Comparison of Early Inflorescence Development between Japanese Pear (Pyrus pyrifolia Nakai) and Quince (Cydonia oblonga Mill.)

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Japanese pear (Pyrus pyrifolia) and quince (Cydonia oblonga) form different inflorescence architectures, the former forms raceme inflorescence with about eight flowers and the latter forms solitary-flowered inflorescence. We observed the floral differentiation of Japanese pear and quince to clarify the differences in their early inflorescence development. Floral differentiation of Japanese pear occurred in late June. After apical meristem turned to a dome-like structure, inflorescence developed by forming lateral flower meristems in axils of bracts. The apex of inflorescence became the terminal flower meristem, two or three meristems were initiated in axils of outer bracts and leaf primordia, and finally approximately eight flower meristems were formed in the inflorescence. Floral differentiation of quince was initiated from late October to November after eight leaf primordia had been initiated. Apical meristem transformed to a dome-like structure and initiated sepal primordia. Axillary meristems of bracts or leaf primordia in Japanese pear differentiate to flower meristem while those in quince remained undifferentiated to form axillary buds in the following growing season, resulting in an inflorescence architecture difference in Japanese pear and quince.

Key Words: floral differentiation, Maloideae, scanning electron microscope.
age of quince trees are unknown. Buds on Japanese pear spurs were collected from May to July in three consecutive floral differentiation seasons from 2003 to 2005. Terminal buds on 5- to 10-cm quince short shoots were also collected from July to January in three consecutive floral differentiation seasons from 2003 to 2006. In addition, the number of flowers, leaves, and elongating shoots emerging from buds were counted to describe flowering morphology at spring bud break in 2005. Although floral buds of Japanese pear sometimes contain secondary inflorescence, so called “Ko-bana” (Furuta, 1965) which is developed occasionally from an axillary meristem that is supposed to develop into a bourse shoot or form an extra axillary meristem in the floral bud, we regarded these floral buds with secondary inflorescence as an exceptional form of inflorescence development and excluded them from the observation in this study.

Observation of floral bud development

The floral bud development of Japanese pear and quince was observed using a scanning electron microscope (SEM). Buds were dissected with forceps under a stereomicroscope. The number of flower meristems, scales, leaf primordia, and bracts in each bud were counted. Scales, leaf primordia, and bracts were defined as leaf-like organs but were brown, leaf-like organs with no flower meristem in the axil, and leaf-like organs with a flower meristem in the axil, respectively. After counting the numbers of organs, the apical portions of trimmed buds were fixed in FAA (3.7% formaldehyde, 5% acetic acid, 50% ethanol). For SEM observation, samples were dehydrated in ethanol series and critical-point-dried in liquid CO$_2$. Dried samples were mounted on stubs and sputter-coated with gold (Hitachi, Tokyo, Japan). Specimens were observed using a Hitachi S-2350 scanning electron microscope (Hitachi), operated at 20 kV, and photographed using Neopan Acros 100 film (Fuji Film, Tokyo, Japan). The phyllotaxy angle of bracts and meristems was manually measured on the photograph.

Results

Flowering morphology of Japanese pear and quince

Bud break of Japanese pear began in late March to early April in Osaka, whereas that of quince began in mid-April in Nagano. The timing difference is most likely a result of the cooler climate of Nagano. The annual average temperatures of Osaka and Nagano are 16.5°C and 11.7°C, respectively. Japanese pear flowers were easily observed after bud break (Fig. 1A), whereas quince flowers could be observed only after the short shoot and leaves were fully elongated and expanded (Fig. 1C).

