Chapter 3

Physiological and Numerical Components of Wheat Yield

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INTRODUCTION

Wheat (*Triticum aestivum* L.) grain yields have increased substantially since the 1950s (Slafer, Satorre, and Andrade, 1993; Simmons, 1987; Schmidt, 1984). About half of this yield improvement has resulted from genetic increases in grain yield and the other half is due to improved production technologies and practices. Genetic improvement in wheat yield can be attributed to selection for improved agronomic characteristics conferring either higher yield potential or greater stress tolerance (Slafer, Satorre, and Andrade, 1993; Simmons, 1987; Schmidt, 1984). The exact physiological basis for the genetic gain in grain yield potential is unknown. However, it stands to reason that the physiological processes controlling wheat yield have been altered during the course of yield improvement, and that new cultural practices have changed how these processes affect wheat growth and development.

Crop physiologists have historically taken a reductionist approach when trying to identify the factors that control yield, usually assuming that improvements in only one or a few processes will result in substantial yield increases. Processes identified as having a significant effect on wheat growth and development include nutrient uptake and metabolism, photosynthesis and respiration, carbon partitioning, leaf senescence, and plant water relations. It is now generally believed that wheat grain yield is a function and integration of all these processes, each of which can be altered by the climatic conditions during the growing season and the cultural practices used to produce the crop. Identifying and understanding how these processes interact to regulate yield will aid in the development

and selection of higher-yielding cultivars for specific production systems. Knowledge of how the different physiological processes interact to control yield will also allow scientists to more accurately predict wheat yield responses to management practices.

In this chapter, we will discuss the physiological traits associated with wheat yield and how these traits affect one another. For wheat, these physiological traits affect the number of kernels per m^2 and/or individual kernel weight. A more thorough discussion of how biotic and abiotic stresses affect wheat growth and development is given in Chapters 2, 4, 5, 8, 9, and 10. We recognize that the various classes of wheat grown throughout the world differ in many important physiological and agronomic characteristics, such as vernalization requirement (see Chapter 2) and grain quality (see Chapter 5). However, there are many physiological traits are common to all of these classes of wheat, which will be the focus of our discussion. As will be pointed out, many of these physiological processes occur not only in wheat, but also in a similar manner in other grain crops, such as soybean (*Glycine max* (L.) Merr.) and corn (*Zea mays* L.).

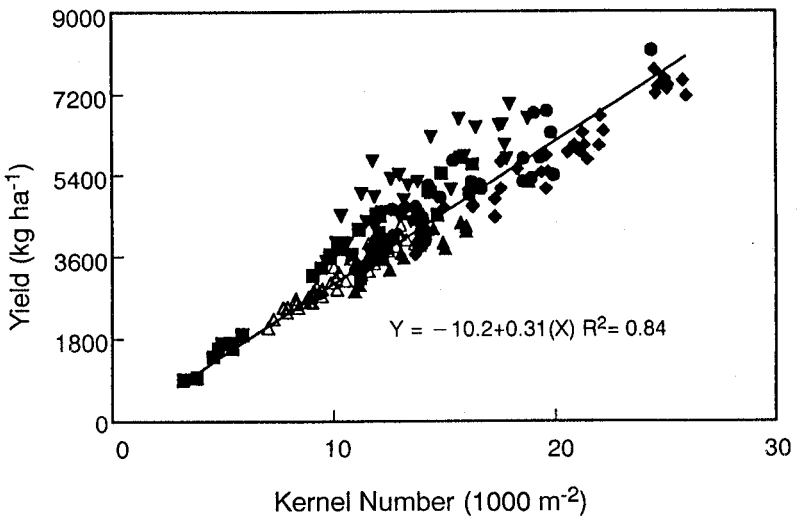
FACTORS AFFECTING KERNEL NUMBER

The number of kernels per m^2 is determined by the number of kernel-bearing tillers per m^2 and the number of kernels per spike. Many factors affect tiller initiation and survival, such as genotype, class of wheat (winter versus spring), cultural practices used (planting date, seeding rate, and soil fertility), and growing conditions (air and soil temperatures, soil water conditions). The effects of these factors are more thoroughly reviewed in other chapters. One aspect of tiller development we would like to discuss briefly is the relationship between timing of tiller appearance and tiller fertility. In general, only those early-formed tillers that are initiated when fewer than four to six leaves are on the main stem will survive to produce a fertile spike (Kirby, 1983). The exact physiological control of this tiller regulation is not known. However, this synchrony in tiller age contributes to a similar anthesis date among tillers on the same plant. Spikelet initiation has been found to occur earlier with respect to leaf appearance and at a faster rate on tillers than on the main stem (Stern and Kirby, 1979), which should also contribute to a synchronized anthesis date among tillers. A similar anthesis date among tillers results in the various stages of grain fill and kernel dry down occurring at about the same time for all spikes on the plant.

