolbori× Dongbori 1 and Oweolbori × Reno showed positive SCA effects for chlorophyll fluorescence (Fv/Fm) in 35-day old plants (Table 6). On the other hand, for 55-day old plants, the crosses of Sacheon 6 × Oweolbori, Sacheon 6 × Dongbori 1, and Sacheon 6 × Reno showed positive SCA effects for

Table 3. Genetic components for photoinhibition ratios (Fv/Fm) to control in 4 parental diallel cross grown in field.

Component	Estimate			
	H-6h†	H-8h	L-10h‡	L-12h
D	307.8 ± 8.5	247.3 ± 6.0	119.5 ± 4.9	98.1 ± 4.0
H_1	63.1 ± 24.8	49.3 ± 17.4	57.6 ± 14.2	50.9 ± 11.6
H_2	67.3 ± 22.9	50.2 ± 16.1	50.3 ± 13.1	44.7 ± 10.7
h^2	77.0 ± 15.0	58.1 ± 10.9	63.8 ± 8.9	52.6 ± 7.3
F	7.1 ± 21.9	4.3 ± 15.4	17.6 ± 12.5	15.9 ± 10.3
E	2.4 ± 3.8	1.1 ± 2.7	0.7 ± 2.2	0.8 ± 1.8
$(H_1/D)^{1/2}$	0.45	0.45	0.69	0.72
$H_2/4H_1$	0.27	0.25	0.22	0.22
K_D/K_R	1.06	1.04	1.12	1.25
h^2/H_2 (K)	1.14	1.16	1.27	1.18
Heritability (B)	0.99	0.99	0.99	0.99
Heritability (N)	0.89	0.90	0.80	0.79

†H-6h and H-8h; 6 and 8 hour photoinhibitions in plants grown for 35 days. ‡L-10h and L-12h; 10 and 12 hour photoinhibitions in plants grown for 55 days.

Table 4. Mean squares of GCA and SCA for photoinhibition ratios (Fv/Fm) to control in 4 parental diallel cross grown in field.

Source	DF	Mean square			
		H-6h†	H-8h	L-10h‡	L-12h
GCA	3	459.8**	369.8**	168.6**	138.0**
SCA	6	22.0**	16.6**	18.2**	15.9**
Error	18	2.41	1.10	0.66	0.81
GCA/SCA		20.90	22.28	9.26	8.68

**Significant at 0.01 probability level. †H-6h and H-8h; 6 and 8 hour photoinhibitions in plants grown for 35 days. ‡L-10h and L-12h; 10 and 12 hour photoinhibitions in plants grown for 55 days.

Table 5. The observed general combining ability effects for photoinhibition ratios to control in 4 parental diallel cross grown in field.

Parents	GCA effect			
	H-6h†	H-8h	L-10h‡	L-12h
Sacheon 6	-7.84	-6.84	-3.99	-3.62
Oweolbori	-6.20	-5.73	-3.25	-2.89
Dongbori 1	3.05	2.67	-0.35	-0.37
Reno	10.99	9.91	7.59	6.88
S.E.(Gi)	0.55	0.37	0.29	0.32
S.E.(Gi-Gj)	0.90	0.61	0.47	0.52

†H-6h and H-8h; 6 and 8 hour photoinhibitions in plants grown for 35 days. L-10h and ‡L-12h; 10 and 12 hour photoinhibitions in plants grown for 55 days.

Table 6. The specific combining ability effects for photoinhibition ratios (Fv/Fm) to control in 4 parental diallel cross grown in field.

		SCA effect			
		[1]	[2]	[3]	[4]
[1]	H-6h†	-1.66	-0.29	3.42	0.19
	H-8h	-1.49	-0.37	3.36	-0.01
	L-10h‡	-6.00	3.82	2.88	5.31
	L-12h	-5.59	3.59	2.74	4.85
[2]	H-6h		-5.39	5.22	5.85
	H-8h		-4.52	3.98	5.44
	L-10h		-1.83	-1.26	1.10
	L-12h		-1.73	-1.52	1.39
[3]	H-6h			-4.27	-0.10
	H-8h			-3.61	-0.12
	L-10h			-1.29	0.96
	L-12h			-0.91	0.60
[4]	H-6h				-2.97
	H-8h				-2.66
	L-10h				-3.68
	L-12h				-3.42
		H-6h	H-8h	L-10h	L-12h
	S.E.(Sij-Sik)	2.00	1.36	1.05	1.16
	S.E.(Sij-Skl)	1.79	1.21	0.94	1.04

