Heredity **82** (1999) 415–421 *Received 16 September 1998, accepted 1 December 1998*

The role of ecophysiological models in QTL analysis: the example of specific leaf area in barley

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Crop modelling has so far contributed little to the genetic analysis of a quantitative trait. This study illustrates how a simple model for crop phenological development, which assumes that crop development rate is affected by daily effective temperature, can assist the identification of Quantitative Trait Loci (QTLs), using specific leaf area (SLA) in barley as an example. The SLA was measured in a field experiment six times during the growing season of 94 recombinant inbred lines (RILs) derived from a cross between cultivars Prisma and Apex. Of the six measurements, one was conducted at the same physiological age for all RILs (at flowering), four were undertaken at specific chronological days prior to flowering, and the last one was taken at 14 days after flowering. When the measured SLA was directly used as the quantitative trait, one to three QTLs were detected for SLA at each measurement time. The major dwarfing gene *denso* segregating in the population was found to affect SLA strongly at all measurement times except at flowering. If SLA of the different RILs was corrected for differences in physiological age at the time of measurement, by the use of the crop development model, QTLs were detected for SLA at only three stages. Furthermore, the effect of the *denso* gene was no longer significant during the preflowering stages. The effect of the *denso* gene detected in the first instance was therefore the consequence of its direct effect on the duration of the preflowering period. This demonstrates the important role that crop development models can play in QTL analysis of a trait that varies with developmental stage. Potential uses of ecophysiological crop growth models in QTL analysis are briefly discussed.

Keywords: crop growth model, *Hordeum vulgare*, quantitative trait loci (QTLs), specific leaf area.

Introduction

The advent of DNA-based molecular markers (e.g. Botstein *et al*., 1980; Vos *et al*., 1995) and new statistical methods (e.g. Lander & Botstein, 1989; Jansen, 1993; Jansen & Stam, 1994) has revolutionized quantitative genetics. They have made it possible to localize polygenes controlling quantitative traits and study the effect of individual genes on the trait, which was difficult in classical quantitative genetics. The acronym QTLs, which stands for Quantitative Trait Loci, has come to refer to genes for a quantitative trait. Numerous studies have been reported on identification of QTLs for various quantitative traits in humans, animals and plants.

QTL analysis in agricultural crops has largely been confined to easily measured traits such as plant height, earliness, yield and its components, economically important quality traits, and resistance to biotic and abiotic stresses. Recently, awareness has been growing of the need for the genetic mapping of physiological traits in crops (e.g. Ellis *et al*., 1997). Not only does mapping provide unequivocal answers to a range of physiological questions, it can also deal with questions that simply cannot be addressed by conventional physiological approaches. For instance, Simko *et al*. (1997) demonstrated that QTL mapping generated new insight into a causal relationship between potato tuber dormancy and abscisic acid content that would have been difficult to obtain by conventional correlation tests.

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An important advance made in crop physiology over the last decades is the development of process-based ecophysiological crop growth models (Loomis *et al.*, 1979). These models are based on integrated knowledge from various disciplines, and are now being increasingly applied in problem-orientated agricultural research (Boote *et al.*, 1996). One of the applications is the explanation of differences in yield potential of genotypes on the basis of individual physiological parameters, and the use of this knowledge for evaluating and designing plant types (Kropff *et al.*, 1995). This is possible because their parameters can be used to mimic genetic characteristics of plants when crop growth models become more mechanistic and comprehensive (Boote *et al.*, 1996). As values of these parameters are genotype-specific, they are often referred to as 'genetic coefficients' (Hoogenboom *et al.*, 1997), reflecting the awareness that the variation of these parameters is under genetic control (Stam, 1996). We have recently demonstrated that techniques for QTL analysis can be eminently suitable for elucidating the inheritance of a specific model parameter as a special type of quantitative physiological trait (Yin *et al.*, 1999).

