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The Utilization of Degree Days for the Characterization of Developmental Stages of 26 Winter Wheat Cultivars

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Abstract. Twenty six winter wheat cultivars representing early maturing (Em), medium early maturing (Mm), and late maturing (Lm) cultivar groups were grown in the field for two growing seasons. The dates at which plants reached the double ridge (DR) and terminal spikelet (TS) stages were determined using anatomical analysis of shoot apices. Thereafter the dates of anthesis (AN) and full maturity (MA) were recorded. The length of the time spans between subsequent developmental stages was then expressed both chronologically (number of days, d) and in terms of thermal time (degree day, °C d) which was calculated with the basal temperature equalling to zero. The results obtained confirmed the suitability of the utilization of degree days for the description of the time course of plant development, because the great differences in the time between subsequent developmental stages recorded between the two growing seasons when expressed in terms of numbers of days markedly diminished when expressed in terms of degree days. For example the period DR-MA expressed in number of days amounted in the year 1986 only to 87 % when related to the number of days recorded in the year 1985, whereas the corresponding value expressed in terms of degree days amounted to 98 %. The utilization of degree days is especially suitable for the AN-MA period (956 and 937 degree days in the years 1985 and 1986, respectively) within which temperature is the main factor determining the rate of plant development. Further analyses of the effects of basal temperatures, vernalization, and daylength appear to be necessary for a better understanding of the length of the period to the DR stage and differences among groups of cultivars and among different cultivars.

The time course of winter wheat crop development in dependence on environmental conditions has been under observation for a number of decades. In this respect, attention had already earlier been focussed on the effects of vernalization and daylength (Krekule 1961, Halse and Weir 1970, Petr 1975). In recent years these problems were again paid great attention with respect to the need of obtaining data necessary for the construction of simulation models (Baker *et al.* 1986, Wright and Hughes 1987). In addition to that, demands for optimum applications of fertilizers, pesticides, and growth regulators have increased with increasing level of the crop cultivation technology (Klepper *et*

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al. 1988). Application optimization also involves the optimization of the dates of the applications, first of all from the viewpoint of the actual developmental stage of plants in a crop canopy. For this reason extensive trials were conducted aimed at obtaining exact descriptions of the course of plant development in dependence on climatic conditions (Kirby *et al.* 1987, Porter *et al.* 1987). And also for this reason attention was again focussed on the demands of cereal crops for vernalization and photoperiod (Saini *et al.* 1986, Wong and Baker 1986).

The level of understanding of many physiological processes is already as high as to allow research workers to describe in quantitative terms the influence of environmental factors on some physiological functions of crop plants and also mutual interactions amoung them. But the construction of simulation models simultaneously results in the emergence of new very specifically formulated questions which can be answered only on the basis of results obtained in new experiments. In this way also the purpose and the aim of mathematical simulation of physiological processes can be formulated (Thornley 1976, Bikhele *et al.* 1980).

When constructing dynamic mathematical models of crop productivity, the construction of a submodel describing the time course of crop development necessarily represents the first step. The time course of plant development is the determining factor for the chronological sequence of the growth of different plant parts and for the production and distribution of photosynthates. The so-called thermal time proved to be useful for the description of the time course of plant development (Baker and Pinter 1986, Porter 1987) which is determined as a sum of daily mean temperatures from which the basal temperature (Tb) was subtracted. This Tb represents that temperature at which the rate of the process under study equals to zero.

However, in agreement with the introductory statement, the construction of mathematical models describing plant development also requires new data. The necessary new data are represented in case of cereal crops by data on the duration of various developmental phases. Experience obtained so far has shown that there exist both species- and cultivar-specificities not only in the duration of different growth phases but also in its dependence on various weather factors (Cao and Moss 1989a, 1989b, 1989c, Marshall *et al.* 1989).

Until the mechanisms regulating the time course of plant development are sufficiently understood, parameters derived from empirically devised experiments must be utilized as input data for complex simulation models. A set of such data characterizing the length of periods between plant development stages of three groups of winter wheat cultivars differing in the time to maturity is the subject of this paper.

