Physiological Basis of Grain Size Variation amongst Barley Cultivars

D. B. Moody[1], R. Flood[1] and N. Fettell[2]

[1] Department of Natural Resources and Environment, Horsham Victoria.
[2] NSW Agriculture, Condobolin Research Station, Condobolin NSW.

ABSTRACT

A population developed from a cross between a tall, large grained barley genotype well adapted to southern Australia, and a semi-dwarf European malting cultivar with inherently smaller grain size, was used to study the physiological basis of grain size in barley. The parents differed in the length of the basic vegetative phase of development, and the population segregated for this trait. Pathway analysis of correlated traits indicated peduncle length, rather than plant height *per se*, was the primary factor influencing grain screenings. Furthermore, despite a positive correlation between grain numbers per spike, for a July sowing date, and relative basic vegetative phase, the direct effect of grain numbers per spike was to increase grain screenings whilst the direct effect of the basic vegetative phase was to lower grain screenings. These results indicate (i) semi-dwarf genotypes with improved grain plumpness can be developed by selection for longer peduncle length, and (ii) long basic vegetative phase may enhance grain plumpness if this trait can be disassociated from grain numbers per spike.

KEY WORDS

Basic vegetative phase, leaf number, plant height, semi-dwarf, peduncle, grain size.

INTRODUCTION

Malting barley breeders seek to improve both grain yield and the reliability with which growers achieve malting quality specifications. Stability of grain size is a key parameter in ensuring reliability of meeting malting quality specifications. Both grain yield and grain size stability are influenced by timing of flowering and by plant stature. An interaction between time of sowing and plant phenological characteristics determine flowering date. Flowering date should be timed to maximise use of growing season rainfall without exposing the grain filling period to extremes of temperature, or severe moisture deficit. Reduction in plant height, as is achieved through the use of genes inducing a semi-dwarf growth habit, improve harvest index and can reduce losses associated with crop lodging and spike loss. A key phenological characteristic influencing flowering date is the length of the basic vegetative phase of development (BVP). Relative BVP is measured as either the minimum leaf number on the main stem, or the minimum number of days to awn emergence for plants grown under long days, after any vernalisation requirement has been satisfied (1). Recent studies have indicated all malting quality varieties in southern Australia, which are adapted to the lower rainfall districts, have a relatively short BVP. These varieties are also of tall (standard) stature. An association between the length of the BVP and grain numbers per spike has been observed, and barley varieties with relatively few grains per spike tend to have superior grain size. In terms of plant height, current standard stature varieties have been observed to have superior grain size compared to the current semi-dwarf varieties.

These studies investigate the association between plant stature, BVP, and grain size.

MATERIALS AND METHODS

Population

A recombinant inbred population was developed from a cross between the large grained breeding line VB9104 and the European semi-dwarf malting variety Chariot. VB9104 was known to have a relatively short BVP, whilst Chariot was assumed to have a relatively long BVP. The population comprised 90 randomly chosen F_2 plants, from which 3 random reselections were made in the F_4 generation. The reselections were propagated until the F_6 generation, at which time one random selection was taken from each line. Seed of these selections was multiplied for this study. Hence the total population consisted of 270 F_6-derived lines. Due to space restrictions in the birdcage environment used in this study, only two selections from each F_2 family were included in these experiments ie a population of 180 randomly chosen inbred lines.

