Relationships between the blade and sheath growth in the same leaf and in successive leaves of winter barley

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Abstract

Winter barley (*Hordeum vulgare* L. cv. Efra) plants were grown till the stage of the fourth leaf under controlled conditions at constant temperatures 26.0 °C, 21.8 °C, 19.6 °C and 15.3 °C. The relationships between the sheath and blade growth was studied. The leaf sheath began to be discernible when it was 0.1 mm long and the blade length was 20 mm. In this stage a correlation (r = 0.812) was found between the length of blade and that of shearth. The sheath length in 20 mm long leaf increased in dependence on leaf insertion. At the time of the beginning of sheath discernibility the elongation growth of the subsequent leaf was initiated. In this stage the sheath length and the length of the subsequent leaf were correlated (r = 0.911). At the beginning of the growth of the subsequent leaf the length of the preceding sheath increased in dependence on insertion. Other relations were derived graphically and a hypothetical model of relationships between the cereal leaf growth and development was formulated.

Introduction

A leaf may be regarded as a correlative system with a relation to all other leaves at the apex (Moorby 1983). One of the ways of comprehending these interrelations consists of studying phyllochron. The concept of phyllochron so far had no unequivocal definition (Tesařová and Nátr 1990). Nevertheless, in the studies of cereals in the present literature it is understood as a length (distance) on the axis of thermal time (Gallagher 1979) within which two successive leaves attain a certain stage,determined beforehand, *e.g.*, the blade tip appears just visible above the sheath of the preceding leaf (Baker *et al.* 1986, Hay and Brown 1988), or the attainment of a certain chosen leaf length measured from the apex is studied - in practice from the level of the substrate (Erickson and Michelini 1975, Zvára and Nátr 1991).

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By application of such procedures the authors using non-destructive methods attempt to come to grips with the fact that the actual elongation zone of the leaf is hidden and, moreover from a certain moment onwards, it is separated into the blade and sheath elongation zones (Rytova 1967). It an early phase meristem on the blade base differentiates into two meristems. One of them differentiates acropetally blade cells and the other basipetally sheath cells. This intercalary meristem is divided into the blade and sheath meristems through the formation of a band of parenchyma cells whose epidermis cells give rise to ligule (Langer 1972). The activity of the blade meristem ceases with the ligule differentiation whereas the sheath meristem continues differentiating and growing (Rytova 1967, Langer 1972, Dale 1988).

Rytova (1967) divides the growth of a fescue-grass leaf into the following phases:
a) blade growth, synchronous with the sheath growth of the preceding leaf - in this phase the synchronization is so pronounced that ligule will get imprinted on the blade of the subsequent leaf;
b) independent blade growth - since the moment when the blade growth rate approximately doubles in comparison with the growth rate of the preceding sheath, and the ligule imprint on the blade appears above the sheath of the preceding leaf;
c) sheath growth - the beginning of this growth sets in at the moment when the blade stops its growth;
d) senescence synchronized with the growth of the next leaf but three - *i.e.* death of the first leaf at the time of the growth of the fourth leaf, *etc.*

Rytova (1967) has also found relations between the initiation of primordia, growth and death of leaves. She has concluded from her findings that there exists a strict rhythmicity and synchronization in the initiation growth and death of grass leaves during the vegetative phase of their growth. These results have led Rytova (1982) to the conception of grass as a colony of metamers in which each metamer, consisting of blade, sheath, bud and internodium, grows gradually with regular overlapping and with regular relations to the growth of the preceding and subsequent metamers.

Rytova's (1982) conclusions that all leaves grow synchronously are interesting and their specification is important for the understanding of leaf growth in cereals. Consequently, the present paper deals with the determination of basic relations between growth of the blade and sheath growths in the same leaf and with their relation to phyllochron, as well as with some aspects of the outllined interdependences of leaves.

Material and methods

Winter barley (*Hordeum vulgare* L. cv. Efra) was grown in plastic pots with perlite in full Knop nutrient solution. The plants were placed in small-volume air conditioning boxes with the photoperioid of 14 h and irradiance of 55 W m^{-2}(PAR), relative air humidity of 80 % to 90 % at the following constant temperatures (Tconst): 26.0±0.5 °C, 21.8±0.3 °C, 19.6±0.3 °C and 15.3±0.8 °C at the level of the plant apices.