There are a number of problems, however, associated with the existing approaches to QTL analysis, such as weak precision in positioning QTL, difficulty of estimating the true number of QTLs, and so on (Kearsey & Farquhar, 1998). Statisticians and quantitative geneticists are exploring new approaches that could provide better accuracy in QTL analysis. But it would seem unlikely that any great increase in reliability can be achieved, and at best some enhanced precision of the tests of significance can be seen (Kearsey & Farquhar, 1998). Support from other disciplines for an improved QTL analysis therefore might become important and should be explored.

Crop growth modelling has so far contributed little to the QTL analysis of a quantitative trait. In this paper, we attempt to show the ability of a crop growth model to assist QTL analysis, using the example of specific leaf area (SLA) in spring barley. SLA is leaf area per unit leaf dry weight, and thus is a crop trait characterizing leaf thickness. It is also an important parameter in crop growth models, both for calculating leaf photosynthesis and for estimating leaf area development (Boote *et al.*, 1996). Its value often varies with developmental stages in many crops, including barley (Grashoff & d'Antuono, 1997). QTLs identified for their genetic variation may therefore be stage-dependent. We show here how a simple model for crop development is useful for QTL analysis of this trait in barley.

Materials and methods

The mapping population and the denso *dwarfing gene*

A population of 94 recombinant inbred lines (RILs) was produced by eight generations of single-seed descent from a cross of two-row spring barley cultivars Prisma and Apex. The two parents are commercial cultivars in the Netherlands. Prisma is shorter than Apex, largely because of a recessive dwarfing gene called *denso* present in Prisma. The *denso* gene, conferring the distinctive prostrate juvenile growth habit (Haahr & von Wettstein, 1976), has been mapped on the long arm of chromosome 3(3H) as a morphological marker (Barua *et al.*, 1993; Laurie *et al.*, 1993; Bezant *et al.*, 1996). In the AFLP marker map constructed from the Prisma × Apex RIL population, the *denso* gene was mapped at the position 126.4 cM of chromosome 3(3H) (Yin *et al.*, 1999). This gene has been found to be associated with a number of traits (Barua *et al.*, 1993; Laurie *et al.*, 1993; Bezant *et al.*, 1996).

The experiment

The 94 RILs were examined in a field experiment conducted on alluvial clay soil in Wageningen (52°N latitude), the Netherlands. Crops were sown on 2 April 1997 and grown under optimal management conditions. Fertilizers (104 kg N, 65 kg P_2O_5 and 60 kg K_2O ha^{-1}) were all applied on the day before sowing. Plants were grown in plots of 10 rows; the rows were 8 m long and the plants were spaced at 13 cm. A randomized incomplete block design was used, with two replicates for each RIL.

Dates for three development stages (emergence, flowering and maturity) were recorded for each RIL. SLA during growth was determined by periodical destructive sampling. Sampling was undertaken at 17 days after emergence (DAE), 27 DAE, 38 DAE, 50 DAE, flowering, and 14 days after flowering (DAF). Green leaf blade area was measured with a LI-1000 leaf area meter (LI-COR Inc., USA). Green leaf blade dry matter was determined after oven-drying at 105°C for at least 15 h. SLA was determined as leaf area divided by leaf dry matter.

Data analysis

The QTL analysis was carried out using MAPQTL 3.0 (van Ooijen & Maliepaard, 1996), based on the AFLP marker map described by Yin *et al.* (1999). Initially, the conventional interval mapping method (Lander &

Botstein, 1989) was performed at 2 cM intervals to identify possible QTLs. Secondly, a more sophisticated QTL mapping model, the MQM mapping method (Jansen, 1993; Jansen & Stam, 1994), was used. In this method, background markers are selected to take over the role of the putative QTLs as cofactors to reduce the residual variance. In our analysis, background markers closest to the indicated region of putative QTLs (LOD ≥ 2.5) were gradually added as cofactors, until no further indicated QTL was found. A threshold LOD value of 3.0 was used to declare the presence of a QTL. Regions with LOD between 2.5 and 3.0 were considered as 'suggestive' for QTLs.

First, the analysis was performed using data of SLA measured at each sampling time. As both flowering and maturity dates were different among RILs (Yin *et al*., 1999), physiological age or developmental stage (DS) differed among RILs at a given sampling date. The QTL analysis was therefore performed secondly using SLA corrected for the same DS of RILs. The correction was conducted by a linear interpolation between the two consecutive measurements based on the following barley development model.

