TEMPERATURE EFFECTS ON INFLORESCENCE DEVELOPMENT AND GRAIN FILLING OF CEREALS

I. R. Brooking
Plant Physiology Division, DSIR,
Private Bag, Palmerston North.

ABSTRACT

The effects of temperature on reproductive development in cereals are reviewed in relation to the developmental phases of leaf primordia production, spikelet primordia production, floret primordia production, floret development/death and grain filling.

Each phase can be quantified in terms of rate and duration, allowing genotypic and environmental comparisons to be made. Both the rates and durations of each phase are affected by temperature, and in some cases there is a clear overall optimum temperature for the phase. For small grain cereals (wheat, barley, oats), these optimum temperatures are quite low for all phases, whereas those for current maize varieties may be higher. The consequences of seasonal temperature changes are discussed in relation to yield components and grain yield, and it is suggested that more emphasis should be placed on screening genotypes for temperature response during floret development and grain filling.

INTRODUCTION

Cereal grain yields depend on many interacting factors, including genotype, agronomic treatment, and environment. Temperature is but one of the environmental parameters, and this review will attempt to summarise its influence on inflorescence and grain development.

Virtually all of the data available has been obtained from glasshouse or controlled environment studies, and caution must be used in extrapolating to the field crop. Different workers have used either constant or fluctuating temperature regimes, and often there has been no attempt to control soil temperature. The latter point is important, as the shoot apex is at or below the soil surface for the initial stages of cereal development, and soil temperature exerts a major control. It is only after stem elongation has raised the apex well above the soil surface that air temperature exerts a more direct control of development.

This review will concentrate on temperature effects on wheat development as more data is available. Relevant data for maize will be included where it is available.

In order to analyse yield development, it is convenient to break grain yield down to its components, namely:

$$\frac{\text{Grain yield}}{\text{Area}} = \frac{\text{Plants}}{\text{Area}} \times \frac{\text{Ears}}{\text{Plant}} \times \frac{\text{Grains}}{\text{Ear}} \times \frac{\text{Weight}}{\text{Grain}}$$

Plant number is the only component which can be fairly directly controlled, by means of planting density. The remainder are affected by environment, as well as genotype and planting density.

The cereal life cycle can also be conveniently partitioned into "growth stages", which aids the determination of temperature effects on more discrete events. In the past, much use has been made of the "double ridge" stage to separate vegetative and reproductive growth phases. However, as pointed out by Kirby (1974), and as evident from Fig. 1, this is hardly a satisfactory marker for quantitative analyses. Instead, it appears more logical to consider development in terms of the processes involved, namely:

a) Leaf primordia production
b) Spikelet primordia production
c) Floret primordia production
d) Floret development/death and
e) Grain filling.

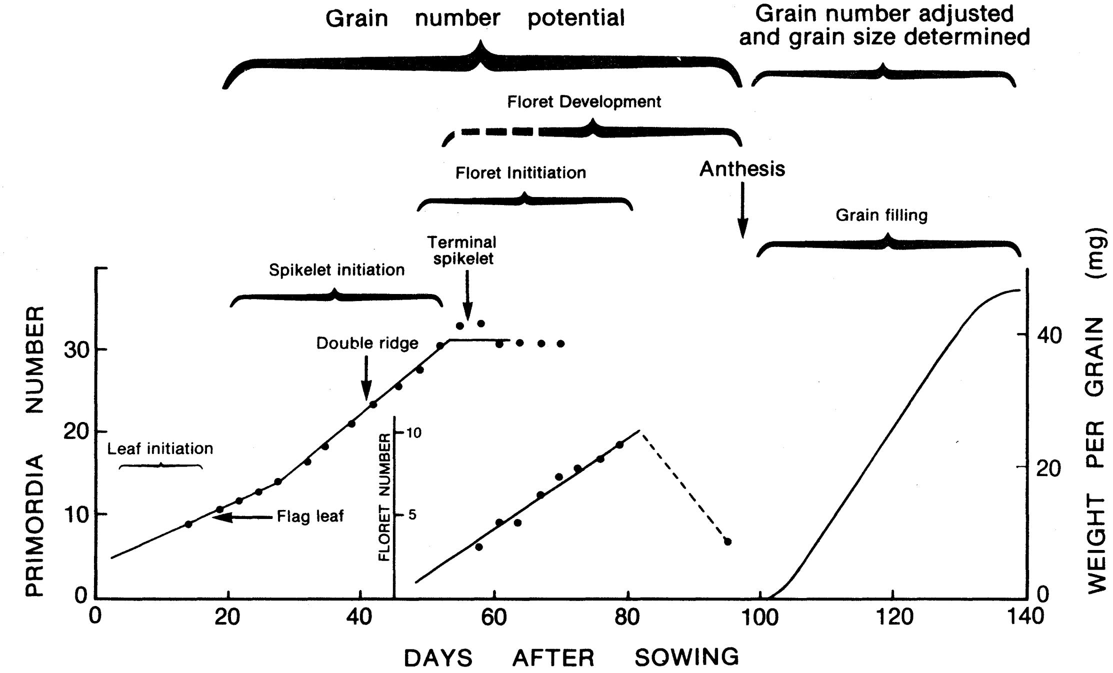
Each of these processes (except floret death) has defined limits (Figs. 1,2) and is amenable to quantitative analysis in terms of rate and duration. Genotypic and environmental comparisons can be made, and each process can be related to final yield components. Grain number is largely a consequence of the pre-anthesis events a) - d), as the sum of these processes determines the number of potentially fertile florets present at anthesis. Events during anthesis/fertilization determine final grain number through effects on floret fertility, and grain weight is influenced mainly by the post-anthesis environment. Thus it is convenient to discuss temperature effects on cereal development in terms of pre-anthesis and post-anthesis events.

