SIMULATION OF WHEAT ONTOGENESIS

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SIMULATION OF WHEAT ONTOGENESIS

Proefschrift

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1. Research on the effects of *Global Change* in agriculture is challenging because it requires simulation of conceived systems based on system analyses and experimentation conducted with existing systems whereas results can be only verified in traditional ways sometimes in the future if it all

2. The possibility of making fascinating computerized images in remote sensing research may paradoxically affect adversely research that only produce insight and knowledge

3. A modeller may be able to exchange ideas with both agronomists and biologists but then he is often considered an agronomist by the biologists and a biologist by the agronomists. This may be frustrating, but it helps to bridge gaps between both

4. Some cooperation projects with developing countries should concern the foundation and operation of agricultural enterprises. This could be demonstrative for local farmers and would increase food production and employement

5. Reductionism in plant physiology is important for its own sake but it is not particularly helpfull for the description of plant development in response to environmental factors
E.Marrè, Ann.Rev.Plant.Physiol., 1991, 42:1-20
This thesis

6. Poor countries require investments from rich ones for rapid development. These are only brought about in a capitalistic environment under ideologic pluralism, and require that development agencies that support cooperation, mitigate inequity effects of the investments and share in the risk

7. There appear to be considerable biological adaptation to elevated carbon dioxide concentration in the proximity of age-old carbon dioxide springs that are abundant in geothermal areas of Central Italy. Further research in these regions helps to predict the changes that will occur in a carbon dioxide enriched world
F.Miglietta & A.Raschi, Vegetatio, 1992, (in press)

8. Institutional memory should be strengthened. It led for instance to the discovery in this thesis that the leaf appearance rate of wheat is independent of the daylength. This crucial observation was also made 25 years ago, but then overshadowed by the misinterpretation of confusing experimentation
W.H.vanDobben, Mediterranea, 1965, 5:54-59
This thesis

9. The effect of stress on plant development cannot be analysed as long as there is no clear understanding of the regulatory effects of temperature and photoperiod on this development under optimal conditions
This thesis

10. Crop models often assume that growth in weight and area are stoichiometrically related. However, there is so little evidence for this that it is much better to develop independent models for these two growth phenomena and place only some small restrictions to minimum and maximum specific weights
Horie et al., Proc.Neth.Ac. of Sci., 1979, 82: p.433
This thesis

11. Hot weather spells, or exceptionally warm years in the weather records are not representative, and even misleading, with respect to the future weather type during the expected greenhouse climate

12. The Dutch should stand for their language

Stellingen behorend bij proefschrift van F.Miglietta:
Simulation of wheat ontogenesis, Wageningen 8 April 1992

to my father

Foreword

Most of the work contained in this thesis comes from ideas and experiments of some years ago. W.H. van Dobben conducted sowing date experiments in the fourties and later experiments on photoperiodic response of cereals in the laboratory with artificial light which already showed that the rate of leaf appearance is independent of the daylength and that synchronization in the time of flowering is a constant characteristic of cereal crops in the field. These two basic observations were then forgotten in most of the scientific literature. So, I'm very much indebted to W.H. van Dobben for his early work as well as for the discussion we had in more recent times in Wageningen. I'm also gratefull to C.T. de Wit who lead me to rediscover, to understand and to reinterpretate that scientific memory, to G.Maracchi, that discussed most of my work and accepted to include it in the programs of his research institute, in Italy. I must then acknowledge E.J.M.Kirby, J.J.R.Groot and J.R.Porter for discussion and F.Sabatini, G.Tagliaferri for technical assistance, Gon van Laar for her help, and friendly assistance. Finally, I am indebted with entire staff of the Departement of Theoretical Production Ecology and in particular with R.Rabbinge, J.Goudriaan and M.Kropff.

The work contained in this thesis was done between the fall of 1986 and the fall of 1990. This was an exciting period of my life that I spent in the laboratory, in the field and at home. My two daughters Giulia and Bianca came into the world during that period.

The only regret is that my father who was visibly happy when I applied for the admission to the doctorate, could not see this work finished. This thesis is dedicated to him.

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- **Chapter 4: Predicting dates of ear emergence and main stem final leaf number**

- Chapter 5: Effect of variety, nitrogen fertilization and water stress on leaf appearance and final leaf number in the field

ACCOUNT

Parts of this thesis have been included, in part or in whole, in the following publications:

Chapter 2: Miglietta,F. 1989. The effect of photoperiod and temperature on leaf initiation rates in wheat. Field Crop Res. 21(2):121-131

Chapter 3: Miglietta,F. 1991. Simulation of wheat ontogenesis: I. Appearance of main stem leaves in the field. Clim.Res. 1:145-150

Chapter 4: Miglietta,F. 1991. Simulation of wheat ontogenesis: II. Predicting dates of ear emergence and main stem final leaf number. Clim.Res. 1:151-160

Chapter 5: Miglietta, F. 1991. Simulation of wheat ontogenesis: III. The effect of variety, nitrogen fertilization and water stress on leaf appearance and final leaf number in the field. Clim.Res. 1:233-242

GENERAL INTRODUCTION

Aims of the study

Development, in wheat, although a continuos process can be divided into categories or stages. Leaves appear successively on the main stem after emergence and the next leaf appears after the ligule of the youngest is visible. Tillering takes place while leaves are being added and ends after the last leaf on the main stem has developed. Subsequently, the stem extends and the head becomes visible, flowering occurs and the seeds develop. When the seed are mature the cycle is completed. The timing of these phases is dependent upon the environment and the genotype.

The purpose of this book is to describe and understand wheat development and to formulate a simulation model for application under field conditions.

Accordingly, research was undertaken to understand the regulatory mechanisms of wheat development, to quantify, as far as possible, the differences between genotypes and to formulate a model that simulates the succession of development phases of any wheat variety, sown in the field, at any latitude and time of the year under different climatic conditions. Moreover, wheat development was studied in relation to plant morphogenesis as a close correlation was found between the morphological structure of the wheat apex and both the duration of development phases and the form of the growing plant. The growth in weight of the wheat plant is not considered in the present study as the growth in weight and both development processes and growth in area are considered to be to some extent independent of each other.

Outline of the work

In Chapter 1 a short description of the main wheat development phases and a review of literature about the effect of environmental factors upon development is given. Then, in Chapter 2, the effects of photoperiod and temperature on leaf initiation rates are considered and a simple temperature dependent model of leaf initiation is formulated and validated by means of the data of an independent field experiment. The simulation of the appearance of main stem leaves in the field and a model to predict the final number of leaves and to calculate the date of heading is considered in Chapter 3 and Chapter 4 In Chapter 5 the effects of nitrogen nutrition and of water stress is studied by comparing simulations with the results of some independent field experiments and of several experiments described in the literature. In conclusion, the application domain of models is discussed together with the areas where further research is needed.

CHAPTER 1

Overview of the problem

1.1. Wheat ontogenesis

Ontogenesis, in plants, can be defined as the transition between vegetative and reproductive development and the problem of ontogeny can be redefined as "the flowering problem". The principal aim of an ontogenetic study is, therefore, to understand the factors that determine the sudden transition of a vegetative growing point from the production of leafy organs to the formation of floral organs (Schwabe, 1987, Kirby,1969).

Wheat ontogenesis can be observed from different point of views. On the one hand it can be observed from the inside, at the apex level, where all vegetative and reproductive structures are formed and, on the other hand, it can be observed from outside, at the so called phenological level. Although the observations made from these two points of view are related, a marked temporal difference may occur between apical and phenological development (Appleyard et al., 1982). However, a correct treatement of ontogenesis implies the use of both descriptive systems.

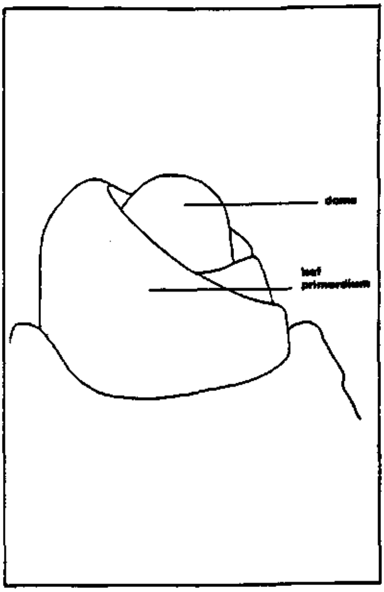

Fig. 1 - A sketch of the wheat apex in the vegetative form (from Kirby & Appleyard, 1986)

1.2. Apical development

In the wheat embryo the apex can be easily observed using a stereo microscope, and accurate descriptions of the different stages of apical development are given by Kirby and Appleyard (1986) and by George (1982). At germination meristematic tissues of the apex become active and more leaf primordia are added. At a later stage, spikelet primordia are formed. Thus, each structure of the wheat plant originates as a primordium by cell division in the shoot apex and the apex can be considered as an early image of the mature plant.

When a wheat seed is sown in suitable conditions it germinates within a few days. At emergence, the coleoptile become visible, at first, above ground and, then, the first leaf emerges from an opening pore at the tip of the coleoptile. At the time of emergence the apex is generally in the vegetative form (Fig.1) and several primordia are visible by dissection. Some of these primordia appear as small bumps on the apex flank, but they can be both leaves or spikelet primordia.

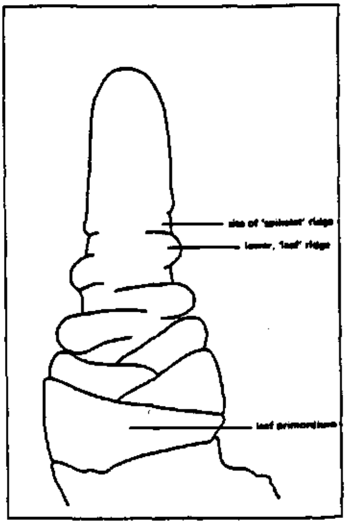

Fig.2 - The wheat apex during the transition from vegetative to reproductive development

This obviously depends on the development stage, that is on the progress made by the plant towards flowering. For this reason a primordium is better designated as "initiated" when its identification as a vegetative or floral structure is univocal. As far as vegetative primordia are concerned, this occurs after a certain size is attained (Dale and Wilson,1979) or, more precisely, when the primordium shape is such that it wraps completely around the apex

dome from which it originates.
The latter definition of "initiated" primordium is used throughout this work. During the vegetative stage of apical development, leaf primordia are subsequently formed and initiated and no great changes occur in the apex structure until floral induction has occurred. The first visible signal of a switch from vegetative to reproductive development is given by the appearance of the double ridges (Fig.2) but it is known that floral induction occurs before the double ridges become visible (Malvoisin,1984, Sharman, 1940, Thomas,1979, Langer and Bussel,1964, Calder,...). When the double ridges are clearly visible at the apex, all the leaves are already initiated and, from this, it may be assumed that the last leaf primordium is initiated shortly before the double ridge stage. Further phases of apical development concern the differentiation and growth of spike structures such as spikelets, glumes, lemmas and florets (Holms,1973, Kirby,1988, Kirby and Appleyard,1986, Pinthus and Nerson,1984, George,1982). These phases are not relevant for the work that is discussed here and thus will not be treated.

1.3. **Phenological development**

When seen from the outside the wheat plant develops through a series of phenological phases that are related with apical development. An early or a late stimulus to floral induction at the apex level has, for instance, a direct effect upon the total number of leaves that are formed and on the earliness or lateness of stem extension and heading. However, some morphogenetic processes like leaf appearance and tillering are only indirectly related to apical development (Klepper et al., 1982, Rickman et al.,1983).

The phenology of the wheat plant has been described since the earliest cereal studies and designation systems were reported by Peterson (1965) to have been in use since 1941. Phenological development is commonly coded by means of descriptive systems. Some are merely a sequence of definitions of the shape and features of the plant as it is seen from the outside and others refer to the so-called growth stage scales. The growth stage scales that are available and in use today differ in the method of designation and in detail. Among them, the methods developed by Feekes (1941), Zadoks (1974) and Haun (1973) are the most widely used. The scale devised by Haun is considered to be the most precise and accurate and it is adopted as a designation system in this work. This scale assigns a number to each leaf on the main stem of the plant. The leaves are numbered consecutively in the order in which they appear. In addition to the leaves, four growth units occur after the last leaf (the flag leaf) is fully developed. These are: flag leaf extension, boot stage, heading and head extension. No designations are provided by the Haun scale for stages of grain growth. Moreover stages of leaf development are divided, in the scale, into sub-stages that result from the calculation of the ratio between the size of the developed leaf and that of the subsequent emerging one. In this way, the Haun scale provides an almost continuous numbering system for the definition of subsequent development phases from germination to anthesis.

1.4. Factors affecting development

Photoperiod and temperature play a major role in determining the developmental response of wheat to the environmental conditions. This is obviously apparent if plants are grown within a range of conditions that can be considered optimal or sub-optimal. However, the effect of moderate stresses upon development patterns of wheat is never large. Neither a moderate reduction of the optimal supply of light nor a moderate water or nutritional stress have a great direct influence upon the timing of development phases (see Chapter 5). Gallagher (1979), found that an increase in the water potential of wheat leaves corresponding to a mild water stress led to a decrease in the rate of epidermal cell extension but had no effect upon the duration of the leaf extension process or upon the timing of phenological development.

Davidson and Campbell (1983) failed to observe, in the growth room, a delay in maturity due to high nitrogen treatments and an acceleration due to moisture stress. Frank and Bauer (1982) and Masle-Meynard (1981) observed that high nitrogen treatments did significantly increase the number of spikelets and kernels per ear but did not affect the duration of the vegetative phase. Friend (1966), Friend et. al. (1967) and Kemp (1981) found that a difference in the total daily radiation received by the plant strongly affected the relative biomass growth rate but did not modify the duration of the growing cycle.

On basis of these observations it is assumed in this work that most of the environmental control of ontogenetic development, in wheat crops, is only dependent upon daylength, temperature, vernalisation and genotype.

1.4.1. **Photoperiod**

The effect of photoperiod on wheat growth and development is studied both in the field and in the growth room. In the field, this is often done by coupling successional sowings with the seasonal and latitudinal fluctuations of natural daylength (VanDobben, 1947, Aitken, 1966, Kirby et al., 1985, Marcellos and Single, 1971, Saini et al., 1986, Stern and Kirby, 1979, Baker et al., 1980, Darwinkel, 1978), by the use of incandescent ligth to extend natural illumination (Paleg and Aspinall, 1964, Paleg and Aspinall,1966, VanDobben, 1964,) and by means of experimental designs involving the transfer of plants from conditions of natural illumination to the dark (VanDobben, 1960, Doroshenko and Rasumow, 1929). In the laboratory, photoperiodic studies are carried out by supplementing the light necessary for growth with a given amount of weak incandescent ligth (Pinthus and Nerson, 1984, Rahman and Wilson, 1977, Rawson, 1971, Riddel et al., 1958a and 1958b, Ryle, 1966, Wall and Cartwright, 1974, Ahrens and Loomis, 1963, Allison and Daynard, 1976, Grant, 1964, Hammes and Marshall, 1980). An illumination of about 700-1000 lux, as provided by incandescent filament lamps, was observed, in fact, to have a strong effect on flowering (VanDobben, 1964).

Wheat is classified as a "long day" plant as development is accelerated by a lengthening in the photoperiod (Vincent-Prue, 1975). In laboratory experiments large varietal differences were found in the dependence of daylength in the number of days from emergence to heading, anthesis or maturity. (Gries et al., 1956, Ahrens and Loomis, 1963, Aitken, 1966, Davidson et al.,1985, Ford et al., 1981, Wall and Cartwright,1974). The photoperiod appears to affect mainly the duration of phases going from germination to double ridge and from double ridge to terminal spikelet intiation (Appleyard et al.,1982, Rahman and Wilson,1977). The first of these two phases coincides, with some approximation, with the vegetative phase of plant growth when the leaves are initiated at the apex. Since leaves are initiated at about the same rate in a constant temperature (Chapter 2), any change in the duration of this phase is therefore, expected to be associated with a change in the final number of leaves that are formed by the main stem. Accordingly, long days were often observed to reduce, together with the duration of the growing cycle, the final main stem leaf number whereas the delay in floral induction and flowering induced by the short days was always associated with an increase in the final number of leaves. Since a close relationship between the final number of leaves formed by the main stem and photoperiodic response of different varieties was demonstrated, the final number of leaves is adopted as a measure of photoperiodic response throughout this work.

There are many references in the literature to differences in tiller number as result of daylength treatement but it was conclusively shown that tillering rate and tiller survival, in wheat as in other graminae, strongly depends on the photosynthetic rate and on the flow of assimilates in the plant (Porter,1985, Dayan et al.,1981). Since only optimal growth conditions are considered in this work, the problem of tillering and tiller survival will be not studied in detail.

Leaf growth, and with this the rate of leaf appearance, was also reported to be affected by daylength, but this was only observed in sowing date experiment in the field where changes in temperature and daylength are correlated. Changes in the rate of leaf appearance were related to the rate of change in the daylength at crop emergence (Baker et al., 1980, Kirby and Eisenberg, 1966, Weir et al.,1984, Travis and Day,1988, Appleyard et al.,1982, Delecolle et al.,1985, Baker and Gallagher, 1983). This was never confirmed in laboratory experiments where daylength and temperature were changed independently of each other (Porter et al.,1987).

Leaf size was also reported to be controlled by daylength. Several authors observed a marked change of the final size of the leaves with their position as result of daylength treatement (Williams and Rijven, 1965, Friend et al.,1967). Kirby and Eisenberg (1966) concluded that the response to the the daylength in terms of changes in leaf size, at least in barley, is closely correlated with the response of ear emergence.

