# CHAPTER 8

# MODELLING GENOTYPE × ENVIRONMENT × MANAGEMENT INTERACTIONS TO IMPROVE YIELD, WATER USE EFFICIENCY AND GRAIN PROTEIN IN WHEAT

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**Abstract**. In breeding trials the complexity of interactions of genotypes (G) with their environment (E) requires extensive field experiments at many locations and seasons to test new traits. Management (M) treatments such as planting density and fertilizer supply are often neglected in such experiments. Moreover, several traits (e.g., increased specific leaf area and faster early root growth) are often changed simultaneously in new genotypes (e.g., early vigour lines) with the contribution of individual traits remaining uncertain.

Using a well-tested simulation model can assist in exploring the impact of new genotypes and the contribution of individual physiological traits on yield by simulating genotypes across many locations, seasons and a range of management options. Recent advances in simulating grain protein concentrations in wheat also allow the analysis of the impact of yield-related physiological traits on grain protein percentage. Simulation analyses have shown that trait effects on yield are location- and season-specific. The contribution of traits to yield varies with growing-season rainfall and soil types. In Mediterranean-type environments, traits of increased specific leaf area and faster early root growth improve grain yields and water use efficiency on low water-holding-capacity soils, but can be detrimental on better water-holding-capacity soils. Increased specific leaf area is often only expressed if N management is adjusted while the positive effect of faster early root growth in sandy soils diminishes with increasing N supply. The sum of individual traits incorporated in early vigour (that is, increased specific leaf area, faster early root growth, earliness, reduced radiation use efficiency) and increased transpiration efficiency is often not the same as the effects when the traits are combined. Another trait for an increased capacity for storing water-soluble carbohydrates can be beneficial for yield and water use efficiency in terminal-drought environments, but is not as effective when growth is limited by water or nutrients during anthesis.

The response of grain protein to yield-related trait modification (such as increased grain-filling rate) is usually negatively related to the response to grain yield. However, under combined water and N limitation, simulations indicated that this negative linear relationship can become non-linear, suggesting that a lower potential yield in such environments might improve grain protein concentrations without reducing the attainable yield.

## INTRODUCTION

In many environments, water supply is a major source of variability in crop yields (Ritchie 1983). The seasonal water use of a wheat crop consists of both crop transpiration and soil evaporation (French and Schultz 1984), with the latter varying between 14% (Angus et al. 1980) and 75% (Cooper et al. 1987) of total water use. Total water use or total evapotranspiration (ET) by a crop can vary substantially due to the limited water available from soil water storage or due to limited rainfall. It can also vary as a result of variation in crop transpiration resulting from management, such as nutrient supply (Shepherd et al. 1987) and sowing time (Connor et al. 1992), or from use of different species (Gregory et al. 1992) or cultivars (Richards and Townley-Smith 1987). For many years, specific traits have been sought to improve water use efficiency and grain yields in rain-fed agriculture (Turner 1986; Whan et al. 1991; Reynolds et al. 1996; Miralles and Richards 1999; Turner and Asseng 2005). However, incorporating new traits into a crop takes 10 to 12 years, and only then it will be known if a new trait has been effective in improving water use efficiency and yield in a specific environment. Simulation modelling can offer an alternative in testing traits in a computer-based experiment across a number of environments, soil types and growing seasons to evaluate the potential benefits from breeding for specific traits. To carry out such simulation experiments, a model needs to be comprehensive, must take into consideration the dynamics of crop-soil-weather interactions and modelled growth processes need to be based on sound physiological principles.

This chapter demonstrates how a crop-soil simulation model was used in evaluating traits in improving yield and water use efficiency (WUE in kg grain yield $mm^{-1}$ ET) and grain protein concentration of rain-fed wheat in a Mediterranean-type climate.

## APSIM-NWHEAT MODEL

The Agricultural Production Systems SIMulator (APSIM) (Keating et al. 2003) for wheat (*Triticum aestivum* L.) (APSIM-Nwheat version 1.55s) is a crop simulation model, consisting of modules that incorporate aspects of soil water, nitrogen, crop residues, crop growth and development and their interactions within a crop-soil system that is driven by daily weather data. A detailed description of APSIM-Nwheat is given by Asseng (2004).

