Phenological Investigations on External Morphological Development and Growth of Japanese Larch Strobili and Cones — Fundamental Studies for Crossing of Larches, I —

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CONTENTS

Introduction

During the interspecific hybridization of Japanese and Dahurian larch and application of the data for practical purposes, one is handicapped by a lack of fundamental knowledge of certain stages in the development of strobili and cones, about information concerning opening of the flower buds and pollination to cone setting and seed fall. BARNER and CHRISTIANSEN (1960) made observations on the process and mechanism of pollination in larches from the internal morphological and cytological point of view. MANZHOS (1959) also made morphological observations on the development of buds from swelling to the end of flowering on Siberian larch. Though they described comprehensively their observations, the identification of the initiation of the receptive period of female strobili is not quite clear. The present authors have also reported their phenological observations on several kinds of characters in some of the previous papers about larches. But these are too fragmentary and less comprehensive to explain such processes as pollination, cone or seed growth in relation to the changes of their external characteristics or various environmental factors, and to identify the most favourable periods for controlled pollination, seed harvest and other procedures.

For the past few years, the authors have undertaken a set of investigations on the Japanese larch trees some of which were girdled on their trunks with the objects of examining the effect of girdling on the induction of flowering (HAMAYA and KURAHASHI 1970), in order to obtain information about the following, viz., favourable periods of controlled pollination and of seed harvest, morphological and phenological changes of strobili and cones from spring to autumn, and pollen dispersal in the re-

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lated surroundings and its effect on natural hybrid production. The results thus obtained will be reported in a series of short articles in preparation for future writing about the main subjects concerning several problems of larch hybridization. And, in this paper, external morphological changes of male and female strobili, cones and related parts of a Japanese larch will be explained in detail in a sequential observation from the early spring to the late autumn of 1968.

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Material and methods

1. Material

Among the Japanese larch trees used for the trials of induction of flowering (HAMAYA and KURAHASHI 1970), especially Nos. 7 and 8 put forth a large number of strobili and cones in 1966 and 1968 as a consequence of the girdling treatment in the years before. It was therefore expected that this might be a good opportunity for making exact observations and detailed accounts on the process of growth of strobili and cones. Tree No. 7 was most suitable for this purpose with its plenty of flowers (see photograph-b, HAMAYA and KURAHASHI, ibid.).

4~6 fertile branches 20~30 cm in length were taken each time from certain parts of the middle height of its crown at the following intervals; 1, 2 or 4 days from 5th April—when the sexes of flower buds became distinguishable to the unaided eye first in that year—to 8th May, and about 10 days from then on to the end of October. Among the flower (or leaf) buds, strobili or cones of these branches, unless mentioned otherwise, 10 male and 3 female strobili were used for observation of their morphological characters, and another set of the same number was used for taking their size and weight. Besides these, each time 15~20 cones were picked from various parts of the middle height of the crown on the same intervals as mentioned above during 19th July to 30th Oct., followed by further 3 days, i.e. 15th and 30th Nov. and 16th Jan. (1969), for investigating the size, weight, water content and colour of the cones as well as the seeds and the germinative ability of the latter. As morphological variations were rather large among the male strobili on branches of different age group, only those on the 2-year-old branches were used in this study. The females were also restricted to those on the 3-year-old. The gathering and investigation were undertaken from 10 a.m. till noon, and after the investigation the materials were preserved in dilute alcohol.

For the sake of comparison, female strobili isolated in bags were also treated in the same way as those collected from the nature (from 18th April to 18th May).

2. Characters and methods of expression

Flower (and leaf) buds, strobili and cones were used to investigate the process and stages of their morphological and phenological changes as described below, applying the sign of expression used in the previous works (HAMAYA et al. 1968,

TAKAHASHI and KUNUGI 1961) to some of the characters. For characters which cannot be quantitatively classified, such as colour, intermediates were selected and adopted as standards for comparison, after glancing over all materials picked during the same time intervals. As far as possible, centesimal or parcentage expressions were applied for other characters.

1) **Leaf buds and needles**

a. Opening of buds. Each time, 10 lateral buds, adjacent to the terminal buds, on the annotinous parts of the leading shoot of a branch among those excised were individually recorded about the degree of their opening. This is expressed as the mean of 10 buds as follows (this expression is nearly the same as that used in the previous paper, HAMAYA et al. 1968); buds obviously swollen: 10; green top of the new needle cluster first appearing through the small crevice of bud scales: 20; new needles half-exposed: 50; needles fully exposed except the base surrounded by bud scales: 80; bud scales fallen and needles in the cluster fully elongated: 100.

b. Terminal bud formation. As previously explained, this phenomenon has been described as the duration when terminal buds are formed on the main axis of the branches and first become visible to the unaided eye.

c. Defoliation. Expressed by the rough ratio (%) of the fallen needles to the whole number of needles on the excised branch (mean of all the branches).