†H-6h and H-8h; 6 and 8 hour photoinhibitions in plants grown for 35 days. ‡L-10h and L-12h; 10 and 12 hour photoinhibitions in plants grown for 55 days. The parents are; [1] Sacheon 6, [2] Oweolbori, [3] Dongbori 1, [4] Reno.

the character. SCA resulting from nonadditive genetic effects are important for the breeding potential of cross-combinations.

Additive and nonadditive gene effects for Fv/Fm from the analysis of variance components were found. Thus, it will be important to evaluate not only the GCA of parents, but also the SCA of the cross-combination when screening barley for chlorophyll fluorescence (CF). This result was different from Zhang *et al.* (2000), who found from analysis of genetic variance components that Fv/Fm was mostly controlled by non-

Table 7. Simple correlation coefficients among freezing resistance and photoinhibition in 4 parental diallel cross.

Variable	CHL1	CHL2	TTC1	TTC2
CHL1	1			
CHL2	0.877**	1		
TTC1	0.883**	0.846**	1	
TTC2	0.867**	0.774**	0.944**	1

†CHL1; 8 hour photoinhibition in plants grown for 35 days. CHL2; 12 hour photoinhibition in plants grown for 55 days. TTC1 and TTC2; absorbance ratios of TTC reduction to control treated with -7°C and -13°C in 35- and 55-day old plants. **Significant at the 0.01 probability level.

Table 8. Linear regression equations for freezing resistance in 4 parental diallel cross.

Linear regression equation	R^2
TTC1† = -39.436 + 1.497 CHL**	0.779
TTC2‡ = 1.631 + 0.957 CHL**	0.751

CHL : Fv/Fm ratio to control treated with 8 hour in 35-day old plants, †TTC1 : absorbance ratio of TTC reduction treated with -7°C in 35-day old plants, ‡TTC2 : absorbance ratio of TTC reduction treated with -13°C in 55-day old plants, **Significant at the 0.01 probability level.

additive genes in the segregating generation of sugarcane.

Correlations between freezing resistance and photoinhibition

The simple correlation coefficients and linear regression equations related to freezing resistance and Fv/Fm were shown in Table 7 and 8. A series of studies suggested that the chromosomes of homologous group 5 of Cheyenne had major genes controlling freezing resistance (Sutka, 1994), expression of antifreeze proteins (Chun *et al.*, 1998) and factors resistant to low temperature-induced photoinhibition (Chun *et al.*, 1997). Thus, these characters were expected to be significantly correlated with each other. The freezing resistance (TTC1 and TTC2) based on dehydrogenase activity treated at -7°C or -13°C for 2 hours were significantly correlated with photoinhibition of PSII (0.883**~0.867**), and significantly fitted by linear regression (R^2 =0.751**~ 0.779**). The chlorophyll fluorescence responses have been found to be highly inheritable and very useful in evaluating relative levels of freezing resistance in barley.

The degree of photoinhibition based on Fv/Fm accounted for about 46-59% of the variation in winter survival of wheat (Chun *et al.*, 1997) and 64% in tea tree (Chun *et al.*, 2000). It appears that the chlorophyll fluorescence is a good parameter to evaluate the cultivars or cross combinations for testing freezing resistance with simple experimental procedure and small amount of sample.

ACKNOWLEDGEMENTS

This work was supported by Korea Research Foundation Grant (KRF-99-041-G00073).

REFERENCES

Binder, W. D. and P. Fielder. 1996. Chlorophyll fluorescence as an indicator of frost hardiness in white spruce seedlings from different latitudes. *New Forests* 11 : 233-253.

Björkma, O. and B. Demmig. 1987. Photon yield of O_2 evolution and chlorophyll fluorescence characteristics at 77K among vascular plants of diverse origins. *Planta* 170 : 489-504.

Bolhar-Nordenkampf, H. R., S. P. Long, and N. R. Baker. 1989. Chlorophyll fluorescence as a probe of the synthetic competence of leaves in the field : a review of current instrumentation. *Funct. Ecol.* 3 : 497-514.