The other component of kernel number per m^2 is the number of kernels per spike. For bread wheat, results from the comparison of old and modern

cultivars suggest that yield improvement has primarily been the result of an increase in the number of kernels per spike and, since spike number has changed little, kernel number per m^2 (see review by Slafer, Satorre, and Andrade, 1993). A very close relationship between grain yield and kernel number per m^2 also occurs in soft red winter wheat (see Figure 3.1). Compared to older cultivars, the higher kernel number per spike for newer cultivars is associated with a greater ratio of spike to total aboveground dry weight at anthesis and a greater partitioning of assimilate to spike formation (and less to vegetative structures) during the three-week period prior to anthesis (Slafer, Andrade, and Satorre, 1990; Siddique, Kirby, and Perry, 1989). This period is also when the flag and penultimate (leaf below

FIGURE 3.1. Soft Red Winter Wheat Grain Yield As a Function of Kernel Number per Square Meter for Four Wheat Cultivars



Note: Grown with two levels of spring-applied N in 1994 (•) and 1995 (▼) as reported by Frederick (1997); wheat grown with different rates of spring-applied N under irrigated and nonirrigated conditions in 1992 (◆) and 1993 (■) as reported by Frederick and Camberato (1995a); and wheat produced with different combinations of surface tillage and deep tillage in 1994 (▲) and 1995 (Δ) as reported by Frederick and Bauer (1997) and in 1996 (○) (unpublished data). Each data point is a plot value for each treatment. Regression equation was developed using individual plot values.

flag) leaves are formed, the two most important leaves with regard to photosynthate production during grain fill. Therefore, the occurrence of photosynthesis-reducing stress during this time should decrease both sink demand (number of potential kernels per head) and source supply (leaf area index) for photosynthate.

If genetic yield improvement is the result of a greater partitioning of assimilate to spike formation prior to anthesis, then factors which increase photosynthate supply during that time, such as a high leaf area index and a high leaf photosynthetic rate, should be important in establishing a high kernel number per m^2 in newer cultivars. Research results indicate these associations occur in wheat. Reductions in leaf photosynthesis and leaf area index due to drought occurring prior to anthesis are correlated with reductions in the number of kernels per spike (Frederick and Camberato, 1995a, 1995b). The uptake rate of most essential wheat nutrients is maximum during stem elongation (Karlen and Sadler, 1990). For example, between 70 and 90 percent of the total aboveground N (nitrogen) is accumulated prior to anthesis (Oscarson et al., 1995; Dalling, 1985; Cregan and van Berkum, 1984). Therefore, nutrient deficiencies during this period should reduce both vegetative development and spike formation. In support of this, we found the application of below recommended rates of spring-applied N to result in lower leaf N concentrations and photosynthetic rates prior to anthesis, lower leaf area indices near anthesis, and fewer kernels per m^2 at maturity, compared to instances when higher N rates are applied (Frederick and Camberato, 1995a, 1995b).

The observed relationship between leaf photosynthesis and kernel number per spike has led to the speculation that spike development is directly regulated by photosynthate availability. Mohaptra, Aspinall, and Jenner (1982) and Scott, Dougherty, and Langer (1975) reported that sucrose supply appears to be important for spikelet development. Shading during floret development has been found to result in fewer florets and fewer kernels per spikelet (Stockman, Fischer, and Brittain, 1983). Loss of leaf area prior to anthesis due to insect feeding and/or foliar diseases reduces leaf photosynthate production and the number of kernels per m^2. As stated above, drought stress reduces both leaf photosynthesis (Frederick and Camberato, 1995b) and kernel number per spike (Frederick and Camberato, 1995a). However, the loss of a water potential gradient in growing spike tissue, rather than reduced carbohydrate supply, may be the primary cause for reduced spike growth under drought stress, as has been reported for vegetative growth (Nonami and Boyer, 1989).

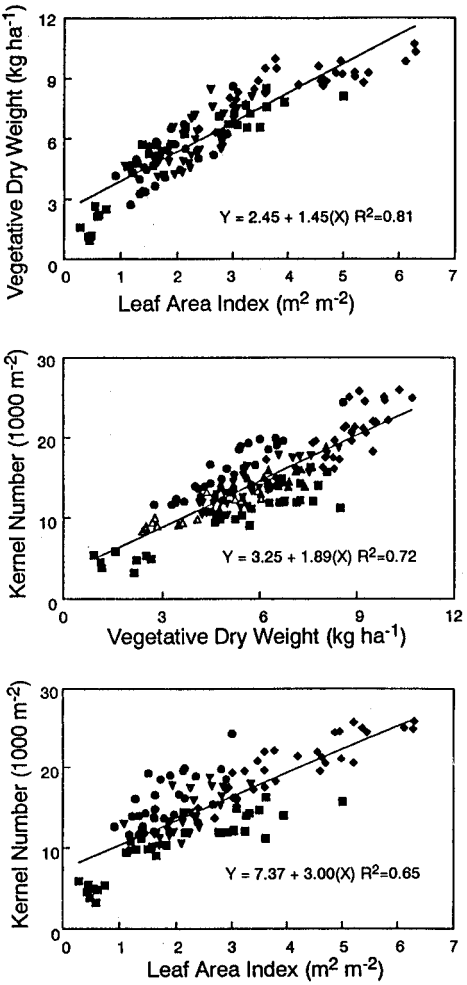
For soft red winter wheat, leaf area index at the boot growth stage (Feekes growth stage 10.0, as described by Large, 1954), total aboveground

