博士論文

Studies on transpiration characteristic of teak plantation in northern Thailand based on sap flow measurements

（樹液流計測に基づく，タイ北部チーク林の蒸散特性に関する研究）

佐藤　貴紀

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Chapter 1

Introduction

1.1 Significance of assessing the energy, water, and carbon cycles in tropical forests

Tropical forests are an important latent energy source and a driving force of atmospheric general circulation, and this latent energy has a strong influence on both regional and global climate (Lean and Warrillow, 1898; Kanae et al., 2001; Mabuchi and Sato, 2005a, b; van der Molen et al., 2006). Zhang et al. (1996a, b) reported decreasing rainfall in tropical forests in the Amazon, Africa, and Asia using numerical simulations in which the tropical forests were converted to grassland and observed a greater decrease in the Amazon and Africa than in Asia. In recent years, various studies have revealed the impact of Asian tropical forests on global and regional climate (Kanae et al., 2001; Mabuchi and Sato, 2005a, b; van der Molen et al., 2006). The deforested area was greater in the Amazon and Africa than in Asia, and the relative rate of tropical deforestation was higher in Asia than in the Amazon or Africa (Food and Agriculture Organization, 1993, 2001; Laurence, 1999). Kanae et al. (2001) reported the actual precipitation change in Southeast Asia based on meteorological station data. A long-term decrease in precipitation over the period 1960-1998 was found in tropical Asia (Malhi and Wright, 2004). A significant decrease in precipitation was also observed for the month of September over Thailand between 1960 and 1994 (Kanae et al., 2001). According to these studies, tropical forests in Asia also play a significant role in global and regional climate.

Several field studies have investigated the energy, water, and carbon exchange between the vegetation and atmosphere in Amazonian tropical rain forests. Recently, studies have been conducted in the tropical forests of Southeast Asia. These forests can be categorized into two types according to rainfall seasonality and topography: tropical rainforest and tropical monsoon forest (Tanaka et al., 2008). Tropical rainforests are distributed near the equator and tropical monsoon forests are affected by the annual cycle of the Asian monsoon. Tropical monsoon forests can be further divided into evergreen and deciduous forests. Field studies that have investigated the exchange of energy, water, and carbon between vegetation and the atmosphere have mainly been conducted in tropical rainforests (Kumagai et al, 2004, Ohkubo et al., 2008; Takanashi et al., 2010) and tropical evergreen forests (Tanaka et al., 2004); few studies have explored tropical deciduous forests (Igarashi 2013; Tanaka et al., 2011; Yoshifuji et al., 2006, 2011, 2014).

Tropical deciduous forests in particular are affected by the Asia monsoon and retain leaves on the canopy during the wet season (April-October) that fall in the dry season (January-March and November-December). In deciduous forest, the energy, water, and carbon exchange between the vegetation and atmosphere are strongly affected by the vegetation phenology, such as leaf out and leaf fall (Maass et al., 1995; Wilson and Baldocchi, 2000; Barr et al., 2004). Previous studies on tropical deciduous forest stands in Southeast Asia revealed an inter-annual variation in the canopy duration and transpiration period according to the inter-annual variation in rainfall seasonality. The variation in canopy duration and the transpiration period spanned around 40 and 60 days, respectively (Yoshifuji et al., 2006). In contrast, the inter-annual variation in canopy duration was reported to be about 10 days in temperate deciduous forests (White et al., 1999; Black et al., 2000; Wilson and Baldocchi, 2000; Barr et al., 2004). Such a large inter-annual variation in canopy duration and transpiration period is possibly strongly affected by differences in the energy, water, and carbon exchange in tropical deciduous forests compared to temperate deciduous forests (Yoshifuji et al., 2006; Igarashi, 2013).

The leaf phenology in tropical deciduous forests is regulated by soil moisture conditions (Reich and Borchert, 1982, 1984; Borchert, 2002), and previous studies have revealed large interspecific and intraspecific variations in the leaf phenology among individual trees (Lieberman, 1982; Lieberman and Lieberman, 1984; Sayer and Newbery, 2003; Elliott et al., 2006). The leaf phenology strongly affected the transpiration and photosynthesis period. Thus, understanding the transpiration characteristics at the individual tree scale is important to determine the energy, water, and carbon exchange between the vegetation and atmosphere in tropical deciduous forests.

1.2 Methods for examining the evapotranspiration from forests

Various types of measurement techniques have been used to quantify evapotranspiration. The most common of these include the use of a porometer, catchment water balance, eddy covariance, and sap flow measurements. The porometer is able to determine the evapotranspiration at the leaf scale, but to convert from the individual leaf scale to tree scale, one must consider the spatial variability in the gas exchange factor (e.g., due to photosynthesis) (Miyazawa et al., 2011).

The catchment balance method is able to reveal the long-term trend in the evapotranspiration using runoff and rainfall data. Previous studies have revealed a change in the amount of evapotranspiration according to changes at the forest level (e.g., thinning or changing the tree species) (Swank and Douglass, 1974; Langford, 1976; Hornbeck et al., 1993; Murakami et al., 2000; Vertessy et al., 2001), and other studies have determined the seasonality in the transpiration from forests using the short-time period water budget method (Suzuki, 1985; Iida et al., 2006). However, the catchment balance method is not able to determine the transpiration at the hourly or diurnal scale. Eddy covariance method is able to reveal the energy, water and carbon exchange between vegetation and atmosphere in hourly to daily scale. Moreover the long-term observation is able to reveal the seasonality of evapotranspiration from forests (e.g., Kumagai et al., 2004).

Sap flow measurements are able to reveal the individual tree scale transpiration using the sap flow sensors inserted into the tree trunk. The unit of obtained data is minute or hourly, and the long term sap flow measurements are revealed the transpiration seasonality. Previous studies have proposed that the method of estimated whole-tree water use (Phillips et al., 1996; James et al., 2002; Delzon et al., 2004; Kumagai et al., 2005, 2007), and scale up from individual tree to stand scale (Hatton et al., 1995; Vertessy et al., 1995; Meinzer et al., 2001; Pataki and Oren, 2003; Čermak et al., 2004; Kumagai et al., 2005; Chang et al., 2006). Taking advantage of the fine spatial and times scale provided by data from sap flow measurements, previous studies demonstrated the effects of forest management (e.g., thinning) to transpiration at the individual tree and plot scale (Morikawa et al., 1986; Bréda et al., 1995; Lagergren et al., 2008; Forrester et al., 2012), and the relationship between forest transpiration and leaf phenology (Meinzer et al., 1999; Pataki et al., 2000; Iida et al., 2013).

1.3 Significance of examining the transpiration from teak plantations and problems in applying sap flow measurements to teak

This study was conducted in a teak (*Tectona grandis* Linn.f.) plantation in northern Thailand. Teak is one of the major tree species planted in tropical regions such as Southeast Asia, the Indian Subcontinent, Central America and Africa (Krishnapillay, 2000). The simple species components and forest structure of a plantation are advantageous for evaluating the energy, water, and carbon exchange between the atmosphere and forest, and the area of land under teak plantations is increasing because of its high commercial value (Kollert and Cherubini, 2012). Teak also has a high potential for carbon storage and biomass production (Kraenzel et al., 2003; Dié et al., 2012). Previous studies have investigated the seasonal change in wood formation (Rao and Rajput, 1999; Priya and Bhat, 1999), and both above and belowground biomass (Singh and Srivastava, 1985; Srivastava et al., 1986; Purwanto and Oohata, 2002) in teak plantations. However, few studies have investigated the transpiration seasonality in teak plantations (Yoshifuji et al., 2006, 2011, 2014; Tanaka et al., 2011; Igarashi, 2013), and there were no studies focusing on the individual tree and plot scale.

In this study, we used the thermal dissipation method (TDM; Granier, 1987) to measure sap flow. The TDM has mainly been applied to coniferous species to estimate water use at both tree and plot scales (Kumagai et al., 2005; Tsuruta et al., 2010; Kume et al., 2011). This method uses Graneir-type sap flow sensors, and is both inexpensive and relatively simple to use, making it a useful tool for measuring sap flow in a large number of trees. However, no previous studies have applied the TDM to teak, a ring-porous species growing in tropical climates. For such species in temperate climates, whole-tree water use has traditionally been underestimated compared to actual water use (Taneda and Sperry, 2008; Bush et al., 2010). This is because the water transport function of large-diameter earlywood vessels is restricted to the outermost annual ring, and these vessels lose their water transport function after 2 years (Umebayashi et al., 2008; Sato et al., 2010). However, the sap flow distribution in teak trunk is not revealed. The information about sap flow distribution in teak trunk is important to apply the sap flow measurement. Moreover there are no studies to estimate whole-tree and plot scale water use in teak using the sap flow measurement established mainly for coniferous species.

1.4 Objectives

The objective of this study was to determine the transpiration seasonality in teak plantation stands in northern Thailand based on sap flow measurements.

Objective in Chapter 2 is to provide an outline of the two study sites; Japanese cedar and Japanese cypress plantation in Kanagawa prefecture, Japan, and teak plantation in northern Thailand. Sap flow measurements were conducted in each study site. In Japanese cedar and Japanese cypress plantation, sap flow measurements were conducted on the steep slope. In teak plantation, meteorological, soil water content, and leaf amount measurements were also conducted. In teak plantation, the sap flow measurements were conducted in two plots at the study site. The differences in soil moisture condition seasonality and leaf penology between the plots is described based on the measurements of soil moisture content and leaf amount at each plot.

Objective in Chapter 3 is to show the adaptation of the TDM for Japanese cedar and Japanese cypress. Japanese cedar and Japanese cypress are coniferous trees which have tracheid, and previous studies have applied the TDM to such species. However, no previous studies have used the TDM to measure sap flow in teak. Thus, we first confirmed that the TDM can be used for Japanese cedar and Japanese cypress, after which we applied the TDM to teak, a ring-porous deciduous species that grows in tropical climates. A lot of previous studies adopted the TDM for coniferous species to estimate whole-tree water use. However, few previous studies indicated that the circumferential variation of sap flow in the tree trunk affected to estimate whole-tree water use (Tateishi et al., 2008; Tsuruta et al., 2010). According to this background, the circumferential variation in sap flow in Japanese cedar and cypress was revealed using sap flow measurements. And the effect of the circumferential variation of sap flow on estimating while-tree water use was discussed.

Objective in Chapter 4 is to discuss the radial distribution of sap flow and the testing the applicability of sap flow measurement to teaks using dye perfusion experiments, absorption experiments, and sap flow measurements in mature teaks. The effects of sap flow distribution in the trunks of teak on the sap flow measurements are also discussed.

Objective in Chapter 5 is to describe difference in the transpiration seasonality in the teak plantation in the leaf-fall period estimated from both sap flow measurements and the eddy covariance method. A comparison of the transpiration seasonality obtained using the two methods revealed that sap flow measurements provide a useful tool for examining the transpiration seasonality in teak plantations.

Objective in Chapter 6 is to discuss the sap flow seasonality in individual teak trees. Sap flow measurements were conducted in two plots that differ in the seasonality of the soil moisture content to observe the effects of the soil moisture content seasonality on the sap flow seasonality in individual teak trees.

This study is concluded in chapter 7.

References

Barr, A. G., Black, T. A., Hogg, E. H., Kljun, N., Morgenstern, K., & Nesic, Z. (2004) Inter-annual variability in the leaf area index of a boreal aspen-hazelnut forest in relation to net ecosystem production. *Agricultural and Forest Meteorology*, 126, 237-255. doi: 10.1016/j.agrformet.2004.06.011

Black, T. A., Chen, W. J. Barr, A. G., Arain, M. A., Chen, Z., Nesic, Z., Hogg, E. H., Neumann, H. H., & Yang, P. C. (2000) Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. *Geophysical Research Letters*, 27, 1271-1274. doi: 10.1029/1999GL011234

Borchert, R., Rivera, G., & Hagnauer, W. (2002) Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain. *Biotropica*, 34, 27-39. doi: 10.1111/j.1744-7429.2002.tb00239.x

Bréda, N., Granier, A., & Aussenac, G. (1995) Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). *Tree Physiology*, 15, 295-306. doi: 10.1093/treephys/15.5.295

Bush, S.E., Hultine, K.R., Sperry, J.S., & Ehleringer, J.R. (2010) Calibration of thermal dissipation sap flow probes for ring- and diffuse-porous trees. *Tree Physiology*, 30, 1545-1554. doi: 10.1093/treephys/tpq096

Čermák, J., Kućera, J. & Nadezhdina, N. (2004) Sap flow measurements with thermodynamic methods, flow integration within trees and scaling up from sample trees to entire forest stand. *Trees*, 18, 529-546. doi: 10.1007/s00468-004-0339-6

Chang, X., Zhao, W., Zhang, Z., & Su, Y. (2006) Sap flow and tree conductance of shelter-belt in arid region of China. *Agricultural and Forest Meteorology*, 138, 132-141. doi: 10.1016/j.agrformet.2006.04.003

Clearwater, M. J., Meinzer, F. C., Andrade, J. L., Goldstein, G., & Holbrook, N. M. (1999) Potential errors in measurement of nonuniform sap flow using heat dissipation probes. *Tree Physiology*, 19, 681-687 doi: 10.1093/treephys/19.10.681

Coder, K. D. (2011) Tree-ring porosity forms in hardwoods. University of Georgia school of forest resources extension publication for99-018. WEB Site = http://warnell.forestry.uga.edu/service/library/for99-018/for99-018.pdf.

Delzon, S., Sartore, M., Granier, A., & Loustau, D. (2004) Radial profiles of sap flow with increasing tree size in maritime pine. *Tree Physiology*, 24, 1285-1293. doi: 10.1093/treephys/24.11.1285

Dié, A., Kitin, P., Kouamé, F. N' G., Bulcke, J. V. d., Acker J. V., & Beeckman, H. (2012) Fluctuations of cambial activity in relation to precipitation result in annual rings and intra-annual growth zones of xylem and phloem in teak (Tectona grandis) in Ivory Coast. *Annals of Botany*, 110, 861-873. doi: 10.1093/aob/mcs145

Elliott, S., Baker, P. J., & Borchert, R. (2006) Leaf flushing during the dry season: the paradox of Asian monsoon forests. *Global Ecology and Biogeography*, 15, 248-257. doi: 10.1111/j.1466-822x.2006.00213.x

Food and Agriculture Organization. (1993) Forest resources assessment 1990 - Tropical countries. FAO Forestry Paper 112, Rome.

Food and Agriculture Organization. (2001) Global Forest Resources Assessment 2000 - main report. FAO Forestry Paper 140, Rome.

Forrester, D. I., Collopy, J. J., Beadle, C. L., Warren, C. R., & Baker, T. G. (2012) Effect of thinning, pruning and nitrogen fertiliser application on transpiration, photosynthesis and water-use efficiency in a young Eucalyptus nitens plantation. *Forest Ecology and Management*, 266, 286-300. doi: 10.1016/j.foreco.2011.11.019

Granier, A. (1987) Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements.

