Physiological and agronomic limits to wheat yield and quality

P. D. Jamieson and D. R. Wilson

New Zealand Institute for Crop and Food Research, Private Bag 4704, Christchurch

Abstract

The key to successful wheat crops is to achieve the right balance of growth between the vegetative and grain fill phases through consistent, balanced crop management. Management during the vegetative phase establishes the yield and quality potential of a crop, and this must be followed by management of appropriate intensity throughout grain fill to realise the potential.

The yield and quality potential of a crop at the end of the vegetative phase can be judged by the amount of dry matter present per unit area, the amount of nitrogen contained in the dry matter, and the number of grains set per unit area. Of these, the amount of dry matter present dominates, because nitrogen accumulation and grain number are closely related to it. Total dry matter at the end of the vegetative phase depends on the amount of solar radiation intercepted up to this point, and this in turn depends on both the incident solar radiation and the duration of the phase. In the absence of stress, management factors that can affect this are the choice of cultivar and sowing time.

The realisation of grain yield and quality depends on the rate and duration of grain fill. Grain growth rates vary little. Therefore the duration of grain fill, which decreases as the mean temperature rises, is the most important determinant of yield realisation. High quality grain means large grains with acceptable protein contents. Its attainment requires enough grains to be set so that they can all be filled completely, and enough nitrogen to be present in the dry matter at the beginning of grain fill to supply most of the requirement for grain protein.

***Key words:** canopy development, phenology, kernel weight, nitrogen, protein.*

Introduction

Most wheat crops fail to achieve their full yield or quality potential because they are exposed to climatic or management stresses such as water or nutrient deficits, or attacks by pests and diseases. The extent of yield and quality reductions below the potential depends on the timing, duration and severity of the stresses, and these effects will be covered in the following papers.

In this paper we will depart from reality by considering completely unstressed crops in order to explore the key environmental and plant factors which determine the upper limits of wheat yield and quality. If we can understand these it should be possible to use the information, first, to help determine crop management strategies to maximise both yield and quality when stresses are present and, second, to identify plant characters associated with better yield and quality which breeders can exploit.

To identify the most important environmental and plant factors and analyze how they determine yield and quality, it is useful to divide the growth and development of a wheat crop into two phases: from planting until the start of grain fill, which for convenience we will call the vegetative phase, and the grain fill phase. During the vegetative phase the potential of a crop to produce yield and quality is established. Whether or not these potentials are fully realised depends on events during the subsequent grain fill phase, and how they influence the crop's ability to retain and fill the grains set in the first phase.

Our aim is to show that the key to successful crops is to achieve the right balance of growth between these two phases through consistent, balanced crop management. Intensive management during the vegetative phase establishes high yield and quality potential, and this must be followed by equally intensive management throughout grain fill to realise the potential. Both yield and quality will be penalised by inadequate management during grain fill. On the other hand, there is little point in intensively managing a low yield potential crop during grain fill.

Vegetative Phase

During this phase no economic yield (i.e., high quality grain) is actually produced, but the potential of a crop to produce yield and quality is established. A crop's potential depends mainly on management during vegetative growth, and most inputs are usually applied (i.e., money is spent) during this period. However, even in unstressed crops, there can be large differences in yield and quality potential by the end of the phase. Our purpose is to consider the cultivar and environmental factors which cause these differences, and how they can be influenced by management.

The yield and quality potential of a crop can be judged by three conditions at the end of the vegetative phase:

- the amount of dry matter present per unit area.
- the amount of nitrogen contained in the dry matter.
- the number of grains set per unit area.

Dry matter production

The amount of dry matter present is the dominant condition. In the absence of any deficiency, nitrogen uptake and accumulation is usually a stable proportion of the amount of dry matter produced (Mirschel *et al.*, 1991). Similarly, potential grain number, which is determined at or soon after anthesis, is related closely to the amount of dry matter accumulated up to that stage of development (Fischer, 1985). Later we will consider the implications for management during grain fill of imbalances due to unusually high or low nitrogen content and/or grain number at the end of the vegetative phase.