APSIM-Nwheat has been tested extensively against field measurements in various studies under a large range of growing conditions (Probert et al. 1995; 1998; Asseng et al. 2000; 2004) and in particular in the Mediterranean climatic regions of Western Australia (Asseng et al. 1998a; 1998b; 2001b). The model was able to reproduce grain yields over the entire range of possible wheat yields from < 0.5 to > 13 t ha$^{-1}$ (Figure 1A).

Recent advances in simulating grain protein concentrations in wheat now allow the analysis of the impact of yield-related physiological traits on grain protein concentration. A comparison of simulated versus observed grain protein contents (in %) is summarized in Figure 1B.
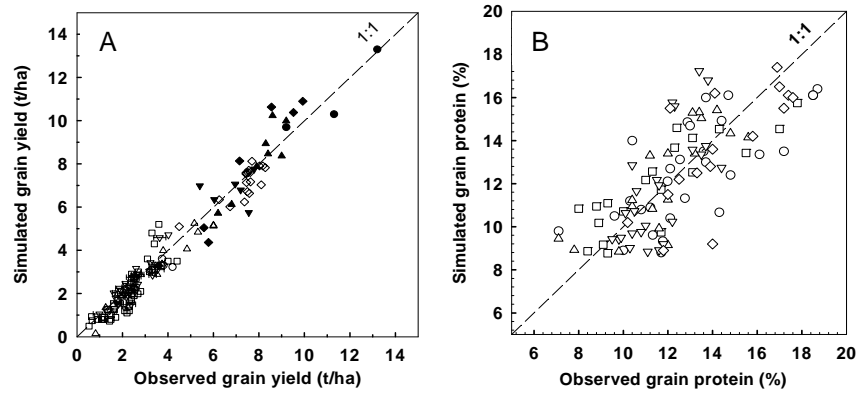
**Figure 1. (A)** *Simulated versus observed grain yield for Western Australia data set I (Asseng et al. 1998b), (▽); Western Australia data set II (Asseng et al. 2002), (□); New South Wales (Asseng and Van Herwaarden 2003), (○); Gatton, Queensland (Asseng et al. 2002), (△); Lincoln, New Zealand (Asseng et al. 2004), (◆); Xiangride, China (Asseng et al. 2002), (●); Arizona, USA (Asseng et al. 2004), (▲); Obregon Mexico (Asseng et al. 2004), (▼); Polder and Wageningen, The Netherlands (Asseng et al. 2000), (◇). (B) Simulated versus observed grain protein (%) for locations in Western Australia (○, ▽, ◇), New South Wales (□) and The Netherlands (△)(after Asseng et al. 2002)*

## MEDITERRANEAN ENVIRONMENT

In the Mediterranean environment of Western Australia, rainfall is very variable, with between two thirds and three quarters of the total annual rain falling in the cropping season. Rainfall between April and October is considered to be the effective growing-season rainfall and ranges in average from 200 mm in the East to 400 mm in the West. The sowing date of wheat varies from late April to the end of July depending on when the first significant rainfall occurs after the dry summer. Depending on sowing date and phenology, wheat crops flower between September and October, and grain filling is often affected by high temperatures and terminal water shortage before maturity in November and December. In addition, soils in the Western Australian wheat belt have a low plant-available water-holding capacity (PAW) in the root zone (PAW: 50–120 mm). As a consequence, grain yields on average are about 2 t ha$^{-1}$, well below average grain yields from temperate environments (Turner 2004).

## MODELLING GENOTYPE × ENVIRONMENT × MANAGEMENT (G×E×M) INTERACTIONS

A number of traits have been suggested to improve yields in the Mediterranean-type environment. A set of these are combined in early vigour as a combination of increased specific leaf area (SLA), faster early root growth, earliness and reduced

radiation use efficiency (RUE) (when early vigour is achieved through increased SLA with less N per unit leaf area), which when linked with increased transpiration efficiency (TE) are considered to improve yields mainly through improved water use efficiency (Condon and Richards 1993). Another trait, an increased capacity to store water-soluble carbohydrate, has been suggested as being particularly efficient in improving yield in terminal-drought environments such as Mediterranean-type environments (Setter et al. 1998). A trait for increased grain filling rate, which has been suggested as increasing yields of lupin in terminal-drought environments (Palta et al. 2004), has also been simulated to investigate its impact on the grain protein content of wheat.

