INTRODUCTION

Barley (*Hordeum vulgare* L.) is the important temperate cereal crop which mostly imports for brewery industry in Thailand. The value added is approximately 1,100 million Baht (about 100,000 tons/year) and tends to be higher every years with an increasing in local consumption. Whereas barley production in Thailand is about 1,000-1,500 tons/year (only 2% of the imported value) due to low yield (Uraikul and Sakapoo, 1991). This yield should be greater than 219 kg / rai in order to encourage farmers to adopt the same trend as soybean yield (Runaphi *et al.*, 1997). One of the most important factor that limits the growth and yield of barley is transient waterlogging or prolonged periods of poor soil drainage in the plantation which causes inadequate soil oxygen supply, especially a heavy paddy soil plantation (Larpruai *et al.*, 1995; Youngsuk *et al.*, 1988).

Under waterlogged soil condition, the diffusion of gases is $1x10^4$ fold less in water than in the air. In consequence, it causes a reduction of O_2 and increase in CO_2 and ethylene concentration in the soil (Jackson and Drew, 1984). These changes in gas composition will affect plant growth and final yield (Jackson and Drew, 1984; Thomson *et al.*, 1992; Huang *et al.*, 1994a). Although barley may not completely die under transient waterlogging, it causes leaf chlorosis and growth limitation after 2-3 days waterlogging at seedling stage which finally causing a low grain yield (Toojinda *et al* ,1992b ; Youngsuk *et al.*,1988). As barley growing area in Thailand still need to be extended as the second crop plantation in paddy field after rice, therefore, the physiological responses of barley as adaptation mechanisms should be considerately investigated.

The majority of the research works in the past concerning waterlogging mechanisms adaptation, were extremely limited by knowing short-term responses of certain economic crops (Vartapetian and Jackson, 1997). Many researchers reported

the root adaptation to waterlogging was due to an anaerobic metabolism (Drew *et al.*,1979 and Jackson,1996) and plant responses to ethylene induction from the roots (Kawase, 1981 and Jackson,1985). Nevertheless, there is a little information on plant growth dynamic under waterlogging throughout crop season. Although, the limitation of nutrient uptake, de-nitrification and leaching of mobile nutrients were studied under waterlogging condition (Trought and Drew, 1980; Drew, 1991; Hale and Orcutt, 1987), nitrogen accumulation and partitioning to each plant parts is still less considering.

Understanding in the physiological responses, along with hypoxic-induced acclimation and identifying genetic differences that can withstand such the stress would improve barley production and breeding program for waterlogging resistance genotype. Thus, the objectives of this thesis were (i) to determine the hypoxic-induced acclimatic adaptation of barley root due to morphological and physiological changes which affected plant growth, yield capacity and seed malt quality, and (ii) to construct the educational mechanistic model which simulated the daily dry matter accumulation of barley genotypes for understanding the responses of barley seedlings under hypoxic condition with various ambient temperatures.

LITERATURE REVIEW

"*Waterlogging*" is defined as the saturation of soil with water. It could be part of the root zone or up to the soil surface, whereas "*flooding*" means only water level above the soil surface. Moreover, The term "*hypoxia*" describes the O_2 status of cells or tissues in which oxidative phosphorylation is slowed by low O_2 concentration (<20%). This term is distinct from "*anoxia*", in which the O_2 concentration is zero which oxidative phosphorylation is regardless to produce energy (Pradet and Bomsel, 1978).

Hypoxia or anoxia of plant roots may also occur by heavy rainfall and the frequency and duration of soil saturation in upland area (Krizek, 1982). Oxygen depletion in soil may require only a few hours (Meek *et al.*, 1983) to several days (Blackwell and Ayling, 1981) by which root respiration and soil microorganisms (Drew and Lynch, 1980; Armstrong and Backett, 1987).

Plant Growth Responses to Waterlogging Condition

Plant growth dealing with dry matter accumulation is most important for grain production in different environments (Tanaka, 1976). It is controlled by two factors; the potential ability of the population to photosynthesize (the source) and the capacity of spikelets to receive the photosynthate (the sink). Types of growth patterns vary according to the combinations of varieties, environmental conditions, and cultural practices.

In general, the most sensitive of waterlogging of cereals and legumes appear to be just prior to flowering or during early flower development. The barley shoot growth is most sensitive to short-term flooding at an early stage of vegetative growth (14 days after emergence). However, younger plants are able to recover more quickly than the older. Barley plants flooded 28 days after seeding shows 55% reduction in grain yield, but only 35% reduction when flooded 35 days after seeding (Krizek, 1982).

The limitation of plant leaf water potential, stomatal conductance, photosynthesis, chlorophyll content, shoot nitrogen content, shoot and root growth, dry matter accumulation, and final grain yield, are reported under waterlogging condition (Jackson and Drew, 1984; Thomson *et al.*, 1992; Huang *et al.*, 1994b). Plant nutrition deficiencies may also occur (Trought and Drew, 1981; Drew, 1991).

Plant with more initial carbohydrates can survive better. Starch content is probably an important factor for waterlogging resistance (Colmer, 1996; Vartapetian and Jackson, 1997). Under submerged condition, plants grown in low nitrogen have high carbohydrate content and high percentage of survival (Palada and Vergara, 1972). In soybeans, photosynthesis is not itself altered by soil flooding, but the flow rate of assimilates from leaves to roots decreases. Whereas in corn, similar results are obtained with respect to the main root, but the flow of assimilate is increased by adventitious roots (Levitt, 1980). However, plant dry weight may not a reliable indicator at early waterlogging damage. Trought and Drew (1980) found that shoot dry weight of wheat increased during the first 4 days of waterlogging in comparison with non-waterlogged plants.

The shoot plant adaptation to waterlogging depends on highly food reserved, increasingly rapid shoot extension, generated new roots as adventitious rooting at the shoot base and some responses such as stomatal closure, leaf epinastic curvature and slow leaf extension. Shoots are normally less susceptible to oxygen deficiency than roots. It causes to suppress carbon assimilation, photosynthate utilization (Vartapetian and Jackson, 1997), high tiller mortality and yellowing leaves (Hobbs, 1990).

