THE OCCURRENCE AND MORPHOLOGY OF TYLOSES AND GUMS IN THE VESSELS OF JAPANESE HARDWOODS

by

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Summary

The occurrence and morphology of natural tyloses and gums in the vessels of 50 Japanese hardwoods (15 ring-, 34 diffuse- and 1 radial-porous woods) were investigated using SEM. Tyloses were present exclusively or predominantly in 23 species (12 ring-, 10 diffuse- and 1 radial-porous woods) and gums in 15 species (3 ring- and 12 diffuse- porous woods). In the pore zones of most of the ring-porous woods both tyloses and gums first occurred in an earlier ring number from the bark than in the diffuse- and radial-porous woods. Tyloses and gums originated from both ray and axial parenchyma cells in most species which have pit pairs connecting these cells to the vessels. Except for four species, the maximum and minimum diameters of the inner pit aperture from vessels to parenchyma cells were greater than 5 and 2 μm, respectively, in those species with tyloses, whereas the diameters were less than these values in species having gums. The forms of tylosis blockings in heartwood vessels were closely related to parenchyma patterns.

Key words: Tylosis, gum, vessel, ray parenchyma cell, axial parenchyma cell, Japanese hardwoods, SEM.

Introduction

A considerable amount of information has been published on the cause and mechanism of tylosis formation, their origin, occurrence, morphology, wall structure and effect on various properties of wood. However, there have been but few reports on those of gums (Côté & Marton 1962; Kóran & Yang 1972; Fujita et al. 1977).

Tylosis and gum formation are considered to be normal physiological processes occurring in many living trees. Studies on their occurrence and morphology in a wide variety of hardwoods are very important for a better understanding not only of their biological properties in different species but also of the inherent peculiarity of the living trees in which they occur from a tree physiology and wood technology standpoint.

The occurrence of tyloses in 94 species of American hardwoods was investigated by Gerry (1914). Similar work was reported by Ito and Kishima (1951) on the presence or absence of tyloses in the heartwood and sapwood of 109 Japanese species. An intensive survey was made of the occurrence of tyloses and secretion of gums in the wood of over 1,100 genera by Chattaway (1949). However, because these studies were not based on the use of fresh material from living trees there were some unanswered questions on the occurrence of natural tyloses. These were:

1) the difference among species in which ring, numbered from the bark, tyloses first occur,
2) the type of parenchyma cell from which tyloses originate, 3) correlation of vessel to parenchyma pit sizes with tylosis formation, and
4) the difference in the morphology of tyloses in heartwood among species. Recently, most of these questions were answered by Bonsen and Kučera (1990) and Bonsen (1991) on the basis of the investigation on 65 species grown in Switzerland. Also, to answer these, the present authors (1992) reported some preliminary observations on the occurrence and morphology of natural tyloses in 28 species grown in Japan.

In the present study this work is extended not only to natural tyloses but also to gums in a further 50 Japanese hardwoods using SEM.
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**Ring-porous wood**