2) **Male buds and strobili**

a. Opening of buds. Represented as the degree of appearance of male strobili using similar signs as that of the leaf buds (mean of 10 male buds).

b. Change of colour of strobili. Combinations of colours are expressed by the abbreviations shown in the notes of Fig. 2 (represented by an intermediate of 5 strobili).

c. Dehiscence of anthers. Ratio (%) of the number of dehisced anthers to the whole in a strobilus (mean of 10 strobili).

d. Fall of strobili. Ratio (%) of the number of strobili fallen by a date to the whole (counting up to 50) on the excised branches.

e. Strobilus stalk. The length of the stalks was measured (mean of 10 strobili). As the strobili grow after the anthesis, the stalks also elongate somewhat and bend, and finally become pendulous in the male while upright in the female. Both the beginning and end of the elongation and bending have been shown in the figure.

3) **Female buds, strobili and cones**

Investigations on the characters of bract and seminiferous scales were performed on all of those which were located in the middle part of a strobilus or cone. And, when the majority of the scales showed a value of a certain degree for a character, this figure was regarded as representative of that date.

3-1) **Buds and strobili**

a. Opening of buds. As indicated for the male strobili (mean of 3 strobili).

b. Recurvature of bract scales. Expressed as centesimal figures to show the angles formed between each part of the bract body or between the latter and the strobilus

axis (cf. Fig. 1): bract body being straightly upright (α=0°, β=0°): 0; distal part of the bract body farther away from the strobilus axis (α=90°, β=0°): 100; the tip beginning to recurve (α=90°, β=ca. 15~20°): 100+20; both fully recurved (α=90°, β=90°): 100+50. The basal part of the bract scale opens a little (γ) during the receptive period. After then, however, they close again preventing further entry of pollen grains after pollination (BARNER and CHRISTIANSEN 1960).

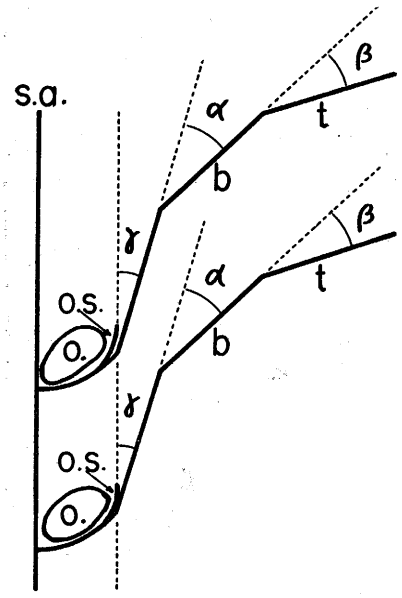

Fig. 1. Schema of bract scales in a female strobilus.
b: bract scale.
t: the top of bract scale.
o: ovule.
o. s.: ovuliferous scale.
s. a.: the axis of strobilus.
α, β, γ: angles.

c. Change of colours of strobili. Mainly shown by those of the bract scale (except midribs) occupying the surface of a strobilus (represented by an intermediate of 3 strobili).

d. Strobilus stalks. (cf. male strobili) (mean of 3 strobili).

e. Appearance of companion needles of female strobili. Expressed in the following sequence (mean of 3 strobili): tips of the new needles appearing between the strobilus and the bud scales: 20; bud scales covering only one tenth of the strobilus body and the needles half expanded: 50; bud scales not covering any part of strobilus and the needles fully expanded: 100.

3-2) **Cones**

a. Appearance of seminiferous scales. The degree of appearance is expressed as follows, based on the external characteristics of young cones (mean of 3 cones): growing scales first appearing from behind and between the adjoining bract scales: 20; cones grown to their full size (when bract scales are nearly hidden behind the seminiferous scales): 100—a little before this, 90, the tips of seminiferous scales begin to bend backwards—.

b. Appearance of seed wings as result of recurvature of seminiferous scales (mean of 3 cones). The seed wings appear as the seminiferous scales recurve their upper part, and, observing the cone from above, its degree is expressed by the rough ratio of visible parts to the whole area of a wing. As the seed wings grow nearly in parallel with the scales, the degree of appearance is arbitrarily fixed as 25% when the scales have fully appeared (90~100%) and begin to recurve.

c. Change of colour of the seminiferous scales. (Represented by an intermediate of 3 cones).

d. Withering and browning process of the seminiferous scales. At maturity the seminiferous scales which have been yellowish brown, are tinged purple and wrinkled longitudinally due to withering. The ratio of wrinkled area to the whole of a scale

is averaged for those obtained from the middle part of a cone (mean of 5 cones): beginning of wrinkling: 20; the whole surface having become grayish brown and rough by withering and wrinkling: 100.

e. Opening of seminiferous scales. From about the time when the withering of the scales is completed, they begin to open gradually increasing the angle between them and the cone axis (mean of 5 cones): at the end of withering the scales begin to lose their imbrication which was tight and close so far: 10; on completion of opening, when the seeds or their scars on the adaxial surface becomes clearly visible from above: 100 (the degree of opening usually showed a highest point of 90 under the outdoor condition due to the high atmospheric humidity, but showed 100 when left under laboratory condition).