Waterlogged soil causes of death in anoxic root cells by insufficient energy generation to sustain cell integrity and by cytoplasmic acidosis. Moreover, it will be also death from metabolic lesions causes by the re-oxygenation after anoxia. Escape mechanism in the root is based on aerenchyma development and internal aeration pathways (Vartapetian and Jackson, 1997) which is reported evidently in barley (Arikado, 1955), wheat (Karishnev, 1958), maize (Jackson *et al.*, 1985), and rice (Setter

et al., 1988). The development of aerenchyma within the roots provides to increase oxygen diffusion. It helps to maintain a high respiration rate in the root tissues (Drew and Dikumwin, 1985; Colmer, 1996). Adventitious rooting relates to ethylene formation as aerenchyma, non-reversible mechanism in a few days (He *et al.*, 1996). But mechanisms by which flooding promotes adventitious rooting are not clear and differ depended on plant species (Vartapetian and Jackson, 1997).

Ethylene Induced Plant Adaptation to Waterlogging

In all vascular plants, key steps are enzymatic conversion of S-adenosyl-L-Met to ACC by ACC synthase and the oxidation of ACC to ethylene by ACC oxidase (Adams and Yang, 1979). Moreover, it is not evidently aerenchyma formation in anoxic roots (Vartapetian and Jackson, 1997). The treatment of anoxic roots with exogenous ethylene also fails to elicit aerenchyma (Jackson *et al.*, 1985). He *et al.* (1996) reported that hypoxia increased the activity of ACC synthase in maize roots, whereas this enzyme was strongly inhibited under anoxic conditions.

Ethylene action induces root aeration pathway which programmes cell death associated with a disorientation of microtubules in cells destined to collapse, cell wall degeneration and increasing cellulase activity, namely aerenchyma. Aerenchyma forms in cortical tissues either by selective cell collapse (*lysigeny*) or by cell separation (*schizogeny*) and differential rates of expansion depending on plant species differing waterlogged tolerant (Armstrong and Armstrong, 1988). It also indicated that ethylene stimulated submerged internode elongation and inhibit leaf growth of deep water rice plants. The enhancement of internode elongation is particularly pronounced in an atmospheric of high CO_2 and low O_2 (Raskin and Kende,1983). Moreover, the oxygen concentration is primarily triggered to increase in ethylene synthesis (Vartapetian and Jackson, 1997).

Chemical Signals between Roots and Shoots under Waterlogging

Some chemical signals transmit between roots to shoots by transpiration stream, integrate roots and shoot physiological changes and limit indirect damage to shoot tissues by soil flooding such as enhance shoot elongation, adventitious root formation, epinastic leaf curvature, slowly growing, stomatal closure, and chlorophyll degradation (Everard and Drew, 1987; Jackson, 1996; Vartapetian and Jackson, 1997). Jackson *et al.* (1978) reported that some of ACC thus accumulated in roots and transports to shoot where the presence of oxygen permited its oxidation to ethylene by ACC oxidase. The fast shoot ethylene production will promote epinastic leave curvature (English *et al.*, 1995). Ethylene in shoots had been observed in broad bean, maize, sunflower, and tomato, but not in rice and barley (Hale and Orcutt, 1987).

Systemic signaling from oxygen deficient roots may change the pattern of gene expression for shoot development responses (English *et al.*, 1995; Neuman and Smit, 1993). It is well recognized that oxygen deficiency inhibits synthesis of indole acetic acid, gibberellins, and cytokinins by roots (Reid and Bradford, 1984) while ABA increases in leaves (Zhang and Davies, 1987). Else *et al.*(1996) studied with waterlogged tomato plant and found that ABA from flooded roots did not export in xylem sap. It revealed that ABA accumulation within foliage due to reduced export. However, the bulk leaf ABA of flooded plants began to increase after stomata closed. Hwang and VanToai (1991) proposed that ABA induced anoxic tolerance by increasing ADH activity before anoxic stress. It was supported by aerenchyma as signals from anaerobic roots which also induced stomatal closure in the leaves.

Jackson and Drew (1984) reported that flooding effected on the shoot arise from modifications to the internal flow of substances between root and shoot. They distinguished that three sorts of internally transmitted chemical messages were, (i) increasing in supply of substances from the flooded roots or soil to the shoot (positive messages), (ii) decreasing supply of substances to the shoot (negative messages), and (iii)accumulating in the shoots of substances usually transported down to the roots (accumulation messages). Water, photosynthate, inorganic nutrients, hormones or their

precursors, and toxins are mostly involved. The effects conduct to survival of the plant (acclimatization) or which constitute injury that may prejudice recovery and set lower limits on post-flooding performance. Some acclimatic responses are among the first reactions to inundation (i.e., within minute or hours), modifying the plant ability to grow and survival if the stress is extended in time.

Hypoxic Acclimation of Plant on Waterlogging Condition

Acclimation involves redistribution of resources towards to most limiting processes, resulting in optimal survival, reproduction and growth under the prevailing environmental conditions (Arp, 1991). Pre-treatment at low oxygen deficiency can induce plant adaptation mechanisms; metabolic and morphological adaptation in both root and shoot (Vartapetian and Jackson, 1997; Johnson *et al.*, 1989). There is much evidence to show plant subjected to hypoxia which has a greatly improved tolerance (Saglio *et al.*, 1988; Hale and Orcutt, 1987).

Metabolic Acclimation to Anoxia Involving Energy Production

Metabolic acclimation apparently contributes to more prolonged survival under anaerobiosis (Saglio *et al.*, 1988; Johnson *et al.*, 1989). This responses in fast (hours) and induces enzymes of glycolysis and alcoholic fermentation (Sachs *et al.*, 1980; Richard *et al.*, 1991) such as LDH in barley roots (Hoffman *et al.*, 1986) and also its aleurone tissues (Hanson and Jacobsen, 1984), LDH and ADH in maize root tips (Robert *et al.*, 1989; Andrews *et al.*, 1993), ADH and pyruvate decarboxylase in rice roots (John and Greenway, 1976). Although anaerobic enzymes activity alone can not explain plant tolerance to flooding (Vartapetian and Jackson, 1996; Xia and Saglio, 1992), but ADH is still the most studied enzyme relating to anaerobiosis. Its activity increases in most plants during waterlogging. In consequence, one component of anoxic tolerant involves alcoholic fermentation which enables some energy production (Kennedy *et al.*, 1992).

