

GENETIC ANALYSIS ON THE COMPETITIVE ABILITY OF BARLEY (*HORDEUM VULGARE* L.) RECOMBINANT INBRED LINES INTERCROPPED WITH OAT (*AVENA SATIVA* L.) WEEDS

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ABSTRACT: Ninety-eight barley recombinant inbred lines (RILs) were studied to determine oat weed competitive ability at Wageningen Agricultural University farm in 1997/98 summer season. The major objectives of the study were to determine: the influence of oat weed competition on the phenotype of barley lines, competitive ability with oat weeds, Quantitative Trait Loci (QTL) responsible for weed competition, and to study the correlation of competitive ability with yield and other agronomic characters. The most important characters determining competitive ability of barley lines were found to be plant height, droopy leaf type, thousand kernel-weight and grain yield (kg/ha). The QTLs identified for these characters revealed the molecular marker 'erect gene' as an aid to select lines that are competitive with oat weeds. The QTLs identified are stable for these characters and are located on chromosome VII at position of 62.6 and 67.6 cM. Correlation analysis also showed that plant height and thousand-kernel weight were positively and moderately correlated with grain yield (kg/ha) in the intercrop environments. Selecting barley lines consisting of traits like droopy leaf type, taller, more number of seeds per ear, with better thousand kernel weight and grain yield (kg/ha) would enable one to determine environmentally friendly way of barley lines to withstand oat weed infestation which could easily be used in local communities. Furthermore, the commonly used herbicide price is soaring from time to time and out of the reach of the poor farmers in the developing countries. Therefore, this method is an alternative which uses a low input and environmentally friendly approach to withstand the oat-weed infestation problem.

Key words/phrases: Barley lines, competitive ability, intercropping, oat-weed, quantitative trait loci

INTRODUCTION

Competitive ability is defined as the sharing ability of essential environmental resources among plants growing together (Harper, 1964). According to Kvist (1992), competition arises when one plant influences the physical environment of the neighbouring plant growth resource utilisation. Competition is indirect and two plants will not compete with each other, unless they are in lack of growth resource(s). They grow as long as they have sufficient water, nutrient, light and other growth factors to satisfy the demands of both plants. Competition begins when the immediate supplies of one single necessary factor fall below the demand for any of the two plants (Donald, 1963).

The growth of plants in a multi-species community is typically influenced at some or all stages of development by biological and physical processes which are frequently referred to as 'competition' (Hall, 1974a). The major problems of crop weed competition are: reduction in yield, degrading the economic value of harvested

product by contamination, hampering crop husbandry practices, attraction of pests and diseases, additional time and expenses needed to control weeds. So far, application of herbicide is the major control measure taken to alleviate crop weed competition. Competition of crops with weeds which are similar in morphology and niche requirement like a case in barley and oat is a serious problem to control both in mechanical or chemical methods (Chancellor, 1976).

Interest to work on competitive ability of barley genotypes arose after observing a barley field completely infested by wild oat weed in North Shewa Ethiopia, during field trips made for collection of crop germplasm. The hypothesis is that would it be possible to identify barley genotypes that could better compete with oat weeds? Moreover, there are different evidences from literature, showing there exists genetic differences among barley genotypes for competitive ability with oat weed. Genetic analysis for competitive ability of barley lines with oat 'weeds' would enable the selection of barley lines that can withstand competition with oat weed.

Competition occurs both for production limiting factors (water, nutrient) and defining factors (light, temperature, crop morphology and phenology) (Lantinga, 1995).

Objectives of the study were to: 1, investigate the influence of weed competition on the phenotype of barley lines grown with oat 'weeds', 2, determine competitive ability of barley recombinant inbred lines (RILs) with oat weed, 3, detect quantitative trait loci (QTLs) responsible for the competitive ability in barley recombinant inbred lines and, 4, analyse possible correlation of competitive ability of weeds with other agronomic traits and yield.

A quantitative trait locus (QTL) is traditionally defined as a trait with a continuous distribution, in contrast to a discrete distribution of qualitative traits. The trait values are usually obtained by measuring. The loci controlling quantitative traits have commonly been referred to as QTL. The genetics of quantitative traits are more complex than those of single factor Mendelian traits. The procedure for finding and locating the QTLs is referred as QTL mapping. It involves the construction of molecular maps and searching for a relationship between traits and polymorphic markers. A significant association between the traits value and the markers distance may be an evidence of a QTL near the traits. Genetic maps show the ordering of loci along a chromosome and the relative distance between them. The developments of molecular markers have enhanced the development of genetic maps in several species of plants including barley. In QTL mapping, marker positions are treated as fixed; but since it represents the best statistical estimate, it is prone to simultaneous and correlated errors when obtained from the same data. It varies with the cross due to epistatic interaction at QTL. For quantitative traits, QTL is a tool for dissecting complex traits into a Mendelian factors, since a target trait may in fact be a QTL for a correlated trait, or a component of the complex target trait, for example, yield is influenced by lateness (Stamp, 1994). In the QTL analysis, the null hypothesis for the presence of segregating QTL is accepted only if the LOD score value at the tested position is greater than the given threshold value and it is rejected otherwise. In this study the recombinant inbred lines were used to study their competitive ability with oat weed under field condition and by analysis of quantitative trait loci (QTL) responsible to oat weed competition. The results of the study would assist to apply the selection methods in Ethiopia with diverse genotypes of plant species,

including barley to alleviate oat-weed competition problems. It also enabled us to get more insight into the genetics of barley genotypes weed competition/suppressing ability.

MATERIALS AND METHODS

Plant material

The plant materials used for this experiment were 98 barley recombinant inbred lines including their two parents namely, GEI which has erect leaf type and high yielder and GUNHILD with droopy leaf type and taller. The barley parents GEI and GUNHILD were crossed to develop the inbred lines. Their progenies in F₂ were grown by single seed descent method until F₈. These lines were intercropped with the two oat weed types BRUNO with the potential of early ground cover, long stem and droopy leaf type and GIGANT with more thousand seed weight and an erect leaf type.

The experiment was conducted from 1st May to 30th August 1998 in the Netherlands at the Wageningen Agricultural University farm, which is located at 51° and 58' North latitude and 5° and 40' East longitude. The soil type of the experimental site was predominantly clay with pH of seven. In the previous cropping season the plot was planted to winter wheat. The field was ploughed twice in autumn and harrowed in spring. Before planting, the barley lines were sieved by three mm sieve mesh to make the seed size as uniform as possible. There was no longevity and seed size difference between the lines. Therefore, all competition differences were assumed to be due to genotypes of both barley lines and oat weeds. A seed-matic row planter machine was used to ensure optimum planting depth and uniform seed rate. No fertiliser was applied to simulate the low input resource poor farmers' situations of the developing countries and to promote competition among the barley lines and oat weed for the scarce resource. All other pertinent cultural practices were applied equally for both barley lines and oat weeds.

Experimental arrangement

An experimental arrangement used in this study was the replacement series, in which the total density of the plants kept constant whilst the relative frequencies of the two species could be varied (Spitters, 1983). This experimental arrangement is most commonly used to investigate

the competition between two-species mixture of plants. The arrangement has proved to be popular because the graphical presentation of yield data allows identification of stronger competitor and the extent of niche overlap between species. The arrangement could also be used to investigate competition for specific nutrients (Hall, 1974a, b).

In this study, 98 barley lines were intercropped with the two oat 'weeds'. Each barley line and oat weeds were also grown as a sole crop for comparison of competitive ability. This makes 294 plots (3 X 98) in the experiment. Each treatment was replicated twice. Sixty incomplete blocks were used to accommodate the treatments. For the intercrop of a 50:50 ratio of barley and oat 'weeds', three rows of barley and three rows of oat were planted alternatively, while six rows were used in the sole cropping of both barley lines and oat weeds. Randomised incomplete block design was used to layout the treatments in the field. The treatments randomly assigned in each replication within an incomplete block. The analysis model was developed to observe whether there exists a difference between blocks, barley lines and treatments.

The model developed for the observation was:

$$Y_{ij} = \mu + \tau_i + \rho_j + E_{ij}$$

$$i=1, 2, \dots, 294$$

$$j=1, 2$$

where i = treatment number; j = block number; μ = population mean; τ_i = the effect of treatment i ; ρ_j = the effect of block j and E_{ij} = the residual effect.

Data collection

For the 98 barley recombinant inbred lines (RILs) and the two oat weeds, the characters that are closely associated with competition were measured. These include, plant height, which was measured in centimetre from the ground level to the top of the spike excluding awns. The first measurement was taken after 30 days of emergence, while the second and third measurements were taken after 45 and 60 days respectively. Plant population was obtained by taking stand count of the plants in each plot. Days to flower, was taken when 50% of plants in the plot have started flowering. Days to maturity were recorded when 75% of plants in the plot reached physiological maturity. Grain filling period, which is the difference of days to maturity and flowering was calculated.

