

Improving Yields in Rainfed Environments Through Physiological Plant Breeding

R.A. Richards^{1,2}, G.J. Rebetzke², A.F. van Herwaarden²,
B.L. Duggan² and A.G. Condon^{1,2}

¹CSIRO Plant Industry, GPO Box 1600, Canberra ACT 2601, Australia

²Plant Science CRC, GPO Box 1600, Canberra ACT 2601, Australia

Abstract: Breeding programs for yield in water-limited environments are plagued by large seasonal variation, low heritabilities and high genotype x environment interactions. A physiological breeding program is described that attempts to identify the principal factors limiting the yield of wheat in Australia. It is notable that the limiting factors identified have more to do with maximizing water use and water use efficiency than with survival under drought. For the characteristics identified, there is substantial genetic variation available in wheat, each having a high heritability so they can be easily screened. They are therefore appropriate for selection in a backcrossing program aimed at retaining the desirable quality and disease resistance characteristics already present in wheats grown in the target region. Identification of highly heritable traits limiting yield and of germplasm containing the desirable expression of the traits also provide valuable parental material and a broader genetic base for empirical breeding programs.

Key words: Wheat, drought, rainfed, breeding, water-use efficiency.

There is a belief that genetic variation for drought tolerance is substantial and that this variation can be used in plant breeding programs to overcome some of the devastating effects of drought in our important crop species. This notion has probably arisen from the array of adaptations to drought exhibited by many perennial species. However, the reality is that it will never be possible to overcome the effects of drought, and that any progress to improve yield under drought is likely to be slow and gains will be small and gradual. Past efforts to improve drought resistance and yield through plant breeding is evidence for this.

Further, grain yield increases in dry regions will come from the adoption of good management practices by farmers and on creative approaches to the development of new crop varieties by plant breeders. The greatest and fastest gains in productivity are generally achieved by adopting management practices that result in: (i) an increase in soil water available for use by the crop, and (ii) greater crop extraction of soil water. Increases in soil-water availability can be achieved by adopting practices that increase soil water storage and reduce water loss from the root profile such as reducing evaporation from the soil surface,

surface run-off, or water loss below the rooting zone. Increases in water extraction by the crop can be achieved by reducing the effect of soil-borne pathogens through the use of break crops and then managing fertilizer supply to match the crops requirements (Angus *et al.*, 1991; Kirkegaard *et al.*, 1994). Plant breeding, on the other hand, can maximize seasonal water use and reduce water loss by better tailoring varieties to regions and cropping practices, and by improving water use efficiency. Breeding can also increase a crop's tolerance to root pathogens or nutrient imbalances which should result in increased water use and yield in regions normally affected by these constraints to growth. The purpose of this paper is to discuss how breeding may contribute to improved adaptation in dry regions by targeting specific traits to overcome limiting factors.

Regional breeding programs have the responsibility to increase or at least maintain grain yields. This is usually achieved by selecting for increased yield and for resistance to pests and diseases. These empirical approaches to yield improvement are very effective and will remain the most wide-spread method of plant improvement in dry regions. It is expected that progress will continue using current approaches providing new genetic variation is incorporated into breeding programs and large numbers of lines are evaluated precisely. It is not our intention to describe the various methods used by breeding programs in dry areas. Instead we shall give an overview of our wheat improvement program. The principal objective of our program is to increase yield in dry regions of Australia through understanding the underlying physiological

factors presumed to be limiting wheat yields and then selecting for them. We have adopted a physiological/morphological approach to wheat improvement as numerous breeding programs in Australia already select primarily for grain yield and we believe our program should complement and build on these.