Relationship between Carbohydrate and Nitrogen Assimilation

Nitrogen can alleviate the adverse effects of waterlogging on shoot growth, but nitrogen alone will not improve shoot growth if the supply of other ions is limited (Huang *et al.*,1994b). Plant species vary widely in their root ability to reduce incoming nitrate, a positive correlation of nitrate reductase in roots and the ratio of organic-N and NO_3^- in xylem exudation. Nitrate reduction in shoot may regulate nitrate uptake by root and is reduced in leaves. Nitrate assimilation takes place in the same compartments; cytosol (NO_3^- reduction to NO_2^-) and chloroplasts (reduction of NO_2^- to NH_4^+ and finally assimilation of glutamate) as sucrose and starch synthesis, respectively. The reduction of NO_2^- to NH_4^+ uses photochemically reducing power; as does the reduction of CO_2 to carbohydrate (Losada, 1976).

Flood-tolerant species markedly increases in nitrate reductase activity in the roots and leaves during waterlogging. Tolerant species also have a greater ability to synthesize amino acids than do intolerant species, thereby facilitating the re-oxidation of $NADH_2$ under conditions of anoxia (Krizek, 1982).

An empirical model of transport and utilization of carbon and nitrogen are measurements of increments of carbon and nitrogen in dry matter of plant parts, assessments of photosynthetic gains and respiration losses, and determination of C:N weight ratios of solutes of xylem and phloem sap serving specific parts of the plant (Pate, 1980). Moreover nitrate reduction and net CO_2 assimilation in leaves are tightly coupled, and that under mild water stress nitrate reduction decreases as a result of stomatal closure (Kaiser and Foster, 1989). In general, leaf photosynthetic rate is correlated linearly or non-linearly with leaf nitrogen or protein content. The shape of the mathematical form may depend on the techniques used for measuring photosynthetic rate, range of experimental conditions, physiological status of plant, and degree of fitness (Yoshida, 1981).

Seed Malting Quality of Barley under Unfavorable Environments

Barley production in Thailand is almost high seed protein content and not to be the standard of malting quality for brewery (Lersrutaiyotin *et al.*,1995 a and b). The standard of barley seeds for brewery should be less 11.5% of protein content, more 40 g of 1,000 seed weight, more 98% of seed germination and vigor during 3 days, more 90% of the 2.5 mm of seed size and cleaned seed from the diseases, insects and impurity (Brummer,1990).

Seed protein content is negative correlation with the seed germination and malt yield. The 1,000 seed weight is negative correlation with the percentage of seed moisture after steeping and the percentage of malt yield (Lersrutaiyotin *et al.*,1995b). Barley malt quality relates to dry matter and nitrogen accumulation from germination until grain filling in the seeds (Pate and Layzell, 1981). Consequently, the size and protein content in the barley seeds are important to evaluate malting quality (Lersrutaiyotin *et al.*, 1995b; Toojinda *et al.*, 1995a; Chumpukaew and Markul, 1992).

Physiological Aspects for Crop Improvement to Waterlogging Resistance

True waterlogged tolerant can vary from only a few hours to many days or weeks depending on species, the directly affected organs, stage of development, and external conditions such as temperature. Plant adaptation to waterlogging involves a combination of physiological traits (Vartapetian and Jackson, 1997).

Some agronomic traits are used for waterlogging selection, such as dry matter accumulation in soybean (Pookpadee *et al.*, 1987) and adventitious rooting in mung bean (Mekanavakul and Laosuwan, 1996). Nelson *et al.*(1983) proposed that the triphenyl tetrazolium chloride reduction method, electrical conductivity method, pressure chamber method, and visual scoring method, were generally good for screening of mungbean, but depending on time-consuming and a large number of samples. Morphological, physiological and biochemical traits of rice, such as aerenchyma formation, dry matter accumulation and possibly ADH enzyme, confer

with resistance to waterlogging (Rosario and Pandey, 1985; Menegus *et al.*,1993; Johnson *et al.*, 1989)

A Simulation Model for Dry Matter Accumulation and Partitioning

Crop simulation models can be used as a tool for agricultural risk analysis. In consequence, researchers can explore potential cropping location and appropriate management strategies. Moreover, a validated crop simulation model could set suitable management and variety rather than carry out extend field management (Mankeb, 1993). Rickman *et al.* (1996) suggested that crop growth simulations needed to help organize our knowledge of plant response to the environment for the purpose of assisting growers in management decisions.

Many crop models generally include yield estimation as a principle objective. The estimates of gross photosynthesis are provided by ecosystem-level models, when correct for respiration, provide good predictions of primary productivity. Economic yields can be derived from that using generalized partitioning factors (Loomis *et al.*,1979), such as the SOYMOD I model (Curry *et al.*,1975) and SOYGRO (Wilkerson *et al.*,1983). Basic physiological processes are considered photosynthesis, respiration, dry matter /nitrogen ratio control of assimilate partitioning, and evaporation. The simulator is validated and adequate for the stage of model development by using translocation photosynthesis and evapo-transpiration sub-models (Loomis *et al.*,1979). Hammer *et al.*(1995) found that the model simulated pod yield, biomass accumulation, crop leaf area were suitable for application over a diverse range of production environments. Murata (1975) suggested the model construction should have the daily rate of respiration which corrected to average air temperature. In general, the 'standardized' respiratory rate was obtained at 30 $^{\circ}$ C. The correction was made on the assumption that the Q_{10} of respiration is 2.0. Moreover, Morrison and Stewart (1995) suggested that the radiation-use efficiency was a parameter that represents a crop canopy's ability to convert intercepted solar energy to dry matter.

Marcelis (1994) reviewed the six approaches model partitioning of dry matter were,(i) descriptive allotment, proposing a predetermined ratio between the (relative) growth rates of the plant organs, (ii) functional equilibrium, based on the ratio of shoot activity to root activity,(iii) transport and sink regulation, based on transport and utilization of carbon and nitrogen,(iv) physical analogue, describing the plant as a set of pools (sinks), each having a performance and potential and each perceiving a common plant potential,(v) potential demand function of sinks, proposing the partitioning to be determined by the potential growth rates of the sinks (organs), and (vi) potential demand with priority functions of sinks, proposing the partitioning to be determined by potential growth rates and affinities (priorities) for assimilates of the sinks (organs). He concluded that the indeterminately growing greenhouse crops which approached the potential demand with or without priority functions, was most suitable to model dry matter partitioning among individual organs such as fruits, or between vegetative and generative growth.