Thousand seed weight and grain yield (kg/ha) were taken after counting thousand seed and weighing 1000 seeds and grain yield (kg/ha) for each plot respectively. Totally eight characters were used to collect data in measuring the competition effects of oat 'weeds' on the barley lines in the three environments (sole cropping, intercrop with taller droopy oat 'weed' and intercropping with tall, erect oat 'weed').

Data analysis

The analysis of variance (ANOVA) was done using the method designed for one main crop grown with a supplementary crop (Federer, 1993). The statistical analysis was computed using the software package of the SAS computer programme, release 6.12 (1997). For barley RILs the analysis was carried out for the characters of plant heights taken at 30, 45 and 60 days after emergence, days to flowering, days to maturity, grain filling period, plant population, thousand grain weight and grain yield per hectare; while number of kernels per ear, thousand-kernel weight, plant population and grain yield (kg/ha) data's were analysed for both oat weeds and barley RILs. Analysis of variance contained the analysis for the effect of block, treatments, and differences within the intercropping, the interaction of RILs by intercropping methods and the interaction of RILs by sole cropping using the adjusted least square means to reduce environmental difference for the characters evaluated.

METHODS OF COMPETITIVE ABILITY EVALUATION

A, Relative crowding coefficient (K)

For barley line 'a' in a 50:50 mixture with oat weed 'b', the formula used was:

$$K_{ab} = \frac{\text{Mixture yield of a}}{2 \times \text{Pure stand yield of a} - \text{Mixture yield of a}}$$

$$K_{ab} = \frac{Y_{ab}}{2 \times Y_a - Y_{ab}}$$

The symbols used in this function are: Y_a = pure stand yield of barley line a; Y_b = pure stand yield of oat weed b; Y_{ab} = Mixture yield of barley line a (in combination with b); Y_{ba} = Mixture yield of oat weed b (in combination with a).

This method has been examined in detail by (De wit and Bergh, 1965; Hall, 1974a, 1974b; Firbank and Watkinson, 1985). The adjusted least square means to reduce environmental difference for the characters evaluated were used to measure relative crowding coefficient value. Each barley line has its own coefficient (K), which gives a measure of whether that line has produced more or less yield than expected. Accordingly, line a has a coefficient less than, equal to, or greater than one implies; it has produced less yield, the same yield, or more yield than 'expected', respectively. The component crop with the higher coefficient is the dominant one. To determine if there is a yield advantage of mixing, the product of the coefficients is formed; this is usually designated as K. If $K > 1$ there is a yield advantage, If $K = 1$ there is no difference and if $K < 1$ there is a yield disadvantage, indicating the presence of severe competition.

B, Relative yield total (RYT)

The adjusted least square means data were used in RYT calculation to reduce environmental difference for the characters evaluated. According to De Wit and Bergh (1965), the RYT values are calculated from the yield data of pure stands and mixtures of A and B component crops.

$$\text{RYT} = \frac{\text{Yield of A in mixture} + \text{Yield of B in mixture}}{\text{Yield of A in pure stand} + \text{Yield of B in pure stand}}$$

The relative yield is expressed as the ratio of the yield of species A in mixture and pure stand plus the ratio of the yield of B in mixture and in pure stand.

If RYT does not differ significantly from one, two component crops have the same demand of nutrients indicating the existence of severe competition. RYT value of greater than one indicates different resource requirements indicating suitability for intercropping. RYT value of less than one implies that mixtures use the environment less efficiently than their components in pure stands. That is both crops suffered from competition. The RYT value of one and less than one indicates that the two crops in the intercrop give no yield advantage; or their yields obtained in the intercrops can be achieved if each one was sown in sole crop in smaller areas, partly with one crop and partly with the other. Considering both crowding coefficient (K) and relative yield total (RYT) methods will enable one to select genotypes that are best competitive.

Methods of mapping quantitative trait loci (QTL)

For QTL mapping three data sources were required. These are the loci data, marker data (which contains molecular markers on each of the seven barley chromosomes for the recombinant inbred lines (RILs) and the trait data, which was obtained by calculating least square means to reduce environmental difference for each of the characters evaluated. The latter was generated from the field experiment by the statistical analysis of least square means obtained by SAS for all eight characters. These data were corresponded to the marker data, using JoinMap version 2.0 developed by Jansen and Stam (1994). The JoinMap computer program used to analyse the gene additive effect to determine the QTL for each trait in the two environments of competition. The RILs competitive ability with oat weed was examined and the morphological marker information was used to look for marker trait associations. The trait data were used for measuring QTL by environment interactions, since the same line can be grown over three different sets of environments (with no weed/sole cropped, with droopy oat 'weed', and with erect oat 'weed').

In this study we used a molecular map based on amplified fragment length polymorphisms (AFLPs) to determine the number, chromosomal location (position), magnitude of effects (additive effects), LOD (measures the probability of linkage between the marker and the QTL loci.) score value, phenotypic variance explained in percentage and the gene action of QTLs controlling important morphologic and yield component characteristics to assess the competitive ability of barley RILs. QTL mapping consisted of two stages; these are Interval QTL mapping and Multiple QTL mapping.

Interval QTL mapping

In interval QTL mapping method genome data of two flanking markers and the quantitative trait values were used for calculating the likelihood of the presence of a QTL for every position on the linkage map. Each chromosome is scanned for the most likely position of QTLs in each marker interval (Stamp, 1994). In this method one QTL at a time scanned ignoring the effects of other QTLs already mapped or to be mapped. It used the neighbouring markers to detect the presence of a QTL in the genome region sided by the markers. The LOD score was used to measure the probability of linkage between the marker and the QTL loci. It gave particularly specified set of trait values for each individual with the observed marker

genotype. The LOD score was calculated as the logarithm of a likelihood ratio $LR = \log [L(\text{data}, r=r') / L(\text{data}, r=0.5)]$ where r' = estimate of recombination frequency in case of linkage and $r=0.5$ if the loci is unlinked. In this mapping the threshold LOD score value was set to be 2.5.

This mapping method used to estimate map position, and it separated the effects of QTL from the effects of recombination between the QTL and its siding markers. However, it could not distinguish multiple linked QTLs in which the mapping was biased and QTLs mapped to wrong positions especially when more than one QTL is identified on a chromosome. Moreover, it over estimated the phenotypic variance explained by the putative QTL to detect the linked QTLs and the interaction of QTLs by environment. Therefore, for a better estimation of the competitive ability and yield components, multiple QTL mapping or composite interval QTL mapping was applied.

Multiple QTL mapping (MQM)

The MQM was done for four traits where QTLs identified by interval QTL mapping and most directly associated with competitive ability namely, plant heights measured at three different growth stages, thousand kernel weight and grain yield (kg/ha). Using appropriate unlinked markers as cofactors can partly account for the segregation variance generated by unlinked QTLs (Lynch and Walsh, 1998). To improve the precision in MQM, putative QTLs identified in interval QTL mapping were used as cofactors (Jansen, 1993; Jansen and Stamp, 1994; Zeng, 1994). Accordingly, in our particular case we used three cofactors which has increased the LOD score value, explained variance and additive effects. It also allowed locating the QTLs at their refined position.

Markers associated to peaks of putative QTLs identified by interval mapping were used as cofactors in searching for the remaining QTLs along the barley genome. The other reason for using MQM is the inability of interval QTL mapping to detect linked QTLs and QTL by environment interactions. Only the most influential markers were chosen to use as cofactors, because the use of non-informative cofactor reduces the power of detecting a QTL. Jansen and Stamp (1994) recommended the number of cofactors should not exceed 2 times the square root of the number of observations and this was applied in scanning MQM. The cofactor markers in the approximate multiple QTL were selected based on the principle that, the marker closest to the estimated map

position of the QTL, or even two markers at either side of this position, was used as cofactors. The cofactors in MQM mapping have reduced the residual variance by the use of cofactor markers, which absorbed the genetic effects of closely linked QTLs. When the LOD values of other markers on the regions reached a significant level, the MQM was done again by considering those new 'peak markers' as a cofactors until a stable LOD profile was recognized. In our case QTLs were identified when the LOD profile threshold value of 2.5 was exceeded. A total of 137 loci for 98 RILs with three neighbouring markers and 200 iterations applied to map the MQM.

RESULTS

The results of data analysis were presented for both barley lines and oat 'weeds'. These two component crops were further separated by their leaf types, as erect (a) droopy (b).