The amount of dry matter produced (DM) depends on the daily growth rate of a crop (C) and the duration of the phase (t):

$$DM = C\,t \qquad (1)$$

If t is expressed in days and DM in g/m^2 then C will have units of g/(m^2.day). The daily growth rate depends on the amount of solar radiation intercepted by a crop (Q) and the efficiency with which it is used to produce dry matter (e):

$$C = e\,Q \qquad (2)$$

With Q in MJ/(m^2.day), e has units of g/MJ. Combining equations (1) and (2):

$$DM = e\,Q\,t \qquad (3)$$

Therefore to understand what causes variations of yield and quality potential at the end of the vegetative phase it is necessary to consider the factors which affect e, Q and t.

Radiation use

The value of e is usually stable for stress-free crops. Most C3 crops, including wheat, produce about 1.2 g of dry matter per MJ of solar radiation intercepted (Monteith, 1977; Kumar and Monteith, 1981; Wilson and Jamieson, 1985). Therefore dry matter production depends much more on the amount of radiation intercepted than on how efficiently it is used.

The amount of radiation intercepted (Q) depends on the total amount available each day, the proportion intercepted by a canopy (the interceptance), and the duration of the phase (t). The amount of radiation available is an uncontrollable environmental factor, but the timing and duration of its interception during a season can be partly controlled by choice of cultivar and sowing time. These affect the seasonal patterns of dry matter production by influencing patterns of interceptance and, therefore, interception.

The results of a computer simulation in Figure 1 show how interceptance patterns and t are affected by changing the time of sowing. These patterns differ among cultivars with different responses to temperature and daylength; this example is for a daylength sensitive cultivar. With earlier sowing this cultivar has the opportunity to intercept more radiation during the vegetative phase, and the duration of the phase is substantially longer than with later sowings. The subsequent grain fill phase starts slightly earlier in earlier sown crops, but its duration is similar for all sowings because early sowings reach senescence slightly earlier than later ones.

The consequences of these interceptance differences for DM production during the vegetative phase are shown in Figure 2. In earlier sowings, the amounts of DM produced are greater even though the phase ends slightly earlier. Thus the earlier sowings have higher grain yield potential.

Although we do not consider constraints caused by pests and disease, water or nutrient stresses in this paper, it is important to note that they reduce growth mainly by decreasing the radiation interceptance, and the growth duration (t). Effects on radiation use efficiency are less important.

Crop development

Leaf number and temperature differences cause variations in the duration of the vegetative phase (t) and interceptance, which are key characteristics of phenological and canopy development respectively.

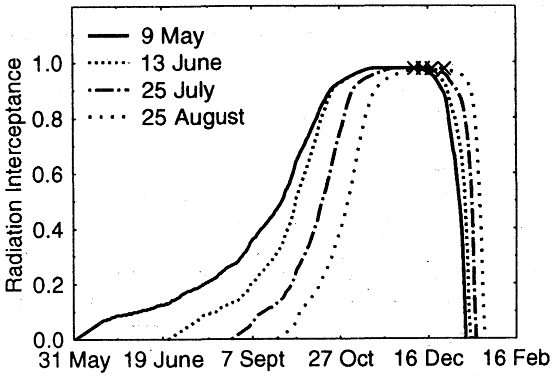

Figure 1. **Computer simulation predictions of the influence of sowing time on radiation interceptance for a daylength sensitive wheat cultivar. The symbol x marks the start of grain fill for each sowing date.**