dry weight near anthesis, and the number of kernels per m^2 at maturity are highly correlated with one another (see Figure 3.2). The good correlation between leaf area and kernel number per m^2 suggests that the number of potential kernels formed and the plant's potential to produce photosynthate to fill these kernels are either directly or indirectly coupled in wheat. The relationship between leaf area index and kernels per m^2 was linear over the entire range of leaf area indices measured. The lack of a plateau in this relationship suggests that additional yield improvement could be made for high-yielding environments by selecting for higher leaf area indices, at least for soft red winter wheat grown in the southeastern United States. However, a point of diminishing return would eventually be obtained with this approach as the wheat leaves begin to shade one another. When this point of increased shading is obtained, Austin et al. (1976) proposed that a more vertical leaf orientation prior to anthesis should be selected for. The relationship between leaf area index and kernel number per m^2 shown in Figure 3.2 also suggests that yield improvement for cultivars to be grown in lower-yielding environments should involve selection for increased stress tolerance, so that leaf area production and spike formation will continue during periods of adverse growing conditions.

FACTORS AFFECTING INDIVIDUAL KERNEL WEIGHT

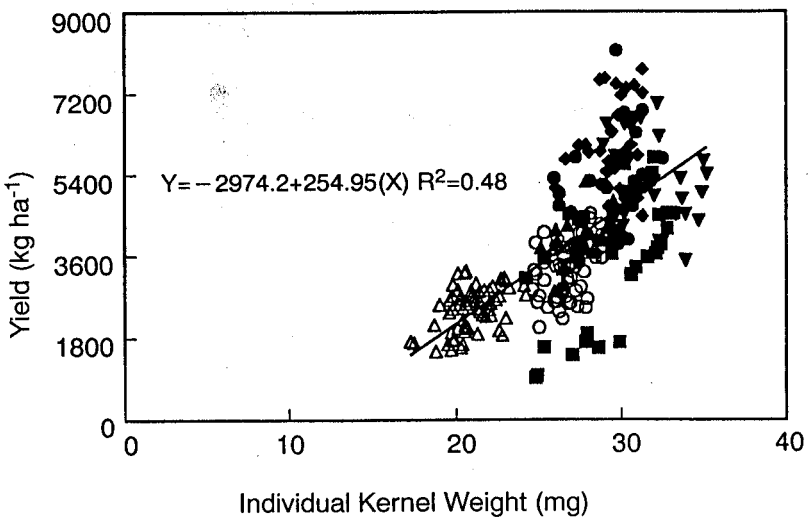
In contrast to kernel number per m^2, there appears to be little relationship between individual kernel weight and grain yield in soft red winter wheat (see Figure 3.3). Reductions in kernel weight generally have less effect on wheat yield than kernel number. For example, shading wheat during the grain-filling period reduces individual kernel weight, but has much less effect on grain yield (see discussion by Slafer, Satorre, and Andrade, 1993). Slafer, Satorre, and Andrade (1993) reported that several studies have shown that kernel weight has been reduced during the course of yield improvement in bread wheat. The lack of association between kernel weight and yield indicates that there has been little success at simultaneously increasing both kernel number per m^2 and kernel weight in wheat. The major limitations to increasing kernel weight under conditions of high kernel numbers are not known, although these limitations must affect the rate and/or duration of grain fill. It seems likely that photosynthate production during grain fill somehow limits kernel weight, as 70 to 90 percent of the grain dry weight comes from photosynthate made during the grain-filling period (Austin et al., 1977; Bidinger, Musgrave, and Fischer, 1977). Only when prolonged periods of photosynthesis-reducing stress occur during grain fill does photosynthate made prior to anthesis

FIGURE 3.2. Vegetative Dry Weight As a Function of Leaf Area Index, Kernel Number per m^2 As a Function of Vegetative Dry Weight, and Kernel Number per m^2 As a Function of Leaf Area Index for Soft Red Winter Wheat



Note: Leaf area index was measured near the boot growth stage and vegetative dry weight was measured near anthesis. Data points are from studies described and referenced in Figure 3.1. Each data point is a plot value for each treatment. Regression equations were developed using individual plot values.