f. Cone stalks. The process of changing of colour from green to brown and withering was recorded.

g. Defoliation. In nearly the same way as that of the ordinary needles.

h. Change in the colour of seeds. The colour was examined on the adaxial surface of the seeds (by the representative set among 6 sets of 50 seeds).

i. Seed fall. On the following 5 days, i.e., 19th and 29th Aug., 9th, 18th and 30th Sept., 6 cones were collected every day as evenly in size and shape as possible. In the 30 cones thus collected, developed seeds (excluding those aborted) were counted, and an average of 70.6 seeds per cone was obtained as a basic seed number in a cone. Seed fall rate is expressed as the ratio (%) of the average number of developed seeds, already shed by cones on each investigation date, to the aforesaid average. (Incidentally it may be noted here that the range of seed number per cone was 59.4～74.4 for No. 7 while 26.6～35.0 for a tree of *Larix gmelinii* var. *japonica* ex Kurile, and that the seed fall rate on 15th Nov. was 96.5% for V-507 and 90.2% for V-307 which grew in other forests and much taller and older than No. 7, showing a value of 61.8%.)

Results

1. Data of investigations

Main parts of the data obtained from the above-mentioned investigations are shown together above a common axis of abscissa marked with calendric time in Fig. 2, and some of them are complementarily explained in the following text. The expressions used in Fig. 2 are only rough representations of general processes of changes of characters, because these are obtained after investigations from only a few branches or different parts of a branch and because some of the individual expressions themselves are based on an eye estimation. The data of several kinds of measurements are also shown in Fig. 3 and in the text.

1-1. Complementary notes

a. Dehiscence of anthers. The dehiscence of anthers and the accompanying pollen dispersal were investigated and represented by the method of expression used in