PRE-ANTHESIS DEVELOPMENT

Tiller production

Small grain cereals rely on their tillering ability to determine ear number per plant. Although tillering ability shows wide species and varietal variation, tiller production and survival is favoured by relatively low temperatures. Friend (1965b), investigating the range 10-30°C, found fertile tiller production to be greatest at 10°C in Marquis spring wheat, and Rawson (1971) obtained more fertile tillers in spring wheat at a mean temperature of 12°C compared with 18°C. Tiller numbers in the field usually reach a maximum at the onset of stem elongation, so presumably soil temperature exerts the major temperature control on tiller production. With spring soil temperatures in the range of 10-15°C in New Zealand, temperature *per se* should not impose any limitation to tiller production in autumn or spring-sown cerals. Increasing air temperatures during stem elongation may, however, influence the survival of these tillers.

Figure 1: Developmental events in the life cycle of a vernalized winter wheat, Cappelle Desprez, grown in a glasshouse (Brooking, unpublished data).



Most commercial maize varieties are non-tillering, and ear number per plant is dependent on prolificacy. Furthermore, prolificacy appears to be more affected by genotype (Duvick, 1974) and density (Russell, 1968) than temperature.

Leaf primordia production and floral initiation

Temperature can influence the time of floral initiation directly, through affecting the rate and number of leaves initiated, or indirectly through vernalization responses. When the vernalization response is absent or satisfied, leaf initiation rate increases with temperature, while leaf number also tends to increase (Friend *et al.*, 1963; Coligado and Brown, 1975; Quinby *et al.*, 1973). As a consequence, the time to floral initiation tends to decrease with increasing temperature, but may increase again at high temperatures (Halse and Weir, 1974; Rahman and Wilson, 1978; Coligado and Brown, 1975; Quinby *et al.*, 1973). However, the exact pattern is modified by the interacting effects of genotype, photoperiod and vernalization response.