1.4.2. **Temperature**

The influence of temperature upon wheat development is complex. The higher the temperature, the higher the rate of formation of new leaf primordia at the apex, the higher cell division and leaf extension rates (Milthorpe,1959, Williams and Rijven,1965) and with this the rate of leaf appearance. Hence, an increase in temperature is expected to promote earliness of phenological and apical development from floral induction to heading, by promoting leaf appearance.

However, high temperature may also delay floral induction because some wheat cultivars (all the "winter" wheats and some of the "spring" ones) have to experience a given amount of low temperatures after germination, before they can be ripe to flower. This conditioning was originally called "jarovization" by Lysenko and later on renamed as "vernalisation". Vernalisation was defined as "the acquisition or acceleration of the ability to flower by a chilling treatement". Vernalisation of wheat generally requires temperatures of 10°C or less but temperatures below -1 or -2°C have no vernalizing effect (Ahrens and Loomis,1963). Very high temperature (above 30°C) may have a "devernalisation" effect, that is, they can cancel the effect of previously experienced cold temperature. It has been supposed that, in the field, vernalisation is the result of the summation of vernalisation and devernalisation reactions (Trione and Metzger, 1970). It is also reported that the cold requirement of the wheat plant decreases with increasing age (Ahrens and Loomis, 1963, Gott, 1957).

A considerable interaction between vernalization and photoperiodism was observed for winter wheat varieties (Hunt,1979, Rahman,1980). For some spring varieties with low vernalisation requirement, continous light of incandescent lamps completely replaces the vernalisation requirement (Rahman and Wilson,1977) but, on the other hand, vernalisation can be replaced by short day treatement in the early growth stages (Evans, 1987, Krekulè,1961).

The need for vernalisation, or high temperature inhibition of reproductive development delays floral development. This ensures that floral induction does not occur, in middle latitudes, in the long days of autumn when temperature is mild and prevents frost damages during head differentiation at the apex by prolonging vegetative development in early spring (Flood and Halloran, 1984).

Genotypic response to vernalisation is extremely variable and often used as classification key of cultivars. A simple classification of wheat varieties is into "spring" and "winter" types on the basis of their vernalisation response but more accurate classifications are given by Hunt (1979) and Davidson et al.(1985), among others.

1.5. Adaptative significance of wheat development

The season of wheat can be divided into two parts: one during which conditions are relatively benign for growth and survival and one during which they are inimical. Reproduction of wheat is timed that seed formation in the inclement part of the season is avoided. In cool-temperate climates, this is the season when cold or freezing weather is exacerbated by dull and short days. In mediterranean, sub-tropical and arid tropics it is more important to avoid the season of drougth and extreme heat.

Wheat crops rely on environmental signals to trigger their developmental responses to avoid the inclement part of the season and when conditions are favorable, to become ripe to flower and to mature the seeds. However, an immediate response to favourable conditions would not be an effective strategy since it is possible that unexpected temporal changes in weather conditions and unseasonal fluctuations may occur. The daylength is a reliable environmental signal with respect to calendar date in non-equatorial latitudes.

1.6. Development models

An intensive effort has been made, in the recent past, to accurately predict wheat development and several development models were proposed. Despite this effort, some of the problems encountered were not solved and accurate predictions are not yet possible (Porter, 1985).

Most of the existing development models are based on the calculation of thermal time and on the assumed linear correlation between temperature sums and development (see VanKeulen and Seligman,1987 for review). More detailed models make use of thermal time corrected for the effect of both vernalisation and photoperiodic response of varieties (Robertson, 1968, Halse and Weir, 1970, Porter, 1983, Weir et al., 1984).

In linear temperature response models, thermal time is normally calculated as the sum of daily or hourly mean temperature above a given base temperature (Monteith, 1981) and its notion is that the fulfillement of a development process requires that the plant experiences a certain number of units (day-degrees) above that base temperature (Roberts and Summerfield, 1987).

In the models where correction factors for photoperiodic and vernalisation response are used, these are calculated in the form of indices that range from zero to one depending on the daylength and the amount of cold temperature experienced by the plant. These indices are used to calculate the daily or hourly contribution of the actual temperature to the temperature sum (Weir et al., 1984). Wheat is a long day plant, and the photoperiodic factor is assumed to decrease linearly from one, when the daylength is above a given optimal value (normally 16 or 20 hours depending on the variety), to zero, when the daylength is equal or below a given lower value (normally 8 hours). The vernalisation factor is calculated on the basis of a vernalisation response curve and on the basis of the estimated total number of days required by a given variety to be fully vernalised. These curves attributes to any given daily mean temperature a relative vernalising effect that equals zero below a lower and above an upper treshold and reaches a maximum between both.

Both the thermal time and the described correction factors are very simple to be used, but neither the former nor the latter have an undoubtful scientific background. The notion of thermal time implicitly assumes a linear relationship between temperature and the rate of development, that was never demonstrated to exist and that is not always confirmed when thermal time is applied in models (Roberts and Summerfield, 1987). Correction factors represent a too large simplification of photoperiodic and vernalisation responses and their use appears to be too remote from what it is known today about photoperiodism and vernalisation and from that part of this knowledge that can be readily used in the formulation of reliable wheat development models.

There are also models that take into account the effect of growing substances and hormones on development (Schwabe and Wimble, 1976, Trewavas,1986), but these models appear to be more speculative than descriptive or predictive. For this reason they will be not considered here.

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CHAPTER 2

The effect of photoperiod and temperature on leaf initiation rates in wheat

2.1 Introduction

One of the most important morphogenetic processes in wheat is leaf appearance. The appearance of a leaf is normally identified with the time when "the laminar tip becomes visible from the heigth of the uppermost ligule" (Baker and Gallagher,1983a) and it is commonly accepted that the rate of leaf appearance is a constant function of time (Malvoisin,1984 , Gallagher,1979).

The effect of photoperiod on those rates is still under debate. Some authors assume that, for a given temperature and genotype, photoperiodic regimes can influence the process. An increase in leaf appearance rate, for a given thermal environment, was hypothesized for longer daylength (Baker et al., 1980, Kirby et al., 1982, Baker and Gallagher,1983b, Porter,1984, Delecolle et al.,1985, Kirby et al.,1985, Porter,1985).

The aim of this work is mainly to clarify the effect of daylength and temperature on the rate of leaf initiation and on the final leaf number. A linear temperature response model is developed on basis of experimental results found in the literature and it is then tested using field experiment data.

2.2 Model development

The morphology of the wheat apex was thouroughly analysed by Williams (1966) and Kirby and Appleyard (1986). Most of the developmental processes can be clearly observed at that level, and the apex itself can be considered as an early image of the future plant. Differences in apex structure are always reflected by the mature plant. It is widely accepted that the main effect of a longer daylength, both in spring and fully-vernalized winter wheats, is an earlier "ripeness" to flower (Wanser,1922, Friend et al.,1966, Kirby, 1969). The phasic switch from vegetative to reproductive development is represented by floral induction, whose first detectable signs are apex elongation and the appearance of double ridges. When double ridges appear, all the vegetative primordia plus a number of spikelet primordia have already been initiated (Malvoisin,1984).

In very sensitive varieties "short days" can strongly delay floral induction. In some cases the number of days from sowing to the appearance of double ridges in "short days" was twice than in "long days" (Rahman and Wilson,1977). The longer the plant remains in the vegetative phase, the higher the number of initiated vegetative primordia and thus, the higher the final main stem leaf number (Rahman,1980 , Pugsley,1966).

To determine the effect of photoperiod on the rate of leaf initiation (Lr), plants grown under different daylengths, but in a similar radiative climate, can be compared. A proportionality between the number of days from sowing to double ridge and the final number of initiated leaves in different photoperiodic treatements would mean both:

- the absence of any daylength effect on the rate of leaf primordium initiation

- and a linear dependence of the number of leaf primordia that are initiated after seed germination, on the length of the period from germination to double ridge.

In one of the experiments found in the literature, (Rahman and

Wilson,1977), 8 wheat varieties, with differing photoperiodic sensitivity were grown under five daylengths, at the constant temperature of 20°C, and with the same basic illumination of 8 hours per day. The existence of a linearity between the observed final leaf number, that corresponds to the number of initiated leaf primordia, and the number of days to double ridge stage, for that particular experiment, is confirmed by the data shown in Fig.1. Hence, in the considered time interval, the rate of leaf primordium initiation was not affected by photoperiodic treatement.

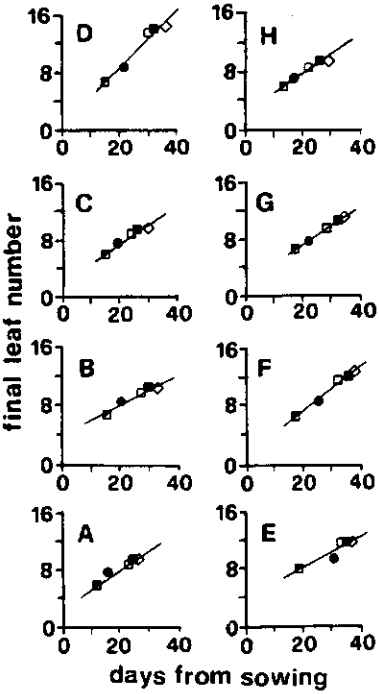

Fig. 1. The final leaf number, i.e. the total number of initiated leaf primordia, observed in different daylength (◇=8, ■=9, □=10, ●=12-15 and ◪=24 h) plotted against the number of days from sowing to double ridge. Fitted lines (see Table 1) are also shown. Variety legend: A, Triple Dirk; B, Gabo; C, Kalyansona; D, Thatcher; E, Selkirk; F, 8-23; G, 8-27; H, Kogat. Data from Rahman and Wilson (1977).

TABLE 1

Linear regression parameters estimated by fitting the final leaf number to time (days) to the occurrence of double ridges, in 8 wheat varieties grown in the laboratory at a mean daily temperature of 20°C (data of Rahman and Wilson, 1977)

Cultivar	Slope (±SE) [primordia/day]	Intercept (±SE) [primordia]	r
Triple Dirk	0.256 (±0.037)	3.33 (±0.795)	0.97
Gabo	0.220 (±0.031)	4.09 (±0.803)	0.97
Kalyansona	0.252 (±0.038)	2.85 (±0.899)	0.97
Thatcher	0.420 (±0.043)	0.65 (±1.200)	0.98
Selkirk	0.213 (±0.052)	4.08 (±0.718)	0.92
8-23	0.299 (±0.023)	1.85 (±0.718)	0.99
8-27	0.250 (±0.017)	2.77 (±0.477)	0.99
Kogat	0.247 (±0.030)	3.26 (±0.030)	0.98
$\bar{x}$	0.270 (±0.066)	2.86 (±1.150)	

Regression coefficients of linear equations fitted on those data are summarized in Tab.1. Intercepts are an estimate of the number of initiated leaf primordia at the time of emergence, which depends on the number of primordia that exist in the embryo. That number normally ranges fom 3 to 4 (Kirby and Appleyard,1986 , Lucas,1972, Kirby et al.,1987). Except for the cultivar Thatcher, slope coefficients range from 0.21 to 0.30 primordia per day, suggesting low genotypic variability in the rate of leaf primordium initiation.

Leaf primordium initiation rates are temperature dependent. For any thermal treatment the mean effect of temperature on the rate of leaf initiation (Lr) can be determined by fitting a straight line to the relationship between the final leaf number and the time from emergence to the double ridge stage. Since Lr is independent of photoperiodic treatements, and its genotypic variability is not large, data of different daylength experiments and different varieties can be pooled. The average intercept of a regression equation represents again the number of primordia already initiated at the time of emergence, whereas slope estimates mean Lr for various temperatures.

The method used to compute Lr implies a definition of "initiated leaf primordium" that differs somewhat from classic observations: a primordium must be considered a "true" initiated leaf when its shape is such to wrap around the apex and not as it first appears, as a small protrusion, on apex flanks. Double ridges appear, in fact, when the last leaf primordium becomes a "true initiated leaf". According to the definition, the time of floral induction can be then separately estimated to occur one plastochrone earlier than the double ridge stage, on the basis of the general form of the relationship between phenological stage and the number of primordia present (Stern and Kirby, 1979).

Data from 148 observations made upon a total of 42 wheat varieties tested in 8 different indoor experiments found in the literature, were used for statistical analysis (Allison and Daynard,1976 , Davidson,1985, Halse and Weir,1970, Holmes,1972, Levy and Peterson,1972, Pirasteh and Welsh,1980, Rahman and Wilson,1977, Rahman,1980). Results obtained for different thermal treatments are summarized in Tab.2, and the linear dependence of Lr on temperature is shown in Fig.2. Points in the figure are fitted by the following regression equation:

$$Lr = -0.0308 + 0.0149\,T \qquad [1]$$

where

T = mean daily temperature in °C

Equation [1] represents a simple, linear temperature response model of leaf initiation, but estimates of Lr response to temperature differ to some extent from those found by other authors (Baker and Gallagher,1983, Kirby et al.,1987). Such a difference, however, simply arises from the different criterion in the definition of an "initiated leaf primordium".

TABLE 2

Linear regression and correlation (r) coefficients estimated by fitting at 4 temperatures, the final leaf number upon the time (days) to the occurrence of the double ridges

Temperature (°C)	N	P_e (±S.E.) [primordia]	L_{ir} (±S.E.) [primordia/day]	r
≈11	59	4.23 (±0.299)	0.1286 (±0.007)	0.915**
≈12	8	5.12 (±0.986)	0.1382 (±0.0033)	0.866**
≈17	8	1.96 (±1.430)	0.2217 (±0.038)	0.964**
≈20	73	3.09 (±0.337)	0.2604 (±0.014)	0.907**

N indicates the number of observations used for calculations. For other variables and data sources, see text.

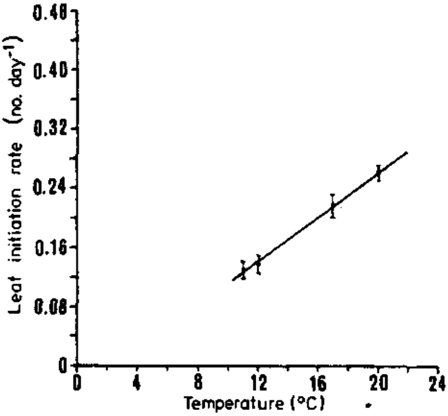

Fig. 2. Linear response of leaf initiation rate (L_{ir} = leaves per day) to temperature (°C). Vertical bars indicate standard errors of mean and the equation of the fitted line is given in the text [Eq.1]. See text for data sources.

To evaluate model errors, the dates of double ridges were recalculated for each observation according to the equation:

$$D = \frac{F_l - E_p}{Lr} \qquad [2]$$

where

D = number of days from germination to the occurrence of the double ridge

F_l = final leaf number observed at ear emergence

E_p = number of vegetative primordia already initiated at plant emergence (average number=3.5)

and results were compared with observed data. The scatter diagram of observed and fitted values of D is given in Fig.3.

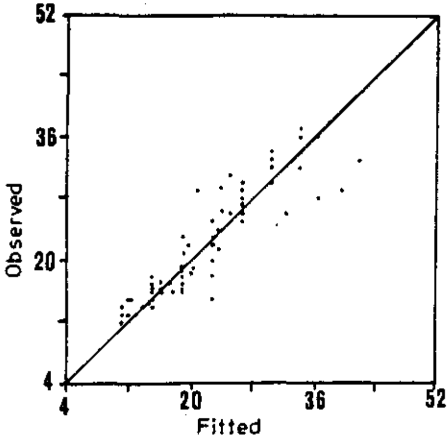

Fig. 3. Scatter diagram of fitted and observed number of days to double ridge for a total of 148 observations on 42 varieties. See text for data sources.

2.3 The field experiment

A field experiment was carried out to evaluate the adaptability of the model to field conditions.

Materials and methods

A winter wheat cultivar (Maris Huntsman) and a durum wheat (Creso) were sown in four large plots on two dates

(November,11th, 1986 and February,5th, 1987, on a clay loam soil, at the experimental farm of Florence University (latitude 43°50" N), following normal agricultural practices . Ten plants from each plot, randomly chosen, were harvested every two or three days from emergence onwards, and the Haun stage was determined scoring main stem leaf development on each plant (Haun,1973). Apex growth was monitored, by microscopic dissection, until the occurrence of the double ridges, and the total number of initiated leaf primordia was recorded. To make field measurements comparable with most of the literature data, where the date of double ridge is recorded, each leaf was considered to be initiated when its shape was such to wrap around the apex. Dry and wet bulb temperatures, soil temperature profiles, global radiation, wind speed and direction were recorded using field mobile meteorological equipment (Benincasa et al.,1984).

2.4 Results

The linear temperature response model of leaf initiation rate given in equation [1] was tested using data of the field experiment. Daily mean soil temperature at 2 cm. depth was used in the calculations, taking into account that the wheat apex remains below ground until the stem starts to elongate. However, model output differences are very small if air, instead of soil, temperature is used. A base temperature of 2°C for apex growth was assumed, according to the intercept of equation [1], but an observation made during an adjacent indoor experiment for seed vernalization showed that very slow apex growth is detectable at 1°C (Miglietta, unpublished data). This implies non-linearity in the lower part of the fitted curve. Due to small variation in results, this aspect was neglected in model runs. In the model, the time of the double ridge stage is estimated as the moment when the last vegetative primordium wraps around the apex, the ordinal number of the last leaf primordium has been inferred by main stem final leaf number measurements, made in the field. Plots of observed and predicted numbers of initiated leaf primordia over time are given in Fig.4, for both sowing dates and tested varieties. Estimated and observed dates of double ridge occurrence and observed final main stem leaf number, are summarized in Tab.3.

