博士論文（要約）

Doctorate Thesis (Abridged)

Influences of ambrosia beetle (*Platypus quercivorus*) attacks on evapotranspiration in a secondary warm-temperate forest

(暖温帯二次林の蒸発散量に及ぼすカシノナガキクイムシ（*Platypus quercivorus*）の加害の影響)

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Influences of ambrosia beetle (*Platypus quercivorus*) attacks on evapotranspiration in a secondary warm-temperate forest

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ABSTRACT

The incidence of Japanese oak wilt (JOW), which is caused by an Ascomycetes fungus *Raffaelea quercivora* vectored by an ambrosia beetle, *Platypus quercivorus*, has been intensified in Japan since late 1980s. Previous studies described that the JOW is likely to cause severe impacts on Fagaceae tree dominated forested ecosystems with canopy loss and changes in water and nutrient uptake. Changes in canopy cover, interception, evapotranspiration (ETI), nutrient, and water uptake have the potential to alter hydrologic processes including stream flow and soil moisture following the incident of JOW.

Therefore, the estimation of changes in ETI rate following JOW is important for assessing the water balance of infested catchments. However, changes of transpiration in infested but surviving oak trees, the transpiration response of surrounding trees to the dead oak and changes of watershed level ETI remain unclear in JOW infested forested catchments in Japan. Therefore, this dissertation contributes to filling the knowledge gap in scientific understanding of these intertwined processes by measuring sap flux density variation of infested but surviving oak trees, the measuring transpiration response of surrounding trees, and evaluating the changes of watershed level ETI after a mass attack of *P. quercivorus*. Thus, the purpose of this study was to investigate the influence of *P. quercivorus* attacks on ETI in secondary warm-temperate forest. The research was conducted in Akazu Research Forest (AKRF), which is a warm-temperate secondary forest own to Ecohydrology Research Institute (ERI), the university of Tokyo Forests in the University of Tokyo. Two main experiments with historical hydro-climatological data analysis were conducted to achieve the objectives.

It was hypothesized that whole-tree sap flux would be reduced in surviving oak trunks owing to sapwood dysfunction; however, part of this reduction would be compensated by enhanced sap flux density (F_d) in the remaining functioning sapwood. To test this hypothesis, 25%, 50%, and 75% of sapwood was removed at breast height to simulate xylem dysfunction for nine *Quercus serrata* trees in AKRF. Granier probes were used to measure the F_d of the treated and three control trees before and after the treatment. Even though tested trees were still alive until at least the end of the second growing season, external symptoms of weakening were detected in 75% treated trees. The analysis using a linear mixed model showed that whole-tree sap flux was significantly reduced in all treatments. However, 25% and 50% treated trees showed significant F_d compensation, whereas 75% treated trees showed significantly smaller whole-tree sap flux than the value expected from the treatment. These results suggest that the threshold of tree weakening lies between 50% and 75% of sapwood removal, above which the F_d compensation cannot be attained. Therefore, whole-tree sap flux in infested but surviving trees varies with respect to the intensity of sapwood damage.

ETI is more variable following the JOW as decreased transpiration from attacked but surviving trees and die-off of oak trees. However, decreased ETI may be offset by increased transpiration by surrounding trees. The transpiration response of individual tree-scale associated with JOW eventually leads to a larger scale response such as stand-scale or catchment-scale. In order to clarify this hypothesize, girdling treatments were applied to the top canopy oak trees in three treatment groups. F_d of 40 neighboring trees representing canopy, sub-canopy, and understory in control and treatment groups were measured for 104 days using Granier sensors in pre and post-treatment conditions. Permanent canopy wilting was observed on 10 days following the girdling treatment.

There were clear seasonal dynamics of F_d s in trees in the control group, with obviously lower F_d values on rainy and cloudy days compared to that of sunny days. Moreover, F_d tended to be decreased with season, showing that whole-tree F_d decreased with season progression from summer to autumn. However, F_d of some trees in the treated groups showed unusual higher F_ds, compared to the controls at two different timings;. (1) the following day of the treatment, (2) after canopy wilt of treated oak. Moreover, F_d decreases with season progression were absent in the trees which showed unusually higher F_ds. Out of the 31 studied trees in the treated groups, 16 trees (52%) showed F_d increases either one of the above-mentioned occasions. The increased F_ds of neighboring trees indicates that transpiration increases in neighboring vegetation following JOW. However, data analysis using LMM showed that F_d increases of neighboring trees in the treatment groups were not significant ($p>0.05$) when compared with the F_d of trees in the control group. In this experiment, F_d measurement was restricted to the first growing season of the study trees. Therefore, time might be the limiting factor for neighboring trees to increase tree leaf foliage and adjusting tree hydraulic architecture for new micro-climatic condition following the oak die-off. Therefore, the result implies that transpiration increases of surrounded vegetation were not large enough to trade-off transpiration losses due dead oak by JOW in the same growing season. Thus, it can conclude that no significant F_d increases imply no transpiration increases in neighboring trees during the first growing season following the girdling treatment. Therefore, ETI reduction can be anticipated in forested watershed following a mass attack of *P. quercivorus*.

In order to study the long-term (7 years) watershed level ETI change before and after the JOW, oak tree mortality and changes of ETI rates were analyzed in North creek (NC) and South creek (SC) a two paired watersheds in AKRF. The first appearance of JOW in the AKRF was reported in 2007, the epidemic peaked in 2011. From January 2008 to Jun 2011 and July 2011 to December 2012 considered as a pre and post infestation period respectively. Before onset of JOW, basal area (BA) composed by *Q. serrata* was reported as 9.4 $m^2\,ha^{-1}$, and 8.7 $m^2 ha^{-1}$ in NC and SC, respectively. The analysis of annually recorded ambrosia beetle attack data from 2007 to 2014 showed that a rapid tree die-off in 2011 and 27% to 33% of oak tree mortality at the end of 2014 in NS and SC, respectively. At the end of 2014 percentage of BA composed by *Q. serrata* was 50% in NC and 49% in SC. The daily observed ETI rates were determined using short-time period water balance method, while potential ETI were calculated using a simple ETI model developed based on the Priestley-Taylor equation. The observed ETI for before infestation period showed good agreement with a similar study in the past. Moreover, calculated ETI was highly correlated (0.84) with observed ETI for before infestation period. To examine how JOW influenced on watershed ETI, an LMM was employed, in which "ETI" was a response variable, "TYPE of ETI" was a fixed effect, and "date" was a random effect. If the observed ETI of each year negative and significantly smaller than 0, it was decided that observed ETI smaller than that of calculated ETI. Results show that there was no significant difference between observed and calculated ETI in the pre-infestation period in both watersheds. In contrast, observed ETIs were significantly smaller in post-infestation period indicating that JOW caused significant ETI reduction. Furthermore, the comparison between annual observed and calculated ETI showed that 6% and 21% reduction in annual ETI in SC and NC respectively.

As shown in the partial sapwood removal experiment, attacked but surviving trees showing significant transpiration reduction owing to sapwood dysfunction. Moreover, tree girdling experiment showed that increased transpiration in neighboring trees did not significant enough to trade-off the ETI reduction due to oak tree die-off. Therefore, a number of dead oak trees, attacked but living trees, as well as transpiration response of surrounding vegetation, are key factors for determining the watershed scale ETI changes following JOW infestation. Comparison between observed and calculated ETI showed a significant ETI reduction following the incident of JOW. The reductions of ETI in two watersheds were not similar. Results showed that the reduction of ETI varied with reduction of BA coverage by *Q. serrata* in spite of the percentage of BA reduction or tree mortality rate. However, the watershed level ETI analysis showed that compensatory sap flux effect and transpiration increases of surrounding vegetation were not significantly trade-offs the ETI reduction due to oak tree mortality. Previous studies suggested that within a first or second growing season, the reduction of stand-scale ETI is more common in spite of increases of individual tree scale transpiration. Moreover, researchers' emphasis that remaining vegetation and newly recruited vegetation seems to offset the loss of ETI within approximately 8 years following a forest disturbance event. In this study, the post disturbance period was limited to 3.5 years. Therefore, it can be assumed that T response of remaining and newly recruited vegetation small compared to the decreased ETI by oak die-off. In other words, the results suggest that transpiration response for 3.5 years following JOW is not significant enough to trade-off the ETI reduction by oak tree die-off. In conclusion, results demonstrate that JOW infested watershed experience a reduction of ETI, due to the reduction of T in attacked but surviving trees and reduction of T and interception by dead oak trees.

Based on the literature review on, it could be stated that this study is the first attempt to investigate hydrological influence of JOW. The identification of whole-tree sap flux compensatory effect in treated but surviving *Q. serrata* trees one of the important findings in this study. Moreover, the observed transpiration response of the neighboring vegetation to the girdling treatment and watershed level ETI reduction response following the JOW will be remarkable recordings for filling the knowledge gaps. This information will be useful in better understanding watershed-scale hydrology in forests disturbed by JOW.