- **Quercus mongolica var. grosseserrata**
  - 9  | 12 | 60 | 1.9| 14 | +  | -  | 4(9)| 1(3)| 6.1| 9.0| -  | -  | 3.9| 6.0|
- **Castanea crenata**
  - 14 | 28 | 27 | 1.2| 3  | +  | -  | 1(4)| 1(3)| 5.4| 10.1| -  | -  | 3.4| 9.0|
- **Castanopsis cuspidata var. sieboldii**
  - 11 | 13 | 46 | 1.9| 20 | +  | (+)| 19(20)| 1.2| 4.9| 10.2| 5.7| 12.3| 3.0| 6.4|
- **Ulmus japonica**
  - 14 | 16 | 64 | 1.2| 18 | +  | -  | 2(19)| 1(3)| 4.0| 10.8| -  | -  | 3.7| 6.6|
- **Zelkova serrata**
  - 14 | 12 | 61 | 1.5| 29 | (+)| +  | 2(28)| 1.2| 3.2| 5.2| 6.6| 13.2| 4.1| 6.6|
- **Morus bombycis**
  - 7  | 8  | 17 | 1.0| 5  | +  | -  | 2(2)| 1.2| 3.2| 5.2| 6.6| 13.2| 4.1| 6.6|
- **Maackia amurensis var. huergeri**
  - 21 | 24 | 49 | 0.5| 4  | +  | -  | 4(5)| 1(3)| 1.3| 3.6| -  | -  | 1.4| 3.9|
- **Robinia pseudo-acacia**
  - 15 | 20 | 22 | 1.0| 5  | +  | -  | 2(3)| 1(3)| 2.9| 7.6| -  | -  | 2.6| 5.4|
- **Phellodendron amurense**
  - 14 | 24 | 59 | 0.8| 9  | -  | +  | 4(7)| 1(3)| 1.2| 3.8| -  | -  | 1.2| 3.6|
- **Rhus javanica**
  - 13 | 12 | 12 | 1.2| 4  | +  | -  | 2(5)| 1.2| 4.3| 7.1| 4.4| 7.0| 2.9| 7.8|
- **Acanthopanax scidophyloides**
  - 10 | 18 | 56 | 3.0| 18 | +  | -  | 8(15)| 1.2| 3.5| 7.7| 3.5| 6.5| 4.3| 7.8|
- **Euvodiptax innovans**
  - 10 | 12 | 79 | 3.2| 55 | +  | (+)| 2(44)| 1.2| 3.3| 14.9| 2.5| 9.1| 2.2| 6.8|
- **Kalopanax pictus**
  - 12 | 13 | 58 | 2.6| 26 | +  | -  | 2(7)| 1.2| 3.2| 6.1| 12.3| 4.9| 10.4| 2.9| 8.8|
- **Frasinus mandshurica var. japonica**
  - 10 | 13 | 57 | 2.1| 22 | +  | (+)| 2(16)| 1(3)| 0.6| 3.3| -  | -  | 0.5| 4.3|
- **Frasinus lanuginosa**
  - 10 | 16 | 65 | -  | -  | +  | (+)| 2(20)| 1(3)| 0.8| 4.8| -  | -  | 0.7| 3.7|

**Radial-porous wood**

- **Quercus acuta**
  - 13 | 13 | 48 | -  | -  | +  | -  | 3  | 1.2| 3.2| 7.4| 3.0| 7.6| 2.2| 6.5|

Legend: 1: Tree height (in m). — 2: d.b.h. (in cm). — 3: Ring numbers at d.b.h. — 4: Sapwood width (in cm): = species without heartwood. — 5: Ring numbers in sapwood: = species without heartwood. — 6: Tyloses: + = present; (+) = occasionally present; - = absent. — 7: Gums: + = present; (+) = occasionally present; - = absent. — 8: Ring numbers from the bark in which tyloses or gums first occurred: ( ) = ring numbers in latewood of ring-porous woods; = species without tyloses or gums. — 9: Kind of parenchyma cells from which tyloses or gums originated; 1 = procumbent ray cell; 2 = upright or square ray cell; 3 = axial parenchyma cell; ( ) = species with homogeneous ray tissue; = species without tyloses or gums. — 10: Means of minimum pit aperture diameter of V-P pits (µm): = absent. — 11: Means of maximum pit aperture diameter of V-P pits (µm): = absent. — 12: Means of minimum pit aperture diameter of V-U pits (µm): = absent. — 13: Means of maximum pit aperture diameter of V-U pits (µm): = absent. — 14: Means of minimum pit aperture diameter of V-A pits (µm): = absent. — 15: Means of maximum pit aperture diameter of V-A pits (µm): = absent.
The inclusions that are most frequent in vessels are tyloses and various amorphous exudations that are gummy, resinous, or chalky in nature (Panshin & De Zeeuw 1980). This paper is not concerned with the chemical composition of the amorphous exudations, but only with the details of their occurrence and morphology, and the term ‘gum’ is therefore used throughout this article to cover all forms of amorphous substances in vessels.

Materials and Methods

Fresh wood samples, from bark to pith, were taken at breast height from living trees of 50 species growing normally at Hokkaido and Wakayama prefectures in Japan. Details of the sample trees are shown in Table 1. Heartwood was distinguished from sapwood in the green condition with the naked eye on the basis of a colour change. Two wood samples were collected from one living tree of each species. They were immediately treated by different methods. One set was fixed in FAA. The other was put into a small box containing solidified CO₂ and were subsequently transferred into an −80°C freezer.