Spikelet production

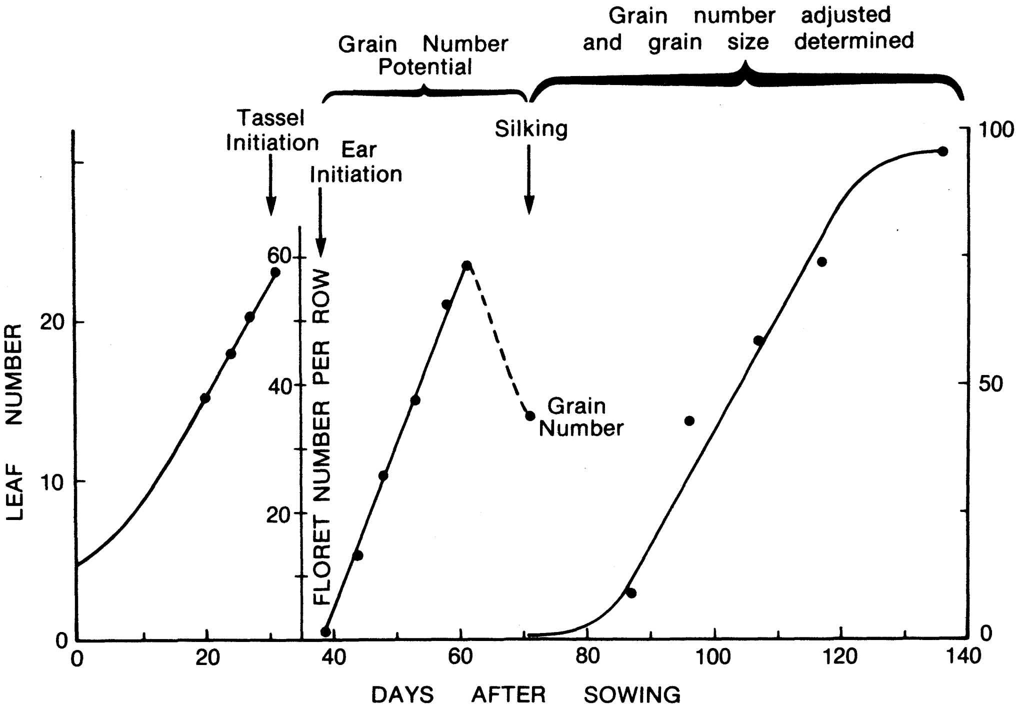
Although there is a large body of information dealing with temperature effects on spikelet number *per se,* there is little accurate data concerning rates and durations of spikelet initiation. This is largely a consequence of using double ridging and terminal spikelet formation to define the spikelet production period, and as is evident from Fig. 1, this leads to inaccuracies in determination of both rate and duration.

From what data is available, it appears that in wheat, the rate of spikelet initiation increases with temperature to a maximum at 20-25°C, and the duration decreases with increasing temperature to a minimum at 25-30°C (Friend, 1965a; Halse and Weir, 1974; Rahman and Wilson, 1978). This results in little overall effect of temperature on spikelet number over the range 10-20°C, if vernalisation responses are first taken into account (Halse and Weir, 1974; Kolderup, 1979; Rahman and Wilson, 1978; Smika, 1974; Wall and Cartwright, 1974). Higher temperatures tend to decrease spikelet numbers. Genotype, photoperiod, and vernalization response are the major interacting factors which affect this temperature response.

At the time of spikelet initiation, the shoot apex is near or below the soil surface, and development rate would be controlled by prevailing soil temperatures. For spring and autumn-sown small-grain cereals in New Zealand, spikelet development generally occurs between September and mid-October, when soil temperatures are around 10-15°C. Temperature *per se* should not therefore be limiting spikelet number production under New Zealand conditions.

For maize, little information is available on spikelet development, and scarcely any on temperature effects. Spikelet production in the maize ear occurs as the stem is elongating, and would presumably be influenced more by air temperature than soil temperature. Hunter *et al.*, (1977) observed a greater number of spikelets on ears of plants grown at constant 20°C compared with 30°C, and some work on tropical maize (CIMMYT, 1974) indicates that the rate of spikelet initiation increases with temperature, while the duration decreases. Of relevance to the New Zealand environment, however, is the genetic variability which apparently exists for

Figure 2: Developmental events in the life cycle of a lowland tropical maize, Tuxpeno planta baja (C6), grown at Tlaltizapan, Mexico (Brooking, unpublished data).



this response. When grown under cool (high altitude) environments, highland varieties show a higher rate of spikelet initiation, and develop more spikelets, than lowland varieties (CIMMYT, 1974). The hybrids currently used in New Zealand are more closely related to tropical lowland maizes (Brown and Goodman, 1977), whereas our temperature environment during the growing season is more closely related to that of the tropical highlands than either the tropical lowlands or the U.S. corn belt (Eagles, 1979). Thus, incorporation of highland germplasm into local hybrids could possibly increase or at least stabilize, grain number potential in maize.

Floret production

In maize and 2-row barley, there is a consistent relationship between spikelet and floret production, as each spikelet produces only one fertile floret, even though 2 or 3, respectively are initiated per spikelet. In 6-row barley, all 3 of the initiated florets per spikelet produce fertile florets. Wheat, however, has an indeterminate meristem in each spikelet, and generally at least 8-10 floret primordia are initiated per spikelet (Kirby, 1974; Langer and Hanif, 1973). Some genotypes can initiate at least 14 primordia (CIMMYT, 1978).

Little is known of how temperature or any other environmental parameter influences floret initiation in wheat, and as 8-10 floret primordia per spikelet are commonly observed, the number initiated may be a fairly fixed genetic character.