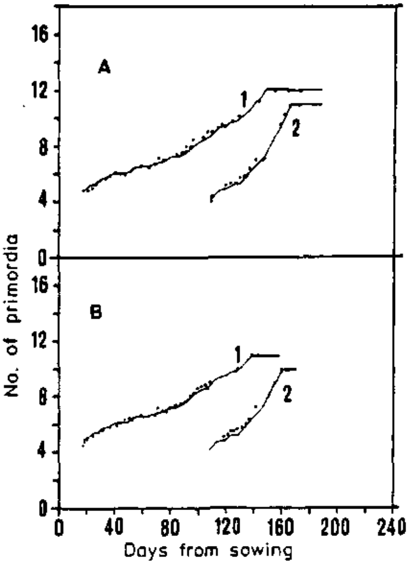

Fig. 4. Simulated (solid line) and observed (dots) number of vegetative primordia, initiated in the field, since the time (days) of the first sowing. A, Maris Huntsman; B, Creso; 1, November sowing; 2, February sowing.

TABLE 3

Observed final main stem leaf number (L_{fn}), observed dates (DR) and model estimates (E) of double-ridges occurrence in the field for both tested varieties and sowing dates

Variety	Sowing date	L_{fn}	DR	E
Maris Huntsman	21 Nov. 1986	12	3- 6 Apr.	4 Apr.
	5 Feb. 1987	11	26-30 Apr.	29 Apr.
Creso	21 Nov. 1986	11	28-30 Mar.	1 Apr.
	5 Feb. 1987	10	20-22 Apr.	22 Apr.

The good agreement between predicted and observed data confirmed both the hypothesis of a low variability of leaf initiation rates among varieties and their independence of photoperiodic regime.

2.5 Conclusions

It is concluded that:

- the rate of vegetative primordium initiation is independent of daylength

- for photoperiodic sensitive varieties, the final leaf number decreases with increasing daylength

- the rate of leaf primordium initiation increases with increasing temperature

- this temperature response curve may differ somewhat for different cultivars, but most genotypic variability is in the response of final leaf number to photoperiod and vernalization

- when the final leaf number can be predicted on basis of photoperiodic sensitivity and vernalization requirements of varieties, the time of floral induction or of the double ridge stage can be estimated by the temperature response of leaf initiation rate.

Since leaves are initiated at the same rate under different photoperiodic regimes, leaf appearance rate is likely to be also independent of the daylength. A detailed study of the mechanism involved in the regulation of leaf primordium extension from the apex to the point of emergence, is, however, needed to explain observed differences in leaf appearance rate among plants sown at different dates.

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CHAPTER 3

Simulation of the appearance of wheat main stem leaves, in the field

3.1 Introduction

Leaf appearance, in wheat, is the result of two distinct processes: leaf primordia initiation and extension. When optimal growth conditions occur, both are mainly controlled by temperature. It was shown, in the previous chapter that leaf primordia initiation is independent from the daylength because a proportionality was, demonstrated to exist between the time taken from sowing to the occurrence of double ridges and the final number of initiated vegetative primordia. If the rate of leaf initiation is independent from daylength, the rate of leaf appearance is expected to be independent as well. However, a difference in the rate of leaf appearance is always observed, for crops sown at different dates, when measured at the same time. Leaves of later sown crops are always observed to appear faster.

Such behaviour can be explained by means of two contrasting hypothesis:

Hypothesis 1 - there is an effect of the date of sowing on the rate of leaf appearance that makes later sown crops to have higher leaf appearance rates

Hypothesis 2 - the time taken by each leaf primordium to extend from the apex to the point of emergence, increases for each subsequent leaf, leading to non-time constant phyllochrones, or, in other words, to a constant decline in the rate of appearance of subsequent main stem leaves

Hypothesis 1 is commonly accepted on basis of the observation that main stem leaves appear at approximately constant rates, when plants are grown under constant conditions (Biscoe et al.,1968, Malvoisin, 1984).

In this paper leaf appearance process is re-discussed, some experimental observations, found in the literature, are analyzed and interpreted by means both of hypothesis 1 and hypothesis 2. Hypothesis 2 is finally assumed to be the more realistic, and on its basis a leaf appearance model is developed and tested by means of original and published field experiment data.

3.2. Model development

Kirby, Appleyard and Fellowes (1985), sowed Norman winter wheat in the field, in Cambridge (Latitude 52°11'N), at four dates, during the season 1980-81. Leaf appearance measurements of different sowings overlapped for certain periods so that it is possible to compare leaf appearance rates of different crops. Linear regression analysis of number of leaves on time for monthly periods of overlapping of leaf production, allows to calculate, for istance, mean monthly leaf appearance rate of September and October sowings. Phyllochrones corresponding to those estimates can be calculated as the reciprocal of observed rates, and, as it is expected, these appear to be almost always shorter in the later sowing. The data are summarized in Tab.1 where the corresponding number of emerged main stem leaves over time, is also given.

Differences among the two sowings can be interpreted by means both of hypothesis 1 and 2:

- in the first case, there is a mean difference of about 11% between phyllochrones of the two sowing dates

- in case of hypothesis 2, the difference between phyllochrones is understood, if it is assumed that each phyllochrone is about 2% longer than its predecessor. A 2% increase amounts to 12 hours of variation between phyllochrones, for an initial phyllochrone of 25 days, and to about 7 hours for an initial phyllochrone of 15 days. The rate of change in subsequent phyllochrones is so small that the decline in leaf appearance rate, easily escape detection in experiments under controlled conditions, and this the more because these are often run at even higher temperatures. If, for istance, the leaf number 6 takes four days to emerge, the leaf number 7 is expected to emerge in four days and two hours.

Month	Lr_1	Lr_2	Ph_1	Ph_2	N_1	N_2
November	0.068	0.074	14.7	13.4	6.0	1.4
December	0.040	0.038	25.0	26.5	7.4	2.6
January	0.035	0.049	28.1	20.5	8.5	4.0
February	0.047	0.049	21.4	20.5	9.8	5.5
March	0.064	0.067	15.5	15.0	11.6	7.4

Table 1. Monthly average of daily leaf appearance rates (*Lr*: leaves d^{-1}) and the corresponding phyllochrones (*Ph*: d), as measured in the field for September (1) and October (2) sowings (data from Kirby et al. 1985). Numbers of emerged main stem leaves (*N*) in each sowing are also reported

Whatever the accepted hypothesis, each leaf primordium has to extend, after initiation, up to a given length before it can emerge from the sheat of the previous leaf, and the distance it has to cover from the shoot apex up to that point, increases for each subsequent leaf (Gallagher,1979). Hence, constant phyllochrones can only occur if leaf extension rate of subsequent leaves increases proportionally to the the increase in the distance from the growing point to the point of emergence. It is practically impossible to determine this by means of leaf extension measurements, because these are cumbersome and rather inaccurate. Various plant parts, as sheats, lamina and internodes, are, in fact, involved in leaf extension as measured by rule or auxanometers (Gallagher,1979).

Plant behaviour can be, better investigated, for that purpose, by comparing the number of emerged leaves (L) with the total number of initiated vegetative primordia (P = emerged leaves+non emerged leaf primordia) at any given time of the growing period until the occurrence of double ridges. For such a comparison, observations made upon several varieties, grown under several climates, can be pooled. If an exact balancing exists between distances and rates of extension, the number of emerged leaves should result from the simple relationship:

$$L = P - 4 \qquad [1]$$

because, at crop emergence, the number of already initiated primordia is about four (see Chapter 1).

In Fig.1, data from both field and laboratory experiments, found in the literature, are shown. In the figure dots denote experimental observations (see legend of Fig.1 for data sources) and the dashed line A indicates the linear relationship of equation [1]. The observations deviate from that straigth line, indicating that phyllochrones are longer than corresponding plastochrones and that this difference tends to increase. This is in accordance with hypothesis 2.

On basis of this hypothesis a model to calculate the number of leaves (L) is now formulated. In the model, the rate of primordia initiation is calculated as a linear function of temperature (see Chapter 1) according to:

$$dP/dt = -0.038 + 0.0149\,T \qquad [2]$$

where

T = temperature, in °C

the rate of leaf appearance, for each subsequent leaf, is then calculated with:

$$dL/dt = dP/dt\,(1 - \alpha L) \qquad [3]$$

Finally, the potential number of emerged leaves is estimated as the integral of leaf appearance rates, according to:

$$L = \int dL/dt \qquad [4]$$

This potential number of emerged leaves is infinite, but the actual number of leaves is of course limited, depending on the genotype and environment.

Parameter α of equation [3], is expected not to be too far from the percentage of increase in phyllochrone time measured by Kirby et al. (1985), in the field. To calculate its value, equations [3] and [4] were fitted to the data of Fig.1 by means of a modified Newton's method of non-linear fitting (Ross,1975). The value of parameter α appears to be very close to field observation (a=0.03), and the line B of Fig.1 presents calculated results.

It is concluded that the increase in the distance between the apex and the point of emergence for each subsequent leaf, is not counterbalanced by higher leaf extension rates. Pending further experimental confirmation, this model of leaf appearance is tested by means of field experiment data found in the literature and obtained from two independent experiments, in Italy.

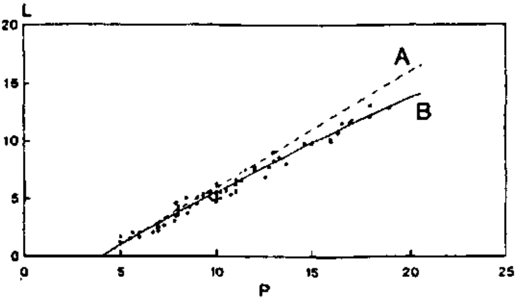

Fig. 1. Relationship between the number of emerged leaves (*L*) and the total number of initiated vegetative primordia (*P*). Data from Williams & Williams (1968), Aitken (1971), Syme (1974), Baker & Callagher (1983), Thomson (1985) and Miglietta (unpubl.) for a total of 40 wheat cultivars. The dashed line A indicates the linear relationship of Eq. (4) and the continuous line B presents fitted values of the non-linear relation given in Eqs. (2) and (3)

3.3. **Experimental**

Experiment 1

A first experiment was carried out in the field at the experimental farm of Florence University (43°,55' N of latitude). A winter wheat (Maris Huntsman) and a durum variety (Creso) were sown at two dates. The first sowing was performed on November 12th,1986, and the second on February 5th,1987, both with 10 cm. row spacing, on four large plots of 1000 m^2 each.

After crop emergence, 25 plants, randomly chosen, were harvested on each plot, every 3 or 4 days. Leaf development was estimated by averaging Haun stage measurements (Haun,1973) made on a sample of 10 plants. Modal plants in the sample were then used for apex observation (Kirby and Appleyard,1986) and primordia counts (see Chapter 1), an the remaining plants for leaf size measurement, leaf area estimation and tillers count. A non destructive sample, of 25 plants per plot, was also used to estimate the final, main stem, leaf number (Kirby and Appleyard, 1986).

Dry and wet bulb temperatures, soil temperature profiles, global radiation, wind speed and direction were recorded every 30 minutes, and daily averaged, all along the season, using a mobile meteorological equipment (Benincasa et al., 1984).

Experiment 2

Winter wheat plants of the variety Maris Huntsman were grown in the open, at Florence University, which is located 1 km. north of the experimental farm, from August 6th,1987, in 8 large pots (50 cm. length, 30 cm. width and 40 cm. depth), on a mixed soil (sand+organic). Two rows were sown on each pot, irrigation was automatically provided, twice a day, and a nutrient solution was weekly added to the irrigation water in order to allow optimal growth. Air temperature was recorded every 30 minutes, and daily averaged. Leaf stage measurements (Haun,1973) were made every 3 days on 24 plants that were not harvested, and every 3 or 4 days 24 plants were harvested for apex observation (Kirby and Appleyard,1986) and primordia counts (see Chapter 1).

In addition to these two experiments, experimental results out of the literature have been used to validate the model. Sources, of these experiments are summarized in Tab.2. Where daily temperatures were not available to calculate the rate of primordia initiation, they were randomly generated from decadic means. The wheat apex remains below ground until the stem starts to elongate, and it is exposed to soil temperatures rather than air temperatures (Hay and Tuncliffe Wilson,1982). Mean soil and air temperature normally have different amplitudes, but comparison of simulation results obtained by the use of soil surface or air mean temperatures, made for data of Experiment 1, showed that differences are, in general, negligible.

Table 2. List of experimental data sources arranged in order of increasing latitude, used for model validation. The table also provides the legend of Fig. 2

Site	Latitude	Sowing date	Variety	Source	Results in:
Rutigliano (I)	40° 10'	30 Nov 83	Creso	Miglietta et al. (1987)	Fig. 2F
Florence (I)	43° 55'	1 = 12 Nov 86	Maris H.	Miglietta (1989)	Fig. 2A
Florence (I)	43° 55'	1 = 12 Nov 86	Creso	Miglietta (1989)	Fig. 2B
Florence (I)	43° 55'	2 = 5 Feb 87	Maris H.	Miglietta (1989)	Fig. 2A
Florence (I)	43° 55'	2 = 5 Feb 87	Creso	Miglietta (1989)	Fig. 2B
Randwijk (NL)	51° 50'	21 Oct 82	Arminda	Groot (1987)	Fig. 2D
Cambridge (UK)	52° 11'	1 = 10 Sep 80	Norman	Kirby et al. (1985)	Fig. 2C
Cambridge (UK)	52° 11'	2 = 24 Oct 80	Norman	Kirby et al. (1985)	Fig. 2C
Cambridge (UK)	52° 11'	3 = 4 Dec 80	Norman	Kirby et al. (1985)	Fig. 2C
Cambridge (UK)	52° 11'	4 = 25 Feb 81	Norman	Kirby et al. (1985)	Fig. 2C
Lelystad (NL)	52° 30'	25 Oct 83	Arminda	Groot (1987)	Fig. 2E

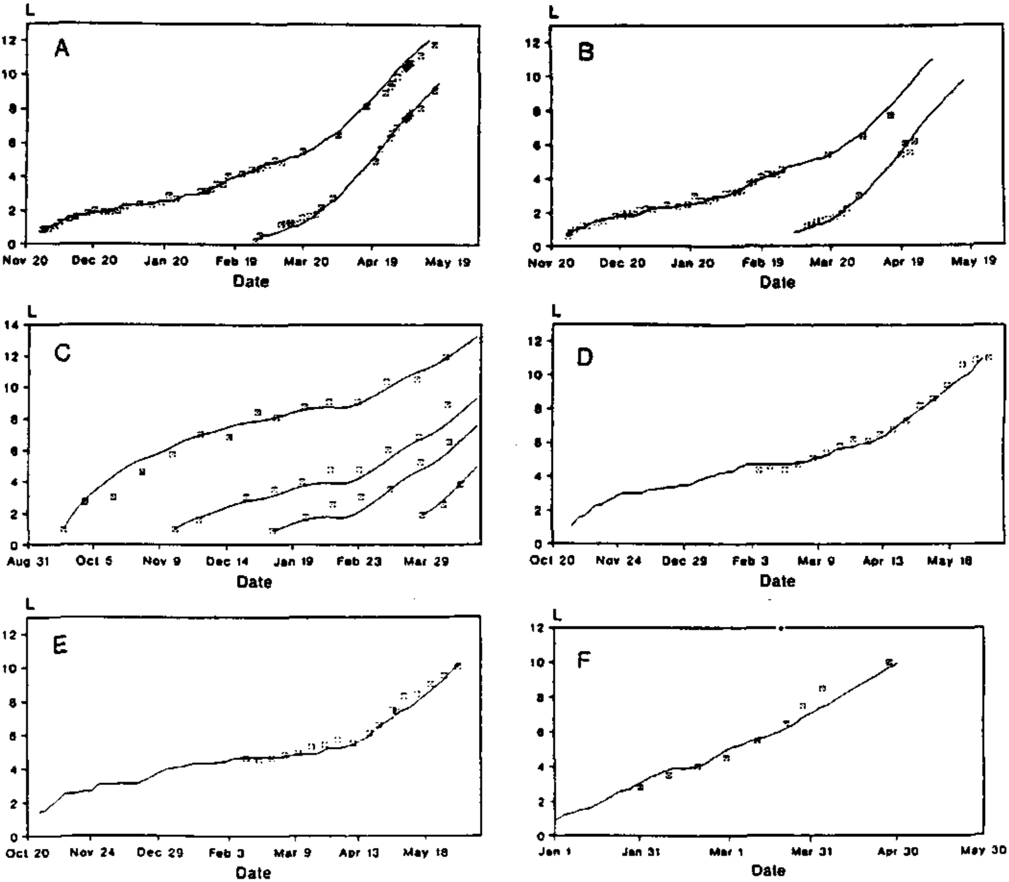

Fig. 2. Simulated (line) and observed (points) number of emerged main stem leaves (*L*) in field experiments (see Table 2 for experimental details

3.4. Results

All results of the experiments referred in Tab.2 are summarized in Fig.2. In spite of the large variation in both sowing dates and latitudes, the agreement between observational points and the calculated lines are excellent over the whole growth period. This confirms hypothesis 2, and the estimate of parameter α of eq.3, obtained by means of data of FIG.1. Subsequently, data of Experiment 2 were used to evaluate model performances under constant temperatures. In that experiment, in fact, the average daily temperature remained almost the same, at 18°C, throughout a period of 32 days, as shown in Fig.3.