FIGURE 3.3. Soft Red Winter Wheat Grain Yield As a Function of Individual Kernel Weight



Note: Data points are from studies described and referenced in Figure 3.1. Each data point is a plot value for each treatment. Regression equation was developed using individual plot values.

become a significant part of grain yield (Bidinger, Musgrave, and Fischer, 1977). Under normal growing conditions, about half of the photosynthate moved into the grain originates from the flag leaf, with the remainder coming from the spike, leaf sheaths, and penultimate leaf (Rawson et al., 1983). Therefore, the rate and/or duration of kernel growth probably is at least partially limited by the rate and/or duration of photosynthate production by the flag leaf during grain fill.

Factors Affecting Kernel Growth Rate

Grain dry weight accumulation is linear during most of the grain-filling period (see reviews by Simmons, 1987 and Egli, 1994). This linear increase is not specific to wheat, but also occurs in other grain crops, such as soybean and corn (Egli, 1994). The rate of increase in wheat kernel weight appears to be under genetic control (Hunt, van der Poorten, and Pararajasingham, 1991; Darroch and Baker, 1990; Bruckner and Frohberg,

1987), with endosperm cell number having a positive effect on kernel growth rate (Brocklehurst, 1977). Individual kernels on the spike differ in rate of growth (Simmons, Crookston, and Kurle, 1982; Simmons and Crookston, 1979; Simmons and Moss, 1978). However, there is little evidence to suggest the growth rate of a kernel at a specific location on the spike and the average kernel growth rate of all kernels on the spike differ in response to a given treatment. In soybean, these two methods for estimating seed growth characteristics are frequently correlated (Egli, 1994).

When comparing genotypes, only a weak association has been found between kernel growth rate and wheat yield (Frederick, 1997; Van Sanford, 1985). The lack of consistent associations between kernel weight and yield and between the rate of kernel growth and kernel weight suggest that little genetic yield improvement can be made by selecting for higher kernel growth rates. Little association between seed growth rate and seed weight or yield has also been found in soybean (see review by Frederick and Hesketh, 1993).

Several researchers have proposed that increases in leaf photosynthetic rate during grain fill should result in higher wheat kernel growth rates (Frederick and Camberato, 1994; Simmons, Crookston, and Kurle, 1982). However, evidence indicates that this may not be true. Frederick and Camberato (1995b) found that increasing the rate of spring-applied N increased flag-leaf photosynthesis of irrigated wheat during the early stages of grain fill, but had little effect on kernel growth rate (Frederick and Camberato, 1995a). Drought stress during grain fill reduces leaf photosynthetic rate, but has little effect on kernel growth rate (Frederick and Camberato, 1995a, 1995b; Egli, 1994). Selection for higher rates of leaf photosynthesis during grain fill has been found to result in little increase in grain yield (Austin, 1989). The lack of correlation between single leaf photosynthesis and yield across genotypes may be caused by other differences between genotypes that affect leaf photosynthetic rate, such as leaf age, leaf area and thickness, and assimilate demand by reproductive structures (see discussion by Frederick and Hesketh, 1993). Within a genotype, the lack of increase in kernel growth rate when leaf photosynthesis is increased indicates photosynthate supply may not be limiting kernel growth rate, at least during the early stages of grain fill before rapid leaf senescence and loss of photosynthetic activity occur. With respect to obtaining high kernel weights, the duration of leaf photosynthesis during grain fill may be just as important as the rate of leaf photosynthesis.

Increases in leaf photosynthesis during the early portion of grain fill are associated with increases in vegetative dry weight (Frederick and Camberato, 1995b; Kiniry, 1993). Nonstructural carbohydrate concentrations also

increase during this time (Kiniry, 1993; Davidson and Chevalier, 1992; Ford et al., 1979) and probably account for most of the vegetative dry-weight increases. These carbohydrate reserves are found primarily in the stem and are utilized for maintenance respiration and grain fill (Austin et al., 1977). The occurrence of drought during grain fill results in smaller increases in vegetative dry weight (Frederick and Camberato, 1995b) and less stored carbohydrate accumulation (Davidson and Chevalier, 1992) during the early stages of grain fill. However, drought increases the proportion of the grain weight originating from stem reserves, with values ranging from near 10 percent under normal conditions to greater than 40 percent when drought or heat stress occur (Davidson and Chevalier, 1992; Austin et al., 1977; Bidinger, Musgrave, and Fischer, 1977; Rawson and Evans, 1971). Stem reserves may serve to maintain a linear rate of kernel growth when photosynthate production declines during the latter portion of grain fill (Simmons, 1987). Under normal growing conditions, the lag period at the end of grain fill may be caused by the depletion of carbohydrate reserves. Little research has been conducted to determine whether the depletion of stored carbohydrates during the latter portion of grain fill directly affects the termination of grain fill.