EXPERIMENT I.

Effects of Transient Waterlogging on Dry Matter Accumulation and Grain Yield of Barley

Objectives

1. To study photosynthetic efficiency, the growth dynamic and yield capacity of barley genotypes differing waterlogged adaptation under different water regimes.
2. To evaluate barley genotypes for representative degrees of waterlogged tolerance.

Materials and Methods

Experimental condition

Field experiment was laid out in a split plot design with 3 replications. Three water regimes of each irrigation interval as main plots imposed throughout barley crop season, were

1. sprinkler irrigation throughout crop season (W1);
2. sprinkler irrigation before 3-4 leaf stage followed by flooding and drainage immediately until maturity (W2);
3. flooding and drainage immediately after emergence throughout the crop season (W3).

Nine barley genotypes represented different waterlogged adaptation, i.e. (SMG1, BRB.2 and BCMU#8 as tolerant genotypes); (BCMU#2, FNBL8403 and FNBLS#140 as moderately tolerant genotypes); and (MKB9601, IBON#108 and BRBRF9629 as susceptible genotypes) were subjected to variable levels of water

observation nurseries under waterlogged soil and were selected by using long green leaf duration and good seedling performance characteristics.

The experiment was conducted on a sandy clay loam soil of rainfed lowland rice field at Lampang Agricultural and Training Center, Lampang, Thailand during the dry season (December – March) of 1997 and 1998. The chemical and physical of soil properties at the experimental site was illustrated in Appendix 2. After harvesting rice, the land was ploughed, rototilled, fertilized inorganic fertilizer with 50 kg /ha each of N, P, and K, and rototilled again. Nine barley genotypes were grown in each 5x3 m main plot size. Seeds were planted in 0.20 m row spacing and 3 m long of each 4 x 3 m subplot size. To ensure uniform crop emergence, 40 mm of sprinkler irrigation was applied to all experimental plots. Weeds were controlled with Butachlor, pre-emergence herbicide at 1.2 kg active ingredient /ha applied after planting. At the 1st fully expanded leaf stage, barley seedlings were thinned to approximately 300 plants /m^2. Monocrotophos at 1 kg active ingredient /ha was used for insect control.

Flooding above soil surface and then drainage suddenly was applied after 3-4 leaf stage in W2 and after the 1st fully expanded leaf stage in W3 throughout the crop season. Different water regime treatments were separated by 2 meter soil ridge width and along the main plot size for the protection of water interference. Sprinkler irrigation in W1 and W2 replenished 40% of pan evaporation in 1997-1998 (Appendix 1) which were approximately 7 days of each irrigation interval. Each transient flooding in W2 and W3 was applied when soil moisture remained 75% field capacity level. The soil moisture content in the field was measured everyday after day for estimating the irrigation interval as described by Kibread and Ananboontarick (1980). Each flooding interval was approximately 4-5 days in this experiment.

Measurements

1. Photosynthetic efficiency can be expressed in terms of photosynthetic rate, transpiration rate, and stomatal resistance on the same time basis. It was measured on intact leaves with the ADC (Analytical Development Company Ltd, Hedderson, Herts, UK) LCA-4 steady-state photosynthesis system with the PLC-4 leaf chamber. Measurements were made on the youngest fully expanded leaf at 13.00 h for the duration of 3-4 leaf, 1st tillering, early booting and heading stage of barley. Each leaf was enclosed in a chamber and left to equilibrate with ambient conditions for approximately 1 min before initiating data collection. During measurement, the photosynthetic photon flux density (PPFD) at the top of plants was 1,500 to 1,700 μ mole/m^2/s. Ten separate measurements were averaged for statistical analyses.

2. Plant growth dynamic was studied by measuring the rates of total dry matter accumulation above the ground and partitioning to the seed. For 90-100 days of barley crops, ten sampling dates of dry matter accumulation were equally separated into vegetative phase (from tillering to heading, every 14 days sampling) and reproductive phase (during grain filling, every 7 days sampling). At each sampling date, plant from 0.5 m^2 area (0.5 m long of 5 rows and 0.25 cm away from the others) of all plots were sampled for growth analysis. Plant sample of each plot was separated into leaf, stems and grains and dried in hot dry air oven at 75 ^{o}C for 24 hours. Both senescent leaves and dead leaves were included in the total leaf dry matter.

Crop, leaf, stem and grain growth rates were calculated as the slope of the linear regression between the dry matter accumulation and the days duration which were a linear reproductive phase as described by McCloud (1974) and Senthong (1979). All means of experimental data including correlation of determination (r^2), were present. The partitioning coefficient of each barley genotype was shown as the percentage of the ratio of grain growth rate divided by crop growth rate (Senthong *et al.*, 1997).

3. Total dry matter at maturity, plant height, grain yield and yield components were determined from 1.2 m^2 area (1 m long of 6 rows and 0.25 cm away from the edges) of each subplot.

Treatment effects of photosynthetic rate, transpiration rate, stomatal resistance, total dry matter at maturity, grain yield and yield components were determined by analysis of variance. Differences among treatment means were separated by the least significant difference at the 0.05 level of probability. Path coefficient analysis was determined the effect of agronomic characteristics and yield components on grain yield under different water regimes.

Results and Discussion

Photosynthetic efficiency

Analysis of variances revealed that there were highly significant difference in the photosynthetic rate, transpiration rate, stomatal resistance of nine barley genotypes under three water regime treatments (Appendix 3). The means of photosynthetic rates of barley genotypes under different water treatments are presented in Table 1.

The photosynthetic rates of all barley genotype at 3-4 leaf and the 1st tillering stage, significantly increased under W2. It was suggested that the early seedling stage of barley was the most sensitive to waterlogging which eventually reduced shoot dry weight (Jongdee and Youngsook,1993). Thus, increases in photosynthetic rates could compensate the reduction of dry matter and returned to the normal growth (Jiang,1995). Under W2 condition, the susceptible genotypes; MKB60, IBON#108, and BRBRF9629 only at 3-4 leaf stage had highest photosynthetic rates than the other genotypes. A similar observation in wheat genotypes was made by Huang *et al.* (1994a). Whereas the other genotypes (tolerant and moderately tolerant) were also significantly high photosynthetic rates under transient waterlogging (W2 and W3) greater than under the control (W1). Plants can adapt to waterlogging by increasing the photosynthetic efficiency for compensation the loss of dry matter accumulation

Table 1 Photosynthetic rate (U mole CO_2 / m^2 /s) of nine barley genotypes at four growth stages under three water treatments.