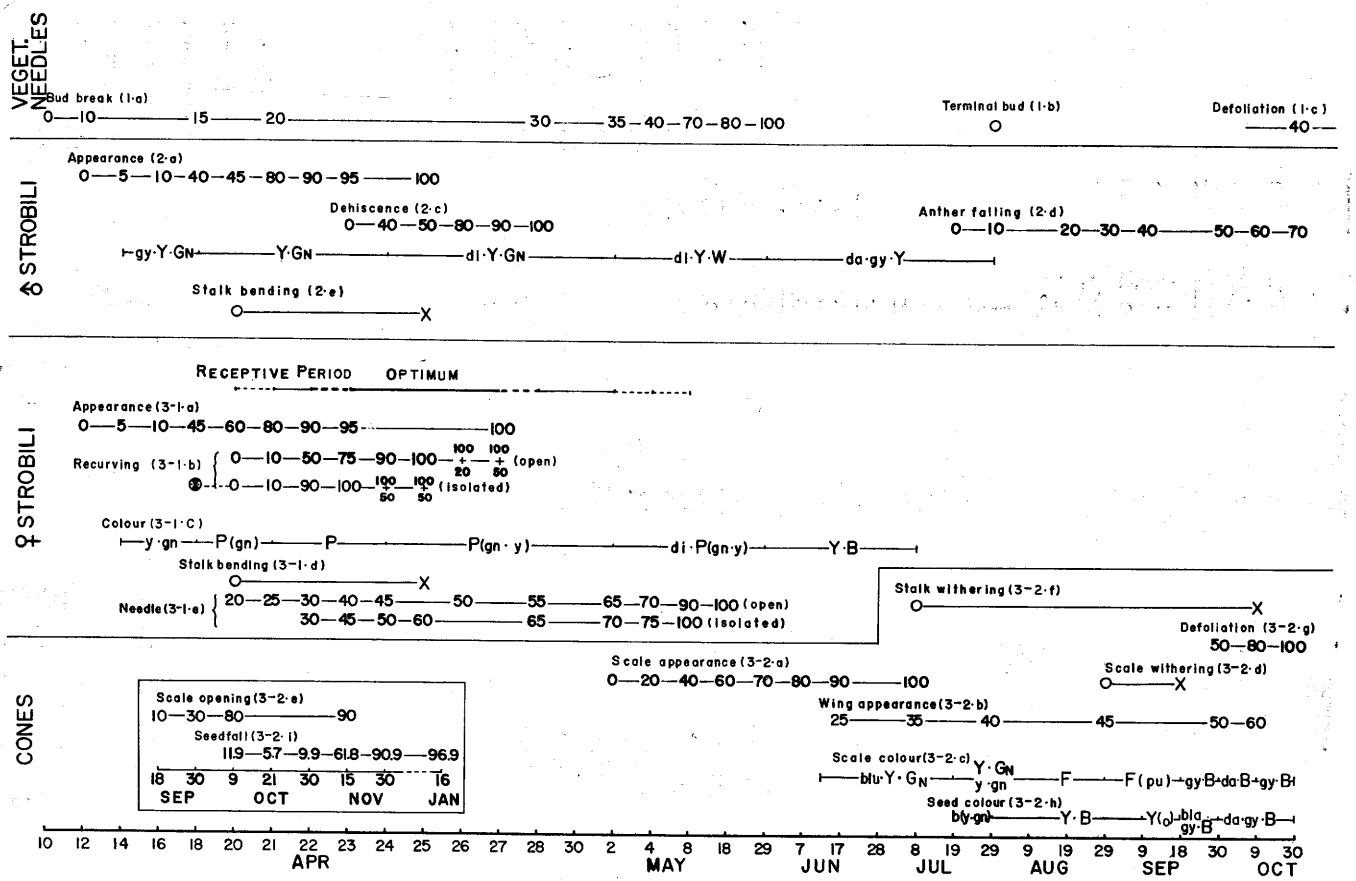

Fig. 2. Phenological investigations on reproductive processes in the No. 7 tree of Japanese larch, in 1968.

N.B.1. The figures in parentheses accompanying the titles show those in the text.

2. ※: date of isolation.

3. Names of colours are abbreviated as follows: b: brown; bla: black; blu: bluish; da: dark; di: dirty; f: fulvescent; gn: green; gy: gray; o: orange; p: pink; pu: purple; w: white; y: yellow. Capitals: main colours. Small letters: auxiliary colours or paleness. ( ): tinged with the colour.

4. ○—×: beginning and end.

the annual phenological observations as follows: a male strobilus fully matured and just before the dehiscence of its anthers: 10; beginning of dehiscence and pollen dispersal: 20; more than half number of anthers dehisced and pollen grains dispersed profusely: 50; almost all anthers having been dehisced and pollen dispersal nearly over: 80; anthers and filaments become dark gray and half-withered: 100. These investigations were carried out on tree Nos. 7 and 8 at some fixed intervals every morning and afternoon.

For reference, the number of pollen grains caught by a pollen trap situated in the vicinity of No. 7 (per day, per cm^2) and daily amounts of pollen obtained from 50 male strobili picked and left in a room are also shown in the Table.

Table. Dehiscence of anthers and pollen dispersal in different expressions

Date	Degree of dehiscence			Pollen grains caught by trap		Pollen amount**
	by present method*	by usual method				
		a.m.	p.m.	no./day·cm^2	(rate to max.)	mg/50 strobili
Apr. 20				0	(0)	370
21				24	(1.3)	451
22				53	(2.9)	488
23	0	10	15	166	(9.2)	467
24	40	15	20	487	(26.9)	449
25	50	40	50	1809	(100.0)	238
26	80	60	75	333	(18.4)	14
27	90	75	80	101	(5.6)	12
28	100	80	90	49	(2.7)	0
30		90	100	41	(2.2)	11
May 2				41	(2.2)	0
4				32	(1.8)	—
8				12	(0.7)	—

* 2)-c in the text.
** cf. Results 1-1. a.

b. Change of the colour of male strobili. The male strobili were yellow-green with grayish tinge when their tips first appeared due to the opening of the buds on 14th April. And just before the earliest dehiscence on the 23rd, they were fully exposed and became yellow-green without the tinge. At this time the anthers were swollen, ovoid in shape, and were green only at the top; and this green colour remained for a while after the dehiscence.

c. Companion needles of female strobili. The needles appeared first on 19th April between the female strobili, which were half exposed, and the bud scales a little later than the vegetative needles. They expanded a little quicker and consequently com-

pleted it conversely earlier than the latter. And, it is possible to say that, as will be mentioned below again, the expansion begins nearly simultaneously with the receptive period and its middle stage (at a point of 65 or 55) can suggest the end of the whole receptive period or the end of the optimum.

d. Colour of bract scales or female strobili. When the strobili first appeared among the bud scales roughly about 14th April, they were light yellow-green. As the anthesis progressed, the bract scales, except for their midribs, changed their colour to pink with a greenish tinge, then once again lost this tinge, and about 23rd or 24th added another tinge of grayish yellow. And at the end the scales assumed a dirty gray colour about 5th May when the receptive period was nearly over.

e. Relative positions of bract scales. About 20th April, the upper part of bract scales having been upright so far, began to open or recurve and became perpendicular to the axis by the 25th. Then, as the axis grew in length, the bract scales themselves grew somewhat with the tips recurving backwards by the 27th. However, because the ovuliferous scales increased in size much faster than the bract after appearing at the end of the receptive period, the bract scales were entirely hidden by the semini- or ovuliferous scales around 8th July. The situation that the upper part of the bract scales is at an angle of about 45° to the axis of the strobilus seems to suggest the beginning of the receptive period, and the recurving of the tips indicates its end.

f. Female strobili isolated in bags. The bract scales and needles of the female strobili in isolated bags grew faster than those of the female strobili in nature even though they started to develop simultaneously (Fig. 2).

1-2. Measurement of size and weight

The changes of the size (length and diameter) and weight of male and female strobili and their stalks are also shown in Fig. 3.