In the model, the DS is defined to have the dimensionless value of 0 at emergence, 1 at flowering and 2 at maturity. The value of DS at any other time is calculated as accumulated daily development rates from emergence. Daily development rate is assumed to increase proportionally with the effective temperature from a base value, 0°C (Dofing, 1997), up to an upper limit, 26°C (Hodges & Ritchie, 1991), above which the rate remains constant. Daily effective temperature is estimated as the average of hourly effective temperatures, and the hourly temperature is estimated from daily maximum and minimum temperature by a sine function assuming that the daily maximum temperature occurs at 14.00 h each day (Yin *et al*., 1997).

Results

Measured values of SLA showed significant differences among RILs ($P < 0.01$) for all sampling times except for the SLA at the 50 DAE sampling ($P > 0.10$). As there is no significant difference in SLA between replicates, the average value of the two replicates was used for QTL analysis.

There were two QTLs detected for SLA at 17 DAE, one for 27 DAE, 38 DAE, flowering and 14 DAF, respectively, by the use of the interval mapping method (Table 1). Two additional minor QTLs for SLA at 14 DAF, one for 17 DAE and one for 38 DAE were detected by the use of the MQM method.

For the time at 50 DAE at which the measured SLA did not differ significantly among RILs, there was only an indication of a marginally significant QTL at the position of the *denso* gene (LOD = 2.44). For other measurement times except for flowering, a much more significant QTL (LOD = 4.25–9.01) was found at or in close proximity to the *denso* locus. The importance of the *denso* locus for the SLA measured at different times is further highlighted in Fig. 1. The additive effect of this gene on SLA varied with times, from negative before flowering to a positive value of 1.485 $m^2\ kg^{-1}$ at 14 DAF (Fig. 1). Plotting mean SLA in the sequence of measurement for the two allelic classes of the *denso* locus shows that SLA increased with stages up to flowering

Table 1 QTLs identified for specific leaf area (SLA) at different measurement times in the 'Prisma' × 'Apex' barley population. Data given in the table are from the MQM method. QTLs marked with an asterisk are detected only by the MQM method, otherwise by both the MQM and interval mapping methods. QTLs with LOD < 3.0 are shown in italics and are considered as 'suggestive'

Time of measurement	Chromosome	cM[a]	LOD	Add. effect[b]	Var. (%)[c]
17 DAE	1(7H)*	142.3	3.05	0.270	10.2
	3(3H)	130.4	4.25	–0.380	20.2
	5(1H)	104.9	4.31	0.330	14.9
27 DAE	3(3H)	126.4	9.01	–0.885	35.7
38 DAE	*2(2H)**	*18.9*	*2.97*	*0.990*	*15.2*
	3(3H)	126.4	6.45	–1.205	22.8
50 DAE	*3(3H)*	*126.4*	*2.44*	*–0.995*	*11.3*
Flowering	4(4H)	4.0	3.39	0.825	17.3
14 DAF	3(3H)	125.2	9.01	1.560	35.8
	*4(4H)**	*2.0*	*2.60*	*0.785*	*8.9*
	*7(5H)**	*92.9*	*2.50*	*–0.685*	*6.8*

[a] The position (in cM) of QTL in the marker map described by Yin *et al*. (1999).
[b] The QTL additive effect = (mean of the 'Prisma' allele – mean of the 'Apex' allele)/2.
[c] The percentage of phenotypic variation accounted for by each QTL.

