トウモロコシの生育相の概念モデル:

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A Conceptual Model of Developmental Phases of Maize on the Basis of the Relationship between Differentiation and Growth of Vegetative and Reproductive Organs*

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The growth stage concept has been introduced to describe a generalized yield determining process of maize[32]. The growth stages proposed were useful in describing a generalized yield determining process, but were inappropriate in the discussion of adaptability and productivity of maize. We therefore have to extend the growth stage concept to the developmental phase concept to overcome this problem.

There are several representative examples of developmental phases proposed recently, those are vegetative *vursus* reproductive phases in plant development, lag-, log-, stationary-, and death-phases in the growth of bacteria, exponential and linear phases in an idealized growth curve[3], and the theory of phasic development emphatically proposed by L.T. LYSENKO. These idea of the developmental phases mentioned above may be summarized as follows. The growth of an organism can be realized by the increase of size such as length, area, volume and mass, and qualitative changes through the development. This process consists of several phases which are quitely different in quality. Each phase may require a definite environmental condition. If the preceding phase has not been completed, then the following phase will not initiate. Therefore, qualitative change in the preceding phase can become an internal precondition for the initiation of the following one.

This developmental phase concept could be applied to estimate the ecological adaptation of cultivars and to evaluate potential productivity of the crops without any modifications in the fundamental idea. TSUNODA (1964)[34] proposed a developmental phase concept to investigate the high productivity of several crops, in terms of matching growth stages with particular environmental conditions. He defined the developmental phases as a quantitative relationship between vegetative and reproductive growth. The migration coefficient, as a ratio of grain (or tuber) weight and total production in dry-matter basis, was regarded as an index of the relationship between both types of growth. VERGARA and CHANG (1976)[35], working on rice, discussed the ecological responses of cultivars to explain the difference between photo-sensitive and non-sensitive cultivars, using the terms of both basic vegetative phase and photoperiod sensitive phase. This method has been developed in maize, by ROOD and MAJOR (1980)[24,25], who used the terms of basic vegetative phase and photo-induced phase for interpreting the genetic diversity of photoperiodic response. EVANS and WARDLAW (1976)[13] presented three developmental phases for interpreting the yield determining process of cereals. The first phase is called vegetative phase, in which the growth of vegetative organs predominates. The second phase is called reproductive period, which determines the rate and extent of floral differentiation in relation to the potential storage capacity of the crop. The third phase is called grain-filling phase, in which the potential grain storage capacity is realized. This method of the division is conventionally used to demonstrate the general process of grain production in cereals.

As mentioned above, the developmental phase concept was usefull for interpreting the principles of adaptability and productivity of the crop, but still not practicable for agronomic purposes, especially for breeding programs. One of the most important reasons seems to be the lack of valuable characters for the breeding programs, which may suggest the need to find out morphological and physiologi-

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cal indices characterizing the developmental phases.

In this study, the author introduces the terms of differentiation and growth to characterize individual developmental phases, using proposed growth stages as transitional points. Differentiation and growth are the two major developmental processes. Usually both take place concurrently during development. There are various kinds of definitions with different expressions in the field of botany[3,12,21,29,36]. In a broad sense, terms are defined as qualitative changes between cells, tissues, or organs, which result from the specialization of cells and many interrelated chemical, physiological, and morphological processes. The term growth is generally defined as increase in lengh, volume, area and mass. In this study the term "differentiation" was used to indicate the process of increment of leaf primordia and floret primordia ; and the term "growth" to indicate the process of morphological changes in size and physiological changes in dry-matter weight.

The objectives of this report are to verify the effectiveness of applying growth stages to different cultivars under different planting conditions, and to imply developmental characteristics in individual phases on the basis of a simplified relationship between differentiation and growth of vegetative and reproductive organs.

Materials and Methods

This field experiment was conducted in the Experimental Farm of Kyoto University, Kyoto. Ten maize cultivars were used : Kho No.3, Chokho No. B411, Mutsumidori, Kho No.9, Pioneer's P3715, P3422, and P3382, Funk's G4553 and G4810, and Dekalb's XL1214. The cultivars used in this experiment show high productivity in Japan and have wide variation in leaf numbers formed on the main stem. Planting was done on 22 April, 19 May, 10 June, and 4 July in 1980. A plot consisted of two rows 4m long, 0.8m interval between the rows and 0.3m interval between the hills, respectively. Three seeds were sown in a hill. The plant density of 41,000 plants per hectare was established by thinning one plant per hill. Fertilizers were applied before planting at rates of 100-100-100kg/ha of N-P-K.