Floret development and death

Overproduction of floret primordia is a common occurrence in all cereals. Small grain cereals produce reproductive tillers which never reach anthesis, maize produces secondary ears which abort on fertilization of the primary ear, and in all cases, spikelets and florets are initiated which never produce fertile florets. Therefore, it would seem logical that the processes involved in floret development and death are important, as the number of fertile florets present at anthesis sets the maximum potential grain number. However, this remains one of the most neglected areas of research into the reproductive development of cereals, presumably due to the technical difficulties involved in quantifying floret development.

No data is available for the effects of temperature on floret development *per se,* as treatments have generally commenced at double ridging or terminal spikelet formation. If it is assumed that temperature has little effect on the number of florets initiated per spikelet in wheat, data of Warrington *et al.* (1977) indicate that floret development was favoured by low (15/10°C) temperatures. Similar results were obtained by Bagga and Rawson (1977) for two varieties of wheat, but a third variety was relatively unaffected over the temperature range 15/5 - 25/10°C. No comparable data is available for maize.

Floret development in all cereals occurs concurrently with rapid stem elongation, so that air temperature would provide the major temperature control. As development is rapid at this stage, assimilate supply is also an important interacting factor. Brooking (unpublished data) has shown that the numbers of floret primordia initiated in a dwarf (Hobbit) and tall (Cappelle Desprez) wheat were identical, but that subsequent partitioning of dry matter during floret development favoured the development of more fertile florets in the dwarf variety.

POST-ANTHESIS DEVELOPMENT

Anthesis and fertilization

Temperature *per se* can affect fertility, with grain set in Gabo wheat being greater at 15/10° than either 21/16° or 27/22°C (Wardlaw, 1970). Kolderup (1979) observed a similar response over the range 12° - 24°C, with 15° or 18° being generally the most favourable, although significant varietal differences occurred. High temperatures at anthesis (>32 °C) have been reported to induce complete sterility in wheat (Owen, 1971).

Grain filling

Of all the periods in reproductive development, grain filling has been the most intensively studied, and a useful summary of temperature effects on wheat, rice, sorghum has been provided by Chowdhury and Wardlaw (1978). An increase in temperature generally causes an increase in the rate of grain growth, whilst decreasing the duration. As with spikelet production, these changes are not complementary, resulting in an optimum temperature range for grain size. For wheat, this temperature is relatively low with Chowdhury and Wardlaw (1978) and Sofield *et al.,* (1977) obtaining maximum grain weights at 15/10 - 18/13°C, while maximum grain weights were obtained at a constant 10°C by Spiertz (1977). In contrast, sorghum exhibited maximum grain weight at 27/22°C (Chowdhury and Wardlaw, 1978). Little data is available for maize, but Hunter *et al.* (1977) obtained heavier grains for plants grown at 20°C compared with 30°C.

Summer temperatures in New Zealand during grain filling are therefore generally above the optimum for development of maximum grain size in small grain cereals, and may be below the optimum for current maize varieties. In both cases, water supply would be the major interacting factor with temperature during this period.

CONCLUSION

For small-grain cereals, the New Zealand temperature environment is favourable for the initial phases of tiller and spikelet production, and floret primordia initiation. In fact an over-abundance of floret primordia are initiated. The subsequent rising temperatures during floret development, anthesis and grain filling then serve to cumulatively reduce yield potential through reductions in the number of fertile florets produced, numbers of grains set and grain size. As genetic variability for temperature sensitivity of at least two of these processes exists (Bagga and Rawson, 1977; Kolderup, 1979) it may be worthwhile to screen breeding material for temperature response during development, in addition to the more commonly accepted photoperiod and vernalization responses.

The temperature response of reproductive development in maize is far less clearly understood, and further work is required. This is particularly relevant for maize growth in New Zealand, where the temperature environment could be regarded as sub-optimal, at least for current varieties. It would be useful to know whether temperature does limit floret development and/or grain filling in New Zealand, either directly, or indirectly through effects on lea area development. If this proves to be the case highland material may provide a suitable source of genetic variability to overcome this limitation (Duncan and Hesketh, 1968, Eagles, 1979), and hence stabilize yields.

REFERENCES

Bagga, A. K., Rawson, H. M. 1977. Contrasting responses o morphologically similar wheat cultivars to temperature appropriate to warm temperate climates with ho summers: A study in controlled environment. *Australian Journal of Plant Physiology 4:* 877-887.

Brown, W. L., Goodman, M. M. 1977. Races of corn. In "Corn and Corn Improvement", Ed. G. F. Sprague American Society of Agronomy, Inc., Madison, U.S.A 49-88.