Tree Physiology, 3, 309-320. doi: 10.1093/treephys/3.4.309

Hatton, T. J., Moore, S. J., & Reece, P. H. (1995) Estimating stand transpiration in a *Eucalyptus populnea* woodland with the heat pulse method: measurement errors and sampling strategies. *Tree Physiology*, 15, 219-227. doi: 10.1093/treephys/15.4.219

Hornbeck, J. W., Adams, M. B., Corbett, E. S., Verry, E. S., & Lynch, J. A. (1993) Long-term impacts of forest treatments on water yield: a summary for northeastern USA. *Journal of Hydrology*, 150, 323-344. doi: 10.1016/0022-1694(93)90115-P

Igarashi, Y. (2013) Studies on heat, water and carbon exchanges between atmosphere and forest at a tropical deciduous forest in Northern Thailand. PhD Thesis, University of Tokyo, Tokyo, Japan.

Iida, S., Nakatani, S., & Tanaka, T. (2006) Evaluation of transpiration from a natural deciduous boreal-leaved forest located at a headwater catchment based on measurement of sap flux density. *Journal of Japan Society of Hydrology and Water Resource*, 19, 7-16. doi: 10.3178/jjshwr.19.7 (in Japanese with English abstract)

Iida, S., Ito, E., Shimizu, A., Nobuhiro, T., Shimizu, T., Kabeya, N., Tamai, K., Araki, M., Chann, S., & Keth, N. (2013) Year-to-year differences in sap flow and crown-level stomatal conductance of two species in a lowland evergreen forest, central Cambodia. *Japan Agricultural Research Quarterly*, 47, 319:327. doi: 10.6090/jarq.47.319

James, S. A., Clearwater, M. J., Meinzer, F. C., & Goldstein, G. (2002) Heat dissipation sensors of variable length for the measurement of sap flow in trees with deep sapwood. *Tree Physiology*, 22, 277-283. doi: 10.1093/treephys/22.4.277

Kanae, S., Oki, T., & Musiake, K. (2001) Impact of deforestation on regional precipitation over the Indochina Peninsula. *Journal of Hydrometeorology*, 2, 51-70. doi: 10.1175/1525-7541(2001)002<0051:IODORP>2.0.CO;2

Kollert, W., & Cherubini, L. (2012) Planted Forests and Trees Working Paper Series; Teak resources and Market assessment 2010 (*Tectona grandis Linn. F.*). FAO working paper FP/47/E

Kraenzel, M., Castillo, A., Moore, T., & Potvin, C. (2003) Carbon storage of harvest-age teak (*Tectona grandis*) plantations, Panama. *Forest Ecology and Management*, 173, 213-225. doi: 10.1016/S0378-1127(02)00002-6

Krishnapillay, B. (2000) Silviculture and management of teak plantations. *Unasylva* 201:14-21.

Kumagai, T., Saitoh, T. M., Sato, Y., Morooka, T., Manfroi, O. J., Kuraji, K., & Suzuki, M. (2004) Transpiration, canopy conductance and the decoupling coefficient of a lowland mixed dipterocarp forest in Sarawak, Borneo: dry spell effects. *Journal of Hydrology*, 287, 237-251. doi: 10.1016/j.jhydrol.2003.10.002

Kumagai, T., Aoki, S., Nagasawa, H., Mabuchi, T., Kubota, K., Inoue, S., Utsumi, Y., & Otsuki, K. (2005) Effects of tree-to-tree and radial variations on sap flow estimates of transpiration in Japanese cedar. *Agricultural and Forest Meteorology*, 135, 110-116. doi: 10.1016/j.agrformet.2005.11.007

Kumagai, T., Aoki, S., Shimizu, T., & Otsuki, K. (2007) Sap flow estimates of stand transpiration at two slope positions in a Japanese cedar forest watershed. *Tree Physiology*, 27, 161–168. doi: 10.1093/treephys/27.2.161

Kume, T., Tsuruta, K., Komatsu, H., Kumaga,i T., Higashi, N., Shinohara, Y., & Otsuki, K. (2010b) Effects of sample size on sap flux-based stand-scale transpiration estimates. *Tree Physiology*, 30, 129-138. doi: 10.1093/treephys/tpp074

Lagergren, F., Lankreijer, H., Kučera, J., Cienciala, E., Mölder, M., & Lindroth, A. (2008) Thinning effects on pine-spruce forest transpiration in central Sweden. *Forest Ecology and Management*, 255, 2312-2323. doi: 10.1016/j.foreco.2007.12.047

Langford, K. J. (1976) Change in yield of water following a bushfire in a forest of eucalyptus regnans. *Journal of Hydrology*, 29, 87-114. doi: 10.1016/0022-1694(76)90007-X

Laurence, W. F. (1999) Reflection on the tropical deforestation crisis. *Biological Conservation*, 91, 109-117. doi: 10.1016/S0006-3207(99)00088-9

Lean, J., & Warrilow, D.A. (1989) Simulation of the regional climate impact of Amazon deforestation. *Nature*, 342, 441-413. doi: 10.1038/342411a0

Lieberman, D. (1982) Seasonality and Phenology in a dry tropical forest in Ghana. *Journal of Ecology*, 70, 791-806. doi: 10.2307/2260105

Lieberman, D., & Lieberman, M. (1984) The causes and consequences of synchronous flushing in a dry tropical forest. *Biotropica*, 16, 193-201. doi: 10.2307/2388052

Maass, J. M., Vose, J. M., Swank, W. T., & Martínez-Yrízar, A. (1995) Seasonal changes of leaf area index (LAI) in a tropical deciduous forest in west Mexico. *Forest Ecology and Management*, 74, 171-180. doi: 10.1016/0378-1127(94)03485-F

Mabuchi, K., & Sato, Y. (2005a) Climatic impact of vegetation change in the Asian tropical region. Part I: Case of the northern hemisphere summer. *Journal of Climate*, 18, 410-428. doi: 10.1175/JCLI-3273.1

Mabuchi, K., & Sato, Y. (2005b) Climatic impact of vegetation change in the Asian tropical region. Part II: Case of the northern hemisphere winter and impact on the extratropical circulation. *Journal of Climate*, 18, 429-446. doi: 10.1175/JCLI-3274.1

Malhi, Y., & Wright, J. (2004) Spatial patterns and recent trends in the climate of tropical rainforest regions. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 359, 311-329. doi: 10.1098/rstb.2003.1433

Meinzer, F. C., Andrade, J. L., Goldstein, G., Holbrook, N. M., Cavelier, J., & Wright, S. J. (1999) Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia*, 121, 293-301. doi: 10.1007/s004420050931

Meinzer, F. C., Goldstein, G., & Andrade, J. L. (2001) Regulation of water flux through tropical forest canopy trees: Do universal rules apply? *Tree Physiology*, 21, 19-26. doi: 10.1093/treephys/21.1.19

Miyazawa, Y., Tateishi, M., Komatsu, H., Kumagai, T., & Otsuki, K. (2011) Are measurements from excised leaves suitable for modeling diurnal patterns of gas exchange of intact leaves? *Hydrological Processes*, 25, 2924-2930. doi: 10.1002/hyp.8107

Morikawa, Y., Hattori, S., & Kiyono, Y. (1986) Transpiration of a 31-year-old Chamaecyparis obtusa Endl. stand before and after thinning. *Tree Physiology*, 2, 105-114. doi: 10.1093/treephys/2.1-2-3.105

Murakami, S., Tsuboyama, Y., Shimizu, T., Fujieda, M., & Noguchi, S. (2000) Variation of evapotranspiration with stand age and climate in a small Japanese forested catchment. *Journal of Hydrology*, 227, 114-127. doi: 10.1016/S0022-1694(99)00175-4

Ohkubo, S., Kosugi, Y., Takanashi, S., Matsuo N., Tani, M., & Nik, A. R. (2008) Vertical profiles and storage fluxes of CO2, heat and water in a tropical rainforest at Pasoh, Peninsular Malaysis. *Tellus*, 60B, 569-582. DOY: 10.1111/j.1600-0889.2008.00367.x

Pataki, D. E., Oren, R., & Smith, W. K. (2000) Sap flux of co-occurring species in a western subalpine forest during seasonal soil drought. *Ecology*, 81, 2557-2566. doi: 10.2307/177474

Pataki, D. E., & Oren, R. (2003) Species differences in stomatal control of water loss at the canopy scale in a mature bottomland deciduous forest. *Advances in Water Resources*, 26, 1267-1278. doi: 10.1016/j.advwatres.2003.08.001

Phillips, N., Oren, R., & Zimmermann, R. (1996) Radial patterns of xylem sap flow in non-, diffuse- and ring-porous tree species. *Plant, Cell & Environment*, 19, 983-990. doi: 10.1111/j.1365-3040.1996.tb00463.x.

Priya, P. B., & Bhat, K. M. (1999) Influence of rainfall, irrigation and age on the growth periodicity and wood structure in teak (*Tectona Grandis*). *IAWA Journal*, 20:181-192.

Purwanto R. H., & Oohara, S. (2002) Estimation of the biomass and net primary production in a planted teak forest in Madiun, East Java, Indonesia. *Forest research, Kyoto*, 74, 59-68.

Rao, K. S., & Rajput, K. S. (1999) Seasonal behaviour of vascular cambium in teak (*Tectona Grandis*) growing in moist deciduous and dry deciduous forests. *IAWA Journal*, 20, 85-93. doi:

10.1163/22941932-90001553

Reich, P. B., & Borchert, R. (1982) Phenology and ecophysiology of the tropical tree, *Tabebuia Neochrysantha* (Bignoniaceae). *Ecology*, 63, 294-299. doi: 10.2307/1938945

Reich, P. B., & Borchert, R. (1984) Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *Journal of Ecology*, 72, 61-74. doi: 10.2307/2260006

Sato, T., Tanaka, N., Inoue, M., Sawada, H., Watanabe, S., & Suzuki, M. (2010) Report on an experiment of dye injection into xylem sap of a *Quercus serrata* tree in University Forest in Aichi. *Miscellaneous information, the University of Tokyo Forests*, 49, 29-41. (in Japanese with English abstract)

Sayer, E. J., & Newbery, D. M. (2003) The role of tree size in the leafing phenology of a seasonally dry tropical forest in Belize, Central America. *Journal of Tropical Ecology*, 19, 539-548. doi: 10.1017/S0266467403003596

Singh K. P., & Srivastava, S. K. (1985) Seasonal variations in the spatial distribution of root tips in teak (*Tectonia grandis* Linn. f.) plantations in the Varanasi Forest Division, India. *Plant and Soil*, 84, 93-104. doi: 10.1007/BF02197870

Srivastava, S. K., Singh, K. P., & Upadhyay, R. S. (1986) Fine root growth dynamics in teak (*Tectona grandis* Linn. F.). *Canadian Journal of Forest Research*, 16, 1360-1364. doi: 10.1139/x86-240

Suzuki, M. (1985) Evapotranspiration estimates of forested watersheds in Japan using the short-time period water-budget method. *Journal of the Japanese Forestry Society*, 67, 115-125. (in Japanese with English abstract)

Swank, W. T., & Douglass, J. E. (1974) Streamflow greatly reduced by converting deciduous hardwood stands to pine. *Science*, 185, 857-859. doi: 10.1126/science.185.4154.857

Takanashi, S., Kosugi, Y., Ohkubo, S., Matsuo, N., Tani, M., & Nik, A. R. (2010) Water and heat fluxes above a lowland dipterocarp forest in Peninsular Malaysia. *Hydrological processes*, 24, 472-480. DOY: 10.1002/hyp.7499

Tanaka, K., Takizawa, H., Kume, T., Xu, J., Tantasirin, C., & Suzuki, M. (2004) Impact of rooting depth and soil hydraulic properties on the transpiration peak of an evergreen forest in northern Thailand in the late dry season. *Journal of geophysical research*, 109, D23107. DOY: 10.1029/2004JD008465

Tanaka, K., Tantasirin, C., & Suzuki, M. (2011) Interannual variation in leaf expansion and outbreak of a teak defoliator at a teak stand in northern Thailand. *Ecological Applications*, 21, 1792-1801. doi: 10.1890/10-1165.1

Tanaka, N., Kume, T., Yoshifuji, N., Tanaka, K., Takizawa, H., Shiraki, K., Tantasirin, C., Tangtham, N., & Suzuki, M. (2008) A review of evapotranspiration estimates from tropical forests in Thailand and adjacent regions. *Agricultural and Forest Meteorology*, 148, 807-819. doi: 10.1016/j.agrformet.2008.01.011

Taneda, H., & Sperry, J.S. (2008) A case-study of water transport in co-occurring ring- versus diffuse-porous trees: contrasts in water-status, conducting capacity, cavitation and vessel refilling. *Tree Physiology*, 28, 1641–1651. doi: 10.1093/treephys/28.11.1641

Tateishi, M., Kumagai, T., Utsumi, Y., Umebayashi, T., Shiiba, Y., Inoue, K., Kaji, K., Cho, K., & Otsuki, K. (2008) Spatial variations in xylem sap flux density in evergreen oak trees with radial-porous wood: comparisons with anatomical observations. *Trees*, 22, 23-30. doi: 10.1007/s00468-007-0165-8

Tsuruta, K., Kume, T., Komatsu, H., Higashi, N., Umebayashi, T., Kumagai, T., & Otsuki, K. (2010) Azimuthal variations of sap flux density within Japanese cypress xylem trunks and their effects on tree transpiration estimates. *Journal of Forest Research*, 15, 398-403. doi: 10.1007/s10310-010-0202-0

Umebayashi, T., Utsumi, Y., Koga, S., Inoue, S., Fujikawa, S., Arakawa, K., Matsumura, J., & Oda, K. (2008) Conducting pathways in north temperate deciduous broadleaved trees. *IAWA Journal*, 29, 247-263.

van der Molen, M. K., Dolman, A. J., Waterloo, M. J., & Bruijnzeel, L. A. (2006) Climate is affected more by maritime than by continental land use change: A multiple scale analysis. *Global and Planetary Change*, 54, 128-149. doi: 10.1016/j.gloplacha.2006.05.005

Vertessy, R. A., Benyon, R. G.,O'sullivan, S. K., & Gribben, P. R. (1995) Relationships between stem diameter, sapwood area, leaf area and transpiration in a young mountain ash forest. *Tree Physiology*, 15, 559-567. doi: 10.1093/treephys/15.9.559

Vertessy, R. A., Watson, F. G. R., & O'Sullivan, S. K. (2001) Factors determining relations between stand age and catchment water balance in mountain ash forests. *Forest Ecology and Management*, 143, 13-26. doi: 10.1016/S0378-1127(00)00501-6

White, M. A., Running, S. W., & Thornton, P. E. (1999) The impact of growing-season length variability on carbon assimilation and evapotranspiration over 88 years in the eastern US deciduous forest. *International Journal of Biometeorology*, 42, 139-145. doi: 10.1007/s004840050097

Wilson, K. B., & Baldocchi, D. D. (2000) Seasonal and interannual variability of energy fluxes over a broadleaved temperate deciduous forest in North America. *Agricultural and Forest Meteorology*, 100, 1-18. doi: 10.1016/S0168-1923(99)00088-X

Yoshifuji, N., Kumagai, T., Tanaka, K., Tanaka, N., Komatsu, H., Suzuki, M., & Tantasirin, C. (2006) Inter-annual variation in growing season length of a tropical seasonal forest in northern Thailand. *Forest Ecology and Management*, 229, 333-339. doi: 10.1016/j.foreco.2006.04.013

Yoshifuji, N., Komatsu, H., Kumagai, T., Tanaka, N., Tantasirin, C., & Suzuki, M. (2011) Interannual variation in transpiration onset and its predictive indicator for a tropical deciduous forest in northern Thailand based on 8-year sap-flow records. *Ecohydrology*, 4, 225-235. doi: 10.1002/eco.219

Yoshifuji, N., Igarashi, Y., Tanaka, N., Tanaka, K., Sato, T., Chatchai, T., & Suzuki, M. (2014) Inter-annual variation in the response of leaf-out onset to soil moisture increase in a teak plantation in northern Thailand. *International Journal of Biometeorology*, 58, 2025-2029. doi: 10.1007/s00484-013-0784-2

Zhang, H., Henderson-Sellers, A., & McGuffie, K. (1996a) Impacts of tropical deforestation. Part I: Process analysis of local climatic change. *Journal of Climate*, 9, 1497-1517. doi: 10.1175/1520-0442(1996)009<1497:IOTDPI>2.0.CO;2

Zhang, H., McGuffie, K., & Henderson-Sellers, A. (1996b) Impacts of tropical deforestation. Part II: The role of large-scale dynamics. *Journal of Climate*, 9, 2498-2521. doi: 10.1175/1520-0442(1996)009<2498:IOTDPI>2.0.CO;2

Chapter 2

This chapter cannot be opened because the content, figures and tables in this chapter will be submitted to the scientific journal within 5 years.