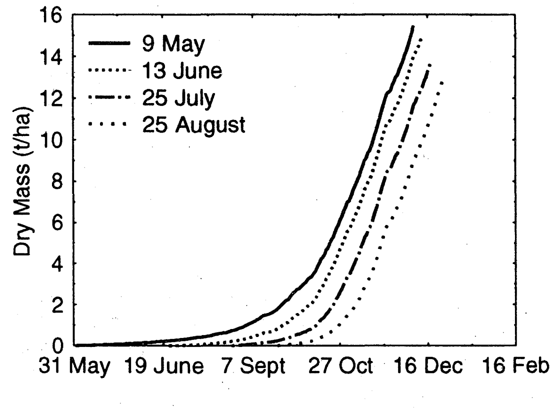

Figure 2. **Computer simulation predictions of the time courses of dry matter production during the vegetative phase for the crops in Figure 1.**

The total number of leaves produced on the mainstem of a wheat plant (final leaf number) is the primary indicator of its phenological and canopy development. This is because the thermal time interval between leaves is very stable (Hay and Kirby, 1991). Cultivars that have an inherent tendency to mature late do so because they produce more leaves before ear emergence. As a result they have a longer chronological duration of the vegetative phase, more opportunity to intercept radiation, and therefore tend to have higher yield potentials.

Some cultivars produce the same final leaf number (typically between 7 and 9) regardless of the environmental conditions they experience. This occurs because their development is insensitive to daylength. The new cultivar Kokako is an example of this type. However, the final leaf number of most cultivars is variable because their development is affected by daylength and, in some, also by chilling (veralisation). Responses to daylength and veralisation are highly heritable, and reflect an adaptation of wheat which results in the convergence of development.

The final leaf number of daylength sensitive cultivars depends on the daylength they experience at plant emergence. They behave like daylength insensitive cultivars, and produce about 7 to 9 leaves if they emerge into long days (i.e., sown in spring), but produce more leaves (up to 14 or more) if they emerge into short days (i.e., sown in winter). This means that the end of the vegetative phase and maturity occur within a short time span, almost regardless of sowing time (Hay and Kirby, 1991). Most cultivars grown in New Zealand are in this category, although the degree of sensitivity to daylength varies among cultivars. For example, Otane has weak sensitivity while Rongotea has stronger sensitivity (I.R. Brooking, personal communication). This means that the convergence of maturity in sowings of Rongotea in winter and spring will be closer than for similar sowings of Otane. Knowledge of these responses influences recommendations about suitable ranges of sowing times for cultivars.

True winter cultivars need a period of exposure to chilling (veralisation) to induce the change from vegetative to reproductive development. When the veralisation requirement is satisfied, the plant apex stops initiating new leaves and begins producing spikelets. If these cultivars are planted in autumn when conditions are still warm they produce more leaves than if planted during winter. When planted in spring, they usually continue to produce leaves indefinitely and fail to develop reproductively. A characteristic of true winter types, such as the European cultivars Crossbow and

Pernel, is that they produce more leaves from a spring than a winter sowing.

Cultivar responses to daylength and veralisation enable adaptation to different conditions. Daylength sensitivity has no advantage at low latitudes where there is little variation in daylength, and true winter habit is a disadvantage where temperatures are never very low. However, these differences give choice and flexibility to the farmer.

The rate of leaf appearance, and therefore the duration of the vegetative phase, both depend on temperature because the intervals between sowing and plant emergence, and of the appearance of successive leaves, are constant in thermal time (Porter *et al.*, 1987; Hay and Kirby, 1991). This is calculated by summing daily mean temperatures when they are above zero, and ignoring them if they are not, (Weir *et al.*, 1984). The thermal intervals between sowing and plant emergence, and between the appearance of successive leaves are about 150 and 100 day °C respectively (Porter *et al.*, 1987; Hay and Kirby, 1991). This means that at a constant mean temperature of 10°C, plant emergence takes 15 days and a new leaf appears every 10 days.