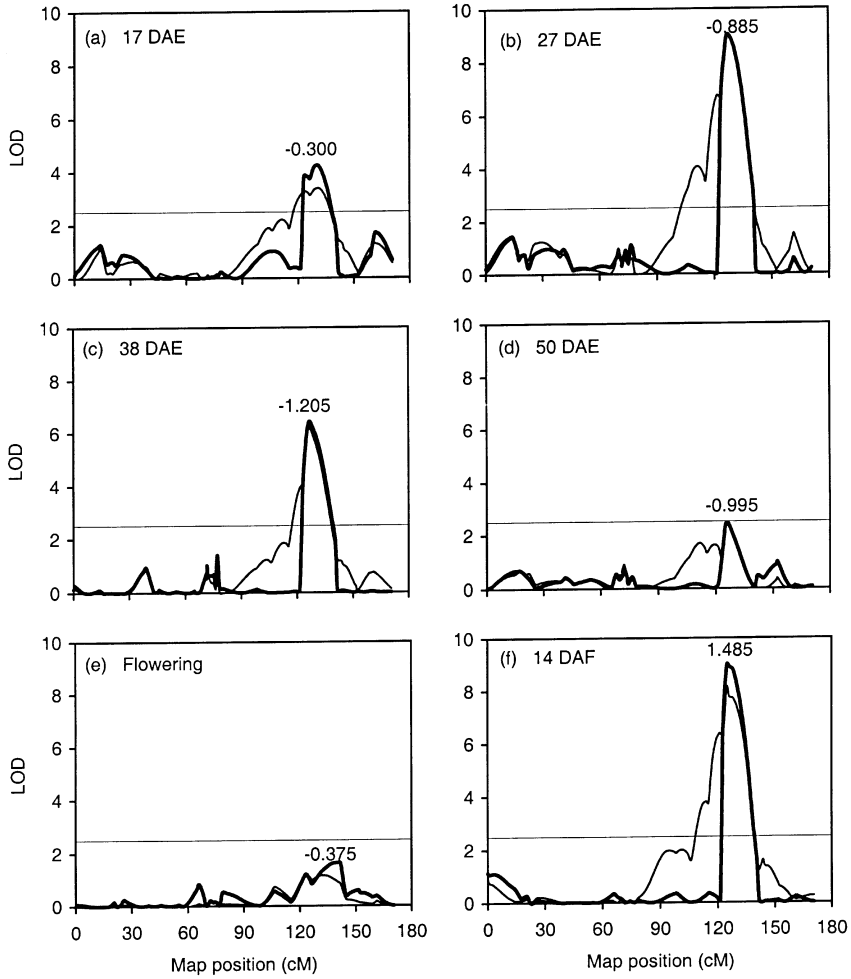

Fig. 1 Plot of LOD scores (the thin curve for the interval mapping and the thick one for the MQM method) over chromosome 3(3H) for SLA measured at different times in the 'Prisma' × 'Apex' barley population. The value shown on the peak of the curve is the additive effect, estimated from the MQM method, of the *denso* locus which has been mapped at 126.4 cM of the chromosome in the marker map used in this study. The horizontal line at a height of 2.5 indicates the LOD threshold for the presence of a QTL.

for both groups, beyond which SLA remained relatively constant for genotypes with the 'Prisma' allele but declined sharply for those with the 'Apex' allele (Fig. 2). Figure 2 also shows that SLA was higher in 'Apex' than 'Prisma' allele genotypes before flowering.

A previous report had shown that the duration from emergence to flowering was strongly affected by the *denso* gene and that the 'Prisma' allele was associated with the late flowering (Yin *et al.*, 1999). Therefore, a given physiological stage would have been at a later DAE for the 'Prisma' allele genotypes than the 'Apex' allele genotypes. Values of SLA corrected by linear interpolation to the same DS were therefore used in the subsequent QTL analysis. Developmental stages of 0.20, 0.35, 0.50, 0.80, 1.00 and 1.28, corresponding roughly to the six measurement times, were used to represent the results. Use of other DS values essentially yielded similar results.

For the corrected SLA, a total of only three QTLs was detected by the interval mapping, one each for the DS 0.35, 1.00 and 1.28, respectively (Table 2). Two additional QTLs, of which one was for the DS 0.35 and the other for the DS 1.28, were suggested by the MQM method. There was no QTL found for the DS 0.20, 0.50 and 0.80, and therefore, no information is given in Table 2 for these stages. For all the QTLs detected, the increasing allele was from Prisma (Table 2). The effect of the *denso* locus, at which the increasing allele was found to derive from Apex when no correction was made (Table 1), no longer had an impact on the corrected SLA before flowering (Fig. 3). The apparent effect of the *denso* gene on SLA shown in Fig. 1 therefore results indirectly from the effect of *denso* on the preflowering duration.