There have been several reports of an inverse relationship between kernel number per m^2 and kernel weight (Frederick and Camberato, 1995a; Frederick and Camberato, 1994; Slafer and Andrade, 1993). Two theories involving kernel growth rate have been put forth to explain this phenomenon (Slafer, Sattore, and Andrade, 1993). First, kernels within the spike differ in rate of dry weight accumulation, with kernels in the proximal location of the spikelet and the central section of the spike tending to have higher kernel growth rates than those further out (Simmons, Crookston, and Kurle, 1982; Simmons and Crookston, 1979; Simmons and Moss, 1978). Therefore, increases in kernel number per spike would result in more kernels produced at locations more distal from the center of the spikelet and spike, locations having slower rates of kernel growth. Second, it has been proposed that, if photosynthate production is not increased proportionally to the increase in kernel number, increases in kernel number per spike should result in more competition between kernels for assimilate, resulting in a lower average rate of kernel growth. The latter theory is not consistent with the fact that photosynthate supply during the early stages of grain fill appears to be in excess of grain demand. Therefore, there should be sufficient assimilate to support the growth of more kernels per spike, at least during the first portion of grain fill when canopy photosynthetic rates and vegetative carbohydrate reserves are high. On the other hand, an increase in kernel number without an increase in photosynthate production would probably

result in a faster depletion of vegetative carbohydrate reserves during the latter portion of grain fill when leaf photosynthetic rates are low. This situation would result in a shorter duration of grain fill and lower kernel weights.

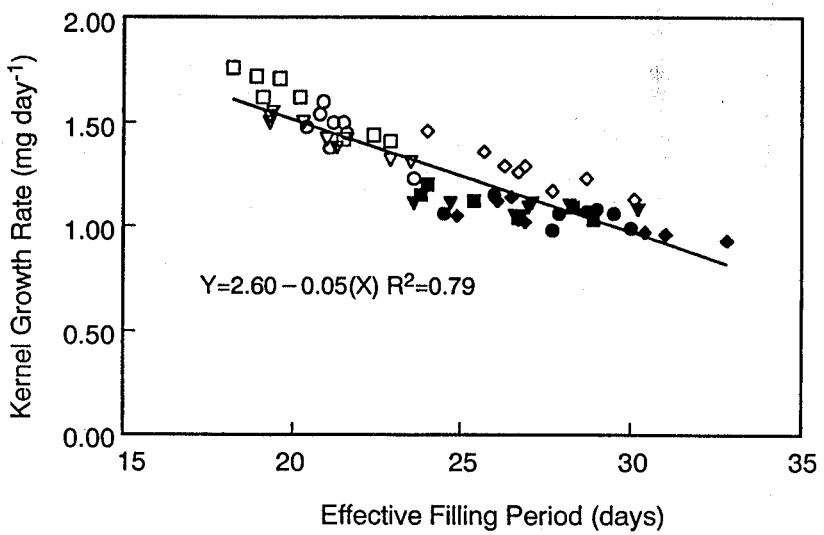
One other explanation may exists for the inverse relationship found between kernel number and kernel weight. The high leaf area index and vegetative biomass associated with a high kernel number per m^2 (Figure 3.2) can result in greater soil water depletion during the growing season and more severe plant water deficits during the grain-filling period. The greater severity of plant water deficits under these conditions results in lower leaf photosynthetic rates and smaller kernels, compared to times when less vegetative growth is produced (Frederick and Camberato, 1995a, 1995b, 1994).

When comparing cultivars, we found an inverse relationship between kernel growth rate and the duration of grain fill (see Figure 3.4). Others have found a similar negative association between these two variables (May and Van Sanford, 1992; Van Sanford, 1985). Frederick and Hesketh (1993) proposed that the high demand for assimilate with high seed growth rates increases leaf senescence, shortens the duration of seed fill, and results in smaller seed in soybean. Similar relationships may also occur in wheat, thus explaining the inverse relationship between the rate and duration of kernel growth shown in Figure 3.4. On the other hand, wheat genotypes with high rates of kernel growth may just proceed through the various stages of kernel development at a faster rate, rather than having a higher kernel growth rate at each stage of kernel development. Breeders must also be aware that selecting for genotypes with high average kernel growth rates can concomitantly cause a selection for fewer kernels per spike (see previous discussion).