1-3. Characteristics indicative of the receptive period

From the explanations and figures in the preceding paragraphs, it is comprehended that some of the characteristics show high phenological correlations between each other. And from the practical point of view, it is desired that these correlations could be indicative of exact times of such invisible phenomena as development and growth of reproductive organs, fertilization and others and could also aid the practical workers in forest tree breeding. The receptive period of female strobili may be a best example for it.

According to the results of the trials of controlled and air pollination and of germination of the seeds obtained, which were carried out simultaneously with the present investigations on the same materials, it is supposed that the female strobili were receptive during a period from 22nd April in nature (from 20th April or earlier in isolation) till 2nd May or later (4th or 8th) showing an optimum from 22nd or 23rd until 27th or 28th April. As seen in Fig. 2 and briefly mentioned in the preceding paragraph, the whole or optimum range of receptive period coincides with the times of dehiscence of anthers, some phases of appearance of female strobili and the companion needles,

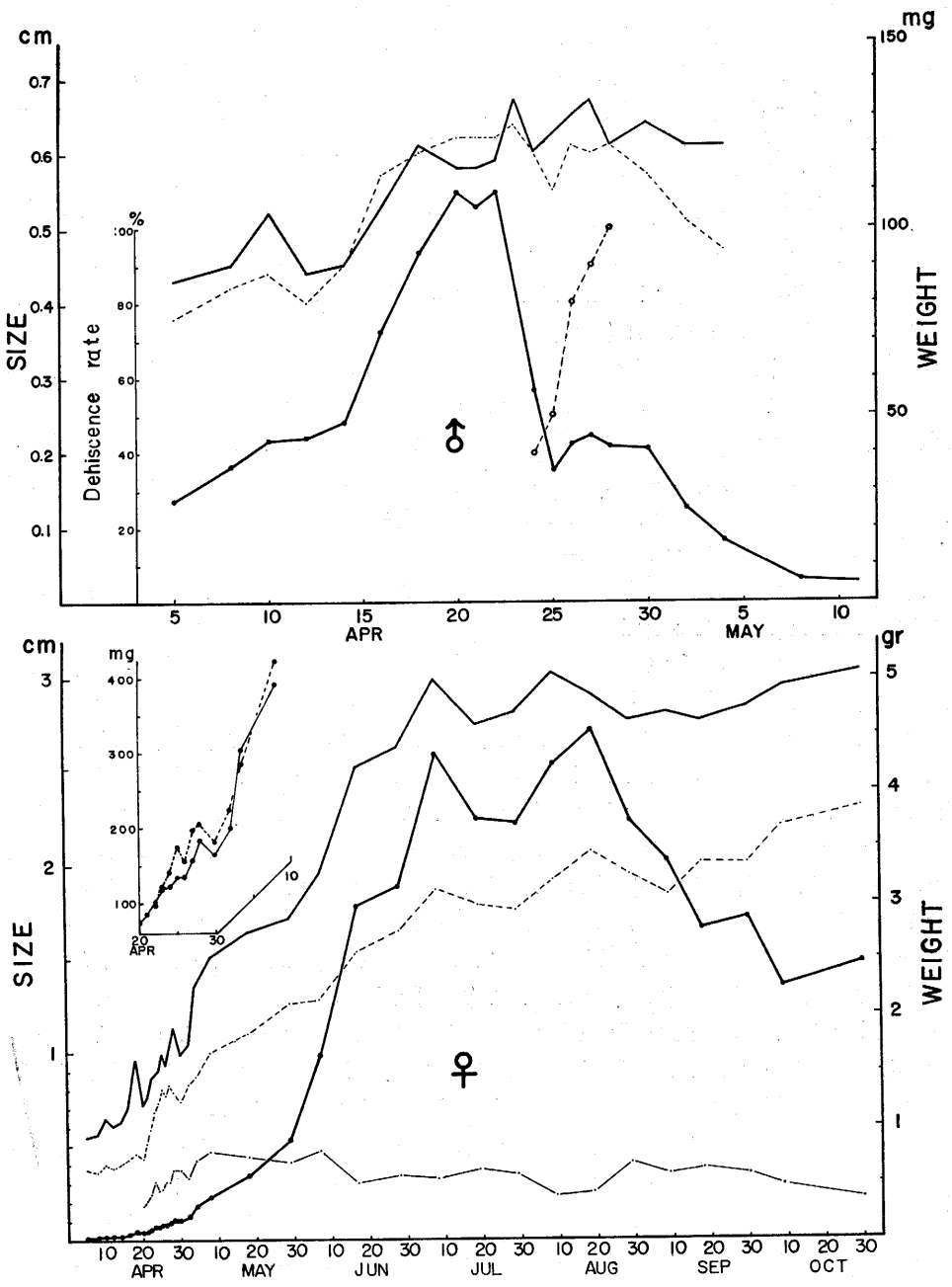

Fig. 3. Process of growth in size and weight of male and female strobili and cones of the No. 7 tree of Japanese larch, in 1968.