Discussion

QTL analysis is now increasingly used to clarify the genetic basis of various physiological traits (e.g. Ellis *et al.*, 1997; Simko *et al.*, 1997), including those physiological parameters used in process-based dynamic crop growth models (Yin *et al.*, 1999). Unlike conventional quantitative traits (such as plant height, earliness, yield and its components, quality and resistance traits),

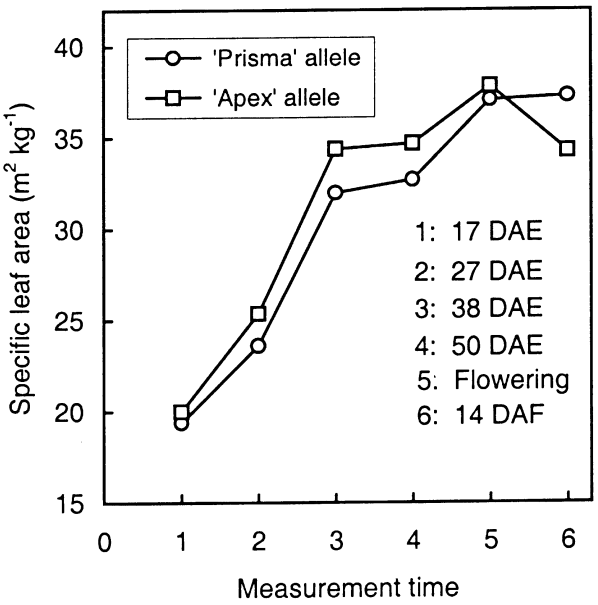

Fig. 2 Mean values of SLA at different measurement times for barley genotypes with the 'Prisma' allele and those with the 'Apex' allele at the *denso* locus.

physiological traits used in ecophysiological models are often dynamic by nature, varying with development stage. The analysis of this type of trait has received little attention from geneticists. Using SLA as an example, we showed here that we did find many QTLs if the analysis was based on SLA measured on the same day for all individuals in a mapping population (Table 1). A more logical measurement should, however, be conducted at the same DS for all individuals. This is practically impossible if the measurement needs to be made at stages that are not clearly marked by morphological changes such as tillering, spike initiation or flowering. Use of an ecophysiologically based crop development model to correct the measured data for the same DS becomes an obvious alternative for such analysis. We demonstrated here the usefulness of a simple development model, assuming that crop development rate is affected by temperature only, in determining quantitative trait values of SLA for QTL analysis. When data on SLA were rescaled by the use of the model to represent a measure at the same DS for all RILs, a very different result was obtained (Table 2). Obviously, attention should be given to the determination of quantitative trait values for the QTL analysis of this type of trait at the same DS. Besides SLA, other traits with a dynamic nature are leaf nitrogen content, coefficient for the fraction of assimilates partitioned into different growing organs, and some more integrated physiological traits such as water or radiation use efficiency.

The precision of QTL analysis depends on a number of factors such as population size, marker density and distribution, data quality and the QTL mapping method used. Despite considerable effort by statisticians, all the methods of QTL analysis yield essentially similar estimates of QTL locations and gene effects (Kearsey & Farquhar, 1998), although there is some improvement in the confidence interval of QTL locations when the more sophisticated methods, such as the MQM method of Jansen (1993) and Jansen & Stam (1994), are used (Figs. 1a,b,c,f and 3f). In general, the power to resolve the location of QTLs is limited by population size and the genetic marker coverage of the genome (McCouch & Doerge, 1995). The fastest way to develop a complete marker map is by the use of AFLP markers (Vos *et al.*, 1995) supplemented with other markers such as RFLP (Botstein *et al.*, 1980) and SSR (Rafalski & Tingey, 1993). There is always a compromise between population size and data quality, and it may be necessary to sacrifice population size to some extent in favour of the quality of both marker and trait data (McCouch & Doerge, 1995). This is especially the case for the genetic analysis of physiological traits, because measuring a physiological trait is often costly and time-consuming. Although improving the precision for QTL analysis is