Factors Affecting the Duration of Grain Fill

Physiological maturity date is controlled by anthesis date, the rate of kernel growth, and the duration of grain fill. The duration of grain fill, in return, is determined by such factors as plant health and nutrient status, reproductive sink demand for assimilate, and air temperature. The duration of grain fill may also be determined by the capacity of the grain to utilize available assimilates, as determined shortly after anthesis by the number of endosperm cells and starch granules formed (Egli, 1994; Brocklehurst, 1977). However, kernel removal (Simmons, Crookston, and Kurle, 1982) and CO_2 enrichment during grain fill (Fischer and Aguilar, 1976; Krenzer and Moss, 1975) have been found to increase mean kernel weight, indicating that maximum kernel weight is usually not obtained

FIGURE 3.4. Relationship Between Average Kernel Growth Rate and the Effective Filling Period for the Soft Red Winter Wheat Cultivars



Note: Cultivars 'Northrup King Coker 9835' (●), 'Northrup King Coker 9803' (▼), 'Andy' (◆), and 'Gore' (■) in 1994 and 'Northrup King Coker' 9835 (○), 'Northrup King Coker' 9803 (▽), 'Andy' (◇), and 'Gore' (□) in 1995. Data taken from Frederick (1997). Each data point is a plot value for each treatment. Regression equation was developed using individual plot values.

under field conditions. Since carbohydrate supply appears to have little effect on kernel growth rate, kernel removal and CO_2-enrichment treatments must increase kernel weight by increasing the amount of stored carbohydrates available for kernel growth during the latter part of grain fill, thus extending the duration of grain fill. Large-seeded genotypes appear to come closer to obtaining their maximum kernel size than smaller-seed genotypes (Blade and Baker, 1991; Simmons, Crookston, and Kurle, 1982), suggesting that extending the duration of grain fill should result in greater kernel weight increases in small-seeded genotypes.

Since kernel growth rate is linear during most of the grain-filling period, the duration of grain fill can be estimated by dividing kernel dry weight at maturity by the rate of kernel growth. This estimate of grain fill has been termed the effective filling period. The shorter the lag period

before and after the period of linear growth, the more accurate the effective filling period is for estimating the actual grain-filling period.

The duration of grain fill may be controlled by the rate of leaf senescence which, in turn, may be regulated by the N status of the plant and the rate of N demand by the developing grain (see review by Frederick and Hesketh, 1993). As for grain dry weight accumulation, the rate of grain N accumulation is linear for most of the grain-filling period (Sofield et al., 1977). Most of the N in the grain originates from N taken up prior to anthesis (Oscarson et al., 1995; Van Sanford and MacKown, 1987; Waldren and Flowerday, 1979). Wheat retains the capacity to take up N after anthesis (Oscarson et al., 1995; Van Sanford and MacKown, 1987), and late applications of N (at boot stage or later) usually increase leaf N concentration and may delay leaf senescence (Tindall, Stark, and Brooks, 1995; Banziger, Feil, and Stamp, 1994). These observations have led researchers to believe that rapid leaf senescence during grain fill is the result of reduced N uptake caused by the depletion of available soil N, in the absence of late N fertilizer applications (Dalling, 1985). Although little is known about root development and activity under field conditions, it is likely that root growth diminishes and root density decreases during grain fill, which may also contribute to the decrease in N uptake during this time. In any case, these observations suggest that the linear rate of grain N accumulation can be met by either the active uptake of N during grain fill and/or from the remobilization of N from vegetative tissue. Nitrogen remobilization probably is the most important source of grain N under most production systems (Simmons, 1987).

Since N is an important component of the chlorophyll molecules and enzymes associated with photosynthesis, the remobilization of vegetative N during grain fill results in the loss of leaf area and photosynthetic activity (Frederick, 1997; Frederick and Camberato, 1995b; Hunt and van der Poorten, 1985). Frederick (1997) found that the photosynthetic activity of wheat flag leaves decreases rapidly when the developing grain reaches about half of its final size. Therefore, once the flag leaf has senesced, remobilization and spike photosynthesis would be the main (and probably only) sources of carbohydrate for grain fill.

Drought stress reduces wheat N accumulation. Therefore, if the rate of N deposition in the grain is not reduced by drought occurring during grain fill, an even greater proportion of the grain N would originate from remobilized N. This increase in N remobilization and loss of photosynthetic activity would at least partially explain why drought stress during grain fill accelerates leaf senescence and shortens the duration of grain fill (Frederick and Camberato, 1995a, 1995b). Drought during grain fill results in

higher grain protein concentrations, and grain N is usually inversely related to grain yield (Slafer, Satorre, and Andrade, 1993; Terman, 1979). The occurrence of drought during grain fill should have little effect on final grain N content if most of the grain N originates from the remobilization of N accumulated prior to anthesis, and drought has little effect on the rate of N remobilization. On the other hand, if most of the grain carbohydrate originates from photosynthate produced during grain fill, the occurrence of photosynthesis-reducing drought during that time would reduce overall carbohydrate supply (current photosynthate and stem reserves). Therefore, the duration of grain fill would be shortened if the rate of grain dry-weight accumulation remained linear. The maintenance of grain N accumulation, but a reduction in total grain carbohydrate accumulation, would explain why grain protein concentration is higher with drought.