Birdcage experiment

Treatments comprised a “normal” (or short) daylength and a long daylength (16.5 hours) with two replications in each treatment, and ten plants per replication. The algorithm “Spades” was used to randomise treatments. The long daylength was achieved by extending normal daylength using incandescent bulbs that gave a light intensity (photo-synthetically-active radiation) of 4μ mol $m^{-2}s^{-1}$ at the soil surface. Seeds from each line were pre-germinated in biodegradable, perforated plastic seedling containers (40mm square by 65mm deep) containing a mixture of loam, peat moss and sand. Ten seedlings of each line were planted into a Wimmera grey cracking clay immediately after emergence in the period 7 to 12 July 1999. Time to awn emergence under both long (DAE_L) and normal (DAE_N) daylength was recorded. Grain filling duration (GFD) was measured as the time from awn emergence to physiological maturity, as measured by colour of the top node, for plants grown under normal daylength. The number of leaves (LN_L) and grain numbers per spike (GN_L) on the main culm was recorded for those plants grown under extended daylength. The length of the peduncle (PED), from the top node to spike rachis, was measured at maturity for plants grown under both natural daylength (PED_N) and extended daylength (PED_L). All measurements were performed on the ten plants per treatment. Treatment means for each parameter were determined using the REML function of Genstat to fit an auto-regressive model to the mean values from the ten plants per treatment. Wald statistics were highly significant for all traits.

Field experiments

The same population of lines was sown in field trials at Horsham and Birchip, with two replications. The algorithm “Spades” was used to randomise treatments. Soils types at Horsham and Birchip were Wimmera grey cracking clays and sodic duplex mallee loams respectively. The Horsham trial was sown on 14 June 1998 and the Birchip trial on 9 June 1999. Each plot consisted of 6 rows, 4.2m in length. Both trials were managed in accordance with local farm practice. Plant height from the base of the plant to the tip of the spike on the tallest tiller, for five plants in each plot, was measured at the Horsham site at maturity. Plot means were calculated and used in subsequent analysis. Unfortunately a late season frost prevented the use of grain yield and grain screenings data from this site. Grain was harvested from the Birchip site and weighed at maturity, and grain sub-samples from this site were assessed for grain size fractions using a Sortimat grain screenings machine. Grain screenings through a 2.8mm screen were subject to natural logarithm transformation, to remove heterogeneity of error variance. Treatment means for plant height (HGT) and transformed grain screenings (SCR) were calculated using the REML function of Genstat to fit an auto-regressive model. Wald statistics were highly significant for both traits at these sites.

Analysis

Correlation matrices were calculated with MS Excel using adjusted treatment means for SCR, DAE_N, DAE_L, LN_L, GFD_N, GN_L, HGT, and PED. Genotypic correlations between SCR and the measured phenotypic traits were partitioned into path-coefficients as described by Dewey and Lu (2). A path coefficient is a standardised partial-regression coefficient that measures the direct influence of one variable upon another, permitting the separation of the correlation coefficient into components of direct and indirect effect. The method of Ortiz and Langie (3) was used to determine the path-coefficients.

RESULTS

The growing season at Birchip during the 1999 season was favourable, with average yields for the parental varieties VB9104 and Chariot being 2.90 and 2.75 t/ha respectively. Due to the favourable spring conditions, grain screenings were relatively low. Hence the percentage grain passing through a 2.8mm screen, as opposed to the more conventional 2.5mm screen, was used to provide effective differentiation between VB9104 (11.0%) and Chariot (25.2%) (?1.2%). Growing conditions at Horsham during the 1998 season were also very favourable, prior to a frost on 28th October. These conditions allowed good discrimination between genotypes in terms of plant height, with the average height of VB9104 and Chariot being 104.1 and 86.2 cm, respectively (?5.5cms).

Birdcage experiments allowed the measurement DAE_N, GFD and relative BVP, in addition to measurements of the effect of daylength on GN and peduncle length. Both leaf number on the main culm and days to awn emergence under extended daylength were used to determine relative BVP. Significant differences in these two measurements of BVP occurred between VB9104 (7.0 leaves, 69.3 days) and Chariot (8.7 leaves, 82.4 days). LN_L amongst progeny ranged from minimum 6.7 (DAE_L = 66.6 days) to a maximum of 9.3 (DAE_L = 86.0 days). Standard errors for these measurements were low (SE LN_L = ? 0.2 leaves; SE DAE_L = ? 1.3 days). Peduncle length was highly correlated between the normal and extended day treatments ($r=0.85$; $p<0.001$), indicating this is a highly heritable trait, and relative ranking of genotypes for this trait are likely to be similar across environments. GN_L was strongly correlated with both LN_L ($r = 0.67$; $p<0.001$) and GN_N ($r = 0.63$; $p<0.001$). However, the correlation between GN_N and LN_L was weaker ($r = 0.25$; $p<0.01$).