Chapter 3

This chapter was based on the article "Circumferential sap flow variation in the trunks of Japanese cedar and cypress trees growing on a steep slope" which was published in Hydrological Research Letters (6, 104-108 [2012]).

Circumferential sap flow variation in the trunks of Japanese cedar and cypress trees growing on a steep slope

3.1 Introduction

Sap flow measurements are useful for investigating transpiration from forests. However, spatial variation (radial or circumferential) in sap flow in the tree trunk may cause significant errors to estimate whole-tree water use. Many studies have described radial variation in sap flow and suggest that sap flow consistently decreases with sapwood depth in some tree species (Phillips et al., 1996; James et al., 2002; Delzon et al., 2004; Kumagai et al., 2005). However, few studies have investigated circumferential variation in sap flow. Tateishi et al. (2008) and Tsuruta et al. (2010) demonstrated circumferential variation using sap flow techniques, and suggested that a sap flow measurement from only one directional aspect generates an error in the estimation of tree transpiration.

Cryptomeria japonica (Japanese cedar) and *Chamaecyparis obtusa* (Japanese cypress) are common plantation tree species in Japan. Most of them grow on steep slopes in mountainous regions. Previous studies have demonstrated that trees growing on slopes tend to exhibit a tree crown that extends toward the lower slope in search of optimum light conditions (Umeki, 1995). Other studies have demonstrated that circumferential variation depends on the direction of sunlight (Granier, 1987) and the location of branches (López-Bernal et al., 2010). Therefore, it is possible that the circumferential variation in sap flow is large in trees growing on a steep slope, and reflects the shape of the tree crown. In this case, information about circumferential variation in sap flow is very important when considering appropriate sampling design for estimating whole tree transpiration using sap flow measurements.

The objective in this chapter, I showed the adaptation of the TDM for Japanese cedar and Japanese cypress standing in the Tanzawa Mountain. Japanese cedar and Japanese cypress is well known coniferous species, and there are some previous studies to apply the TDM to estimate the whole-tree water use. However, according to above background, the information about the circumferential variation of sap flow in the tree trunk is needed to estimate the whole-tree water use. Thus, sap flow measurements were conducted for upper and lower slope aspects and in four directions (north, east, south, and west), and measured the width of the tree crown to examine the effect of sunlight. The goal of this chapter was to examine circumferential variation in sap flow in Japanese cedar and cypress, and to provide an appropriate sap flow sampling design for estimating whole tree transpiration.

3.2 Materials and methods

3.2.1 Study site

This study was conducted in the Oborasawa Watershed, located in the eastern part of the Tanzawa mountains, and the western part of Kanagawa Prefecture, Japan (latitude: 35° 28′ N, longitude: 139° 12′ E, altitude: 432–878 m). A description of the study site is provided in Chapter 2. Sap flow measurements were conducted in Japanese cedar and Japanese cypress stands located on adjoining northwest-facing and southeast-facing slopes: slope angles were 30° and 25°, respectively.

3.2.2 The width of tree crown

We measured the tree crown widths of nine Japanese cedar trees and nine Japanese cypress trees on the northwest-facing slope, and three Japanese cedar trees on the southeast-facing slope. The width of the tree crown was measured as the horizontal distance from the center of the tree trunk to the edge of the tree crown. We measured the horizontal distance in eight directions (north, northeast, east, southeast, south, southwest, west, and northwest).

3.2.3 Sap flow measurement

Sap flow velocity (F_d; cm h^{-1}) was measured by the TDM. The detail of the TDM was shown in chapter 2.

To determine the circumferential variation in F_d, sensors were installed to measure sap flow for the upper and lower slope aspects and in four directions (north, south, east, and west). Table 3.1 lists tree numbers, diameter at breast height (DBH), tree height, sapwood depth, slope aspect, and location of sensors.

The region of the trunk where the sensors were installed was fully insulated using aluminum foil, avoiding any effects from direct radiation and natural thermal gradients along the trunk. Measurements were conducted on trees on the northwest-facing slope from 25 June to 19 December, 2010, and on trees on the southeast-facing slope from 20 September to 19 December, 2010. For analysis, we selected the data for the northwest-facing slope from 21 August to 13 September, 2010, and for the southeast-facing slope from 26 September to 18 October. We excluded all data collected on rainy days and interpolated any lost data based on a linear relationship with F_d measured in each direction.

Table 3.1 Characteristics of the study trees and position of the sensors. Upper: upper slope aspect, Lower: lower slope aspect.

No.	Species	Diameter at breast height (cm)	Tree height (m)	Sapwood depth (N, S) (cm)	Slope	Location of sensors
1008	*C. japonica*	17.3	16.0	3.3, 3.7	NW	N, S
1018		18.0	15.3	3.2, 4.7	NW	N, S, Upper, Lower
1024		27.3	18.1	4.4, 4.7	NW	N, S, Upper, Lower
1023	*C. obtusa*	18.9	16.3	3.8, 2.9	NW	N, E, S, W
1032		19.6	16.1	2.4, 2.6	NW	N, E, S, W
1031		19.4	15.9	2.4, 3.0	NW	N, E, S, W
2001	*C. japonica*	65.9	32.7	4.1, 2.4	SE	N, S, Lower, Upper
2002		47.4	27.3	3.5, 3.1	SE	N, S, Lower, Upper
2003		53.7	30.5	4.6, 3.8	SE	N, S, Lower, Upper

3.2.4 Relationship between the number of circumferential measurements and the difference in average F_d estimates

To examine the effect of circumferential variation, we examined the relationship between the number of circumferential measurements (n) and the difference in average F_d estimates (Tsuruta et al., 2010; Kume et al., 2011). We changed n from 1 to 4. For each n, we selected F_d from all possible combinations of the four measurement directions and estimated the average F_d. For example, when n = 2, six possible combinations of the measurement aspect exist (i.e., (1) north and east, (2) north and south, (3) north and west, (4) east and south, (5) east and west, and (6) south and west in Japanese cypress). We assumed that an accurate F_d was found when n = 4. The difference in average F_d estimate (%) was calculated as the difference between the accurate F_d and the average F_d estimated from all possible combinations for each n.

3.3 Results and Discussion

3.3.1 The relationship between slope and width of the tree crown

Figure 3.1 shows the horizontal length from the center of the tree trunk to the tree crown edge for the northwest-facing slope and southeast-facing slope. On the northwest-facing slope, tree crowns were widest in the west, northwest, north, and northeasterly directions; on the southeast-facing slope, tree crowns were widest in the east, southeast, south, and southwesterly directions. Based on these results, Japanese cedar and Japanese cypress trees at this study site appear to be influenced by light conditions, and to extend tree crown growth toward the lower slope.

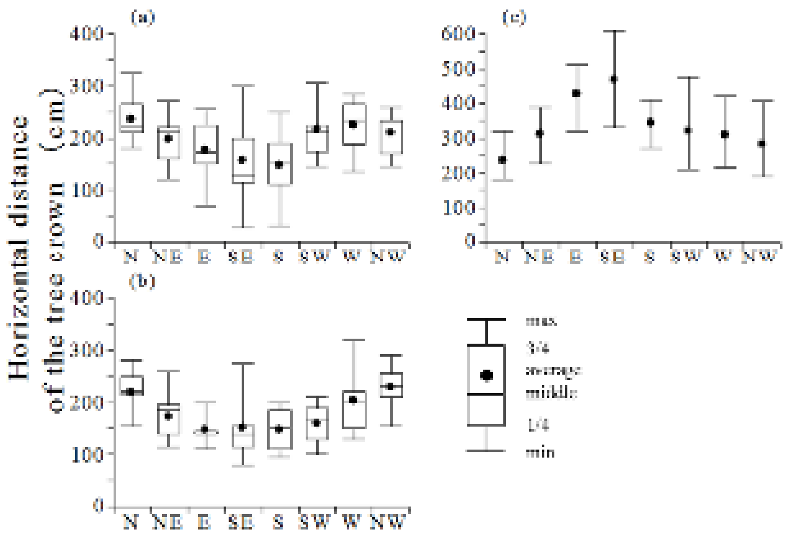

Figure 3.1 Horizontal width of the tree crown. (a): Japanese cedar growing on the northwest-facing slope (n = 9), (b): Japanese cypress growing on the northwest-facing slope (n = 9), (c): Japanese cedar growing on the southeast-facing slope (n = 3).

3.3.2 Circumferential variations in sap flow

Figure 3.2 shows the diurnal time course of solar radiation, vapor pressure deficit (*VPD*), and F_d at 0–20 mm depth for the four aspects in tree Nos. 1024, 1023, and 2001 on a sunny day. Considerable circumferential variation was observed in F_d measured around noon. Figure 3.3 shows the relationship between daily F_d for the northerly aspect and one other aspect in tree Nos. 1024, 1023, and 2001 during all measurement periods. Daily F_d for the northerly aspect and one other aspect had a strong linear relationship. This trend was displayed by all sample trees, and did not change during the measurement period.

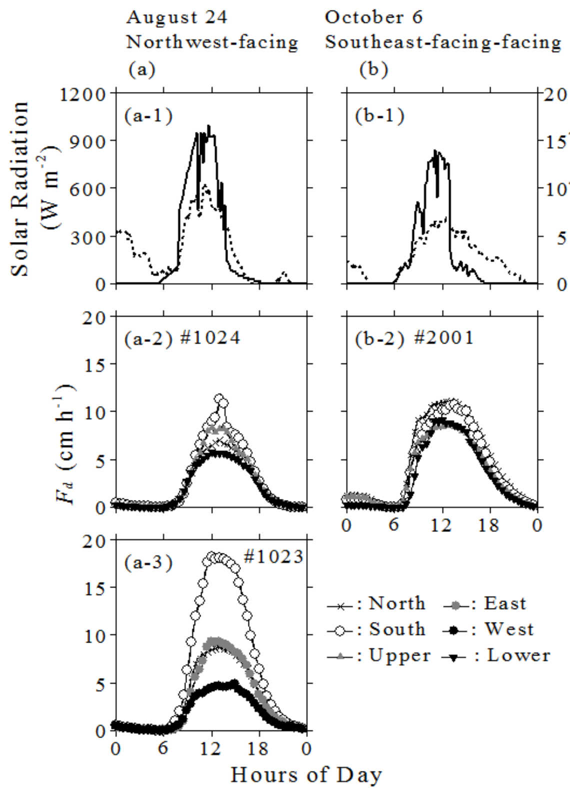

Figure 3.2 Diurnal patterns in solar radiation, vapor pressure deficit (*VPD*), and F_d for each measurement aspects at 0-20 mm depth. Upper: upper slope aspect, Lower: lower slope aspect. (a): Northwest-facing slope. Data were obtained on August 24, 2010. (b): Southeast-facing slope. Data were obtained on October 6, 2010. (a-1) and (b-1) represent solar radiation (solid line) and *VPD* (dotted line), respectively. (a-2), (a-3), and (b-2) are F_d values for four directions in tree Nos. 1024, 1023, and 2001 respectively. In (a-2) and (b-2) (Japanese cedar), F_d was measured for the north, south, upper, and lower aspects; in (a-3) (Japanese cypress), F_d was measured for the north, east, south, and west aspects. Results are shown in 10-minute increments (solid line) and symbols represent 30-minitue increments.

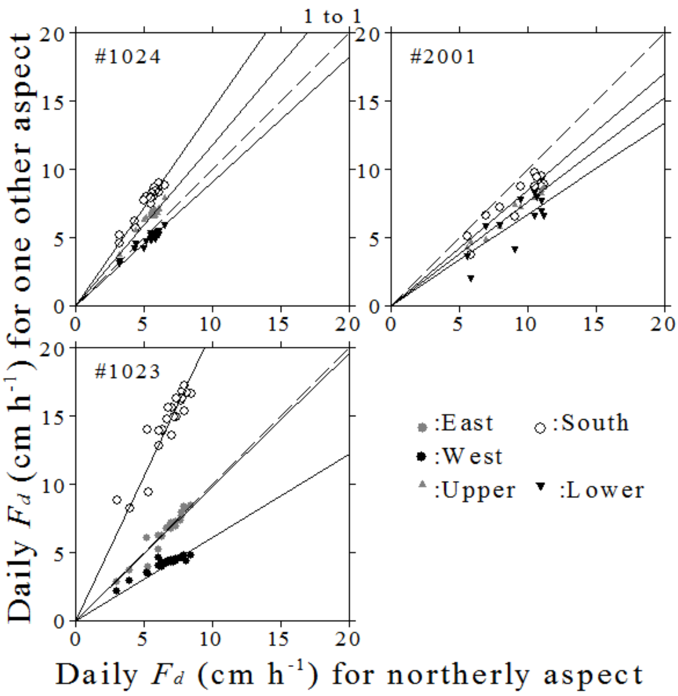

Figure 3.3 The relationship between daily F_d to the north and the other aspects for all trees. Daily F_d were averaged value of F_d from 10:00 to 15:00. Upper: upper slope aspect, Lower: lower slope aspect. Solid lines are regression lines and broken lines are 1:1 lines. Tree No. 1024 was a Japanese cedar standing on the northwest-facing slope. Daily F_d was measured for north, south, upper, and lower aspects (r^2 = 0.92, 0.92, 0.86). Tree No. 1023 was a Japanese cypress standing on the northwest-facing slope. Daily F_d was measured for north, east, south, and west aspects (r^2 = 0.79, 0.92, 0.74). Tree No. 2001 was a Japanese cedar standing on the southeast-facing slope. Daily F_d was measured for north, south, upper, and lower aspects (r^2 = 0.85, 0.98, 0.66).