Samples of eight plants were taken daily, or every other day. The length of the entire leaf, blade and sheath was measured in a destructive way. During the initial phases, the blade and sheath lengths were measured under a stereomicroscope.

The measured data were related not to the real but to the thermal time (Gallagher 1979) where the effective temperature is a sum of mean daily temperature (Tu). Therefore the symbol Tu, *i.e.* mean daily temperature, is used and not T const (*i.e.* constant temperature) although in this particular case it holds that T const = Tu.

From the linear part of leaf growth phyllochron was calculated after described by Zvára and Nátr (1991). When assigning phyllochrons numbers a phyllochron was regarded as completed when the given leaf attained 50 mm in length (for instance: 50 mm in the fifth leaf terminates the fifth phyllochron).

Coeficients of linear regression and correlations were calculated by usual statistical methods.

Results

The evaluation of the linear part of growth of the entire leaf has shown that in all thermal regimes (Tu) under study the leaf growth rate increased in dependence on leaf insertion. The values of regression coefficient increased with mean daily temperature (Tu) up to Tu = 21.8 °C with an abrupt decrease at a still higher temperature Tu = 26 °C (Fig. 1).

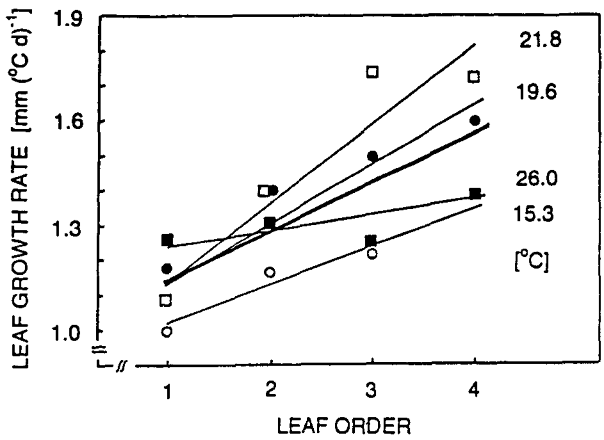

Fig. 1. Rate of the linear phase of growth in subscequent leaves of plants grown at different constant temperatures (Tu). Measured values (*points*) and linear regression (*lines*) are presented. For all Tu's: y = 0.143 x + 0.998, r = 0.732 (*thick line*)

The mean growth rate of all leaves of the given variant was not identical even when expressed in terms of thermal time. The fact that there exists a limit to the linear relation between the increasing temperature and the rate of a number of growth processes has been pointed out *e.g.* by Bauer (1984).

The sum of effective temperatures for the first three phyllochrons (ΣTu_{1-3}) increased with increasing daily temperature means (Tu) and the regression correlation corresponded to the following expression:

$$Tu_{1-3} = 3.5\ Tu + 181.29 \qquad (r = 0.988)$$

Consequently, the development was slowed down due to increase of mean daily temperature in thermal time. To same dependence was displayed independently by various phyllochrons (Fig. 2). For comparison the shortening of the third phyllochron is shown, *i.e.* the acceleration of the development as due to the rise in Tu in real time (Fig. 2).

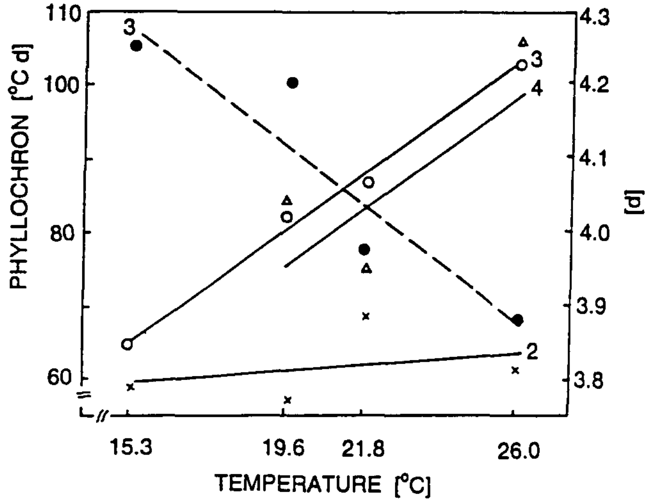

Fig.2. The dependence of the 2nd, 3rd, and 4th phyllochrons, expressed in thermal time [°Cd] (*full line*), and dependence of the 3rd phyllochron expressed in real time [d] (*dashed line*), on temperature. Measured values (*points*) and linear regression (*lines*) are presented.