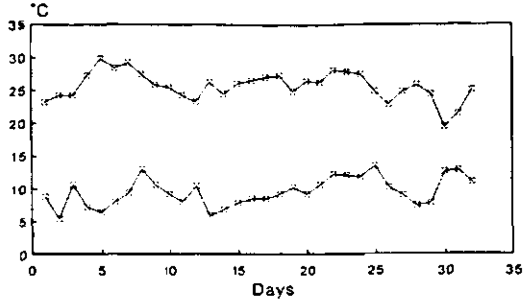

Fig. 3. Mean daily maximum and minimum temperature (°C), measured from plant emergence onward, in Expt 2

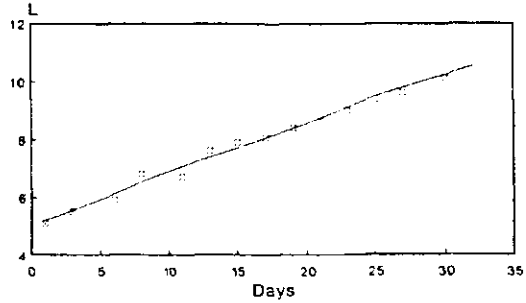

Fig. 4. Observed (points) and calculated (line) number of emerged leaves (L) in Expt 2

Primordia counts showed that leaves were initiated at a constant rate of about 0.23 primordia per day and a good estimate of this rate is obtained by means of equation [3]. Then, the number of leaves exposed on the main stem calculated by the model (solid line) is compared with observations (dots), in FIG.4, and an excellent agreement is found. The small bending of the solid line, in the figure, is hardly detectable by eye, and this confirms the idea that the decline in leaf apperance rates of subsequent leaves easily escapes detection in controlled condition experiments.

Hence, the observation of approximately the same leaf appearance at constant temperature does not support hypothesis 1.

3.5. Discussion and Conclusions

It was shown, that with increasing age of wheat plants, the number of emerged main stem leaves lags more and more behind the number of initiated leaf primordia, so that a small and constant increase in the length of subsequent phyllochrones occurs. This leads to the following conclusions:

- phyllochrones are longer than corresponding plastochrones as it was already reported by Bunting and Drennan (1966).

- the higher rate of extension of subsequent leaves, that was observed in wheat plants (Gallagher,1979), does not exactly counterbalance the longer distance the tip of the lamina has to cover from the growing point, where leaves are initiated, to the point of emergence

- there is a constant increase in the length of the period from initiation to emergence for each subsequent leaf

- that increase is so small, that differences between subsequent phyllochrones are probably too small to be observed even under controlled conditions

- expected decline in the rate of leaf appearance of subsequent leaves, provides a good explanation about differences in the rate of leaf appearance at a given date, for crops sown at different dates.

Leaf appearance models, based on hypothesis 1 assume phyllochrones to be constant and express them in thermal time (Delecolle and Gurnade, 1980, Kirby and Perry, 1987, Weir et al.,1984), whereas the daylength is assumed to have an effect upon the rate of leaf appearance and differences in the rate of leaf appearance among sowings are related to the rate of change in daylength at crop emergence (Baker et al.,1980).

The use of thermal time contraddicts with the conclusions reached in this paper, because degree days can only be used if phyllochrones are constant and linearly related to temperature.

The assumption made about daylength effects contraddicts with results of a number of experimental observations, with some unpublished scientific experience of M.A.Ford and R.B.Austin (referenced in Kirby et al.,1987), and W.H.Van Dobben and C.T.DeWit, (personal communications) and with the fact that wheat plants become sensitive to daylength only after vernalization requirements are fully met (Davidson et al.,1985, Rahman,1980).

Moreover, models that estimate leaf appearance rates on basis of the rate of change in daylength, need to be calibrated for different latitudes (Delecolle et al.,1980, Kirby et al.,1987) because they take a steady characteristic of plant growth, as a variable one.

The problem of the simulation of leaf appearance under field conditions, is simplified, to a large extent, by the model which is here discussed.

Hence, provided that the final leaf number is known, phasic development and some morphogenetic features of wheat growth can be predicted on basis of leaf appearance. Shoot apex development is, in fact, co-ordinated with leaf appearance as well as with the total number of formed leaves (Aitken, 1971, Kirby,1988), and both tillering and stem extension processes take place at particular stages of leaf development (Klepper et al. 1984, Friend,1966, Masle-Maynard and Sebillotte,1981). Thus, a next step is to calculate the final number of leaves initiated by wheat at different latitudes and sowing dates, under different climates. Calculations must be based on a better understanding of the interaction of temperature, photoperiodism and vernalization upon wheat development.

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CHAPTER 4

Predicting Dates of Ear Emergence and Main Stem Final Leaf Number

4.1. Introduction

By reinterpreting the results of several experiments under controlled conditions and in the field a model of leaf appearance was developped in the two previous chapters. For this purpose, it was first shown that the rate of leaf initiation on the main stem of wheat depends on temperature, but it is both independent of the daylength and of the rate of change in daylength. Then, it was shown that the length of the period from initiation to appearance increases linearly with increasing leaf number. This interpretation of the experimental results was confirmed by an excellent agreement between model calculations and experimental data for the number of leaves in course of time for wheat sown at widely different dates in widely different locations.

The problem that remains to be solved in this chapter, is how many leaves are formed, on the main stem, or, to formulate the same problem otherwise, at what moment the last leaf appears. For this purpose it is important to remark that the time of heading, and with this, the time of appearance of the last leaf is to a large extent independent of the time of sowing for wheat grown in temperate climates (Titta, 1934, VanDobben, 1947, Pfeiffer, 1949, Orsi,1953, Pal et al.,1959, Henriksen, 1961, Shulze and Zabel, 1962, Lovato and Amaducci,1965, Tandoi,1967, Vez, 1974, Collald, 1984, Photiades and Hadijchristodoulou, 1984, Reinink et al., 1985, Green and Ivins, 1985, Tuttobene et al.,1985, Mucci et al., 1985, Porter et al., 1987). An example is given in FIG.3.

This synchronisation is attributed to a combined effect of vernalization, photoperiod and temperature and its existence simplify to a large extent the problem of the prediction of the final number of leaves. It suffices, in fact, to calculate the final leaf number for a suitable chosen sowing date.

In this chapter, the effect of daylength upon the final number of main stem leaves is quantified for wheat varieties of different origin of which the vernalisation requirements have been met. Together with the earlier model of leaf appearance, this information is used to calculate the date of appearance of the last leaf or the date of heading in dependence of the sowing date. Subsequently the effect of vernalisation and temperature on the date of appearance of the last leaf or on the date of heading is investigated. This is done by comparing observed heading dates of wheat sown at a wide range of dates with calculations. The comparison reveals a period at which vernalisation requirements are fullfilled in a very early stage of growth that can serve as a base for the development of a model to estimate the final number of leaves on the main stem of any wheat cultivar for any latitude, sowing date and weather. Comparison of model results with experimental results all over Europe and USA shows an excellent agreement.

4.2. Model development

Photoperiodic response of wheat varieties

At first, spring wheats, that do not require vernalisation, and winter wheats that are vernalised by pre-sowing treatements, are considered. Such plants, in fact, are expected to respond immediately after emergence to the length of the day (Rahman, 1980, Hunt,1979).

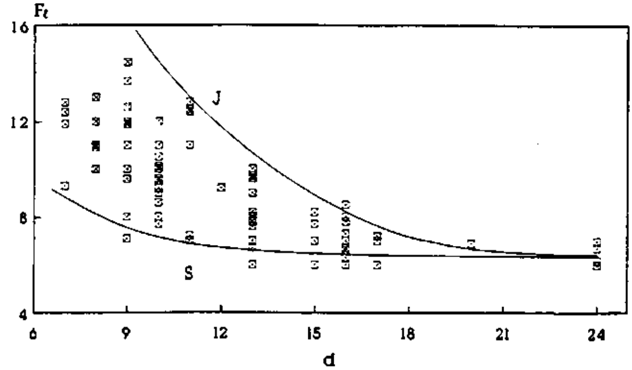

Fig. 1. Final number of leaves (F_l) formed by wheat main stem under different photoperiodic regimes plotted against daylength (d, hours). Lines are fitted curves [see Table 1 and Eq. (1)] of cultivar Justin (J), originating from northern latitudes of Canada, and Sunset (S), that originates much further south. Data from: Halse & Weir (1970), Holmes (1972), Levy & Peterson (1972), Allison & Daynard (1976), Rahman & Wilson (1977), Rahman (1980), Pirasteh & Welsh (1980)

The final leaf number in dependence of the daylength is given in FIG.1 for 35 of such varieties, grown in 12 photoperiodic controlled environments. Wheat is a "long day" plant, but some varieties are much more responsive to the daylength than others.

When plants are grown under optimal inductive conditions, the number of leaves is at minimum 6-7. Early investigations with rye suggested that this minimum number of leaves may be necessary before the plant responds to external inductive conditions (Purvis,1934), but later on, it was also suggested that this minimum number equals the number of leaves that already differentiated in the embryo (Holdsworth,1956).

Whatever the case, a mean number of 6.5 leaves may be assumed to be a good value for all wheat varieties that have been investigated. It appears that, for a given variety, the number of leaves in dependence of the daylength can be satisfactorely described by the following equation:

$$F_l = \sigma \exp(-\beta P) + 6.5 \qquad [1]$$

where

F_l = final leaf number

P = daylength in hours

β = parameter governing the curvature of the relation. It may be set at 0.25 for all varieties

σ = coefficient characterizing the sensitivity for the daylength of the variety

Values of coefficient σ are given in TAB.1 for each of the varieties of which data are reported in FIG.1. The coefficient varies from about 18.69 (σ_{min}) for the variety that is least sensitive to the daylength to about 72.52 (σ_{max}) for the most sensitive one, and it can be assumed to be correlated with the the latitude at which the variety is selected (δ, in degrees), according to :

Cultivar	σ	Source
8–23	50.03	Rahman & Wilson (1977)
8–27	32.31	Rahman & Wilson (1977)
Gabo	30.49	Rahman & Wilson (1977)
Galgalos	65.19	Levy & Peterson (1972)
Justin	72.52	Levy & Peterson (1972)
Kalyansona	32.81	Rahman & Wilson (1977)
Kogat	30.24	Rahman & Wilson (1977)
Marquis	47.74	Holmes (1972)
Natadores	61.95	Levy & Peterson (1972)
Pitic 62	21.50	Levy & Peterson (1972) Holmes (1972)
Selkirk	35.71	Rahman & Wilson (1977)
Siete Cerros	29.53	Allison & Daynard (1976)
Sonora 64	32.83	Allison & Daynard (1976) Pirasteh & Welsh (1980) Levy & Peterson (1972)
Tokwe	18.39	Allison & Daynard (1976)
Triple Dirk	34.52	Rahman & Wilson (1977) Rahman (1980)
Triumph	68.20	Levy & Peterson (1972)
Zambesi 2	32.74	Allison & Daynard (1976)

Table 1. Photoperiodic sensitivity (coefficent σ of Eq. [1]) of a number of spring and vernalized winter wheat varieties. Data source is indicated

$$\sigma = \frac{(\sigma_{max} - \sigma_{min})}{(\delta_{max} - \delta_{min})} (\delta - \delta_{min}) + \sigma_{min} \qquad [2]$$

where

δ_{max} = 57° latitude

δ_{min} = 20° latitude

A relation between sensitivity to the daylength and latitude of origin can be, in fact, supposed. Photoperiodic sensitivity can be assumed to be a consequence of different selection strategies at lower or higher latitudes. At lower latitudes varieties are normally selected for a weak photoperiodic response in order to enable earliness and escape drought, whereas at higher latitudes the varieties are selected for high photoperiodic response to enable a wide range of sowing dates to fill grains in the optimal period around the longest day of the year. The existence of an adaptation of varieties to their photoperiodic environment was often observed and discussed (VanDobben,1965, Kirby,1969, Hunt,1979, Napp-Zinn,1987, Hunt,1979, Krekulè,1987, Hoogendoorn,1986).

Model calculations for varieties that do not require vernalisation

It is possible, on the basis of eq. 1, to formulate a model that calculates the final leaf number and the date of ear emergence for the main stem for any given sowing date and any latitude, but only for plants that respond immediately after emergence to the length of the day. This is the case for plants do not require vernalisation or are vernalized before emergence.

The model requires the following procedural steps:

1] estimate the time needed from sowing to emergence as a function of temperature. Provided that the soil is moist, this may be done on the basis of air temperature according to Porter et al.

(1987)

2] determine the length of the day at the time of emergence according to Goudriaan and Van Laar (1978) taking into account the twiligth zone

3] calculate the final leaf number of the variety from the daylength by means of eq. 1, using the appropriate value of coefficient σ. This value may be determined in experiments under controlled conditions, or derived by means of eq.2

4] calculate initiation and appearance of subsequent leaves from emergence to the moment of the appearance of the last leaf, by using daily mean air temperature and by means of the leaf appearance model that is presented in the first Chapter

5] Estimate heading to occur just after the appearance of the ligule of the flag leaf

This procedure was used to calculate the curve that relates the heading date to the sowing date on the basis of the daily mean air temperatures as measured in Lelystad (The Netherlands) during the Autumn and Winter season 1977-78 and for a variety selected at that latitude. This place, period and variety were chosen because they allow comparison with experimental results that are presented later on in this chapter.

Calculated results are presented in three ways. In FIG.2a and 2b with the heading date along the vertical axis and the date of emergence and sowing, respectively, along the horizontal axis and in FIG.2c with the final number of leaves along the vertical axis and the date of sowing along the horizontal axis. For subsequent discussion the graphs with the date of sowing along the horizontal axis are divided in four sowing periods, A,B,C and

D. The corresponding periods in the graph with dates of emergence along the horizontal axis are indicated by A',B',C',D'.

For sowing periods before November, in period A, calculated heading dates are very early, in May, because these plants emerge at a time when photoperiod is still so long that the number of leaves is low. Plants sown around half November (period D) emerge in the second half of December, when daylength is very short. The number of leaves is at the highest and heading is postponed to the middle of July. In the winter sowing (period C) the heading dates are amost synchronised because the photoperiod increases and the number of leaves decreases when the crops are sown later and the plants that are sown earlier do not have any advantage of this because the temperature, in winter is very low. This is otherwise in the spring (period D) when the synchronisation breaks down.

A comparison with a field experiment

A sowing date experiment was done by Reinink et al. (1986) at the same place and in the same season with a dutch winter wheat variety (Lely). The results are reported in FIG.3 with the same scale as FIG.2a . The division between the periods A,B,C and D are also added for easy comparison. Obviously the period of synchronisation starts now already early in autumn instead of in winter. This is because for the calculated curve, the seeds of all sowings are supposed to be vernalized, whereas in the actual experiments the autumn sowings are only vernalized in winter when the temperature is sufficiently low. The final leaf number of autumn sowings is, thus, determined by the daylength when vernalization requirement is fullfilled and plants become sensitive to photoperiod and not by the daylength at the time of emergence. By this lack of vernalization, the plant escape the early heading dates of period A and the late heading dates of period B. On the other hand, plants sown in period C are fully vernalised from the beginning by the low temperatures of winter, so that their final leaf number and heading

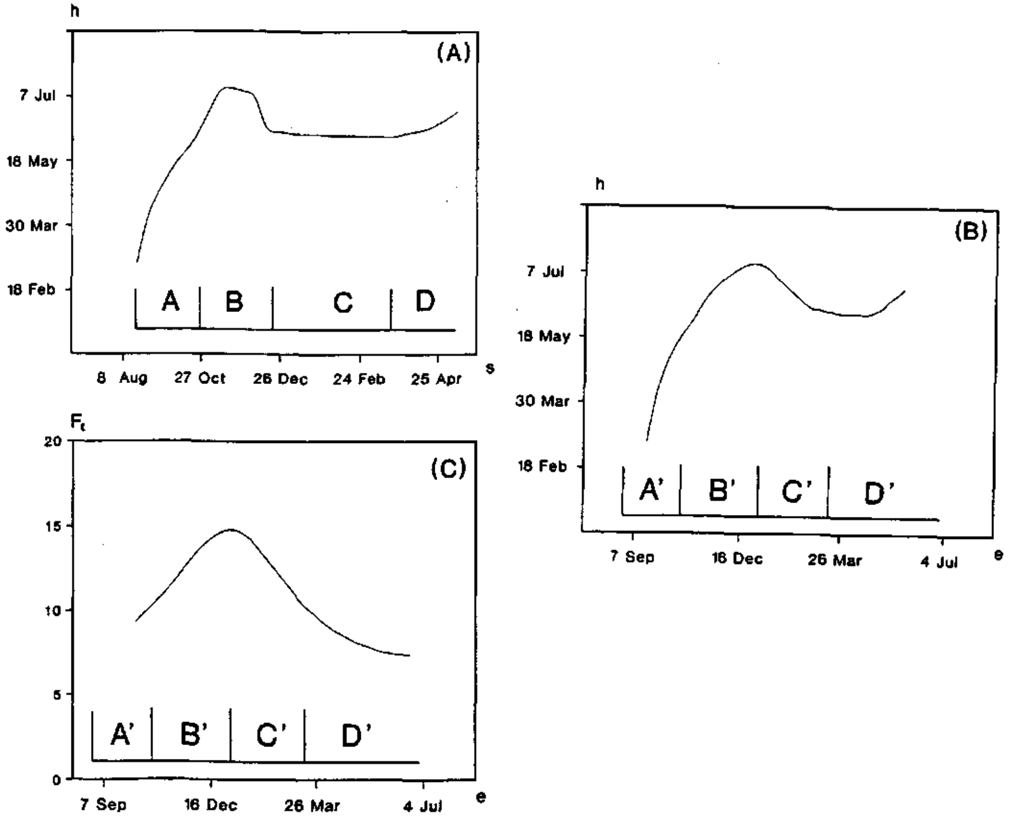

Fig. 2. Development parameters calculated using the procedure described in the text, and on the basis of temperature records measured at Lelystad, The Netherlands, in the season 1977–78. (A) Date of heading (h) plotted versus corresponding date of sowing (s); (B) date of heading (h) versus corresponding date of emergence (e); (C) final number of leaves (F_f) versus date of emergence (e)

date almost coincide with those calculated in FIG.2. The small difference between calculated and measured values may be very well due to the circumstance that the daylength sensitivity of the variety used was not determined in the laboratory and had to be estimated from the latitude according to eq.1 and 2. The plants of the spring sowings, in period D are of course not vernalised, but their synchronisation breaks down anyhow because the higher temperature makes that the early sowings remain earlier than the late sowings.