The major growth stages and their criteria proposed in the preceding studies[32] were summarized as follows. The first stage, emergence stage, was defined the time when coleoptiles appeared in more than 50 per cent of the hills. The second and third stages ; tassel and ear initiation stages, were determined by the number of visible leaf collars measured on 10 plants per plot every three or four days. The relationship between the number of leaf collars and both stages in each cultivar had already been confirmed by dissecting several plants grown in the satellite plots. The fourth stage, the beginning of silk elongation on basal parts of the first ear, was estimated by using the date for the increase of leaf collar and the position of ear-bearing leaf measured at silking. The fifth stage, silking stage, was determined by the stage at which more than 50 per cent plants have silks. The sixth stage, the beginning of starch accumulation, was determined by colour change from milky to pale-yellow on the surface of kernels. The seventh stage, the initial stage of physiological maturity, was determined by observing the formation of a black layer in the upper kernels of an ear.

The number of leaves produced on the main stem and the vegetative tillers and the position of nodes bearing the uppermost ear on the main stem for all the plants in a plot were measured at about 7 days after the silking stage.

Results and Discussion

1. *Growth stages and their effectiveness*

The growth stage concept is necessary to study the critical stages in yield determining process of maize, because developmental progress of yield components is implicated with definite growth stages. HANWAY (1963)[16] presented the growth stages concerned with Corn Belt cultivars, and these have been widely used for agronomic purposes until the present. The author devised the growth stages of maize to be applied to agronomic studies and cultural practices on the basis of the knowledges obtained by studies on developmental morphology of maize. The number of collars, a joint part between blade and sheath in a leaf, and gross morphological development of florets or kernels, as visual indices, have received considerable attention. Transitional changes in both of them are easily identified by field observations.

External leaf growth of a plant can be observed by the increase in number of visible collars represented by two linear equations connected at a point, the turning point. The increasing rate of collars was more rapid in the second half after the turning point than in the first half before the turning point. The turning point of leaf emergence occurs as a result of rapid and simultaneous elongation in the upper internodes[31]. The relationships between the number of visible collars, i.e. the number of leaves fully expanded, and tassel and ear initiation stages are shown in Table 1. The relationship given in each cultivar was retained for different planting dates. This suggets that the number of visible collars can be used as an indication for identifying the tassel and ear initiation stages, although the number itself varies with different cultivars.

The number of potential rows of kernels per ear is determined at around the ear initiation stage. The number of potential spikelets is determined by the initial stage of silk elongation, in spite of indeterminate characteristics of ear development. This stage is approximately identified by the appearance of an ear-bearing leaf collar. Strictly speaking, therefore, the number of potential florets is determined in the period between the ear initiation stage and the initial stage of silk elongation.

When the silks emerged, the cob, ear shank and husks began to grow rapidly. The kernels consisted of nucellus mainly. The embryo and endosperm were initiated 4-5 days after the silking. The cob, ear shank and husks ceased to grow, as the kernels reached the blister stage. A couple of days after this stage, a pale-yellow colour appeared on the kernel surface without regard to endosperm types. This colour change coincided with the beginning of starch accumulation in the endosperm and the differentiation of plumule and radicle in the embryo.

The black layer appeared in the upper kernels of an ear. This indicated that the kernels reached the initial stage of physiological maturity. Another 7 to 10 days were reguired to observe the black layers in entire kernels. The kernels per ear indicated a linear growth in dry-matter during the filling process between the initial stages of starch accumulation and physiological maturity.

The results of major growth stages proposed were easily identified in the field and were verified to be applicable in every cultivars.

2. *Brief description of the proposed model*

Before giving an explanation of the proposed model, we review the historical changes of plant types in maize breeding to

Table 1. Varietal differences in the number of leaves indicating the major growth stages, final leaf number, and the number of leaves increased between the successive stages. Data were processed by the randomized complete block design with four replications, or four planting dates. Means with the same letter are not significantly different ($P<0.05$).