The consequences of these principles for the duration of the vegetative phase are illustrated in Figure 3. The length of the phase decreases as the mean temperature increases, and as final leaf number decreases. For a given location, winter and spring sowings are represented by low and higher mean temperatures respectively in Figure 3. The figure can be used to illustrate the difference that daylength sensitivity makes to the flexibility of a cultivar. Consider the difference in duration between autumn and spring sowing. The daylength insensitive cultivar will always have 7 leaves on the main stem. The change in temperature exposure is the only influence on it, so that the change in its duration with sowing time is quite small. If sown in May it will be exposed to a mean temperature over the season of about 8°C and will have a duration only about 20 days longer than the same cultivar sown in August (mean temperature exposure 9.5°C). In contrast, a daylength sensitive cultivar will extend its duration by adding extra leaves if sown early. In addition, it will develop more slowly in the cooler temperatures. Its extended vegetative duration means that it also experiences some of the warmer temperatures in early summer that are missed by the daylength insensitive cultivar because of its early maturity. Hence a cultivar producing 13 leaves when sown in May will have a mean temperature exposure over the season of 8.9°C. The same cultivar sown in August will have only 7 leaves, and its duration is about 75 days shorter. The May sowing extends the duration of this cultivar by about 65 days. The most obvious effect in the field is that the maturity times of the two sowings are much closer together than for the daylength insensitive cultivar. A good illustration of this is in Figure 1 where the daylength sensitive cultivar had a small span of times for the end of the vegetative phase.

There are two important consequences of this difference. First, daylength sensitivity confers a considerable advantage in extending the opportunity to intercept radiation. Second, a daylength insensitive cultivar sown early is put at risk, because it will flower early when there is a high probability of frost damage.

Nitrogen content and grain set

Nitrogen accumulation and grain set are usually closely related to the amount of dry matter accumulated during the vegetative phase. In unstressed crops, usually about 13 grains are set per g of dry matter present at the end of the phase in New Zealand (P.D. Jamieson, unpublished data) and the nitrogen content of the dry

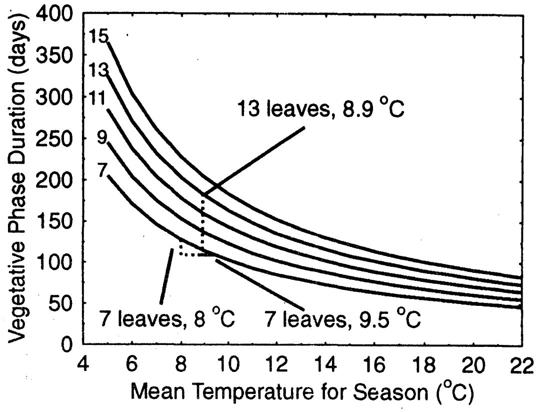

Figure 3. Vegetative phase duration versus mean temperature during the phase. Each curve represents a plant with a different number of leaves on the mainstem. The broken vertical lines show the change in duration for early and late planting of a daylength insensitive (7 leaf) and a daylength sensitive (13 leaf going to 7 leaf) cultivar.

matter is about 1.5% (Mirschel *et al.*, 1991). In well balanced crops, these values lead to the ranges of potential yield and quality shown in Table 1, in terms of the criteria listed earlier. Stresses and variations in nitrogen availability may upset the balance between dry matter production, nitrogen content and grain number, so that typically, values range between 11 and 15 grains set per g of dry matter, and nitrogen contents from 1.1% to 1.8% (Mirschel *et al.*, 1991). The consequences for grain yield and quality of these departures from a well balanced crop are discussed in the next section.

Grain Fill

During this phase the potential grain yield and quality may or may not be realised. From the beginning of grain fill the potential cannot be increased further - the aim during the phase is to minimise potential losses. Therefore it is important to ensure that the established potential yield and quality are realised as far as possible by retaining and completely filling all grains with assimilate with an appropriate nitrogen content. High quality in a milling wheat means large grains with high protein content. The fulfilment of this aim requires that the potential must be realisable within the limits imposed by the environment.