![Fig. 1. Inflorescence architecture of Japanese pear and quince. Photograph (A) and schematic illustration (B) of Japanese pear ‘Housui’, which has an indeterminate inflorescence with approximately eight flowers. Numbers indicate the order of flower opening. Schematic photograph (C) and schematic illustration (D) of quince, which bears solitary flowers at the terminal end of current-year shoots that have approximately eight leaves. Leaves subtend small axillary buds (arrow).](image-url)
Floral buds of the Japanese pear trees used in this study contained a primary inflorescence with approximately eight flowers, one or two leaves, and one elongating bourse shoot that was subtended by a leaf (Table 1). There were floral buds containing secondary inflorescences, but we excluded these floral buds from the observation as mentioned in Materials and Methods. The frequency of secondary inflorescence development in this study, however, seemed to be less than in other observations (Furuta, 2000). Flowers opened in progression acropetally from the side-lateral to the terminal (Fig. 1B). Quince floral buds contained a single

Table 1. The number of organs emerged from a floral bud of Japanese pear and quince.

<table>
<thead>
<tr>
<th></th>
<th>Japanese pear (n = 80)</th>
<th>Quince (n = 40)</th>
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<tbody>
<tr>
<td>Number of flowers</td>
<td>8.0 ± 2.1†</td>
<td>1.0 ± 0.0</td>
</tr>
<tr>
<td>Number of leaves</td>
<td>1.6 ± 1.4</td>
<td>7.6 ± 1.0</td>
</tr>
<tr>
<td>Number of bourse shoots</td>
<td>0.6 ± 0.6</td>
<td>0</td>
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</tbody>
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† The number of buds examined.

Mean ± SD.

Fig. 2. Floral differentiation of Japanese pear ‘Housui’ in 2005 in Osaka, Japan. Flat apical meristem in late May and early June (A). Slightly expanded apical meristem in mid-June (B). Expanded and swollen apical meristem in late June. This stage was defined as the visible sign of the initiation of floral differentiation (C, D). Initiation of the lateral flower meristem and development of inflorescence (E, F). Initiation of four or five lateral flower meristems and termination of inflorescence development to initiate the terminal flower meristem in late June to early July (G, H). Initiation of lateral flower meristems 6–8 (arrow) on the outer-basal position of the primary inflorescence in early July (I–K). Flower organ differentiation in each flower meristem in mid-July. The terminal flower completed development first, and the outer-basal flower (arrow) developed last (L). M = Apical meristem, INF = Inflorescence meristem, LF = Lateral flower meristem, TF = Terminal flower meristem, B = Bract, S = Sepal, UM = Undifferentiated meristem.
Table 2. The number of organs in a floral bud of Japanese pear and quince.

<table>
<thead>
<tr>
<th></th>
<th>Japanese pear (n = 48)</th>
<th>Quince (n = 105)</th>
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<tbody>
<tr>
<td>Number of scales</td>
<td>15.5 ± 1.4 y</td>
<td>6.4 ± 0.9 y</td>
</tr>
<tr>
<td>Number of leaf primordia</td>
<td>1.1 ± 0.5 z</td>
<td>7.6 ± 1.2</td>
</tr>
<tr>
<td>Number of bracts</td>
<td>8.7 ± 1.1 x</td>
<td>—</td>
</tr>
<tr>
<td>Number of flower meristem</td>
<td>7.6 ± 0.8 z</td>
<td>1.0 ± 0.0 z</td>
</tr>
<tr>
<td>Number of undifferentiated meristem</td>
<td>1.0 ± 0.6 z</td>
<td>0</td>
</tr>
</tbody>
</table>

* The number of buds examined.

* Mean ± SD.

* Scales were defined as leaf-like organs but were brown.

* Leaf primordia were defined as leaf-like organs with no flower meristem in the axil.

* Bracts were defined as leaf-like organs with a flower meristem in the axil.

* Undifferentiated meristem is supposed to develop to bourse shoot.

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**Fig. 3.** Floral differentiation of quince in 2005 in Nagano, Japan. Apical meristem in July and August (A, B). Narrow apical meristem surrounded by several leaf primordia in late August and September (C, D). Expansion of the apical meristem in October (E, F). Initiation of the flower meristem in October (G, H). Initiation of sepals on the fully swollen flower meristem in November (I–K). Flower with five sepals in January (L). M = apical meristem, L = leaf primordia, F = flower meristem, S = sepal.
flower borne at the terminal end of a current-season shoot. Each shoot had approximately eight leaves (Table 1, Fig. 1D). Although axillary buds subtended by leaves were initiated on the shoot, none of these buds grew into a bourse shoot.