Growth stage	Water treatment	Barley genotypes									
		SMG1	BRB2	BCMU#8	BCMU#2	FNBLS8403	FNBLS#140	MKB60	IBON#108	BRBRF9629	mean
3-4 leaf	W1	2.37	4.61	2.28	1.78	1.78	2.61	3.43	2.43	3.43	2.75
stage	W2	4.06	4.82	5.28	4.11	3.31	3.84	8.48	8.19	8.35	5.60
	W3	4.07	3.72	3.78	2.03	2.16	3.10	4.07	3.38	3.42	3.30
	mean	3.50	4.38	3.78	2.64	2.42	3.18	5.33	4.67	5.07	
LSD at 0.05 of (WxG) at 3-4 leaf stage =						1.82					
1st tiller	W1	10.67	12.47	11.38	11.54	12.68	11.04	10.55	11.62	10.94	11.43
stage	W2	17.14	14.89	14.55	16.90	14.35	18.58	16.13	12.52	14.68	15.53
	W3	15.09	11.29	15.17	11.01	12.01	16.14	14.25	14.30	10.74	13.33
	mean	14.30	12.88	13.70	13.15	13.01	15.25	13.64	12.81	12.12	
LSD at 0.05 of (WxG) at 1st tiller stage =						2.68					
Early	W1	14.16	13.60	11.81	15.83	13.88	14.27	10.64	10.80	9.84	12.76
booting	W2	8.92	9.55	10.30	13.01	8.71	9.96	10.69	9.39	9.85	10.04
stage	W3	12.78	7.43	12.27	9.42	10.64	14.12	7.19	10.61	9.10	10.40
	mean	11.95	10.19	11.46	12.75	11.08	12.78	9.51	10.27	9.60	
LSD at 0.05 of (WxG) at earley booting stage =						2.35					
Heading	W1	12.15	11.41	9.45	10.14	10.83	13.77	10.50	10.72	9.12	10.90
stage	W2	12.44	12.04	9.67	13.11	12.32	13.17	10.25	9.37	9.02	11.27
	W3	12.56	9.24	7.63	9.34	8.39	9.64	7.10	10.85	8.79	9.28
	mean	12.38	10.90	8.92	10.86	10.51	12.19	9.28	10.31	8.98	
LSD at 0.05 of (WxG) at heading stage =						2.20					

Note : Water treatments on each irrigation interval : W1 = sprinkler irrigation throughout crop season; W2= sprinkler irrigation during seedling stage followed by flooding and drainage until maturity, and W3 = flooding and drainage throughout crop season. (W) = water treatment, (G) = barley genotypes,

(Krizek, 1982; Tanaka, 1976). The waterlogged tolerant feature should maintained stomatal opening during waterlogging and after termination of waterlogging (Huang *et al.*, 1994b).

At the early booting stage, the photosynthetic rates of all barley genotypes under transient waterlogging decreased lower than under the control (W1), but were not significantly difference at heading stage. The younger plants are mostly sensitive to waterlogging than the older (Krizek, 1982). In addition, a barley genotype may possibly acclimatic adaptation to transient waterlogging after tillering stage (Saglio *et al.*, 1988; Johnson *et al.*, 1989).

Two interesting barley genotypes, FNBLS#140 and BCMU#2 exhibited the same results as SMG1 (tolerant genotype) under transient waterlogging at 3-4 leaf and at early booting stage, but had a low rate under W3 at heading stage. SMG1, BRB2 and FNBLS#140 had the highest photosynthetic rate under W2 as compared to the control (W1). BRBRF9629 genotype tended to be greatly affected by transient waterlogging.

The responses of all barley genotypes to waterlogging on transpiration rates at 3-4 leaf stage were similar to their photosynthetic rates and also had the same effects on the other growth stages (Table 2). Jiang (1995) also found that short term (24 hrs) waterlogging on strawberry plants promoted higher CO_2 assimilation rate and transpiration rate. The stomatal resistance of all genotypes was the same response as changes in photosynthetic rate (Table 3). Surprisingly, the tolerant genotypes at 3-4 leaf stage grown under W1 had low photosynthetic rate and high stomatal resistance (Table 1 and 3). These were argued by the previous studies in wheat (Huang *et al.*, 1994a; Trought and Drew, 1980). It may be the cementing of soil surface by sprinkler irrigation that caused insufficient soil water for barley growth. These results markedly affected the data recorded before irrigation.

Table 2 Transpiration rate (mole H_2O /m^2 /s) of nine barley genotypes at four growth stages under three water treatments.

Growth stage	Water treatment	Barley genotypes									
		SMG1	BRB2	BCMU#8	BCMU#2	FNBLS8403	FNBLS#140	MKB60	IBON#108	BRBRF9629	mean
3-4 leaf stage	W1	0.55	0.64	0.58	0.53	0.32	0.64	0.35	0.62	0.76	0.55
	W2	0.82	0.83	0.59	0.85	0.47	0.95	1.05	0.98	0.97	0.83
	W3	1.12	1.01	0.73	1.14	0.51	0.88	0.92	0.53	0.33	0.80
	mean	0.83	0.83	0.63	0.84	0.43	0.82	0.77	0.71	0.69	
LSD at 0.05 of (WxG) at 3-4 leaf stage =						0.61					
1st tiller stage	W1	2.92	3.92	3.84	4.06	3.26	3.67	3.59	3.14	3.46	3.54
	W2	3.95	3.85	4.10	4.05	3.48	4.19	3.94	3.46	3.89	3.88
	W3	3.28	3.07	3.50	2.17	1.94	3.69	2.80	2.78	1.50	2.75
	mean	3.38	3.61	3.81	3.43	2.89	3.85	3.44	3.13	2.95	
LSD at 0.05 of (WxG) at 1st tiller stage =						0.76					
Early booting stage	W1	3.51	3.01	2.92	3.56	3.14	2.94	2.67	2.76	2.89	3.04
	W2	2.27	2.64	1.85	2.07	2.25	1.80	2.30	2.18	1.90	2.14
	W3	2.88	2.81	3.05	2.57	2.58	2.93	2.04	2.77	1.31	2.55
	mean	2.89	2.82	2.61	2.73	2.66	2.56	2.34	2.57	2.03	
LSD at 0.05 of (WxG) at earley booting stage =						0.48					
Heading stage	W1	3.39	2.77	1.88	2.16	2.46	3.12	2.67	2.76	2.89	2.68
	W2	3.97	3.33	2.93	3.39	3.09	3.72	2.30	2.18	1.90	2.98
	W3	2.84	3.02	2.20	2.63	3.27	3.04	2.05	2.77	1.31	2.57
	mean	3.40	3.04	2.34	2.73	2.94	3.29	2.34	2.57	2.03	
LSD at 0.05 of (WxG) at heading stage =						0.48					