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LIST OF ABBREVIATIONS

AIC	Akaike information criterion
AKRF	Akazu Research Forest
ANRF	Ananomiya Research Forest
AT	After treatment
BA	Before attack
BT	Before treatment
C	Canopy
DBH	Daimeter at breast height
DOY	Day of year
E	Evaporation
EEMD	Empirical Ensemble Mode Decomposition
Eq.	Equation
ERI	Ecohydrology Research Institute
ETI	Evapotranspiration
GSALS	Graduate School of Agriculture and Life Science
ha	hectare
I	Interception
IUFRO	International Union of Forest Research Organizations
JOW	Japanese oak wilt disease
LMM	Linear mixed model
LTER	Long-term ecological research
NC	North creek
P	precipitation
PWD	Pine wilt disease
RH	relative humidity
SC	South creek
SC	Sub-canopy
SD	solar radiation
T	Transpiration

T_a	Temperature
UN	Understory
UTokyo	The University of Tokyo
VPD	vapor pressure deficit
Q	discharge
NSC	no significant change

CHAPTER 1 GENERAL INTRODUCTION

1.1 Background and motivation

The collective term, evapotranspiration (ETI) is the total loss water via vaporization in a given watershed. The main three components of ETI are the evaporation of intercepted water (I), transpiration by plants (T), and evaporation from the earth surface (E) (Suzuki 1980; Adams *et al*., 2012). ETI is an important natural process in which 60-95% of precipitated water in terrestrial ecosystem transfers to the atmosphere (Wilson *et al*., 2001; Mathney *et al*., 2014). Changes in forest structure and functioning subsequent disturbances may have an effect on ETI (Matheny *et al*., 2014; Nolan *et al*., 2014). Forest disturbances like wildfires, insects/pest disease, harvesting and silvicultural treatments play a major role in determining forest structure, composition, and natural cycles that can alter ETI (Brown *et al*., 2005; Matheny *et al*., 2014; Surfleet and Skaugset 2013; Ayres *et al*., 2000). In the forest hydrology, ETI is a major component of catchment water budget (Adams *et al*., 2012; Hubbard *et al*., 2013; Mathney *et al*., 2014). Thus understanding how changes in forest cover affect ETI, is critical to understand the effects of disturbance on water yield, water quality at different temporal scales, and on peak and low flows (Brown *et al*., 2005; Noguchi *et al*., 2004).

In recent decades, researchers found the large levels of tree mortality due to a combination of drought, warmer temperature and infestation by pathogen and /or pests (Adams *et al.*, 2012; Pugh 2012; Mikkelson *et al*., 2013; Hubbard 2013; Schäfer *et al*., 2014). However, watershed related studies have been focused on the impact of forest management activities and very few studies relevant ecohydrological consequences following the large-scale tree mortality (Potts 1984; Adams *et al*., 2012). Among the available studies related to tree mortality and hydrological consequences, were limited to coniferous forests and most studies were recorded in the North American continent, few from Europe (Adams *et al*., 2012; Mikkelson *et al*., 2013).

In the Japanese context, pine wilt disease (PWD) induced by the pinewood nematode, *Bursaphelenchus xylophilus*, was a great threat to pine forests in Japan (Mamiya, 1988). It was reported 110 mm annual ETI reduction following PWD in 20 years old Japanese black pine (*Pinus thunbergii*) forest (Abe and Tani, 1985). Mass mortality of trees belonging to the family Fagaceae by Japanese oak wilt disease (JOW) is a major issue in Japan from 1980s (Kuroda and Yamada, 1996; Ito and Yamada, 1998; Kamata *et al*., 2002). The wide spread of JOW in Japanese islands is expected to be accelerated as a result of global warming (Kamata *et al*., 2002; Sanguansub, 2012). The mass mortality of oak trees due to JOW reduces canopy cover and tree density, which has a major impact on the landscape, dynamics, and conservation of temperate forests in Japan (Hata *et al*., 2014; Kamata *et al*., 2002). Tree mortality results in loss of canopy cover and thus directly alters E, T, and canopy I in the hydrologic cycle. As indirect effects of tree mortality, alteration of the watershed hydrologic processes such as infiltration, percolation, runoff, and stream discharge can be highlighted (Adams *et al*., 2012). Therefore, the influence of JOW on vegetation changes by tree mortality has the potential of alteration of ETI and finally may change the catchment water budget. Therefore, estimation of changes in ETI following the JOW is important for assessing the water balance and crucial for future watershed management's activities in infested watersheds. However, studies related to hydrological consequence following the JOW have not been reported so far

Photo: Nobuaki Tanaka, 2010

Figure 1.1 A photograph of Seto Mixed Forest Site, a warm-temperate forest infested with Japanese oak wilt disease (JOW) in 2010. Wilted oak canopies can be identified in brow color

1.1.1 Japanese oak wilt disease (JOW)

Incidences of JOW have been recorded since the 1930s in Japan, with epidemics being documented since the late 1980s (Hijii *et al*., 1991; Kamata *et al*., 2002; Kobayashi and Ueda, 2005). A rapid increasing of the epidemic was observed after 2002 onward, and disease has become an national issue (Forest Agency, 2012). Consequently, the mass mortality of trees belonging to the family Fagaceae during the summer months has become a serious problem (Kuroda and Yamada, 1996; Ito and Yamada, 1998). JOW is caused by an Ascomycetes fungus *Raffaelea quercivora* (Kubono and Ito, 2002) that is vectored by an ambrosia beetle *Platypus quercivorus* (Murayama) (Ito and Yamada, 1998; Kubono and Ito, 2002). A male beetle excavates an entrance hole into sapwood and uses a pheromone to attract both male and female beetles (Kamata *et al*., 2002). Because only females have mycangia, in which they carry ambrosia fungi, infection by R. quercivora occurs after female starts to construct a gallery in sapwood. Raffaelea quercivora spreads into sapwood from the gallery surface and cause necrosis followed by discoloration. The discolored area spreads surrounding the beetle galleries. Vessels in the necrosis are non-conductive (Kuroda and Yamada, 1996; Kuroda, 2001). If many beetles attack the host tree until the necrosis stop water conductance, wilting with foliage discoloration will appear (Saito et al., 2001) resulting in branch dieback or tree mortality (Kuroda and Yamada, 1996). However, some trees can survive even if they receive the insect attack (Kamata et al., 2002; Murata et al., 2007; Yamasaki et al., 2014). It has been reported that *P. quercivorus* prefers large trees, dense forest (Kobayashi and Ueda, 2005; Yamasaki *et al*., 2013; Oguro *et al*., 2015). In general, *P. quercivorus* use weakened and fallen trees as hosts (Wood, 1982, Kamata *et al*., 2002). Ultimately, this phenomenon results in branch dieback or even tree mortality (Kuroda and Yamada, 1996) (Figure 1.1). However, some infested trees survive after the initial attack without receiving a mass attack and those trees do not show even branch dieback and externally similar to healthy trees (Kamata *et al*., 2002; Murata *et al*., 2007; Yamasaki *et al*., 2014).

JOW is prevalent in 31 out of 47 prefectures in Japan, damaging 325,000 m^3 in (Forest Agency, 2012; Matsuda *et al*., 2012). A drastic change in vegetation is occurs following the mass attack and followed tree mortality of oak (Kuroda *et al*., 2011). Tree mortality is due to JOW differs among the species. Out of 50 susceptible Fagacea tree species in Japan, dieback has been recorded to happen in only 15 species (Yamada, 2008). However, tree mortality in *Quercus crispula* Blume and *Quercus serrata* is more common. With reference to *Q. crispula*, the mortality of attacked trees was about 40% (Kamata *et al*., 2002).

Even though damaged forests will recover with natural resilience (Kuroda *et al*., 2012; Nolan *et al*., 2014), the mass mortality directly effects on timber production, charcoal production and secondary products such as mushrooms cultivation (Kondoh *et al*., 2015). In addition, mass mortality of oak trees reduces canopy cover and tree density, which has a major impact on the landscape, dynamics, and conservation of forests by degrading the quality of the ecosystem (Kuroda *et al*., 2012; Hata *et al*., 2014). After a mass attack, the average canopy coverage of severely damaged forest was reported as 28% and 47% in *Q. crispula* and *Q. serrata* dominated forests respectively (Saito and Shibata, 2012). The reduction of canopy covers giver negative impact on ecosystem services due to changes in the hydrological cycle of forests by altering forest ETI (Bonan, 2008; Hubbard *et al*., 2013; Mikkelson *et al*., 2013; Mathney *et al*., 2014; Nolan *et al*., 2014). Plant-water relations are an important component of ecohydrology, because plant T is important for the hydrological cycle, and influences the water budget in forested watersheds (Wang *et al*., 2010; Guardiola-Claramonte *et al*., 2011; Hubbard *et al*., 2013; Adams *et al*., 2012; Mikkelson *et al*., 2013; Mathney *et al*., 2014).