Vernalisation is obviously not a limiting factor for earliness for sowings made in period C, or, in other words, around the coldest period of the year. This was also reported by Van Dobben (1947).

Hence the final leaf number and the heading date of a crop that is supposed to be sown at the beginning of the coldest period of the year, can always be calculated by means of the procedure described earlier for vernalized plants. The final leaf number of earlier sowings can be calculated assuming they are more or less synchronised in heading with this late sown crop, but for later sowing this calculation

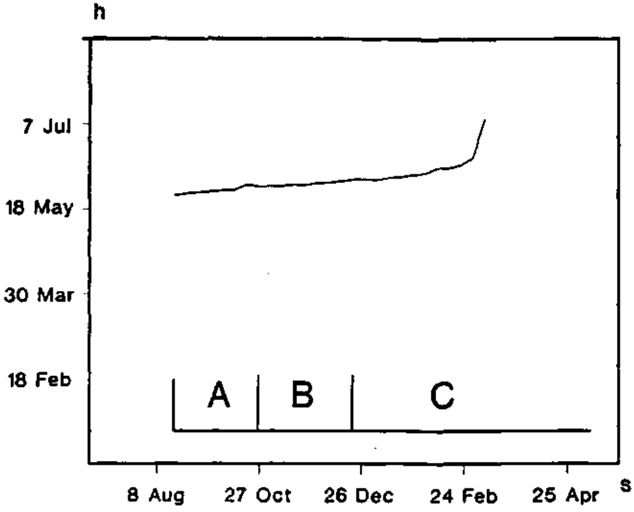

Fig. 3. Heading (*h*) and sowing dates (*s*) observed for winter wheat (cv. Lely) at Lelystad, The Netherlands, in the season 1977–78 (Reinink et al. 1986)

may break down because of the lack of vernalisation in early spring. But this is of no practical consequence because winter wheats are never sown that late.

4.3. Imperfect synchronisation

Synchronisation may be assumed to be perfect, but, in practice the heading is somewhat later for later sowings as illustrated in FIG.3. It was found by Orsi (1953) that synchronisation is better the colder the climate in winter, by O'Leary et al.(1985) and Reinink et al.,(1986) that it is better the colder the winter and by Van Dobben (1947) that synchronisation is less for species like rye that continue to grow at low temperatures. This is due to the circumstance that the higher temperatures in winter, the more earlier sowings can gain an advantage over late sowings, as explained in par. 3.

If it is assumed that a crop sown at the beginning of the coldest period of the year is vernalised when it emerges, it can also be assumed that any earlier sowing is fully vernalised at that time. The final leaf number of this early sown crop will be, equal, at the minimum, to the final leaf number of the later sown one and it will be given, at the maximum, by the sum of this number and the number of leaves that are already appeared on its main stem (F_e) when the later sown one emerges. Hence, the actual number of leaves formed by this crop (F_t) can be calculated as follows:

$$F_t = F_l + \mu F_e \qquad [3]$$

where

F_l = final number of leaves calculated for a crop sown at the beginning of the coldest period of the year according to eq.2

μ = empirical coefficient ranging from 0 to 1

The value of the coefficient μ was calculated on basis of field experiment data of Reinink et al.(1986) for the season 1976-77, 1977-78 and 1978-79. In every season the sowing date closest to the beginning of the coldest period of the year was identified at first. Then, the final number of leaves of any earlier sowing (F_l) and the number of leaves formed by the same crop before the coldest period of the year (F_e), were calculated by the simulation of leaf appearance from the date of emergence to the date of the appearance of the ligule of the flag leaf (Zadoks's stage 39). Finally, values of coefficient μ were estimated by solving eq.3.

These values showed a very small variability among sowings and years (0.666 ± 0.033 in 1976-77, 0.0637 ± 0.054 in 1977-78 and 0.673 ± 0.054 in 1978-79), although some differences in the climatic conditions of the three seasons were observed. The mean value of μ =0.65 seems to be, therefore, appropriate in order to estimate, according to eq.3, the final leaf number of any crop sown at any date and under any climatic condition, in middle latitudes.

4.4 Model description

Model input are:

- Date of sowing
- Date of crop emergence (if known)
- Latitude of the site
- Records of average daily air temperature

- Varietal data:
    - Winter or spring wheat
    - Experimentally determined value of coefficient σ or, if this is not available, the latitude at which the variety was selected

Model outputs are:

- Date of appearance of subsequent main stem leaves from emergence to heading
- Final number of main stem leaves at heading
- Date of the initiation of the last leaf at the apex
- Date of heading

Calculation procedure is as follows:

Firstly the five procedural steps described in par.3 are executed to estimate the date of emergence and the final number of leaves, of a crop sown at the beginning of the coldest period of the year (period C). This period is identified, in the model, by means of the five days running average of daily air temperature.

Then, the number of main stem leaves formed by the crop sown at the actual date is simulated, in the course of time, by means of the model described in Chapter 3, and the final number of leaves is estimated, at the time of emergence of the crop sown at the beginning of the coldest period of the year, according to eq.3.

Finally, heading is assumed to occur immediately after the date of the full appearance of the last leaf.

4.5 Model evaluation

To evaluate the model, a large number of experimental data was collected over a wide range of climatic and photoperiodic conditions. For some experiments, the final leaf number and dates of heading were measured, but in others only the latter. The experiments concern 58 experimental crops in 26 locations throughout Europe and USA. Maps with the experimental locations are given in FIG.4 and reference to data sources in TAB.2. Observed and calculated values of the date of heading and, where available, of the final leaf number are given in TAB.2 and in the graphs of FIG.5 and 6. In general, the model performs very excellent under a wide range of experimental conditions and thus provides a good starting point to develop more satisfactory ontogenetic models than are available at present.

4.6 Discussion and conclusions

The model clarifies the role of temperature, photoperiod and temperature within the global development strategy of the wheat plant.

Vernalization increases the range of sowing dates for which the date of heading can be synchronized, by keeping plants insensitive to the still "long days" of autumn and to the "short days" of early winter. Photoperiodism determines the final number of leaves on the main stem and contributes, together with the low temperatures to the synchronization of heading. Thus, a global function seems to be optimized, in field crops, that makes the time of flowering to occur around the same optimal date for a wide range of sowing dates. The best date for flowering depends on the latitude for which wheat varieties are selected, that is, on their photoperiodic response.

Baker, Gallagher and Monteith (1980) found a positive correlation between the rate of leaf appearance expressed in number of leaves per degree days, and the rate of change in the daylength at emergence, in experiments where the sowing dates varied from autumn to spring. This

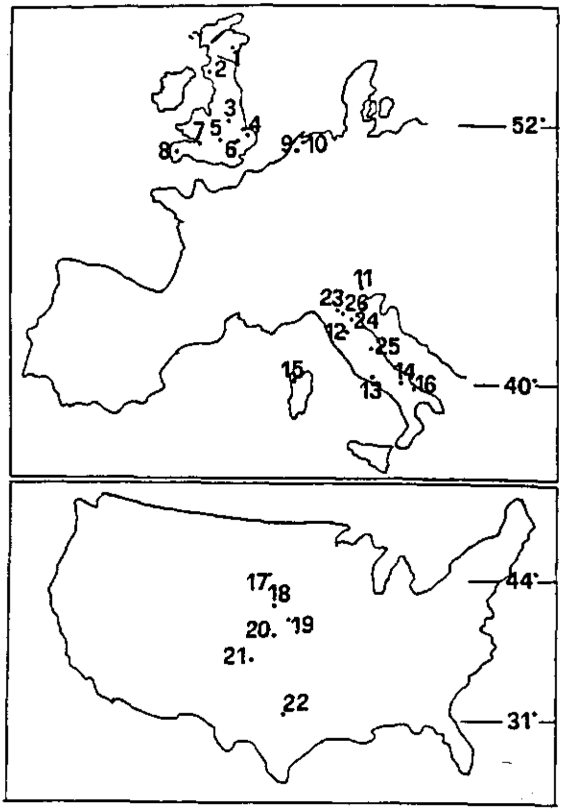

Fig. 4. Western Europe and United States, showing locations of experiments used to validate the model. Site names, countries, latitudes, sowing dates and data sources are listed in Table 2

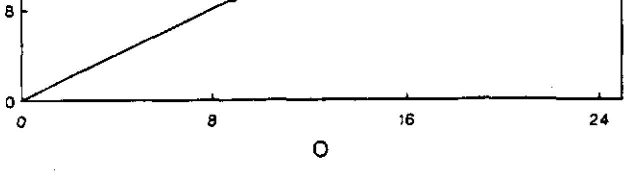

Fig. 5. Scatter diagram of predicted final leaf number (*P*) against corresponding observations (*O*) made in the field experiments listed in Table 2

relation was confirmed by others but only in field experiments, and not under controlled conditions where daylength, temperature and change in daylength were varied independently from each other.

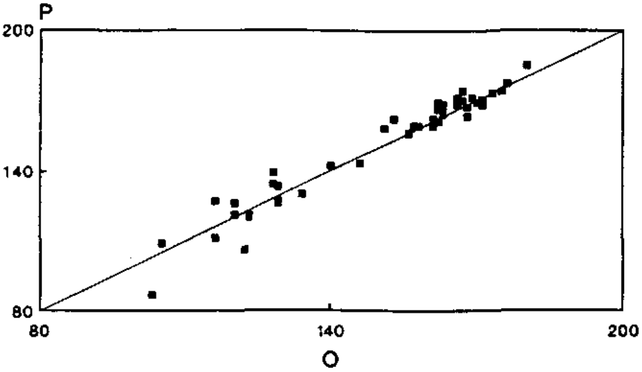

Fig. 6. Scatter diagram of calculated dates of ear emergence (*P*, days from 1 January) against corresponding observations (*O*), made in the field experiments listed in Table 2

The existence of this correlation is confirmed by the model presented in this work, as it is illustrated by the simulated data for Lelystad experiments (Reinink et al. 1986). In that example, the simulated number of appeared main stem leaves, for a number of sowing dates ranging from autumn to spring, was related to the number of degree days from emergence to the appearance of last leaf, as illustrated in FIG.7. Subsequently, slopes of the fitting lines were related to the rate of change in the daylength calculated at the time of emergence of each sowing (FIG.8). The simulated slope of this relation appears to be similar to those found experimentally, both in direction and magnitude. The explanation is that the period from initiation to appearance of a leaf increases with increasing the leaf number as quantified in Appendix 3.

This makes that the average rate of appearance is lower the larger the final number of leaves, as illustrated in FIG.7. Since the final number of leaves is lower in spring when the days lengthen than in autumn when the days shorten, there has to be a correlation between the rate of leaf appearance and the rate of change in the daylength. This correlation, significant as it is, does however not reflect a causal relation.

Table 2. Final leaf number (F_l) and date of ear emergence (H) calculated for different years, locations and sowing dates are compared with corresponding observed values (F_{lo} and H_o). * Missing values. Numbers correspond to locations in Fig. 4. Data sources are coded as follows: 1 = Porter et al. (1987); 2 = Beni (1984); 3 = Miglietta (1989); 4 = Biancolatte et al. (1982); 5 = Wittmer (1986); 6 = Biancolatte et al. (1983); 7 = Miglietta et al. (1987); 8 = Arkin et al. (1979a, b); 9 = Consorzio Emiliano-Romagnolo Aziende Sperimentali (1977–1986); 10 = Farina et al. (1958); 11 = Capodaglio & Tandoi (1959); 12 = Tandoi (1960–67); 13 = Groot (1986)

No.	Place	Country	Sowing date	F_l	J	F_{lo}	H_o	Source
1	Aberdeen	UK	14 Sep 83	11.4	22 Jun 84	12.3	*	1
	Aberdeen		12 Oct 83	9.9	26 Jun 84	10.0	*	1
	Aberdeen		16 Nov 83	9.0	4 Jul 84	8.9	*	1
2	Auchincruive	UK	14 Sep 83	14.1	18 Jun 84	16.0	*	1
	Auchincruive		12 Oct 83	12.3	20 Jun 84	12.6	*	1
	Auchincruive		16 Nov 83	10.7	22 Jun 84	10.2	*	1
3	Sutton B.	UK	14 Sep 83	14.2	15 Jun 84	16.0	*	1
	Sutton B.		12 Oct 83	11.8	17 Jun 84	12.0	*	1
	Sutton B.		16 Nov 83	10.2	20 Jun 84	10.0	*	1
4	Edmunds	UK	14 Sep 83	14.3	17 Jun 84	15.4	*	1
	Edmunds		12 Oct 83	11.5	19 Jun 84	13.8	*	1
	Edmunds		16 Nov 83	9.7	23 Jun 84	10.8	*	1
5	Cambridge	UK	14 Sep 83	15.0	8 Jun 84	14.8	*	1
	Cambridge		12 Oct 83	12.7	10 Jun 84	12.1	*	1
	Cambridge		16 Nov 83	10.6	12 Jun 84	9.9	*	1
6	Harpenden	UK	14 Sep 83	13.4	17 Jun 84	15.0	*	1
	Harpenden		12 Oct 83	11.2	19 Jun 84	12.0	*	1
	Harpenden		16 Nov 83	10.6	22 Jun 84	10.8	*	1
7	Bristol	UK	14 Sep 83	15.3	11 Jun 84	16.0	*	1
	Bristol		12 Oct 83	12.9	13 Jun 84	13.0	*	1
	Bristol		16 Nov 83	10.8	16 Jun 84	10.5	*	1
8	Newton Abbot	UK	14 Sep 83	15.5	5 Jun 84	15.5	*	1
	Newton Abbot		12 Oct 83	12.9	8 Jun 84	13.0	*	1
	Newton Abbot		16 Nov 83	10.8	10 Jun 84	11.4	*	1
9	Wageningen	Netherlands	21 Oct 82	11.0	8 Jun 83	11.0	10 Jun 83	13
	Wageningen		25 Oct 83	9.6	18 Jun 84	10.0	18 Jun 84	13
10	Nagele	Netherlands	21 Oct 82	10.5	11 Jun 83	11.0	6 Jun 83	13
	Nagele		25 Oct 83	9.4	19 Jun 84	10.0	4 Jun 84	13
11	Lonigo	Italy	28 Oct 83	9.5	20 May 84	*	20 May 84	2
12	Firenze	Italy	21 Nov 86	11.5	11 May 87	12.0	17 May 87	3
	Firenze		21 Nov 86	10.3	29 Apr 87	11.0	4 May 87	3
13	Roma P. G.	Italy	5 Nov 81	14.3	1 May 82	*	4 May 82	4
14	Foggia	Italy	13 Dec 85	9.9	7 May 86	*	9 May 86	5
15	Ottava	Italy	29 Dec 82	9.9	30 Apr 83	*	3 May 83	6
16	Rutigliano	Italy	11 Nov 82	12.8	1 May 83	*	29 Apr 83	7
	Rutigliano		30 Nov 83	11.3	10 May 84	*	14 May 84	7
	Rutigliano		28 Nov 84	10.9	16 Apr 85	*	2 May 85	7
17	Pierre	USA	4 Sep 78	14.3	15 Jun 79	*	11 Jun 79	8
18	Pickstown	USA	8 Sep 78	14.6	12 Jun 79	*	13 Jun 79	8
19	Norfolk	USA	18 Sep 78	13.4	11 Jun 79	*	7 Jun 79	8
20	Grand Isl.	USA	18 Sep 78	13.5	7 Jun 79	*	30 May 79	8
21	Goodland	USA	13 Sep 78	13.3	23 May 79	*	26 May 79	8
22	Blackland	USA	19 Oct 78	14.9	28 Mar 79	*	14 Apr 79	8
23	Mezzano	Italy	12 Nov 76	17.4	2 May 77	*	10 May 77	9
24	Ravenna	Italy	9 Nov 78	12.0	12 May 79	*	21 May 79	9
	Ravenna		15 Nov 79	16.2	16 May 80	*	20 May 80	9
	Ravenna		7 Nov 80	10.7	8 May 81	*	17 May 81	9
	Ravenna		22 Oct 80	12.4	8 May 81	*	16 May 81	9
25	Macerata	Italy	26 Nov 57	11.4	14 May 85	*	8 May 58	10
	Macerata		20 Nov 58	11.1	21 Apr 59	*	26 Apr 59	11
	Macerata		17 Nov 59	11.6	7 May 60	*	26 Apr 60	12
	Macerata		17 Nov 60	11.3	19 Apr 61	*	15 Apr 61	12
	Macerata		21 Nov 61	11.4	19 May 62	*	8 May 62	12
	Macerata		22 Nov 62	10.0	13 May 63	*	9 May 63	12
	Macerata		15 Nov 63	10.4	6 May 64	*	30 Apr 64	12
	Macerata		20 Nov 64	10.7	13 May 65	*	8 May 65	12
	Macerata		15 Nov 66	10.4	3 May 67	*	27 Apr 67	12
26	Boara	Italy	10 Nov 80	9.3	5 May 81	*	16 May 81	9

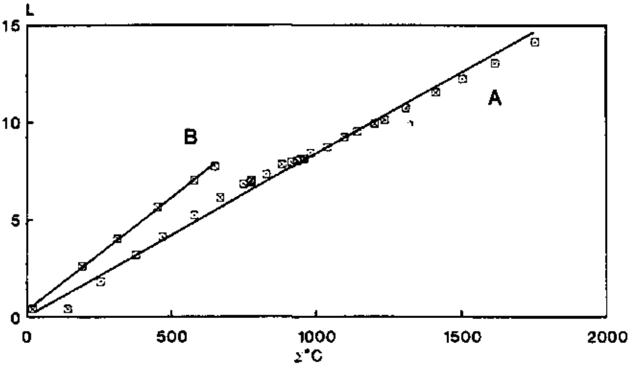

Fig. 7. Simulated number of appeared main stem leaves (*L*) plotted versus thermal time calculated from emergence (Σ °C), for 2 of the 50 sowings made in the field experiment reported by Reinink et al. (1986). A: sown on 31 August 1978; B: sown on 29 May 1979

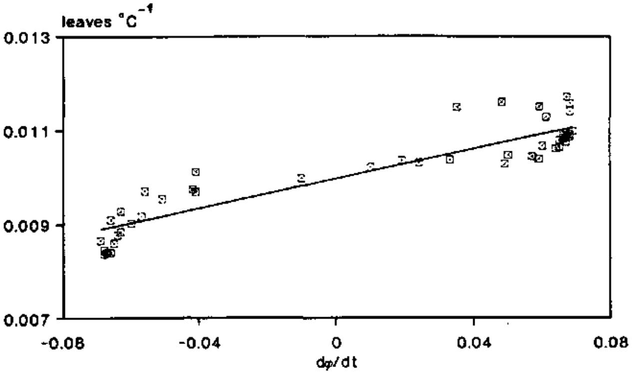

Fig. 8. Rates of leaf appearance calculated by the regression of the simulated number of appeared leaves on thermal time (leaves °C^{-1}) plotted against rate of change in daylength at crop emergence (dφ/dt). Line represents the linear relationship found by Baker et al. (1980)

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CHAPTER 5

The effect of variety, nitrogen fertilization and water stress on leaf appearance and final leaf number in the field.