Figure 3.4 shows the distribution of daily F_d values and the coefficients of variation (CV) for all sample trees. The daily F_d was the measured F_d averaged from 10:00 to 15:00. Individual trees exhibited circumferential variation in F_d, but variations in sap flow in the tree trunk did not appear to be dependent on direction or upper or lower slope aspects. The variation of daily F_d in Japanese cedar and Japanese cypress was 5 to 7 cm h^{-1} and 5 to 15 cm h^{-1}, respectively. For Japanese cedar standing on the northwest-facing slope, the maximum daily F_d was 1.92 times as large as the minimum for tree No. 1018. In the same stand, the CV ranged from 20.9 % to 28.4 %. For Japanese cypress standing on the northwest-facing slope, the daily F_d exceeded 10 cm h^{-1} locally, and the daily F_d in each tree varied considerably. The maximum daily F_d was 3.80 times as large as the minimum for tree No. 1031. In the same stand, the CV ranged from 49.2 % to 58.9 %. For Japanese cedar standing on the southeast-facing slope, the maximum daily F_d was 1.60 times as large as the minimum for tree No. 2002. In the same stand, the CV ranged from 15.3 % to 19.3 %. Compared with Japanese cedar, Japanese cypress varied greatly in F_d, and large local values of F_d were recorded in tree trunks. Daily F_d values in this study are same range to those reported in previous studies that applied the TDM to these species (Kumagai, et al., 2005; Kume et al., 2010; Tsuruta et al., 2010). Previous studies have reported circumferential variation in F_d in some tree species, with coniferous trees having a larger degree of circumferential variation in F_d than broad-leaved trees. In coniferous trees (Kominami and Suzuki, 1993; Tsuruta et al., 2010), the maximum F_d tends to be about 3 times as large as the minimum and the CV ranges from 30 % to 50 %. In broad-leaved trees (Lu et al., 2000; Tateishi et al., 2008; Kume et al., 2011), the maximum F_d tends to be about 2 to 3 times the minimum and the CV ranges from 15 % to 30 %. The circumferential variation in F_d in the Japanese cypress observed in this study was within, or slightly higher than, the ranges reported in previous studies. In contrast, the Japanese cedar observed in this study had smaller circumferential variation in F_d than previous reported in coniferous trees. Morikawa (1974) conducted sap flow measurements in Japanese cypress standing on flat ground and isolated from other trees and found similar F_d values measured in all directions. These results suggest that Japanese cypress standing on flat ground have a symmetrical crown, experience uniform sunlight conditions, and thus have less circumferential variation in F_d than in the present or previous studies.

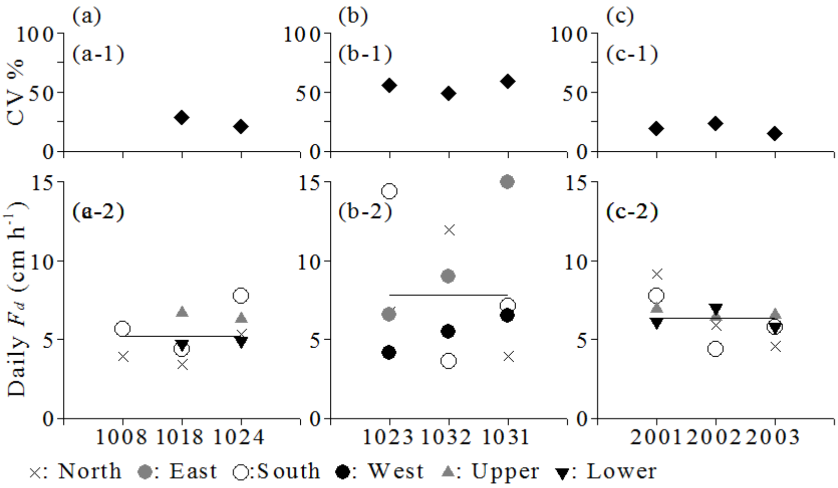

Figure 3.4 Distribution of daily F_d values and the coefficient of variation (CV) for each sample tree. Upper: upper slope aspect, Lower: lower slope aspect. Solid lines are the average of the daily F_d obtained for each site and species: (a) is a Japanese cedar; (b) is a Japanese cypress standing on the northwest-facing slope; (c) is a Japanese cedar standing on the southeast-facing slope; (a-1) to (c-1) show the CV and (a-2) to (c-2) show daily F_d.

In our study, Japanese cedar and Japanese cypress trees were growing on a steep slope and extended their tree crowns toward the lower slope. However, we did not find a relationship between circumferential variation in F_d and the shape of the tree crown. Rudinsky and Vite (1959) conducted dye perfusion experiments with 31 conifer trees to examine patterns of water transport in tree trunks. Kozlowski and Winget (1963) also conducted dye perfusion experiments in three conifer trees and seven broad-leaved trees. They found some patterns in water transport in each species and suggested that turning water transport is more common than vertical water transport. Morikawa (1974) performed a dye perfusion experiment on Japanese cypress and confirmed this finding: the path of ascent in the tree trunk was turning, not straight. Takizawa et al. (1996) conducted a dye perfusion experiment and suggested that sap flow in tracheids can move more easily in the circumferential direction than in the radial direction. These previous studies suggested that Japanese cedar and Japanese cypress exhibit turning water transport, and thus circumferential variation in F_d would not correspond with the shape of the tree crown or the direction of the tree trunk.

Figure 3.5 shows the relationship between the number of circumferential measurements and the difference in average F_d estimates. In Japanese cedar and Japanese cypress, the difference was about 20 % and 40 %, respectively. When the number of circumferential measurements decreased, the difference in Japanese cypress increased sharply compared with Japanese cedar. These results suggest that, by ignoring circumferential variation in F_d, we create large errors in estimates of whole tree transpiration in both species, and that Japanese cypress shows larger circumferential variation in F_d than Japanese cedar. Therefore, when estimating whole tree transpiration using the sap flow technique, we need to use sensors to capture the circumferential variation in F_d. When we conduct sap flow measurements on a steep slope, we can insert the sensors randomly and need not consider the shape of the tree crown or the direction of the tree trunk.

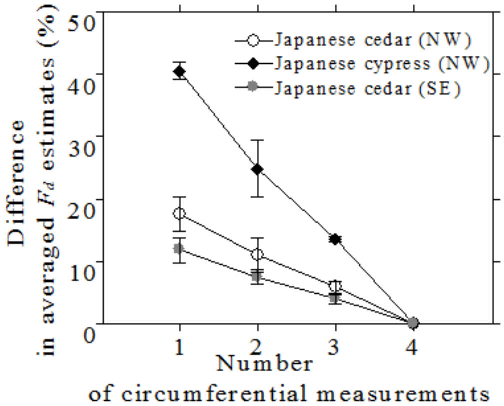

Figure 3.5 Relationship between the number of circumferential measurements and the difference in average F_d estimates. Each symbol shows the average of the difference at each number of circumferential measurements. Error bars indicate standard deviations. For Japanese cedar standing on the northwest-facing slope (NW), average value was calculated from two sample trees. For Japanese cypress standing on the northwest-facing slope and Japanese cedar standing on the southeast-facing slope (SE), average values were calculated from three sample trees.

Previous studies have examined the spatial and tree-to-tree variation in F_d, and suggested that the effect of the spatial variation was a minor source of error to estimate stand- and catchment-scale evapotranspiration compared with tree-to-tree variation (Ford et al., 2007; Kume et al., 2011). In this study, we only discussed circumferential variation in F_d. We need to conduct additional sap flow measurements to investigate circumferential, radial, and tree-to-tree variation in Japanese cedar and Japanese cypress trees growing on steep slopes.

3.4 Conclusion

Sap flow measurements were conducted for upper and lower slope aspects and in four directions on a steep slope. The daily F_d in Japanese cedar and Japanese cypress in this study was almost same value compared with previous studies applied the TDM to Japanese cedar and Japanese cypress. This study found that individual trees displayed circumferential variations in F_d. Japanese cypress had large F_d values, and these values varied more than in Japanese cedar. However, variations in F_d values did not appear to be dependent on direction or slope aspect. These results suggest that when circumferential variation in F_d is ignored, large errors are produced during the estimation of whole tree transpiration. Therefore, we need to use sensors to capture the circumferential variation in F_d. Sensors can be inserted randomly without the need to consider the shape of the tree crown or the direction of the tree trunk. At our site, more sap flow sensors need to be used with Japanese cypress to capture circumferential variation in F_d compared with Japanese cedar.

References

Delzon, S., Sartore, M., Granier, A., & Loustau, D. (2004) Radial profiles of sap flow with increasing tree size in maritime pine. *Tree Physiology*, 24, 1285-1293. doi: 10.1093/treephys/24.11.1285

Ford, C. R., Hubbard, R. M., Kloeppel, B. D., & Vose, J. M. (2007) A comparison of sap flux-based evapotranspiration estimates with catchment-scale water balance. *Agricultural and Forest Meteorology*, 145, 176-185. doi.org/10.1016/j.agrfomet.2007.04.010

Granier ,A. (1987) Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiology*, 3, 309-320. doi: 10.1093/treephys/3.4.309

James, S. A., Clearwater, M. J., Meinzer, F. C., & Goldstein, G. (2002) Heat dissipation sensors of variable length for the measurement of sap flow in trees with deep sapwood. *Tree Physiology*, 22, 277-283. doi: 10.1093/treephys/22.4.277

Kominami, Y., & Suzuki, M. (1993) Comparison of transpiration rate measured by heat pulse method and uptake water in single trees of *Chamaecyparis obutsa* and *Pinus densiflora*. Exchanging processes at the land surface for a range of spaceand time scales. Bolle H-J, Feddes RA, Kalma JD (eds). IAHS Publication No. 212. IAHS Press: Wallingford; 27-34.

Kozlowski, T. T., & Winget, C. H. (1963) Patterns of Water Movement in Forest Trees. *Botanical Gazette*, 4, 301-311.

Kumagai, T., Aoki, S., Nagasawa, H., Mabuchi, T., Kubota, K., Inoue, S., Utsumi, Y., & Otsuki, K. (2005) Effects of tree-to-tree and radial variations on sap flow estimates of transpiration in Japanese cedar. *Agricultural and Forest Meteorology*, 135, 110-116. doi: 10.1016/j.agrformet.2005.11.007

Kume, T., Otsuki, K., Du, S., Yamanaka, N., Wang, Y., & Liu, G. (2011) Spatial variation in sap flow velocity in semiarid region trees: its impact on stand-scale transpiration estimates. *Hydrological Processes*, 26, 1161-1168. doi: 10.1002/hyp.8205. doi: 10.1002/hyp.8205

López-Bernal, Á., Alcántara, E., Testi, L., & Villalobos, F. J. (2010) Spatial sap flow and xylem anatomical characteristics in olive trees under different irrigation regimes. *Tree Physiology*, 30, 1536-1544. doi: 10.1093/treephys/tpq095

Lu, P., Müller, W. J., & Chacko, E. K. (2000) Spatial variations in xylem sap flux density in the trunk of orchard-grown, mature mango trees under changing soil water conditions. *Tree Physiology*, 20, 683-692. doi: 10.1093/treephys/20.10.683

Morikawa, Y. (1974) Sap flow in *Chamaecyparis obtusa* in relation to water economy of woody plants. *Bulletin of the Tokyo University Forests*, 66, 251-297. (in Japanese with English abstract)

Oda, T., Suzuki, M., Egusa, T., & Uchiyama, Y. (2013) Effect of bedrock flow on catchment rainfall-runoff characteristics and the water balance in forested catchments in Tanzawa Mountains, Japan. *Hydrological Processes*, 27, 3864-3872. doi: 10.1002/hyp.9497

Phillips, N., Oren, R., & Zimmermann, R. (1996) Radial patterns of xylem sap flow in non-, diffuse- and ring-porous tree species. *Plant, Cell & Environment*, 19, 983-990. doi: 10.1111/j.1365-3040.1996.tb00463.x

Rudinsky, J. A., & Vite, J. P. (1959) Certain ecological and phylogenetic aspects of the pattern of water conduction in conifers. *Forest science*, 5, 259-266.

Shiraki, K., Wakahara, T., Ishikawa, Y., Suzuki, M., & Uchiyama, Y. (2007) Characteristics of Rainfall and Runoff of the Oborasawa Watershed. *Results of Scientific Research on the Tanzawa Mountains*, 405-409. (in Japanese)

Takizawa, H., Kubota, J., & Tsukamoto, Y. (1996) Distribution of water flow velocity at a stem cross-section. *Journal of the Japanese Forestry Society Japanese Forestry Society*, 78, 190-194. (in Japanese with English abstract)

Tateishi, M., Kumagai, T., Utsumi, Y., Umebayashi, T., Shiiba, Y., Inoue, K., Kaji, K., Cho, K., & Otsuki, K. (2008) Spatial variations in xylem sap flux density in evergreen oak trees with radial-porous wood: comparisons with anatomical observations. *Trees*, 22, 23-30. doi: 10.1007/s00468-007-0165-8

Tsuruta, K., Kume, T., Komatsu, H., Higashi, N., Umebayashi, T., Kumagai, T., & Otsuki, K. (2010) Azimuthal variations of sap flux density within Japanese cypress xylem trunks and their effects on tree transpiration estimates. *Journal of Forest Research*, 15, 398-403. doi: 10.1007/s10310-010-0202-0

Umeki, K. (1995) Modeling the relationship between the asymmetry in crown display and local environment. *Ecological Modelling*, 82, 11-20. doi: 10.1016/0304-3800(94)00081-R

Chapter 4

This chapter was based on the article "Applicability of thermal dissipation method (TDM) for sap flow measurement of teak tree" in Bulletin of the university of Tokyo forests (submitted).