1.1.2 University of Tokyo Forests

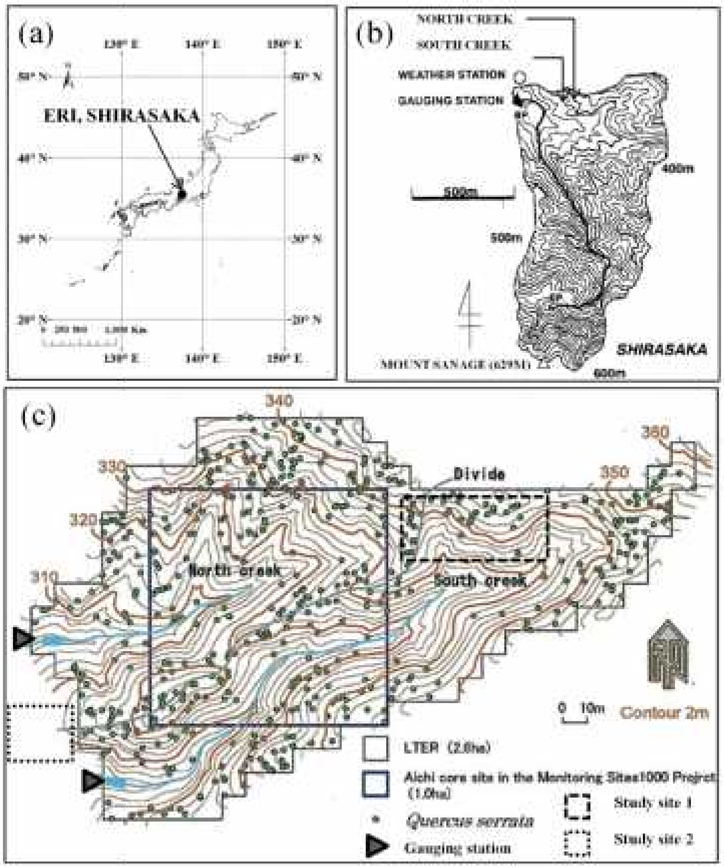
The first national university in Japan, the University of Tokyo (UTokyo) was established in 1877. As a leading research university, UTokyo offers courses in both undergraduate and graduate levels in all essential academic disciplines and conducts research to create and disseminate new knowledge. The university aims to provide a multidisciplinary academic environment that ensures opportunities for both intellectual development and the gaining of professional knowledge and skills. In the recent history, from the year 2014, 2015 the UTokyo took 23rd place on international ranking of Universities in the world and the first place among Japanese universities.

With more than 130 years history, at present Graduate School of Agricultural and Life Sciences (GSALS), is one of the brilliant graduate school, among the 10 graduate schools in the UTokyo. The University of Tokyo Forests was established in 1894 and now under the GSALS as one of the major institute out of the 12 departments and 8 affiliated institutions. The University of Tokyo Forests" of the UTokyo consist with 7 university forests in various parts in Japan. Among the 7 university forests, Ecohydrology Research Institute (ERI) is the one allocated for Ecohydrology is an interdisciplinary field studying interactions between water and ecosystems (UTokyo 2016; ERI, 2008) (Figure 1.2).

1.1.3 Ecohydrology Research Institute (ERI)

The University of Tokyo Forests established in 1922. ERI is one of the main research sites own to the University of Tokyo forests. ERI is located in northeastern part of Aichi Prefecture, central Japan (137° 10' E, 35° 12' N) (Figure 1.2). ERI has owned administrative and research facilities at Gozuka-cho seto city and three research forests namely; Akazu Research Forest (AKRF, 745ha), Inuyama Research Forest (IRF, 442ha) and Ananomiya Research Forest (ANRF, 77ha).

AKRF is a secondary forest in the warm-temperate zone and is composed of a mixture of deciduous and evergreen broadleaved trees and evergreen conifers (Figure 1.2). The forest canopy is mainly composed of *Q. serrata, Chamaecyparis obtusa,* and *Pinus densiflora*. Mean tree height is approximately 20 m. The average topographical inclination is 25°, while elevation ranges from 330 to 360 m. The mean annual temperature and mean annual precipitation were 12.8 ºC and 1860 mm, respectively (1985–2014) (ERI, 2015). AKRF provides a unique study site for researchers with more than 80 years old (1928-2015), rainfall-runoff processes data at two paired watersheds with timely collected climatological data (1985 – 2015) accompanying with long-term ecological research in permanent plot (LTER) data. Long-term hydrological measurements it enables evaluating the effects of anthropogenic manipulation, effects of ongoing climate change around AKRF and irregularly occurring forest disturbance such as forest decline due to JOW, on water yield from the forested watersheds (ERI, 2015). The first appearance of JOW in the AKRF was reported in 2007, the epidemic peaked in 2011 (Sawada, 2012; Sawada *et al*., 2014), and by 2014, most *Q. serrata* (80%) in the forest had been attacked by *P. quercivorus*. Out of the attacked *Q. serrata,* 35% died, while the remaining 65% of trees survived (Sato *et al*., 2016). The ecohydrological consequences after tree mortality have rarely been studied; it is because of lack of pre and post disturbance data (Guardiola-Claramonte *et al*., 2011; Adams *et al*., 2012). With hand long-term hydro-climatological data with tree mortality data for pre and post JOW infestation, AKRF is providing the best study site for evaluating the influences of *P. quercivorus* attacks on ecohydrological consequences.



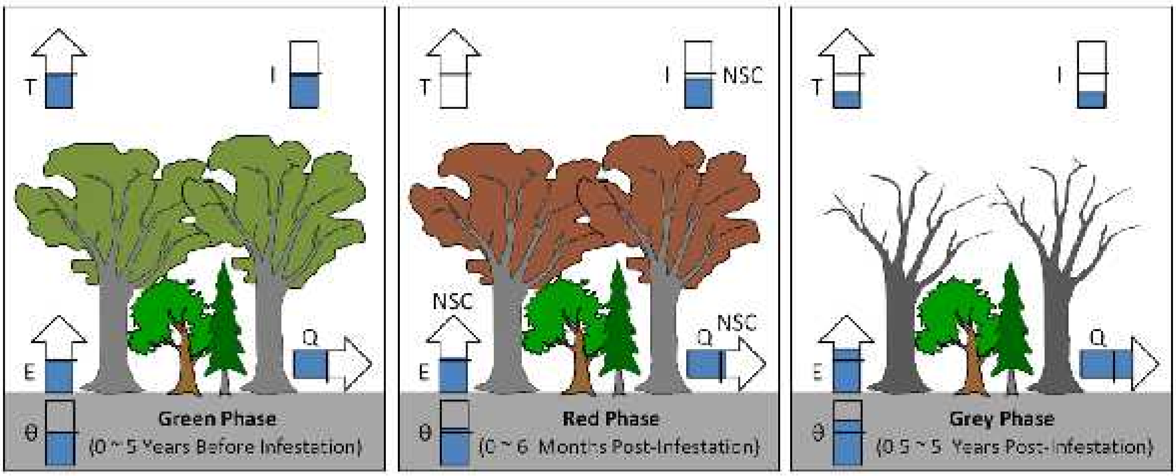
Source: Kazuhiro Yabe, 2003; ERI, 2012

Figure 1.2 Location of the study site. (a) Geographical location of Ecohydrology Research Institute (ERI) and Shirasaka watershed in Japan, (b) Topography of the Shirasaka main watershed and location of North creek (NC), South creek (SC) sub-watersheds , gauging station for the Shirasaka watershed and Akazu weather station. Location of the mount Sanage the highest point of the watershed also located in the map, (c) Topography of the NC, and SC sub-watersheds and distribution of *Q. serrata* trees. Location of the stream gauging stations (V-notch weir), long-term ecological research plot, and Aichi core site plot also shown. Location of the Study site 1, and Study site 2 also shown in the map which will describe in chapter 2 and chapter 3 respectively.

1.2 Objectives of the research

1.2.1 Hypothesis

Changes in forest condition by weakening an individual tree and or wilting of trees by JOW have the potential to alter the ETI in infested forests. Changes of ETI may induce changes in soil moisture and stream flow since all are components of forest hydrological cycle. Before the infestation (Green phase in Figure 1.3) all component of the hydrological cycle is in well balance. After JOW (Red phase in Figure 1.3), ambrosia beetle constructs galleries and introduce ambrosia fungus into the sapwood. With the spreading of necrosis and followed by discoloration immediately restricts the water and nutrient flow to the canopy. The T reduction is anticipated in infested but surviving trees. With the mass attack, the leaves of attacked tree turn green to red within one to two weeks. In the red phase, tree T gradually decreased and with full blockage of xylem conduits physiological activities stop and trees not further transpire. However, due to the resource release (water, nutrient, and sunlight) T of the surrounded vegetation could increase. After approximately 6 months or more, the tree appears gray (Gray phase in Figure 1.3) and leaves drop off to the forest floor, thus reduction of canopy cover decrease the I of precipitated water. In the gray phase, decaying of stem and tree branches start and eventually fall to the forest floor (Figure 1.3).



Modified after Mikkelson *et al.*, 2013; Hubbard *et al.*, 2013

Figure 1.3 A visual representation of the three primary phases of JOW infestation, with the accompanying elements of the hydrologic cycle. Fluxes are denoted with arrows and storage reservoirs as rectangles with the associated hypothetical increase or decrease in the process depicted by the fill departure above or below the center line. While filled-in portion displays the general trend even though magnitude may vary. T = transpiration, E = ground evaporation, I =interception, θ = soil moisture, and Q = water yield/discharge. NSC=no significant change.