When modelling G×E×M interactions with APSIM-Nwheat, a specific trait was altered in the model and then compared with the unaltered crop across more than 80 seasons using contrasting soils appropriate to the Mediterranean-type region of Western Australia; a sand with 55 mm PAW and a clay with 109 mm PAW and a range of N management options. Trait effects were then analysed individually and in combination with other traits.

## THE IMPACT OF SOIL TYPE, N SUPPLY AND RAINFALL ON TRAIT EXPRESSION

In a simulation study, Asseng et al. (2003) showed that on a sandy soil, doubling specific leaf area increased yields by 15%, but only when sufficient N was supplied. On a clay soil, doubling SLA reduced yield under low N supply, but was marginally beneficial with a high N supply. A trait for faster early root growth, increased grain yields by more than 15% on a sandy soil with low N input by assisting the crop to capture more N from deeper in the soil, but this trait became less important with high N input on a sand and gave little benefit on average on a clay (Figure 2A, C). Traits of earliness, increased transpiration efficiency (TE) and reduced radiation use efficiency all affected yield, but their impact varied with soil type and N supply. WUE usually changed in parallel to yields (Figure 2B, D) as the impact of these traits on ET was often less than on yield. For example, increased SLA stimulated growth and the increased crop water use was then offset by reduced soil evaporation due to the increased leaf cover of the soil.

When the traits of increased SLA, faster early root growth, earliness, reduced RUE and increased TE were combined, the effect on yield and WUE was greater than the sum of the individual yield effects due to non-linear interactions among the traits (Figure 2). For example, with low N on sand, the sum of the individual trait effects was 18% yield increase, while the combined trait effect was 32%.

On a clay soil, the simulated effect of the combined traits on yield in the low-rainfall region increased yields by 30% on average (Figure 3A). With high N input the average yield advantage remained at 30% as rainfall increased, but with low N input the average yield advantage was reduced to 10%. However, on a deep sand the average yield was increased by 20–30% by the combined set of traits with low N input and by about 20% when the N input was high across all rainfall environments (Figure 3B).
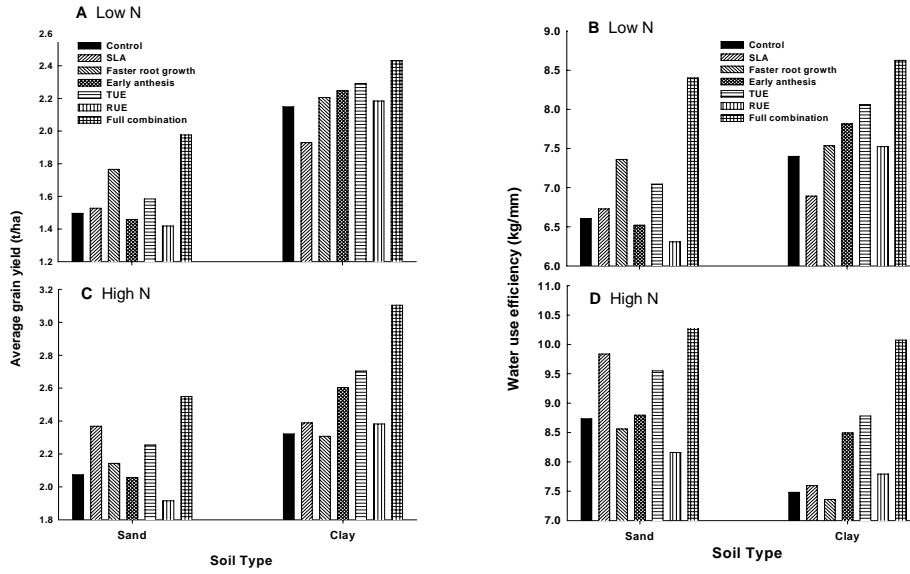
*Figure 2. Simulated average effects of individual traits (standard, increased SLA, faster early root growth, earliness, increased transpiration efficiency (TE), reduced radiation use efficiency (RUE) and all traits in combination) on (A, C) wheat yields and (B, D) WUE on a deep sand and a clay soil with (A, B) low N and (C, D) high N fertilizer input, for a medium-rainfall location in Western Australia (322 mm mean growing-season rainfall)*
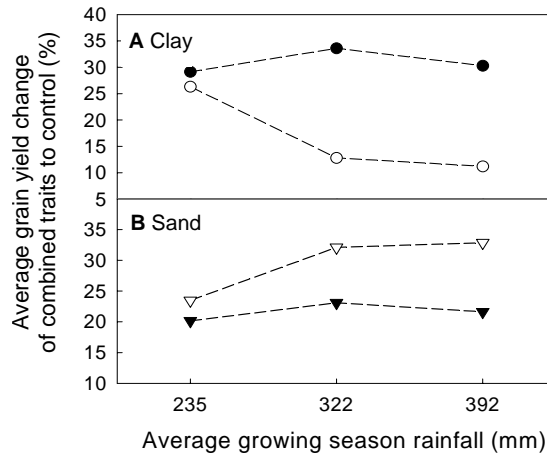