Applicability of thermal dissipation method (TDM) for sap flow measurement of teak tree

4.1 Introduction

In order to access forest water uptake on a stand scale, it is necessary to quantify water uptake by individual trees and to scale them up to a stand scale. Measurements of tree-to-tree variations in sap flow and within-tree spatial variations (both circumferential and radial) are essential for this procedure (Philips et al., 1996; James et al., 2002; Delzon et al., 2004; Kumagai et al., 2005; Tateishi et al., 2008; Tsuruta et al., 2010; Kume et al., 2011). Estimations of two levels of variability in an actual forest stand require several sap flow sensors. The thermal dissipation method (TDM; Granier, 1987), which uses Granier-type sap flow sensors, is both inexpensive and relatively simple to operate. In fact, in recent years, circumferential, radial and tree-to-tree distributions of sap flow were investigated using several Granier-type sap flow sensors (Kumagai et al., 2005; Kume et al., 2010b, 2011). Ease of calculation is an additional advantage provided by the TDM: sap flow averaged over a sensor cross-section is readily obtainable from an empirical equation with only two coefficients that are applicable to various tree species (Granier, 1987). Thus some previous studies used the TDM to estimate whole-tree and stand scale water use (e.g., Delzon et al., 2004; Kumagai et al., 2005). Nevertheless, other studies have reported substantial errors when the TDM was applied to broader range of tree species (Goulden and Field, 1994; Clearwater et al., 1999). Especially, sap flow is greatly underestimated by the TDM when it is used with ring-porous species (Taneda and Sperry, 2008; Bush et al., 2010).

The cause of such underestimation was considered by the large sap flow distribution in the tree trunk of ring-porous species (Clearwater et al., 1999; Bush et al., 2010). Sap flow distribution in the trunk of ring-porous tree species may be much greater than variation in the trunks of coniferous and diffuse-porous species (Umebayashi et al., 2008). Thus, the existence of radial variation in sap flow indicates that wide-scale application of the TDM to ring-porous species will require a full exploration of the sap flow distribution in tree trunks. Most of the previous studies testing the applicability of the TDM to ring-porous tree species have been performed in the laboratory on field-collected branch and stem segments (Taneda and Sperry, 2008; Bush et al., 2010). Although it is considered that water transport pattern in the sample segments was quite different from natural condition (Renninger and Schäfer, 2012), few studies have examined the applicability of the TDM to ring-porous trees growing in natural settings (Granier et al., 1994). Furthermore, no study has tested the applicability of this method to ring-porous forest canopy trees that are mature and have large diameters.

Teak (*Tectona grandis* Linn. f.) is a well-known ring-porous tree species (Coder, 2011) that is widely planted in tropical regions, including Southeast Asia, the Indian subcontinent, Central America and Africa, because of its considerable commercial value (Krishnapillay, 2000; Kollert and Cherubini, 2012). However most studies of sap flow distribution in ring-porous species and the applicability of the TDM have been conducted in the north-temperate climate (Umebayashi et al., 2008; Sato et al., 2010).

The objective in this chapter is to investigate radial distribution of sap flow for teaks and to test the applicability of TDM for this species. Toward this goal, the following field procedure on mature plantation teaks: dye perfusion experiments to investigate the radial distribution of sap flow in tree trunks, and simultaneous measurements of tree water uptake and sap flow using the TDM to compare with the actual water uptake and estimated water uptake by the TDM.

In Chapter 3, we showed that circumferential variation in F_d is important for whole-tree estimates of water use based on the TDM. Thus, in this chapter we considered the circumferential variation in F_d in teak trunks and applied the original coefficient of Granier (1987) to produce estimates of whole-tree water use using the TDM.

4.2 Materials and methods

4.2.1 Plant materials

Experiments on teak were conducted in the Mea Mo teak plantation, which is located in Lampang Province, Thailand (18° 25' N, 99° 43' E; 380 m above sea level). The details of the study site was shown in chapter 2.

Teak is a deciduous broadleaved tree classified as ring-porous by its vessel distribution in the xylem (Coder, 2011). It has large earlywood vessels that are 200-300 μm in diameter arrayed along annual rings, and small latewood vessels with diameters of <100μm (Saeki, 1982).

4.2.2 Dye perfusion experiment

To determine the radial distribution of sap flow in the trunks, dye perfusion experiments were conducted for individuals listed in Table 4.1. Three sample trees differing in DBH were selected and named D1, D2 and D3. The dye perfusion experiments were conducted on the following dates: 2009/11/17, 2012/10/25, and 2012/10/26.

A 1 % acid fuchsin solution was used as the perfusion liquid. The movement of this solution matches that of sap flow, because the dye molecules do not adhere to the vessel walls and move together with the sap through the vessels (Iida et al., 1992; Sano et al., 2005). Thus, it is supposed that the flow of the acid fuchsin solution matched sap flow movement in the vessels.

The bottles used for injecting the dye solution were attached to tree trunks 90 cm above ground level (Figure 4.1(a)). On each tree, a hole, the diameter and depth were 10 and 50 mm, was made through the bark and into the trunk xylem 80 cm above ground level using an electric drill. To avoid xylem vessel cavitation, a simple water reservoir was attached to the tree trunk and the hole was made under water. After made the hole, the dye solution was injected into each hole for a set period of time (Table 4.1). To avoid leakage of the dye solution, the hole and the bottle outlet were connected with a silicone cap, after which the water reservoir was detached (Figure 4.1(a)). Before starting the dye solution injection, the hole on the bottle was made using a gimlet. Following dye injection, the experimental trees were felled and all branches were immediately cut free to prevent further ascent of the dye solution. Sample disks were cut out of the trunks at intervals of 10-100 cm, until the dyed section on the disks surface became ambiguous.

To distinguish the dyed and non-dyed section on the surface of each sample disk, the dyed section was shaved using a chisel and immediately marked out the borders using a ball-point pen. According to examine the surface of disks, radial thicknesses of the bark, sapwood, heartwood and dyed section were measured, and the annual rings of the sapwood, heartwood and dyed area were counted.

The dye ascent velocity (D_s; cm h^{-1}) was calculated as:

$$D_s = h/T \times 60 \tag{4.1}$$

where h (cm) is the height above the injection hole and T (min) is the duration of dye solution injection.

4.2.3 Absorption experiment

Details of the trees used in the absorption experiment are provided in Table 4.2. Three sample trees differing in DBH were selected and named A1, A2 and A3. The absorption experiments were conducted on the following dates: 2010/10/23-25, 2011/10/14-17 and 2012/10/27-29.

A water holding collar was attached to each experimental tree 80 cm above ground and sealed with silicon caulk to prevent water leakage (Figure 4.1(b)). On the day of the experiment, we used an electric drill and a chisel to cut a groove about 40 mm depth and 20 mm width through the bark and xylem around the circumference of the trunk 90 cm above ground level (See Figure 4.1(b)). The groove was deep enough to reach the heartwood. To reduce the effects of xylem cavitation, this operation was performed predawn under the premise that sap does not flow. After visible sawdust on the water holding collar was removed as possible as clearly, the water holding collar was filled with water. Bubbles were removed manually from the surface of the groove cut in the trunk.

The water absorbed by the sapwood was supplied from a measuring cylinder and the amount of supplied water was recorded. The actual absorbed water ($Q_{\_act}$, kg h^{-1}) was calculated as follow;

$$Q_{\_act} = Q/IT \times 60 \tag{4.2}$$

where Q (kg) was the amount of supplied water during interval and IT (minute) was interval times of water supply. To compare with sap flow measurements, $Q_{\_act}$ was made at 30 min interval by interpolation.

4.2.4 Sap flow measurements

Sap flow velocity (F_d) on the teaks using the TDM were measured during the course of the absorption experiments. Details of the sap flow measurement on each experimental tree are provided in Table 4.2. To determine the spatial (circumferential and radial) variation in tree trunk, sap flow sensors were installed to measure sap flow at a depth of 0-1 cm on 2-4 trunk directions (north, east, south, and west), and at a depth of 1-2 cm depth on a north direction. The detail of the TDM was shown in chapter 2.

The estimated absorbed water using the TDM ($Q_{\_cal}$; cm^3 h^{-1}) was calculated as follows:

$$Q_{\_cal} = F_{d\_0\text{-}1} \times A_{s\_0\text{-}1} + F_{d\_1\text{-}2} \times A_{s\_1\text{-}2} + F_{d\_2\text{-}3} \times A_{s\_2\text{-}3} \tag{4.3}$$

where $F_{d\_0\text{-}1}$, $F_{d\_1\text{-}2}$ and $F_{d\_2\text{-}3}$ are F_d values measured at a depth of 0-1, 1-2 and 2-3 cm, respectively, and $A_{s\_0\text{-}1}$, $A_{s\_1\text{-}2}$ and $A_{s\_2\text{-}3}$ are the sapwood areas (cm^2) occupied at each depth by the sap flow sensor. To consider the circumferential variation in $F_{d\_0\text{-}1}$, $Q_{\_cal}$ was calculated using averaged $F_{d\_0\text{-}1}$ values for two or four directions, and F_d values for just one direction. Each of the calculated $Q_{\_cal}$, $F_{d\_1\text{-}2}$ and $F_{d\_2\text{-}3}$ value was used for northerly direction.

To compare the diurnal pattern of F_d in experimental and non-experimental trees, sap flow measurements were conducted to other teak trees standing in the plantation simultaneously. The relative F_d values measured on the non-experimental trees were indicated in Figure 4.3 (gray dashed lines).

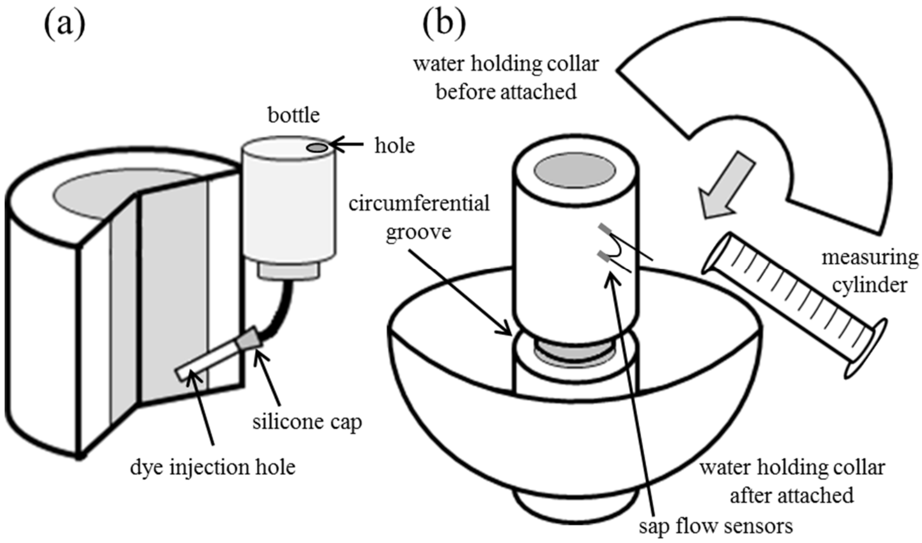

Figure 4.1 Schematics of the dye perfusion (a) and water uptake (b) experiments. The diameter and depth of the drilled dye injection hole were about 10 mm and 50 mm, respectively. The hole on the bottle was made using a gimlet. The depth and width of the circumferential groove were about 40 mm and 20 mm, respectively. In the dye perfusion experiment, the bottle and dye injection hole were connected through a silicone cap. In the absorption experiment, water absorbed from the sapwood was supplied with a measuring cylinder. Sap flow sensors were installed 1.3 m above ground level and two or four directions.

Table 4.1 Information on experimental teak specimens and details of the dye perfusion experiments.

	Date of experiment	Tree height (m)	Diameter at breast height (cm)	Sapwood thickness (cm)	Sapwood annual rings	(total)	Aspect of hole	Duration of experiment (total dye injection time min)
D1	2009/11/17	20.0	16.0	1.4	11	(33)	N	09:30 - 10:30 (60)
				1.5	11		SE	09:50 - 10:30 (40)
				1.2	10		SW	10:10- 10:30 (20)
D2	2012/10/25	18.0	17.6	1.6	15	(32)	N	11:00 - 11:30 (30)
				1.9	13		SE	
				1.1	8		SW	
D3	2012/10/26	23.3	28.2	2.1	10	(35)	N	10:30 - 11:00 (30)
				2.0	11		SE	
				1.5	13		SW	

Table 4.2 Information on experimental teak specimens and details of the procedures for the absorption experiments and sap flow measurements.

	Date of experiment	Tree height (m)	Diameter at breast height (cm)	Sapwood thickness (cm)	Sapwood annual rings	(total)	Positions of sensors aspect	Depth (cm)
A1	2010/10/23-25	21.9	27.0	2.5	8	(31)	N	0-1, 1-2, 2-3
				1.2	9		E	0-1
				1.9	9		S	0-1
				2.8	9		W	0-1
A2	2011/10/14-17	21.2	16.0	1.8	15	(26)	N	0-1, 1-2
				1.6	15		S	0-1
A3	2012/10/27-29	22.8	22.9	1.6	12	(36)	N	0-1, 1-2
				2.1	11		E	0-1
				2.1	10		S	0-1
				1.8	12		W	0-1

4.3 Results

4.3.1 Dye perfusion experiment

The maximum dye ascent heights, maximum D_s values, and numbers of dyed annual rings on sample disks at breast height and maximum dye accent height are summarized in Table 4.3. Figure 4.2 presents the image of the surface of dyed disks cut at 0.4 m (i.e. at breast height) and 8.7 m above the dye injection point on the north side of D3. The circumferential variation in the maximum dye ascent heights for D1 (Table 4.3) may be attributed to differences in the total dye injection time on each of the trunk sides (Table 4.1): the highest and lowest dye ascent heights were observed for directions with the longest (northerly direction) and shortest (southwesterly direction) dye injection times (Table 4.1), respectively. For D2 and D3, the maximum dye ascent heights differed considerably by directions (Table 4.3) even though the total dye injection time was consistent (30 min) in the two individuals (Table 4.1), indicating large circumferential variation in sap flow in the trees.

The number of dyed annual rings on sample disks cut out at breast height (0.4 m above the dye injection height) varied from five to seven. At the maximum height of dye ascent, the number varied from three to five, except among those taken from the SW direction on D3, which had only one dyed annual ring (Table 4.3 and Figure 4.2). The maximum D_s varied from 440 to 2840 cm h^{-1} at each injection point. Thus, some vessel conduits may be functional for at least 5 years. However during our visual observations, we were unable to find any relationship between functionality and the anatomical features of the vessels (i.e., between the vessels in earlywood and latewood).

Table 4.3 Numbers of sapwood annual rings, maximum dye ascent speed (D_s) and dyed annual rings 0.4 m above the dye injection point and at the maximum height to which the dye ascended (for three trunk geographical aspects).