The wood samples fixed in FAA were used for the tylosis observations. The others which were preserved at low temperature were used for the gum observations. Small blocks were cut from the wood samples sequentially from the outermost sapwood to near the pith. A careful check was made whether abnormal tissues were present to avoid traumatic tyloses and gums. The radial surfaces of the normal wood to be observed were cut with a new razor blade. Transverse and tangential surfaces to be observed were also prepared, if necessary. Their finished size was c. 5 × 7 × 2 mm. The samples for tylosis observations were critical-point dried with liquid CO₂. Those for gum observations were dried at room conditions to avoid gum dissolution in solvents (Kóran & Yang 1977). Both samples were mounted on SEM specimen stubs using electrically conductive past, and then coated with carbon and gold in a high vacuum evaporation unit. They were examined at 15 kV in a JSM-35CFII scanning electron microscope.

To decide the types of parenchyma cell from which tyloses and gums originate, three methods were used. The first was to observe, from the vessel lumen, those pits from which tylosis buds or gum droplets were arising (Figs. 1 & 2). The second was to detect solitary gum lumps existing on the vessel to procumbent ray cells (V-P), vessel to upright (or square) ray cells (V-U) or vessel to axial parenchyma cells (V-A) pits in the vessel walls (Fig. 3). The third was to detect from the tylosis lumen side the opened pit pairs through which the tyloses had emerged (Fig. 4).

In order to measure the diameters of the inner pit apertures of vessel to parenchyma cell pits in the vessel walls, SEM micrographs of V-P, V-U and V-A pits were taken from the vessel lumen side at 2,000–10,000 magnifications. Fifty pits of each kind were selected randomly from the micrographs and their maximum and minimum diameters at right angles to each other were measured at the broadest parts of the inner pit apertures (Fig. 5).

Results and Discussion

Presence of tyloses and gums

The presence of tyloses and gums in the 50 species (13 ring-, 34 diffuse- and 1 radial-porous woods) examined are shown in Table 1. Tyloses were found in 30 species (13 ring-, 16 diffuse- and 1 radial-porous woods). Gums were found in 23 species (7 ring- and 16 diffuse-porous woods). Although both tyloses and gums were found in 15 species, either one or the other predominated. Consequently, tyloses were confirmed to be present exclusively or predominantly in 23 species (12

Fig. 1. Bud tyloses arising from V-P pits. Rhus javanica. — Fig. 2. Small droplets of gums (arrows) arising from V-A pits. Gums of type 3. Prunus sargentii. — Fig. 3. Irregular lump of gums arising from V-A pits. Gums of type 2. Maackia amurensis var. buergeri. — Fig. 4. Arrow indicates V-U pit opening from which tylosis originated. Tylosis of type 4. Magnolia oborata. — Fig. 5. Pit apertures of V-P pits. Solid line = maximum diameter; broken line = minimum diameter. Fagus crenata. — Fig. 6. Thin-walled tylosis. Zelkova serrata.
ring-, 10 diffuse- and 1 radial-porous woods) and gums exclusively or predominantly in 15 species (3 ring- and 12 diffuse-porous woods). The species having predominantly gums were *Zelkova serrata* and the 6 species belonging to *Prunus*. Tyloses were rarely present and all of the enlarged ones had very thin walls (Fig. 6).

Of the 15 ring-porous woods examined, tyloses were present exclusively or predominantly in 12 species. On the other hand, of the 34 diffuse- and one radial-porous woods examined, tyloses were present exclusively or predominantly in 11 species and gums in 12 species. This result indicates a general tendency that tyloses occur in those species with larger vessels and gums occur in those with smaller vessels as found by Bonsen and Kučera (1990) and Bonsen (1991).

Although tyloses and gums were not present in 12 species, all of these were diffuse-porous woods in which heartwood was not found except for *Magnolia salicifolia* and *Clerodendron trichotomum*.

**Ring number, from the bark, in which tyloses or gums first occur**

Of the 23 species having tyloses exclusively or predominantly, in 9 out of 12 ring-porous woods the tyloses first occurred in earlier ring numbers from the bark in the pore zone than in the 10 diffuse-porous woods and in one radial-porous wood. Tyloses occurred in the current annual ring or in the previous year’s annual ring in the pore zone of the ring-porous woods except for three species (*Quercus mongolica* var. *grosseimera*, *Castanopsis cuspidata* var. *sieboldii*, *Acanthopanax scidophylloides*). However, the first occurrence of tyloses in the latewood varied widely among the 12 ring-porous woods and appeared later than in the pore zone in most of them. In the diffuse-porous woods, ring numbers in which tyloses first occurred varied among species. Tyloses first occurred in the middle of the sapwood in *Salix sachalinensis* and *Juglans ailanthifolia*, species in which tyloses first occurred earliest in the diffuse-porous woods. They first occurred however near the transitional region from sapwood to heartwood in the other species having heartwood and at the inner regions (more than 16th ring number from the bark) in the 3 species lacking heartwood.