Table 2 QTLs identified for specific leaf area (SLA) corrected for the same developmental stage in the 'Prisma' × 'Apex' barley population. Data given in the table are from the MQM method. QTLs marked with an asterisk are detected only by the MQM method, otherwise by both the MQM and interval mapping methods. QTLs with LOD < 3.0 are shown in italics and are considered as 'suggestive'

Developmental stage	Chromosome	cM[a]	LOD	Add. effect[b]	Var. (%)[c]
0.35	*3(3H)**	*33.7*	*2.50*	*0.425*	*13.6*
	7(5H)	*37.6*	*2.88*	*0.410*	*13.4*
1.00 (Flowering)	4(4H)	4.0	3.19	0.810	16.3
1.28	3(3H)	126.4	7.65	1.320	30.1
	*4(4H)**	*2.0*	*2.87*	*0.810*	*11.3*

[a] The position (in cM) of QTL in the marker map described by Yin *et al.* (1999).
[b] The QTL additive effect = (mean of the 'Prisma' allele − mean of the 'Apex' allele)/2.
[c] The percentage of phenotypic variation accounted for by each QTL.

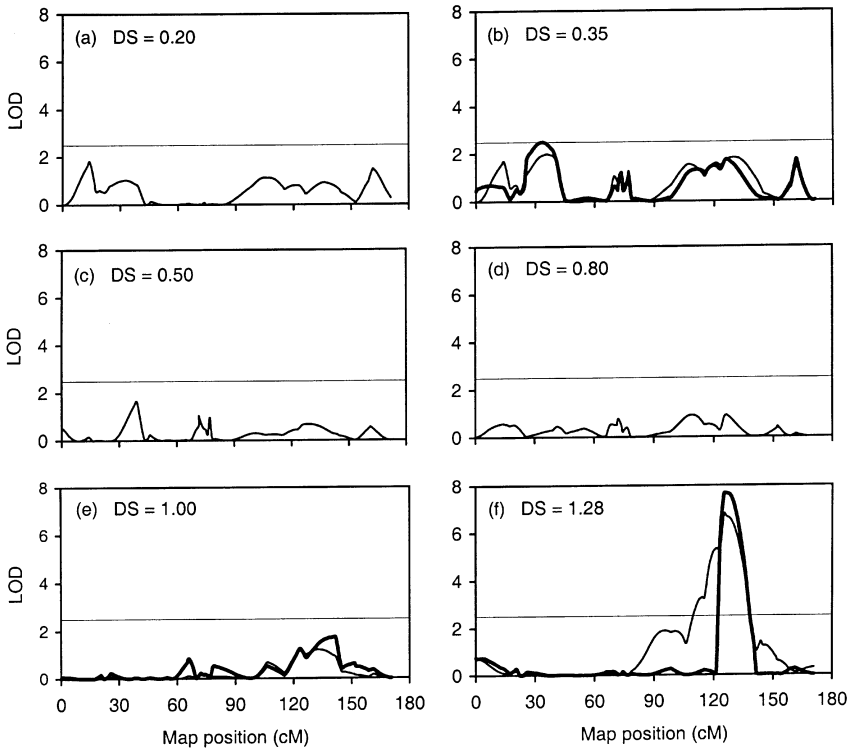

Fig. 3 Plot of LOD scores (the thin curve for the interval mapping and the thick one for the MQM method) over chromosome 3(3H) for SLA corrected at the same development stage (DS) in the 'Prisma' × 'Apex' barley population. The LOD scores are not shown for the MQM method in (a), (c) and (d) of this figure because no QTL was detected by the interval mapping for the corresponding stages. The horizontal line at a height of 2.5 indicates the LOD threshold for the presence of a QTL.

largely the task of quantitative geneticists and biometricians, the example presented in this study showed that it no longer remains the privilege of those specialists. Physiologists and crop modellers should play a role in guaranteeing the quality of data for trait values.