Actual grain yield, the final product of growth during grain fill, can be described as the product of the grain number and the mean grain size or, independently, as the product of the mean grain growth rate and its duration. In contrast, the potential yield is the product of the maximum kernel weight, which is biologically determined and depends on cultivar, and the grain number. To achieve maximum weight each kernel must grow sufficiently fast for long enough. The maximum kernel growth rate is nearly constant for a cultivar (Nass and Reiser, 1975), although it is weakly dependent on temperature (Vos, 1985), so that the chief constraint is the duration of grain fill.

Table 1. Typical ranges of the three crop conditions that represent potential yield and quality in well balanced crops at the end of the vegetative phase.

Dry Matter (kg/ha)	Nitrogen (kg/ha)	Grains/m^2
10000	150	13000
11000	165	14300
12000	180	15600
13000	195	16900
14000	210	18200
15000	225	19500

In unstressed crops, the thermal duration of grain fill is stable at about 700 day °C, and is similar for all cultivars (Hay and Kirby, 1991; Loss *et al.*, 1989). Therefore the chronological duration decreases as the temperature rises. For example, at 13°C grain fill takes 54 days, but at 16°C it takes 44 days. Since realisable yield depends primarily on the duration of the phase, its response to temperature mirrors that of the phase duration (Fig. 4). Consequently yields are higher in cool environments like Southland than in warmer ones like Canterbury.

Even though the thermal duration of grain fill is independent of cultivar, the temperature experienced during grain fill can vary with sowing time and cultivar because these determine the time of the season when grain growth occurs. Therefore chronological durations of grain fill can vary.

Balancing potential with realisable yield

It is vital to maintain the balance between potential to produce yield and quality and the possibility of achieving it. The biological determinant of potential yield is the

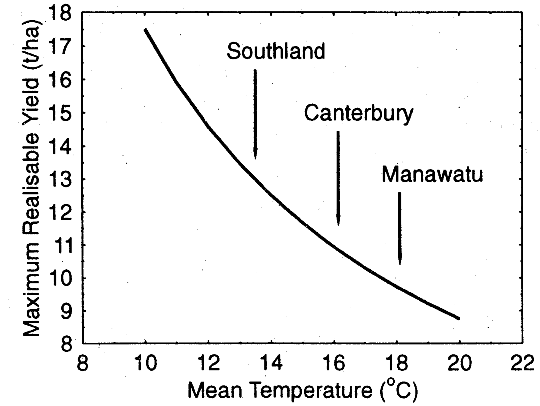

Figure 4. **Maximum realisable yield versus mean temperature during the grain fill phase. Arrows indicate typical mean temperatures during grain fill for New Zealand's three main wheat production regions.**

grain number, which is determined before grain fill starts. The environmental determinant of realisable yield is the duration of grain fill, which depends on the temperature during the phase. These two determinants must be balanced. Conditions and management during the vegetative phase may result in a high grain number, but temperature during grain fill may be too high so that there is insufficient time for the grains to fill completely. There is a corresponding quality penalty because the insufficiently filled grains will be small and the screening percentage will tend to be high.

To some extent, the climate cooperates in making it possible to set a suitable yield potential. In warm climates crop development during the vegetative phase is rapid, and this limits the potential to produce too much dry matter by the beginning of grain fill. Conversely, the vegetative phase is longer in cool climates, and dry matter production is high. The Canterbury climate may be inherently out of balance for wheat production, because relatively cool springs are often followed by hot summers. Therefore conditions may favour the establishment of high yield potential but are not conducive for realising it during grain fill. Hence it is important not to push a crop beyond its realisable yield by excessive management during the vegetative phase, or the result will be small grains and high screenings. Table 2 shows the effects on yield and kernel weight of setting various yield potentials (in terms of grain number) during the vegetative phase when the environment during grain fill is capable of realising a maximum yield of only 8 t/ha. Setting a low yield potential results in a low yield of good sized grain. When the potential yield is the same as the maximum realisable yield, then that potential is realised with good sized grain. However, if the potential is set too high and only the realisable yield is attained, then the grains are small with a high likelihood of unacceptable screenings.