—●— weight (open). -------- diameter.
---●--- weight (isolated). —·—·— stalk length.
——— length. ---o--- dehiscence rate.

some phases of colour-change and recurving of bract scales, and bending of stalks. Among them, the recurving process of bract scales is naturally regarded as a direct indication of the receptive period. However, the degree of opening of the female buds (or appearance of female strobili) must be more convenient as practical indications for isolation and artificial pollination of them. It may be concluded that the time when the strobili just appear may be an indication of the earliest point of receptiveness and that isolation should be carried out before this stage. The receptiveness is probably preserved, even though very weak, until the time the seminiferous scales first appear. Furthermore, the period of time they begin to represent a value of 80 degree of appearance until that showing 100 must be regarded as the optimum.

BARNER and CHRISTIANSEN (1960) suggest that the position of bracts is less reliable as a sign (criterion) for receptiveness than the shape of the bracts and the protrusion of stigmatic flaps from them. And they have recommended the key characters for identifying each of the 3 parts of the receptive period. The criteria given by the present authors above, however, seem to be sufficient for practical use under the present situation, because the receptiveness, fertility and flowering condition of larch species are considerably variable.—It is rather difficult to detect the exact receptive period (especially its first part) by testing in controlled condition.

2. Calendar of reproductive cycle

Considering collectively the results and facts shown in Fig. 2 and in the preceding paragraphs, a phenological calendar may be composed for the reproductive cycle of Japanese larch at Yamabe, after the idea proposed by STANLEY (1958) and ASAKAWA (1965). In this calendar shown in Fig. 4, the reproductive cycle is divided into several distinct periods with accompanying subperiods. The definition, explanation, and some of the remarkable time-points are as follows. Among them, however, the times of metaphase I of PMC, pollen grain formation, embryo sac formation, fertilization and flower bud differentiation are not based on the observation of the present authors, but are borrowed from the data of YANAGIHARA (1958, 1959), YOKOYAMA et al. (ASAKAWA 1965), HASHIZUME and IMAI (1966) and KAZI (1971) with small corrections on consideration of latitudinal and climatic differences between Nagano Pref. and Yamabe or Kōshunai. On the other hand, the time (earliest) of formation of terminal buds on long shoots is decided by the present authors' own investigation.

① Dormant bud period. A long priod from the formation of buds on the current-year short shoots till they become active in the following spring (early mid-April). As lateral buds are successively formed on the new long shoots and terminal buds on the short shoots also do so as early as in May, this period extends through nearly a full year.

② Period of bud opening. After the beginning of the flower bud opening (about 14th April) and before the bract scales of the female strobili and the anthers begin to open or to dehisce.

4:12 (12th April): Beginning of opening of vegetative buds.

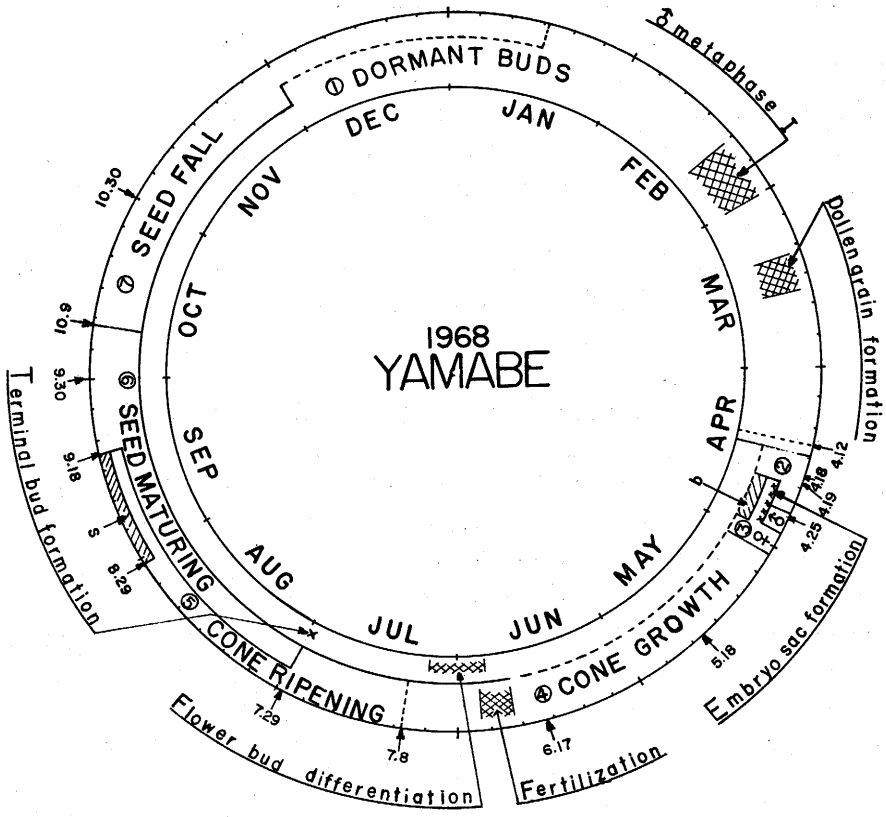

Fig. 4. Calendar of reproductive cycle of Japanese larch, based on the investigations of the No. 7 tree in 1968.

