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Ethylene evolution changes in the stems of *Metasequoia glyptostroboides* and *Aesculus turbinata* seedlings in relation to gravity-induced reaction wood formation

Received: 18 December 2002 / Accepted: 7 May 2003 / Published online: 21 June 2003
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Abstract Two-year-old *Metasequoia glyptostroboides* and 3-month-old *Aesculus turbinata* seedlings were tilted at a 45° angle to induce compression wood formation on the lower side of the former species and tension wood on the upper side of the latter. Two weeks later, the seedlings were tilted in an opposite direction at 45° so that the upper and lower sides changed to each other. This reverse tilting was kept for 7 weeks for *M. glyptostroboides* and 6 weeks for *A. turbinata*. The seedlings were sampled and analyzed at intervals throughout each experimental period so that an ethylene evolution kinetic was monitored. Ethylene evolution from the cambial region of the upper and lower sides of tilted stems was measured separately by gas chromatography with a flame ionization detector. Xylem production expressed as wood area during each experimental period was microscopically determined. In both tilting and reverse tilting periods, the rates of ethylene evolution from the lower side of *M. glyptostroboides* and the upper side of *A. turbinata*, where xylem production was accelerated and compression or tension wood formation was induced, had increased to high levels, whereas those from the opposite sides had either remained low (in tilting period) or rapidly recovered to low levels (in reverse tilting period). The cambial activity quantified by wood formation, including reaction wood, in both species showed the same tendency as ethylene evolution. The stem side with vigorous ethylene evolution, xylem development and reaction wood formation reversed with the reversal of tilting orientation. The roles of accelerated ethylene evolution in reaction wood formation in the tilted seedlings of gymnosperm and angiosperm trees are compared and discussed.

Keywords *Aesculus turbinata* · Cambial growth · Ethylene · Gravitropism · *Metasequoia glyptostroboides*

Introduction

Many investigations demonstrated that ethylene evolution in stems or branches of woody plants is enhanced by various kinds of physical stresses such as bending (Leopold et al. 1972; Brown and Leopold 1973; Robitaille and Leopold 1974; Robitaille 1975; Nelson and Hillis 1978; Blake et al. 1980), shaking (Telewski and Jaffe 1986; Rinne 1990; Telewski 1990) and stem reorientation (Yamamoto and Kozlovski 1987c; Little and Eklund 1999). These stresses often locally stimulate cambial activity and wood formation. For instance, even a slight change of gravity vector through plant axis by stem tilting can cause reaction wood formation in both conifers and woody angiosperms.

The reaction wood forming on the lower side of tilted stems of gymnosperms is called compression wood, which contains much lignin in comparison with normal and opposite wood; whereas the reaction wood forming on the upper side of tilted stems of angiosperm woody plants is called tension wood, which is characterized by unlignified gelatinous fibers (Zimmermann and Brown 1971; Timell 1986a). It has been suggested that ethylene produced by stem reorientation may have important roles in reaction wood formation (Brown and Leopold 1973; Nelson and Hillis 1978; Barker 1979). The evidence supporting this hypothesis for compression wood formation in conifers includes findings that ethylene evolution was greater from the lower sides of *Cupressus arizonica* branches (Blake et al. 1980) and the tilted stems of *Abies balsamea* (Little and Eklund 1999), where compression wood formed, than from the upper sides. Savidge et al. (1983) reported that 1-aminocyclopropane-1-carboxylic acid (ACC), a direct precursor of ethylene, was detected in the lower-side cambium where compression wood formation occurred but not in the cambium on the opposite side in *Pinus contorta* branches. In addition, in

This work was presented at the 5th Pacific Region Wood Anatomy Conference, Yogyakarta, Indonesia, 9–14 September 2002

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vertical *A. balsamea* stems ringed with *N*-1-naphthylphthalamic acid (NPA), an inhibitor of indole-3-acetic acid (IAA) transport, both tracheid production and ethylene evolution were stimulated at and above the application point, where compression wood formation was induced (Little and Eklund 1999).