Responses of wheat to management practices designed to extend the duration of grain fill and increase kernel weight may partially depend on the climatic conditions during the grain-filling period. There have been many reports of late N fertilizer applications increasing leaf N concentration and grain protein concentration, but having little effect on kernel weight or grain yield (see discussions by Tindall, Stark, and Brooks, 1995 and Slafer, Satorre, and Andrade, 1993). These responses may partially be due to adverse growing conditions during grain fill. For example, if drought occurs during that time, photosynthesis would be reduced even if leaf N concentrations are high. Consequently, there would be more vegetative N for remobilization to the grain when N is applied near anthesis, but little additional photosynthate produced. This situation would result in a higher grain protein concentration with late N applications, but little increase in kernel weight or grain yield. On the other hand, cool air temperatures and good soil moisture conditions during the latter portion of grain fill would favor delayed leaf senescence, an extended period of photosynthate production, and a longer grain-filling period (Wiegand and Cuellar, 1982), especially with late N applications (Banziger, Feil, and Stamp, 1994). Therefore, under these conditions, the uptake of N during grain fill may result in higher kernel weight and grain yield (Evans, Wardlaw, and Fischer, 1975).

SUMMARY AND STRATEGIES FOR FUTURE YIELD IMPROVEMENT

Research results indicate that genetic yield gains in wheat have been due to a greater partitioning of assimilate to reproductive development, and less to vegetative dry matter production, during the period of spike formation prior to anthesis (see review by Slafer, Satorre, and Andrade,

1993). These changes have resulted in modern wheat cultivars having a high kernel number per spike and kernel number per m^2 (Figure 3.1; Slafer, Satorre, and Andrade, 1993). Less partitioning of assimilate to vegetative tissue may have resulted in modern cultivars having less leaf area per plant and/or less vegetative carbohydrate reserves prior to anthesis than older cultivars. Therefore, newer cultivars are probably more yield sensitive than older cultivars to stresses that reduce photosynthetically active leaf area and leaf photosynthetic rates during the period of spike formation and grain set. This greater reliance of newer cultivars on photosynthate production during the period of spike formation prior to anthesis would explain why yield differences between old and new cultivars are greater in high-yielding (high-photosynthate producing) environments than in low-yielding environments (Slafer and Andrade, 1993; Austin, Ford, and Morgan, 1989). Obviously, there is a limit to the magnitude of yield improvement that can occur by increasing kernel number per m^2 without increasing leaf area, as sink demand would eventually exceed photosynthate production. The linear relationship between leaf area index and kernel number shown in Figure 3.2 suggests that further increases in kernel number of wheat cultivars to be produced in high-yielding environments could be accomplished by selecting for a higher leaf area index. The amount of yield improvement that could be achieved with this approach would depend on the increase in leaf shading at higher leaf area indices.

Selecting for higher kernel numbers in wheat would also take advantage of the better growing conditions that usually occur prior to anthesis, compared to during the grain-filling period. In most wheat-producing areas, air temperatures generally increase and soil water levels decrease during the spring growing season. Good growing conditions prior to and at anthesis would allow the genetic potential for high kernel numbers to be expressed. There appears to be less potential for increasing grain yield by selecting for heavier kernels (Figure 3.3), especially under conditions of high kernel number per m^2. Neither a high kernel growth rate nor a long duration of grain fill have been consistently found to be closely associated with a high kernel weight. The kernel growth rate of wheat cultivars appears to be controlled by the physiological and/or anatomical characteristics of the kernel and/or spike, rather than carbohydrate supply (Thornley, Gifford, and Bremner, 1981; Jenner and Rathjen, 1978; Simmons and Moss, 1978). With respect to kernel demand, it appears that wheat will usually produce photosynthate in excess of grain demand or respirational needs during the first part of the grain-filling period and possibly not enough photosynthate during the latter part of grain fill. Carbohydrate produced in excess of grain needs is stored primarily in wheat stems. The

accumulation of carbohydrate reserves appears to have at least an evolutionary advantage, serving as a source of carbohydrate to maintain grain fill during periods of drought stress (Kiniry, 1993; Gallagher, Biscoe, and Hunter, 1976).

Leaf N concentrations, leaf photosynthesis, and stem carbohydrate reserves all decrease to low levels during the latter portion of grain fill (Frederick and Camberato, 1995b; Kiniry 1993; Ford et al., 1979). Little research has been conducted to determine whether physiological maturity and the termination of grain growth under normal growing conditions in the field are caused by the lack of available photosynthate near the end of grain fill or whether the depletion of carbohydrate reserves is timed to coincide with physiological maturity. Plant water stress probably occurs to some degree during grain fill in nonirrigated wheat. Water stress accelerates leaf senescence, reduces leaf photosynthesis, and results in lower levels of vegetative carbohydrate reserves. These reductions in photosynthate supply are associated with a shorter grain-filling period, indicating that the duration of kernel growth may depend at least partly on carbohydrate availability near the end of grain fill under field conditions.