1.2.2 Objectives

1. To investigate transpiration reduction by means of sap flux measurement in infested but surviving *Q. serrata* trees
2. To elucidate the threshold percentage of vessel dysfunction for weakening a *Q. serrata* tree flowing JOW.
3. To clarify the transpiration response of neighboring trees following the wilting of oak individuals
4. To estimate long-term hydrological consequences of evapotranspiratin change of JOW infested watershed

Understanding of the mechanism of forest responses to particular disturbance event is especially important for future predictions of forest recovery and preventing of underestimation of forest functions or services (Adams *et al*., 2012 Schäfer *et al*., 2014; Matheny *et al*., 2014). In this thesis, I provide a synthesis and insight of changes of T in individual tree-scale, stand-scale, and watershed-scale ETI of *Q. serrata* dominated temperate forest in Japan.

CHAPTER 2 WHOLE-TREE SAP FLUX IN *Quercus serrata* TREES AFTER THREE LEVELS OF PARTIAL SAPWOOD REMOVAL TO SIMULATE JAPANESE OAK WILT

Content of this chapter already published in Ecohydrology

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Authors	G.G.T.CHANDRATHILAKE, Nobuaki TANAKA, and Naoto KAMATA
Key Words;	Tree transpiration; Granier method; ambrosia beetle; ambrosia fungi; *Raffaelea quercivora*; *Platypus quercivorus*; tree mortality; radial growth
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2.1 Introduction

Q. serrata is a deciduous oak, which is a dominant tree species in a secondary forest in warm-temperate region in Japan. It has been reported that more than half of *Q. serrata* survive even after JOW disturbance (Urano, 2000; Saito and Shibata, 2012). The infested but surviving trees may appear externally identical to trees without *P. quercivorus* attacks. However, these trees may be weakened internally owing to blockages of sap flow (Kuroda and Yamada, 1996). *Q. serrata* is a canopy-dominant tree species in secondary forests, and may be important in determining watershed-scale canopy transpiration. Therefore, before assessing JOW impact on watershed-scale hydrology, we must investigate changes to the magnitudes of tree transpiration in infested but surviving *Q. serrata* trees.

Several methods have been developed to assess and quantify tree transpiration. Sap flow measurements allow whole-tree sap flux to be estimated, and are widely used in measuring tree transpiration (Granier, 1987; Ladekarl, 1998; Oren, 1999; Wilson, 2001; Wang, 2010). Sap transports water and nutrients from the roots to foliage and to living cells in trees (Tyree and Sperry, 1988). The combined effect of differences in water-potential among the soil, the plant, and the atmosphere, as well as the capillary action of the xylem, causes sap to flow from the roots to canopy foliage (Tyree and Sperry, 1988; Tyree and Ewers, 1991). Whole-tree sap flux can be obtained from spatially averaged sap flux density over the sapwood cross-section of a tree and the hydro-active sapwood area of the tree (Granier, 1987; Gartner and Meinzer, 2005; Ford *et al*., 2007). Out of the various methods available to measure sap flux density, Granier sensors (thermal dissipation probe) allow plant water use to be estimated *in situ* at relatively low cost, and are easy to use in complex terrains (Ladekarl, 1998; Kume *et al*., 2009; Wang *et al*., 2010).

In this study, Granier sensors were used to detect changes to whole-tree sap flux in relation to mechanical sap wood removal, which simulated sapwood dysfunction by the JOW. We hypothesized that whole-tree sap flux would be reduced in infested but surviving oaks trees, due to partial sapwood dysfunction. However, we further hypothesized that, due to enhanced sap flux density in remaining healthy sapwood, the decline in the whole-tree sap flux would be less than expected from the dysfunctional sapwood area (hereafter termed “compensatory effect”). To test these hypotheses, this study aimed to (1) investigate the relationships between whole-tree sap flux and the percentage of xylem dysfunction; (2) examine whether sap flux density had a compensatory effect in the healthy part of sapwood, and (3) elucidate the threshold percentage of vessel dysfunction for weakening a tree. We also examined compensatory radial growth in treated trees as a possible cause for the compensatory effect of sap flux. Insights gained from the present study would improve knowledge of how *Q. serrata* trees with partially damaged sapwood influence the magnitude of tree transpiration; this information may be a prerequisite to understanding watershed-scale hydrology in forests infested by JOW.

2.2 Materials and methods

2.2.1 Study site

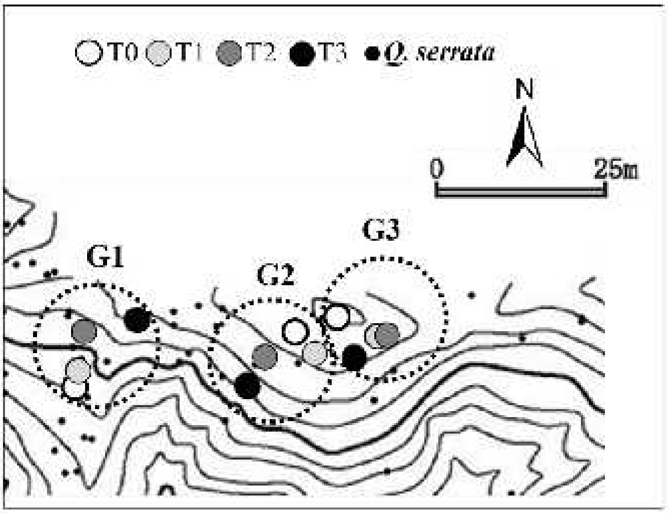

Figure 2.1 Location of the study site and test trees. (a) Location of the study site in northern end of the South creek location of Akazu Research Forest (AKRF) in Japan, (b) Topography of the study site in AKRF and the distribution of tested *Quercus serrata* trees within this site. T0, control; T1, 25% of sapwood removal; T2, 50% of sapwood removal; T3, 75% of sapwood removal.

The study was conducted in the “study site 1” SC of the Shirasaka sub-watershed in the AKRF, ERI, UTokyo. The distribution of the test trees, and lay out of the study groups in the study site 1 is shown in Figure 2.1.

2.2.2 Test trees and sapwood removal

Twelve *Q. serrata* individuals that reached the top canopy layer were selected as test trees (Table 2.1). The geographical location and history of *P. quercivorus* attacks were considered as the selection criteria. Before starting the experiment, the trunks of the test trees were covered with plastic sheets to prevent natural *P. quercivorus* attacks during the study. The test trees were divided into three groups (G1, G2, and G3) according to the geographical distribution considering the ease of sharing electrical equipment and closer to the electric power source for conducting sap flux measurements (Figure 2.1). Each group consisted of a control tree (no treatment, T0), a 25% treated tree (with 25% sapwood being removed on the north aspect of the trunk, T1), a 50% treated tree (with 50% of sapwood being on the north–east aspect of the tree, T2), and a 75% treated tree (with 75% of sapwood removal at west–north–east aspect, T3) (Figure 2.2). On July 18, 2014 (day of the year, DOY=199), sapwood was removed to simulate vessel dysfunction due to *R. quercivorus* vectored by *P. quercivorus*. An approximately 2-cm width of sapwood band, about 4-cm below reference sensors (see section Sap flux density measurement), was removed using a chainsaw and a chisel (Figure 2.2).

Table 2.1 Test trees (*Quercus serrata*) for measurement of sap flux density with information on group, treatment, diameter at breast height (DBH), ambrosia beetle attack history, and period of sap flux density data available in the sapwood removal experiment.

Group	Treatment*	DBH (cm)	Ambrosia beetle attack history (year)							Sap flux density data availability (DOY)**
			2007	2008	2009	2010	2011	2012	2013	
G1	T0	25.5	No	No	No	No	Yes	No	No	196 - 325
	T1	21.0	No	No	No	No	Yes	No	No	196 - 274
	T2	23.9	No	No	No	No	Yes	No	No	196 - 325
	T3	30.7	No	No	No	No	Yes	No	No	196 - 325
G2	T0	31.2	No	No	No	Yes	No	No	No	196 - 324
	T1	22.6	No	No	No	Yes	No	No	No	196 - 318
	T2	34.1	No	No	No	Yes	No	No	No	196 - 325
	T3	22.9	No	No	No	Yes	No	No	No	196 - 325
G3	T0	24.5	No	No	No	Yes	No	No	No	196 - 321
	T1	25.5	No	No	No	Yes	No	No	No	196 - 325
	T2	27.4	No	No	No	Yes	No	No	No	196 - 323
	T3	26.8	No	No	No	Yes	No	No	No	196 - 325

*: T0, control, T1, 25% of sapwood removal, T2, 50% of sapwood removal, T3, 75% of sapwood removal
**: Day of the year 2014