MATERIAL AND METHODS

The development of the ear on the main stalk was studied in 26 cultivars and lines of winter wheat (*Triticum aestivum* L.) during two growing seasons (1984/1985 and 1985/1986). Using the characteristic inferred by Šíp and Škopík (1987) on the basis of an evaluation of the time span from seedling emergence to ear emergence, the cultivars involved in the experiment were divided to three groups, as follows:

1. Early maturing (Em): Super Zlatná, Košútka, Sava, Vala.
2. Medium early maturing (Em): Mexico 50/B 21, Karlik, Roazon, BU-17, UH 1072, Slavia, Amika, NA-4, Kavkaz, Ilyichovka, Mironovskaya 10, Mironovská.
3. Late maturing (Lm): Maris Fundin, Maris Marksman, Maris Huntsman, Weihenstephan 378, Kormorán, Margin, Caribo, Zora, Fakir, Chlumecká 12.

Their seeds were drilled using a drilling machine onto experimental field plots belonging to the Research Institute of Crop Production. The amount of sown seeds equalled to 4.5 millions of viable seeds per hectare. Seeds were drilled on October 5, 1984, and on October 4, 1985, respectively. Because measurements were conducted always after the winter season, the first experimental growing season is in the text of this paper referred to as 1985 and the second one as 1986.

During April and May, five plants were sampled each week in the cultures of all the above cultivars from each of the three replicate parcels for the determination of the stage of organogenesis of the shoot apex of the main stalk. The dates at which plants reached double ridge stage (DR), terminal spikelet (TS) stage, anthesis (AN), and maturity (MA) were recorded. Those dates were considered to be the dates of DR and TS stages at which the same stage of ontogenesis was recorded in 90 % of the analyzed shoot apices. The date of anthesis was recorded by that day on which 70 % of ears on experimental plants showed extruded stamina.

Daily average effective temperatures were calculated according to Porter (1984) using records of daily minimum and maximum temperatures with the basal temperature equalling to 0 °C. Sums of these effective temperatures were then calculated for periods from DR to TS (DR-TS), from TS to AN (TS-AN), and from AN to MA (AN-MA). Thereafter values for DR-AN, DR-MA, and TS-MA also were calculated.

Data on the sum of effective temperatures with basal temperatures in the range from 1 °C to 10 °C with a gradient of 1 °C were evaluated only for the comparison of the variability of results obtained in the two growing seasons. Statistical significance of differences between groups of genotypes and between growing seasons was determined using the t-test.

TABLE 1

Duration [d] of different periods delimited by double ridge (DR). terminal spikelet (TS). anthesis (AN). and maturity (MA) recorded with 26 winter wheat cultivars grown in the growing seasons 1984/1985 (indicated 1985) and 1985/1986 (1986). Dates at which cultivars reached double ridge are presented in the first two columns. Differences between means accompanied by different letters are statistically significant.

Cultivars	Period of development													
	DR		DR-TS		TS-AN		AN-MA		DR-AN		TS-MA		DR-MA	
	Years													
	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986
EARLY (Em)														
Vala	8.4.	14.4.	34	24	24	22	55	53	58	46	79	75	113	99
Košútka	6.4.	13.4.	31	21	26	20	56	54	57	41	82	74	113	95
Sava	8.4.	13.4.	30	24	26	20	57	55	56	44	83	75	113	99
Super Zlatná	5.4.	13.4.	33	24	25	21	57	54	58	45	82	75	115	99
Mean Em	7.4.	13.4.	32.0	23.3	25.3	20.8	56.3	54.0	57.3	44.0	81.5	74.8	113.5	98.0
			a	a	a	a	a	a	a	a	a	a	a	a
MEDIUM (Mm)														
Slavia	11.4.	14.4.	33	28	22	24	55	45	55	52	77	69	110	97
Mironovskaya 10	11.4.	24.4.	32	16	23	27	56	47	55	43	79	74	111	90
Mironovská	12.4.	14.4.	31	28	21	22	56	49	52	50	77	71	108	99
Iliichovka	11.4.	19.4.	31	19	25	23	55	54	56	42	80	77	111	96
UH 1072	12.4.	24.4.	33	21	19	19	56	49	52	40	75	68	108	89
Kavkaz	11.4.	21.4.	35	21	22	28	55	44	57	49	77	72	112	93
Mexico 50	8.4.	18.4.	34	19	24	24	58	51	58	43	82	75	116	94