In the stereomicroscope the sheath was discernible at the time when its length was about 0.1 mm, which corresponded to the blade length of about 20 mm. At the time when the sheath began to be discernible and measurable a linear correlation with the coefficient r = 0.812 was found between the length of blade and that of sheath (Fig. 3).

The relationship between the blade and sheath length of the same leaf at the time when the sheath began to be discernible exhibited moderate deviations dependent both on leaf insertion and on Tu. The sheath length of a 20 mm long leaf increased with the insertion level of the leaf (Fig. 3). For various temperatures the sheath of a 20 mm long leaf was the longer, the lower Tu, *i.e.* -0.072 mm, 0.108 mm, 0.110 mm and 0.130 mm for 26.0 °C, 21.8 °C, 19.6 °C and 15.3 °C, respectively.

The correlation coefficient r = 0.911 was found for the relation between the sheath length at the time when the sheath begins to be discernible in the stereomicroscope and the length of the subsequent leaf. In this phase the subsequent leaf was always longer than the sheath of the preceding leaf (Fig. 4). However, owing to different growth rates (see below) it helds in all cases that the length of the subsequent leaf for a calculated zero length of the blade was negative. This shows that the formation of the sheath precedes the growth of subsequent leaf. This growth (not primordium initiation and formation) of the next leaf sets in at the time when the sheath of the preceding leaf is about 0.13 mm in length (Fig. 4).

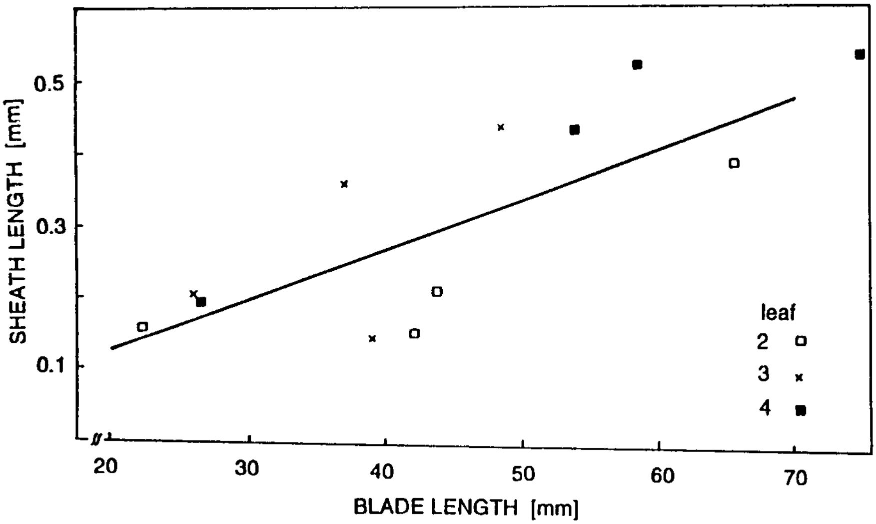

Fig.3. Relation between the blade and sheath length of the same leaf at the time of visual appearance in the stereomicroscope of the sheath. Line fitted to the experimental points of the 2nd, 3rd and 4th leaves corresponds to fuction: $y = 0.008x - 0.026$, $r = 0.812$

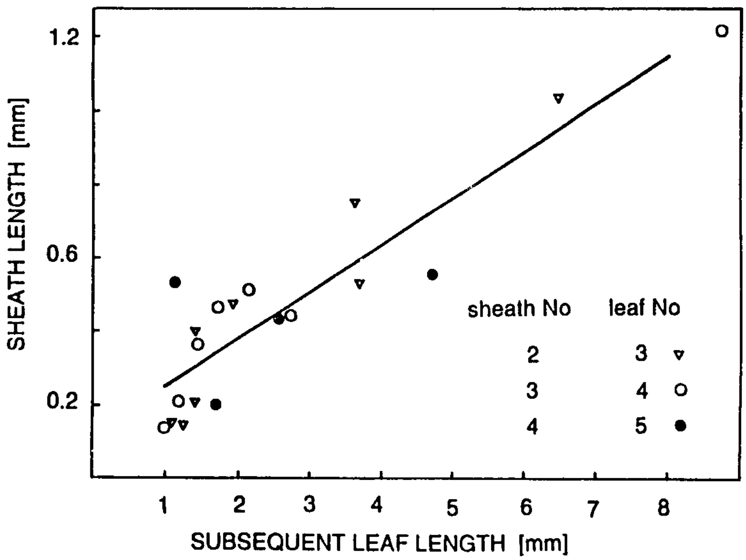

Fig.4. Relationship between the first stage of the sheath growth and the length of the lengtn of next leaf. Line fitted to the all experimental points correspond to fuction: $y = 0.30x + 0.133$, $r = 0.911$