The heritability corresponding to an individual QTL largely determines whether the QTL can be detected or not (Kearsey & Farquhar, 1998). The detection of low heritability QTLs often depends on the test environment, because of large trait-by-environment interaction effects (e.g. Tinker *et al.*, 1996). The impact of environmental conditions has to be minimized to identify the true genetic effect. Crop development models separate different aspects of responses of flowering or maturity to photothermal environments (Yin *et al.*, 1997). Coefficients in a physiologically robust model are genetically determined and are not altered by environment, but predict flowering or maturity date of a genotype in a wide range of environments. If those conditions are met, the model is able to capture and to quantify the genotype × environment interaction (Roberts *et al.*, 1996). Similarly, ecophysiologically based crop growth models separate the different processes that determine yield ability and explicitly account for environmental effects on these processes (Bindraban, 1997). Parameters used in crop growth models are also known as 'genetic coefficients' (Hoogenboom *et al.*, 1997). It is expected that the QTLs, detected for the model parameters, will be environment-independent, and therefore that ecophysiological crop growth models can potentially be used to resolve QTL × environment interaction.

Acknowledgements

The work was supported by a 'Stimulans' subsidy from The Netherlands Organization for Scientific Research to the C. T. de Wit Graduate School for Production Ecology of Wageningen Agricultural University.

References

BARUA, U. M., CHALMERS, K. J., THOMAS, W. T. B., HACKETT, C. A., LEA, V., JACK, P. *et al.* 1993. Molecular mapping of genes determining height, time to heading, and growth habit in barley (*Hordeum vulgare*). *Genome*, **36**, 1080–1087.

BEZANT, J., LAURIE, D., PRATCHETT, N., CHOJECKI, J. AND KEARSEY, M. 1996. Marker regression mapping of QTL controlling flowering time and plant height in a spring barley (*Hordeum vulgare* L.) cross. *Heredity*, **77**, 64–73.

BINDRABAN, P. S. 1997. *Bridging the gap between plant physiology and breeding. Identifying traits to increase wheat yield potential using systems approaches.* PhD Thesis, Wageningen Agricultural University, The Netherlands.

BOOTE, K. J., JONES, J. W. AND PICKERING, N. B. 1996. Potential uses and limitation of crop models. *Agron. J.*, **88**, 704–716.

BOTSTEIN, D., WHITE, R. L., SKOLNICK, M. AND DAVIS, R. W. 1980. Construction of a genetic linkage map in man using

restriction fragment length polymorphisms. *Am. J. Hum. Genet.*, **32**, 314–331.

DOFING, S. M. 1997. Ontogenetic evaluation of grain yield and time to maturity in barley. *Agron. J.*, **89**, 685–690.

ELLIS, R. P., FORSTER, B. P., WAUGH, R., BONAR, N., HANDLEY, L. L., ROBINSON, D. *et al*. 1997. Mapping physiological traits in barley. *New Phytol.*, **137**, 149–157.

GRASHOFF, C. AND D'ANTUONO, L. F. 1997. Effect of shading and nitrogen application on yield, grain size distribution and concentrations of nitrogen and water soluble carbohydrates in malting spring barley (*Hordeum vulgare* L.). *Eur. J. Agron.*, **6**, 275–293.

HAAHR, V. AND VON WETTSTEIN, D. 1976. Studies of an induced high yielding dwarf-mutant of spring barley. In: *Proc. 3rd Int. Barley Genet. Symp., Garching, 1975*, pp. 215–218. Verlag Karl Thiemig, Munich.

HODGES, T. AND RITCHIE, J. T. 1991. The CERES-wheat phenology model. In: Hodges, T. (ed.) *Predicting Crop Phenology*, pp. 133–141. CRC Press, Boca Raton, FL.

HOOGENBOOM, G., WHITE, J. W., ACOSTA-GALLEGOS, J., GAUDIEL, R. G., MYERS, J. R. AND SILBERNAGEL, M. J. 1997. Evaluation of a crop simulation model that incorporates gene action. *Agron. J.*, **89**, 613–620.