Further selection for higher kernel numbers per m^2 in wheat, without increasing leaf area index, may result in an earlier remobilization of vegetative C and N during grain fill due to the higher sink-to-source ratio. If the rate of kernel growth is not altered, then a faster rate of leaf senescence and shorter duration of grain fill would result due to the increased demand for C and N. These relationships between kernel number, leaf area, and kernel weight would at least partially explain why kernel weight has decreased as breeders have selected for higher kernel numbers during the course of yield improvement (see review by Slafer, Satorre, and Andrade, 1993).

One possible solution to maintaining the duration of grain fill and kernel weight under conditions of high assimilate demand (high kernel number per m^2) may be to select for a stay-green (delayed senescence) characteristic in wheat, as is found in modern corn hybrids. Most leaves of higher-yielding, modern U.S. corn hybrids remain green and retain chlorophyll until physiological maturity, whereas the leaves of lower-yielding, older U.S. corn hybrids senesce prior to physiological maturity, as in wheat. This stay-green characteristic is different from the delayed leaf senescence associated with a low assimilate demand by developing grain (see Frederick and Hesketh, 1993). In corn, the stay-green characteristic has been reported to be associated with a greater lodging and biotic stress resistance (Duvick, 1992), a greater drought tolerance (Nissanka, Dixon, and Tollenaar, 1997; Frederick et al., 1989), a higher kernel number per

ear (Frederick et al., 1989), a greater total (Tollenaar, McCullough, and Dwyer, 1993) and vegetative (Frederick, Below, and Hesketh, 1990) biomass during the latter portion of grain fill, a greater N uptake during grain fill under both irrigated and nonirrigated conditions (Frederick, Below, and Hesketh, 1990), and a longer duration of kernel fill (Cavalieri and Smith, 1985). Genetic yield improvement in corn appears to have occurred without a large change in leaf area index at anthesis (Tollenaar, McCullough, and Dwyer, 1993). Therefore, modern corn hybrids probably have a higher sink-to-source ratio than older hybrids, as has been proposed for wheat (Slafer, Satorre, and Andrews, 1993). Sustained photosynthetic activity and the high levels of vegetative carbohydrate reserves late into the grain-filling period may allow the duration of grain fill to be extended (or at least maintained) in modern corn hybrids under conditions of high assimilate demand (high kernel number per ear). If this is true, then selecting for a similar stay-green characteristic in wheat should increase the duration of kernel fill and kernel weight of genotypes having a high kernel number per m^2 to leaf area index ratio (high sink-to-source ratio for photosynthate), assuming genes for this trait can be found in wheat.

Carbohydrate reserves have been shown to be of value in maintaining kernel growth during periods of photosynthesis-reducing drought stress in wheat (Kiniry, 1993). On the other hand, vegetative carbohydrate reserves are low during the latter portion of grain fill in wheat (Kiniry, 1993), which should reduce the plant's ability to buffer itself during periods of drought occurring during that time. In addition, carbohydrate reserves used to support grain growth during drought occurring later in the grain-filling period probably cannot be replenished in wheat once the stress is relieved because of the decline in leaf area and photosynthate capacity during that time. The earlier utilization of stem reserves and the loss of photosynthetic capacity when drought occurs late in the grain-filling period would limit carbohydrate supplies, which, in addition to accelerated leaf senescence, may explain why the duration of wheat grain fill is shortened by drought. For corn, the duration of grain fill may not be shortened by drought because of the high levels of stored carbohydrates and the capacity to continue photosynthesis late into the grain-filling period once the stress is relieved. These traits would account for the greater drought tolerance of modern corn hybrids. It seems very likely that a similar trait would benefit wheat produced in regions of the world where drought stress is common during grain fill.

The stay-green characteristic may be of little value for improving wheat yield in most wheat-producing areas if reproductive demand for assimilate is not also increased. Without a concurrent increase in kernel number per

m^2 (increase in assimilate demand), incorporating a stay-green characteristic in wheat would theoretically result in a lengthening of the grain-filling period, as has been proposed for the late application of N fertilizer near anthesis. If growing conditions are warm and dry throughout grain fill (conditions that favor accelerated leaf senescence and a shortened grain-filling period), the stay-green characteristic would have little benefit. However, in wheat-producing areas where climatic conditions are conducive to a long grain-filling period, a stay-green characteristic may enhance photosynthate production during the latter portion of grain fill, resulting in heavier kernels.

In conclusion, there appears to be significant opportunity to further increase the genetic yield potential of wheat. The most promising approach appears to be for breeders to continue selecting for a higher kernel number per m^2, especially for areas where growing conditions become warm and dry during the grain-filling period. There appears to be less opportunity for genetic yield improvement by selecting for heavier kernels either by way of higher kernel growth rates and/or a longer duration of grain fill. Data indicate there has been little success at increasing kernel weight, especially when kernel number is high. However, we have identified several possible limitations to kernel-weight increases under these conditions. Solutions to these limitations may partially depend on the climatic conditions normally encountered during the growing season.

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