Very little evidence from tension wood formation in woody angiosperms supports the aforesaid hypothesis. Nelson and Hillis (1978) reported that more ethylene emanated from the upper sides of longitudinally bisected stems in leaning *Eucalyptus gomphocephala* stems. In contrast, Robitaille (1975) found higher ethylene concentrations on the lower side than on the upper side of horizontally oriented *Malus domestica* shoots. Yamamoto and Kozłowski (1987c) also reported that there was no significant difference in ethylene evolution between the upper side and the lower side of tilted *Acer platanoides* seedlings.

The application of 2-chloroethylphosphonic acid, named Ethrel or Ethephon, an ethylene-generating compound, to stems also increases wood formation in conifers (Barker 1979; Telewski et al 1983; Yamamoto and Kozłowski 1987a, 1987b; Ekund and Little 1995, 1996) and in woody angiosperms (Yamamoto et al. 1987; Yamamoto and Kozłowski 1987c). However, the anatomical characteristics of increased xylem tissue by Ethrel application were different from those of compression wood in *P. taeda* (Telewski et al. 1983), *P. halepensis* (Yamamoto and Kozłowski 1987a), *P. densiflora* (Yamamoto and Kozłowski 1987b), and *A. balsamea* (Eklund and Little 1996), and of tension wood in *Acer platanoides* (Yamamoto and Kozłowski 1987c), and *Ulmus americana* (Yamamoto et al 1987). When applied to tilted stems, Ethrel even blocked the development of certain characteristics of compression wood in *P. densiflora* (Yamamoto and Kozłowski 1987b) and tension wood in *A. platanoides* (Yamamoto and Kozłowski 1987c). Therefore, the regulatory roles of ethylene in the formation of compression and tension wood are still not fully understood.

With the foregoing considerations in mind, comparative measurements of ethylene evolution from stems were performed on two species of tree, *Metasequoia glyptostroboides*, a gymnosperm, and *Aesculus turbinata*, an angiosperm. A primary objective was to compare the responses of ethylene evolution from the cambial region of these seedlings to the induction of reaction wood formation by stem reorientation. The roles of ethylene in both compression and tension wood formation are discussed.

Materials and methods

Plant materials

One-year-old *Metasequoia glyptostroboides* Hu et Cheng seedlings grown in pots were purchased from a garden center in Sho-oh town, Okayama prefecture in March 2000, transplanted into plastic pots (18.5×14.5 cm) containing sand and compost (2/1, v/v) and grown in the greenhouse of Tottori University for 1 more year. On 8 June 2001, 50 2-year-old seedlings were selected for uniformity of size and development at the beginning of the experiment. The average heights and stem diameters at 2.5 cm above the ground were 57.8 cm and 8.2 mm, respectively.

Aesculus turbinata Bl. seedlings were grown from seeds sown in March 2001, in plastic pots (18.5×14.5 cm) in the greenhouse of Tottori University. On 26 July 2001, 40 3-month-old seedlings were selected for uniformity of size and development at the beginning of the experiment. The average heights and stem diameters at 2.5 cm above the ground were 33.2 cm and 6.8 mm, respectively.

Tilting treatments and samplings

The *M. glyptostroboides* seedlings and the *A. turbinata* seedlings were divided into 10 and 8 groups, respectively. Groups of each species consisted of five seedlings. One group of each species was immediately harvested for the determination of the rate of ethylene evolution from stems just before tilting. The remaining seedlings were tilted at a 45° angle to the horizontal to induce gravitational stress on the cambial region of stems (Fig. 1). One group of tilted seedlings of each species was selected for anatomical investigation of the xylem formed during the experimental period. To identify the amount of xylem produced prior to and during the treatment, pin-markings were made on the stems of those seedlings with an insect-