We take the view that any improvement in yield must have a physiological basis and if we were able to identify the factors limiting yield then we would be able to effectively target them. That is, target parent lines that have the most desirable expression of the characteristic, devise effective selection procedures for the trait, and if highly heritable, incorporate the trait into the best cultivars that also have desirable grain quality and are resistant to diseases. Empirical approaches to yield improvement in dry environments are often limited by a lack of suitable genetic variation, and poor correlation of genotype performance when assessed across other environments (Rosielle and Hamblin, 1981). Our physiological framework aims to identify characteristics associated with yield but which do not suffer the penalties of low heritability or a negative cost to yield when extended to target environments other than the selection environment. Furthermore, because many of the characteristics we believe are important are genetically unlinked they can be readily combined to broaden adaptation and genotypic stability. There is also the benefit of the availability of new genes from which to broaden the genetic base from which selection can be made. Hence, progress from selection across all environments may be greater than for empirical approaches targeting specific 'stress' en-

vironments but with a view to broader adaptation.

Physiological Factors Limiting Yield in Dry Regions

The identification of critical traits limiting yield is the most important yet most difficult aspect to improving productivity under drought. To some extent it can be viewed as a lottery. The literature on drought resistance has ample examples of traits that are clearly important in protecting plants from the devastating effects of drought. However, few, if any of these traits are useful to crops as they are often more important for protection against drought than for increasing productivity.

Passioura (1977) proposed an identity based on resource utilization and efficiency rather than drought protection and this has been responsible for changing the way we think about agricultural plants grown under water-limited conditions. Passioura proposed that when water is limited, the production of biomass is a function of the amount of water used by the crop (W) and how efficiently the crop uses this water, i.e., the water use efficiency (WUE , biomass/water use), where:

$$\text{Biomass} = W \times WUE \quad \dots (1)$$

Water use can be further partitioned into its components E (water lost through evaporation from the soil surface), and T (water transpired by the crop). If grain is the economic product, then biomass is partitioned into grain as the proportion of biomass, i.e., the harvest index (HI), such that:

$$\text{Grain yield} = W \times WUE \times HI \quad \dots(2)$$

As this identity always holds true, and because W , WUE and HI are likely to be somewhat independent of each other, then an improvement in any one of them should result in increased yield. Using this model it is then possible to assess whether a candidate trait for selection is likely to increase any one of the components, thereby increasing yield under drought.

To further refine trait identification for use in a breeding program, there are several other principles that are important. Firstly, the time scale over which the trait is effective will determine its importance for overall crop growth and yield. Secondly, the level of organization (molecule, cell, organ, plant, crop) where the trait is expressed determines its likely influence on crop growth and yield. Thus, a change at the molecular level is less likely to influence yield than a change at the crop level. Thirdly, an understanding of the target environment is critical. For example, if crops already extract all the available water from the soil profile, there is little point in breeding for deeper roots. Similarly, there is little point in developing cultivars with deeper roots if soil water is not being used because of the presence of root pathogens or mineral toxicities. Instead, greater progress will be achieved by breeding for greater tolerance to these factors. A fuller description of the above considerations is provided by Richards (1996).

In the rest of this paper, we shall discuss the traits that we consider are most likely to increase wheat yield in different water-limited regions of Australia. Wheat growing regions in Australia differ markedly in both the amount and timing of rainfall. Rainfall varies from regions which are more summer-

dominant to others which are winter-dominant, while other regions experience a more evenly distributed rainfall pattern throughout the year. Wheat is typically planted in early winter and harvested early summer. The predominant wheat varieties are spring types which are relatively insensitive to both vernalization and photoperiod. Thus the crop is sown under conditions where water is typically plentiful and vapour-pressure deficit low, and then matures into a terminal drought when vapour pressure deficit is high. Although the physiological traits have been targeted to overcome limitations to yield in Australia, most will have application elsewhere. The reasons for their choice are also described and these will provide an overview of factors we suggest must be considered in developing a physiologically-based breeding program targeting greater yields in drier environments.