Floral bud differentiation in Japanese pear and quince
Since floral differentiation of Japanese pear and quince for three consecutive floral differentiation seasons showed the same pattern, here we describe the results obtained in 2005. Japanese pears in Osaka initiated floral differentiation in late June, about 75 days after full bloom. Before this, the apical meristem was narrow and flat (Fig. 2A, B). After 14 to 17 scales (average 15.5) were initiated, the apical meristem expanded and swelled to form a dome-like structure (Table 2, Fig. 2C, D). The domed apical meristem ballooned, and bracts and leaf primordia, which were indistinctive at this stage, were initiated from the basal part (Fig. 2E–G). Lateral flower meristems were initiated in all bract axes, except for the two or three outermost. The average phyllotaxic divergence angle of bract and flower meristem initiation was 139° (Fig. 2F, K). After the initiation of bracts and lateral flower meristems on the flanks of the domed apical meristem, the apex transformed into a terminal flower meristem (Fig. 2H). Following the initiation of this terminal flower meristem, two or three additional lateral flower meristems were developed in the axes of the two or three outermost bracts (Fig. 2I–K). Thus, approximately eight flower meristems comprised the inflorescence (Table 2, Fig. 2K). Finally, an undifferentiated meristem was developed in the axil of leaf primordium that was located at the outermost position of the inflorescence. After the inflorescence formed, flower organs (sepals, petals, stamens, and pistils) began to differentiate, first in the terminal flower, then in lateral flowers (Fig. 2L). The inflorescence and flower meristems developed very quickly. Once the dome-like structure, a visible sign of floral differentiation, formed in late June (Fig. 2C, D), the development of the inflorescence was completed within a few days, by early July (Fig. 2E, K). Flower organs in the flower meristems differentiated, for the most part, in mid-July (Fig. 2L).

The floral differentiation of quince in Nagano took place from late October to early November, or about 160–180 days past full bloom. The cooler climate of the Nagano region, compared to Osaka, leads to later floral differentiation. Our preliminary comparisons of the floral differentiation time among several pear cultivars indicated that floral initiation in Osaka is about one month earlier than in Nagano (data not shown). In quince, the apical meristem remained narrow and small and slowly produced scales and leaf primordia until the dome-like structure formed in October (Fig. 3A–G). Approximately six scales and eight leaf primordia were initiated, with an average phyllotaxic divergence angle of 135°, before the apical meristem transformed into a dome-like structure (Table 2, Fig. 3D). After the dome-like apical meristem formed, sepal primordia were initiated, with the same phyllotaxy as that of the scales and leaf primordia (Fig. 3H–K). The apical meristem neither elongated nor protruded to form an inflorescence, and the entire apical meristem converted to a single flower meristem (Fig. 3L).

Discussion
The subfamily Maloideae (Rosaceae), which contains a variety of fruit tree species such as apple, pear, quince, and loquat, shows great diversity in phenological and morphological characteristic, and its various inflorescence architectures are particularly interesting characters (Phipps et al., 1990; Robertson et al., 1992; Rohrer et al., 1991, 1994). The inflorescence architecture of quince, which forms only solitary flowers, was quite different from that of Japanese pear. However, if we consider that a flower or leaf represents one node, the number of nodes was approximately the same in quince and Japanese pear (Table 1). As a quince axillary meristem is generally subtended by a leaf, both flower and bourse shoots of Japanese pear are regarded as equivalent to a quince axillary bud and are considered to be derived from an axillary meristem. Genetic factors that determine the fate of axillary meristems seem to be diverged in quince and Japanese pear, leading to their different inflorescence morphology.