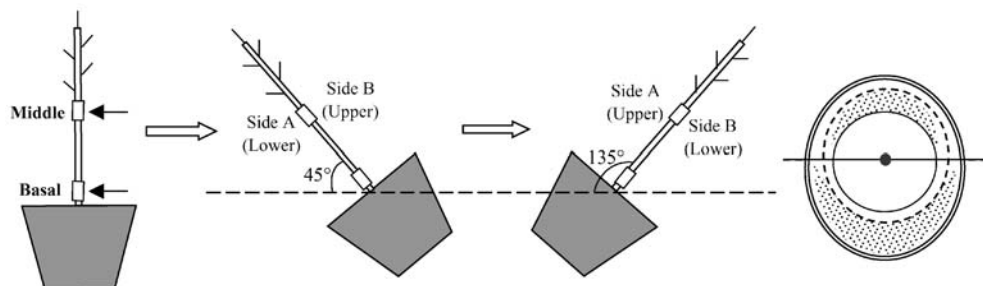


Fig. 1 Schematic drawings illustrating how the seedlings were tilted and reverse tilted, where the basal and middle segments were taken for measurements of cambial region ethylene evolution (rectangles), where the pin-marks and transverse sections were made for anatomical observations (narrow solid arrows), and how the microscopic measurements were carried out. The transverse section (right drawing) was divided into sides A and B by a pith-

passing horizontal line. Solid and dashed single circles represent the beginning of tilting and reverse tilting treatments, respectively, which were identified by pin-marks. Areas of newly formed xylem tissues before and after the reverse tilting in both sides were measured microscopically according to the demarcation circles and line. Stippled areas show reaction wood formation

mounting needle (0.3 mm in diameter) according to the method of Wolter (1968). The pin-marked positions were at 3 and 30 cm above the ground level for the *M. glyptostroboides* seedlings and at 3 and 15 cm for the *A. turbinata* seedlings. Those positions are denoted as basal point and middle point in Fig. 1.

The seedlings of other groups of each species were sampled for ethylene determination. During the first 2 weeks, three groups of seedlings were sampled one by one at 4, 7, and 14 days for *M. glyptostroboides* and two groups were sampled at 7 and 14 days for *A. turbinata*.

At 14 days after stress initiation, the seedlings of the remaining groups, including those for anatomical investigations, were tilted in an opposite direction at 45° so that the upper and lower sides changed relative to each other. This reverse tilting was kept for 7 weeks for *M. glyptostroboides* and 6 weeks for *A. turbinata* (Fig. 1). The seedlings for anatomical investigation were pin-marked again just before the reversal at the same heights as the first time, but on different points on the circumferences. Then the seedlings for ethylene determination were sampled group by group at 4, 7, 14, 28, and 49 days after reverse tilting for *M. glyptostroboides*, and at 7, 14, 28, and 42 days for *A. turbinata*. For each species, the group for anatomical investigation was sampled simultaneously with the last sampling for ethylene determination.

Ethylene determination

Ethylene evolution in both species was measured for bark segments located at the basal and middle portions of stems, corresponding to the pin-marked portions of the seedlings for anatomical investigation (Fig. 1). Four-centimeter-long stem segments taken from both portions were bisected longitudinally into upper and lower halves in tilted seedlings and randomly chosen halves in untilted seedlings. As cambium was reported to be the major source of endogenous ethylene production in stems (Yamanaka 1985; Eklund and Little 1998), about 4 cm² (1×4 cm) bark segments including the cambial region were obtained from the bisected stem segments with knives and a pair of forceps for determining ethylene evolution. The outer epidermis of the bark segments was removed using a pair of fine-nosed forceps. Thus, the bark segments contained cambium, differentiating xylem, and differentiating and mature phloem.

Each bark segment was placed in a 5 ml glass vial immediately after excision, sealed with a rubber stopper and incubated at 30°C in an incubator (Sanyo MIR-152) for 2 h for *M. glyptostroboides* samples and 1 h for *A. turbinata* samples. Several references (Yamanaka 1985, 1986; Eklund and Little 1998) and our preliminary experiments confirm that wound-induced ethylene is limited within these incubation periods. After incubation, a 1 ml air sample was drawn from the head space of each vial with a gas-tight syringe and injected into a gas chromatograph (Hitachi 263-50, Hitachi, Japan) with a flame ionization detector and a spiral glass column (0.35×200 cm) packed with 60/80 mesh activated alumina. Chromatographic conditions were as follows: column, injector, and detector temperatures were 80°C, 120°C, and 120°C, respectively; carrier gas (He), 35 ml min⁻¹. Ethylene concentration was calculated on the basis of surface area of cambial region by reference to the chromatographic data of a 10.6 mg l⁻¹ nitrogen-balanced ethylene standard (Sanso, Japan). The sample volume was measured and subtracted from the vial volume, and the surface area of cambium was determined soon afterwards.