Cultivar	The number of leaves indicating the initiation of			Final leaf number	Number of leaves increased between successive stages		
	tassel (A)	ear (B)	silk elongation (C)	(D)	A-B	B-C	C-D
Kho No.3	6.0	9.3^{bc}	13.8^{bc}	20.3^{e}	3.3^{abc}	4.5^{ab}	6.5^{bcd}
Chokho No. B411	6.0	9.5^{b}	13.8^{bc}	20.0^{e}	3.5^{ab}	4.3^{abc}	6.3^{cd}
Mutsumidori	7.0	10.5^{a}	15.5^{a}	22.5^{b}	3.5^{ab}	5.0^{a}	7.0^{b}
Kho No. 9	7.0	10.3^{a}	15.0^{a}	21.8^{c}	3.3^{abc}	4.8^{a}	6.8^{bc}
P3715	6.0	8.8^{c}	12.0^{d}	18.3^{g}	2.8^{c}	3.3^{c}	6.3^{cd}
P3422	6.0	9.0^{bc}	12.3^{d}	19.3^{f}	3.0^{bc}	3.3^{c}	7.0^{b}
P3382	6.0	9.0^{bc}	13.3^{c}	19.3^{f}	3.0^{bc}	4.3^{abc}	6.0^{d}
G4553	6.0	8.8^{c}	12.3^{d}	19.3^{f}	2.8^{c}	3.5^{bc}	7.0^{b}
G4810	6.0	9.0^{bc}	14.3^{b}	21.0^{d}	3.0^{bc}	5.3^{a}	6.8^{bc}
XL1214	7.0	10.8^{a}	15.3^{a}	23.3^{a}	3.8^{a}	4.5^{ab}	8.0^{a}

help further understanding of the model. The comprehensive picture of historical development in maize plant types was shown by GALINAT (1977)[15]. According to this picture, the history was characterized by phased condensations within the branch, the shank, and the rachis in ear morphology and the inhibition of tillering to uniculm type. The primitive types such as teosinte and some popcorn races had vigorous tillering ability and very small spikes scattered on the stem. In comparison with the primitive type, the modern Corn Belt dent has a single stem with a large ear. A remarkable change has occurred in the source-sink relationship (or unit) of an individual plant. In the primitive type, there were many source-sink units which became on the stem such as in soybean. The modern type have single source-sink unit as a whole. This process could be compared with the origin of the monochasal head and stout single stem of the cultivated sunflower, through a suppression of the many small lateral heads of the wild sunflower.

The proposed model of developmental phases for the cultivated maize was shown in Fig. 1. The framework of this model consisted of the main stem and the primary lateral branches produced by the co-growing relation in the process of leaf primordium differentiation, and seven major growth stages. The development of the main stem and the metamorphosis of the primary branches characterize this model primarily. The relationship between differentiation and growth in vegetative and reproductive organs were schematically represented on the main stem, two lower branches and two uppermost branches. The main stem leading the development of an individual plant produces leaf primordia of the lateral branches from the bottom to the top, under the co-growing relation. The lower branches have ability to develop the tassel and ears as well as the main stem. The upper branches will develop into the ears.

Secondary characteristics were those of that the seven growth stages ; they were effectively used for the baseline, which showed the transition of developmental phases with a dynamic relationship between differentiation and growth of vegetative and reproductive organs. The emergence stage ((1) in the Figure) was regarded as the beginning of leaf primordium differentiation for the convenience of measurement. The tassel initiation stage (2) indicated the ceasation of production of leaf primorida on the main stem and the beginning of differentiation of florets in the tassels of the main stem and the lower branches. The ear initiation stage (3) and the initial stage of silk elongation (4) indicated the beginning and end of the floret differentiation on the ear. At the silking stage (5), basic structure and function of the tassel and the ears have been accomplished, and the next generation initiated in the caryopses by fertilization. The initial stage of starch accumulation (6) was considered to indicate the maturation of vegetative organs and the beginning of kernel growth. Finally, the initial stage of physiological matuity (7) showed physiological maturation of caryopses, or kernels.

From the results, leaf primordia were exclusively produced from the emergence stage to the tassel initiation stage. Floret primordia of the tassel and ears were produced from the tassel initiation stage to the silking stage. Strictly speaking, the floret primordia on the uppermost ear were produced by the initial stage of silk elongation. The rapid growth of leaf primordia initiated at the tassel initiation stage. The gross morphology of vegetative organs were established up to the silking stage and consequent physiological maturity occurred in the period from the silking to the initial stage of starch accumulation. The floret primordia began to grow gradually in the early stage of embryogeny, from the silking stage to the initial stage of starch accumulation, and showed rapid growth in the following period until the initial stage of physiological maturity.