Phenology

Like most water-limited environments, changes in phenology, or flowering time, have resulted in the most significant yield increases in crops in Australia. That the manipulation of time of flowering continues to result in yield increases in wheat is somewhat surprising considering flowering time has been altered over the past 150 years by selection and breeding (Siddique *et al.*, 1989). Most of the changes in Australia have been towards earlier flowering (Kirby *et al.*, 1989; Richards, 1991) and to the avoidance of drought. It is now likely that an optimum flowering time has been achieved for a given sowing date in most of Australia such that the risk of flowering too early and be damaged by frost, on the one hand, and flowering

too late and experience drought and high temperatures, on the other, is now minimized. Whereas it is unlikely there will be further changes in the time of flowering, it is likely that an earlier sowing date will be more widely adopted by farmers and that varieties will need to be developed that are better suited to an earlier sowing and these will require a longer duration to flower. Changes in sowing date are being made possible by improved herbicides, altered cropping practices, new machinery, and by the awareness of the benefits of sowing before the onset of winter. It is likely that with the genetic variation available in wheat to manipulate phenology, significant yield increases will continue to be made with a changed phenology.

The ideal sowing time is one that will ensure maximum crop growth and water use occurs at a time when water is most likely to be available to the crop and that the water is used as economically as possible. Sowing wheat as early as possible in autumn, or at the break of the season in Mediterranean environments, has been found to result in the highest potential yields in water-limited environments. Earlier sowing results in a longer crop duration. It ensures that early growth is faster because soil temperatures are warmer. The longer duration can also result in deeper root growth and increased water use from deep in the soil profile. Crop water use is also more economical. Firstly, because an early sowing results in more water use by the crop and less evaporation from a bare soil surface and secondly, because transpiration efficiency is inversely proportional to vapour pressure deficit. A higher crop biomass and yield should result.

Incorporation of genes that delay floral initiation in wheats have provided opportunities for earlier planting in Australia and so greater yields (Anderson and Smith, 1990; Gomez-Macpherson and Richards, 1995; Penrose, 1993; Woodruff and Tonks, 1983). The longer crop duration may, in turn, require further genetic modification to the crop. For example, Gomez-Macpherson and Richards (1995) have shown that winter wheats sown in mid-April produce double the biomass of spring wheats sown in mid-May but with only marginally greater grain yields. Furthermore, only small differences in yield were reported between winter wheats sown early and spring wheats sown at their optimal time in over 200 trials conducted in southern New South Wales (Penrose, 1993). This may partly be explained by greater pre-anthesis water use with less remaining for use during grain filling (Fischer, 1979; Passioura, 1977). However, our evidence suggests that two other factors also contribute to the lower yields of winter wheats sown in April. Firstly, the longer vegetative period results in the production of more leaves and therefore more internodes and longer stems. This excessive stem growth occurs at the expense of water soluble carbohydrate storage and ear growth, thereby limiting yield potential. Secondly, the longer vegetative period results in an excessive number of tillers, most of which abort without producing grain. Dry matter wasted in the production of these tillers could otherwise have been stored as water-soluble carbohydrates or used for ear growth.

Several sources of dwarfing genes are now being introduced into winter wheats to reduce their plant height and therefore

competition between stems and ears. We are also incorporating the tiller inhibitor (*tin*) gene into winter wheats to reduce the production of excessive tillers (Richards, 1988).

Increased Early Vigor

The early growth and vigor of wheat is very conservative compared to other cereals (Lspez-Castaqeda and Richards, 1994). Whereas this is not a disadvantage in environments where there is adequate water for growth (e.g. where there is irrigation and high fertility), the conservative growth of current wheat cultivars may limit yield in many drier regions around the world. Yield penalties from poor early growth arise where crops are largely reliant on current rainfall such as exists with Mediterranean-like environments. In these environments the topsoil is maintained wet by frequent rainfall events of 5-10 mm. If the soil cover provided by the crop is inadequate then a considerable proportion of the rain that falls may be evaporated from the soil surface. This loss of water can be as much as 60% of the season's rainfall in Mediterranean climates (Cooper *et al.*, 1987), and so represents a potentially substantial yield loss in environments where rainfall is a major determinant of yield. A more vigorous wheat stand should reduce water loss from the soil surface resulting in greater transpiration as a proportion of total water use (T). Transpiration efficiency (biomass per unit of water transpired) is also enhanced in a vigorous crop because of a more favorable exchange of water vapour for carbon dioxide early in the season when the air

Table 1. Comparison of high vigor selection, Vigour18, with Indian and Chinese parents, and low vigor control lines (cvs Amery and Hartog) for early vigor characteristics measured on plants at the 4 leaf stage. Values represent the mean of four replications.