Anatomical investigation

At the end of both experiments, stem segments containing the pin-marked portions of the seedlings were taken for anatomical investigation and fixed in 70% ethanol. Transverse sections (10–15 µm) were made at the reference points with sliding microtome. The sections were stained with safranin and fast green solution, and mounted in Eukitt. For each section, the areas of newly formed xylem tissues in the upper and lower sides produced before and

after stem reorientation were measured separately with a light microscope (Olympus BHS 323) in combination with a video micrometer (Olympus Flovel VM-31, Flovel, Japan).

Statistical analysis

Analysis of variance was applied to each data set, and the multiple comparisons among mean values were performed using Duncan's test.

Results

At the beginning of the experiment for *M. glyptostroboides*, ethylene evolution from the cambial region was around 3.5 nmol cm⁻² h⁻¹, and no significant difference was observed between the bisected counterparts or the two sampling heights (Fig. 2, upper). However, at 4 days after tilting, the lower side of stems (side A) indicated higher rates of ethylene evolution than that of the upper side (side B), with a more significant difference in the basal portions of stems. Ethylene evolution from the lower side gradually increased over 14 days, whereas little change was observed in the upper side. The lower-upper ratios (side A / side B) of ethylene evolution also showed an increasing trend throughout this period. The ratios in basal stem portions were constantly greater than those in middle portions, except at the beginning of the experiment (Fig. 2, lower).

After the seedlings were reverse tilted, ethylene evolution from side A, the former lower side, decreased rapidly, while that from the side B, the new lower side, gradually increased. The lower-upper ratios (side B / side A) of ethylene evolution reached about 1.0 within 4 days after stem reorientation, with a rapid recovery in the basal stem portion. At 14 days after stem reorientation, the ethylene evolution from the new lower side (side B) of both basal and middle stem portions reached to almost the same levels as the corresponding levels of the former lower sides (side A) before stem reorientation. For the lower side of the middle portion, ethylene evolution rate peaked at 28 days after stem reorientation, whereas the basal portion had not shown an ethylene evolution peak by the end of the treatment. However, the lower-upper ratio of ethylene evolution in the basal portion decreased at 49 days after stem reorientation.

The dynamics of ethylene evolution in the experiment of the *A. turbinata* seedlings was similar to that of the *M. glyptostroboides* seedlings; however, greater ethylene evolution was constantly detected in the upper side of tilted stems of this species but not in the lower side (Fig. 3). Accordingly, the upper-lower ratios of ethylene evolution calculated in this experiment corresponded to the lower-upper ratios in the experiment on *M. glyptostroboides* seedlings. After 14 days tilting, ethylene evolution from the upper side rapidly increased in both basal and middle portions, while the upper-lower ratios substantially increased. After the seedlings were reverse tilted, however, both the increase in ethylene evolution of

Fig. 2 Ethylene evolution rates from lower- and upper-side cambial region of tilted stems and the lower-upper ratios throughout the tilting and reverse tilting period in *M. glyptostroboides*. Data points (or columns) and error bars in this and subsequent figures represent means and standard errors, respectively ($n=5$). Means accompanied by common letters in this and subsequent figures are not significantly different at $P < 0.05$