	Direction	max dye ascent height from the dye injection point (m)	Dye injection time (min)	Maximum dye ascent speed (cm h^{-1})	number of dyed annual rings (total rings in sapwood)	
					*0.4 m above dye injection point	Maximum dye height
D1	N	8.7	60	870	5 (11)	4 (13)
	SE	4.2	40	630	6 (10)	3 (12)
	SW	2.7	20	810	5 (11)	4 (14)
D2	N	2.2	30	440	6 (15)	3 (16)
	SE	3.2	30	640	6 (13)	3 (14)
	SW	7.2	30	1440	6 (8)	4 (12)
D3	N	14.2	30	2840	7 (10)	5 (8)
	SE	9.2	30	1840	7 (11)	5 (10)
	SW	7.2	30	1440	7 (13)	1 (8)

*breast height (1.3 m above ground)

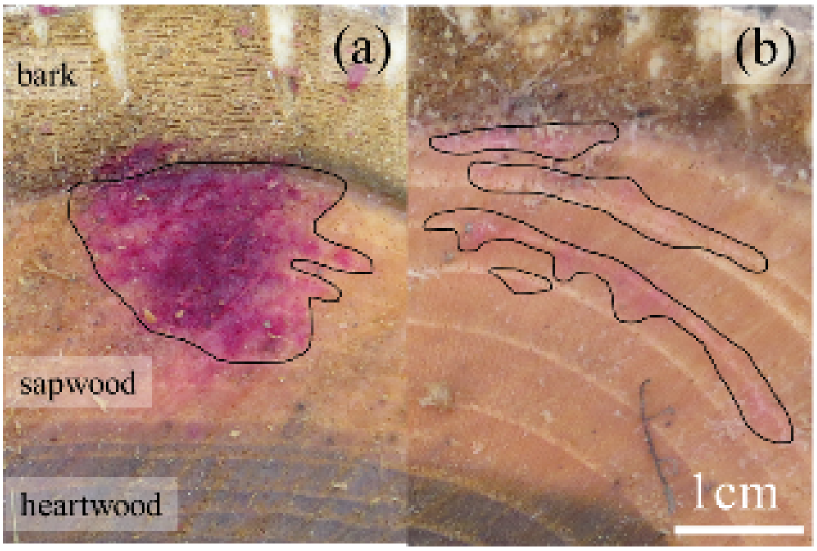

Figure 4.2 Surfaces of dyed disks cut 0.4 m (a) and 8.7 m (b) above the dye injection point on the north side of D3. The bark sides are uppermost and pith sides are lowermost in these images. The light brown and dark brown sectors are sapwood and heartwood, respectively. The peripheries of the marked areas in each figure enclose dyed sections visible to the unaided eye.

4.3.2 Sap flow based on the TDM

Figure 4-3 shows the diurnal patterns in F_d (for the three individuals listed in Table 4.2), in relation to the above-canopy solar radiation (S_d) and atmospheric vapor pressure deficit (*VPD*). The bold horizontal solid lines indicate the periods of water supply to the water holding collar. Before removing xylem, the diurnal pattern of F_d corresponded well with S_d in all individuals examined (Figure 4.3). On the other hand, the diurnal pattern of F_d after removing xylem was depressed in comparison with the relative F_d, particularly in A3 (gray dashed line in each panel of Figure 4.3). The changes in the diurnal pattern of F_d were more obvious at a depth of 0-1 cm than at depths of 1-2 and 2-3 cm, except in A3 (central and row of panels in Figure 4.3). F_d declines might be attributed to vessel clogging by minute dust particles in the water holding collar, although most visible dust had been removed, the effect of cavitation while removing the xylem, and the formation of traumatic tylose because of having injured the xylem. Anyhow the illustrated diurnal patterns of F_d after the xylem removals in Figure 4.3 should be taken as those different from relative F_d. However, for the purpose of comparing with $Q_{\_act}$ and $Q_{\_cal}$, the obtained F_d data could be used.

On days 24 (A1), 16 (A2), and 28 (A3), circumferential variation in F_d was detected, particularly in A1. The average daily value of $F_{d\_0\text{-}1}$ (10:00–15:00) in A1 was 13.26, 16.42, 18.83, and 21.08 in the northerly, easterly, southerly, and westerly directions, respectively. The maximum circumferential variation in $F_{d\_0\text{-}1}$ was about 1.6 times that in the northerly and westerly directions.

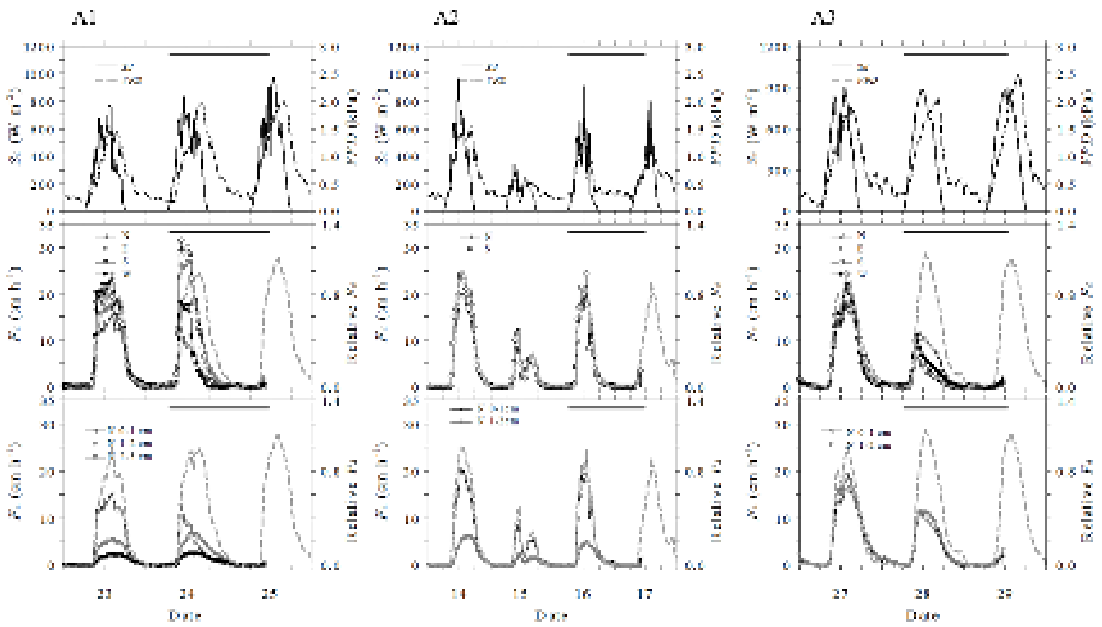

Figure 4.3 Diurnal patterns in solar radiation (S_d), atmospheric vapor pressure deficit (*VPD*) and sap flow velocity (F_d). A1 was measured from October 23-25, 2010. A2 was measured from October 14-17, 2011. A3 was measured from October 27-29, 2012. The upper box showed the *Sd* and *VPD*, the middle box showed the circumferential variation of F_d and the lower box showed the radial variation in F_d. A gray dashed line was the relative F_d measured from another teaks standing in Mae Mo plantation simultaneously. A horizontal solid line indicates the period of supplying water to the water holding collar.

4.3.3 Comparison of $Q_{\_act}$ and $Q_{\_cal}$

Figure 4.4 compares the diurnal patterns in $Q_{\_act}$ and $Q_{\_cal}$ for the three teak tree listed in Table 4.2. In general, $Q_{\_cal}$ underestimated $Q_{\_act}$ in all individuals, even when circumferential variation in $F_{d\_0\text{-}1}$ was taken into consideration (see the dashed lines in Figure 4.4); the underestimations were more pronounced for A1 than for A2 and A3. Table 4.4 lists details for the amount of $Q_{\_act}$ and $Q_{\_cal}$ calculated from 07:00 on the first experimental day through 07:00 on the next. The amount of $Q_{\_cal}$ for A1 was 14.64 kg (i.e., 14.5 % of the amount of $Q_{\_act}$). The amount of $Q_{\_cal}$ for A2 and A3 were 44.1 % and 62.4 % of the corresponding $Q_{\_act}$, respectively (Table 4.4). Despite our consideration of the circumferential variation in $F_{d\_0\text{-}1}$, $Q_{\_cal}$ was underestimated compared to $Q_{\_act}$.

Figure 4.5 shows the relationship between $Q_{\_act}$ and $Q_{\_cal}$ for all individuals. The broken lines represent 1:1 ratios, and the gray solid lines are fitted regression lines. The regressions show that the hourly $Q_{\_cal}$ was lower than the hourly $Q_{\_act}$. The points in the regressions plots were scattered in an approximately elliptical pattern, especially in the graph for A3. For periods when the sap flow was increasing, $Q_{\_cal}$ relatively underestimated $Q_{\_act}$, but when the sap flow was decreasing, $Q_{\_cal}$ relatively overestimate $Q_{\_act}$. The hourly $Q_{\_act}$ and $Q_{\_cal}$ were positively correlated except in the case of A3 (A1; r = 0.99, A2; r = 0.89, A3; r = 0.54).

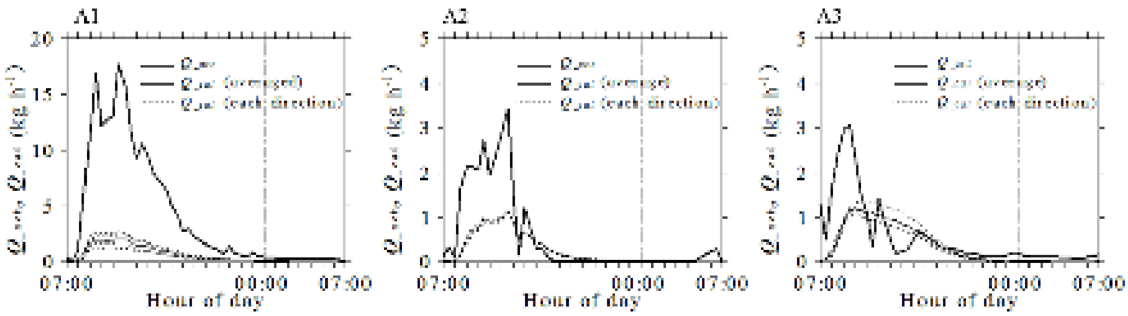

Figure 4.4 Diurnal patterns of hourly $Q_{\_act}$ and $Q_{\_cal}$. $Q_{\_act}$ is represented by thick solid lines; $Q_{\_cal}$ is represented by thin lines. Thin dashed lines represent estimated water uptake calculated as sap flow velocity (F_d) in each direction.

Table 4.4 Comparisons between the amount of $Q_{\_act}$ and $Q_{\_cal}$. The amount of $Q_{\_act}$ and $Q_{\_cal}$ calculated from 07:00 on the first experimental day through 07:00 on the next.

experimental trees	A1	A2	A3
$Q_{\_act}$ (kg)	101.15	13.42	13.72
$Q_{\_cal}$ (kg)	14.64 max: 18.46 (E) min: 10.17 (N)	5.92 max: 6.00 (S) min: 5.85 (N)	8.56 max: 10.18 (N) min: 7.52 (S)
ratio	6.91	2.27	1.60

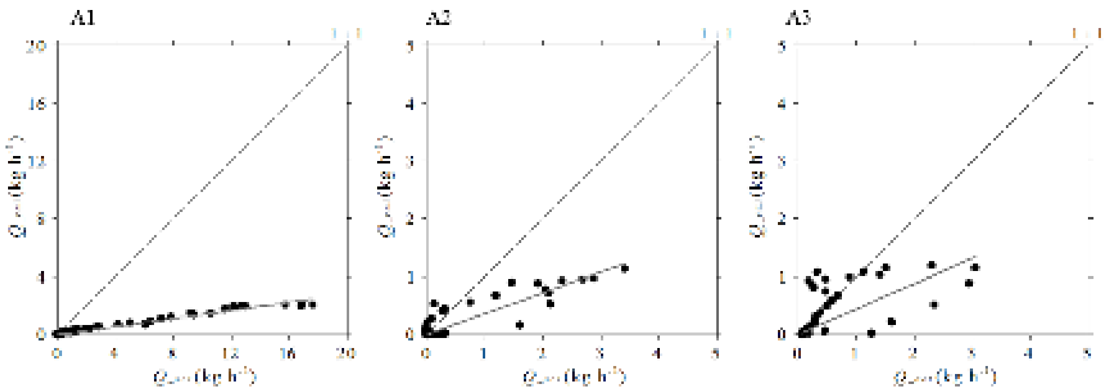

Figure 4.5 Relationship between hourly $Q_{\_act}$ and $Q_{\_cal}$. Broken lines represent ratios of 1:1; gray solid lines are fitted regression line. The correlation coefficients (r) for A1,A2 and A3 are 0.99, 0.89 and 0.54, respectively.

4.4 Discussion

Dye perfusion experiment visualized the sap flow distribution in teak trunks. At the maximum height of dye ascent, the number of dyed annual rings varied from one to five (Table 4.3 and Figure 4.2). However, we were unable to discern the distribution of dyed section in the annual ring by visual observation. The velocity of water in a channel is proportional to the fourth power of its internal radius (Hagen-Poiseuille Low). Since the vessel diameter is large, the sap flow velocity must also be large (Tyree and Zimmermann, 2002). In teak trees, the diameter of the vessels in earlywood ranges from 200 to 300 µm, but in latewood it is <100 µm (Saeki, 1982). Thus, the sap flow velocity in earlywood should exceed that in latewood. Our experiment was conducted during the rainy season; thus, the outermost annual ring retained a water transport function. Moreover, our results indicate that the dyed section spanned more than one annual ring (Figure 4.2b). Thus, large diameter earlywood vessels have water transport functions across more than one annual ring in teak trunk. Dye perfusion experiments on ring-porous species growing in cool temperate climates (Taneda and Sperry, 2008; Umebayashi et al., 2008; Bush et al., 2010; Sato et al., 2010) have demonstrated a restricted water transport function in large diameter earlywood vessels occurring in the outermost annual ring. The freezing cavitation of large diameter earlywood vessels during winter is likely responsible for destruction of the transport function in older vessels (Tyree and Zimmermann, 2002). In contrast, we showed that tropical teaks, which are never exposed to freezing, are able to maintain their water transport function across more than one annual ring. The cavitation of large-diameter vessels occurred due to water stress in the trunk because of soil drought. However Lianas, which are common vine species in tropical climates, have large diameter vessels which the size was same range to the ring-porous species, the large diameter vessels retain their water transport function for many years despite enduring a dry season (Frank et al., 1997). The water transport function of these large diameter vessels is thought to be maintained as a result of refilling due to root pressure (Frank et al., 1997). It is thought that the same phenomenon occurs in teak.

We measured $Q_{\_act}$ in mature teaks in a plantation and compared them with $Q_{\_cal}$. $Q_{\_cal}$ underestimated $Q_{\_act}$ in our experimental trees. The ratio of underestimation varied between approximately one half and one sixth (Table 4.4). An elliptical form in the scatter relationship between hourly $Q_{\_act}$ and $Q_{\_cal}$ indicates a hysteresis, especially A3 (Figure 4.5). This result indicates that the ratio of underestimation differed between periods of increasing and decreasing sap flow. However, the relationship between hourly $Q_{\_act}$ and $Q_{\_cal}$ was linear in cases other than A3 (Figure 4.5); hysteresis between $Q_{\_act}$ and $Q_{\_cal}$ was less obvious in A1 and A2. Thus, a linear fit regression was inappropriate for A3.