*Figure 3. Simulated relative average yield increases for wheat with the full compliment of traits associated with early vigour and high TE in three rainfall regions of Western Australia with low N (open symbols) and high N (filled symbols) fertilizer supply on (A) a clay soil and (B) a deep sand (after Asseng et al. 2003)*

## THE IMPACT OF SEASONAL RAINFALL DYNAMICS ON GENOTYPE EXPRESSION

Increasing the capacity to accumulate assimilates in the pre-grain-filling period for later remobilization by 20% in a simulation experiment over 78 growing seasons, increased yields by up to a maximum of 12% in moderate seasons, but had little effect in poor or very good seasons. This was because several factors affected the amount of carbohydrates stored rather than the storage capacity itself, namely: (i) poor growth due to water or N deficits in the weeks prior to and shortly after anthesis (when most of the assimilates are stored for later remobilization) (Figure 4, Phase A); (ii) a small number of kernels due to little growth for most of the pre-anthesis season and hence poor sink demand by grains (Phase A); or (iii) a high photosynthetic rate during grain filling that is sufficient to fill grains (Phase C). Thirty-five of the 74 seasons shown in Figure 4 (note 4 seasons of the 78 simulated had no sowing opportunity due to lack of rainfall) resulted in > 5% yield increase due to the increased storage capacity. Further analysis of the simulated data revealed that 63% of >5% yield increases were in seasons with above average biomass accumulation at anthesis. Forty-nine percent of the yield increases > 5% were associated with late sowing opportunities (later than the simulated long-term average) that often resulted in a shorter grain-filling period due to water shortage and high temperatures arising from the delayed flowing. Thus, the simulation suggests that increasing the potential storage capacity for remobilization increases grain yields under conditions of terminal drought when the growing conditions up to the start of grain filling are favourable. Increasing the supply of N in Phase C in Figure 4 increased yields with an increased storage capacity, suggesting that the yields were N-limited, rather than water-limited.

Since water use was little affected by changes in the storage capacity of water-soluble carbohydrates, WUE reflected the simulated yield and yield changes (Figure 4B).