Plant height

After 30 days of emergence barley lines have shown significant difference in growth in all environments and there are significant differences among the three intercropping environments in plant heights at ($P < 0.05$) (Table 1). However, barley lines in the intercrop after 45 days of emergence were taller and slimmer showing the effect of competition compared to the sole cropped. Furthermore, there existed highly significant differences among the barley lines in the two intercropping methods. There was also an interaction effect between lines and for the differences between sole cropping and intercropping. After 60 days of emergence, this was two weeks after blossoming, the treatment effects were clearly observed. There was significant difference among lines, intercropping methods and lines by intercropping method. Interactions for the difference between sole and intercropped lines and within the two intercrops were also observed for the character. Plant heights of sole crop barley lines in the early growing period of 30 days after emergence were taller for both erect and droopy leaf types than in the intercrop, indicating that at this stage the competition for light did not start. For plant height measured 45 days after emergence, barley lines with droopy leaf type in the intercrop had very similar height to sole crop, showing their strong competitive ability with oat weeds, while erect ones were more affected by

competition. Through development over time, plant height was taller and slimmer in intercropped environment than sole cropped (Table 2), due to competition for light by the barley lines to overcome the shading effect of oat weeds. Furthermore, for plant height measured 60 days after emergence barley lines with droopy leaf type intercropped with both erect and droopy oat weeds were taller than sole cropped, showing stronger competitive ability with oat 'weeds' at the later growth stage.

Phenological characters

The barley lines in the sole crop were earlier to flower than intercropped. There were significant differences within the intercrop environments to

delay the barley lines timely flowering. Because, the nutrient and light obtained by the barley lines in the intercrop environment was lower for the timely resumption of the reproductive phase. This was also true for days to maturity. Barley lines were delayed to reach physiological maturity due to the effect of competition. Due to this, there was significant difference among barley genotypes, within intercropping and an interaction of barley lines by the two intercropping environments in delaying days to maturity. There was also an interaction effect of intercropping by RILs in delaying days required to fill the grain. Long grain filling period was observed in intercropped barley lines, because maturity was delayed compared to sole cropped barley lines (Table 2).

Table 1. Mean Plant heights in (cm) as affected by intercropping environments at three different growth stages.

Intercropping environment	Plant height 1	Plant height 2	Plant height 3
Sole crop	48.0b	80.7a	82.1a
Barley lines with oat weed 1	46.4a	82.9b	85.6c
Barley lines with oat weed 2	46.4a	82.3b	84.8b

Oat 1, taller droopy oat 'weed', oat 2, tall erect oat 'weed'.

Values with the same letters are not significantly different while values with different letters are significantly different.

Table 2. The effect of intercropping environment on the average performance of erect and droopy leaf type barley RILs for the characters evaluated.

Character	Genotype	Environments			Differences
		B	B01	B02	
PH1	erect	45.63	44.41	44.04	1.41
	droopy	48.87	47.30	47.62	1.41
PH2	erect	73.40	75.40	76.34	-2.47
	droopy	83.57	86.20	81.71	-0.38
PH3	erect	74.33	78.56	77.78	-3.38
	droopy	84.02	87.44	86.75	-3.08
DF	erect	51.84	52.35	52.15	-0.41
	droopy	52.63	52.80	52.67	-0.11
DM	erect	93.95	94.79	94.87	-0.88
	droopy	93.56	94.83	94.42	-1.06
GFP	erect	42.11	42.44	42.73	-0.47
	droopy	40.93	42.03	41.75	-0.96
NEM	erect	811.82	827.24	789.74	3.36
	droopy	796.89	776.11	787.49	15.09
NKE	erect	21.73	20.68	20.85	0.97
	droopy	20.63	20.72	20.66	-0.06
TKW	erect	47.12	38.86	40.34	7.52
	droopy	50.48	47.15	48.59	2.62
YLD	erect	8254.30	6232.80	6391.80	1942.00
	droopy	8118.90	7531.30	7495.60	605.47

B, sole cropping; B01, intercrop with droopy oat 'weed'; B02, intercrop with erect oat 'weed'; PH1, PH2, PH3, plant heights measured at 30, 45 and 60 days after emergence in cm; DF, days to flower; DM, days to maturity; GFP, grain-filling period; NEM, number of ears per square meter (plant population); NKE, number of kernels per ear; TKW, thousand kernel weight in gram and YLD, grain yield (kg/ha).

Yield and its components

Yield components used for competitive ability study included characters like, number of kernels per ear, thousand-kernel weight, plant population and grain yield. For the number of kernels per ear, the barley lines were significantly different to each other. But there was no significant difference within the two intercropping environments. An interaction of barley lines and intercropping environment was observed. The number of kernels per ear was lower in the intercrops than in sole crop environment. Genetically, oats have more number of kernels than barley. However, they decreased in the intercrop more than the barley lines did (Fig. 1). Thousand-kernel weight was observed as a better estimate of competition than the former characters. It was noted that, there existed significant differences among barley lines, intercropping and an interaction of lines by intercropping environments. The barley lines in the sole crop environment had more thousand-kernel weight than when intercropped, while the oat 'weeds' gained in thousand-kernel weight in intercropping environment (Fig. 2). This indicates

that the oat 'weeds' in competition for the environmental resources dominated the barley lines. Genetically, barley has greater thousand kernel weight than oat, but the decrease in weight due to competition environment was more obvious for barley lines than for the oat 'weeds' in the intercropping environment. Plant population has largely reduced for oat, but not so much for barley (Fig. 3). Barley lines grown with an erect oat 'weed' have showed the highest plant population, even though there was no significant difference between the two intercropping environments. The increase in plant population of barley lines show that barley lines were more competitive than oat 'weeds' for this trait. Grain yield was the best estimate of competition effect among the characters evaluated. The yield decrease of more than one ton in an intercrop with droopy leaf type oat 'weed' and 0.8 ton with an erect leaf type oat 'weed' was observed (Fig. 4). Individual lines differed significantly from each other in grain yield due to competition. Genetically, barley is high yielder than oats. But the difference in grain yield among barley lines was more than oat 'weeds.'

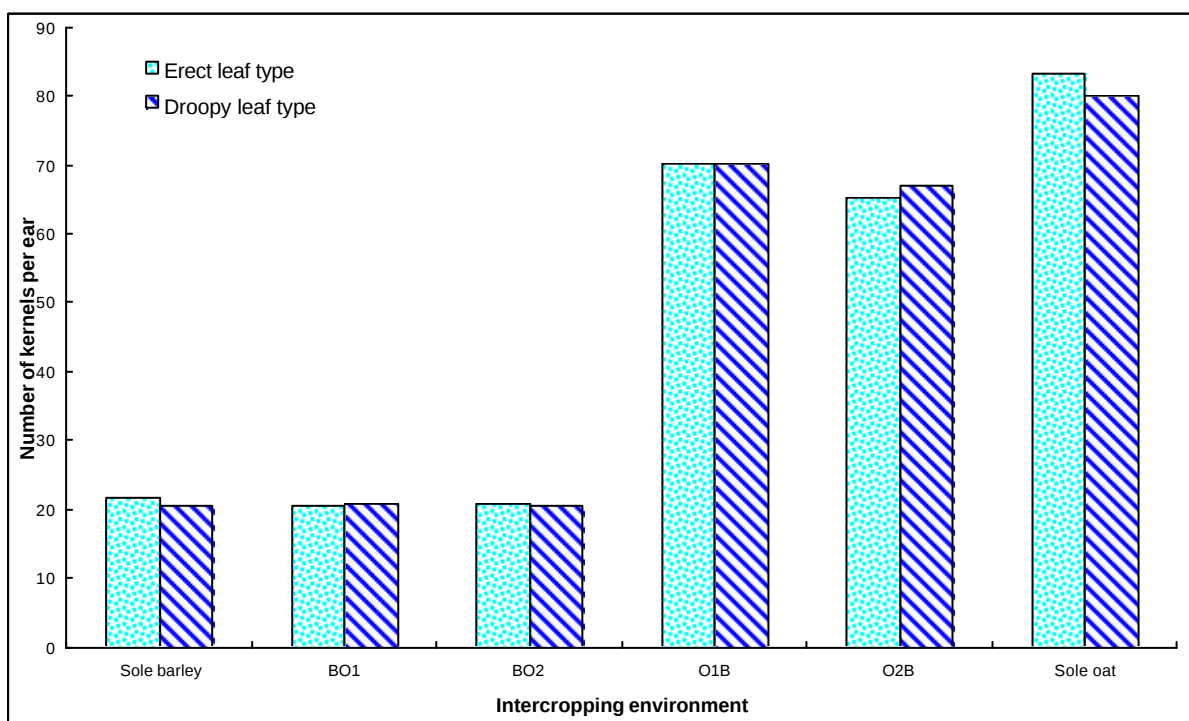


Fig. 1. Comparing the competition effects on the erect and droopy leaf types of barley lines and oat 'weeds' for number of kernels per ear. BO1, barley lines with droopy oat 'weed'; BO2, barley lines with erect oat 'weed'; O1B, droopy oat with barley lines; O2B, erect oat weed with barley lines.