Trait	High vigor lines			Controls	
	Vigor 18	Indian parent	Chinese parent	Amery	Hartog
Breadth of 1st leaf (mm)	6.3	5.4	6.0	3.9	4.7
Length of all leaves (mm)	650.0	603.0	608.0	495.0	524.0
Plant leaf area (mm)	54.0	39.0	46.0	27.0	33.0

is cooler and vapour pressure deficit lower (Tanner and Sinclair, 1983).

There are several other penalties associated with the low vigor of current wheats. One is their inability to effectively compete with weeds (Lemerle *et al.*, 1996). This results in reduced yields, greater herbicide use and faster emergence of herbicide resistance in weeds. Another penalty associated with the poor vigor of wheat is its lower yield when planted late. A more rapid development of the leaf canopy would lead to greater light interception and subsequently higher crop growth rates. Greater biomass at anthesis should, in turn, increase grain yield relative to crops with smaller crop growth rates and less biomass.

Investigations into the underlying factors that contribute to fast early growth and vigor of wheat has revealed the importance of five characteristics: a large embryo, high specific leaf area, fast seedling emergence, a high frequency of large coleoptile tillers and the absence of major gibberellic-acid-insensitive dwarfing genes (Lpez-Castañeda *et al.*, 1996; Liang and Richards, 1994; Richards, 1992). We have been unable to find sufficiently useful genetic variation for embryo size, specific leaf area, or large coleoptile tillers among Australian or CIM-MYT-bred wheats. However, germplasm

from China, India and Canada and lines from a composite cross population have been identified which have high expression of the above characteristics (Table 1). Some of these characteristics have been pyramided together into parent lines to use as donors in a backcrossing program with low vigor Australian cultivars. The donor parent, Vigour18, combines the large specific leaf area and embryo size of its Chinese and Indian parents to produce a 100% greater leaf area than the low vigor Australian cultivar, Amery (Table 1).

Genetic studies have been initiated to understand the extent to which gain from selection can be made for early vigor. Parent-offspring estimates of narrow-sense heritability show that seedling leaf area and biomass are under complex genetic control, and are of low narrow-sense heritability ($h^2 = 0.30 - 0.40^*$). On the other hand, leaf breadth and total leaf length are more highly heritable ($h^2 = 0.60 - 0.80^{**}$), their higher heritability indicating greater progress from selection when screening segregating wheat populations for these characters. Given that leaf breadth has a strong and positive genetic correlation with leaf area ($r_g = 0.76 - 0.82^{**}$), selection of plants with larger leaf breadths should produce greater leaf area than selection for leaf area itself. Selection for leaf breadth

Table 2. Coleoptile length for cultivars containing different plant height reducing genes. Coleoptile length for each cultivar is presented as the mean of six replicates grown at each of three temperatures (11°, 15° and 19°C)

Height gene	Cultivar	Coleoptile length (mm)
Rht1 (GA-insensitive)	Janz	77
Rht2 (GA-insensitive)	Stiletto	83n.s.
Rht8 (GA-insensitive)	Mara	93*
Rht8 (GA-sensitive)	Chuan-Mai 18	108**
rht1 rht2 (GA-sensitive)	Ghurka	119*
rht1 rht2 (GA-sensitive)	Stockade	126**

n.s. Not statistically different from Janz at $P = 0.05$ using a Dunnett's test.

*,**Statistically different from Janz at $P = 0.05$ or $P = 0.01$ using a Dunnett's test.

over leaf area is advantageous for other reasons including it is non-destructive and much quicker to screen segregating populations. Plants can also be screened much earlier in the season.