5.1. Introduction

A model to calculate the appearance of subsequent main stem leaves and to predict phasic development of wheat was presented in the two previous papers of this series. The model assumes that both initiation and appearance of main stem leaves are a function of temperature and independent of daylength (Miglietta,1989) and that the time between initiation and appearance of a leaf linearly increases with the leaf number (Miglietta,1990a). Phasic development of wheat is described in terms of the number of emerged leaves. The final number of leaves depends on the photoperiodic response of the variety and on flower synchronisation which in turn also depends on temperature and vernalization (Miglietta,1990b). The photoperiodic response of spring wheats and fully vernalized winter wheats is described by an exponential decrease of the final number of main stem leaves with increasing daylength to a minimum of 6 leaves.

The model was validated by means of a comparison with both original and published field experiment data and its performances was excellent for a wide range of environmental conditions.

In the model, differences between varieties are only considered in terms of a different response of the final number of leaves to daylength. The effect of variety on the rate of leaf initiation and appearance is considered to be negligible. This was concluded on the basis of an analysis of experiments under controlled conditions but it was only verified for 2 varieties in a single field experiment.

The effects of nitrogen fertilization and of water stress on the rate of leaf initiation and appearance, on the final leaf number and on the phasic development of wheat are not considered in the model.

In this paper, the results of published field experiments and of a series of original field experiments are considered in order to study leaf appearance rates of different varieties and to analyse the effect of nitrogen fertilization and water stress on both leaf appearance and final leaf number. Published data comes from a large scale collaborative experiment in North America. Original experiments were conducted in Italy, in a joint research project involving different Institutions and experimental farms.

Simulation accuracy of the model is tested in this paper by means of a comparison between observed and calculated values of the final main stem leaf number, of the date of heading and of the appearance of main stem leaves in the course of time.

5.2. Materials and methods

Field experiments in the USA and Canada

A comparative study called "Agricultural Microclimatological measurements for Comparing Production Functions and Water Use Efficiency" was sponsored, in 1984-86, by the US National Science Foundation, by Agriculture Canada and by the Agricultural Research Service of USDA. The response of selected wheat cultivars to climate and to water and nitrogen applications was studied simultaneously at 5 sites in North America. A common experimental design was employed and the same instruments and techniques were used to make measurements of microclimate and plant growth conditions (Reginato et al.,1988). Phenological observations were made at each site but complete data set are only available for Manhattan,KS (39° 09'N, 96° 37'W) and Mandan, ND (46° 46'N, 100° 55'W) (Bauer et al., 1988).

Wheat development was weekly determined from emergence onwards by the Haun and the Zadoks-Chang-Konzak scales (Bauer et al.,1983) on 2 different varieties (V1 and V2) . These were the cultivars Colt and Brule in Manhattan,KS and Colt and Norstar in Mandan,ND. The variety Colt was grown at each site for easy comparison of the effect of climate on development (Bauer et al.,1988). Other variables in the experiments that are here taken into consideration are soil water level (W1=dryland or rainfed conditions, W2=well-watered condition) and nitrogen fertilization (N1=50-60 Kg NO3 - N / ha and N2=160 kg NO3-N / ha). Details of experimental design and water and nitrogen treatements are given by Reginato et al. (1988).

Field experiments in Italy

Three field trials were performed in the 1988-89 winter season in a joint research project established by 2 research Institutes (CE.S.I.A. and I.A.T.A., Florence) and 2 agricultural extension Institutions (CERAS and ERSA Emilia-Romagna, Bologna). Three italian winter wheat varieties with a marked difference in earliness of maturity (PANDAS early,CENTAURO medium and SALMONE late) were grown in the 1988-89 season under two fertilization treatements at 3 experimental farms located in Emilia-Romagna (Martorano 5 , Ostellato and Stuard). Plots of 65 square meters were sown at a row distance of 10 cm. at the same date (October 31st) in each location and replicated twice. In the first fertilization treatement no-nitrogen was applied to the plots and in the second one 140-160 kg ha_{-1} N in the form of NO3 were applied at two dates (3010/2003). The same amount of Phosphorus (120 kg./ha) and Potassium (60 kg/ha) was applied to each plot. Data of the cultivar SALMONE in the Ostellato experiment are not considered due to the failure in crop emergence and the variety CENTAURO was replaced by a variety having comparable earliness (COSTANTINO) in the Stuard experiment.

Weather data were daily recorded throughout the growing season by means of the automatic weather stations of ERSA that were located close to the experimental fields.

Haun stage measurements and counts of the final main stem leaf number were performed on each plot. Phenological stages of development were recorded using the Zadok's scale.

5.3. **Results and discussion**

The effect of variety

The model that is discussed in this series of papers assumes that the difference in the rate of leaf appearance between varieties is generally small and , thus, it can be neglected in the simulation model (Miglietta,1989, Miglietta,1990a). This assumption was based upon observations made in several laboratory experiments in which the total number of leaf primordia formed by the wheat plant and the time taken by the plant from emergence to the double ridge stage were measured (Rahman & Wilson,1977, Levy & Peterson, 1972, Holmes, 1972, Allison & Daynard, 1975, Pirasteh & Welsh, 1980). In these experiments the calculated rate of leaf primordia initiation was observed to be almost the same for the different varieties tested and it was inferred that the rate of leaf appearance was likely to be independent of the variety as well. This conclusion was confirmed by the comparison of leaf appearance rates recorded in 2 varieties of different origin in a field experiment (Miglietta,1990a), but it was not validated further.

Data obtained in the field experiments in the USA and in Italy are here used to evaluate the effect of different varieties on the leaf appearance rate. Haun stage measurements made in the field from emergence to heading and the calculated rates of leaf appearance are compared and statistically analysed. Results of the comparison are given in Fig.1A for the experiment conducted at Manhattan and in Fig.1B for the experiment conducted at Mandan.

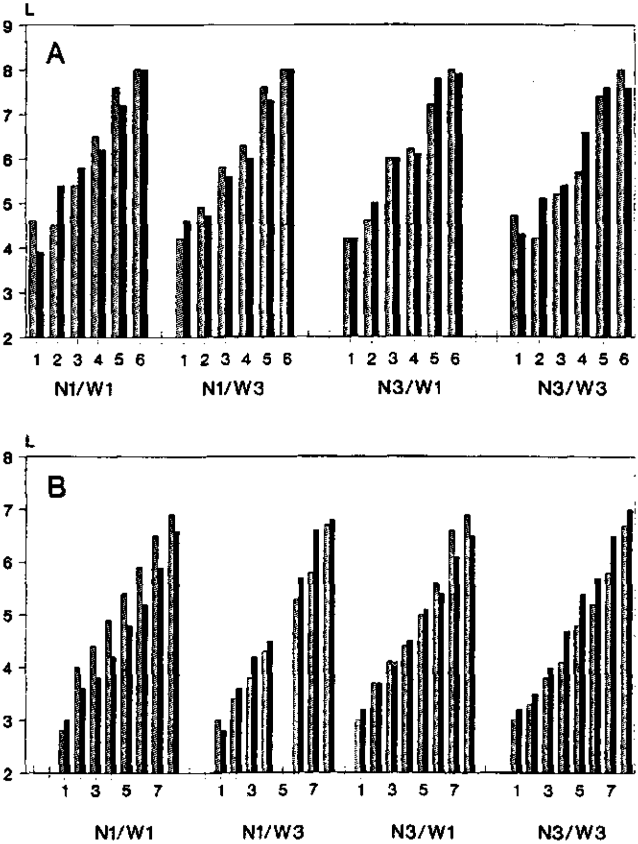

Fig. 1. Number of main stem leaves emerged (L) at each weekly sampling date (numbers on horizontal axis indicate subsequent samples) in each one of the 4 nitrogen/irrigation treatments (see 'Materials and methods') at (A) Manhattan, Kansas, and (B) Mandan, North Dakota, USA. Observations are shown for the variety 'Colt' (filled bars) and for the varieties 'Brule' (Manhattan) and 'Norstar' (Mandan) (hatched bars)

Table 1. Multifactor variance analysis of leaf appearance rates recorded in Manhattan, Kansas, USA, in the 1984–85 season. The effect of observation date is always significant because it is dependent upon the different thermal conditions occurring between 2 subsequent observations

Source of variation	Sum of squares	df	Mean square	*F*-ratio
Variety	0.0000864	1	0.0000864	0.002^{ns}
Fertilization	0.0902358	1	0.0902358	2.560^{ns}
Irrigation	0.0619635	1	0.0619635	1.758^{ns}
Observation date	0.5718128	6	0.0953021	2.704*
Residual	1.6212285	46	0.0352441	
Total (corr.)	2.3453270	55		

^{ns} Not significant; * significant at $p = 0.05$

Table 2. Multifactor variance analysis of leaf appearance rates recorded in Mandan, North Dakota, USA in the 1985–86 season. The effect of observation date is always highly significant because it is dependent upon the different thermal conditions occurring between 2 subsequent observations

Source of variation	Sum of squares	df	Mean square	*F*-ratio
Variety	0.0003710	1	0.0003710	0.167^{ns}
Fertilization	0.0000284	1	0.0000284	0.013^{ns}
Irrigation	0.0001854	1	0.0001854	0.083^{ns}
Observation date	0.0812282	4	0.0203070	9.129**
Residual	0.0711797	32	0.0022244	
Total (corr.)	0.1529928	39		

^{ns} Not significant; ** significant at $p = 0.01$

In the figures the tested varieties are compared by plotting, for each nitrogen and water treatement, the number of leaves that have appeared on the main stem versus time of sampling. Differences in the number of leaves formed by the 2 varieties at successive dates of observation appear to be very small for all the considered treatements. The effect of the variety on the rate of leaf appearance is considered in the multifactor variance analysis (Table 1 and 2) and it is not significant.

Data of the 3 varieties grown in the experiments performed in Italy are separately compared for each experiment and for each nitrogen treatement. Haun stage measurements taken in the plots with no nitrogen fertilization are reported in Fig. 2 for the experiments performed at Martorano 5, Stuard and Ostellato. Measurements taken on fertilized plots are illustrated in the same order in Fig. 2 . The mean rates of leaf appearance calculated for the different treatements and summary results of the multifactor variance analysis are reported in Table 3.

Data in Fig. 3 clearly shows that the difference in the number of leaves between varieties are negligible at whatever date of sampling. The results of the multifactor variance analysis reported in Table 3 indicate that there is no effect of the variety upon the rate of leaf appearance.

The results obtained in these experiment are in contrast with those of a field experiment reported by Syme (1974) where the rate of leaf appearance was found to be slightly different for different varieties. In that experiment a split-plot design with 4 times of sowing and 2 replications was adopted and two plants per plot were tagged in order to record leaf appearance. Data from the 4 sowings were then pooled and the mean rate of leaf appearance was calculated, for each variety, as the slope of the line fitted between the number of appeared main stem leaves and the number of days from sowing. However, since the rate of leaf appearance decreases for every subsequent leaf (Miglietta,1990a), the change in the final

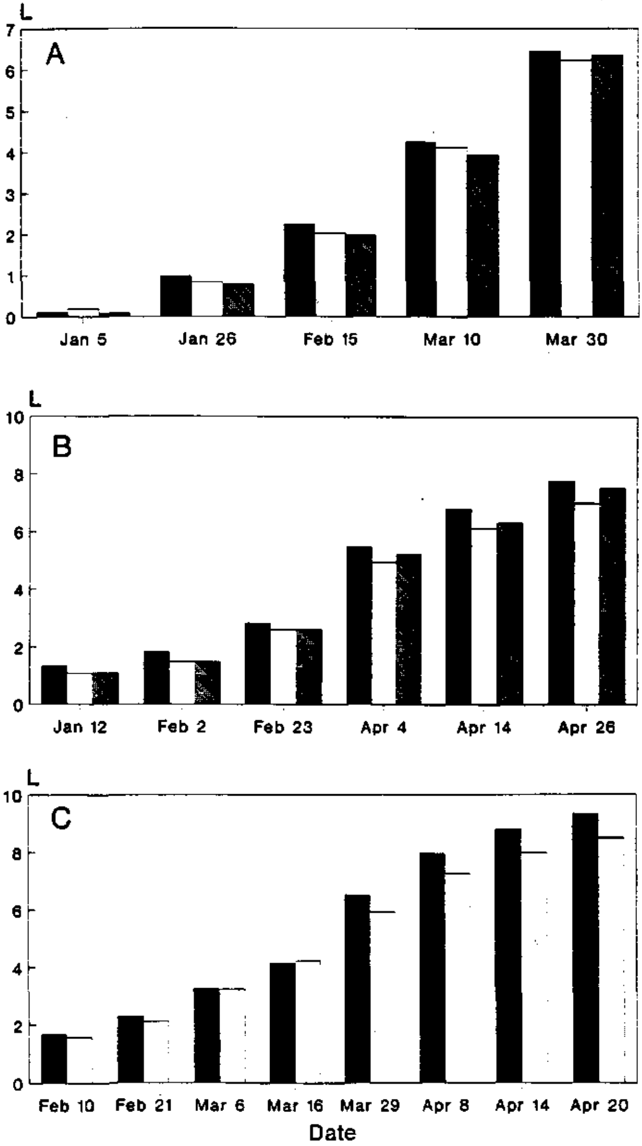

Fig. 2. Number of main stem leaves emerged (L) at each sampling date (1989) in non-fertilized experimental plots at (A) Martorano 5, (B) Stuard and (C) Ostellato farms in Italy. Filled bars: cultivar 'Pandas'; open bars: cultivar 'Centauro' or 'Costantino'; hatched bars: cultivar 'Salmone'

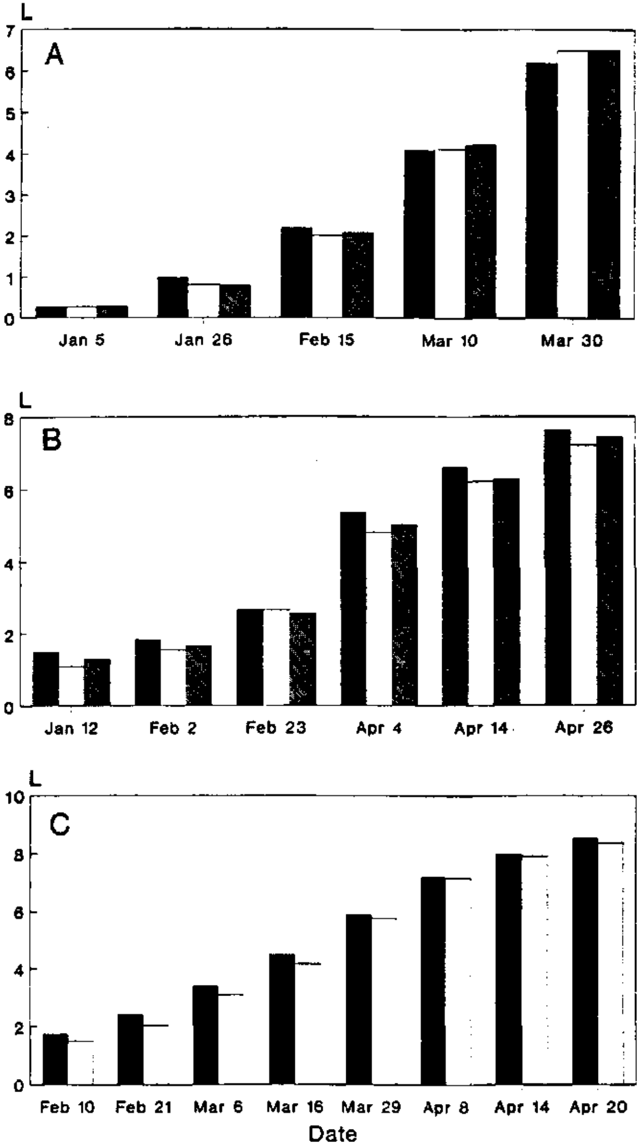

Fig. 3. Number of main stem leaves emerged (L) at each sampling date (1989) in experimental plots fertilized with nitrogen, at (A) Martorano 5, (B) Stuard and (C) Ostellato farms in Italy. Filled bars: cultivar 'Pandas'; open bars: cultivar 'Centauro' or 'Costantino'; hatched bars: cultivar 'Salmone'

leaf number that is expected to occur for the different sowing dates makes the rate of leaf appearance calculated in this way not sufficiently reliable (Miglietta,1990b). Hence, the calculation procedure adopted by Syme (1974) does not provide a full evidence that the rate of leaf appearance is different for the different varieties.