Chowdhury, S. I., Wardlaw, I. F. 1978. The effect of temperature on kernel development in cereals. *Australian Journal of Agricultural Research 29:* 205-223.

CIMMYT. 1974. Maize Improvement. El Batan, Mexico.

CIMMYT. 1978. CIMMYT Review. El Batan, Mexico.

Coligado, M. C., Brown, D. M. 1975. Response of corn (*Zea mays* L.) in the pre-tassel initiation period to temperature and photoperiod. *Agricultural Meteorology 14:* 357-367

Duncan, W. G., Hesketh, J. D. 1968. Net photosynthetic rates, relative leaf growth rates, and leaf numbers of 22 races of maize grown at eight temperatures. *Crop Science 8:* 670-674.

Duvick, D. N. 1974. Continuous backcrossing to transfer prolificacy to a single-eared inbred line of maize. *Crop Science 14:* 69-71.

Eagles, H.A. 1979. Cold tolerance and its relevance to maize breeding in New Zealand. *Proceedings Agronomy Society of N.Z.* 9.

Friend, D. J. C. 1965a. Ear length and spikelet number of wheat grown at different temperatures and light intensities. *Canadian Journal of Botany 43:* 345-353.

Friend, D. J. C. 1965b. Tillering and leaf production in whea as affected by temperature and light intensity. *Ibid: 43.* 1063-1076.

Friend, D. J. C., Fisher, J. E., Helson, V. A. 1963. The effect of light intensity and temperature on floral initiation and inflorescence development of Marquis wheat. *Ibid. 41.* 1663-1674.

Halse, N. J., Weir, R. N. 1974. Effects of temperature on spikelet number of wheat. *Australian Journal of Agricultural Research 25:* 687-695.

Hunter, R. B., Tollenaar, M., Breuer, C. M. 1977. Effects of photoperiod and temperature on vegetative and reproductive growth of a maize *(Zea mays)* hybrid. *Canadian Journal of Plant Science 57:* 1127-1133.

Kirby, E. J. M. 1974. Ear development in spring wheat. *Journal of Agricultural Science (Camb.) 82:* 437-447.

Kolderup, F. 1979. Application of different temperatures in three growth phases of wheat. II. Effects on ear size and seed setting. *Acta Agriculturae Scandinavica 29:* 11-16.

Langer, R. H. M., Hanif, M. 1973. A study of floret development in wheat *(Triticum aestivum* L.) *Annals of Botany 37:* 743-751.

Owen, P. C. 1971. Responses of a semi-dwarf wheat to temperatures representing a tropical dry season. II. Extreme temperatures. *Experimental Agriculture 7:* 43-47.

Quinby, J. R., Hesketh, J. D., Voigt, R. L. 1973. Influence of temperature and photoperiod on floral initiation and leaf number in sorghum. *Crop Science 13:* 243-246.

Rahman, M. S., Wilson, J. H. 1978. Determination of spikelet number in wheat. III. Effect of varying temperature on ear development. *Australian Journal of Agricultural Research 29:* 459-467.

Rawson, H. M. 1971. Tillering patterns in wheat with special reference to the shoot at the coleoptile node. *Australian Journal of Biological Science 24:* 829-841.

Russell, W. A. 1968. Test crosses of one- and two-ear types of

Corn Belt maize inbreds. I. Performance at four plant stand densities. *Crop Science 8:* 244-247.

Smika, D. E. 1974. Optimum crown depth soil temperature for reproductive development of four wheat varieties. *Plant and Soil 40:* 573-580.

Sofield, I., Evans, L. T., Cook, M. G., Wardlaw, I. F. 1977. Factors influencing the rate and duration of grain filling in wheat. *Australian Journal of Plant Physiology 4:* 785-797.

Spiertz, J. H. J. 1977. The influence of temperature and light intensity on grain growth in relation to the carbohydrate and nitrogen economy of the wheat plant. *Netherlands Journal of Agricultural Science 25:* 182-197.

Wall, P. C., Cartwright, P. M. 1974. Effects of photoperiod, temperature and vernalization on the phenology and spikelet numbers of spring wheats. *Annals of Applied Biology 76:* 299-309.

Wardlaw, I. F. 1970. The early stages of grain development in wheat: Response to light and temperature in a single variety. *Australian Journal of Biological Science 23:* 765-774.

Warrington, I. J., Dunstone, R. L., Green, L. M. 1977. Temperature effects at three developmental stages on the yield of the wheat ear. *Australian Journal of Agricultural Research 28:* 11-27.