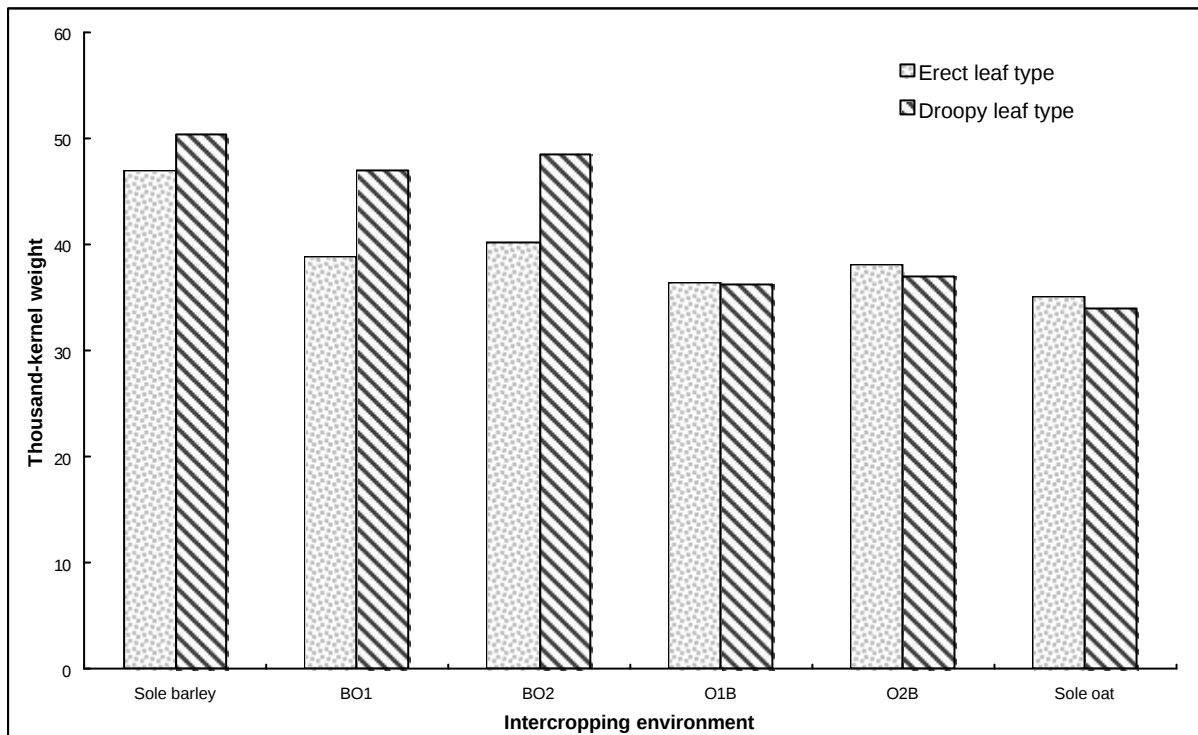


Fig. 2. Competition effects of erect and droopy leaf types of barley lines and oat 'weeds' for thousand-kernel weight. BO1, barley lines with droopy oat 'weed'; BO2, barley lines with erect oat 'weed'; O1B, droopy oat with barley lines; O2B, erect oat with barley lines.

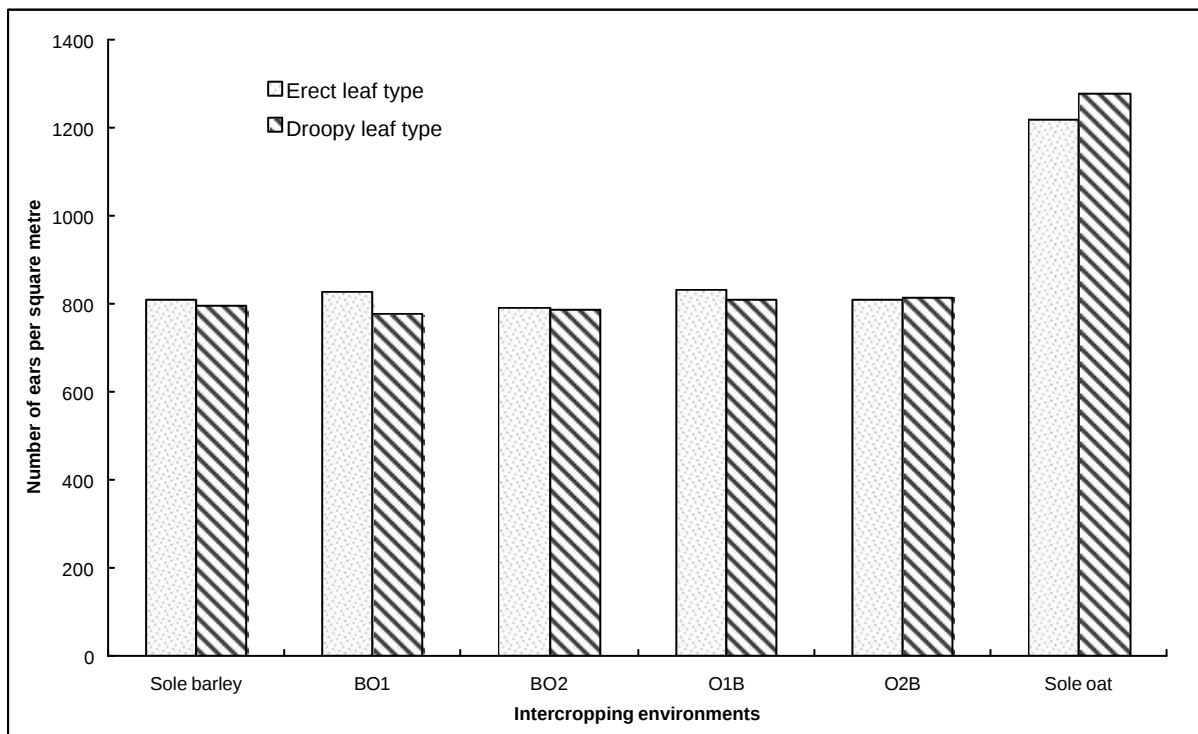


Fig. 3. Comparing the competition effect of an erect and droopy leaf types of barley lines and oat 'weeds' for the number of ears per square metre. BO1, barley lines with droopy oat 'weed'; BO2, barley lines with erect oat 'weed'; O1B, droopy oat with barley lines; O2B, erect oat with barley lines.

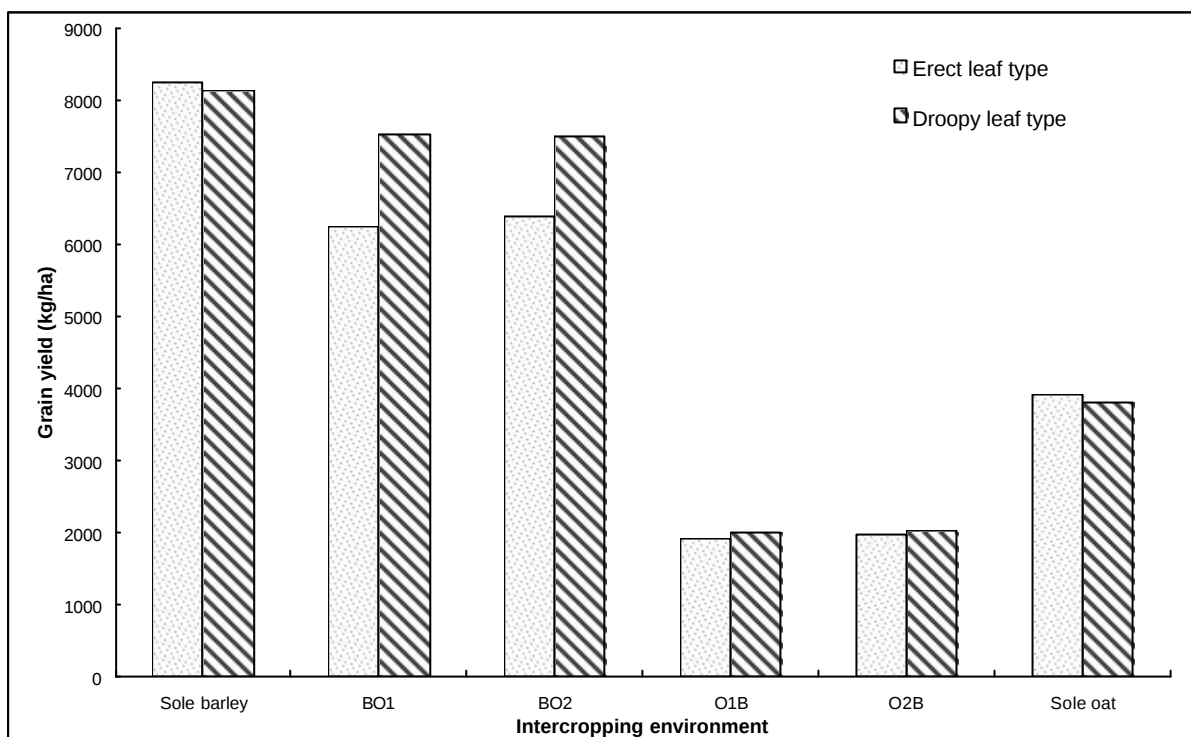


Fig. 4. Comparing the competition effects on an erect and droopy leaf types of barley lines and oat 'weeds' for grain yield (kg/ha). BO1, barley lines intercropped with droopy leaf oat weed; BO2, barley lines intercropped with erect leaf oat weed; O1B, droopy leaf oat weed with barley lines; O2B, erect leaf oat weed with barley lines.