Consequently, the author could propose the hypothetical model shown in Fig. 1. The first phase is particularly characterized by the differentiation of leaf primordia. This period is called vegetative phase in general. The second phase is a significant period for the establishment of source and sink relation, because distinct events characterized by the growth of leaf primordia and the differentiation of floret primordia occurred simultaneously. This phase is called reproductive phase[35] or reproductive period[13]. The third phase is characterized by competitive growth between the vegetative and reproductive organs. This phase is called lag period or lag phase[8,13,19] in the

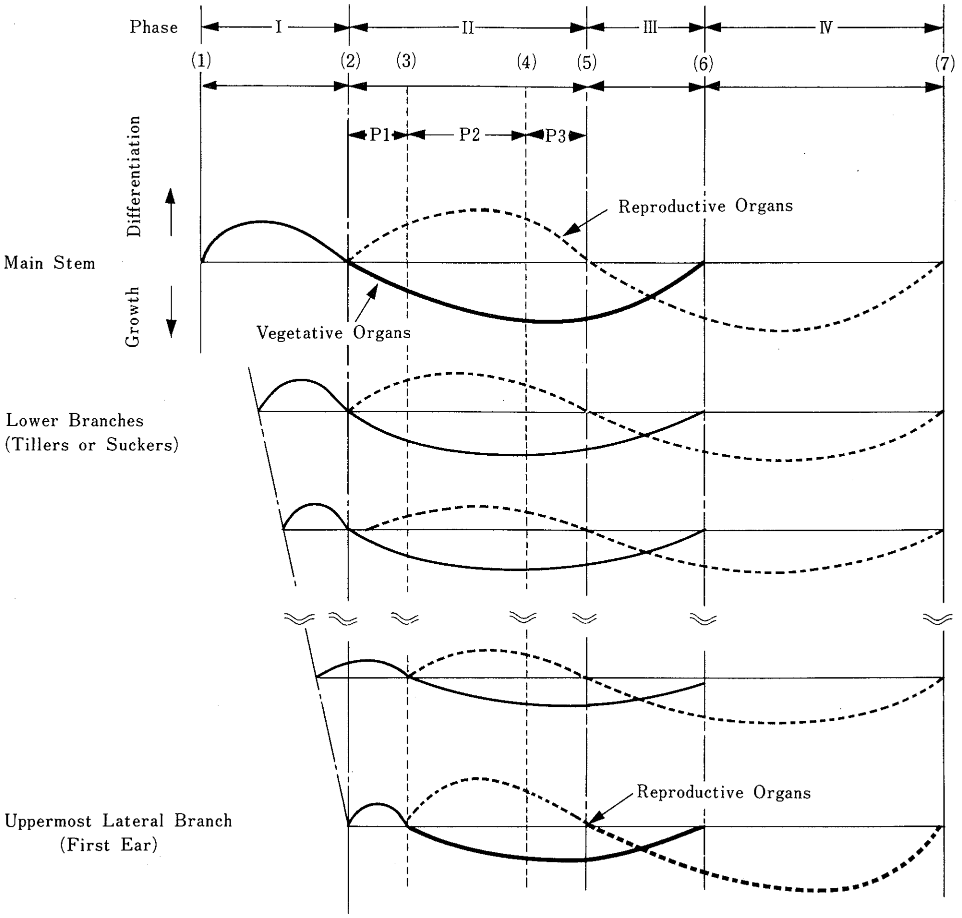

Fig. 1. A hypothetical model of the developmental phases for the cultivated maize, on the basis of the relationship between differentiation and growth of vegetative and reproductive organs. The numbers with parentheses indicate the major stages as follows : 1, emergence stage ; 2, tassel initiation stage ; 3, ear initiation stage ; 4, initial stage of silk elongation ; 5, silking stage ; 6, initial stage of starch accumulation ; 7, initial stage of physiological maturity. Heavy solid and deshed lines indicate that the growth of vegetative and reproductive organs is realized in modern maize cultivars.

pattern of kernel growth. The fourth phase is characterized by predominant growth of the kernels. This phase is called the grain filling period, effective filling period, or effective filling period duration (EFPD)[9,10].