Of the 15 species having gums exclusively or predominantly, gums in pore zone of 2 out of 3 ring-porous woods occurred first in an earlier ring number than in the 12 diffuse-porous woods. Gums in the pore zone of all the ring-porous woods first occurred in earlier ring numbers than in the late wood. It is especially noteworthy that gums first occurred in the previous year’s annual ring in the pore zone of *Zelkova serrata*. In the diffuse-porous woods, gums first occurred near the transitional region from sapwood to heartwood in those species having heartwood, and at 15th and 25th ring numbers from the bark in the 2 species having no heartwood.

The experimental data obtained in the present study are based on the survey of limited samples in one living tree of each species. Therefore, our results do not consider variability within the species.

It has been recognised that tyloses and gums are the means by which vessels that have lost their water-conducting capacity were sealed off from functioning tissues (Zimmermann 1983). As pointed out by Saioto et al. (1992), the positional differences of the first occurrence of tylosis among species, especially between ring- and diffuse-porous woods, are considered to result from the positional differences of the water conducting vessels and subsequent embolised ones in the living trees. Such a relation in the living trees may also hold true in the positional differences of the first occurrence of gum among species.

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Fig. 7. Tyloses of type 1. *Robinia pseudo-acacia*.
Fig. 8. Tyloses of type 2. *Cinnamomum camphora*.
Fig. 9. Tyloses of type 3. *Ficus erecta*.
Fig. 10. Tyloses of type 5. *Fraxinus lanuginosa*.
Fig. 11. Gums of type 1. *Phellodendron amurense*.
Fig. 12. Gums of type 4. Pit apertures (arrows) are covered with thin layer of gums. *Illicium religiosum*.
Fig. 13. Thin layer of gums deposited between bars. *Alnus hirsuta*. 

The types of parenchyma cell from which tyloses or gums originated

Tyloses were traced to both ray and axial parenchyma cells in 17 of the 23 species having tyloses exclusively or predominantly. They originated from both procumbent and upright (or square) ray cells in all species having pit pairs connecting these cells to vessels. In Castanopsis cuspidata var. sieboldii, Pterocarya rhoifolia, Carpinus laxiflora and Ficus erecta, the kind of parenchyma cells from which tyloses originated could not be decided, because of the low percentage of vessel and parenchyma contact and the little tylosis development. A more detailed survey is needed.

In Salix sachalinensis and Cinnamomum camphora, tyloses were not traced from axial parenchyma cells, though vessels came in contact with axial parenchyma cells in both species. Vessel to axial parenchyma pits were found in the vessel walls in Cinnamomum camphora but not in Salix sachalinensis. The reasons why tyloses did not originate from axial parenchyma cells in the former could not be elucidated in the present study.

Gums were also traced to both ray and axial parenchyma cells in 13 of the 15 species having gums exclusively or predominantly. They originated from both procumbent and upright (or square) ray cells in all of the species with heterogeneous ray tissue. The type of parenchyma cell from which gums originated could not be decided in Illicium religiosum and Cornus controversa, because no

Fig. 14. Relationship between the mean values of maximum and minimum pit aperture diameters of vessel to parenchyma cell pits and the occurrence of tyloses or gums. ● = V-P pits in species with tyloses; ○ = V-P pits in species with gums; ▲ = V-U pits in species with tyloses; △ = V-U pits in species with gums; ■ = V-A pits in species with tyloses; □ = V-A pits in species with gums.

The types of parenchyma cell from which tyloses or gums originated

Tyloses were traced to both ray and axial parenchyma cells in 17 of the 23 species having tyloses exclusively or predominantly. They originated from both procumbent and upright (or square) ray cells in all species having pit pairs connecting these cells to vessels. In Castanopsis cuspidata var. sieboldii, Pterocarya rhoifolia, Carpinus laxiflora and Ficus erecta, the kind of parenchyma cells from which tyloses originated could not be decided, because of the low percentage of vessel and parenchyma contact and the little tylosis development. A more detailed survey is needed.

In Salix sachalinensis and Cinnamomum camphora, tyloses were not traced from axial parenchyma cells, though vessels came in contact with axial parenchyma cells in both species. Vessel to axial parenchyma pits were found in the vessel walls in Cinnamomum camphora but not in Salix sachalinensis. The reasons why tyloses did not originate from axial parenchyma cells in the former could not be elucidated in the present study.