Correlation among characters evaluated in the two intercropping environments

In general, the correlations of characters were more prominent under the intercropping environments than in sole cropping, showing the dependency of characters on each other in the intercropping environment (Table 3). For example, plant height was positively and moderately correlated with grain yield in the intercropping environment. But not correlated with grain yield in a sole crop environment. The character thousand-kernel weight was also positively and moderately correlated in the intercrop environment with grain yield, while it had no correlation with grain yield in sole cropping environment. Grain yield had a positive correlation with days to flower and number of kernels per ear in the intercrop with tall, erect oat 'weed', but a negative correlation was observed with plant population. The only positively and significantly correlated character with grain yield was number of kernels per ear in a sole cropping environment. This shows that, in a sole crop environment without the effect of oat-weed competition, selecting barley lines with higher number of kernels per ear, more thousand kernel weight and erect leaf type can result in an increased grain yield (kg/ha).

Relative crowding coefficient (K)

When the crowding coefficient was used to measure competitive ability among barley lines and oat 'weeds', it was observed that barley genotypes with erect leaf type suffered in competition with oat 'weeds' with droopy leaf type (Table 4). This was true for the characters of plant height measured at 30 and 45 days after emergence, days to maturity, grain-filling period, number of kernels per ear, thousand-kernel weight and grain yield. On the other hand, erect leaf type oat 'weed' suffered in competition with droopy leaf type barley lines for the characters of plant height measured in 45 and 60 days after emergence, days to flower and maturity. The competition between droopy leaf type barley lines and oat 'weed' was severe for the characters of plant population. A difference in leaf morphology was a major factor for both crops to cause severe competition. The droopy leaf type oat suppressed more than the droopy leaf type barley lines in competition for the characters grain yield (kg/ha) and thousand-kernel weight. Because oat weeds were taller than barley lines and their shading effect was more compared to barley lines.

Table 3. Correlation coefficient of agronomic characters in the three combined intercropping environments (sole, BO1 and BO2).

Character	PH2	PH3	DF	DM	GFP	NKE	TKW	NEM	YLD
PH1	0.44*	0.30*	-0.49*	-0.49*	-0.18	-0.50*	0.37*	0.22*	-0.01
	0.40*	0.14	-0.56*	-0.52*	-0.02	-0.32*	0.43*	0.20*	0.20
	0.13	0.17	-0.54*	-0.55*	-0.09	-0.38*	0.35*	0.19*	0.15
PH2		0.93*	0.18	-0.04	-0.26*	0.02	0.44*	0.25*	-0.06
		0.82*	0.17	0.01	-0.20*	0.20*	0.76*	-0.36*	0.59*
		0.90*	0.07	0.02	-0.06	0.09	0.30*	0.07	0.07
PH3			0.40*	0.14	-0.22*	0.13	0.45*	-0.35*	-0.09
			0.46*	0.22	-0.27*	0.33*	0.61*	-0.19*	0.64*
			0.50*	0.30*	-0.21*	0.42*	0.60*	-0.27*	0.53*
DF				0.71*	-0.05	0.61*	0.03	-0.50*	-0.02
				0.72*	-0.24*	0.54*	0.05	-0.25*	0.25*
				0.75*	-0.20*	0.61*	0.08	-0.34*	0.19*
DM					0.66*	0.46*	-0.08	-0.28*	0.09
					0.49*	0.35*	-0.01	-0.18	0.17
					0.50*	0.39*	-0.03	-0.09	0.09
GFP						-0.01	-0.15	0.13	0.15
						-0.18	-0.08	0.05	-0.08
						-0.22*	-0.15*	0.29*	-0.12
NKE							-0.21*	-0.73*	0.20*
							0.01	-0.60*	0.12
							0.01	-0.63*	0.28*
TKW								-0.23*	0.01
								-0.41*	0.59*
								-0.30*	0.44*
NEM									0.03
									0.09
									-0.19*

Values with * are significantly different at ($p < 0.05$).

PH1, plant height measured after 30 days of sowing; PH2, plant height measured after 45 days after sowing; PH3, plant height measured 60 days after sowing; DF, days to flowering; DM, days to maturity; GFP, grain filling period; NKE, number of kernels per ear; TKW, thousand kernel weight; NEM, number of ears per meter square; YLD, gain yield (kg/ha).

Table 4. Relative crowding coefficient (K) for erect and droopy genotypes of barley lines and oat 'weeds' for agronomic characters evaluated.

Character	Barley genotypes	Oat 'weeds'	
		Droopy	Erect
PH1	erect	0.90	0.94
	droopy	0.95	0.96
PH2	erect	1.06	1.40
	droopy	1.08	0.98
PH3 3	erect	1.15	1.11
	droopy	1.08	1.06
DF	erect	1.02	1.01
	droopy	1.02	1.0
DM	erect	1.02	1.02
	droopy	1.03	1.02
GFP	erect	1.03	1.04
	droopy	1.06	1.05
NEM	erect	0.92	0.94
	droopy	1.02	1.02
TKW	erect	0.71	0.76
	droopy	0.89	0.94
NEM	erect	1.12	1.05
	droopy	1.03	1.13
YLD	erect	0.63	0.65
	droopy	0.90	0.90

$K < 1$, oat reduces value of neighbouring barley lines more than barley lines would do.

$K = 1$, oat reduces value of neighbouring barley lines equally as barley would do.

$K > 1$, oat reduces value of neighbouring barley lines less than barley would do.

A, erect genotype; b, droopy genotype; PH1, plant height measured after 30 days of sowing; PH2, plant height measured after 45 days after sowing; PH3, plant height measured 60 days after sowing; DF, days to flowering; DM, days to maturity; GFP, grain filling period; NKE, number of kernels per ear; TKW, thousand kernel weight; NEM, number of ears per meter square; YLD, gain yield (kg/ha).

Relative yield total (RYT)

When the relative yield total (RYT) was considered to measure competitive ability among barley lines and oat 'weeds', the erect leaf type barley lines suffered more in competition with droopy leaf type oat 'weed' for the characters of thousand kernel weight and grain yield (Table 5). These characters are the major yield determining ones in the intercropping environments. Droopy leaf type barley lines were more competitive than erect leaf type oat 'weed' for the character of number of kernels per ear. As seen in crowding coefficient, droopy leaf type barley lines were most competitive with droopy leaf type oat 'weed' for the characters of grain yield (kg/ha) and plant

population. The droopy leaf type barley lines had the better ability to compete with oat-weed.

QTL mapping

The molecular map of 137 amplified fragment length polymorphism (AFLP) markers and two morphological markers for the barley lines with erect (a) and droopy (b) leaf types respectively are spanned along all seven barley chromosomes. It had a total length of 788 centiMorgan (cM) and an average distance between markers was six cM. QTLs for competitive ability of barley lines were determined in each three environments (Tables 6 and 7).

Table 5. Relative yield total value for four yield components measured in erect and droopy leaf types of barley lines and oat 'weeds'.

Character	Barley genotypes		Oat 'weeds'
NKE	erect	Droopy	Erect
		1.86	1.90
TKW	droopy	1.88	1.81
	erect	1.88	1.96
NEM	droopy	1.98	2.07
	erect	1.15	1.19
YLD	droopy	1.08	1.14
	erect	1.32	1.36
	droopy	1.44	1.45

a value of 2 means equal to the mono culture situation; where as less than 2 indicates the presence of competition in both oat weeds and barley lines. a, erect genotype; b, droopy genotype; NKE, number of kernels per ear; TKW, thousand kernel weight; NEM, number of ears per square meter; YLD, grain yield (kg/ha).

Table 6. Chromosomal locations and additive effects of putative QTLs determined by interval QTL mapping for the characters evaluated in the three intercropping environments (Sole crop, BO1, BO2).

Character	Sole crop		BO1		BO2	
	Chr	Add	Chr	Add	Chr	Add
PH1	2 (28.8)	-1.71	1 (34.4)	-1.70	2 (28.8)	-1.60
	7 (67.6)	-2.28	7 (67.6)	-1.71	7 (67.6)	-2.10
PH2	7 (42)	-6.0	7 (67.6)	-5.7		
	7 (47)	-5.7				
PH3	7 (67.6)	-6.2	1 (99.2)	-3.59		
			7 (67.6)	-5.05		
DF	1 (52.3)	-1.63	1 (52.3)	-1.70	1 (52.3)	-1.78
	2 (37.4)	1.08	2 (28.8)	1.13	2 (28.8)	1.14
DM	1 (57.3)	-2.89	1 (57.3)	-2.35	1 (52.3)	-2.49
GFP	1 (42.3)	-1.1			2 (57.3)	-0.9
					2 (39.7)	-0.9
NEM	2 (28.8)	-44.61	2 (44.7)	-61.95	2 (44.7)	-57.61
TKW	2 (31.7)	-2.25	2 (28.8)	-2.37	2 (31.7)	-2.75
	7 (42.0)	-2.35	7 (67.6)	-5.13	7 (67.6)	-4.95
YLD (kg/ha)			7(67.6)	-727.2	7 (62.6)	-624.6

Chr, chromosome on which QTL determined by interval mapping; values in brackets are approximate position in centiMorgan; Add, additive effects of QTLs on the character evaluated genotypes (a-b)/2; BO1, intercrop with droopy oat 'weed'; BO2, intercrop with erect oat 'weed'; PH1, plant height measured after 30 days of sowing; PH2, plant height measured after 45 days after sowing; PH3, plant height measured 60 days after sowing; DF, days to flowering; DM, days to maturity; GFP, grain filling period; NKE, number of kernels per ear; TKW, thousand kernel weight; NEM, number of ears per meter square; YLD, grain yield (kg/ha).