Poor Emergence

The adoption of semidwarf spring wheats around the world has been rapid with most wheat cultivars now having either of the gibberellic acid (GA) insensitive genes, Rht1 or Rht2. These dwarfing genes reduce plant height to reduce lodging and increase partitioning of dry matter to the ears of current varieties. However, these genes also reduce cell size (Keyes *et al.*, 1989) and result in short coleoptiles (Table 2) that lead to reduced emergence and poor seedling vigor when compared to older, taller wheats (Allan *et al.*, 1962; Richards, 1992). This reduced emergence is accentuated when seed is sown deep in order to seek moisture. Seedling emergence of current cultivars is particularly impaired where conservation farming is practiced as seedlings must emerge through stubble and/or from hard seed beds.

Combining the desirable features of both reduced plant height and better establishment and vigor should result in greater wheat yields in water-limited environments. Small gains may be made by selection for longer coleoptiles in wheats with dwarfing genes but substantially greater progress is possible using alternative sources of genes for reduced plant height. We have identified a number of genetically unrelated germplasm stocks containing major and minor GA-sensitive genes for reduced plant height and increased coleoptile length (Table 2). Unlike the GA-insensitive genes derived originally from Norin-10, these wheats reduce plant height whilst maintaining sensitivity to GA at the seedling stage. Increased cell elongation and expansion in response to endogenous GA produces longer coleoptiles and greater seedling leaf area. Field observations indicate that wheat seedlings containing GA-sensitive genes for reduced plant height are far more vigorous than current wheats containing GA-insensitive genes. Our preliminary studies have shown that the major GA-sensitive genes for reduced plant height (e.g. Rht8) may provide

Table 3. Grain yield ($t\ ha^{-1}$) for low and high near-isogenic groups evaluated at Condobolin and Wagga Wagga in 1996

	Condobolin	Wagga Wagga	Mean
Low	3.39*	5.31	4.35*
High	3.17	5.14	4.16
Location	3.27	5.22	-

*Low and high means statistically different at $P = 0.05$.

the greatest genetic gains for increased coleoptile length and vigor owing to their high repeatability of expression across environments and large gene action.

Greater transpiration efficiency

More growth and yield per unit of rainfall is one of the most important yet elusive goals in agriculture. All plants discriminate against the rarer ^{13}C in the air relative to ^{12}C in the fixation of carbon dioxide during photosynthesis. The amount of this discrimination is inversely proportional to the transpiration efficiency of crops with the C_3 photosynthetic pathway (Farquhar and Richards, 1984). Plants that have low discrimination against ^{13}C have a high transpiration efficiency and therefore use less water to produce dry matter. This is a distinct advantage to all crops when it is dry. However, in more favorable environments high discrimination is related to high yield (Condon *et al.*, 1987). Thus ^{13}C discrimination can be important in both favorable and unfavorable environments. We have been actively selecting for low ^{13}C discrimination (Δ in backcross populations developed from crosses between high and low (Δ) wheat parents to improve grain yields in dry environments. Preliminary studies using near-isogenic wheat populations showed that low (Δ) to be associated with between a 3 and 7% yield increase

across environments representing high and low grain yield potentials but each with a terminal drought (Table 3). Indeed some low Δ lines yielded 20% more than the recurrent, widely-grown, commercial parent when averaged over both field sites.