Gums were also traced to both ray and axial parenchyma cells in 13 of the 15 species having gums exclusively or predominantly. They originated from both procumbent and upright (or square) ray cells in all of the species with heterogeneous ray tissue. The type of parenchyma cell from which gums originated could not be decided in Illicium religiosum and Cornus controversa, because no
small droplets of gums were found on the vessel-parenchyma pits in either species (see Table 3).

From the results described above, it is suggested that tyloses and gums arise from ray cells [both procumbent and upright (or square) in species with heterogeneous ray tissue] and from axial parenchyma cells in most of the species having pit pairs connecting these cells to vessels, as pointed out by Bonsen (1991). This indicates, therefore, that there are no functional differences between ray [procumbent and upright (or square) ray cells] and axial parenchyma cells for the formation of tyloses and gums in most species which have them.

Relationship between the size of vessel to parenchyma cell pits and the occurrence of tyloses or gums

Figure 14 shows the relationship between the mean values of maximum and minimum pit aperture diameters of vessel to parenchyma pits and the occurrence of tyloses or gums. The mean values were greater than c. 5 and 2 μm, respectively, in species having tyloses exclusively or predominantly and were less than these values in species having gums exclusively or predominantly. Four species were exceptional: *Zelkova serrata*, *Illicium religiosum*, *Fraxinus mandshurica var. japonica* and *Fraxinus lanuginosa*.

In *Zelkova serrata*, only the maximum diameters of V-P, V-U and V-A pits were greater than 5 μm. In *Illicium religiosum*, only maximum diameters of V-U and V-A pits were greater than 5 μm. In the two species belonging to *Fraxinus*, however, both the maximum and minimum diameters of vessel-ray and -axial parenchyma pits were less than 5 and 2 μm, respectively. It is concluded, therefore, that the occurrence of tyloses or gums were more closely related to the minimum diameters than to the maximum ones except for the two species belonging to *Fraxinus*.

The results obtained indicate that there is a critical minimum size of pit aperture on the vessel side between vessel and parenchyma cells above which tyloses form and that there is a critical maximum size below which gums secrete. In order to elucidate this problem, essentially the size of the actual pits from which tyloses or gums have arisen should be measured. However, such measurements were very difficult to make in the present study. Chattaway (1949) reported that tyloses were

Fig. 15. Morphological types of tyloses: 1 = closely packed tyloses; 2 = closely packed tyloses at intervals; 3 = uniseriate tyloses of which upper and lower walls are in contact; 4 = uniseriate tyloses which are not contiguous; 5 = collapsed tyloses.
Table 2. Morphological types of tyloses and parenchyma pattern.

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<tr>
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<th>5</th>
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</tr>
<tr>
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<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
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<td>2</td>
</tr>
<tr>
<td>Pterocarya rhoifolia</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
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<td>2</td>
</tr>
<tr>
<td>Juglans ailanthifolia</td>
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<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Ostrya japonica</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Fagus crenata</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Ficus erecta</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
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<td>1</td>
</tr>
<tr>
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<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
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<td>2</td>
</tr>
<tr>
<td>Magnolia obora-ta</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
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</tr>
<tr>
<td>Cinnamomum camphora</td>
<td>+</td>
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<td>+</td>
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<tr>
<td>Quercus mongolica var. grosseserrata</td>
<td>(+)</td>
<td>(-)</td>
<td>(-)</td>
<td>- (+)</td>
<td>(-)</td>
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<td>Castanea crenata</td>
<td>(+)</td>
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<td>- (-)</td>
<td>- (+)</td>
<td>- (-)</td>
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</tr>
<tr>
<td>Castanopsis cupidata var. sieboldii</td>
<td>(+)</td>
<td>- (-)</td>
<td>+ (+)</td>
<td>- (+)</td>
<td>- (-)</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
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<td>- (-)</td>
<td>- (+)</td>
<td>- (+)</td>
<td>+ (-)</td>
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<td>- (-)</td>
<td>+ (+)</td>
<td>- (-)</td>
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<td>- (+)</td>
<td>- (-)</td>
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<td>1</td>
</tr>
<tr>
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<td>- (-)</td>
<td>+ (+)</td>
<td>- (+)</td>
<td>- (-)</td>
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<td>+ (+)</td>
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<td>- (-)</td>
<td>+ (+)</td>
<td>- (+)</td>
<td>- (-)</td>
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<td>1</td>
</tr>
<tr>
<td>Kalopanax pictus</td>
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<td>+ (+)</td>
<td>- (-)</td>
<td>- (-)</td>
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</tr>
<tr>
<td>Fraxinus mandshurica var. japonica</td>
<td>- (-)</td>
<td>- (-)</td>
<td>- (-)</td>
<td>- (+)</td>
<td>+ (-)</td>
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<td>1</td>
</tr>
<tr>
<td>Fraxinus lanuginosa</td>
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<td>- (-)</td>
<td>- (+)</td>
<td>+ (-)</td>
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<tr>
<td>Quercus acuta</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
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</table>