It shoud be noted that the uppermost branch begins to develop from the tassel initiation stage This is based upon an interpretation of an implicit interval between tassel initiation of the main stem and ear initiation of the uppermost branch, which may realize after the increase of three plastochrones evaluated by the number of leaf collars. In maize, floral induction may occur in the apex of the main stem and extend to the upper branches acropetally. On the contrary, the ears initiate basipetally from the apex of the uppermost branch. How can we interprete this interval. Here, we are making the assumption that the co-growing relation indicated in the tillering habit of rice plants[20] and soybean[23,33] was assumed to be applicable to the process of tillering in maize. When the tassel initiates on the main stem, the uppermost branch may develop a shoot apex with less than a leaf primordium. It may be necessary for floral induction of the uppermost branch to produce several leaf primordia which may correspond to the number of leaves above the ear node. This is assumed to be one of the representative phenomena of apical dominance.

One more thing to be noticed is that every lateral branch does not grow. The modern dent grown in Corn Belt exhibits the growth of the main stem and the uppermost branch, and, on contrary, other lateral branches are ordinarily inhibited to grow. This growth regulation is known to be one of the representative examples of the sunflower effect.

3. *Analytical approach to the developmental phases*

The proposed developmental phases were briefly divided into two parts by silking. Of these, the former two phases are based on the number of leaves (leaf collars) and the latter two phases on the development of kernels, respectively. Here, we discuss how to analyze each developmental phase.

The number of leaves (leaf collars) on the main stem were used for an index in one half of the developmental phase. The number of leaves produced on the main stem is primarily determined by genotype and serves as the basis of an index of maturity[1,4,6,26]. It is a well-known fact that two major environmental factors, day length and temperature, have predominant effects in changing the number of leaves by controlling the timing of floral induction.

The photoperiod response of maize has been investigated by many researchers [2,5,7,14,17,18,22,27,30]. In general, as photoperiod is extended, the number of leaves increased under a wide range of temperatures. It was concluded, by Coligado and Brown (1975)[7], that the increase in leaf number with increasing photoperiod resulted from the prolongation of the time of tassel initiation, because there was a small change in the rate of leaf initiation with photoperiod. The effects of temperature on the number of leaves produced on the main stem has also been investigated by several researchers[7,11,17]. In general, the number of leaves increased with increasing temperature. An interesting experiment suggested that the increase in leaf numbers with an increasing temperature of more than 25℃ was brought about by the remarkable increase (nearly double) of leaf initiation rate[7]. In spite of these results mentioned above, the number of leaves for the modern cultivars was commonly considered to be a genotypic trait given wide expression in a variety of growing conditions. The result shown in Table 1 revealed that the number of leaves (leaf collars) as the indices of the three major stages and final leaf number were regarded as stable morphological characters of genotype.

The first phase (Phase I in the Figure) was characterized by the differentiation of leaf primordia. Five leaf primordia were produced through the process of embryogeny[28]. The leaves, therefore, subtracted by five leaves from final leaf number are differentiated in this phase. This phase is characterized by two components, the differentiation rate of leaf primordia (internal plastochrone) and the number of differentiated leaf primordia. These characters may be correlated with the external characters, the increasing rate of leaves (leaf collars) and the number of leaves at the tassel initiation stage. The number of leaves (leaf collars) indicating the tassel initiation showed less variation than the final leaf numbers (see Table 1). This suggested that genotypic differences might be detected on the differentiation rate of leaf primorida.

The second phase (Phase II) was divided into three distinctive periods. This first period was from the tassel initiation to ear initiation stages and was regarded as the preceding period for preparing the infrastructure of floral induction on the uppermost branch because of the effect of apical dominance. This period is characterized by the number of leaf primordia and their initiation rate on the uppermost branch. The number of leaf primordia on the uppermost branch may correspond with that of leaves above the uppermost ear node on the main stem. Externally, this period was analyzed by the number of leaves (leaf collars) increased from the tassel initation to ear initiation stages and its rate. The number of leaves increased between both stages were ordinarily 3.0 in spite of small difference shown in Table 1. The second period, from ear initiation stage to the initial stage of silk elongation, was defined as the duration of floret primordium production. This period, therefore, is considered to be a critical period for the formation of sink capacity[13]. It may be characterized by the number of differentiated florets and the differentiation rate of floret primordia. Externally, the number of leaves increased between both stages and its increasing rate are the components. There was a relatively large variation in the number of leaves observed in this experiment. The third period was characterized by stem elongation and silk protrusion. This period was externally analyzed by the number of leaves increased from the initial stage of silk elongation to the silking stage and its increasing rate. The increasing rate may depend upon stem elongation, since the growth of leaves in longitudinal axis ceased already.