Table 7. Chromosomal positions and additive effects of putative QTLs for the characters evaluated to determine competition effects on sole cropping environment, crowding coefficient values with oat 1 (kv1) and with oat 2 (kv2).

Character	Difference		kv1		kv2	
	Chr	Add	Chr	Add	Chr	Add
PH2	7 (67.6)	-3.42	7 (67.6)	-0.23		
	7 (55.9)	-3.03				
PH3			7 (62.6)	-6.3		
TKW	7 (62.6)	2.68	7 (62.6)	-0.1	7 (62.6)	-0.1
YLD	7 (67.6)	674.4	7 (67.6)	-0.1	7 (62.6)	-0.1

Chr, chromosome on which the QTL determined, values in the brackets are approximate positions of QTL in centiMorgan
Add, additive effects of the QTLs on the competition effects evaluated (a-b)/2. positive value indicates effect due to genotype (b) is smaller than (a); negative value indicates effect due to genotype (b) is greater than (a);
Difference, sole cropping minus an average of the two intercrop environments shows the competition effect on the character evaluated; PH2, plant height measured after 45 days after sowing; PH3, plant height measured 60 days after sowing; TKW, thousand kernel weight and YLD= gain yield (kg/ha).

Plant heights

In the multiple quantitative trait loci mapping (MQM) method, two QTLs were identified for sole crop environment on chromosomes II and VII. Interval mapping also identified these QTLs. However, the position of QTLs was on 28.8 cM in interval mapping and changed to 13.6 cM in MQM, but the location was on chromosome II on both cases. Furthermore, the additive effect and explained phenotypic variance also improved by using MQM (Table 8).

For the barley lines intercropped with the droopy leaf type oat 'weed', an additional one QTL was identified, making three QTLs for this environment. This QTL was identified at position 34.6 cM with LOD score value greater than seven and additive effect of -1.8 on the molecular marker of erect gene which was also a marker for QTL identified on chromosome VII and had an

explained phenotypic variance of 28 percent. For the barley lines intercropped with erect leaf type oat 'weed', however, one additional QTL was identified on chromosome II at position of 28.8 cM with a LOD score value of 6.4 and explained phenotypic variance of 25.6 percent.

Thousand-kernel weight

For this character, one additional QTL for difference due to competition was identified on chromosome VII at position 53.1 cM with LOD score value greater than seven. It had additive effect of 2.6 and explained phenotypic variance of 31 percent. The rest were found in the same position to the interval QTL mapping. In most cases, the QTLs were identified on chromosome VII at molecular markers of E32M61-83, E45M51-6(n), erect gene and E35M48-256(7Q) (Table 8).

Table 8. Chromosomal locations and additive effects of putative QTLs determined by MQM for the characters of plant heights (PH, PH2, PH3) thousand kernel weight and grain yield (kg/ha) in the three intercropping environments.

Character	Sole crop		BO1		BO2	
	Chr	Add	Chr	Add	Chr	Add
PH1	2 (13.6)	-2.2	1 (42.3)	1.4	1 (39.4)	1.6
	7 (67.6)	-2.1	2 (34.6)	-1.8	2 (34.6)	-2.1
			7 (67.6)	-1.5	2 (34.6)	-2.1
PH2					7 (52.0)	-1.8
	7 (67.6)	-5.8	7 (67.6)	-5.6		
			1 (99.2)	-3.5	7 (67.6)	-5.1
PH3					7 (62.6)	-6.2
					7 (52.0)	-3.8
			7 (67.6)	-3.4	7 (67.6)	-3.9
TKW	2 (28.8)	-1.6	7 (53.1)	-3.9	7 (50.4)	-448.7
			7 (67.6)	-545.2	7 (62.6)	-619.9
YLD (kg/ha)			7 (51.1)	-437.2		
			7 (62.6)			

Chr, chromosome on which the QTL determined, values in the brackets are approximate positions of QTL in centiMorgan;
Add, additive effects of the QTLs on the competition effects evaluated (a-b)/2; positive value indicates effect due to genotype (b) is smaller than (a); negative value indicates effect due to genotype (b) is greater than (a);
Difference, sole cropping minus an average of the two intercrop environments shows the competition effect on the character evaluated;

PH1, plant height measured after 30 days of sowing; PH2, plant height measured after 45 days after sowing; PH3, plant height measured 60 days after sowing; TKW, thousand kernel weight and YLD, gain yield (kg/ha).

Grain yield (kg/ha)

By the MQM the QTLs doubled from five to ten for this character (Figs. 5–10). Four cofactors were used to run MQM. An addition of one QTL for intercrop with droopy oat ‘weed’ and with erect oat ‘weed’ was found on chromosome VII. The intercrop environments had two QTLs each on chromosome VII. For the difference due to competition three QTLs were identified. The locus on position 51.1 cM had the greatest LOD score (5.1) with the additive effect of -545.2 and 22.7

percent explained phenotypic variance. For the competitive ability, three QTLs were identified. Two for the competition with droopy oat ‘weed’ and one for the competition with an erect oat ‘weed’. The locus on position 51.1 cM had the greatest LOD score (4.8) with the explained phenotypic variance of 21.3 percent. Surprisingly, for this character, all the QTLs were identified on chromosome VII and molecular markers associated with these QTLs were E35M55-436, E33M54-218 (7Q), E32M61-121 and erect genes (Table 8).

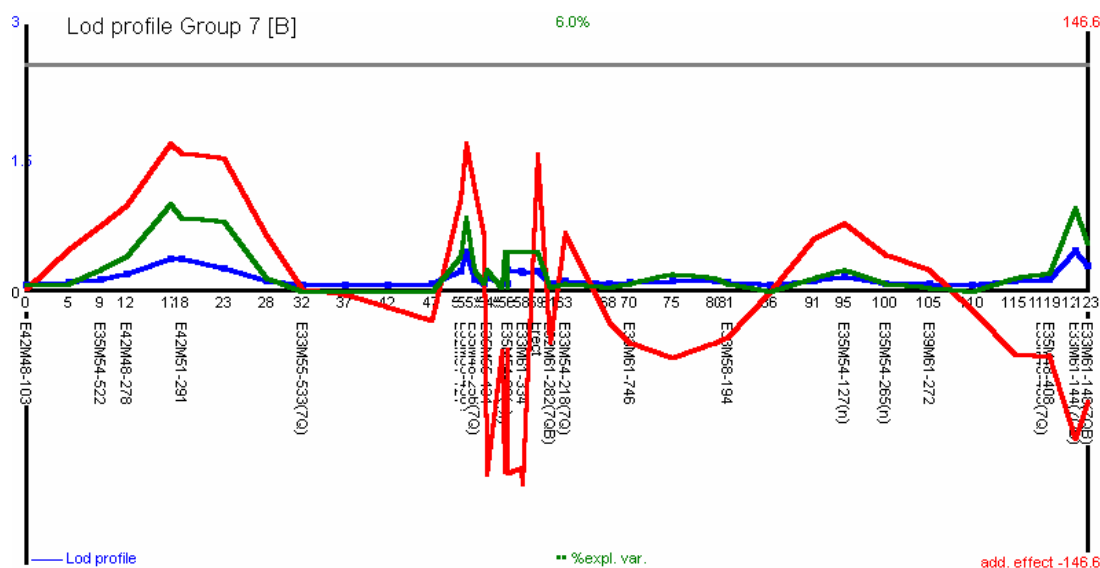


Fig. 5. The QTL map for the sole crop environment in which no QTL was identified. Results of the multiple QTL maps for the character grain yield (kg/ha).