Reduced Tillering

Conserving soil moisture for grain filling is essential for maximizing grain yields in dry environments. This is particularly the case where crops are grown on stored soil moisture. Some of the water used by a crop is wasted in the pre-anthesis production of tillers that later abort. A genetic reduction in the number of sterile tillers produced by a wheat plant does not significantly compromise leaf area development in the vegetative period but after the commencement of stem elongation leaf area is less, thereby resulting in less transpiration prior to flowering and more water available for grain filling. Reduced tillering can be achieved by planting current cultivars later in the season, or by sowing into low fertility soils, neither of which is desirable for maximizing yield. Incorporation of a gene that inhibits tiller formation (*tin*) enables tiller number to be reduced under favorable conditions, allowing plants to concentrate resources into productive tillers (Richards, 1988). The *tin* gene has been incorporated

Table 4. Effect of fertilizer nitrogen on the biomass, water soluble carbohydrate (WSC) and grain yield of wheat in two contrasting environments

Fertilizer N (kg ha ⁻¹)	Anthesis		Maturity		
	Biomass (t ha ⁻¹)	WSC (t ha ⁻¹)	Biomass (t ha ⁻¹)	WSC (t ha ⁻¹)	Grain yield (t ha ⁻¹)
Ginninderra					
0	10	2.4	14	0.03	6.1
200	11	1.8	17	0.02	7.9
Wagga Wagga					
0	10	2.1	11	0.02	3.7
200	11	1.2	11	0.02	2.8

into several Australian commercial wheat backgrounds and these are currently being assessed for yield in drier regions of the Australian wheat belt. We suggest that plants that produce 2 to 4 fertile tillers only at a plant density of about 150 plants m⁻² would be sufficient to maximize yield in most environments.

Increased Storage of Water Soluble Carbohydrates

Due to low rainfall and high evaporation in most of Australia's wheatbelt, wheat crops usually experience drought during grain filling which substantially reduces yield. The dryland cultivation of high-protein wheats currently carries with it the risk of overfertilisation, which can lead to haying-off, resulting in substantial economic losses. Haying-off is a worldwide disorder of cereal crops leading to incomplete grain filling under conditions of post-anthesis drought. It normally follows vigorous vegetative growth stimulated by high soil nitrogen, resulting in a low harvest index, and shriveled grain of high protein concentration (van Herwaarden *et al.*, 1997).

Results from this group confirmed previous studies (Barley and Naidu, 1964; Fischer and Kohn, 1966) showing haying-off to be associated with reduced post-anthesis assimilation in response to a lack of soil water. However, the reduction in soil water available for post-anthesis use does not explain why grain yields can decrease in response to high soil nitrogen rather than plateau. We found that the absolute amount of water soluble carbohydrates (WSC) present in high-nitrogen crops at anthesis was less than in low-nitrogen crops, despite a greater biomass (Table 4).

The lack of this form of assimilate, available for transfer to the grain, was the greatest single contributor to the yield reduction of crops of high nitrogen status. This reduction in WSC with increased biomass is most likely due to assimilates being used to a greater extent for the production of structural materials (e.g., Snyder, 1993) and increased respiration rates of leaves at higher nitrogen concentration (Amthor, 1989; Winzeler *et al.*, 1989), thereby reducing the net carbon gain in dense canopies at high nitrogen (van Her-

waarden *et al.*, 1996). Provided there is little or no water stress (e.g., Ginninderra, Table 4), a high nitrogen crop can fill grain from current photosynthesis and remobilise WSC reserves during periods of peak assimilate demand. However, in the event of water deficit, and therefore reduced current photosynthesis, the lack of WSC reserves results in haying-off (e.g., Wagga Wagga, Table 4). A low nitrogen crop does not face the same degree of water stress as a high nitrogen crop because lower anthesis biomass results in reduced pre-anthesis water use. Higher yields at low nitrogen are achieved through greater current photosynthesis and greater reserves of pre-anthesis WSC.

The proposed model also accounts for high levels of WSC in crops with a low spike density. We speculate that the reputation of tall or winter varieties for increased haying-off is explained by low pre-anthesis reserves of WSC due to greater assimilate demand by larger stems. It also leads to speculation that while haying-off is a problem in closed-canopies, it is likely to be less of a problem in regions where leaf area index is low due to low photothermal quotient or nutrient deficiency, as these crops are more likely to contain higher levels of pre-anthesis stored WSC.