The effect of nitrogen fertilization

Based upon the observation that crops grown with high nitrogen stay green longer than crops grown with low nitrogen, it is often concluded that high nitrogen slows down the development of the wheat. However, more careful laboratory observations showed that nitrogen treatements may have a positive effect on the number of spikelets and kernels per ear but do not affect the duration of the vegetative phase (Davidson & Campbell, 1983, Masle-Meynard & Sebillotte, 1985, Frank & Bauer, 1982).

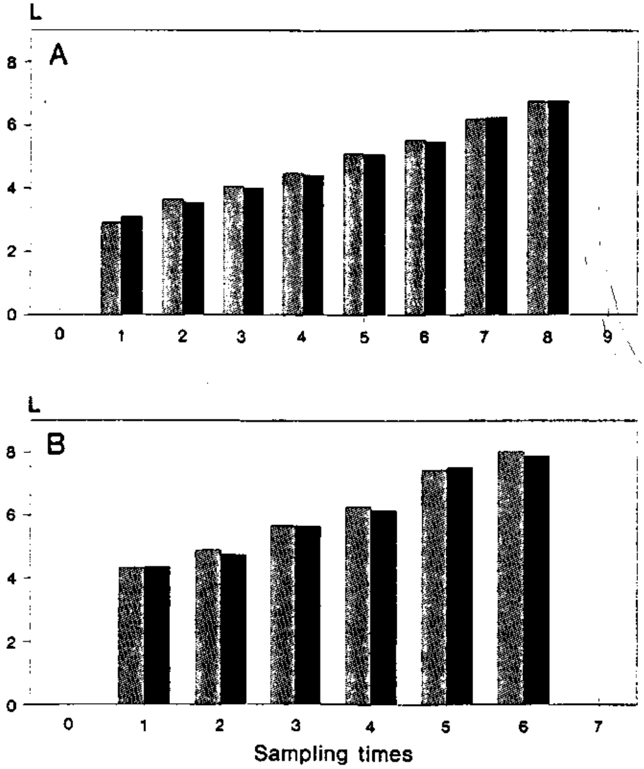

Fig. 4. Number of main stem leaves emerged (L) at each weekly sampling date (number on horizontal axis indicate subsequent samples) in plots with high nitrogen (solid bars) and low nitrogen (hatched bars) fertilization, at (A) Manhattan, Kansas, and (B) Mandan, North Dakota, USA

Table 3. Variance analysis of leaf appearance rates measured in the field at 3 farms in Italy. The effect of observation date is always highly significant because it is dependent upon the different thermal conditions occurring between 2 subsequent observations

Source of variation	Sum of squares	df	Mean square	*F*-ratio
Martorano 5				
Variety	0.0002132	2	0.0001066	1.237^{ns}
Fertilization	0.0000269	1	0.0000269	0.312^{ns}
Observation date	0.6190572	4	0.1547643	1000^{**}
Residual	0.0403174	468	8.61482×10^{-5}	
Total (corr.)	0.6604542	475		
Ostellato				
Variety	0.0001950	1	0.0001950	0.598^{ns}
Fertilization	0.0000294	1	0.0000294	0.090^{ns}
Observation date	1.4884941	8	0.1860618	570.87^{**}
Residual	0.1104873	339	3.25921×10^{-4}	
Total (corr.)	1.5996196	349		
Stuard				
Variety	0.0004976	2	0.0002488	0.740^{ns}
Fertilization	0.0002563	1	0.0002563	0.762^{ns}
Observation date	0.7885398	5	0.1577080	469.081^{**}
Residual	0.2380338	708	3.36206×10^{-4}	
Total (corr.)	1.0273895	716		

^{ns} Not significant; ** significant at $p = 0.01$

Mean rates of leaf appearance and final numbers of leaves at low and high nitrogen are given in Fig.4 for the Manhattan and Mandan experiments. This was done for averages across varieties since leaf appearance rates are independent of the variety. The figure confirms that leaf appearance rates are not affected by the level of nitrogen fertilization. It is worthwhile noting that the effect of nitrogen fertilization on final yield was substantial in the two experiments. Yields in N1 and N2 treatment plots were respectively 2.585 t ha^{-1} and 2.707 t ha^{-1} of grains in Manhattan,KS and of 1.832 t ha^{-1} and 3.162 t ha^{-1} of grains in Mandan,ND (Major et al.,1988a). Results obtained in the experiments in Italy are given in Fig.5 for the Martorano 5, Ostellato and Stuard farms. Here, an average difference of 8-10% in final grain yield was obtained by nitrogen fertilization.

Data from all the experiments clearly indicates that nitrogen fertilization has no effect upon the rate of leaf appearance. This is also confirmed by the results of the multifactor variance analysis (Table 1,2 and 3). The timing of developmental phases and the final leaf number are also unaffected as they are the same for both nitrogen treatments.

The effect of water shortage

As regards water stress, Gallagher et al. (1979), found that mild water stress led to a decrease in the rate of epidermal cell extension but had no effect upon the duration of the leaf extension process or upon the timing of phenological development. It is also well known that even moderate water stress can affect crop assimilation rate and thus the final yield.

Crops sown at Manhattan,KS and in Italy did not suffer from lack of water but in Mandan the effect of irrigation upon the growth rate and the final yield of both crops grown with low (N1) or high (N2) nitrogen fertilization was great. In the N1 treatement the grain yield was 1,074 kg/ha for rainfed conditions and 1,161 kg/ha for well

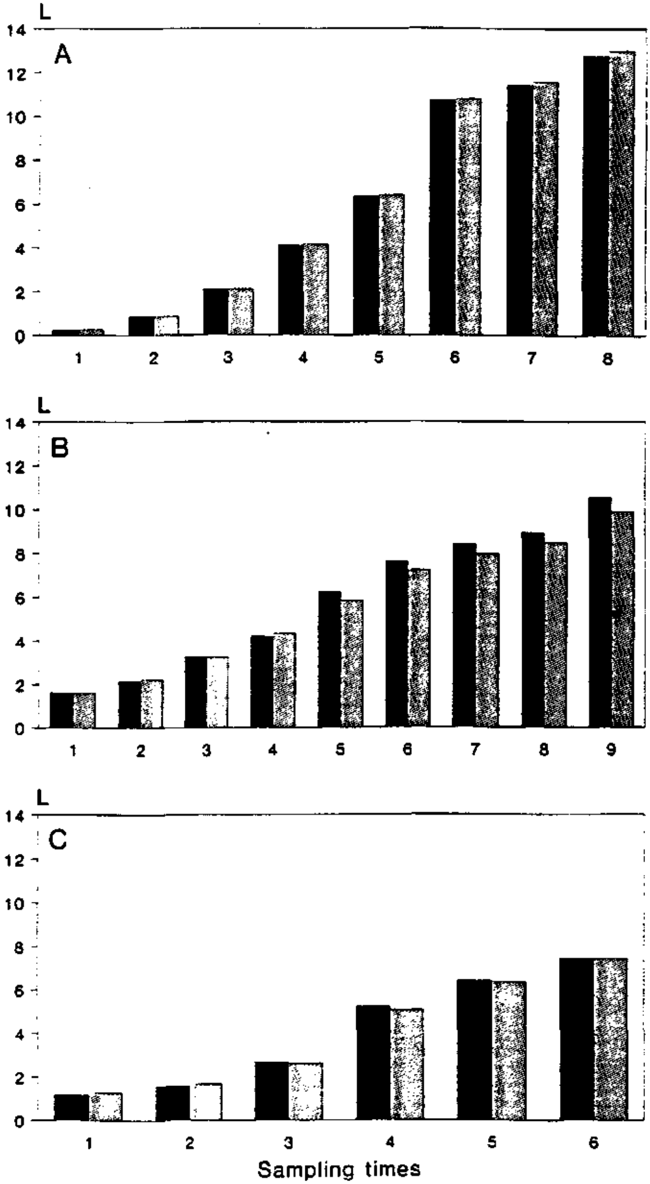

Fig. 5. Number of main stem leaves emerged (L) at each weekly sampling date (numbers on horizontal axis indicate subsequent samples) in plots with high nitrogen (solid bars) and low nitrogen (hatched bars) fertilization, at (A) Martorano 5, (B) Stuard and (C) Ostellato farms in Italy

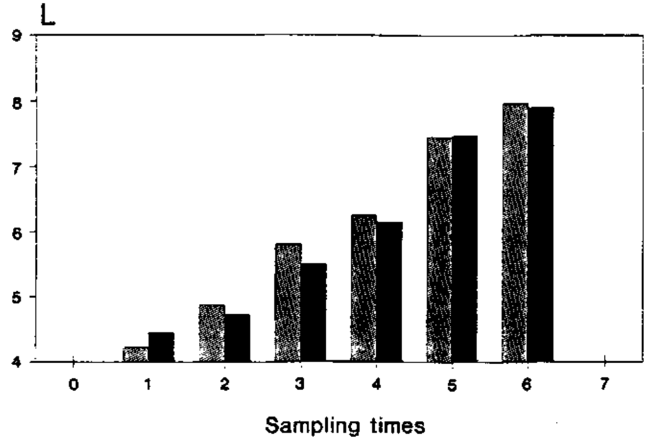

Fig. 6. Mean number of main stem leaves emerged (L) at each weekly sampling date (numbers on horizontal axis indicate subsequent samples), in well-watered (solid bars) and non-irrigated (hatched bars) plots of the 2 varieties tested at Mandan, North Dakota, USA, in the 1988–89 season

watered plots. In the N2 treatement yields ranged from 2,064 to 3,092 kg/ha. The mean growth rate of irrigated plots was 17.36 g/m2 day-1 whereas that of non irrigated ones dropped to 8.49 g/m2 day-1 (Major et al., 1988a, Major et al., 1988b). Nevertheless, the rate of leaf appearance appears to be unaffected by the irrigation treatements as is clearly shown in Fig.6 and statistically confirmed by the results of the variance analysis reported in Table 2. Also the date of heading and with this the final leaf number are unaffected by the irrigation treatements as they remained the same for both irrigation treatments.

It may be concluded that both wheat development and the leaf appearance process are independent of one of the major limiting factors for biomass growth and yield.

Simulation accuracy

The model under discussion makes it possible to predict the final leaf number of a crop sown at any date before the coldest period of the year and to simulate the appearance of the leaves on the main stem. The accuracy of predictions and simulations can be evaluated by comparing model preformances with field data. For such purposes a model parameter concerning varietal response to photoperiod has to be estimated at first and, then, model performances must be evaluated.

Table 4. Field experiments from which data were used to estimate photoperiodic sensitivity (σ) of the wheat variety 'Colt'. Last column indicates the difference found between calculated and observed dates of heading

Experimental sites	Lat. (N)	Long. (W)	Season	Difference (d)
Lethbridge (Canada)	49° 42′	112° 50′	1984–85	−1
			1985–86	1
Sandhills (NB, USA)	41° 37′	100° 50′	1984–85	1
			1985–86	2
Mandan (ND, USA)	46° 46′	100° 55′	1984–85	−3
Manhattan (KS, USA)	39° 09′	96° 37′	1985–86	3

Table 5. Field experiments in Italy from which data were used to estimate photoperiodic sensitivity (σ) of cultivars tested in the experiments conducted in Italy. Last 3 columns indicate the differences between observed dates of heading and those calculated using values of σ equal to 40.0 for the variety 'Salmone', 24.5 for 'Pandas' and 32.09 for 'Centauro'

Experimental sites	Lat. (N)	Long. (E)	Season	Difference (d)		
				Salmone	Pandas	Centauro
Avanella (Firenze)	43° 46′	11° 23′	1981–82	−2		
			1982–83	−3		
Basiliano (Udine)	46° 02′	13° 05′	1984–85	0	1	2
Nespoledo (Udine)	46° 01′	13° 03′	1980–81	2		
Braccagni (Grosseto)	42° 53′	11° 05′	1982–83	2		
Torviscosa (Udine)	45° 47′	13° 20′	1981–82	2		
			1984–85	−4	0	−1
Cremona	45° 08′	10° 01′	1982–83	−1		
			1983–84	3		
			1984–85	2	5	6
Caorle (Venezia)	45° 39′	12° 50′	1982–83	3		
			1983–84	6		
			1984–85	−1	1	2
Catania	37° 30′	15° 06′	1984–85	−7	−10	−10
Fano (Pesaro)	43° 51′	13° 03′	1982–83	−2		
			1984–85	−1	0	0
			1985–86	0	1	−1
Fontarronco (Arezzo)	43° 37′	11° 50′	1982–83	−1		
Ponte Galeria (Roma)	41° 52′	12° 27′	1981–82	−1		
Cavriglia (Arezzo)	43° 30′	11° 31′	1981–82	8		
Cesa (Arezzo)	43° 21′	11° 46′	1982–83	3		
S. Angelo Lod. (Milano)	45° 15′	9° 25′	1981–82	−2		
			1982–83	−2		
			1984–85	−2	5	6
Ravenna	44° 25′	11° 35′	1981–82	5	0	0
			1982–83	−3	1	−1
			1983–84		0	1
			1984–85	−6	−2	−1
Cadriano (Bologna)	44° 30′	11° 10′	1981–82	−1	−2	−5
			1982–83	−4	0	2
			1983–84		0	0

The model assumes that different wheat varieties can have a different response to photoperiod. This response is expressed by the relationship between daylength (P = hours day^{-1}) and the final number of leaves that are formed in the main stem (F_l) and it is quantified, in the model, in the following equation (Miglietta,1990b):

$$F_l = \alpha * \exp^{(-0.25\,P)} + 6.5$$

The photoperiodic response coefficient α can be estimated in laboratory experiments by counting the final number of leaves in vernalized or non vernalization requiring plants that are grown under different daylength or, when laboratory data are not available, it can be estimated on the basis of the latitude for which any given variety has been artificially selected (Miglietta,1990b).

Moreover, estimates of α can be directly obtained on the basis of data obtained in field experiments. In this case, the model itself can be used to estimate the photoperiodic response of varieties. This can be done by running it in an iterative way and by changing, at each run, the photoperiodic response of the variety under study. This procedure aims to find the value of α that minimizes the difference between observed and calculated final leaf number or heading date. The estimates of α obtained in this way for any given variety are obviously more reliable where the range of latitudes and the number of years for which experimental observations are available, are larger.

The variety Colt was grown in the experiments performed in the USA. No laboratory data are at present available to estimate with accuracy the photoperiodic response of the variety and it is not known to the author the latitude for which that particular variety was selected. The iterative procedure described above was therefore used in order to estimate the coeffient α. A list of the field

Table 6. Calculated and observed dates of heading, predicted and observed final leaf number, for the different fertilization/irrigation treatments in all the experiments

Site	Variety	Date of heading		Final leaf number	
		Observed	Predicted	Observed	Predicted
Manhattan (KS, USA)	Colt	3 May	3 May	7	9.5
Mandan (ND, USA)	Colt	8 Jun	7 Jun	8	9
Martorano 5 (Italy)	Pandas	27 Apr	25 Apr	10	9.8
	Centauro	1 May	30 Apr	10	10.3
	Salmone	5 May	4 May	11	11
Ostellato (Italy)	Pandas	28 Apr	28 Apr	9	9.3
	Centauro	1 May	2 May	10	9.8
Stuard (Italy)	Pandas	6 May	4 May	9	9.3
	Costantino	9 May	8 May	9	9.7
	Salmone	11 May	11 May	10	10.2

experiments used in the estimation procedure is given in Table 4 (Hubbard et al., 1988) together with the difference, in days, found between observed and calculated dates of heading. The value of α that minimizes the difference between observed and calculated dates of heading for the variety Colt is 29.5.

Laboratory data to estimate the photoperiodic response coefficient of the 4 varieties tested in the experiments conducted in Italy are also not available. A rough evaluation of the photoperiodic response coefficient for these varieties is therefore possible on the basis of the latitude for which the varieties were selected but this method cannot take into account developmental differences which are the result of different breeding programs developed at the same breeding Institute. In fact, the variety Pandas which develops faster and Centauro which develops slower were both bred by the Società

Produttori Sementi in Bologna. Hence, the photoperiodic response of these varieties was again estimated on the basis of independent experimental data obtained in the field at several sites and in several years (CERAS, 1960-89, Bindi and Miglietta, 1990). Iterative model runs were again performed according to the optimizing procedure that is described above and estimated values of the coeffient α were found to be 24.5±1.96 for PANDAS, 32.09±1.83 for CENTAURO and COSTANTINO and 40±1.71 for SALMONE. A list of the field experiments used in the estimation procedure is given in Table 5 together with the difference in days found between observed and calculated date of heading. Results of the experiments performed in the season 1988-89 are not included in the data set, thus keeping calibration and validation data independent of each other.