For Tu = 15.3 °C and Tu = 19.6 °C the length of preceding sheath for zero length of the subsequent leaf was 0.002 mm whereas for two higher Tu (21.8 °C and 26.0 °C) it was 0.2 mm.

At the evaluation according to the insertion in each next pair of leaves the length of the preceding sheath for the zero length of the subsequent leaf increased.

As already mentioned, in an early phase the growth rate of the sheath and that of the subsequent leaf, growing more or less simultaneously with it, were not identical. At the time when the sheath began to be discernible its mean growth rate amounted only to 13 % of the mean growth rate of the subsequent leaf.

Changes of the ratio of the initial sheath and the subsequent leaf growth rates have been found to depend on the insertion level. In contrast to the preceding pair (of sheath and the subsequent leaf) each subsequent pair displayed a larger difference between the sheath growth rate and the growth rate of the subsequent leaf, namely in favour of the leaf growth (Fig. 4). In other words: the lower insertion, the shorter the preceding sheath at the beginning of elongation of the subsequent leaf and the less the ratio of the sheath growth rate to the growth rate of subsequent leaf (Fig. 4).

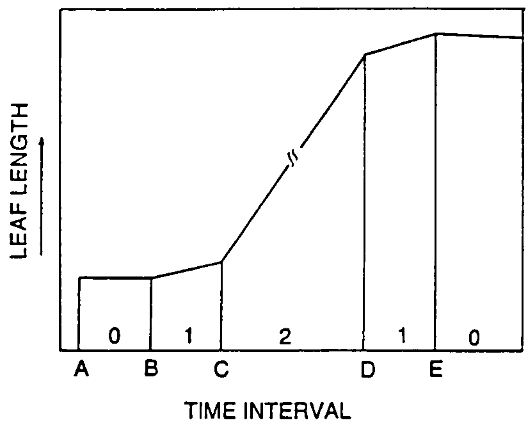

Fig.5. A schematic diagram of cereal leaf growth divided into stages. The same diagram is used for the whole leaf growth as well as for the sheath or blade growth. The values of length and time interval are relative: by values 0 to 2 relative growth rate is denoted. The intervals are delimited from their beginnings to the beginning of the next interval: A: from the appearance, B: from the beginning of measurable extension growth, C: from the beginning of linear extension growth, D: from the end of linear extension growth, E: from the end of extension growth onwards.

Discussion

The increased growth rate with insertion of the first four leaves under study is in accordance with a normal development of this barley cultivar (Tesařová and Nátr 1990). It indicates, that even under the applied controlled conditions no strong stress reactions occurred which might have changed the characteristics of leaf growth. For Tu = 19.6 °C and Tu = 21.8 °C the mean growth rates of 1.48 mm $L(^{o}Cd)^{-1}$ and

1.41 mm L(°Cd)$^{-1}$ were very similar to the results of field trials where the mean growth rate of this cultivar were 1.36 mm L(°Cd)$^{-1}$ to 1.41 mm L(°Cd)$^{-1}$.

A relationship between the blade and sheath lengths at the sheath emergence of the same leaf was estabilished. At the latest up to the leaf length of 20 mm blade and sheath are differentiated in a visible form. The linear part of the growth curve always involves the growth of the blade and sheath in changing mutual proportion. Consequently, when phyllochron is studied the additive activity of both elongation zones is considered too.