It is proposed that the incidence of haying-off could be reduced by increasing storage of WSC in the crop. This may be achieved by increasing light infiltration into the canopy of a crop through the use of reduced-tillering cultivars, progressively reducing leaf size after the commencement of stem elongation (as in barley cultivars), and/or increasing the erectness of flag

leaves. This improved canopy efficiency and/or reduced production of structural material should result in higher storage of WSC and lead to improved yield over current cultivars. These changes to crop architecture are only expected to be an advantage at high nitrogen status.

Conclusions

A feature of all the aforementioned traits is that selection for each is very efficient and straight-forward. From a detailed physiological understanding of each trait, we have developed selection techniques that are very precise and target the trait rather than a linked marker. All traits can be measured non-destructively before anthesis, which means that selected plants can be used in hybridization, an important consideration where the trait is being backcrossed into an adapted genetic background. There are a number of other advantages associated with selection for each trait. Large numbers of plants can be processed, plants can be screened out of season and several generations can be grown in a year. Furthermore, all traits have a high heritability and backcrossing can be used to incorporate the traits into current cultivars. Identification of new characters to improve adaptation also provide longer-term benefits in the availability of new genes and a subsequent broadening of the genetic base from which selection will be made.

So far we have not found evidence of undesirable pleiotropic or linkage effects associated with any of the traits. However, we are conscious of possible associations between embryo size and milling yield, and between greater vigor and earlier flow-

ering. The latter association may, in fact, be a desirable one.

References

- Allan, R.E., Vogel, O.A. and Peterson, C.J. 1962. Seedling emergence rate of fall-sown wheat and its association with plant height and coleoptile length. *Agronomy Journal* 54: 347-350.
- Amthor, J.S. 1989. *Respiration and Crop Productivity*. Springer-Verlag: New York.
- Anderson, W.K. and Smith, W.R. 1990. Yield advantage of two semi-dwarf compared with two tall wheats depends on sowing time. *Australian Journal of Agricultural Research* 41: 811-826.
- Angus, J.F., van Herwaarden, A.F. and Howe, G.N. 1991. Productivity and break crop effects of winter-growing oilseeds. *Australian Journal of Experimental Agriculture* 31: 669-677.
- Barley, K.P. and Naidu, N.A. 1964. The performance of three Australian wheat varieties at high levels of nitrogen supply. *Australian Journal of Experimental Agriculture and Animal Husbandry* 4: 39-48.
- Condon, A.G., Richards, R.A. and Farquhar, G.D. 1987. Carbon isotope discrimination is positively correlated with grain yield and dry matter production in field grown wheat. *Crop Science* 27: 996-1001.
- Cooper, P.J.M., Gregory, P.J., Keatinge, J.D.H. and Brown, S.C. 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: 67-84.
- Farquhar, G.D. and Richards, R.A. 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Australian Journal of Plant Physiology* 11: 539-552.
- Fischer, R.A. 1979. Growth and water limitation of dryland wheat yield in Australia: a physiological framework. *The Journal of the Australian Institute of Agricultural Science* 45: 83-94.
- Fischer, R.A. and Kohn, G.D. 1966. The relationship of grain yield to vegetative growth and post-flowering leaf area in the wheat crop under conditions of limited soil moisture. *Australian Journal of Agricultural Research* 17: 281-295.
- Gomez-Macpherson, H. and Richards, R.A. 1995. Effect of sowing time on yield and agronomic characteristics of wheat in south-eastern Australia. *Australian Journal of Agricultural Research* 46: 1381-99.
- Keyes, G.J., Paolillo, D.J. and Sorrells, M.E. 1989. The effects of dwarfing genes Rht1 and Rht2 on cellular dimensions and rate of leaf elongation in wheat. *Annals of Botany* 64: 683-690.
- Kirby, E.J.M., Siddique, K.H.M., Perry, M.W., Kae-sehagen, D. and Stern, W.R. 1989. Variation in spikelet initiation and ear development of old and modern Australian wheat varieties. *Field Crops Research* 20: 113-128.
- Kirkegaard, J.A., Gardner, P.A., Angus, J.F. and Koetz, E. 1994. Effect of brassica break on crops on the growth and yield of wheat. *Australian Journal of Agricultural Research* 45: 529-545.
- Lemerle, D., Verbeek, B., Cousens, R.D. and Coombes, N. 1996. The potential for selecting wheat varieties strongly competitive against weeds. *Weed Research* 36: 505-13.
- Liang, Y.L. and Richards, R.A. 1994. Coleoptile tiller development is associated with fast early vigor in wheat. *Euphytica* 80: 119-124.
- Lopez-Castañeda, C. and Richards, R. A. 1994. Variation in temperate cereals in rainfed environments. 3. Water use and water-use efficiency. *Field Crops Research* 39: 85-98.
- Lopez-Castañeda, C., Richards, R.A., Farquhar, G.D. and Williamson, R.E. 1996. Seed and seedling characteristics contributing to variation in early vigor among temperate cereals. *Crop Science* 36: 1257-1266.
- Passioura, J.B. 1977. Grain yield harvest index and water use of wheat. *The Journal of the Australian Institute of Agricultural Science* 43: 117-120.
- Penrose, L.D.J. 1993. Yield of early dryland sowing of wheat with winter and spring habit in southern and central New South Wales. *Australian Journal of Experimental Agriculture* 33: 601-8.
- Richards, R.A. 1988. A tiller inhibitor gene in wheat and its effect on plant growth. *Australian Journal of Agricultural Research* 39: 749-757.