Legend: 1–5: tyloses of type 1–5, respectively; + = present; – = absent; ( ) = latewood of ring-porous woods. — 6: Ray composition: 1 = contact ray; 2 = contact-isolation ray. — 7: Axial parenchyma arrangement: 1 = paratracheal parenchyma; 2 = apotracheal parenchyma.

developed in those species in which the widths of the apertures of the pits from vessels to ray cells exceed approximately 10 μm. However, the critical value (5 μm) of the maximum diameter obtained in the present study is considerably smaller than her value. Bonsen and Kučera (1990) and Bonsen (1991) reported that the minimum pit aperture diameter of vessel-parenchyma pits was greater than 3 μm in species with tyloses and less than 3 μm in species with gum only. This value corresponds closely to that obtained in our study.

The morphological types of tyloses and gums

Tyloses in the heartwood (or in the inner region of those species without heartwood) of species having tyloses exclusively or predominantly present were divided into the following five types on the basis of the form of their blockings in the longitudinally cut vessel cavities (Fig. 15). Type 1: numerous closely packed tyloses occlude entire vessel cavities along the vessel axes (Fig. 7). Type 2: numerous closely packed tyloses occlude vessel
Tyloses and gums in Japanese woods

Tyloses and folia chiefly small, inus and extremely walls (K6nin cheal cies include larly losses, nantly. ring-porousported Saitoh, species are (Ishida in to three woods, although tyloses include all the wood, having thin, lignified, multi-lamellate and lack parallel arrangement of microfibrils and intercellular layers. Tyloses of the species belonging to Fraxinus are, therefore, assumed to be unique in their morphology and wall structure.

However, it is noteworthy that vessel occlusions in Fraxinus excelsior and F. ornus have been defined as gums by Bonsen (1991), on the basis of morphological structure and staining with safranine-astrablue of their developmental stages. The occlusions in the two Fraxinus species examined have been interpreted as tyloses in this paper, because of their outer appearances in the SEM micrographs. In order to elucidate their true nature, a more detailed study from various aspects is needed.

Table 2 shows the morphological types of tyloses and parenchyma pattern in those species having tyloses exclusively or predominately. Rays were divided into two types, contact and contact-isolation rays, based on the classification by Braun (1970). Axial parenchyma was divided into two kinds, paratracheal and apotracheal. Parenchyma patterns are defined by means of the combination of ray composition and axial parenchyma arrangement.

The occurrence of the types of tyloses described above was confirmed to be related to the diameter of vessels, as pointed out by Saitoh et al. (1991). Types 1 and/or 3 were found in the pore zone of ring-porous woods except for three species with type 5, although tyloses of type 1 were often found in larger vessels. Type 3 and/or 4 were found in the late wood of all the ring-porous woods and in all of the diffuse- and radial-porous woods. Although tyloses of type 1 were also found in three diffuse-porous woods, they were also commonly present in Juglans ailanthifolia having larger vessels. Tyloses of type 2 were found in only two species. Tyloses of type 5 were limited to the pore zone in three ring-porous woods. It has been already reported that tyloses of this type in Ulmus japonica begin to collapse in the intermediate zone (Ishida & Ohtani 1968; Ohtani & Fujikawa 1991). The tylosis wall of this type in the 2 species belonging to Fraxinus were the thinnest in all the species examined. That tylosis walls of the other species in this genus are extremely thin has been reported in F. americana (Körn & Côté 1965), F. nigra, F. oregona and F. profunda (Isenberg 1933). Isenberg (1933) has reported that tyloses of the 3 Fraxinus species have very thin walls composed chiefly of lignin to which are added perhaps small, irregular patches of cellulose. Sano and Fukazawa (1991) have reported that the tylosis walls of F. mandshurica var. japonica are thin, highly lignified, multi-lamellate and lack parallel arrangement of microfibrils and intercellular layers. Tyloses of the species belonging to Fraxinus are, therefore, assumed to be unique in their morphology and wall structure.

