Lignification of ray parenchyma cells in the xylem of trees

Summary

The stem of many trees has sapwood (sW) and heartwood (hW). In most of the trees, ray parenchyma cells are involved in the formation of hW, which has a major effect on wood quality. In sW, ray parenchyma cells remain alive for several years at least, and play an important role in physiological activities. The hW is the non-living part of the stem and has no apparent physiological role. The transition zone (TZ) is the intermediate region between sW and hW. In the TZ, ray parenchyma cells are partially living and are responsible for the conversion of primary metabolites (fat and starch) to hW extractives. Transformation of sW to hW is a complex developmental biological process and an essential part of secondary growth.

The research about lignification procedure of ray parenchyma cells in softwood and hardwood supply integrated literature in lignification of ray parenchyma cells. In another hand, as known, hW extractives cause pitch problems in pulp and paper manufacture. Ray parenchyma cells play an important role in the formation of hW, especially in the conversion of primary metabolites (fat and starch) into hW extractives. The death and lignification of ray parenchyma cells are involved as the sign of hW formation. The research about the lignification of ray parenchyma cells from sW to hW may helpful to reveal the mechanism of hW formation. Therefore, it is important to clarify the lignification procedure of ray parecnchyma cells, which may helpful to improve the quality of wood in paper manufacture.

The lignification process from sW to hW in ray parenchyma cells of softwood (*Pinus densiflora*) and hardwood (*Phellodendron amurense*) has been analysed by means of microscopic and microchemical investigations in this research.

In some conifers such as *Pinus*, rays consist of ray tracheids and ray parenchyma cells. Ray tracheids are located predominantly at the upper and lower edges of individual rays, and ray parenchyma cells mainly in the middle regions in the case of *Pinus densiflora*. The lignification degree of ray parenchyma cells of softwood *Pinus densiflora* has been analysed by means of ultraviolet (UV) microscopy, acetyl bromide lignin determination, and time-of-flight secondary ion mass spectrometry (TOF-SIMS). The cell wall layers were localized by polarized optical microscopy (POM). POM revealed that ray parenchyma cells have almost no secondary wall in sW, and have only the outer layer of secondary wall (S_1) in the TZ and hW. UV microscopic observations indicated that the secondary wall of ray parenchyma cells, which are in contact with ray tracheids, begin to lignify in sW, while the secondary wall of ray parenchyma cells, which are not in contact with ray tracheids, are partially lignified in the TZ. The secondary wall of both types of ray parenchyma cells are completely lignified in hW. The acetyl bromide lignin content in sW is slightly lower than that in hW. In the TOF-SIMS measurements, the relative intensities of the secondary ions of guaiacyl-lignin in the rays in sW are significantly lower than those in hW. In summary, the conversion of sW to hW is accompanied by the proceeding of ray parenchyma cells secondary wall differentiation and lignification ending up in the cell death.

Moreover, the lignification of ray parenchyma cells in sW and hW of *Pinus densiflora* was investigated by thioacidolysis and subsequent Raney nickel desulphuration. Samples rich and less rich in ray parenchyma cells were prepared by laser microdissection (LMD). Whole sections burned randomly by the laser served as controls. Guaiacyl (G) monomers were detected in all samples, and *p*-hydroxyphenyl (H) monomers were detectable only in trace amounts, while syringyl (S) units were absent, as expectable in a softwood. In sW samples rich in ray parenchyma cells, the yields of G monomers are significantly lower than in other samples. Various types of G-G and one G-H dimers were detected, and the β-1′, β-5′, and 5-5′ type dimers were dominant. The relative distributions of lignin interunit linkages were very similar in all samples, regardless of the abundance of ray parenchyma cells in sW or hW tissues.

The morphology of rays is different between in softwood and in hardwood. In softwood, rays consist of ray parenchyma cells and ray tracheids, and usually are uniseriate rays. In hardwood, such as *Phellodendron amurense*, rays consist of ray parenchyma cells only, and usually are fusiform rays. It was reported that the position within a ray and neighboring short-lived vessel and fiber elements might affect the timing of cell death and differentiation of ray parenchyma cells. Therefore, positional information might be an important determinant of the control of cell death, differentiation and lignification of ray parenchyma cells in hardwoods, as is the case in conifers.

The lignification process of ray parenchyma cells of hardwood *Phellodendron amurense* were investigated by means of microchemical methods. Samples rich in ray

parenchyma cells were successfully prepared by means of LMD in contiguous annual rings containing sW, TZ, and hW. The samples were submitted to thioacidolysis. The thioacidolysis monomer analysis showed that the lignin content in ray parenchyma cells increases from annual ring 1 to 7, especially in the boundary of sW and hW. Moreover, ray parenchyma cells contain less lignin than fiber elements in the beginning of the sW. The S/G ratio in ray parenchyma cells obviously increase from sW to hW, while there is almost no difference in fiber elements.

Thus, lignification of ray parenchyma cells progressed form sW to hW, especially in the TZ in both softwood (*Pinus densiflora*) and hardwood (*Phellodendron amurense*) by means of microscopic and microchemical investigations.