Model results concerning the predicted final leaf number and the date of heading in all the considered field experiment are given in Table 6. Simulation accuracy for leaf appearance is illustrated in Fig. 7 for Manhattan, KS and Mandan, ND experiments and in Fig. 8 for the experiments in the Martorano 5, Ostellato and Stuard farms.

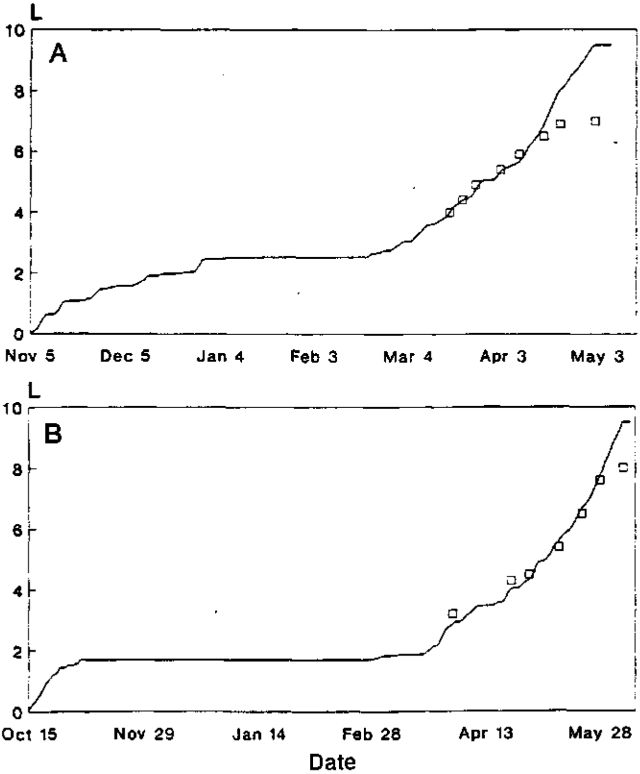

Fig. 7. (—) Simulated and (□) observed number of emerged main stem leaves (L) of the variety 'Colt' at (A) Manhattan, Kansas, in the 1985–86 season and (B) Mandan, North Dakota, in the 1984–85 season

The model overestimates the final leaf number in the two experiments in the USA but the date of heading is accurately calculated for both.

5.4. Conclusions

It has been demonstrated that neither variety, nitrogen fertilization nor mild water stress have an effect upon leaf appearance, final number of main stem leaves, phasic development or the timing of the different apical stages, in the field. Hence, the previous conclusion that wheat development is mainly controlled by temperature, photoperiod and vernalization is confirmed. This makes the model that was presented in the two previous papers of this series widely applicable at the field level.

The accuracy of model performances was confirmed by the comparison of predicted and simulated data with field observations made in the experiments conducted in the USA and in Italy. The problems encountered in the parametrization of varietal response to photoperiod suggested that the rough evaluation of photoperiodic response of varieties on the basis of the latitude for which they were selected is not always applicable. However, the iterative procedure developed for such an evaluation revealed that difficult and expensive daylength experiments in the laboratory are often not necessary. This conclusion should encourage stronger efforts for the collection and the circulation of variety and meteorological data as recorded in the many variety trials that are conducted around the world.

Simulation models are useful tools in research and application (de Wit,1978). In particular, a model that simulates and predicts the development of wheat, in the field, can be of great value for agronomy (Kirby,1988), of help to breeders as well as to researchers involved in the study of the impact of climate changes upon agriculture (Miglietta & Porter,1990).

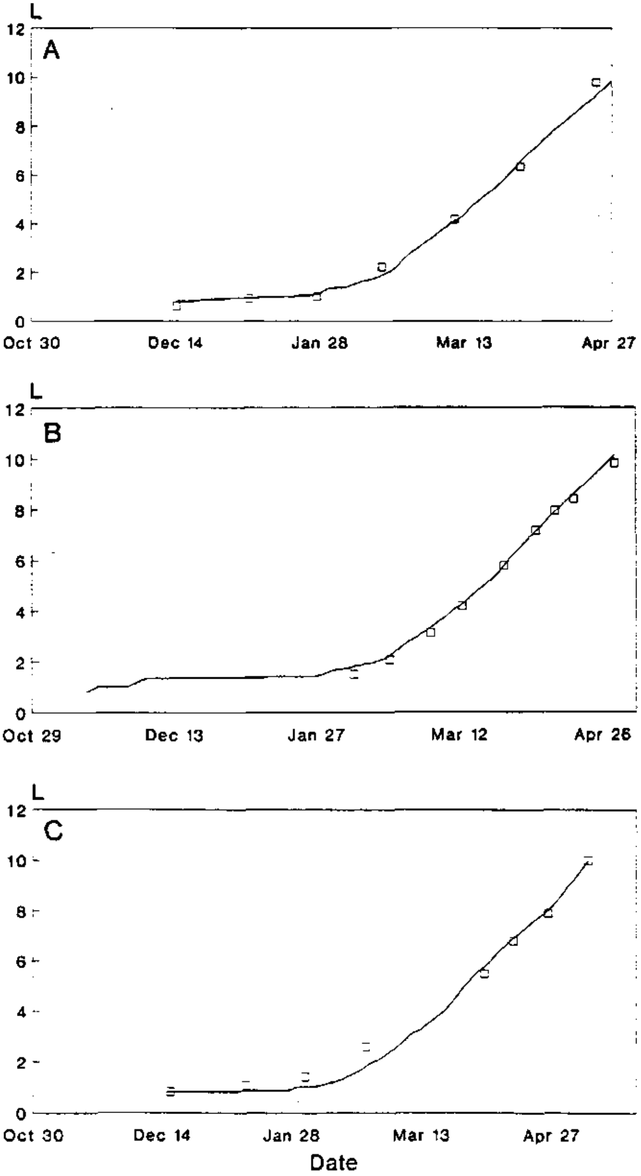

Fig. 8. (—) Simulated and (□) observed number of emerged main stem leaves (L) of the variety 'Colt' at (A) Martorano 5, (B) Stuard and (C) Ostellato farms in Italy, in 1988–89

The optimal time for the application of fertilizers and of hormone based herbicide is more related to apical and leaf development than to calendar dates. The discussed model makes it possible to predict with sufficient accuracy the time of floral induction and to simulate the appearance of subsequent main stem leaves.

The screening of varieties for earliness and adaptation to a given environment implies knowledge of photoperiodic and vernalisation responses of the different genotypes. Since the final number of leaves formed in the field by the different varieties is an interesting selection criterium. Thus, a model that predicts the final number of main stem leaves of crops grown at any latitude and under any climate can be succesfully applied in breeding programs.

The effect of expected climate changes related to the increase in the atmospheric CO2 can also be studied by means of this model. Model runs can be performed both to assess the direct effect of increasing temperatures upon wheat development and to define the ideotype variety which will be better adapted to such changes.

However, further research is needed to come up with a complete onto-morphogenetic model for wheat. This model, in fact, should be able to estimate the effect of variety, climate, mineral nutrition and water stress on the final size of main stem and tillers leaves and on the development of leaf cover under field conditions.

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SUMMARY

The main purpose of this study is to understand wheat ontogenesis and to formulate a simulation model of the development of wheat for application under field conditions. The basic idea that is behind this work is that plant development can be accurately simulated on the basis of leaf appearance provided that the final number of leaves is known. Apex and leaf development are in fact coordinated and in plants with terminal flowers, flowering occur when all the leaves are appeared on the stem. Wheat ontogenesis, apical and phenological development of wheat are described at first in the introductory chapter. A brief review of current knowledge about factors affecting wheat development and some information about existing ontogenetic models are also given.

Subsequently, data of some experiments in the literature are compared and statistically analysed to confirm the assumption of independence of wheat leaf initiation from daylength, and to evaluate the effect of temperature. Independence for any daylength treatement is demonstrated by the strict proportionality between the total number of initiated leaf primordia and the time to double ridges. The temperature response of leaf initiation rate is evaluated as the slope of a regression line between these two variables for different thermal treatments. On such a basis a linear model is constructed where daily leaf primordium initiation rates are calculated as a function of temperature. Data from a specific field experiment are then used to test the model. In the experiment, two varieties (Maris Huntsman and Creso) and two sowing dates (late November and early February) are compared. Predicted and observed dates of double ridge appearance and the predicted number of initiated primordia match rather accurately for both sowing dates and varieties, confirming the previous hypothesis. It is concluded that vmost of the genotypic variabllity in wheat ontogenesis is accounted for by the effect of photoperiod on

earliness of floral induction and, therefore, on the final main stem leaf number.

However, rate of leaf appearance differs among wheat crops sown in the field at different dates. This can be interpreted either as a direct effect of the date of sowing on the rate of leaf appearance or as an indirect effect of an ontogenetic decline in the rate of leaf appearance as the plant ages. This decline is attributed to the increasing distance that has to be traversed the youngest leaf in the apparent stem that is formed by the leaf sheets of the older leaves. Analysis of data from both laboratory and field experiments leads to the conclusion that the second hypothesis is more likely. A simulation model of leaf appearance is formulated on the basis of this hypothesis, and tested using experimental results from the literature and 2 original experiments carried out in Italy. A good agreement between experimental data and simulation results is found. The model simplifies the problem of simulation of leaf appearance considerably compared with existing models that are based on a spurious relation between the rate of change in daylength at crop emergence and the rate of leaf appearance, which does not have a physiological base.

The problem of the prediction of the final number of leaves is then approached. The role of photoperiod in the regulation of wheat development and on final main stem leaf number is analysed by means of literature data from a number of laboratory experiments. A procedure is developed to calculate the final number and the date of heading of plants that do not require vernalisation. Subsequently, differences between calculations and field observation are ascribed to an effect of vernalisation. This allows the formulation of a model to predict the final number of leaves and date of heading of any given wheat variety. The model involves the following assumptions: (1) wheat varieties have different sensitivities to the daylength; (2) wheat varieties that require vernalisation are vernalised at a very early stage of growth if sown at the beginning of the coldest period of the year; (3) wheat varieties that are vernalised at a very early stage of growth immediately respond to external photoperiodic conditions; (4) wheat crops sown within a range of sowing dates tend to synchronize time of flowering. It is concluded that if the final main stem leaf number of a crop sown at a given date is known, the date of heading and the corresponding final leaf number of main stem leaves of every other sowing can be found. The model is validated using field data from 58 experimental trials performed in the USA and Europe.

In the last part of the work, the effect of nitrogen fertilization, water shortage and of the genotype on both the rate of leaf appearance and the final leaf number are considered. Results of field experiments conducted in USA and of original experiments performed in Italy are used for such a purpose. Data analysis shows that leaf appearance, final leaf number and phasic development of wheat are independent of nitrogen fertilization and water shortage and that genotypic effect is restricted to the control of the final number of leaves but not of the rate of leaf appearance.

Finally, the formulated models are extensively validated on basis of data recorded in field experiments and it is concluded that these appear to be well suited for monitoring wheat ontogenesis under field conditions. The models can be used in agronomy, for analyses of the influence of weather on the development of wheat and of the adaptation of varieties to different environments and for studying the impact of climatic changes on agriculture.

SAMENVATTING

Belangrijke doelen van dit onderzoek zijn een bijdrage te leveren aan een beter begrip van de ontogenese van tarwe en het opstellen van een simulatieprogramma voor de ontwikkeling van tarwe onder veldomstandigheden. Het uitgangspunt van het onderzoek is dat de ontwikkeling volledig wordt bepaald door de snelheid waarmee de bladeren verschijnen, het uiteindelijke aantal bladeren en de coördinatie tussen de ontwikkeling van de apex en de bladeren en dat bij planten met een terminale bloeiwijze het bloeien direct begint na het verschijnen van de bladeren.

Het eerste hoofdstuk betreft de ontogenese en de apicale en fenologische ontwikkeling van tarwe. Het geeft een kort overzicht van de factoren die de ontwikkeling beïnvloeden, en gaat in op bestaande ontogenetische modellen.

In het volgende hoofdstuk zijn de resultaten van een aantal experimenten uit de literatuur vergeleken en statistisch geanalyseerd om aan te tonen dat de snelheid waarmee de bladeren worden geïnitialiseerd onafhankelijk is van de daglengte en om het effect van de temperatuur op deze snelheid vast te stellen. Deze onafhankelijkheid blijkt uit de strikte recht-evenredigheid tussen het totaal aantal bladprimordia dat wordt geïnitialiseerd en de tijd die verloopt totdat het "double ridge" stadium wordt bereikt in proeven waarbij de planten aan verschillende daglengten zijn blootgesteld. De helling van de regressie lijn tussen temperatuur en snelheid van initialisatie voor de verschillende behandelingen geeft de reactie op de temperatuur weer. Dit maakt het mogelijk de initialisatiesnelheid van de bladprimordia voor iedere dag te berekenen als functie van de temperatuur. Het hierop gebaseerde model is getest met gegevens van een onafhankelijk veldexperiment met twee tarwe cultivars (Maris Huntsman and Creso) en twee zaaidatums (eind november en begin februari). Voorspelde en waargenomen gegevens over de datum van bereiken van het " double ridge" stadium en over het aantal geïnitialiseerde primordia komen goed overeen voor zowel de variëteiten als de zaaidatums en bevestigen zodoende de uitgangsveronderstellingen. Zo blijkt dat vrijwel alle genotypische variatie in de ontogenese van tarwe tot expressie komt door de invloed van de fotoperiode op de tijd van inductie van de bloei en zodoende op het uiteindelijke aantal bladeren aan de hoofdstengel.

Niettemin is het zo dat de snelheid waarmee de bladeren verschijnen wel afhangt van de tijd waarop het tarwegewas wordt gezaaid. Dit zou gezien kunnen worden als een direct effect van de tijd van zaaien op de snelheid van verschijnen van de bladeren of een indirect effect van een ontogenetische vertraging van de snelheid van verschijnen bij het ouder worden. Deze vertraging zou dan samenhangen met de toenemende afstand die door het jongste blad moet worden afgelegd in de schijnstengel die wordt gevormd door de oudere bladeren. Een analyse van zowel laboratorium als veldexperimenten geeft aan dat de tweede hypothese het meest waarschijnlijk is. Op grond hiervan is een simulatiemodel ontworpen dat vervolgens is getoetst met behulp van experimentele resultaten uit de literatuur en van twee eigen proeven in Italië. Hierbij werd een goed verband tussen gemeten en gesimuleerde resultaten vastgesteld. Het model vereenvoudigt de simulatie van het verschijnen van de bladeren aanzienlijk, dit in vergelijking met bestaande modellen die zijn gebaseerd op een niet-oorzakelijke correlatie tussen de snelheid waarmee de daglengte verandert bij het opkomen van het gewas en de snelheid van het verschijnen van de bladeren.

Vervolgens komt de voorspelling van het aantal bladeren aan de orde. Hierbij is de invloed van de fotoperiode op de regulering van de ontwikkeling van tarwe en het uiteindelijke aantal bladeren aan de hoofdstengel geanalyseerd met behulp van literatuur gegevens en een procedure uitgewerkt voor de berekening van dit aantal voor planten die geen vernalisatie behoeven. Door verschillen tussen berekeningen en de veldwaarnemingen toe te schrijven aan vernalisatie is het mogelijk een model op te stellen waarmee bladaantal en datum van in aar schieten kunnen worden voorspeld voor welke cultivar dan ook. Het model steunt op de volgende veronderstellingen: (1) cultivars verschillen in hun gevoeligheid voor daglengte;(2) tarwe cultivars die vernalisatie behoeven, worden gevernaliseerd aan het begin van de groei, indien er wordt gezaaid aan het begin van de koudste periode van het jaar; (3) tarwe cultivars die in een vroeg stadium van de groei zijn gevernaliseerd, zijn direct daarop gevoelig voor de daglengte; (4) tarwe gewassen die op verschillende tijden zijn gezaaid, hebben de neiging hun bloei te synchroniseren. Op basis hiervan kan het uiteindelijke aantal bladeren, de datum van in aar schieten en daarmee het uiteindelijke aantal bladeren worden berekend voor een heel scala van cultivars, zaaidatums en breedtegraden. Het model is gevalideerd met behulp van literatuurgegevens over 58 experimenten in de USA en Europa.

Vervolgens is de invloed van stikstofbemesting, watertekorten en genotype op zowel de snelheid van het verschijnen van bladeren als het uiteindelijke aantal bladeren onderzocht. Hiervoor zijn resultaten van veldexperimenten in de USA opnieuw geanalyseerd en eigen proeven gedaan in Italië. Het blijkt dat de verschijning van de bladeren, het uiteindelijk aantal bladeren en de overige kenmerken van ontwikkeling van de tarwe niet worden beïnvloed door stikstofbemesting en watertekort en dat genotypische verschillen zich niet uitstrekken tot de snelheid van verschijnen van de bladeren, maar zich beperken tot verschillen in aantal bladeren.

Tot slot zijn alle modellen uitvoerig gevalideerd op basis van gegevens ontleend aan veldexperimenten en wordt op grond hiervan geconcludeerd dat deze modellen uitermate geschikt zijn voor het voorspellen van de ontogenese van tarwe onder veldomstandigheden. De modellen kunnen in de landbouwkunde gebruikt worden voor het analyseren van de invloed van het weer op de ontwikkeling van tarwe, van de bruikbaarheid van cultivars onder uiteenlopende omstandigheden en van de invloed van klimaatsveranderingen op de landbouw.

Curriculum vitae

F.Miglietta was born in Genoa, Italy, on 7 August 1954. He got his degree in Agricultural Sciences at Florence University in 1980. Since 1984 he works as research scientist at IATA-CNR of Florence and he spent a six month period at the Departement of Theoretical Production Ecology of Wageningen Agricultural University in 1986.

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He is author of several papers on refereed journals dealing with remote sensing, agrometeorology, crop modelling and environmental physiology.