Choe, B. H. 1998. New Mystat. Chungnam National Univ. pp. 101.

Chun, J. U., I. H. Jeong, and M. Griffith. 1997. Difference in photoinhibition in wheat chromosome substitution lines for freezing resistance. *Korean J. Breed.* 29(3) : 359-367.

Chun, J. U., X. M. Yu, and M. Griffith. 1998. Genetic studies of antifreeze proteins and their correlation with winter survival in wheat. *Euphytica* 102 : 219-226.

Chun, J. U., H. I. Jeong, and H.K. Choi. 2000a. A simple method for testing freezing resistance based on chlorophyll fluorescence in tea (*Camellia sinensis* L.). *Korean J. Crop Sci.* 45(5) : 322-327.

Chun, J. U., S. W. Kang, D. S. Song, and J. Choi. 2000b. Establishment of simple method for freezing resistance with use of electrical conductivity and 2, 3, 5-tripenyl tetrazolium chloride in tea (*Camellia sinensis* L.). *J. Kor. Tea Soc.* 6(3) : 121-133.

Genty, B., J.-M. Briantais, and N. R. Baker. 1989. The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. *Biochim. Biophys. Acta* 990 : 87-92.

Greer, D. H., C. Ottander, and G. Öquist. 1991. Photoinhibition and recovery of photosynthesis in intact barley leaves at 5°C and 20°C. *Physiol. Plant* 81 : 203-210.

Griffing, B. 1956. Concept of general and specific combining ability in relation to diallel crossing systems. *Aust. J. Biol. Sci.* 9 : 463-493.

Hayman, B. I. 1954. The theory and analysis of diallel crosses. *Genetics* 39 : 789-809.

Hurry, V. M. and N. P. A. Huner. 1991. Low growth temperature effects a differential inhibition of photosynthesis in spring and winter wheat. *Plant Physiol.* 96 : 491-497.

Hurry, V. M. and N. P. A. Huner. 1992. Effects of cold hardening on sensitivity of winter and spring wheat leaves to short-term photoinhibition and recovery of photosynthesis. *Plant Physiol.* 100 : 1283-1290.

Krause, G. H. and E. Weis. 1991. Chlorophyll fluorescence and photosynthesis : The basics. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 42 : 313-349.

Levitt, J. 1980. Chilling, freezing, and high temperature stresses. *In* Responses of Plants to Environmental Stresses. Ed 2. Vol, 1. Academic Press, New York.

Lindgren, K. and J. E. Hallgren. 1993. Cold acclimation of *Pinus contorta* and *Pinus sylvestris* assessed by chlorophyll fluorescence. *Tree Physiol.* 13 : 97-106.

Moffatt, J. M., R. G. Sears, T. S. Cox, and G. M. Paulsen. 1990. Wheat high temperature tolerance during reproductive growth. II. Genetic analysis of chlorophyll fluorescence. *Crop Sci.* 30 : 886-889.

Mohammed, G. H., W. D. Binder, and S. L. Gillies. 1995. Chlorophyll fluorescence : A review of its practical forestry applications and instrumentation. *Scand. J. For. Res.* 10 : 383-410.

Öquist, G. and N. P. A. Huner. 1991. Effects of cold acclimation on the susceptibility of photosynthesis to photoinhibition in Scots pine and in winter and spring cereals : a fluorescence analysis. *Funct. Ecol.* 5 : 91-100.

Powles, S. B. 1984. Photoinhibition of photosynthesis induced by visible light. *Annu. Rev. Plant Physiol.* 35 : 15-44.

Steponkus, P. L. and G. O. Lanphear. 1967. Refinement of triphenyl tetrazolium chloride method of determining cold injury. *Plant Physiol.* 42 : 1423-1426.

Sutka, J. 1994. Genetic control of frost tolerance in wheat (*Triticum aestivum*). *Euphytica* 77 : 277-282.

Zhang, M.-Q., R.-K. Chen, J. Luo, J.-L. Lu, and J.-S. Xu. 2000. Analyses for inheritance and combining ability of photochemical activities measured by chlorophyll fluorescence in the segregating generation of sugarcane. *Field Crops Research* 65 : 31-39.