## EFFECT OF GRAIN-FILLING RATE ON YIELD AND GRAIN PROTEIN CONCENTRATION

Using long-term historical weather records and simulating an increased yield potential by increasing the potential grain-filling rates resulted, as expected, in a large range of mostly negative but linear protein-yield relationships (Figure 5). A large proportion of these seasons had a combination of water and N limitations that gave the wide spread of lines. However, some non-linear relationships occurred in which, below a certain yield, grain protein decreased without a change in grain yield despite different potential grain-filling rates. In some cases, there was no change in simulated yield over the whole range of grain-filling rates but protein still declined. This unexpected result was caused by differences in dry-matter accumulation and N accumulation dynamics by the grain at the different potential grain-filling rates and a dependency of dry matter and N accumulation at extreme low and high rates (Asseng et al. 2002). In these years, the higher potential grain-filling rates initially
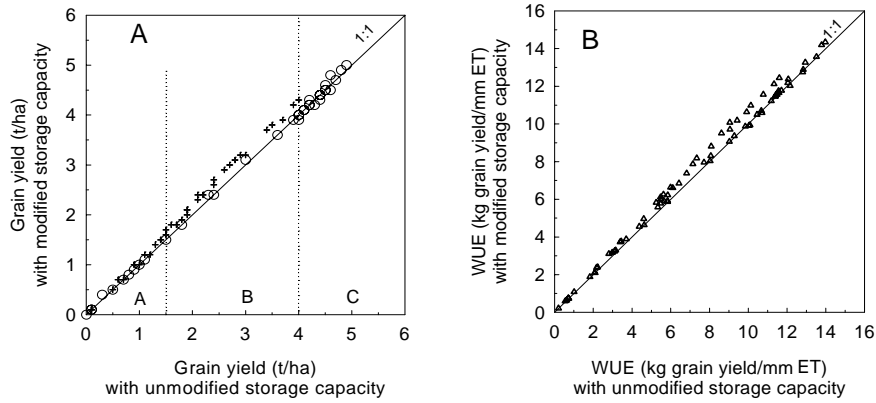
**Figure 4.** **(A)** *Simulated grain yields and* **(B)** *water use efficiency (WUE) with a 20% increased capacity to store pre-grain-filling assimilates for potential remobilization to the grain compared with an unmodified storage capacity at Barellan, New South Wales, with 90 kg N ha$^{-1}$, using weather records from 1915–1992. Yield change in* **(A)** *of >5% (+) and <5% (○). The diagonal shows the 1:1 line. In* **(A)** *the vertical lines separate different response scenarios. Phase A, dry years with yields of < 1.5 t ha$^{-1}$; Phase B, moderate years with a terminal drought and yields of 1.5–4.0 t ha$^{-1}$; and Phase C, wet years with yields of > 4 t ha$^{-1}$ (after Asseng and Van Herwaarden 2003)*
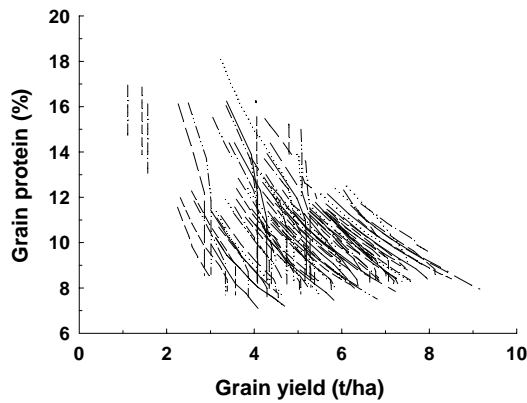


**Figure 5.** *Simulated relationship between grain protein percentage and grain yield with seven different potential grain-filling rates (rates increase with increasing yield or decreasing protein) for 104 years (lines connect the different potential rates, a range of different types of line is used for each year) at Kojonup (high-rainfall location), Western Australia, with 150 kg N ha$^{-1}$ (after Asseng and Milroy 2006)*

allowed a higher rate of dry-matter accumulation in the grain, but had no effect on the rate of N accumulation because it was limited by N supply. The higher filling rate resulted in an earlier depletion of the available carbohydrates and the crop then relied solely on the supply of carbohydrates from current photosynthesis, which was also low by this stage. This led to brief restrictions in N accumulation because of the limits on the ratio of grain N to dry-matter accumulation in the model. The shortfall in N accumulation remained until maturity. With a low grain-filling potential, grain filling continued at the potential rate for longer. Thus the N accumulation, which proceeded at the same rate as in the plants with a high filling rate, could also continue for longer. Eventually the accumulated grain dry matter reached the same mass as in the high-potential-rate scenario, but N accumulation had been restricted less frequently by the low rate of dry-matter accumulation. The result was an altered protein content but the same grain yield.