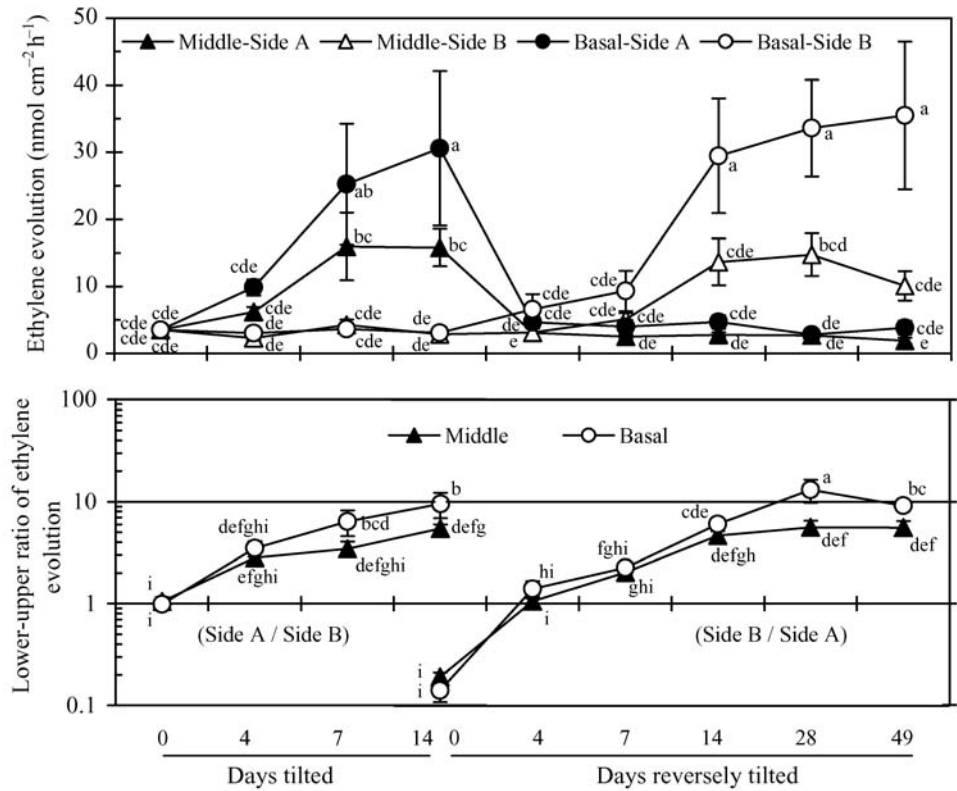
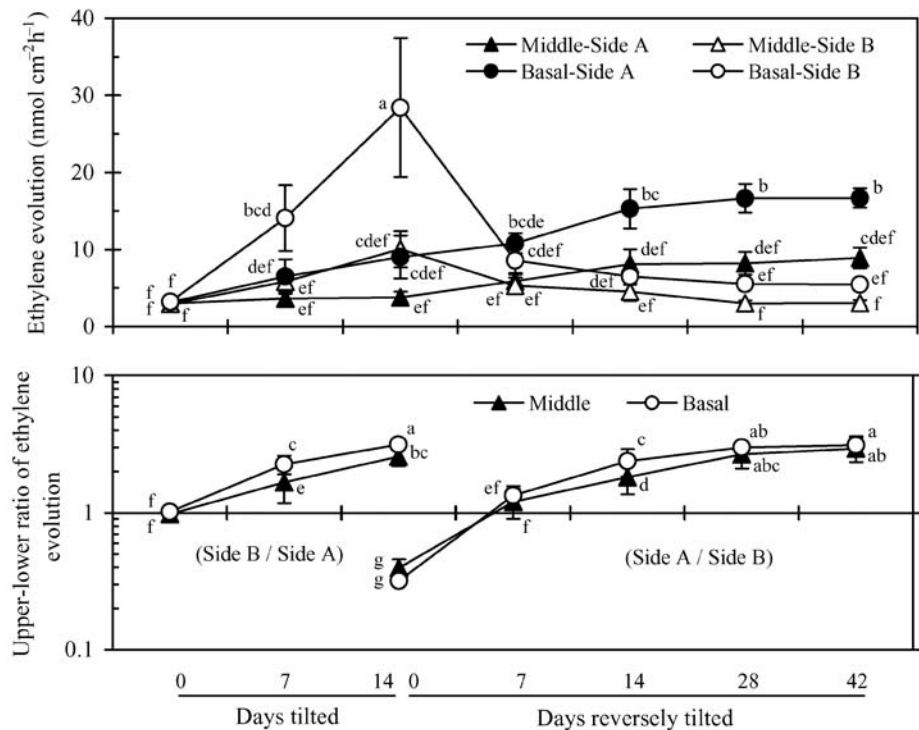


Fig. 3 Ethylene evolution rates from lower- and upper-side cambial region of tilted stems and the upper-lower ratios throughout the tilting and reverse tilting period in *A. turbinata*



the new upper side and the decrease of the new lower side were relatively gradual. The maximum rates of ethylene evolution from both portions were determined at 42 days after stem reorientation. Nevertheless, at 28 days of

reverse tilting, the upper-lower ratios had already recovered to the levels close to those before the reorientation.