The third phase (Phase III) was characterized by the development of caryopsis and the vegetative growth of ear shank, bracts, and cob structure occurring in the uppermost branch. There was little difference in this period between the genotypes and planting dates used in this experiment. The period ranged from 12.5 to 13.8 days in genotype despite large differences between plant types and growing days. This evidence may suggest that the third phase may depend upon the early development of embryogeny in maize.

The fourth phase (Phase IV) was exclusively characterized by kernel growth. Carbohydrates accumulate into the kernels. This period was analyzed by kernel weight and kernel growth rate, since there was a linear growth of the kernels during this phase.

Of these morphological and physiological characters mentioned above, the number of leaves (leaf collars) indicating the tassel and ear initiation stages shoud be determined by microscopic dissection. Other characters will be derived from the observations of leaf increase pattern, principal morphological traits, and yield components which can be measured in almost all of the experiments. The results show that these characters may become useful indices to characterize the developmental phases of maize.

Summary

A conceptual model of developmental phases in maize was developed by designating major growth stages, to establish a dynamic pattern between differentiation and growth in vegetative and reproductive organs. The effectiveness of growth stages was verified by using ten cultivars and four planting dates. The framework of the model shown in Fig. 1 consisted of the main stem and the primary lateral branches produced by the co-growing relation in the process of leaf differentiation, and seven growth stages. The whole growing period of maize was divided into four developmental phases.

The first phase, from emergence to tassel initiation, was characterized by the differentiation of leaf primordia.

The second phase, from tassel initiation to silking, was indicated by quite different processes between the growth of leaf primordia and the differentiation of floret primordia. This phase could be subdivided into three distinctive periods. The first period, from tassel initiation to ear initiation, was regarded as the preparatory stage for floral induction on the uppermost lateral branch. The second period, from ear initiation to the beginning of silk elongation, was difined as the duration of floret primordium production. The third period, from the beginning of silk elongation to silking, was characterized by internode elongation and silk protrusion.

The third phase, from silking to the beginning of starch accumulation, was characterized by a competitive growth between leaf primordia and floret primordia, and there was little variation between cultivars and planting dates.

The fourth phase, from the beginning of starch accumulation to physiological maturity, was exclusively indicated by the growth of floret primordia, i.e. kernel growth.

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*In Japanese with English summary

**In Japanese

〔和 文 摘 要〕

トウモロコシの生育相の概念モデル

―栄養器官と生殖器官における分化と生長との相互関係を基礎にして―

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主要生育段階を基準にして，栄養器官と生殖器官の分化と生長の動的なパターンによるトウモロコシの生育相の概念モデルを提案した．主要生育段階は品種ならびに播種期を異にしても変わることがなく，基準として利用できる．モデルの骨格は，第1図に示すように，葉原基分化過程における同伸葉・同伸分げつ関係により形成される主茎ならびに一次分枝と7主要生育段階とからなる．その結果，トウモロコシの全生育期間は4生育相に分けられる．

第一相は出芽期から雄穂分化期までの期間で，葉原基の分化によって特徴づけられる．

第二相は雄穂分化期から絹糸抽出期までの期間であり，葉原基の生長と穎花原基の分化という質的に異なる過程が並行して進む．この相はさらに3つの期間に細分することができる．第一期は雄穂分化期から雌穂分化期までの期間であり，最上位側枝が花芽誘導に至るまでの準備期間とみなしうる．第二期は雌穂分化期から絹糸の伸長開始期までの期間であり，穎花原基の形成期間である．第三期は絹糸の伸長開始期から絹糸抽出期までで，上位の節間伸長と絹糸の突出とにより特徴づけられる．

第三相は絹糸抽出期から澱粉蓄積始期までの期間で，葉原基の生長と穎花の原基の生長とが競合する．この期間は品種とか播種期を異にしても変異はほとんど見られない．

第四相は澱粉蓄積始期から生理的成熟期までの期間で，穎花の生長により特徴づけられる．