## DISCUSSION AND CONCLUSIONS

The analysis of trait effects on yield and WUE has indicated that yield and WUE of wheat crops in the Mediterranean-climatic region of Western Australia vary markedly depending on soil water-holding capacity, N management and rainfall amount. The degree of variation in yield and WUE is difficult to quantify from field experimentation alone. Thus, simulation modelling provides a powerful means of integrating all these factors, of linking these to traits, and when combined with long-term climatic data and regional soil information is able to markedly extend the interpretation possible from limited experimental studies. The results suggest that there is large potential for increasing yield and WUE through increased N application, in particular in the high- and medium-rainfall zones of Western Australia on soils with high water-holding capacity (Asseng et al. 2001a). Breeding for early vigour (increased SLA, faster early root growth, earliness, reduced RUE), together with increased TE, will further increase yields and WUE in this environment. The full combination of traits related to early vigour and increased TE can increase yields by up to 30% regardless of soil type. However, the different traits associated with early vigour and increased TE have been shown to have different impacts on yield depending on soil type, management and rainfall season. While the trait of faster early root growth could increase yields particularly with low N supply on a sandy soil, an increased SLA required high N fertilization for a positive impact on yield.

The simulation study with an increased capacity for storage of water-soluble carbohydrates highlighted that increasing the storage capacity may not always be effective in increasing grain yields even in a Mediterranean environment with frequent terminal water shortage. The analysis pointed out that the relative contribution of remobilization to grain yield depends primarily on source/sink interactions during grain filling in each environment and confirms results from shading experiments by Conocono (2002). If growth is restricted around anthesis due to lack of water or N resulting in a low grain number (Fischer 1985), then even if rainfall is low a small assimilate demand for total grain growth can be entirely met

by photosynthesis during grain filling (e.g., Palta and Fillery 1995) and results in little water use by the crop during grain filling (Asseng et al. 2001a). A high N supply and high water use before anthesis can result in a high assimilate demand during grain filling, but the high pre-anthesis water use can reduce water availability after anthesis if the post-anthesis rainfall is low (Fischer 1979). Therefore, increasing the storage capacity will not be effective if (i) growth shortly before and after anthesis, when most assimilates are accumulated for remobilization (Conocono 2002; Schnyder 1993) is limited by periods of drought; or (ii) when yield is not limited by water supply and it is N supply which limits yield. Additional yield increases of more than 10% were simulated in some seasons and selecting for larger storage capacity of soluble carbohydrates appears to be worthwhile for terminal-drought environments. The simulation experiment indicated that assimilates stored prior to the main storage period around anthesis can also be important for grain yields in some seasons where growth rates are high for the first part of the growing season but low during the second part starting well before anthesis. While genetic variation for storage of soluble carbohydrates in the period up to 14 days after anthesis has been demonstrated (Nicolas and Turner 1993), it still needs to be shown that genotypic variation exists for the ability to accumulate significant amounts of assimilate well before anthesis for remobilization during grain filling.

The variation between different seasons in the protein-yield curves with the increased potential grain-filling rate indicated a large impact of rainfall, and consequently water and water by N interaction, on this relationship. The simulated change in protein content with no change in grain yield in some seasons was unexpected, but can be explained by the model through an intermittently restricted carbohydrate supply that occurred at different frequency with the different grain-filling rates. Hence N accumulation, which is constrained by periods of low grain dry-matter accumulation, was interrupted to varying extents. The frequency of changes in protein content without change in yield was higher at low N supply and at low-rainfall locations (Asseng and Milroy 2006). From these responses it is hypothesized that a higher genetic grain protein potential can be achieved via a lower genetic yield potential without compromising the *achievable* grain yield under water- and N-limited conditions. Cultivars with moderate yield potential might therefore be more suitable for growth-limited environments: attaining a higher grain protein but still achieving the environmental yield potential.

In summary, the G×E×M analysis has shown that using a well tested simulation model is a powerful tool in exploring the impact of new genotypes and the contribution of individual physiological traits on yield and WUE by simulating the responses of genotypes or traits across many locations, seasons, soil types and management options.

## REFERENCES

Angus, J.F., Nix, H.A., Russell, J.S., et al., 1980. Water use, growth and yield of wheat in a subtropical environment. *Australian Journal of Agricultural Research,* 31 (5), 873-886.

Asseng, S., 2004. *Wheat crop systems: a simulation analysis.* CSIRO, Melbourne.