In both species, upward bending of the tilted stems occurred first in shoot apices and proceeded basipetally.

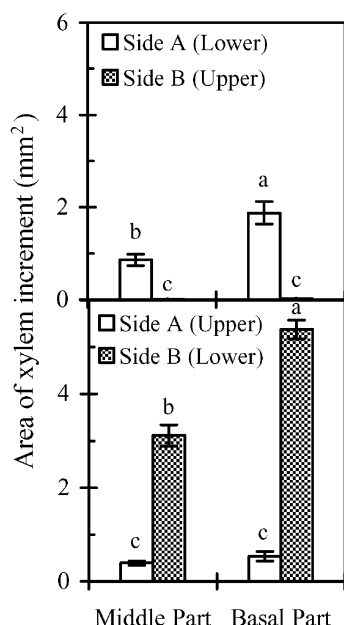


Fig. 4 Areas of xylem increment before (*top*) and after (*bottom*) reverse tilting in both sides in *M. glyptostroboides*

At the end of both experimental periods, the top half of each stem had almost become vertical, whereas the basal stem portions were still leaning. The anatomical observations of transverse stem sections revealed that in both the middle and basal stem portions compression and tension wood had formed in *M. glyptostroboides* and *A. turbinata* seedlings, respectively. In both species, xylem production was promoted on the side of reaction wood formation, with a basipetal increase in the degree of eccentricity in the form of the transverse sections (Figs. 4, 5).

Discussion

Tilting of seedlings not only induced eccentric radial growth and reaction wood formation, but also accelerated ethylene evolution by the cambial region that differentiates reaction wood (compression wood on the lower side of *M. glyptostroboides* and tension wood on the upper side of *A. turbinata*). These results are consistent with the previous reports that ethylene evolution was positively correlated with cambial activity in gymnosperms (Telewski and Jaffe 1986; Yamamoto and Kozłowski 1987a, 1987b; Eklund 1990, 1991, 1993; Ingemarsson et al. 1991; Eklund and Little 1995, 1996; Little and Pharis 1995; Eklund and Tiltu 1999). They also support to some extent the suggestion that ethylene plays a role in compression wood formation (Little and Eklund 1999; Eklund and Klintborg 2000).

It is commonly accepted that compression wood formation and eccentric radial growth are not causally related, although they typically occur together (Timell

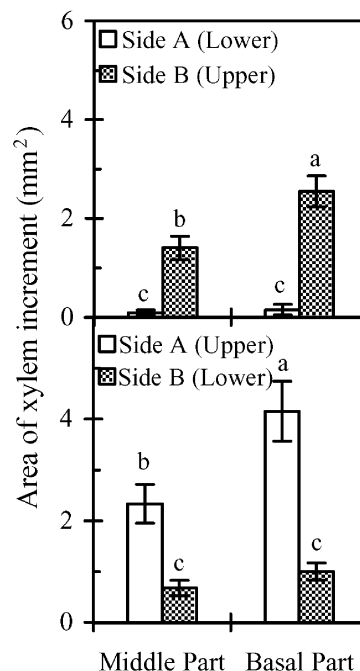


Fig. 5 Areas of xylem increment before (*top*) and after (*bottom*) reverse tilting in both sides in *A. turbinata*