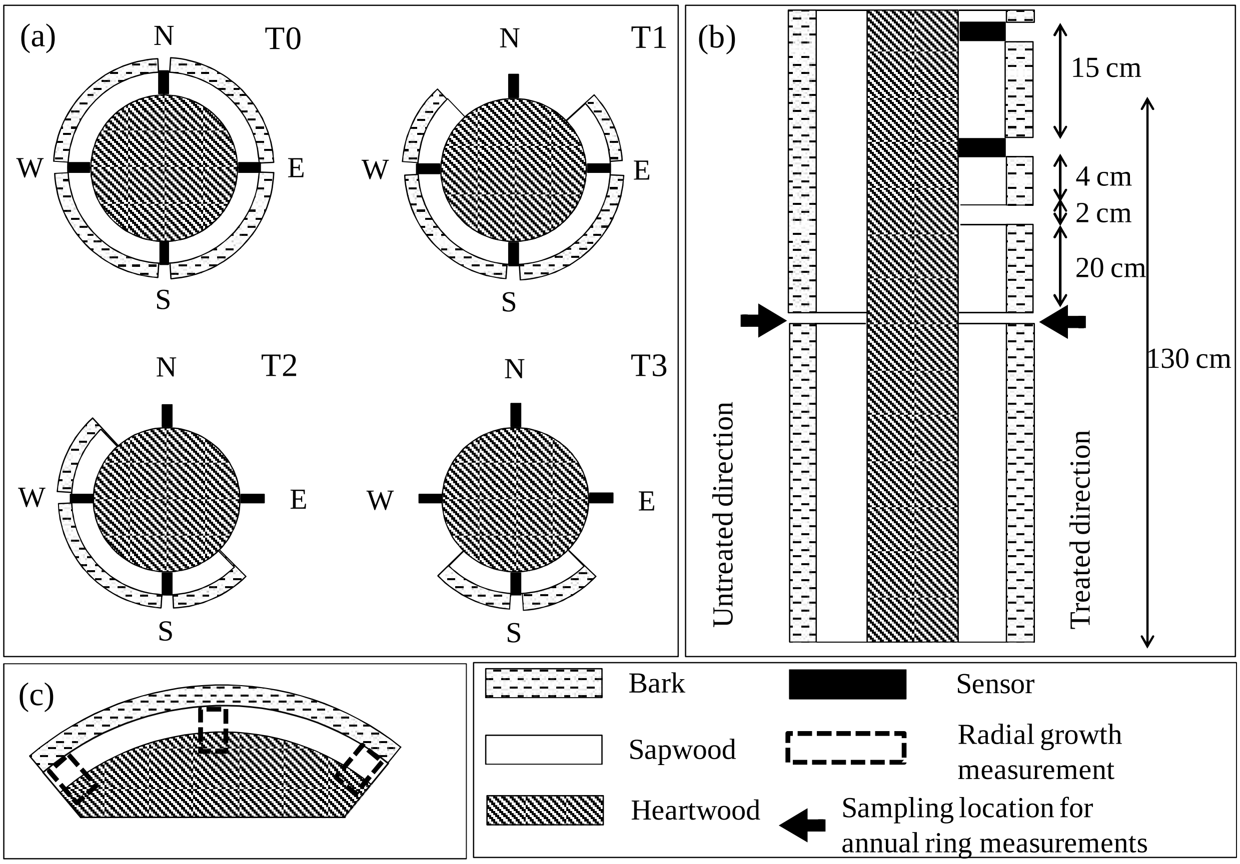

Figure 2.2 Sapwood removal treatments and Granier probes monitoring sap flux density. T0, control; T1, 25% of sapwood removal; T2, 50% of sapwood removal; T3, 75% of sapwood removal. N, North; E, East; S, South; W, West. (a) Horizontal cross sections, (b) Vertical cross section, (c) Wood sample used to measure radial growth.

2.2.3 Sap flux density measurements

Sap flux densities in four azimuthal directions (north, east, south, and west) of all of the test trees were measured with handmade Granier-type sensors (Granier, 1987) for 130 days from July 15 (DOY = 196) to November 21, 2014 (DOY = 325). Each sensor unit had a continuously heating upper probe and an unheated lower probe (Granier, 1987). A dye injection experiment in a mature *Q. serrata* in the AKRF reported that conductive sapwood thickness varies between 2 and 3 cm at breast height (Sato *et al.*, 2010). Therefore, 20-mm long probes were used for this study. Several studies suggested that the direct use of the Granier method could underestimate sap flow due to heterogeneous sap flux along the sensor length, especially in ring porous tree species (Chiu *et al.*, 2014; Bush *et al.*, 2010; Clearwater *et al.*, 1999). However, I did not calibrate the sensor for *Q. serrata*, since the purpose of this study was to detect temporal changes (before and after the treatment) in observed sap flux.

Each probe had a copper-constantan thermocouple in the middle and was covered with an aluminum tube to obtain homogeneous temperature distribution along the probe length. In each direction at breast height of the trunk, two pieces of bark (1.5 × 1.5 cm in size), 15 cm apart from each other vertically, were removed until the cambium was exposed. Two holes (2.5 mm in diameter and 20 mm in depth) were made on the trunk surface in the center of the two sections of exposed cambium. A probe was inserted into each hole. The upper probe contained a heating coil that was connected to a continuous 0.2 W power supply (Granier, 1987). The unheated lower probe detected the reference temperature. Constantan ends from the two probes were connected together, while the copper ends were connected to a multiplexer (AM16/32B, Campbell Scientific Inc., UT, USA), which was controlled by a data logger (CR1000, Campbell Scientific Inc., UT, USA). After installing the probes, exposed cambium areas were covered with silicone gel to prevent contamination or contact with water. The installed sensors were covered with aluminum foil to prevent exposure to direct sunlight. The temperature difference (ΔT) of the two probes was measured every 30 s. The 10-min averages of twenty 30-s measurements were recorded by the data logger.

The canopy of all tested trees was monitored for foliage discoloration, wilted leaves, and branch dieback by observation from the ground. The trees were monitored throughout the period of data collection, and between summer and fall of the following year.

2.2.4 Data screening

Before data analysis, ΔT data were screened. Each sensor was checked for a data spike or a noisy pattern in a 10-min ΔT time series (Figure 2.3 a). Irregular patterns in ΔT may have been caused by an electric surge, because both the data logger and the multiplexer were powered by commercial power. Thus, ΔT data that produced a spike or noise were removed from the dataset.

2.2.5 Sap flux density

Recorded temperature differences were converted to sap flux densities (F_d; cm^3 m^{-2} 10 min^{-1}) by modifying Granier's empirical equation (Granier, 1985, 1987):

$$F_d = (119 \times 10^{-6} \left(\frac{\Delta T_M - \Delta T}{\Delta T}\right)^{1.2})600 \qquad (1),$$

where ΔT_M is the maximum temperature difference, representing the value of ΔT when F_d is assumed to be zero (that usually occurs predawn) (Granier, 1985, 1987; Lu *et al.,* 2004; Du *et al.,* 2011). In Eq. (1), '600' was introduced to convert seconds to 10 minutes. Determination of ΔT_M is crucial for the calculation of F_d using Eq. (1) (Granier, 1985, 1987; Lu *et al.,* 2004). When calculating ΔT_M, we considered predawn zero sap flux as well as drift of ΔT_M over the period of measurement. Because our ΔT time series showed considerable daily variations in ΔT_M (see an example in Figure 2.3 b), ΔT_M was estimated over any given duration of 10 minutes using the linear interpolation method, based on an assumption that F_d was zero at the time when the daily maximum ΔT was observed. The maximum temperature (ΔT_M) of each sensor on h th date at time t was defined by the following equation (see also Figure 2.3 b):

$$\Delta T_M(t) = \Delta T_M(h) + \left(\frac{\Delta T_M(h+1)-\Delta T_M(h)}{M \quad (h+1)-M \quad (h)}\right) * (t - M \qquad (h)) \qquad (2),$$

where Maxtime is the time when maximum temperature was recorded on a given day. In the 10-min F_d calculation based on Eq. (1), I input ΔT_M (t) given by Eq. (2) as ΔT_M. When ΔT (t) > ΔT_M (t), we set ΔT (t) as ΔT_M (t), because Eq. (1) cannot be applied in this case.

After treatment, the F_d for the treated directions was considered as zero (no sap flow movement). The 10-min F_d was averaged over the four directions for each individual. For each individual, daily F_d was calculated from the 10-min averaged F_d time series. In the data analyses, both 10-min and daily F_d were separated into 2 groups: before and after applying the treatment.

2.2.6 Normalized sap flux density index

To exclude variation in F_d among individual test trees, both 10-min and daily F_ds were normalized using each of the averaged F_d values before treatment for each individual. The normalized indices were used in subsequent data analyses. The normalized sap flux density index (nF_d) of *i* th tree in *j* th group at time/date t was defined by the following equation:

$$nF_d i(t) = \frac{F_{d_{AT}} \quad (t)}{F_{d_B} \quad m \quad\quad i} \qquad (3),$$

where $F_{d\,AT\,ij}$ is the F_d of *i* th tree in *j* th group after treatment and $F_{d\,BT\,mean\,ij}$ is the mean F_d of *i* th tree in *j* th group before treatment.

2.2.7 Linear mixed model (LMM)

To examine how each treatment influenced whole-tree sap flux, a linear mixed model (LMM) (R core Team, 2014) was employed, in which either “10-min or daily nF_d” was a response variable, “treatment (T0 (control), T1 (25% treated tree), T2 (50% treated tree), and T3 (75% treated tree))” was a fixed effect, and “group” and “date and time” were random effects.