Asseng, S. and Van Herwaarden, A.F., 2003. Analysis of the benefits to wheat yield from assimilates stored prior to grain filling in a range of environments. *Plant and Soil,* 256 (1), 217-229.

Asseng, S. and Milroy, S.P., 2006. Simulation of environmental and genetic effects on grain protein concentration in wheat. *European Journal of Agronomy,* 25 (2), 119-128.

Asseng, S., Fillery, I.R.P., Anderson, G.C., et al., 1998a. Use of the APSIM wheat model to predict yield, drainage, and $NO_3$-leaching for a deep sand. *Australian Journal of Agricultural Research,* 49 (3), 363-377.

Asseng, S., Keating, B.A., Fillery, I.R.P., et al., 1998b. Performance of the APSIM-wheat model in Western Australia. *Field Crops Research,* 57 (2), 163-179.

Asseng, S., Van Keulen, H. and Stol, W., 2000. Performance and application of the APSIM Nwheat model in the Netherlands. *European Journal of Agronomy,* 12 (1), 37-54.

Asseng, S., Dunin, F.X., Fillery, I.R.P., et al., 2001a. Potential deep drainage under wheat crops in a Mediterranean climate. II. Management opportunities to control drainage. *Australian Journal of Agricultural Research,* 52 (1), 57-66.

Asseng, S., Turner, N.C. and Keating, B.A., 2001b. Analysis of water- and nitrogen-use efficiency of wheat in a Mediterranean climate. *Plant and Soil,* 233 (1), 127-143.

Asseng, S., Bar-Tal, A., Bowden, J.W., et al., 2002. Simulation of grain protein content with APSIM-Nwheat. *European Journal of Agronomy,* 16 (1), 25-42.

Asseng, S., Turner, N.C., Botwright, T., et al., 2003. Evaluating the impact of a trait for increased specific leaf area on wheat yields using a crop simulation model. *Agronomy Journal,* 95 (1), 10-19.

Asseng, S., Jamieson, P.D., Kimball, B., et al., 2004. Simulated wheat growth affected by rising temperature, increased water deficit and elevated atmospheric $CO_2$. *Field Crops Research,* 85 (2/3), 85-102.

Condon, A.G. and Richards, R.A., 1993. Exploiting genetic variation in transpiration efficiency in wheat: an agronomic view. *In:* Ehleringer, J.R., Hall, A.E. and Farquhar, G.D. eds. *Stable isotopes and plant carbon water relations.* Academic Press Inc., San Diego, 435-450.

Connor, D.J., Theiveyanathan, S. and Rimmington, G.M., 1992. Development, growth, water-use and yield of a spring and a winter wheat in response to time of sowing. *Australian Journal of Agricultural Research,* 43 (3), 493-516.

Conocono, E.A., 2002. *Improving yield of wheat experiencing post-anthesis water deficits through the use of shoot carbohydrate reserves.* PhD Thesis, University of Western Australia.

Cooper, P.J.M., Gregory, P.J., Keatinge, J.D.H., et al., 1987. Effects of fertilizer, variety and location on barley production under rainfed conditions in northern Syria. 2. Soil water dynamics and crop water use. *Field Crops Research,* 16 (1), 67-84.

Fischer, R.A., 1979. Growth and water limitation to dryland wheat yield in Australia: a physiological framework. *Journal of the Australian Institute of Agricultural Science,* 45 (2), 83-94.

Fischer, R.A., 1985. Number of kernels in wheat crops and the influence of solar radiation and temperature. *Journal of Agricultural Science,* 105 (2), 447-461.

French, R.J. and Schultz, J.E., 1984. Water use efficiency of wheat in a Mediterranean-type environment. I. The relation between yield, water use and climate. *Australian Journal of Agricultural Research,* 35 (6), 743-764.

Gregory, P.J., Tennant, D. and Belford, R.K., 1992. Root and shoot growth, and water and light use efficiency of barley and wheat crops grown on a shallow duplex soil in a mediterranean-type environment. *Australian Journal of Agricultural Research,* 43 (3), 555-573.