- Richards, R.A. 1991. Crop improvement for temperate Australia: Future opportunities. *Field Crops Research* 26: 141-169.
- Richards, R.A. 1992. The effect of dwarfing genes in spring wheat in dry environments. II. Growth, water use and water use efficiency. *Australian Journal of Agricultural Research* 43: 529-539.
- Richards, R.A. 1996. Defining selection criteria to improve yield under drought. *Plant Growth Regulation* 20: 157-166.
- Rosielle, A.A., and Hamblin, J. 1981. Theoretical aspects of selection for yield in stress and non-stress environments. *Crop Science* 21: 943-946.
- 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: 233-245.
- Siddique, K.H.M., Belford, R.K., Perry, M.W. and Tennant, D. 1989. Growth, development and light interception of old and modern wheat cultivars in a Mediterranean-type environment. *Australian Journal of Agricultural Research* 40: 473-487.
- Tanner, C.B. and Sinclair, T.R. 1983. Efficient water use in crop production: Research or re-search? In *Limitations to Efficient Water Use in Crop Production* (Ed. H.M. Taylor), pp. 1-27. ASA, CSSA and SSSA: Madison.
- van Herwaarden, A.F., Farquhar, G.D., Angus, J.F., Richards, R.A. and Howe, G.N. 1997. 'Haying-off', the negative grain yield response of dryland wheat to nitrogen fertilizer. I. Biomass, grain yield and water use. *Australian Journal of Agricultural Science* (in press).
- van Herwaarden, A.F., Farquhar, G.D., Angus, J.F. and Richards, R.A. 1996. Physiological responses of six spring wheat varieties to nitrogen fertilizer. In *Proceedings of the 8th Australian Agronomy Conference*, pp. 570-573. Australian Society of Agronomy, Toowoomba, Queensland.
- Whan, B.R. 1976. The association between coleoptile length and culm length in semidwarf and standard wheats. *The Journal of the Australian Institute of Agricultural Science*. 42: 194-196.
- Winzeler, M., McCullough, D.E. and Hunt, L.A. 1989. Leaf gas exchange and plant growth of winter rye, triticale, and wheat under contrasting temperature regimes. *Crop Science* 29: 1256-1260.
- Woodruff, D.R. and Tonks, J. 1983. Relationship between time of anthesis and grain yield of wheat genotypes with differing developmental patterns. *Australian Journal of Agricultural Research* 34: 1-11.