Before investigating whether F_d had a compensatory effect in the healthy part of sapwood, we calculated an F_d index (hereafter termed “offset F_d”) that would have been observed if the treatment had not been implemented. For each treatment tree, we first derived the proportion of the sum of F_d in the treated direction(s) in relation to the sum of F_d in the four directions using directional F_d data before the treatment (p). Then, the offset F_d indices at the time/date t for *i* th tree in *j* th group were calculated by the following equation:

$$o\ F_{d}i_{j}(t) = \frac{nF_{d}i_{j}(t)}{p_{i}} (4),$$

The calculated offset values (osF_d) of treated trees were compared with the nF_d values of control trees by LMM, in which “10-min or daily osF_d” was a response variable, “treatment” was a fixed effect, and “group” and “date and time” were random effects. If the osF_d of each treatment was positive and significantly greater than 0, it was judged that a compensatory effect of F_d in the untreated portions of treated trees was present. In contrast, if the osF_d of each treatment was negative and significantly lower than 0, the treated trees were judged to be weakened.

In order to test the treatment effect on F_d variation at different intervals, the study period was separated into three seasons—S1 (from July 19 to August 8), S2 (from August 9 to October 1) and S3 (from October 2 to November 21) based on data availability and data gaps of individuals trees (specially G1T1)(Table 2.1). The 3 seasons S1, S2, and S3 represent the mid-summer, late-summer, and autumn respectively. LMMs were used for both 10-min and daily data of S1, S2, S3, and S1–S3 (whole study period).

2.2.8 Annual growth ring measurement

We hypothesized that compensatory radial growth in treated trees was one of cause for compensatory sap flux in the untreated direction. Two pieces of minor-segment wood samples were collected from each test tree on December 9, 2015, using a hand saw and a chisel (Figure 2.2 c). The samples were taken from the north (treated direction) and the south (untreated direction) directions of a trunk at approximately 20 cm below the position of sapwood removal (Figure 2.2 b). Radial growth in each year from 2013 to 2015 was determined at three positions for each wood sample by microscopic observation (SZX7, Olympus, Japan) (Figure 2.2 c). For both treated and untreated directions, the ratios of radial growth (2014 growth/2013 growth and 2015 growth/2013 growth) were compared between T0 (control) and all other treatments. A linear model (LM) was used, in which the “ratio” was a response variable and the “treatment” was an explanatory variable.

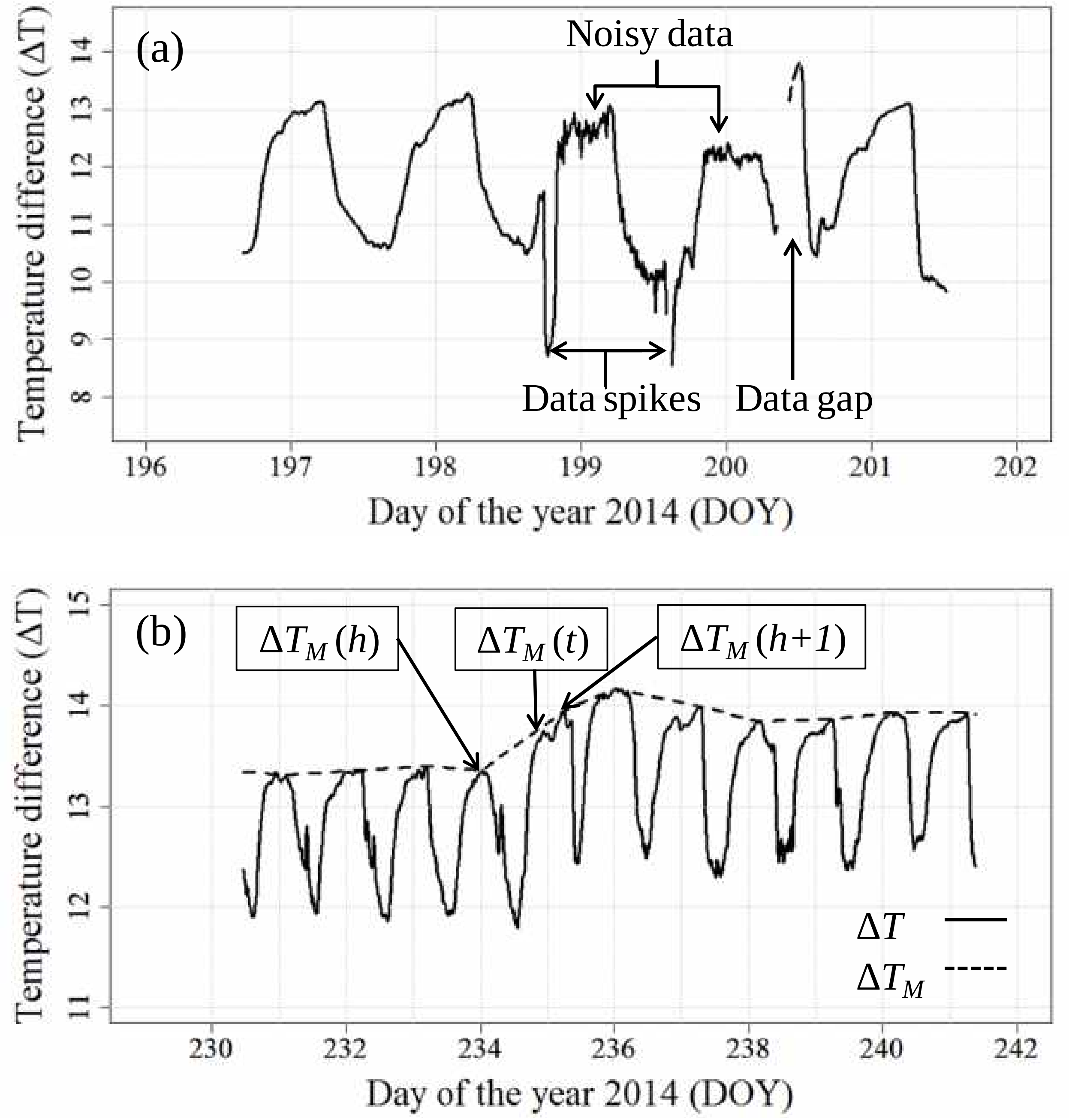

Figure 2.3 Diurnal variation in temperature difference (ΔT) in 10-min intervals, (a) graph showing noisy data, data gaps, and data spikes for the south direction of the T3 tree (75% of sapwood removed) in study group 2 (G2), (b) determination of maximum temperature differences (ΔT_M) with linear interpolation method for east direction of the T0 tree (control) in study group 1 (G1). "*h*" represents day 1.

2.3 Results

Foliage coloration indicated that all individuals of the control and treated trees were still alive at the end of the experimental. Branch dieback was also absent in all test trees during the experiment period up to mid-October 2015. However, twigs with no living leaves and relatively sparse canopy foliage were detected for T3 (75% treated trees) (Figure 2.4).

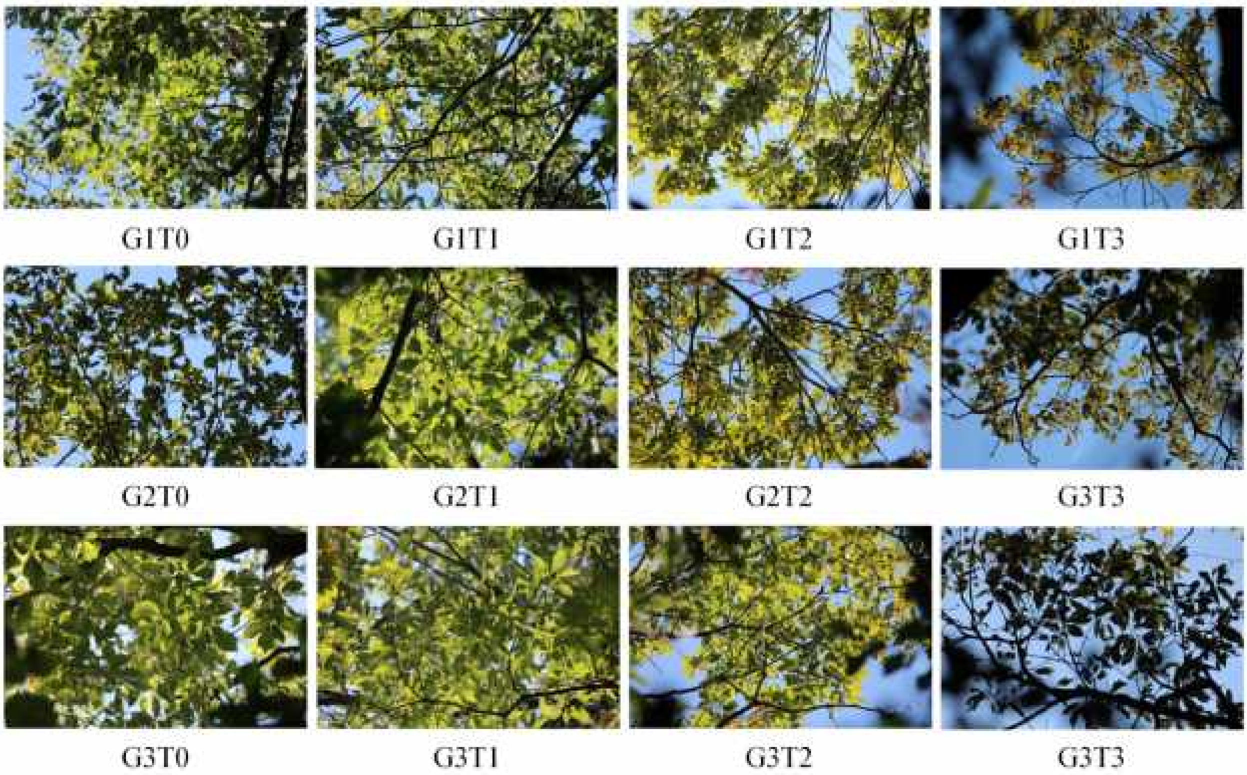

Figure 2.4 Canopy photos in the year following sapwood removal, which were used to detect symptoms of tree weakening. Photos were taken in October 2015. G, group ID; T, treatment ID. T0, control; T1, 25% of sapwood removal; T2, 50% of sapwood removal; T3, 75% of sapwood removal.