JANSEN, R. C. 1993. Interval mapping of multiple quantitative trait loci. *Genetics*, **135**, 205–211.

JANSEN, R. C. AND STAM, P. 1994. High resolution of quantitative traits into multiple loci via interval mapping. *Genetics*, **136**, 1447–1455.

KEARSEY, M. AND FARQUHAR, A. G. L. 1998. QTL analysis in plants; where are we now? *Heredity*, **80**, 137–142.

KROPFF, M. J., HAVERKORT, A. J., AGGARWAL, P. K. AND KOOMAN, P. L. 1995. Using systems approaches to design and evaluate ideotypes for specific environments. In: Bouma, J., Kuyvenhoven, A., Bouman, B. A. M., Luyten, J. C. and Zandstra, H. G. (eds) *Eco-Regional Approaches for Sustainable Land Use and Food Production*, pp. 417–435. Kluwer, Dordrecht.

LANDER, E. S. AND BOTSTEIN, D. 1989. Mapping Mendelian factors underlying quantitative traits using RFLP linkage maps. *Genetics*, **121**, 185–199.

LAURIE, D. A., PRATCHETT, N., ROMERO, C., SIMPSON, E. AND SNAPE, J. W. 1993. Assignment of the *denso* dwarfing gene to the long arm of chromosome 3 (3H) of barley by use of RFLP markers. *Pl. Breed.*, **111**, 198–203.

LOOMIS, R. S., RABBINGE, R. AND NG, E. 1979. Explanatory models in crop physiology. *Ann. Rev. Pl. Physiol.*, **30**, 339–367.

MCCOUCH, S. R. AND DOERGE, R. W. 1995. QTL mapping in rice. *Trends Genet.*, **11**, 482–487.

RAFALSKI, J. A. AND TINGEY, S. V. 1993. Genetic diagnostics in plant breeding: RAPDs, microsatellites and machines. *Trends Genet.*, **9**, 275–279.

ROBERTS, E. H., QI, A., ELLIS, R. H., SUMMERFIELD, R. J., LAWN, R. J. AND SHANMUGASUNDARAM, S. 1996. Use of field observations to characterise genotypic flowering responses to photoperiod and temperature: a soyabean exemplar. *Theor. Appl. Genet.*, **93**, 519–533.

SIMKO, I., MCMURRY, S., YANG, H. M., MANSCHOT, A., DAVIES, P. J. AND EWING, E. E. 1997. Evidence from polygene mapping for a causal relationship between potato tuber dormancy and abscisic acid content. *Pl. Physiol.*, **115**, 1453–1459.

STAM, P. 1996. Quantitative genetics: a moving frontier to the benefit of crop production. In: *Annual Report for 1995*, pp. 6–9. The C. T. de Wit Graduate School for Production Ecology, Wageningen Agricultural University, The Netherlands.

TINKER, N. A., MATHER, D. E., ROSSNAGEL, B. G., KASHA, K. J., KLEINHOFS, A., HAYES, P. M. *et al*. 1996. Regions of the genome that affect agronomic performance in two-row barley. *Crop Sci.*, **36**, 1053–1062.

VAN OOIJEN, J. W. AND MALIEPAARD, C. 1996. *MapQTL (tm) version 3.0: Software for the calculation of QTL position on genetic maps*. CPRO-DLO, Wageningen, The Netherlands.

VOS, P., HOGERS, R., BLEEKER, R., REIJANS, M., VAN DE LEE, T., HORNES, M. *et al*. 1995. AFLP: a new technique for DNA fingerprinting. *Nucl. Acids Res.*, **23**, 4407–4414.

YIN, X., KROPFF, M. J., HORIE, T., NAKAGAWA, H., CENTENO, H. G. S., ZHU, D. AND GOUDRIAAN, J. 1997. A model for photothermal responses of flowering in rice. I. Model description and parameterization. *Field Crops Res.*, **51**, 189–200.

YIN, X., STAM, P., DOURLEIJN, C. J. AND KROPFF, M. J. 1999. AFLP mapping of quantitative trait loci for yield-determining physiological characters in spring barley. *Theor. Appl. Genet.* (in press).