Note : Water treatments on each irrigation interval : W1 = sprinkler irrigation throughout crop season; W2= sprinkler irrigation during seedling stage followed by flooding and drainage until maturity, and W3 = flooding and drainage throughout crop season. (W) = water treatment, (G) = barley genotypes,

Table 3 Stomatal resistance (s /cm) of nine barley genotypes at four growth stages under three water treatments.

Growth stage	Water treatment	Barley genotypes									
		SMG1	BRB2	BCMU#8	BCMU#2	FNBLS8403	FNBLS#140	MKB60	IBON#108	BRBRF9629	mean
3-4 leaf	W1	28.63	26.95	29.16	17.88	16.57	14.63	12.22	12.88	15.82	19.42
stage	W2	16.83	15.42	12.21	10.67	9.33	17.29	8.34	8.61	9.21	11.99
	W3	15.73	12.85	12.44	18.40	19.40	20.22	17.82	18.68	14.31	16.65
	mean	20.40	18.41	17.94	15.65	15.10	17.38	12.79	13.39	13.11	
LSD at 0.05 of (WxG) at 3-4 leaf stage =						9.32					
1st tiller	W1	18.83	12.20	10.39	8.82	14.20	11.47	11.19	11.54	12.42	12.34
stage	W2	7.73	8.45	7.60	8.88	11.87	7.13	8.61	11.54	8.72	8.95
	W3	11.28	15.05	11.07	13.00	19.15	9.70	9.26	10.35	12.00	12.32
	mean	12.61	11.90	9.69	10.23	15.07	9.43	9.69	11.14	11.05	
LSD at 0.05 of (WxG) at 1st tiller stage =						7.88					
Early	W1	5.77	9.72	8.97	5.68	7.56	8.60	11.06	8.82	8.49	8.30
booting	W2	9.77	6.95	13.67	10.17	7.99	13.81	10.38	9.10	10.97	10.31
stage	W3	10.47	14.76	10.21	12.44	11.33	10.09	17.81	10.12	11.56	12.09
	mean	8.67	10.48	10.95	9.43	8.96	10.83	13.08	9.35	10.34	
LSD at 0.05 of (WxG) at earley booting stage =						3.67					
Heading	W1	10.47	18.42	15.01	19.25	13.14	10.05	11.06	9.32	8.49	12.80
stage	W2	8.42	11.51	11.61	10.16	10.64	9.32	10.38	9.10	10.97	10.23
	W3	18.98	15.41	28.11	21.78	13.79	16.70	17.81	12.62	12.31	17.50
	mean	12.62	15.11	18.24	17.06	12.52	12.02	13.08	10.35	10.59	
LSD at 0.05 of (WxG) at heading stage =						3.04					

Note : Water treatments on each irrigation interval : W1 = sprinkler irrigation throughout crop season; W2= sprinkler irrigation during seedling stage followed by flooding and drainage until maturity, and W3 = flooding and drainage throughout crop season. (W) = water treatment, (G) = barley genotypes,

Dry matter accumulation rate and partitioning coefficients

The growth rates of nine barley genotypes under different water treatments are presented in Table 4. All barley genotypes exhibited higher stem growth rate than leaf growth rate under different water treatments. Leaf growth rates of all genotypes decreased under transient waterlogging (W2 and W3). The responses of the moderately tolerant genotypes were not significantly different under W2 as compared to under W3. Vartapetian and Jackson (1997) suggested that plant adaptation to waterlogging needs highly food reserved in the shoots. In this study, the susceptible genotypes decreased leaf growth rate under transient waterlogging lower than the other genotypes. Although their photosynthetic rates were high (Table 1), they did not compensate the reduction of leaf dry weight. It might be transient waterlogging increased the chlorosis of lower leaves (Jongdee and Youngsook, 1993) and reduced leaf area duration and shoot growth during waterlogging (Jackson and Drew, 1984; Thomson *et al.*, 1992).

The tolerant genotypes were not significantly difference in grain growth rates and crop growth rates under different water regimes. These results may depended on the ability of photosynthetic efficiency which contributed to be high grain growth rates and their partitioning coefficient (Pate, 1980; Vartapetian and Jackson, 1997). These might be acclimatic adaptation to waterlogging (Huang *et al.*, 1994a ; Wignarajah *et al.*,1976). The moderately tolerant genotypes; BCMU#2, FNBL8403 and FNBLS#140 also had high leaf and stem growth rate but low in grain growth rate. Crop growth rates of all barley genotypes under W1 were slightly higher than under transient waterlogging. A similar result in wheat was also reported by Meechoui (1985). However BRBRF9629 had the lowest crop growth rate under transient waterlogging (Table 4).

Dry matter partitioning of all barley genotypes under different water treatments is presented in Table 5. During grain filling period, all tolerant genotypes including FNBL8403 and FNBLS#140 genotypes consistently partitioned dry matter to the seeds under transient waterlogging as compared with under W1. Among nine barley

Table 4 Leaf, stem, grain and crop growth rates (g /m^2 /day) for nine barley genotypes under three water treatments.