The LMM results on the effects of “treatment” on nF_d (Table 2.2) showed that intercepts (and so the sap flux) of control trees decreased with season. The coefficients of all three treatments were significantly negative in each of the three seasons and for all seasons combined (S1–S3), with one exception, showing that whole-tree sap flux was significantly reduced by sapwood removal. The only exception was T1 (25% treated tree) in S3, where the obtained negative coefficient did not significantly differ from 0 for daily data, but did significantly differ for 10-min data. The absolute values of the coefficients were greatest for T3 (75% treated tree) followed by T2 (50% treated tree), with a greater reduction in whole-tree sap flux occurring as the percentage of sapwood removal increased. The absolute values of the coefficients tended to decrease with season, showing that the reduction in whole-tree sap flux decreased with season.

The LMM results on the compensatory effects (Table 2.3) showed that the coefficients of T1 (25% treated tree) and T2 (50% treated tree) were all positive and significantly differed from “0,” indicating significant F_d compensation in the untreated sapwood. The positive coefficient (and so compensatory effect) of T2 (50% treated tree) was consistently greater than that of T1 (25% treated tree). In the 10-min data, the coefficients of T3 (75% treated tree) were negative and significantly differed from “0” in S1 and S2, indicating that the reduction in whole-tree sap flux was greater than that expected from sapwood removal. The coefficient of T3 (75% treated tree) in S3 was positive, but not significantly different from “0,” indicating no F_d compensation in the untreated sapwood. The coefficients of T3 (75% treated tree) were all negative without any significant difference to “0” for the daily data. The coefficient values of T2 (50% treated tree) and T3 (75% treated tree) in both the 10-min and daily time scales, tended to increase from S1 to S3, indicating that the compensatory effect increased with season. The coefficient value of T1 (25% treated tree) in both the 10-min and daily time scale was greatest in S3, followed by S1.

The relationship between whole-tree sap flux and percentage of sapwood removal in treated and control trees is presented in Figure 4. Using the post-treatment daily nF_d dataset (23 days where nF_d are available for all examined individuals), we calculated the total nF_d for each individual during this period, and then the calculated totals were averaged for each treatment type (i.e., T0 (control) –T3 (75% treated tree)). Whole-tree sap flux decreased gradually as the percentage of sapwood removal increased (Figure 4). In contrast, for T1 (25% treated tree) and T2 (50% treated tree), F_d compensation was detected, which was shown by the greater incidence of whole-tree sap flux than the expected (Figure 4). Compensatory effect was greater in T2 (50% treated tree) than T1 (25% treated tree) (Figure 4). In contrast, observed whole-tree sap flux in T3 did not differ from the expected value (Figure 4).

The trunks of trees grew radially in both treated (south) and untreated (north) directions, even after treatment, because the ratio of radial growth was greater than 0 (Figure 2.6). However, the treatment depressed the radial growth of the treated direction, because the ratios of T1 (25% treated tree) –T3 (75% treated tree) were smaller than those of T0 (control) (Figure 2.6 a, and b). In contrast, in both years, the ratio for the untreated direction was significantly greater in T1 (25% treated tree) than in T0 (control) (LM, $p < 0.01$; Figure 2.6 c and d), supporting compensatory radial growth in the treatment group. For T2 (50% treated tree) and T3 (75% treated tree), no significant difference from T0 (control) was found in the ratio for the untreated direction (LM, $p > 0.05$; Figure 2.6 c and d).

Table 2.2 Results of the linear mixed models for analyzing the effects of sapwood removal over three seasons and for all seasons combined. Control trees were used as base models. (a) 10-min normalized sap flux density data; (b) daily normalized sap flux density data.

(a)

Season (day of the year 2014)	Treatment	Estimate	t value	Pr(>|t|)
S 1 (200 – 220)	Intercept	0.81	12.06	< 0.01 **
	T1	-0.16	-34.19	< 0.01 **
	T2	-0.34	-74.98	< 0.01 **
	T3	-0.62	-136.03	< 0.01 **
S 2 (201 – 274)	Intercept	0.61	10.57	< 0.01 **
	T1	-0.12	-43.89	< 0.01 **
	T2	-0.20	-73.76	< 0.01 **
	T3	-0.47	-177.60	< 0.01 **
S 3 (275 – 325)	Intercept	0.42	12.56	< 0.01 **
	T1	-0.03	-8.69	< 0.01 **
	T2	-0.07	-24.36	< 0.01 **
	T3	-0.31	-111.60	< 0.01 **
S 1 – S 3 (200 – 325)	Intercept	0.57	12.93	< 0.01 **
	T1	-0.09	-46.71	< 0.01 **
	T2	-0.17	-96.11	< 0.01 **
	T3	-0.44	-240.72	< 0.01 **

(b)

Season (day of the year 2014)	Treatment	Estimate	t value	Pr(>|t|)
S 1 (200 – 220)	Intercept	0.82	10.82	< 0.01 **
	T1	-0.16	-6.43	< 0.01 **
	T2	-0.35	-14.35	< 0.01 **
	T3	-0.64	-25.89	< 0.01 **
S 2 (201 – 274)	Intercept	0.61	10.42	< 0.01 **
	T1	-0.11	-6.13	< 0.01 **
	T2	-0.19	-10.86	< 0.01 **
	T3	-0.47	-26.54	< 0.01 **
S 3 (275 – 325)	Intercept	0.44	12.72	< 0.01 **
	T1	-0.03	-1.58	0.114
	T2	-0.07	-3.97	< 0.01 **
	T3	-0.32	-17.97	< 0.01 **
S 1 – S 3 (200 – 325)	Intercept	0.59	13.24	< 0.01 **
	T1	-0.09	-7.01	< 0.01 **
	T2	-0.18	-14.01	< 0.01 **
	T3	-0.45	-36.50	< 0.01 **

T1, 25% of sapwood removal; T2, 50% of sapwood removal; T3, 75% of sapwood removal
Statistical significance: ‘**’ 0.01, ‘*’ 0.05

Table 2.3 Results of the linear mixed models used to analyze -*F*d compensation (or compensatory effects on whole-tree sap flux) following sapwood removal over three seasons and for all seasons combined. Control trees were used as base models (a) 10-min normalized sap flux density data; (b) daily normalized sap flux density data.

(a)

Season (day of the year 2014)	Treatment	Estimate	t value	Pr(>|t|)
S 1 (200 – 220)	Intercept	0.81	5.45	0.03 *
	T1	0.05	10.70	< 0.01 **
	Intercept	0.82	5.68	0.03 *
	T2	0.16	31.31	< 0.01 **
	Intercept	0.79	11.77	< 0.01 **
	T3	-0.02	-5.82	< 0.01 **
S 2 (201 – 274)	Intercept	0.61	4.26	0.04 *
	T1	0.02	5.79	< 0.01 **
	Intercept	0.59	4.42	0.04 *
	T2	0.27	80.26	< 0.01 **
	Intercept	0.60	29.21	< 0.01 **
	T3	-0.02	-6.91	< 0.01 **
S 3 (275 – 325)	Intercept	0.38	3.07	0.09
	T1	0.08	20.59	< 0.01 **
	Intercept	0.38	5.69	0.03 *
	T2	0.33	83.59	< 0.01 **
	Intercept	0.43	24.08	< 0.01 **
	T3	0.01	1.78	0.07
S 1 – S 3 (200 – 325)	Intercept)	0.56	4.28	0.02 *
	T1	0.05	24.66	< 0.01 **
	Intercept	0.55	5.30	0.03 *
	T2	0.28	117.60	< 0.01 **
	Intercept	0.56	35.23	< 0.01 **
	T3	-0.01	-4.59	< 0.01 **

(b)