1986b; Little and Eklund 1999). A postulated role for ethylene in compression wood formation was supported by the observation that tracheid production was greater in the basal segment than in the apical segment in the lower side of tilted *Abies balsamea* seedlings but there was no difference in ethylene evolution, i.e. tracheid production and ethylene evolution were not related (Little and Eklund 1999). However, the data presented here with *M. glyptostroboides* showed that both the ethylene evolution rate from the lower side and the lower-upper ratio of ethylene evolution in tilted stems were higher in basal than in middle parts (Fig. 2), coinciding with the difference in total tracheid production (Fig. 4). In addition, reports on ethylene evolution or effects of applications of ethylene-releasing compounds in coniferous species are more often correlated with increased cambial activity, such as increases in bark thickness and tracheid production, no matter whether compression wood forms or not (Brown and Leopold 1973; Barker 1979; Telewski et al. 1983; Telewski and Jaffe 1986; Yamamoto and Kozłowski 1987a, 1987b; Little and Pharis 1995; Eklund and Little 1996, 1998). Therefore, the evidence for a causal relationship between increased ethylene evolution and compression wood formation is still not proven.

The investigations on tension wood formation in woody angiosperms in relation to ethylene have been relatively few. Corresponding to the results from gymnosperms, ethylene evolution by bisected stems of tilted *A. turbinata* seedlings was also positively correlated with xylem development (Figs. 3, 5), partially supporting the suggestion that ethylene plays a role in tension wood

formation (Nelson and Hillis 1978). However, as in the case of gymnosperms, whether the increased ethylene evolution was related to tension wood formation itself or to the entirety of accelerated xylem production is as yet indeterminable. Moreover, the results from exogenous ethylene application rejected a probable role for this hormone in tension wood formation, as applied Ethrel blocked the formation of tension wood in tilted *Acer platanoides* stems though the total wood formation was increased (Yamamoto and Kozlowski 1987c).

Auxin has long been recognized as a main factor in regulating the formation of both compression and tension wood. It is generally agreed that whereas compression wood is associated with an excessively high level of auxin, formation of tension wood is induced by a deficiency of auxin, and both kinds of reaction wood could be induced in upright stems by administration of auxin-related chemicals locally (Timell 1986b). Savidge et al. (1983) observed that exogenous ACC together with IAA was more effective than IAA alone in causing formation of compression wood in defoliated *P. contorta* seedlings, suggesting that ethylene might interact with IAA in tracheid differentiation. The possible involvement of ethylene in the regulation of compression wood formation was further interpreted as a factor inducing increase either in IAA level or in sensitivity to IAA (Little and Eklund 1999). In brief, both auxin and ethylene are positively correlated with cambial growth, including the formation of compression wood in conifers. In the case of woody dicotyledons, however, the results turned out to be unexpected in that cambial growth and ethylene evolution were promoted while auxin level was supposed to be decreased on the upper side of tilted stems where tension wood formation was induced.

The interactions between ethylene and auxin seem to be complicated and of great importance to wood formation. Investigations to date showed that these two hormones could regulate each other's activities and levels (Abeles et al. 1992). It has been hypothesized that ethylene application inhibits the capacity of basipetal IAA transport, resulting in a local accumulation of IAA that stimulate the development of xylem (Burg and Burg 1967; Wood 1985; Suttle 1988; Abeles et al. 1992; Lomax et al. 1995; Eklund and Little 1996, 2000). Auxin also has an effect on promoting ethylene biosynthesis (Abeles et al. 1992). Hence, it is not known whether the elevated rate of ethylene evolution in one side of a tilted stem regulates the level of auxin or vice versa.

The present experiments showed a positive correlation between ethylene evolution and xylem production in both softwood and hardwood species. During the reverse tilting period of *A. turbinata* seedlings in the present experiment, ethylene evolution in the upper side samples was generally not as high as that before the reversal (Fig. 3), probably reflecting a gradually slowing of radial growth during this period (August and September). Compared with the data of lower-upper ratios in *M. glyptostroboides*, the upper-lower ratios of ethylene evolution in *A. turbinata* were as a whole lower and corresponded to a

relatively low eccentricity in radial growth (Figs. 4, 5). It can be concluded that ethylene evolution from cambial region is closely correlated with the stem displacement and consequent changes in wood formation. There may be a role for ethylene in the formation of compression or tension wood, but it remains to be determined whether the enhanced ethylene evolution is related to reaction wood formation per se or the entirety of accelerated xylem production.

Acknowledgements This research was supported by a Grant-in-Aid for Scientific Research (B) (No. 12460070) from the Ministry of Education, Culture, Science and Technology, Japan.

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