4:18: Change of the colour of strobili (male: deep yellow tinge, female: changing from light yellowish green to greenish pink).

4:19: Beginning of bending of strobilus stalks.
Beginning of expanding of companion needles.

③ Periods of flowering. For the female strobili, from the time the bract scales begin to recurve till the time the ovuliferous scales begin to appear from behind the bracts (according to BARNER and CHRISTIANSEN 1960, before this time the stage of receptiveness has been undoubtedly over also in *Larix decidua*). And for the male, from the beginning of the anther dehiscence until its end.

b: The process of recurvature of bract scales is distinguishable as a subperiod (21st or 22nd~27th April) and must be a good sign of the optimum receptiveness.

4:25: Completion of bending of strobilus stalks.

④ Period of cone growth. From the end of the former period (end of April or beginning of May), when the female strobili appreciably begin and continue to increase their size taking a form of cones, until around the cessation of the increase in size (ca. 10th July).

5:18: Both kinds of needles nearly fully expanded.
6:17: Beginning of recurvature of seminiferous scales and of appearance of seed wings.
7: 8: Beginning of browning of cone stalks.

⑤ Period of cone ripening. From the time the cones and the seminiferous scales complete their growth in size (the cone stalks also begin to become brown) until the time the scales complete the process of withering.

s: The withering process is characteristic enough to be divided as a subperiod occupying the last part (from the end of August till about 20th Sept.) of this period lasting for about 70 days. And during this subperiod the water content of them also reduces from 55% down to 25% (according to the authors' unpublished data).

7:29: Beginning of shedding of withered male strobili (anthers).
8:29: Beginning of withering of seminiferous scales.
9:18: End of the withering and beginning of opening of seminiferous scales.

⑥ Period of maturation of the seeds. After the time the adaxial surface of the seeds becomes deep white in colour with yellowish brown tinge and changes to yellowish brown (late in July) before spontaneous seed fall begins (9th Oct.). It is naturally not easy to mention what character can indicate the beginning of seed maturation. Undoubtedly seeds begin to develop after the fertilization late in June, and come to show the first sign of their germinative ability around 20th Aug. (according to the data presented by the present authors at the annual meeting of Hokkaido Branch, Japanese Forestry Society, Hakodate, 1971) (cf. HÅKANSSON 1961). It is also supposed that the weight and water content of the seeds reach their maxima late in July (20th or 30th) nearly at the same time as in the cones (unpublished data). Taking these three points of time and that of colour change into consideration, it seems more reasonable to divide the period concerning seed ripening, from the fertilization till the beginning of seed fall, into two, i.e. the period of seed growth from the fertilization till the time of maximum weight (late in July or early in August) and that of seed maturation from then or the first sign of germinative ability till the time of seed fall. However the latter period only is shown in this calendar which is based mainly upon reproductive phenology by external characters.

9:30: Beginning of defoliation of companion needles.
10: 9: Grayish-brown colouring of cone stalks.

⑦ Period of spontaneous seed fall. From the time the spontaneous seed fall is first recorded [this coincides also with the time when the seminiferous scales reach 80 degree of opening (9th Oct.)] till the time more than 90% of seeds have fallen except those at the basal and apical parts of cones (30th Nov.). The seed fall stays at a level of about 10% for the first 20 days, but within the following half month most of the fertile seeds fall.

10:30: Completion of defoliation of the companion needles, and beginning of that of the vegetative needles (40%).

Summary

In order to obtain fundamental knowledge of the male and female strobili and cones, various investigations were carried out on Japanese larch at Yamabe, Hokkaido, on the basis of the criteria previously determined for each of their characters from the point of view of the reproductive phenology. Measurement of size and weight were regularly maintained. The results of these investigations are shown together with a common axis of abscissa marked with calendric time in a figure, and those of the measurements in another (Figs. 2 and 3). Collective consideration on them gives a well-defined image to the reproductive cycle of this species in Hokkaido. This cycle shown as a circular calendar (Fig. 4) can be divided into several characteristic periods, and serves as a guide for undertaking breeding in the natural conditions.