Barley genotypes	Leaf growth rate (g /m^2 /day)						Stem growth rate (g /m^2 /day)					
	W1		W2		W3		W1		W2		W3	
		r^2		r^2		r^2		r^2		r^2		r^2
SMG1	1.31	0.970**	0.93	0.815*	1.17	0.941**	1.41	0.959**	1.69	0.982**	1.67	0.904**
BRB2	1.21	0.895**	1.25	0.866*	0.82	0.880**	1.67	0.8578*	1.46	0.876**	1.57	0.854*
BCMU#8	1.18	0.941**	1.11	0.969**	0.59	0.954**	1.55	0.963**	1.37	0.862*	1.63	0.940**
BCMU#2	1.65	0.928**	0.84	0.966**	0.83	0.989**	2.09	0.976**	1.73	0.978**	1.84	0.960**
FNBLS8403	1.29	0.942**	0.78	0.981**	0.88	0.891**	1.69	0.970**	1.48	0.934**	1.27	0.972**
FNBLS#140	1.64	0.966**	1.04	0.949**	1.02	0.957**	1.87	0.975**	1.24	0.952**	1.79	0.953**
MKB60	0.70	0.853*	0.51	0.871**	0.14	0.905**	1.47	0.878**	1.32	0.872*	1.18	0.938**
IBON#108	0.57	0.879*	0.39	0.963**	0.16	0.862*	1.34	0.945**	1.56	0.974**	1.46	0.981**
BRBRF9629	0.36	0.978**	0.19	0.871**	0.14	0.876**	1.29	0.960**	1.42	0.942**	1.28	0.939**

	Grain growth rate (g /m^2 /day)						Crop growth rate (g /m^2 /day)					
	W1		W2		W3		W1		W2		W3	
		r^2		r^2		r^2		r^2		r^2		r^2
SMG1	2.01	0.920**	2.09	0.987**	2.37	0.981**	2.53	0.973**	2.53	0.966**	2.65	0.929**
BRB2	1.81	0.862*	1.21	0.907**	1.87	0.834*	2.35	0.810*	2.21	0.838*	2.38	0.898**
BCMU#8	1.14	0.984**	0.97	0.931**	1.07	0.824*	2.37	0.832*	2.04	0.952**	2.31	0.891**
BCMU#2	2.08	0.969**	1.27	0.958**	1.54	0.925**	3.04	0.961**	2.24	0.923**	2.75	0.909**
FNBLS8403	1.81	0.868*	1.24	0.992**	1.46	0.955**	2.86	0.960**	2.04	0.880**	2.03	0.957**
FNBLS#140	2.10	0.955**	1.42	0.986**	1.77	0.927**	3.28	0.971**	2.01	0.880**	2.70	0.890**
MKB60	1.89	0.945**	1.32	0.979**	1.07	0.985**	2.64	0.924**	2.08	0.892**	2.00	0.959**
IBON#108	1.62	0.919**	1.08	0.979**	1.34	0.973**	2.57	0.968**	2.08	0.919**	2.26	0.983**
BRBRF9629	1.04	0.973**	0.82	0.987**	1.01	0.987**	1.45	0.914**	1.63	0.911**	1.97	0.988**

Note : Water treatments on each irrigation interval : W1 = sprinkler irrigation throughout crop season; W2= sprinkler irrigation during seedling stage followed by flooding and drainage until maturity; and W3 = flooding and drainage throughout crop season.

*,** Significant at 0.05 and 0.01 probability levels, respectively.

genotypes, SMG1 had the highest partitioning of assimilate to the seeds in all water treatments. This result might be the best acclimatic adaptation to waterlogging of tolerant genotypes for a long period of growth (Huang *et al.*, 1994a). BRBRF9629 was the least dry matter partitioning to the seeds under transient waterlogging especially under W3.

Table 5 Partitioning coefficients of nine barley genotypes under three water treatments.

Barley genotypes	Partitioning coefficient (%)		
	W1	W2	W3
SMG1	79.42	82.62	89.43
BRB2	76.94	77.62	78.55
BCMU#8	48.02	47.45	46.55
BCMU#2	68.84	56.57	55.90
FNBL8403	63.25	60.96	71.98
FNBLS#140	63.83	70.38	65.51
MKB60	71.48	63.64	53.51
IBON#108	63.29	51.94	59.09
BRBRF9629	71.69	50.64	51.11

Note : W1 = sprinkler irrigation throughout crop season; W2= sprinkler irrigation during seedling stage followed by flooding and drainage until maturity; and W3 = flooding and drainage through out crop season. Partitioning coefficients (%) = $\frac{\text{grain growth rate}}{\text{crop growth rate}} \times 100$

Total dry matter accumulation at maturity of all barley genotypes was highly significant difference which depending on either barley genotypes or water treatment effect ($P<0.01$). There was no significant difference among barley genotypes which grown under different three water treatments (Appendix 4). All barley genotypes grown under W2 had total dry matter lower than under W1 and W3 (Table 6). These results may be associated with low growth rate during vegetative phase affecting the final dry matter accumulation at maturity (Krizek, 1982; Levitt, 1980; and Pate, 1980). Chafai-Elalaoui and Simmons (1988) stated that more surviving tillers under transient waterlogging by acclimatic adaptation contributed substantially the amounts of dry matter for growth, especially longer vegetative phase of barley genotypes. Among all genotypes under three water treatments, SMG1, BRB2 and BCMU#2 produced the highest total dry matter at maturity whereas MKB9601 and BRBRF9629 had the lowest (Table 6).

Grain yield and yield components

Barley grain yield and yield components of each barley genotypes were highly significant difference under water treatments ($P<0.01$) (Appendix 4). The average yield components and grain yield of nine barley genotypes are presented in Table 6.

All barley genotypes, except FNBL8403 and FNBLS#140, had lower spikes /m^2 under W2 than under W3. The earlier seedlings under several transient flooding as W3 treatment, might induce acclimatic adaptation and recover quickly than the older plant affected transient waterlogging (Krizek, 1982). Moreover, it revealed that the susceptible genotypes were greatly affected under W2 more than the other genotypes. Transient waterlogging possibly reduced tillering ability and plant growth at seedling stage (Jongdee and Youngsook,1993).

Among nine barley genotypes, SMG1 and BRB2 grown under W3 produced higher seeds /spike than the other genotypes. All tolerant and moderately tolerant genotypes except for SMG1 under W2 had lower seeds /spike as compared to under W1 and W3. The susceptible genotypes including BCMU#2 had consistent in seeds /

Table 6 Average total dry matter accumulation at maturity, grain yield and its yield components of nine barley genotypes under three water treatments.