TABLE 1
(continued)

Cultivars	Period of development													
	DR		DR-TS		TS-AN		AN-MA		DR-AN		TS-MA		DR-MA	
	Years													
	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986
Amika	12.4.	18.4.	31	20	23	24	55	50	54	44	78	74	109	94
NA 4	10.4.	21.4.	35	21	20	19	57	54	55	40	77	73	112	94
BU 17	10.4.	20.4.	34	22	22	26	56	49	56	48	78	75	112	97
Roazon	9.4.	20.4.	35	18	20	24	58	53	55	42	78	77	113	95
Karlik	12.4.	18.4.	30	20	22	25	57	51	52	45	79	76	109	96
Mean Mm	11.4.	19.4.	32.8	21.1	21.9	23.8	56.2	49.7	54.8	44.8	78.1	73.4	110.9	94.5
			a	a	b	b	a	b	b	a	b	ab	b	b
LATE (Lm)														
Chlumecká 12	14.4.	20.4.	35	26	20	27	55	44	55	53	75	71	110	97
Maris Fundin	8.4.	14.4.	38	30	23	26	55	46	61	56	78	72	116	102
Maris Marksman	13.4.	14.4.	35	31	23	29	53	43	58	60	76	72	111	103
Margin	11.4.	24.4.	38	22	22	32	51	42	60	54	73	74	111	96
Maris Huntsman	12.4.	21.4.	35	23	21	26	56	47	56	49	77	73	112	96
Caribo	8.4.	20.4.	41	25	19	25	54	47	60	50	73	72	114	97
Fakir	9.4.	24.4.	38	22	23	27	54	45	61	49	77	72	115	94
Kormorán	13.4.	18.4.	32	27	19	28	55	41	51	55	74	69	106	96
Weihenstephan 378	11.4.	20.4.	35	26	26	29	51	42	61	55	77	71	112	97
Zora	12.4.	20.4.	35	26	21	30	55	41	56	56	76	71	111	97
Mean Lm	11.4.	19.4.	36.2	25.8	21.7	27.9	53.9	43.8	57.9	53.7	75.6	71.7	111.8	97.5
			b	b	b	c	b	c	a	b	c	b	ab	a
Total mean	10.4.	18.4.	34.0	23.2	22.3	24.9	55.3	48.1	56.3	48.1	77.7	73.0	111.7	96.2

TABLE 2

Duration (expressed in terms of 0 °C d) of winter wheat plant development periods delimited by double ridge (DR), terminal spikelet (TS), anthesis (AN), and maturity (MA) recorded with 26 winter wheat cultivars grown in the growing seasons 1984/1985 (indicated 1985) and 1985/1986 (1986). Differences between means accompanied by different letters are statistically significant.

Cultivars	Period of development: DR-TS		TS-AN		AN-MA		DR-AN		TS-MA		DR-MA	
Years	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986
EARLY (Em)												
Vala	310	312	424	345	956	969	734	657	1380	1314	1690	1626
Košútka	263	230	427	342	954	1005	690	572	1381	1347	1644	1577
Sava	253	304	428	330	991	998	681	634	1419	1328	1672	1632
Super Zlatná	288	304	412	344	987	971	700	648	1399	1315	1687	1619
Mean Em	279	288	423	340	972	986	701	628	1395	1326	1673	1614
	a	a	a	a	a	a	a	a	a	a	a	a
MEDIUM (Mm)												
Slavia	341	359	383	369	956	881	724	728	1339	1250	1680	1609
Mironovskaya 10	312	260	406	395	973	898	718	655	1379	1293	1691	1553
Mironovská	304	359	360	343	973	934	664	702	1333	1277	1637	1636
Iliichovka	289	278	444	353	945	994	733	631	1389	1347	1678	1625
UH 1072	241	335	329	296	963	934	570	631	1292	1230	1533	1565
Kavkaz	372	316	378	403	943	908	750	719	1321	1311	1693	1627
Mexico 50	310	276	424	370	1007	938	734	646	1431	1308	1741	1584