Several earlier studies calibrated the TDM in diverse woody species. Some reported satisfactory TDM performance for a variety of trees, including gymnosperms with tracheid (Granier, 1987; Čermák et al., 1992; Catovsky et al., 2002), tropical tree species (Lu and Chacko, 1998; Lu et al., 2002; Clearwater et al., 1999; McCulloh et al., 2007), diffuse-porous species (Braun and Schmid, 1999; Clearwater et al., 1999; Catovsky et al., 2002; Taneda and Sperry, 2008; Bush et al., 2010) and ring-porous species (Catovsky et al., 2002; Granier et al., 1994). However, other reports indicated that TDM calculated sap flow substantially underestimated actual sap flow in diffuse porous species (Taneda and Sperry, 2008; Hultine et al., 2010; Steppe et al., 2010), ring-porous species (Taneda and Sperry, 2008; Bush et al., 2010) and bamboo (Kume et al., 2010a). Bush et al. (2010) calibrated the TDM in four ring-porous (*Elaeagnus angustifolia*, *Gleditsia triacanthos*, *Qercus gambelii* and *Sophora japonica*) and two diffuse-porous (*Populus fremontii* and *Tilia cordata*) species, demonstrating that the TDM severely underestimates actual sap flow in only ring-porous species. Taneda and Sperry (2008) also conducted a TDM calibration using the ring-porous species *Q. gambelii* and the diffuse-porous species *Acer grandidentatum*; they found that the underestimation was more serious for *Q. gambelii*. Likewise, Montague and Kjelgren (2006) compared the actual water uptake of containerized diffuse-porous (*Pyrus calleryana*, *Populus detoides* and *Liquidambar styraciflua*) and ring-porous (*Q. rubur* × *Q. bicolor*) species with TDM-based estimates and found the most serious underestimations by the TDM in the ring-porous tree. These comparative studies indicate that TDM measurement of sap flow produces a greater error for ring-porous than for diffuse-porous tree species. The current study shows that, also in ring-porous teak, TDM underestimates actual sap flow indeed.

$Q_{\_cal}$ was estimated considering the circumferential variation in F_d in teak trunks. In A1, the maximum circumferential variation in $F_{d\_0\text{-}1}$ was about 1.6 times. In the analyses reported in Chapter 3, the circumferential variation in $F_{d\_0\text{-}2}$ was about 1.92 and 3.80 times that in Japanese cedar and Japanese cypress, respectively. Compared to Japanese cedar and Japanese cypress, the circumferential variation in F_d in A1 was nearly equal or a bit smaller. However, $Q_{\_cal}$, as calculated using equation (4.3) was underestimated compared to $Q_{\_act}$.

The high velocity sap flows in ring-porous species may provide partial explanations for these underestimations. In the TDM, heat generated by the sensor is transferred to the sap and transported by the flow. However the large sap flow velocities in large diameter earlywood vessels prevent temperature equilibration between the sensor and sap. Anfodillo et al. (1993) inserted a heater into tree trunks to observe heat transfer by thermographic procedures and found no thermal loading in the outermost annual rings of the ring-porous species (*Fraxinus excelsior*). According to this result, he indicated that the heat could not move to the sap sufficiently because of large sap flow velocity. In our results, however, the relationship between $Q_{\_act}$ and $Q_{\_cal}$ was not a saturation relationship; the relations in our data were either linear or hysteretic (Figure 4.5). So, other explanations are required to account for TDM underestimations in teak trees.

TDM underestimation in ring-porous species may also be explained by a non-uniform sap flow distribution over the sap flow sensors. Clearwater et al. (1999) showed that when there was a large sap flow gradient over the sensor, the sap flow estimated by the average ΔT at the sensor underestimated the actual sap flow because of the nonlinear relationship between sap flow and ΔT (Equation 2.4). A large sap flow gradient over the sensor is more likely to occur when part of the sensor is inserted into heartwood with no water transport function, and when the water transport function is limited in the outermost annual ring, which is the case in ring-porous species. Clearwater et al. (1999) showed that the degree of underestimation increased in proportion to the area of non-conducting tissue in the trunk, and they proposed a correction procedure for modifying the original Granier calibration by taking into account the proportions of conducting and non-conducting tissues sampled by the sap flow sensor. In our comparison of $Q_{\_act}$ and $Q_{\_cal}$, the ratio of underestimation for A1 was larger than for A2 and A3 (Table 4.4). Interestingly, A1 had wider annual rings (i.e. a lower ring density) in its sapwood than the other two teaks (Table 4.2). The wood density of ring-porous species is so high that the density of the annual rings becomes greatly reduced and the width of the earlywood does not vary across annual rings. In contrast, the width of latewood, which comprises small-diameter vessels and non-conducting tissue, varies across annual rings (Shimaji et al., 1985). Even teak, a ring-porous species found in tropical climates, exhibits this tendency (Priya and Bhat, 1999). Therefore, the sap flow sensor inserted into A1 was exposed to a larger area of latewood than the sensors inserted into A2 and A3. The results of our dye perfusion experiment indicate that the sap flow gradient between earlywood and latewood in a single annual ring is large, and that this trend is repeated across several annual rings, producing a wave-like pattern in the sap flow profile. Accordingly, we believe that the sap flow sensor inserted into A1 encountered fewer waves in the sap flow profile than the sensors inserted into A2 and A3; thus, the conducting area on the sap flow sensor inserted into A1 was smaller than the conducting areas in A2 and A3. Although our experiment examined only three individuals, the evidence suggests that the conducting area on the sap flow sensor change with the number of annual rings functioning in water transport. Hence, the degree of underestimation will vary among individuals.

4.5 Conclusion

To test the applicability of the TDM to mature plantation teak trees, dye perfusion experiments and simultaneous measurement of water uptake and sap flow using the TDM were conducted. The teak trees exhibited water transport across more than one annual ring. Based on the vessel distribution in the annual rings of ring-porous species, and the relationship between vessel diameter and sap flow velocity, we propose that large diameter earlywood vessels have water transport functions across more than one annual ring. We compared the actual water uptake with the uptake estimated by the TDM. $Q_{\_cal}$ estimated using the coefficient proposed by Granier (1987) was underestimated compared to $Q_{\_act}$, even when circumferential variation was considered. Moreover, the ratio of underestimation varied at each individual. Thus, estimates of sap flow velocity by the TDM are strongly affected by the unique sap flow distribution in teak tree trunks; the number of functional annual rings is an important determinant of sap flow underestimation measured by the TDM. However we found a linear relationship between hourly $Q_{\_act}$ and $Q_{\_cal}$. This result indicated that the TDM was useful tool to examined the diurnal and seasonal change of sap flow in teak using the relative value.

References

Anfodillo, T., Sigalotti G.B., Tomasi, M., Semenzato, P., & Valentini, R. (1993) Applications of a thermal imaging technique in the study of the ascent of sap in woody species. *Plant, Cell & Environment*, 16, 997-1001. doi: 10.1111/j.1365-3040.1993.tb00524.x

Braun, P., & Schmid, J. (1999) Sap flow measurements in grapevines (Vitis vinifera L.) 2. Granier measurements. *Plant and Soil*, 215, 47-55 doi: 10.1023/A:1004708119821

Bush, S. E., Hultine, K. R., Sperry, J. S., & Ehleringer, J. R. (2010) Calibration of thermal dissipation sap flow probes for ring- and diffuse-porous trees. *Tree Physiology*, 30, 1545-1554. doi:10.1093/treephys/tpq096

Catovsky, S., Holbrook, N. M., & Bazzaz, F. B. (2002) Coupling whole-tree transpiration and canopy photosynthesis in coniferous and broad-leaved tree species. *Canadian Journal of Forest Research*, 32, 295-309. doi: 10.1139/X01-199

Čermák, J., Cienciala, E., Kučera, J., & Hällgren, J. E. (1992) Radial velocity profiles of water flow in trunks of Norway spruce and oak and the response of spruce to severing. *Tree Physiology*, 10, 367-380. doi: 10.1093/treephys/10.4.367

Clearwater, M. J., Meinzer, F. C., Andrade, J. L., Goldstein, G., & Holbrook, N. M. (1999) Potential errors in measurement of nonuniform sap flow using heat dissipation probes. *Tree Physiology*, 19, 681-687 doi: 10.1093/treephys/19.10.681

Coder, K. D. (2011) Tree-ring porosity forms in hardwoods. University of Georgia school of forest resources extension publication for99-018. WEB Site = http://warnell.forestry.uga.edu/service/library/for99-018/for99-018.pdf.

Delzon, S., Sartore, M., Granier, A., & Loustau, D. (2004) Radial profiles of sap flow with increasing tree size in maritime pine. *Tree Physiology*, 24, 1285-1293. doi: 10.1093/treephys/24.11.1285

Ewers, F. W., Cochard, H., Tyree, M. T. (1997) A survey of root pressures in vines of a tropical lowland forest. Oecologia, 110, 191-196. doi: 10.1007/s004420050149

Goulden, M. L., & Field, C. B. (1994) Three methods for monitoring the gas exchange of individual tree canopies: ventilated-chamber, sap-flow and Penman-Monteith measurements on evergreen oaks. *Functional Ecology*, 8, 125-135. doi: 10.2307/2390121

Granier, A. (1987) Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiology*, 3, 309-320. doi: 10.1093/treephys/3.4.309

Granier, A., Anfodillo, T., Sabatti, M., Cochard, H., Dreyer, E., Tomasi, M., Valentini, R., & Bréda, N. (1994) Axial and radial water flow in the trunks of oak trees: a quantitative and qualitative analysis. *Tree Physiology*, 14, 1383-1396. doi: 10.1093/treephys/14.12.1383

Hultine, K. R., Nagler, P. L., Morino, K., Bush, S. E., Burtch, K. G., Dennison, P. E., Glenn, E. P., & Ehleringer, J. R. (2010) Sap flux-scaled transpiration by tamarisk (*Tamarix spp.*) before, during and after episodic defoliation by the saltcedar leaf beetle (*Diorhabda carinulata*). *Agricultural and Forest Meteorology*, 150, 1467-1475. doi: 10.1016/j.agrformet.2010.07.009

Iida, I., Zhao, G. J., Shi, W. C., & Wang, W. T. (1992) Dyeing of xylem utilizing the sap flow of living trees. (3) Investigation of permeable dyes for wood. *Bulletin of Kyoto Prefecture University Forests*, 36, 29–36.　(Japanese with English abstract)

James, S. A., Clearwater, M. J., Meinzer, F. C., & Goldstein, G. (2002) Heat dissipation sensors of variable length for the measurement of sap flow in trees with deep sapwood. *Tree Physiology*, 22, 277–283. doi: 10.1093/treephys/22.4.277

Kollert, W., & Cherubini, L. (2012) Planted Forests and Trees Working Paper Series; Teak resources and Market assessment 2010 (*Tectona grandis Linn. F.*). FAO working paper FP/47/E

Krishnapillay, B. (2000) Silviculture and management of teak plantations. *Unasylva*, 201, 14-21.

Kumagai, T., Aoki, S., Nagasawa, H., Mabuchi, T., Kubota, K., Inoue, S., Utsumi, Y., & Otsuki, K. (2005) Effects of tree-to-tree and radial variations on sap flow estimates of transpiration in Japanese cedar. *Agricultural and Forest Meteorology*, 135, 110-116. doi: 10.1016/j.agrformet.2005.11.007

Kume, T., Onozawa, Y., Komatsu, H., Tsuruta, K., Shinohara, Y., Umebayashi, T., & Otsuki, K. (2010a) Stand-scale transpiration estimates in a Moso bamboo forest: (1) Applicability of sap flux measurements. *Forest Ecology and Management*, 260, 1287-1294. doi: 10.1016/j.foreco.2010.07.012

Kume, T., Tsuruta, K., Komatsu, H., Kumaga,i T., Higashi, N., Shinohara, Y., & Otsuki, K. (2010b) Effects of sample size on sap flux-based stand-scale transpiration estimates. *Tree Physiology*, 30, 129-138. doi: 10.1093/treephys/tpp074

Kume, T., Otsuki, K., Du, S., Yamanaka, N., Wang, Y., & Liu, G. (2011) Spatial variation in sap flow velocity in semiarid region trees: its impact on stand-scale transpiration estimates. *Hydrological Processes*, 26, 1161–1168. doi: 10.1002/hyp.8205

Lu, P., & Chacko, E. (1998) Evaluation of Granier's sap flux sensor in young mango trees. *Agronomy for Sustainable Development*, 18, 461-471. doi: 10.1051/agro:19980703

Lu, P., Woo, K. C., & Liu, Z. T. (2002) Estimation of whole-plant transpiration of bananas using sap flow measusremnts. *Journal of Experimental Botany*, 53, 1771-1779. doi: 10.1093/jxb/erf019

McCulloh, K. A., Winter, K., Meinzer, F. C., Garcia, M., Aranda, J., & Lachenbruch, B. (2007) A comparison of daily water use estimates derived from constant-heat sap-flow probe values and gravimetric measurements in pot-grown saplings. *Tree Physiology*, 27, 1355-1360. doi: 10.1093/treephys/27.9.1355

Montague, T., & Kjelgren, R. (2006) Use of thermal dissipation probes to estimate water loss of containerized landscape trees. *Journal of Environmental Horticulture*, 24, 95-104.

Phillips, N., Oren, R., & Zimmermann, R. (1996) Radial patterns of xylem sap flow in non-, diffuse- and ring-porous tree species. *Plant, Cell & Environment*, 19, 983-990. doi: 10.1111/j.1365-3040.1996.tb00463.x

Priya, P. B., & Bhat, K. M. (1999) Influence of rainfall, irrigation and age on the growth periodicity and wood structure in teak (*Tectona Grandis*). *IAWA Journal*, 20, 181-192.