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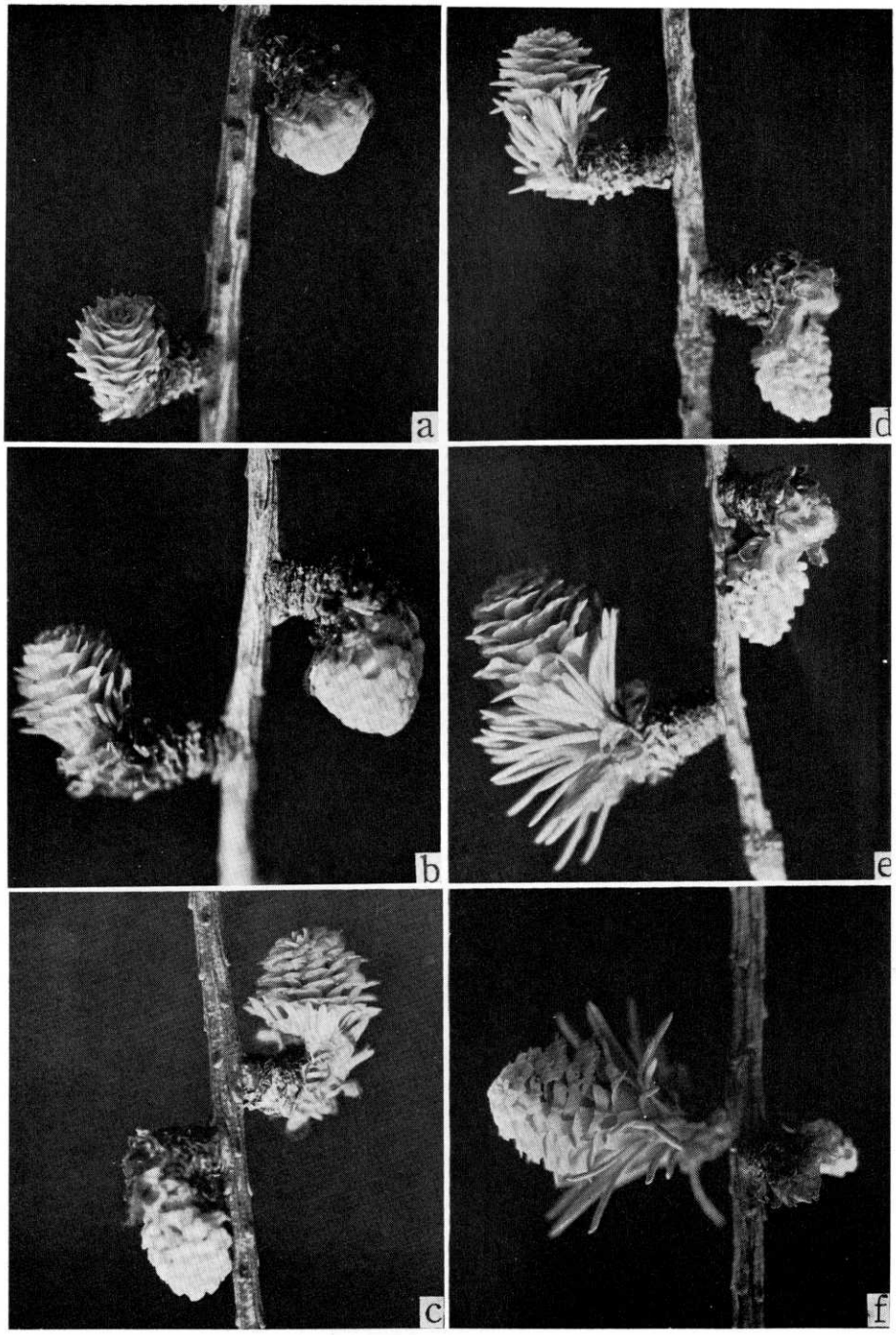

Photo. a—f. Development of male and female strobili on a Japanese larch tree (No. 7) in 1968.

a: Apr. 20.
b: Apr. 22.
c: Apr. 25.
d: Apr. 27.
e: May 1.
f: May 7.

カラマツ花部発育の季節的推移
—カラマツ類交雑のための基礎的研究 I—

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和文摘要

カラマツ類交雑のための基礎的な研究の一つとして，カラマツの花部の季節的時期的な発育過程を調べた。調査観察は，東京大学北海道演習林山部苗畑内の着花促進試験中の植栽木が1968年に多量の球花を着けたので，そのうちの1本を対象に，4月初めより翌年1月まで続けられた。形質ごとに，従来用いられてきた，あるいは新たに決めた，方法によって表示し，1図にまとめて相互の間の時間的な関係がみられるようにした (Fig. 2)。また，大きさ，重さ等の計測できる一部の形質についてもその時間的な変化を調べた (Fig. 3, Table)。

以上の結果を綜合して，カラマツの生殖的サイクルをいくつかの期間 (段階) に区切ることもできる。ここでは，その各期間を一つの円周上に配列して，円形のカレンダーを作つた (Fig. 4)。このカレンダーには，文献に基いて若干の器官形成学的時点を加え，空白の一部を埋めた。

これによつて，山部，ひいては道央地区でのカラマツの生殖暦に一通りの像を与えることができる。今後，平行してあるいは別途に行われた実験ないし観察の結果をこれと比較することによつて，年による差異を考慮に入れてもなお，交配から採種に至る過程の各々の段階で行うべき処理や操作の適期を判定する基準を示すことができると期待している。例えば，いくつかの形質が雌花の受粉可能期間を示す目印となりうる。