Figure 4 shows schematic diagrams of the order of flower meristem initiation and flower organ differentiation of Japanese pear. Interestingly, although neither the order of flower meristem initiation nor flower organ differentiation was indeterminate, blooming occurred acropetally from the outer basal to the terminal flower, which is often observed in an indeterminate inflorescence (Fig. 1B). Typically, four to five lateral flower meristems formed acropetally at first and finally a terminal flower meristem formed. However, once a terminal flower meristem formed, two to three additional lateral flower meristems were initiated in axils of outer bracts, which made an inflorescence with approximately eight flowers. Flower organ differentiation of the terminal flower meristem started first and then those of lateral meristems proceeded as indicated Figure 4C. Undifferentiated meristem developed in the axil of outermost leaf primordium was supposed to develop into a bourse shoot or secondary inflorescence at blooming time in spring. The previous observations of the floral differentiation of Japanese pear ‘Nijisseiki’ in Tottori, Japan, where the annual average temperature is 14.6°C, correspond well with ours, although they did not fully describe inflorescence development (Banno et al., 1986). We present here more detailed photographs which indicate the order of flower meristem initiation and development in early inflorescence.

Floral differentiation of quince initiated from late October to early November. To our knowledge, this is
the first report observing the floral differentiation of quince. Quince appeared to have fewer scales than Japanese pear (Fig. 5); however, the total number of quince leaf primordia plus bracts was almost the same as that of Japanese pear. Therefore, excluding scales, the total node numbers in Japanese pear and quince buds were the same.

Foster et al. (2003) observed the floral differentiation of apple (*Malus domestica* Borkh.) using SEM. They proposed that apical meristem doming is the first morphological indication of the transition to flowering and reflects a commitment to floral development. They described four distinct stages of inflorescence development: 1) the domed apical meristem initiates four-six lateral meristems, each subtended by a bract showing 137° divergence-angle phyllotaxy; 2) the apical meristem transforms to a terminal flower meristem; 3) the terminal flower initiates sepals, while the lateral flower meristems initiate bractlets; and 4) sepals are initiated in the lateral meristem acropetally from the basal meristem to that next to the terminal flower meristem. The maloid fruit species we examined showed a similar phyllotaxy in floral differentiation. Furthermore, the first stage of Japanese pear inflorescence development appeared to be quite similar to that of apple until four or five lateral flower meristems were developed; however, we observed additional lateral flower meristem initiation on the basal axillary of the Japanese pear inflorescence. Unlike apples, Japanese pears are competent to initiate additional lateral flower meristems, which may lead to the different inflorescence architecture of Japanese pear and apple.

Evans and Dickinson (2005) observed the floral differentiation of several maloid species. They found various differences at early inflorescence development of maloid species, such as *Photinia* Lindl. and *Rhaphiolepis* Lindl., although their mature inflorescence architectures resembled panicle types. Inflorescence of *Sorbus* L. was complex with a number of partial inflorescences and was hardly observed in the early stage of development. Furthermore, they investigated *Chaenomeles speciosa* Nakai and observed small inflorescence with a cluster of three flowers. *Chaenomeles* species were considered closely related to *Cydonia*, *Malus*, and *Pyrus* species; however, their inflorescence was fascicle; a cluster with 1–6 flower buds (Robertson...
et al., 1991; Rumpunen, 2002). Interestingly, intergeneric hybrids between pears and quince, so called “Pyronia”, formed 1–3 flowered inflorescences which were most likely intermediate phenotype of the two species (Shimura et al., 1983; Trabut, 1916). We believe these hybrids or closely related species could be effectively used to comprehend the mechanisms of inflorescence architecture development in maloid species.

This study showed that the number of leaf primordia in a quince floral bud is almost the same as the total number of bracts plus leaf primordia in a Japanese pear floral bud. Thus, we propose that Japanese pear bracts may arise ontogenetically from the same tissues as quince leaf primordia. In other words, genetic factor characteristics of Japanese pear and quince could differentiate the fate of their axillary meristems.

Acknowledgments

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