Renninger, H. J., & Schäfer, K. V. R. (2012) Comparison of tissue heat balance- and thermal dissipation-derived sap flow measurements in ring-porous oaks and a pine. *Frontiers in Plant Science*, 3, 103. doi: 10.3389/fpls.2012.00103

Saeki, H. (1982) The structure of domestic and imported wood in Japan. Japan forest technology association, Tokyo (in Japanese)

Sano, Y., Okamura, Y., & Utsumi, Y. (2005) Visualizing water-conduction pathways of living trees: selection of dyes and tissue preparation methods. *Tree Physiology*, 25, 269-275. doi: 10.1093/treephys/25.3.269

Sato, T., Tanaka, N., Inoue, M., Sawada, H., Watanabe, S., & Suzuki, M. (2010) Report on an experiment of dye injection into xylem sap of a *Quercus serrata* tree in University Forest in Aichi. Misc. Inform. *The University of Tokyo Forests*, 49, 29-41. (in Japanese with English abstract)

Shimaji, K., Saeki, H., Harada, H., Shiokura, T., Ishida, S., Shigematsu, T., Sudo, A. (1985) Structure of woods-woodscience 1. Bunei-do, Tokyo (in Japanese)

Steppe, K., De Pauw, D. J. W. D., Doody, T. M., & Teskey, R. O. (2010) A comparison of sap flux density using thermal dissipation, heat pulse velocity and heat field deformation methods. *Agricultural and*

Forest Meteorology, 150, 1046-1056. doi: 10.1016/j.agrformet.2010.04.004

Taneda, H., & Sperry, J. S. (2008) A case-study of water transport in co-occurring ring- versus diffuse-porous trees: contrasts in water-status, conducting capacity, cavitation and vessel refilling. *Tree Physiology*, 28:1641-1651. doi: 10.1093/treephys/28.11.1641

Tateishi, M., Kumagai, T., Utsumi, Y., Umebayashi, T., Shiiba, Y., Inoue, K., Kaji, K., Cho, K., & Otsuki, K. (2008) Spatial variations in xylem sap flux density in evergreen oak trees with radial-porous wood: comparisons with anatomical observations. *Trees*, 22, 23-30. doi: 10.1007/s00468-007-0165-8

Tsuruta, K., Kume, T., Komatsu, H., Higashi, N., Umebayashi, T., Kumagai, T., & Otsuki, K. (2010) Azimuthal variations of sap flux density within Japanese cypress xylem trunks and their effects on tree transpiration estimates. *Journal of Forest Research*, 15, 398-403. doi: 10.1007/s10310-010-0202-0

Tyree, M. M. & Zimmermann, M. H. (2002) Xylem structure and the ascent of sap. Springer Series in Wood Science. Ed. T.E.Timell. Springer, New York, 113-117

Umebayashi, T., Utsumi, Y., Koga, S., Inoue, S., Fujikawa, S., Arakawa, K., Matsumura, J., & Oda, K. (2008) Conducting pathways in north temperate deciduous broadleaved trees. *IAWA Journal*, 29, 247-263.

Chapter 5

Differences in the seasonality of transpiration estimated using sap flow measurements and the eddy covariance method

This chapter cannot be opened because the content, figures and tables in this chapter will be submitted to the scientific journal within 5 years.

Chapter 6

The influence of soil moisture conditions on sap flow seasonality in individual teak trees

This chapter cannot be opened because the content, figures and tables in this chapter will be submitted to the scientific journal within 5 years.

Chapter 7

Summary and conclusion

This study examined the seasonal variation in transpiration in individual teak trees growing in northern Thailand using sap flow measurements. The sap flow distribution in the trunk of each teak tree was also determined using the thermal dissipation method (TDM). There are no studies applying the TDM in teak, a ring-porous species found in tropical climates. Thus, this study also examined the sap flow distribution in Japanese cedar and Japanese cypress, located in the Oborasawa Watershed (Kanagawa prefecture, Japan). Japanese cedar and Japanese cypress is coniferous species and there are some previous studies applying the TDM in Japanese cedar and Japanese cypress.

Chapter 1 described the importance of, and problems associated with, the study of energy, water, and carbon exchanges between the vegetation and atmosphere in tropical forests, especially tropical deciduous forests. In addition, the usefulness of sap flow measurements in examining the water cycle in tropical deciduous forests was described. Tropical forests have a strong influence on both regional and global climates. In particular, tropical deciduous forests in Southeast Asia are affected by the Asian monsoon; the leaves in the canopy are retained during the wet season and fall during the dry season. Inter-annual variation in the duration of the canopy and transpiration period is affected by inter-annual variation in rainfall to a greater extent in tropical deciduous forests than in boreal and temperate deciduous forests. On the other hand, the leaf phenology in tropical deciduous species varies widely not only between but also within species. Transpiration seasonality also varies with variation in leaf phenology, even if the forest is composed of uniform species. Canopy duration time is strongly affected by the transpiration period. Thus, it is necessary to focus on transpiration seasonality at the individual tree scale in tropical deciduous forests. Sap flow measurements can be used to examine the transpiration in a forest at the individual tree level using a diurnal or seasonal time scale. Therefore, sap flow measurements can be used to examine transpiration seasonality in tropical deciduous forests. In this study, sap flow measurements were conducted at a teak plantation to examine the seasonality in transpiration for individual trees. The simple species component and forest structure of the plantation facilitated the evaluation of transpiration seasonality according to changes in canopy structure. Teak is a popular tree species in tropical regions. The information about seasonal variation in transpiration gained in this study will enable appropriate water resource management at teak plantations. Sap flow measurements were also conducted for Japanese cedar and Japanese cypress. Japanese cedar and Japanese cypress are popular species for planting in Japan, and sap flow measurements have been widely used to examine water use by these species at the whole-tree and stand scales. However, circumferential variation in sap flow in the trunk of Japanese cedar or Japanese cypress is poorly understood, especially for trees on a steep slope. Thus, the effect of circumferential sap flow variation in Japanese cedar and Japanese cypress on estimates of whole-tree water use was discussed.

Chapter 2 described the study sites where the sap flow measurements were made for Japanese cedar and Japanese cypress in Kanagawa prefecture, Japan (35° 28′ N, 139° 12′ E, altitude 432-878 m; Oborasawa Watershed), and for teak at the Mae Mo plantation in northern Thailand (18° 25′ N, 99° 43′ E, altitude 380m; Mae Mo plantation). An outline of the sap flow measurements made using the TDM was also presented in Chapter 2. Meteorological measurements were conducted in an open space on a ridge at the Oborasawa Watershed. Sap flow measurements were conducted in Japanese cedar and Japanese cypress stands located on adjoining northwest- and southeast-facing slopes; the slope angles were 30° and 25°, respectively. Sap flow measurements were made from 21 August, 2010, to 26 September, 2010. At the Mae Mo plantation, meteorological measurements and measurements of gas exchange by the eddy covariance method were conducted at a scaffold tower (height, 40 m). Sap flow measurements were made in two different plots at the Mae Mo plantation (plots A and B) from March, 2010, to March, 2013. The soil water content at depths of 10, 20, 40, and 60 cm, and the downward solar radiation under the canopy (S_b) were also measured in plots A and B. The downward solar radiation above the canopy (S_d) was measured from the scaffold tower. In each plot, the relative extractable water, $\Theta_{0\text{-}60}$, was calculated from the soil water content at each depth, and the negative logarithmic values of the ratio (NLR), which is an index of leaf area, was calculated from S_d and S_b. A handy dynamic corn penetrometer was used in plots A and B to examine the soil depth. Plots A and B were located approximately 400 m apart (to the east and west). Plot B, which was located at the foot of a mountain, had a gentle slope, while the topography in plot A was flat. The soil depths in plots A and B were 150-400 cm and 50-150 cm, respectively. During the transition from the dry to the wet season, the timing of the increase in $\Theta_{0\text{-}60}$ and NLR was almost synchronized following heavy rainfall in each plot. On the other hand, during the transition from the wet to the dry season, the progress of decreasing $\Theta_{0\text{-}60}$ was earlier in plot B than in plot A; similarly, the NLR value in plot B began to decrease earlier than in plot A.

In Chapter 3, circumferential sap flow variation in the trunks of Japanese cedar or Japanese cypress trees growing on a steep slope was described, and the effect of circumferential sap flow variation on estimates of whole-tree water use was discussed. Japanese cedar and Japanese cypress growing on a steep slope extended their crowns toward the lower slope. The circumferential distribution of sap flow in Japanese cedar and Japanese cypress was confirmed; however, no relationship between circumferential sap flow variation and tree crown shape was detected. The potential error in our estimates of whole-tree water use for Japanese cedar and Japanese cypress using the general method was at most 20 and 40%, respectively, when circumferential sap flow variation in the trunk was ignored.

Chapter 4 described the sap flow distribution in teak trunk based on dye perfusion experiments. In addition, the amount of water absorbed from the cut xylem surface, $Q_{\_act}$ (kg h^{-1}), and the estimated amount of water absorbed using the TDM, $Q_{\_cal}$ (kg h^{-1}), were compared. Dye perfusion experiments were conducted using three teaks located in plot A. The dye ascent speed varied from 440 to 2840 cm h^{-1}. At the maximum height of dye ascent, the number of dyed annual rings varied from one to five. However, it was impossible to determine the relationship between the functionality and anatomical features of the vessels (i.e., between the vessels in earlywood and latewood) based on a visual observation of the dyed disks. The relationship between sap flow velocity and vessel diameter indicates that the sap flow distribution in annual rings will be skewed toward earlywood. Moreover, the results of the dye perfusion experiment indicated the existence of more than one functional annual ring, suggesting that the radial sap flow distribution in teak trunk has a wave-like pattern. Absorption experiments and sap flow measurements were conducted simultaneously in three teak trees located in plot A. $Q_{\_cal}$ was underestimated compared with $Q_{\_act}$, and the ratio of underestimation varied from 1.5 to 6.0 times at each individual. In Chapter 3, we demonstrated that circumferential variation in sap flow within the trunk is important for whole-tree water use estimates. However, when $Q_{\_cal}$ was estimated considering circumferential variation in $F_{d\_0\text{-}1}$ in teak trunks, $Q_{\_cal}$ was underestimated compared with $Q_{\_act}$. Moreover, the ratio of underestimation varied among individuals. The extent of underestimation was greatest in the teak tree with the lowest annual ring density. According to the radial sap flow distribution in teak trunk shown by the dye perfusion experiments, the conducting area on the sap flow sensor will change according to the number of annual rings that are active in water transport, and the degree of underestimation will therefore vary among individuals.

Chapter 5 described the difference in transpiration seasonality at a teak plantation estimated using sap flow measurements and the eddy covariance method. The mean stand sap flow velocity, J_s (cm h^{-1}), was calculated using the TDM for five teaks located in plot A. The stand sapwood area, $SWA_{\_stand}$ (cm^2), in plot A was estimated from extracted xylem cores. The estimated transpiration rate based on sap flow measurements, $E_{\_sap}$ (mm day^{-1}), was calculated by multiplying the values of J_s and $SWA_{\_stand}$. The latent heat flux, LE (W m^{-2}), measured using the eddy covariance method, is composed of transpiration from the canopy, LE_c (W m^{-2}), and soil evaporation, LE_s (W m^{-2}). Thus, the value of LE_c was estimated by subtracting LE from LE_s. LE_c was converted to the height of water, $E_{\_eddy}$ (mm day^{-1}), for comparison with the $E_{\_sap}$.

The relationship between $E_{\_sap}$ and $E_{\_eddy}$ was examined between October 19 and 30, 2011; the effect of LE_s was ignored because of crown closure. A linear relationship was detected between $E_{\_sap}$ and $E_{\_eddy}$ (R^2 = 0.72), and the $E_{\_sap}$ value was about one-tenth the $E_{\_eddy}$ value. Subsequently, the $E_{\_sap}$ value modified by that relationship was compared with the $E_{\_eddy}$ value from October 2011 to March 2012. The relative $E_{\_sap}$ and $E_{\_eddy}$ values exhibited a linear relationship (R^2 = 0.72). Thus, the transpiration estimated from TDM was useful for examining transpiration seasonality in the teak canopy. From December to January, the relative $E_{\_sap}$ was greater than the relative $E_{\_eddy}$. The objective spatial scale of sap flow measurements is narrower than that using the eddy covariance method. Thus, the estimated value of $E_{\_sap}$ based on our sap flow measurements reflected the transpiration characteristics of the teak trees standing in plot A.

Chapter 6 described the sap flow seasonality for individual teak trees using the sap flow measurements from plots A and B, as well as the effect of soil water content on sap flow seasonality. The relative sap flow velocity, *SF*, was used to compare the sap flow seasonality for each individual. The TDM was used in plot A, while the heat pulse method (HPM) was used in plot B. Granier-type and heat pulse sensors were inserted into the two teaks standing in plot A, and sap flow measurements were made simultaneously. According to this result, the relative values obtained with the TDM and HPM could be used to compare the seasonal sap flow in each individual. In plot A, the seasonality of the relative *SF* for each individual was revealed using sap flow measurements collected from March, 2010, to March, 2013. The seasonality of the relative *SF* during the leaf flush period was largely synchronized in each plot according to the increases in $\Theta_{0\text{-}60}$ and relative NLR. On the other hand, the seasonality of the relative *SF* during the leaf fall period varied for each individual about every 30 days. The seasonality of the relative *SF* in plots A and B, which had different soil water contents, was compared from March, 2010, to March, 2011. The timing of the increase in relative *SF* was nearly identical between the plots, the value of $\Theta_{0\text{-}60}$ when the relative *SF* exceeded 0.2 was about 0.2 $m^3\ m^{-3}$ in both plots. On the other hand, during the leaf fall period, the relative *SF* in plot B began to decrease earlier than in plot A. Moreover, the relative *SF* in plot B stopped earlier than in plot A. The value of $\Theta_{0\text{-}60}$ when the relative *SF* was below 0.8 was about 0.1 $m^3\ m^{-3}$ in both plots, and the day that the value of $\Theta_{0\text{-}60}$ reached 0.1 in plot B was earlier in plot A. Thus, the seasonal variation in sap flow from teak standing in plot A and plot B corresponded with the soil water content.

Sap flow measurements using the TDM is a useful technique to estimate whole-tree or plot scale water use in mainly coniferous spices. This study determined the circumferential variation in sap flow in Japanese cedar and Japanese cypress using the TDM, and the effect of that variation on estimates of whole-tree water use was discussed. There are no previous studies applying the TDM to teak. Thus, it was necessary to examine the sap flow distribution in teak in order to take sap flow measurements using the TDM.

The sap flow velocity in teak trunks was greater than that in the coniferous and diffuse-porous species, and the large sap flow velocity occurred in more than one annual ring. The estimated whole-tree water use based on the TDM was underestimated compared with the actual water use, and the ratio of underestimation varied among individuals. This indicates that the large sap flow velocity and annual ring width in sapwood resulted from non-uniform heat distribution across the Granier-type sap flow sensor. Transpiration from the teak canopy was estimated using both the TDM and eddy covariance method, and the results were compared. Although the sap flow measurement was about one-tenth the value produced using the eddy covariance method, the two methods showed a linear relationship. Our results indicate that the relative value obtained using the TDM in teak can be used to examine transpiration seasonality.

The seasonal variation in sap flow in individual teak trees was determined by making sap flow measurements in two plots with different soil water contents and different leaf phenology. The seasonal variation in sap flow strongly affected the soil water content at the stand and plot scales. Thus, the seasonal variation in sap flow in teak varied in response to the soil water content, even for trees in the same plantation.

Previous studies of the energy balance and water and carbon cycles at teak plantations utilized the eddy covariance method and were conducted on the stand or catchment scale. The present study demonstrated that the individual tree scale is important for examining the transpiration characteristics of teak plantations. The variation in sap flow among individual teak trees shown in this study was equal to the inter-annual variation in transpiration shown in previous studies. Thus, the variation in sap flow in each individual teak tree will have a large influence on the energy balance and water and carbon cycles in teak plantations.

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