Water treatment	Barley genotypes									
	SMG1	BRB2	BCMU#8	BCMU#2	FNBLS8403	FNBLS#140	MKB60	IBON#108	BRBRF9629	mean
	Total dry matter at maturity (g /m^2)									
W1	202.9	243.5	166.2	256.7	181.0	244.4	100.8	161.5	175.0	192.4
W2	138.3	111.7	108.7	120.5	98.3	126.9	83.0	123.2	100.0	112.3
W3	216.3	238.0	182.6	243.0	161.4	194.0	133.8	170.5	159.2	188.7
mean	185.8	197.7	152.5	206.7	146.7	188.4	105.9	151.7	144.7	
LSD at 0.05 of	(W) = 38.20				(G) = 38.30					
	Spikes /m^2									
W1	340	318	350	262	310	243	368	377	372	326
W2	327	240	227	178	303	195	200	180	190	227
W3	402	362	418	288	302	233	337	330	332	334
mean	356	307	332	243	305	224	302	296	298	
LSD at 0.05 of (WxG) =	61.00									
	Seeds / spike									
W1	25	26	20	16	28	27	14	15	15	21
W2	26	26	19	17	17	16	15	14	15	18
W3	31	39	20	18	25	29	15	15	16	23
mean	27	30	20	16	23	24	15	15	15	
LSD at 0.05 of (WxG) =	6.00									
	1,000 grain weight (g)									
W1	41.6	37.6	49.5	48.9	39.5	39.8	45.9	44.0	44.8	43.5
W2	39.9	37.2	49.9	52.8	33.9	34.0	25.5	33.3	27.9	37.2
W3	41.6	38.8	52.0	57.9	42.3	46.2	34.7	39.5	45.3	44.2
mean	41.0	37.9	50.5	53.2	38.5	40.0	35.4	38.9	39.3	
LSD at 0.05 of (WxG) =	8.4									
	Grain yield (g /m^2)									
W1	205.2	220.5	157.7	176.8	238.5	224.7	169.9	202.5	195.2	199.0
W2	120.0	92.6	82.1	70.9	78.5	88.6	88.2	94.5	67.6	87.0
W3	382.0	257.7	203.6	197.6	239.9	243.8	174.1	209.2	183.7	232.4
mean	235.7	190.3	147.8	148.5	185.7	185.7	144.1	168.7	148.8	
LSD at 0.05 of (WxG) =	82.3									

Note : Water treatments: W1 = sprinkler irrigation throughout crop season; W2= sprinkler irrigation during seeding stage followed by flooding and drainage until maturity; and W3= flooding and drainage throughout crop season.

spike and were lower seeds/spike than the other genotypes. This may be associated with the genetic ability of the two rows spike type (Wych *et al.*,1985). Pintasen *et al.* (1997) reported that the adverse effect of waterlogging might reduced the number of florets /spike which relevantly low in photosynthetic rate at early booting stage.

The 1,000 grain weight of all barley genotypes except for tolerant genotypes, decreased under W2. BCMU#8 and BCMU#2 genotypes had the highest 1,000 grain weight in all water treatments. In contrast, the susceptible genotypes, MKB9601, IBON#108, and BRBRF9629 under transient waterlogging had the lowest 1,000 grain weight.

Grain yield of all barley genotypes under W2 significantly decreased greater than under W1 and W3. SMG1 and BCMU#8, tolerant genotypes under W3 had a significantly higher in grain yield than under W1 and W2 whereas the other grain yields of barley genotypes under W3 were not significantly different from under W1. It is therefore confirmed that the tolerant genotypes could induce acclimatic adaptation in both growth and grain yield to waterlogging (Vartapetian and Jackson, 1997). In addition, it was possibly less severe waterlogged damage due to have a good drainage in the sandy clay loam soil of this field experiment and probably gets more nitrogen and water (Krizek, 1982). In this experiment, BRBRF9629 under W2 was the lowest in grain yield.

Agronomic effects on grain yield

Path coefficient analysis was used in order to explain some agronomic effects on grain yield under different water regimes. This study was found that plant height, spikes /m^2, seeds / spike and total dry matter at maturity, had highly significant effects on grain yield (R^2=0.81**). These characters affected directly on grain yield (Table 7). This revealed that the expression of these characters identified the ability of barley plant to survive under waterlogging and the ability to recover and giving yield. All these confirmed the results concluded by Krized (1982); Drew (1997); and Vartapetian and Jackson (1997). Among yield components, the number of spikes/m^2 greatly affected

the grain yield (Table 7). This effect may be associated with the ability of tillers to produce spikes (Trought and Drew, 1980).

Table 7 Path coefficient analysis of correlation variables on the direct (diagonal) and indirect (off- diagonal) effect of some agronomic characters of nine barley genotypes under three water treatments on grain yield. (N=81)

Variables					Over all effect (in row)
Plant height at maturity	0.262	0.071	0.037	0.114	0.484**
Spikes /m^2	0.051	0.363	0.057	0.093	0.563**
Seeds / spike	0.035	0.074	0.278	0.133	0.520**
TDM	0.104	0.118	0.130	0.286	0.637**

Note : TDM = Total dry matter at maturity. Residual effect = 1 - R^2 = 1-0.811 = 0.189.

** highly significant at P<0.01. All analysed data showed in Appendix 5.

To evaluate waterlogged tolerant among nine barley genotypes, SMG1 was the best tolerant genotype due to high crop growth rate, high dry mater partitioning to the seeds, and high grain yield under transient waterlogging. It revealed that the waterlogged tolerant genotypes with high initial dry matter or carbohydrates can survive better than non-waterlogged tolerant (Colmer, 1996; Vartapetian and Jackson, 1997). Moreover, SMG1 genotype also produced a large amount of total dry matter at maturity. Whereas the moderately tolerant genotype, FNBLS#140 had the same responses of SMG1 but in low level. BRBRF9629 was evaluated as the representative susceptible genotype due to the lowest responses in crop growth rate, total dry matter accumulation at maturity and yield capacity. These three representative barley genotypes were used to investigate the physiological responses and seed malt quality under waterlogging in the next experiment.