TABLE 2
(continued)

Cultivars	DR-TS		TS-AN		AN-MA		DR-AN		TS-MA		DR-MA	
	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986
Amika	304	284	406	362	956	931	710	646	1362	1293	1666	1577
NA 4	364	316	326	310	992	994	690	626	1318	1304	1682	1620
BU 17	350	320	383	377	973	971	733	697	1356	1348	1706	1668
Roazon	358	274	336	362	1007	999	694	636	1343	1361	1701	1635
Karlik	281	284	372	373	991	997	653	657	1363	1350	1644	1634
Mean Mm	319	305	379	360	973	947	698	665	1352	1306	1671	1611
	b	a	b	a	a	b	a	a	b	a	a	a
LATE (Lm)												
Chlumecká 12	394	383	348	387	940	903	742	770	1288	1290	1682	1673
Maris Fundin	394	392	389	372	940	935	783	764	1329	1307	1723	1699
Maris Marksman	383	408	380	415	918	892	763	823	1298	1307	1681	1715
Margin	412	348	369	501	884	891	781	849	1253	1392	1665	1740
Maris Huntsman	378	349	361	389	959	960	739	738	1320	1349	1698	1698
Caribo	434	369	336	357	924	951	770	726	1260	1308	1694	1677
Fakir	403	348	384	387	929	926	787	735	1313	1313	1716	1661
Kormorán	312	380	336	402	943	859	648	782	1279	1261	1591	1641
Weihenstephan 378	310	383	418	419	916	879	728	802	1334	1298	1644	1681
Zora	378	383	361	440	943	859	739	823	1304	1299	1682	1682
Mean Lm	380	374	368	407	930	906	748	781	1298	1312	1678	1687
	c	b	b	b	b	c	b	b	c	a	a	b
Total mean	336	329	382	375	956	937	718	704	1338	1312	1674	1641

Period of development; Years

RESULTS

The classification of cultivars according to the dates of maturing allowed to distinguish on the basis of the dates at which they reached the DR stage only Em cultivars from the other two groups between which no differences were recorded in any of the two growing seasons (Table 1). In the course of further ontogenesis, the Em group did not show any period which was shorter in the two growing seasons than in the Mm group. When compared with the Lm group, only the DR-TS period in the Em group was in both growing seasons shorter by approximately three days (Table 1). By contrast, the TS-AN period in the 1985 growing season and the AN-MA period in the 1986 growing season were longer in the Em group than in the other two cultivar groups. When compared with the mean of all cultivars, the period DR-MA was longer in the Em group by two days (Table 1).

The longest DR-TS period was recorded in both growing seasons in the Lm group. In contract to this, the AN-MA period was shorter in the Lm group than in the other two groups (Table 1).

The highest differences in the time within which the cultivars reached the DR stage and also in the length of different periods recorded during wheat plant ontogenesis were found when the two growing seasons were compared. The DR stage was reached in the above cultivar groups in the 1986 growing season by 6 to 8 days later than in the 1985 growing season. The highest differences were recorded in the length of the DR-TS period which lasted in the 1985 growing season in average (all cultivars taken into account) 34 days, and in the 1986 growing season in average only 23.2 days. Within the experimental groups of cultivars, the TS-AN period was longer in the Em group only in the 1985 growing season. The AN-MA period was longer in the 1985 growing season in all three groups of cultivars. That means that an earlier DR date in the 1985 growing season was followed by a longer DR-MA period which lasted in the 1985 growing season 111.7 days whereas only 96.2 days in 1986. But such time course of ontogenesis was not recorded without exception in each particular case. Under certain weather conditions an early date of the DR stage can be followed by a fast time-course of ontogenesis and thus by short subsequent periods of plant ontogenesis. The differences in the length of the DR-TS and AN-MA periods were in both growing seasons consistent in all three groups of cultivars which means that this period was shorter in the 1986 growing season. The same applies for the whole DR-MA period. What is conspicuous is the differential response of cultivar groups as far as the length of the TS-AN period is concerned which was in the 1986 growing season shorter in the Em group by 4 days but longer by 6 days in the Lm group.