Grain quality, nitrogen and protein

Grain growth relies on assimilate from two sources during grain fill (Austin *et al.*, 1977). Current photosynthesis provides between 70 and 100% of the assimilate. The rest comes from assimilates accumulated during the vegetative phase which are re-mobilised and translocated from storage in the stems and leaves. These can provide up to 30% of grain dry weight. The latter are used to "top-up" demand by the grains for assimilate when production by current photosynthesis is too slow to meet their growth requirements. This dual source is one reason that the grain growth rate is nearly constant for much of the grain fill phase.

In contrast to carbon, up to 90% of the nitrogen contained in the dry matter present at the beginning of grain fill can be mobilised and translocated to the grain (Gregory *et al.*, 1981). This means that in unstressed crops, most of the nitrogen requirement of the grain can be met from reserves in the stems and leaves, provided they contain enough. How this translates to grain protein content depends on the nitrogen content of the vegetative dry matter and the grain yield. Figure 5 shows the grain protein content that results from the translocation into the grain of 90% of the nitrogen in the dry matter at the beginning of grain fill, assuming a range of dry matter nitrogen concentrations. The calculations were based on

Table 2. Yield and grain weight for a 8 t/ha achievable crop at various grain populations.

Grain number (1000/m^2)	10	16	25
Potential Yield (t/ha)	5	8	12.5
Actual Yield (t/ha)	5	8	8
Kernel Weight (mg)	50	50	32

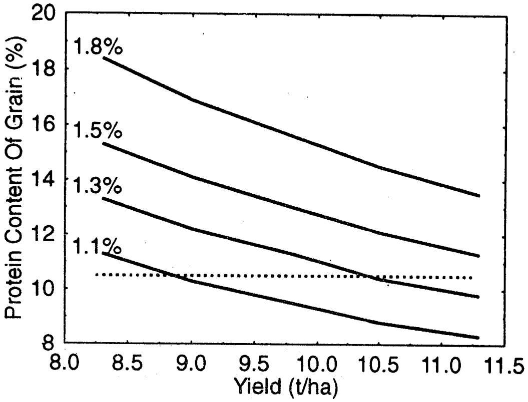

Figure 5. Protein content of grain versus grain yield. Curves represent responses assuming different dry matter nitrogen contents (shown on the lines) at the beginning of grain fill. The horizontal line shows the current acceptable lower limit for protein content in bread wheats (R. Hanson, personal communication).

an assumed 15 t/ha of dry matter at the beginning of grain fill, with potential yields calculated for a range of 11 to 15 grains per g of dry matter.

The achievement of high yield and quality means that nitrogen management should aim to produce grain in the upper right portion of Figure 5. If the nitrogen content of the dry matter and available soil nitrogen are insufficient, then more nitrogen must be added at the beginning of grain fill to make up the deficit and maintain the balance. This is especially so if a cool spring with plentiful rainfall results in high biomass with low nitrogen content at the beginning of grain fill. This is likely to lead to crops with grain in the lower right of Figure 5.

Nitrogen reserves in the leaves and stems are in the form of proteins and amino acids, especially chlorophyll. During grain growth, nitrogen relocation to the grains exceeds nitrogen uptake and assimilation (Spiertz and Vos, 1985). This reduces the photosynthetic capacity of leaves, and hastens their senescence. The grain growth rate, and ultimately yield, are reduced since most of the material for grain growth comes from current assimilate. Hence it is important to have an adequate soil nitrogen supply during grain fill to maintain the nitrogen content of the leaves and delay their senescence through continued nitrogen uptake (Spiertz and Ellen, 1978).

Conclusions

The limits to wheat production and quality are set by environmental, physiological and agronomic factors. Although only agronomic factors are under direct control, knowledge of physiological responses to the environment allows choices, such as sowing time and cultivar, to be made that maximise the benefits and minimise the costs of environmental variation. For example, the potential yield of daylength sensitive cultivars can be increased by sowing early. Conversely, lack of daylength sensitivity is useful if early maturity is required, for instance as a way of avoiding the driest period of summer.