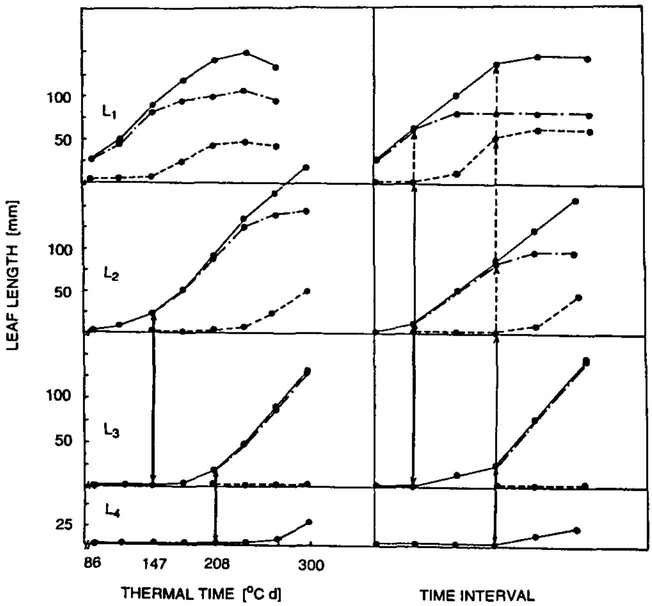

Fig.6. Dependence of the growth [mm] on thermal time (°C d) in sheath (*dashed line*), blade (*dashed and dotted line*) and blade plus sheath (*full line*) in the 1st (L1), 2nd (L2), 3rd (L3) and 4th (L4) leaves of winter barley plants grown at a constant temperature of 15.3 °C.
In the left the measured values;. in the right these values for the schematics growth diagram (derived from Fig.5) was used. *Thick vertical lines* - measured relationships, *thin lines* - assumed relatioships, *dashed lines* - hypothetic relationships.

In addition, a connection between the initial growth phase of sheath and that of the subsequent leaf was established. However, this was not the case of the same growth rate as mentioned by Rytova (1967) in fescue-grass. The leaf growth rate was always higher than the sheath growth rate of the preceding leaf. The growth (not the initiation) of the subsequent leaf started at the time when the sheath of the preceding leaf was about 0.13 mm long, *i.e.* when it began to be discernible.

The calculated statistical correlation between the sheath and blade growth rates of the same or subsequent leaf should further be experimentally verified. However, it seems expedient to formulate a hypothesis, albait a simplified one.

In a hypothetical model of correlations between the growth and development of cereal leaves the simplified leaf growth curve was divided into five intervals. The intervals differ in the elongation growth rates quantified in the three basic degrees from 0 to 2. The beginnings of intervals are denoted by A to E (Fig. 5). The individual intervals are passed through by the leaf as a whole but also by its parts, *i.e.* blade and sheath.

Connections are assumed to exist between the beginnings of the intervals. These relations can most easily be derived from the beginning of the visible existence of the sheath. This moment is related both to the beginning of the linear phase of growth of the same leaf, and with the onset of elongation growth of the subsequent leaf (Fig.6). From these relations the probabillity of shifting of intervals at the growth of successive leaves follows in the way indicated in Table 1.

Table 1. Hypothetical model of leaf and inter-leaf growth relations of cereals (definition of intervals see Fig.5. and Fig.6.). The blade and the entire leaf are regarded as identical up to the moment of the sheath appearance

		Interval				
1st leaf	ENTIRE	C	C	C	D	E
	blade	C	D	E	E	E
	sheath	A	B	C	D	E
2nd leaf	ENTIRE	B	C	C	C	C
	blade	B	C	C	D	E
	sheath		A	A	B	C
3rd leaf	ENTIRE	A	B	B	C	C
	blade	A	B	B	C	C
	sheath				A	A
4th leaf	ENTIRE	A	A	A	B	B

The growth rate of the entire leaf is co-determined by the blade and sheath growth rates in changing mutual proportions as follows from Fig. 6.

Although the above-mentioned model corresponds to the preliminary results of several field trials (not published as yet) and also to the results of the present experiment in controlled conditions it should only be regarded as a working hypothesis for the orientation of further research.

Experimental evidence cannot be regarded as sufficient. Only two of the indicated correlations have been verified. The other are only derived graphically from the growth curves of the mentioned field trials and of the present experiment under controlled conditions. Nevertheless, the hypothesis that the repeatedly established rhythmicity of growth processes and the multi-level effect of regulative signals play a role also in the observed phenomena of leaf growth appears to be attractive.

Should other assumed relations be confirmed for instance the relationships between the beginning of discernibility of the leaf sheath of a given insertion (Li-1) and the end of the linear phase of growth of a leaf with insertion lower by two degrees (Li-2), and other possible vertical connections (Fig. 6) as well, it would be possible to assess the growth intervals of the preceding or subsequent leaves from the growth interval of one of the leaves. This would contribute to a significant improvement of the description of leaf growth and of models of cereal growth and productivity as well.

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