There can be no doubt that the rate of the time-course of plant ontogenesis is determined by the interaction of genetic specificity of cultivars with weather conditions. This also is obvious from a simplified analysis of the influence of

TABLE 3

A comparison of the duration (%) of different developmental periods of three winter wheat cultivar groups in the 1986 growing season when related to the 1985 growing season (= 100 %) and when expressed either in terms of days (d) or in terms of degree days (°C d).

Group of cultivars	% days							% degree days
	Periods of plant development							
	DR-TS	TS-AN	AN-MA	DR-MA	DR-TS	TS-AN	AN-MA	DR-MA
Early (Em)	72,8	82,2	95,9	86,9	103,2	80,4	101,4	96,4
Medium (Mm)	64,3	108,2	88,4	85,2	95,6	95,0	97,3	96,5
Late (Lm)	74,1	141,6	81,1	89,9	98,4	110,6	97,4	100,5
Mean	69,6	115,3	86,8	87,2	97,9	98,2	98,0	98,0

weather conditions in the two growing seasons when only the influence of temperature was evaluated by means of thermal time (Table 2), with the influence of vernalization and photoperiod being neglected. The length of individual periods of ontogenesis expressed in terms of degree days shows several specific characters. The period DR-TS was in both years approximately equally long. The shortest DR-TS period was recorded in the Em group of cultivars and the longest in the Lm group. The mean length of the TS-AN period of all cultivars also was the same in both growing seasons. In this case however, differential behaviour of cultivar groups was recorded in different growing seasons. In case of Em cultivars, this period was shorter in the 1986 growing season, whereas both growing seasons were nearly equal in case of Mm cultivars. In contrast to that, the TS-AN period was longer in the 1986 growing season in the Lm group. And finally small differences were recorded in degree days in the AN-MA period between the two growing seasons. But this period was shortest in both growing seasons in the Lm group.

TABLE 4

Variation coefficients (%) of values expressing the length of different development periods when expressed in terms of days (d) or in degree days (°C d). Mean values obtained with all 26 cultivars in both growing seasons.

Period	d	°C d	Tb (°C)
DR-TS	27.5	20.6	0
TS-AN	19.6	17.5	0 to +5
AN-MA	9.7	3.6	+4 to +6

Note: In case of the TS-AN period, the same °C d values were obtained for Tb in the range from 0 °C to +5 °C.

Whereas the DR-MA period corresponded in the 1986 growing season only to 87 % of the length of this period in 1985 in terms of days, it corresponded to 98 % when expressed in terms of degree days, and thus the length of this period was in both growing seasons nearly the same (Table 3). The length of each period of ontogenesis expressed in terms of days (mean value of all cultivars and both growing seasons) always showed higher variability expressed in terms of the value of the coefficient of variation (CV) than when the periods were characterized in terms of degree days. Very low CV values were obtained for the AN-MA period in which case the coefficient of variation equalled at Tb = 0 °C to 4.1 and at Tb = 10 °C to 5.8. The lowest value was found at Tb from 4 °C to 6 °C. Thermal times with such basal temperatures at which the lowest variation coefficients were obtained are presented in Table 4. The application of basal temperatures higher than zero did not result in higher CV values till anthesis. Basal temperature range from 4 to 6 °C appeared to be suitable only for the AN-MA period. But the difference from Tb = 0 °C was relatively small and therefore thermal times with Tb = 0 °C are also presented in Table 2 for the AN-MA period for reasons of a better comparison of the length of the studied periods of ontogenesis.