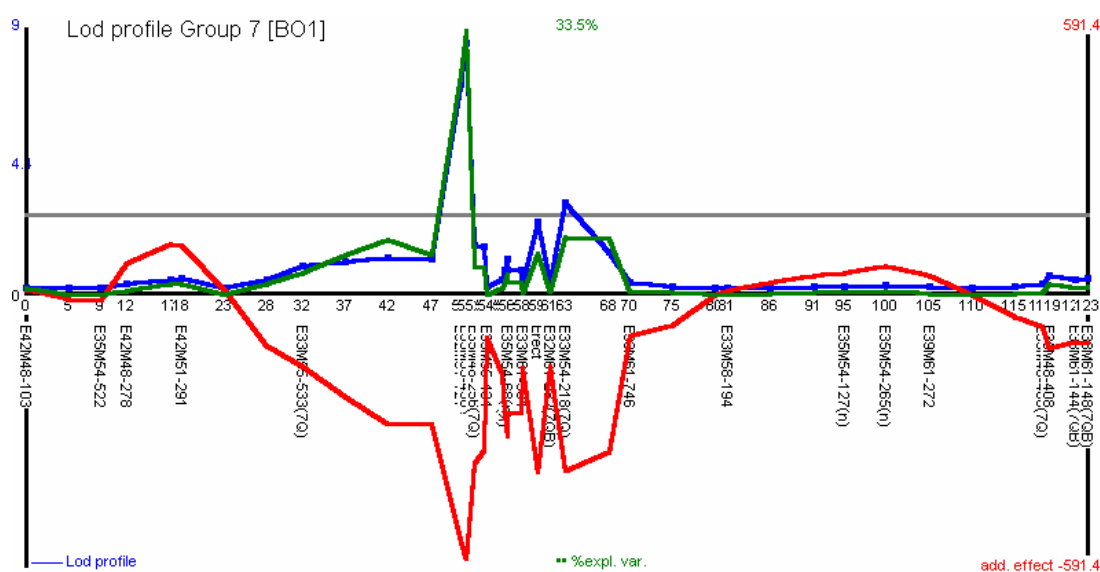


Fig. 6. The QTLs identified by MQM in the intercrop of taller droopy leaf type oat ‘weed’ with RILs. Results of the multiple QTL maps for the character grain yield (kg/ha).

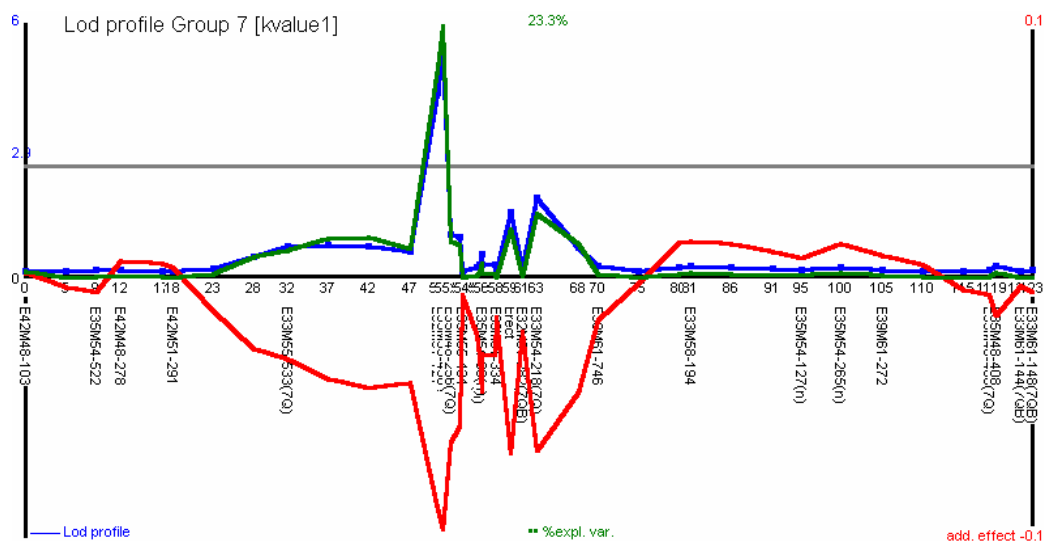


Fig. 7. The QTL identified for the competitive ability of RILs with taller, droopy leaf type oat 'weed'.

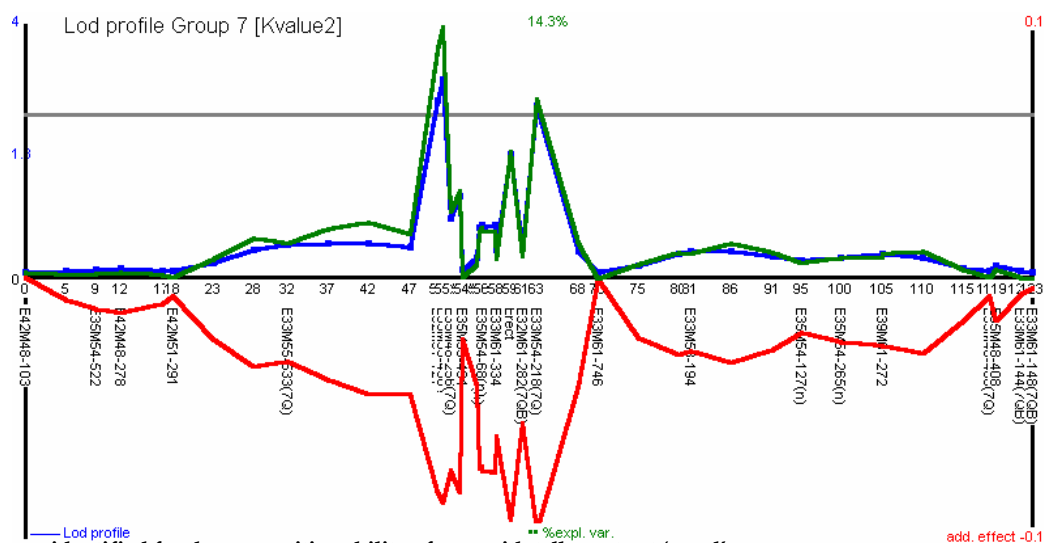


Fig. 8. The QTLs identified for the competitive ability of RILs with tall, erect oat 'weed'.

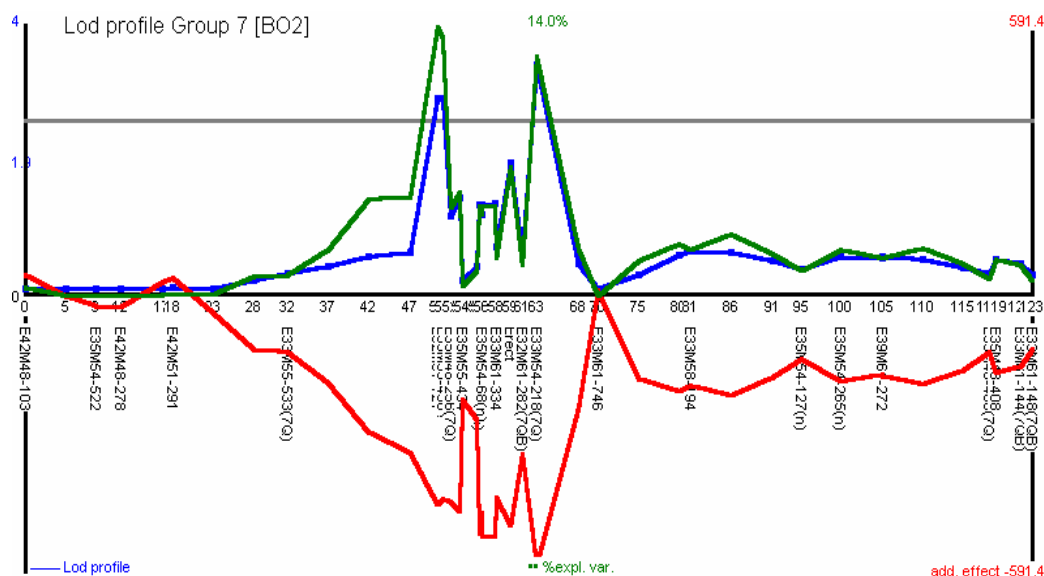


Fig. 9. The QTLs identified by MQM in the intercrop with tall erect oat 'weed'.

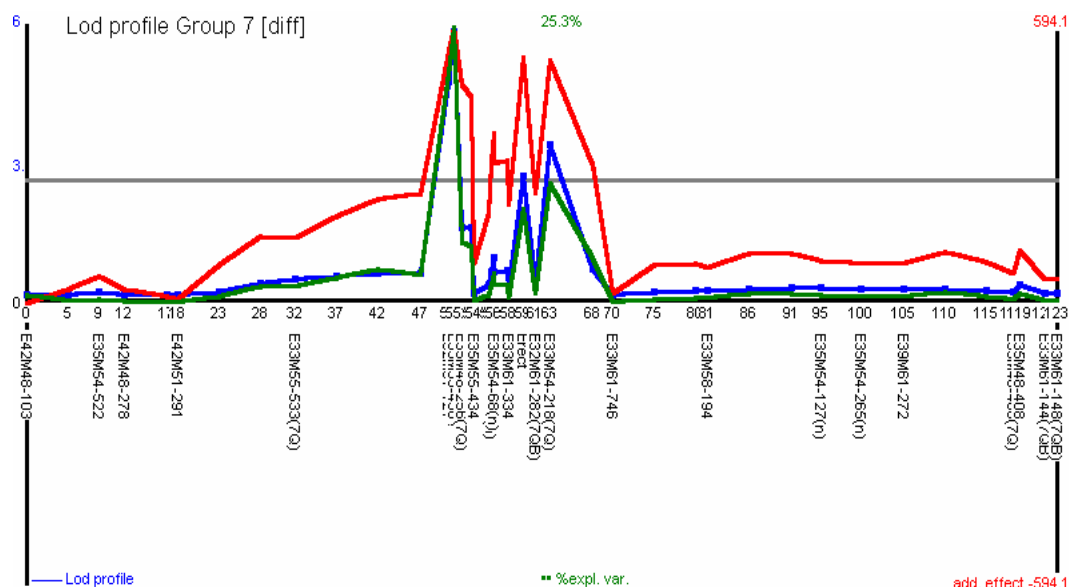


Fig. 10. The QTLs identified by MQM for the difference due to competition with two oat 'weed'.