Fig. 16 shows the relationship between tylosis types and parenchyma pattern. In the ring-porous woods, tylosis types were only counted in the pore zone. Type 1 was found in the 12 species in which all parenchyma patterns were included. Type 2 was found in the only 2 species having contact ray and paratracheal parenchyma. Type 3 was found in 15 species and type 4 in 10 species, in which three parenchyma patterns, except for a combination of contact-isolation ray and paratracheal parenchyma, were included. Type 5 was found in the only 3 species having contact ray and paratracheal parenchyma. Comparing

![Percentage of parenchyma (%)](image)

Fig. 16. Relationship between tylosis types and parenchyma pattern. Hatched = contact-paratracheal; white = contact-apotracheal; cross-hatched = contact, isolation-paratracheal; black = contact, isolation-apotracheal.
Table 3. Morphological types of gums and parenchyma pattern.

<table>
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<td><strong>Diffuse-porous wood</strong></td>
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</tr>
<tr>
<td>Betula maximowicziana</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<td>2</td>
</tr>
<tr>
<td>Alnus hirsuta</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Illicium religiosum</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>1</td>
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</tr>
<tr>
<td>Prunus pendula forma ascendens</td>
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<tr>
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<tr>
<td>Prunus ssiori</td>
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<td>-</td>
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<tr>
<td>Prunus buergeriana</td>
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<tr>
<td>Sorbus alnifolia</td>
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<tr>
<td>Tilia japonica</td>
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<td>+</td>
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<tr>
<td>Cornus controversa</td>
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</tbody>
</table>

| **Ring-porous wood**             |   |   |   |   |   |   |
| Zelkova serrata                  | + (+) | + (+) | + (+) | + (-) | 1 | 1 |
| Maackia amurensis var. buergeri  | + (-) | + (-) | + (-) | + (+) | 1 | 1 |
| Phellodendron amurense           | + (+) | + (+) | + (+) | - (-) | 1 | 1 |

Legend: 1–4: gums of type 1–4, respectively; + = present; − = absent; ( ) = latewood of ring-porous woods. — 5: Ray composition: 1 = contact ray; 2 = contact-isolation ray. — 6: Axial parenchyma arrangement: 1 = paratracheal parenchyma; 2 = apotracheal parenchyma.

types 1, 3 and 4, the proportion of species having contact ray and paratracheal parenchyma was highest in type 1 and decreased gradually from types 1 to 4, while the proportion of the combination of contact-isolation ray and apotracheal parenchyma increased from types 1 to 4 and was highest in type 4. This fact suggests that the form of tylosis blocking in heartwood vessels is closely related to the parenchyma pattern. Gums in heartwood (or in the inner portion in those species without heartwood) of species having gums exclusively or predominantly were divided into four types on the basis of their shapes and sizes in vessel lumina (Fig. 17). Type 1: partitions across the vessel lumina (Fig. 11). Type 2: irregular lumps on the inner vessel wall (Fig. 3). Type 3: small droplets on the vessel-parenchyma pits (Fig. 2). Type 4: thin layers lining the inner vessel wall (Fig. 12).

Table 3 shows the morphological types of gums and parenchyma pattern in those species having gums exclusively or predominantly. No distinct differences of gum types were found, not only between ring- and diffuse-porous woods but also among all the species. All types of gums were found in 4 species. Types 1, 2 and 3 were found in each of 12 out of the 15 species having gums. Although type 4 was found in 7 species, in Illicium religiosum and Cornus controversa only type 4 was found. In all four species having scalariform perforation plates, thin layers deposited between their bars were found (Fig. 13). The same types of gums were present in 6 species belonging to Prunus.

Out of the species having gums exclusively or predominantly, only one, Cornus controversa, had contact-isolation rays. Although each of types 1, 2 and 3 occurred in the species having two different parenchyma patterns (two combinations, contact ray and paratracheal parenchyma, and contact ray and apotracheal parenchyma), the proportion of those
within each type was not distinctly different among types. Type 4 occurred in the species having three different parenchyma patterns. This suggests that the morphological types of gums are not always related to the parenchyma pattern.

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References