Simple correlation analysis indicated DAE_N ($r = 0.30$), HGT ($r = –0.23$), and PED ($r = –0.40$) had the greatest influence on grain screenings (Table 1). The influence of maturity on grain screenings was mainly due to a direct effect. Of more interest, was the path coefficient for PED which was high (-0.51) whilst the direct effect of plant height on grain screenings was very small (-0.06). Strong direct influences of LN_L (-0.29) and GN_N (0.38) on grain screenings were detected, even though both these traits were poorly correlated with grain screenings. GFD was strongly negatively correlated with DAE_N ($r = -0.50$; $p<0.001$) but showed no direct effect on grain screenings.

DISCUSSION

The observation that long BVP varieties in southern Australia produce higher screenings than short BVP varieties has resulted in malting barley breeders actively selecting against long BVP genotypes in their breeding programs. Pathway analysis of the phenological characteristics influencing grain screenings in the population derived from VB9104/Chariot, which segregates for relative BVP, indicates BVP, as measured by LN_L, is negatively related to grain screenings (Table 1). That is, increasing BVP provides a mechanism for reducing grain screenings if the indirect effects associated with BVP can be avoided. Pathway analysis also confirmed GN_N had a large, direct and positive effect on increasing grain screenings. The correlation between LN_L (BVP) and GN_N was relatively weak, with an early July sowing date, indicating the potential to select for long BVP genotypes, with relatively low grain numbers per spike and plump grain size. It is expected the correlation between grain numbers per spike and BVP would increase with delayed sowing although it is unlikely growers in the medium to low rainfall districts of southern Australia would wish to sow later than early July. However, the potential for yield increase through enhanced grain numbers per spike will be limited by an increased propensity for high grain screenings.

In the case of plant height, pathway analysis indicates peduncle length has a greater influence on grain size than does plant height. Although peduncle length and plant height are strongly correlated ($r=0.66$; $p<0.001$), plant height has little direct influence on grain size whilst peduncle length is strongly associated with a reduction in grain screenings. Selection for longer peduncle, when selecting amongst semi-dwarf germplasm, should improve the efficiency of identifying large grain semi-dwarf varieties.

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Table 1. Direct and indirect genetic effects of physiological parameters on grain screenings for the population derived from the cross VB9104 X Chariot.

Character	Direct Effect	Indirect effect via							Total correlation (direct + indirect) with grain screenings
		Days to Awn Emergence (Normal daylength)	Days to Awn Emergence (Long Days)	Leaf Number (Long Days)	Grain Fill Duration	Grain Number (Long Day)	Plant Height	Peduncle Length	
Days to Awn Emergence (Normal daylength)	0.19		0.03	-0.09	-0.06	0.11	0.00	0.14	0.30
Days to Awn Emergence (Long Days)	0.07	0.08		-0.25	-0.01	0.09	0.00	0.11	0.09
Leaf Number (Long Days)	-0.29	0.06	0.06		-0.01	0.09	0.01	0.15	0.07
Grain Fill Duration	0.12	-0.09	-0.01	0.02		-0.10	0.01	0.04	-0.01
Grain Number (Normal Days)	0.38	0.05	0.02	-0.07	-0.03		-0.02	-0.17	0.12

Plant Height	-0.04	0.01	0.00	0.04	-0.03	0.14		-0.34	-0.23
Peduncle Length	-0.51	-0.05	-0.01	0.09	-0.01	0.13	-0.03		-0.40