Overall the QTLs for competitive ability and characters associated with it were identified on chromosomes VII, I and II (Table 9). For plant height, the QTLs were identified on chromosomes I, II and VII while for thousand kernel weight on chromosomes II and VII. For grain yield and for crowding coefficient exclusively the QTLs were identified on chromosome VII. For competitive ability alone, in general, six QTLs were identified for the characters of plant height, thousand-kernel weight, and grain yield. From these, for the competitive ability with droopy oat 'weed', three QTLs for the characters of plant height measured after 45 days, thousand kernel weight and grain-

yield were identified. For the competitive ability with erect oat 'weed' similarly, three QTLs were identified; for the thousand-kernel weight one, and grain yield two. This shows that the erect oat 'weed' had competitive effect on reducing grain yield because of competition for underground nutrient more than for the above ground shading effect. The QTLs identified for these characters revealed that the molecular marker erect gene is an aid to select lines that are competitive with oat weeds. The QTLs were stable for these three characters and located on chromosome VII at position of 62.6 and 67.6 cM.

Table 9. Chromosomal locations and additive effects of putative QTLs determined by MQM for the characters evaluated to assess competitive ability.

Character	Difference		KV1		KV2	
	Chr	Add	Chr	Add	Chr	Add
PH2	7 (67.6)	-3.3	7 (67.6)	0.2		
TKW	7 (53.1)	2.6	7 (53.1)	-0.1	7 (52.0)	-0.1
	7 (62.6)	2.5				
YLD (kg/ha)	7 (62.6)	529	7 (51.1)	-0.1	7 (51.1)	-0.1
					7 (62.6)	-0.1

Chr, chromosome on which QTLs determined, values in brackets are approximate position of QTLs in centiMorgan
Add, additive effects of QTLs on competition for the characters evaluated (a-b)/2

positive: effect due to genotype (b) is smaller than (a)

negative: effect due to genotype (b) is greater than (a)

Difference, sole crop minus an average of the two intercrop environments, shows the competition effect on the character evaluated; PH2, plant height measured after 45 days after sowing; TKW, thousand kernel weight and YLD, gain yield (kg/ha).

DISCUSSIONS

The study of competitive ability of barley lines with oat weeds revealed that there were considerable differences among the two intercropping environments and their effects on the performance of erect leaf type barley lines for the character of plant height. When the character plant height was investigated in both sole cropped and intercropped barley lines with oat weeds for the competition effect, the barley lines in the sole crop were taller than the intercropped during the early growth stage of 30 days after emergence. This shows that barley lines in the intercrop were suffered in competition with oat weeds more for underground nutrients compared to oat 'weeds' in the early growth stage. Later on after 45 days, the barley lines intercropped with oat weeds were taller and slimmer than sole cropped. Indicating, competition for above ground and below ground resources like light and nutrient respectively was stronger with oat 'weeds' starting from 45 days and barley lines were affected in competition for both above ground and underground resources starting from this time.

The phenological characters which included days to flower, maturity and grain-filling period were prolonged. The delaying effect of maturity and grain-filling period in intercrop to the sole crop was again because of the shading effect of oat weeds. The competition effect of barley lines with oat weeds has delayed both timely flowering and maturity for the intercropped barley lines. Because the intercropped barley lines could not reach the reproductive stage at the same time with the sole cropped barley lines due to limitation of both underground and above ground resources as the result of competition.

The characters of yield and its components value (number of kernels per ear, thousand-kernel weight, plant population and grain yield) considered for competitive ability were decreased due to resource limitation in the intercropping environments. There was no interaction effect for the plant population due to oat weed competition for erect leaf type barley lines indicating the effect of plant population in barley lines was independent of cropping system. However, the effect was negative for droopy leaf types in both component crops. In the contrary, plant population was higher in both genotypes of sole crop environment than the intercrops. The reduction in plant population in intercrop for droopy leaf type

barley lines was much more than erect types due to strong competition effect, since the droopy types were taller and shaded the erect types. Both barley lines and oat weeds in the sole crop had more number of kernels per ear than intercropped. The erect leaf type barley lines reduced three times lower than droopy leaf types due to competition for the traits of thousand-kernel weight and grain yield per hectare. The erect leaf type barley lines suffered more than the droopy leaf type in the intercrop with the two oat weeds. On the other hand, the droopy leaf type oat weed was more competitive with erect leaf type barley lines, while the erect leaf type oat weeds suffered in competition with droopy leaf type barley lines, but benefited in competition with erect leaf type barley lines. Therefore, leaf angle in barley lines was more important for competition than in oat. The most indicative character for the competitive ability study was droopy leaf type, tall height, more thousand-kernel weight and higher grain yield (kg/ha). Decrease of 0.8 to one ton grain yield per hectare was observed due to oat weed competition for barley lines intercropped with oat weeds compared to sole cropped.

According to Baeumer and de Wit (1967), when barley and oat weed were grown in competition, barley clearly had the advantage over oats, because it is able to claim the available space at an earlier stage, therefore, by the time the oat weeds are able to claim their share, a disproportionate part of space is already occupied by barley. This is in agreement with our observation where the barley genotype with droopy leaf type and tall were found to be competent, when intercropped with oat weeds starting from the early growth stages.

The interaction of genotype by environment is a basic remarkable concept in applied plant breeding, because the selection of suitable variety that adapts to a given growing condition largely depends on its stable performance across the environments. In general, genotype is regarded as stable when its performance across environments does not depart much from the average performance of the group of standard genotypes (Schut and Dourleijn, 1998). In this principle, the barley lines that have droopy leaf type, taller, having more thousand seed weight and with more grain yield per hectare were found to be consistently better competitive when grown with the two oat weeds of erect and droopy leaf types in a 50:50 plant population.

CONCLUSION

From the investigations made on competitive ability of barley lines intercropped with oat weeds the following conclusions were made. The statistical analysis revealed that there was a significant difference between the sole cropping and intercropping environments. There was a significant interaction effects of barley lines by intercropping environments to most of the characters evaluated for the competitive ability. The competition effect with oat weeds increased plant heights which presumably resulted in lodging, prolonged days to flower, maturity and grain-filling period and reduced number of kernels per ear, thousand kernel weight, plant population and grain yield (kg/ha) in barley lines. The pleiotropic effect of the erect (ert-g) gene on chromosome VII for most of the traits evaluated was found to be consistent. The additive effects of the alleles from the parent Gunhild (with morphological marker of droopy leaf type) on various traits was consistent with the result of correlation among the traits. But there were cases where alleles from the erect leaf type parent affected traits in such a way that it was inconsistent. For most of the characters studied, QTLs for the competitive ability were detected on chromosome VII and in close positions. For example, grain yield, thousand-kernel weight and plant height QTLs were localized on chromosome VII at or near the ert-g gene.

The erect gene increases yield in sole crop environment and decrease in the intercrop environment. The mapping method MQM was superior to interval QTL mapping by clearly positioning and increasing the number of QTLs for the competitive ability studied. The alleles from droopy leaf type barley parent Gunhild had contributed superior effects for competitive ability for all the characters in almost all of the cases, while the alleles from erect leaf type barley parent GE119 contributed for the character grain yield only in the sole crop environment. Therefore, the selection of barley lines for the competitive ability with oat weeds should be based on the five most useful characters. These are tall barley lines, with droopy leaf type, more thousand-kernel weight and higher grain yield (kg/ha). Indicating, selection of barley lines with a morphological marker of tall, droopy leaf type and molecular marker of an erect gene with higher thousand kernel weight and grain yield can enable to adopt an environmentally friendly way to reduce the

effect of oat weed competition. Because, the application of herbicide for weed control is toxic to animals, humans and have a deleterious effect for the crops growing along with weeds. Further more, herbicide price is soaring from time to time, which is out of the reach of the poor farmers in the developing countries.

ACKNOWLEDGEMENTS

The author would like to thank Prof. Dr. Piet Stamp and Dr. Johan Dourleijn, Wageningen Agricultural University, Department of Plant Breeding for their support and valuable advice.

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