In this paper we have stressed the concept of balance in two senses. The first is the balance between vegetative and grain production: the potential yield set during the vegetative phase must be realisable during the grain fill phase. The second is the balance between biomass production and nitrogen content, needed to ensure that grain protein levels are sufficiently high to ensure good baking quality. This requires that the crop's need for nitrogen is recognised and quantified.

References

Austin, R.B., Edrich, J.A., Ford, M.A. and Blackwell, R.D. 1977. The fate of dry matter, carbohydrates and ^{14}C lost from the leaves and stems of wheat during grain filling. *Annals of Botany* ***41***, 1309-1321.

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

Gregory, P.J., Marshall, B. and Biscoe, P.V. 1981. Nutrient relations of winter wheat 3. Nitrogen uptake, photosynthesis of flag leaves and translocation of nitrogen to grain. *Journal of Agricultural Science, Cambridge* ***96***, 539-547.

Hay, R.K.M. and Kirby, E.J.M. 1991. Convergence and synchrony - a review of the coordination of development of winter wheat. *Australian Journal of Agricultural Research* ***42***, 661-700.

Kumar, M. and Monteith, J.L. 1981. Remote sensing of crop growth. *In* Plants and the Daylight Spectrum (ed. H. Smith) pp. 133-144. Academic Press, London.

Loss, S.P., Kirby, E.J.M., Siddique, K.H.M. and Perry, M.W. 1989. Grain growth and development of old and modern Australian wheats. *Field Crops Research* ***21***, 131-146.

Mirschel, W., Kretschmer, H., Matthäus, E. and Koitzsch, R. 1991. Simulation of the effects of nitrogen supply on yield formation in winter wheat with the model TRITSIM. *Fertilizer Research* ***27***, 293-304.

Monteith, J.L, 1977. Climate and the efficiency of crop production in Britain. *Philosophical Transactions of the Royal Society, London,* ***B281***, 277-294.

Nass, H.G. and Reiser, B. 1975. Grain filling period and grain yield relationships in spring wheat. *Canadian Journal of Plant Science* ***55***, 673-678.

Porter, J.R., Kirby, E.J.M., Day, W., Adam, J.S., Appleyard, M., Ayling, S., Baker, C.K., Beale, P., Belford, R.K., Biscoe, P.V., Chapman, A., Fuller, M.P., Hampson, J., Hay, R.K.M., Hough, M.N., Matthews, S., Thompson, W.J., Weir, A.H., Willington, V.B.A. and Wood, D.W. 1987. An analysis of the morphological development stages in Avalon winter wheat crops with different sowing dates and at ten sites in England and Scotland. *Journal of Agricultural Science, Cambridge* ***109***, 107-121.

Spiertz, J.H.J. and Ellen, J. 1978. Effects of nitrogen on crop development and grain growth of winter wheat in relation to assimilation and utilisation of assimilates and nutrients. *Netherlands Journal of Agricultural Science* ***26***, 210-231.

Spiertz, J.H.J. and Vos, J. 1985. Grain growth of wheat and its limitation by carbohydrate and nitrogen supply. *In* Wheat growth and modelling (eds. W. Day and R.K. Atkin) pp. 129-141. Plenum Press, New York.

Vos, J. 1985. Aspects of modelling post-floral growth of wheat and calculations of the effects of temperature and radiation. *In* Wheat growth and modelling (eds. W. Day and R.K. Atkin) pp. 143-148. Plenum Press, New York.

Weir, A.H., Bragg, P.L., Porter, J.R. and Raynor, J. H. 1984. A winter wheat model without water or nutrient limitations. *Journal of Agricultural Science, Cambridge* ***102***, 371-382.

Wilson, D.R. and Jamieson, P.D. 1985. Models of growth and water use of wheat in New Zealand. *In* Wheat growth and modelling (eds. W. Day and R.K. Atkin) pp. 211-216. Plenum Press, New York.