The low value of the variation coefficient of thermal time representing the length of the AN-MA period suggests that (1) the utilization of thermal time is suitable for the expression of the length of the period from anthesis to maturity and that (2) temperature is the relevant factor which determines the length of this period. By contrast, the high value of the coefficient of variation of data characterizing the length of the DR-TS period probably is the result of mutual interactions between vernalization and photoperiod, that is between those two factors which were not taken into consideration in this evaluation.

DISCUSSION

The utilization of degree days for the description of environmental conditions of crop plant development does not represent a novel approach to this problem (see the review by Monteith 1981). But there are some new biological aspects and the clearly defined necessity of using exact data including genotype specificity (Krekule 1987) also can be considered to be new.

Weir *et al.* (1984) include in their model of the development of winter wheat crops termal time values which are in the period from seedling emergence to anthesis modified by the coefficients of vernalization and daylength. In contrast to this, relevant factors can tentatively be reduced to sole thermal time in other climatic conditions. There is no doubt that in conditions in which our field trials were conducted, the development of plants of the above winter wheat cultivars could be influenced by both vernalization and daylength. However, vernalization is always completed before the onset of spring growth in a winter season with normal weather conditions corresponding to a long-term average and when wheat crops are sown at an early date. In our particular case, in total 113 d with average temperatures below 10 °C occurred in the period from October 15, 1984, to February 15, 1985, and 114 d in the year 1986. The influences of the photoperiod can show higher variability both in different growing seasons and in case of different cultivars. We consider the daylength influence to be the main cause of differences among the cultivar groups, especially in the duration of the DR-TS period. The general influence of daylength on the double-ridge stage date has been described by a number of authors. But there also exists evidence that daylength can influence the course of the period which follows after the DR stage (Wright and Hughes 1987, Dellecolle *et al.* 1989, Ellis *et al.* 1989). Innes *et al.* (1985) inferred that the date of ear emergence on winter wheat plants is also predetermined by genes controlling their sensitivity to daylength. The corresponding algorithm is also formulated in similar way in the model devised by Weir *et al.* (1984).

Basal temperatures can represent another source of variability in the length of thermal time calculated by us. With the exception of data given in Table 4, only values calculated for Tb = 0 °C are presented in this paper. In contrast to this Weir *et al.* (1984) chose Tb = 1 °C for the period from seedling emergence to anthesis, and Tb = 9 °C for the AN-MA period. Pozo *et al.* (1987) experimentally inferred Tb = 2 °C for seed germination, seedling emergence, tillering and leaf growth, but Tb = 6 °C for most other processes. Numbers of degree days calculated by us for particular developmental periods using temperature bases in the range from 1 °C to 10 °C did not indicate distinct or more clear-cut or unequivocal conclusions and therefore these data are not presented in the paper.

It can be assumed that the value of the basal temperature, basal parameters characterizing demands for vernalization (and thus also its duration under various combinations of minimum, maximum, and mean day temperature) and photoperiod (its duration at certain daylengths) will belong to the group of the basal parameters characterizing different cultivars. It can be expected that these parameters will be difficult to obtain and that the experiments will be time-consuming. But on the other side it can be expected that aims formulated in such definite terms will allow to simplify the necessary experimental scheme.

The characterization of the length of particular periods of winter wheat plant development in terms of degree days offers not only define data which can be used for the determination of parameters of different cultivars, but also repeatedly proves the suitability of the conception of thermal time, with the mean values of the cultivar groups and also of the whole set of the cultivars involved supplying basal data. However, also in this case the utilization of mean values does not represent the final aim (see also Roberts *et al.* 1988). They rather represent a basis for the construction of a model and for the arrangement of an experiment aimed at (1) describing all the above indicated parameters determining the velocity of plant development, and at (2) inferring the cultivar-specific parameters.

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