Keating, B.A., Carberry, P.S., Hammer, G.L., et al., 2003. An overview of APSIM, a model designed for farming systems simulation. *European Journal of Agronomy,* 18 (3/4), 267-288.

Miralles, D.J. and Richards, R.A., 1999. Sensitivity to photoperiod during the reproductive phase changes grain number in wheat and barley. *In: Combined conference abstracts: 42nd annual ASBMB, 38th annual ASPP and 20th annual NZSPP conferences, Adelaide, Australia, 1998.* Australian Society of Plant Physiology.

Nicolas, M.E. and Turner, N.C., 1993. Use of chemical desiccants and senescing agents to select wheat lines maintaining stable grain size during post-anthesis drought. *Field Crops Research,* 31 (1/2), 155-171.

Palta, J.A. and Fillery, I.R.P., 1995. N application enhances remobilization and reduces losses of pre-anthesis N in wheat grown on a duplex soil. *Australian Journal of Agricultural Research,* 46 (3), 519-531.

Palta, J.A., Turner, N.C. and French, R.J., 2004. The yield performance of lupin genotypes under terminal drought in a Mediterranean-type environment. *Australian Journal of Agricultural Research,* 55 (4), 449-459.

Probert, M.E., Keating, B.A., Thompson, J.P., et al., 1995. Modelling water, nitrogen, and crop yield for a long-term fallow management experiment. *Australian Journal of Experimental Agriculture,* 35 (7), 941-950.

Probert, M.E., Dimes, J.P., Keating, B.A., et al., 1998. APSIM's water and nitrogen modules and simulation of the dynamics of water and nitrogen in fallow systems. *Agricultural Systems,* 56 (1), 1-28.

Reynolds, M.P., Rajaram, S. and McNab, A. (eds.), 1996. *Increasing yield potential in wheat: breaking the barriers: proceedings of a workshop held in Ciudad Obregón, Sonora, Mexico.* CIMMYT, Mexico.

Richards, R.A. and Townley-Smith, T.F., 1987. Variation in leaf area development and its effect on water use, yield and harvest index of droughted wheat. *Australian Journal of Agricultural Research,* 38 (6), 983-992.

Ritchie, J.T., 1983. Efficient water use in crop production: discussion on the generality of relations between biomass production and evapotranspiration. *In:* Taylor, H.M., Jordan, W.R. and Sinclair, T.R. eds. *Limitations to efficient water use in crop production.* American Society of Agronomy, Wisconsin, 29-44.

Schnyder, H., 1993. The role of carbohydrate storage and redistribution in the source-sink relations of wheat and barley during grain filling: a review. *New Phytologist,* 123 (2), 233-245.

Setter, T.L., Anderson, W.K., Asseng, S., et al., 1998. Review of the impact of high shoot carbohydrate concentrations on maintenance of high yields in cereals exposed to environmental stress during grain filling. *In:* Nagarajan, S., Singh, G. and Tyagi, B.S. eds. *Wheat: research needs beyond 2000AD: proceedings of an international conference, 12-14 August 1997, Karnal, India.* Narosa Publishing House, New Delhi, 237-255.

Shepherd, K.D., Cooper, P.J.M., Allan, A.Y., et al., 1987. Growth, water use and yield of barley in Mediterranean-type environments. *Journal of Agricultural Science,* 108 (2), 365-378.

Turner, N.C., 1986. Crop water deficits: a decade of progress. *Advances in Agronomy,* 39, 1-51.

Turner, N.C., 2004. Sustainable production of crops and pastures under drought in a Mediterranean environment. *Annals of Applied Biology,* 144 (2), 139-147.

Turner, N.C. and Asseng, S., 2005. Productivity, sustainability, and rainfall-use efficiency in Australian rainfed Mediterranean agricultural systems. *Australian Journal of Agricultural Research,* 56 (11), 1123-1136.

Whan, B.R., Anderson, W.K., Gilmour, R.F., et al., 1991. A role for physiology in breeding for improved wheat yield under drought stress. *In:* Acevedo, E., Conesa, A.P., Monneveux, P., et al. eds. *Physiology breeding of winter cereals for stressed Mediterranean environments, Montpellier, France, 3-6 July 1989.* INRA, Paris, 179-194.