Season (day of the year 2014)	Treatment	Estimate	t value	Pr(>|t|)
S 1 (200 – 220)	Intercept	0.81	4.98	0.03 *
	T1	0.05	2.48	0.02 *
	Intercept	0.82	5.29	0.03 *
	T2	0.16	5.58	< 0.01 **
	Intercept	0.80	9.37	< 0.01 **
	T3	-0.04	-1.09	0.28
S 2 (201 – 274)	Intercept	0.62	4.21	0.05 *
	T1	0.02	1.12	0.27
	Intercept	0.59	4.16	0.04 *
	T2	0.28	3.61	< 0.01 **
	Intercept	0.61	16.58	< 0.01 **
	T3	-0.03	-1.07	0.28
S 3 (275 – 325)	Intercept	0.38	2.91	0.09
	T1	0.09	6.60	< 0.01 **
	Intercept	0.40	5.66	0.02 *
	T2	0.33	17.17	< 0.01 **
	Intercept	0.45	13.43	< 0.01 **
	T3	-0.01	-0.40	0.68
S 1 – S 3 (200 – 325)	Intercept	0.57	4.30	0.05 *
	T1	0.05	4.55	< 0.01 **
	Intercept	0.56	5.18	0.03 *
	T2	0.28	18.94	< 0.01 **
	Intercept	0.58	20.17	< 0.01 **
	T3	-0.03	-1.33	0.18

T1, 25% of sapwood removal; T2, 50% of sapwood removal; T3, 75% of sapwood removal

Statistical significance: ‘**’ 0.01, ‘*’ 0.05

2.4 Discussion

The LMM analysis treatment effect and compensatory effect indicated that the coefficients of the treatments differed significantly from 0, which means that tree-to-tree F_d variation was low compared to the F_d variation due to the treatment. Therefore, three replicates (n=3) per treatment type were sufficient to ensure that the final results were accurate.

In trees, water (sap flow) transport from roots to leaves relies on negative pressures established in continuous water columns in xylem conduits as described in cohesive tension theory. On the other hand, sap flow movement of a tree largely depends on total conductive sapwood area (Granier, 1985; Granier, 1986;Granier *al.*, 1994;Wullschleger and Norby 2001; Gartner and Meinzer, 2005; Ford *et al.*, 2007; Gebauer *et al.*, 2008). Therefore, sap wood removal treatment caused greater reduction of hydraulic conductivity through reduction in the number of conduits (xylem) supporting the same canopy foliage compared to the before treatment condition. Moreover, the treatment also reduced water storage capacity which determines the ability of trees to survive water stress conditions (Tyree and Ewers, 1991). Loss of water storage capacity, and decreased hydraulic conductance of xylem may lead to a reduction in the water potential in leaves, which might impair plant physiological activities and possibly lead to the eventual death of the plant (Nardini *et al.*, 2011). Therefore, in this experiment it was expected that loss in xylem hydraulic conductivity would be proportional to reduced sapwood area. However, our results showed that loss of hydraulic conductivity in treated trees was not proportional to the sapwood removal percentages.

The “pipe model theory of plant form” (Shinozaki *et al.*, 1964) regards a plant as an assemblage of “unit pipes,” in which each pipe supports a unit of leaves in the canopy. This theory predicts sectoral canopy wilting and/or branch dieback even if the spiral ascent of sap that has been reported for other species belonging to the genus *Quercus* (Kozlowski and Winget, 1963; Waisel *et al.*, 1972) occurs in *Q. serrata*. However, neither canopy wilting nor branch dieback were observed in treated trees. Yet, continuous radial growth was identified at the position below the treatment site in the year following the treatment (Figure 2.6 b). This result provides evidence for the horizontal movement of carbohydrates. Previous studies on sap flow analysis using deuterium oxide (D_2O) tracing techniques have reported the axial and radial transport of water within a tree stem (James *et al.*, 2003). The radial movement of sap in the stem is significant with intervessel pits in between early wood vessels and late wood vessels (Kitin *et al.*, 2004). Therefore, horizontal water movement in the stem may cause foliage to survive in the treated directions.

However, F_d compensation occurred in the remaining sapwood of treated trees, making up for reduced sap flow by sapwood removal (Table 2.3, Figure 2.5). Given that F_d compensation increased with the ratio of removed sapwood to remaining sapwood, the ratio would be 0.33 (= 25/75), 1 (= 50/50), and 3 (= 75/25) in T1 (25% treated tree), T2 (50% treated tree), and T3 (75% treated tree), respectively. These expected ratios indicated that compensation was greatest in T3 (75% treated tree) followed by T2 (50% treated tree). However, whole-tree sap flux in T3 (75% treated tree) was smaller than expected, probably because the trees in T3 (75% treated tree) were highly stressed by a greater proportion of sapwood removal and had begun to weaken. Twigs without leaves and sparse canopy were observed in T3 (75% treated tree) the following year (2015), representing symptoms of weakening. We proposed a threshold for compensation and weakening between 50 and 75% of sapwood dysfunction (Figure 2.5).

In T1 (25% treated tree) and T2 (50% treated tree), the F_d compensation was not enough to recover reduced F_d, which was proportional to sapwood removal. However, signs of weakening and branch dieback were not detected in T1 (25% treated tree) and T2 (50% treated tree). Sap flux may have been enhanced in the remaining sapwood after treatment. Sapwood removal reduces the total number of vessels in the stem without decreasing the amount of canopy foliage and water absorbent area (root hairs), which may increase the velocity of sap flow. Speeding up sap flow movement in the remaining sapwood could be a major mechanism of the compensatory effect detected in this experiment.

After applying heat treatment to *Pinus halepensis* stems in early spring, the opposite side of the trunk to the treated direction achieved higher radial growth than the mean radial growth at the breast height level of the tree (Ducrey *et al.*, 1996). The recovery of hydraulic conductivity in ring porous *Fraxinus excelsior* after winter embolism has also been reported to be entirely dependent on the production of new early wood conduits (Hacke and Sauter, 1996). The compensatory radial growth observed in the untreated direction of T1 (25% treated tree) (Figure 2.6 c) may also cause compensatory sap flux in the treatment group. However, no significant compensatory radial growth was found in T2 (50% treated tree) (Figure 2.6 c), despite the compensatory sap flux observed in the treatment group (Figure 2.5). Therefore, compensatory radial growth was not the only cause of compensatory sap flux. However, the gradual recovery of whole-tree sap flux in treated trees with seasonal progression (Table 2.3) provides indirect evidence for compensatory radial growth, because a certain amount of time is required for radial growth and vessel formation to occur following treatment.

The annual rings of ring porous wood consist of early wood vessels with large diameters and late wood vessels with narrow diameters (Bush *et al.*, 2010). Consequently, water conductance is mostly restricted to the outermost annual growth ring (Granier *et al.*, 1994; Bush *et al.*, 2010; Sato *et al.*, 2010; Chiu *et al.*, 2014; Taneda and Sperry, 2008). However, there is considerable sap flow movement in the old inner xylem, as shown by sap flux studies of ring porous ash (*F. excelsior*) (Gebauer *et al.*, 2008), and *Quercus petraea* and *Quercus robur* (Granier *et al.*, 1994); a similar conclusion was reached in vessel refilling studies in *Quercus gambelii* (Taneda and Sperry, 2008), and in a dye injection experiment in *Q. serrata* (Sato *et al*., 2010). The ability of sap flow movement in the inner rings increases significantly, after decreasing in the outermost rings, so that the sap flow rate remained unchanged (Granier *et al*., 1994). Recent studies on xylem physiology, have suggested three important mechanisms for the generation of the positive pressure required for refilling embloized conduits: (1) an increase in the osmotic pressure of the remaining sap layer at the inner conduit wall with solutes - this could lower the osmotic potential in the embolized conduits and cause them to refill; (2) reversale of osmotic pressure by starch hydrolysis in adjacent tissues and development of a kind of pumping mechanism to pressurize embolized vessels and refill them under positive pressure; (3) an increase phloem pressure by hormone mediation might drive water transport to the embolized conduit (Taneda and Sperry, 2008; Salleo *et al*., 2009; Nardini *et al*., 2011; Christman *et al*., 2012). To compensate for the loss of hydraulic conductance in treated *Q. serrata* trees, sap flow in the inner conductive xylem might be enhanced by the above described positive pressure refilling mechanisms. Therefore enhanced sap flow in the inner xylem (but within sensor reach) might also have contributed to the compensatory effect detected in this experiment.

Variation in the symptoms shown by the canopy foliage among the treated trees in this study may serve as a rough indicator of the impact of JOW on watershed-scale canopy transpiration. If most infested oaks in a stand are free from the external symptoms of JOW, as shown for T1 (25% treated tree) and T2 (50% treated tree), the impact of JOW on watershed-scale canopy transpiration is expected to be small. This is because the reduction of whole-tree sap flux in infested oaks is mitigated by the compensatory effect. In contrast, if most infested trees exhibit canopy discoloration or twig dieback, as shown for T3 trees, watershed-scale canopy transpiration is significantly reduced. This is because sapwood damage of infested oaks is beyond the threshold for the detected compensatory effect (Figure 2.5). Of course, because an oak with a permanently wilted canopy stops tree transpiration, the mortality rate represents another important indicator of the impact of JOW on canopy transpiration at the watershed-scale.

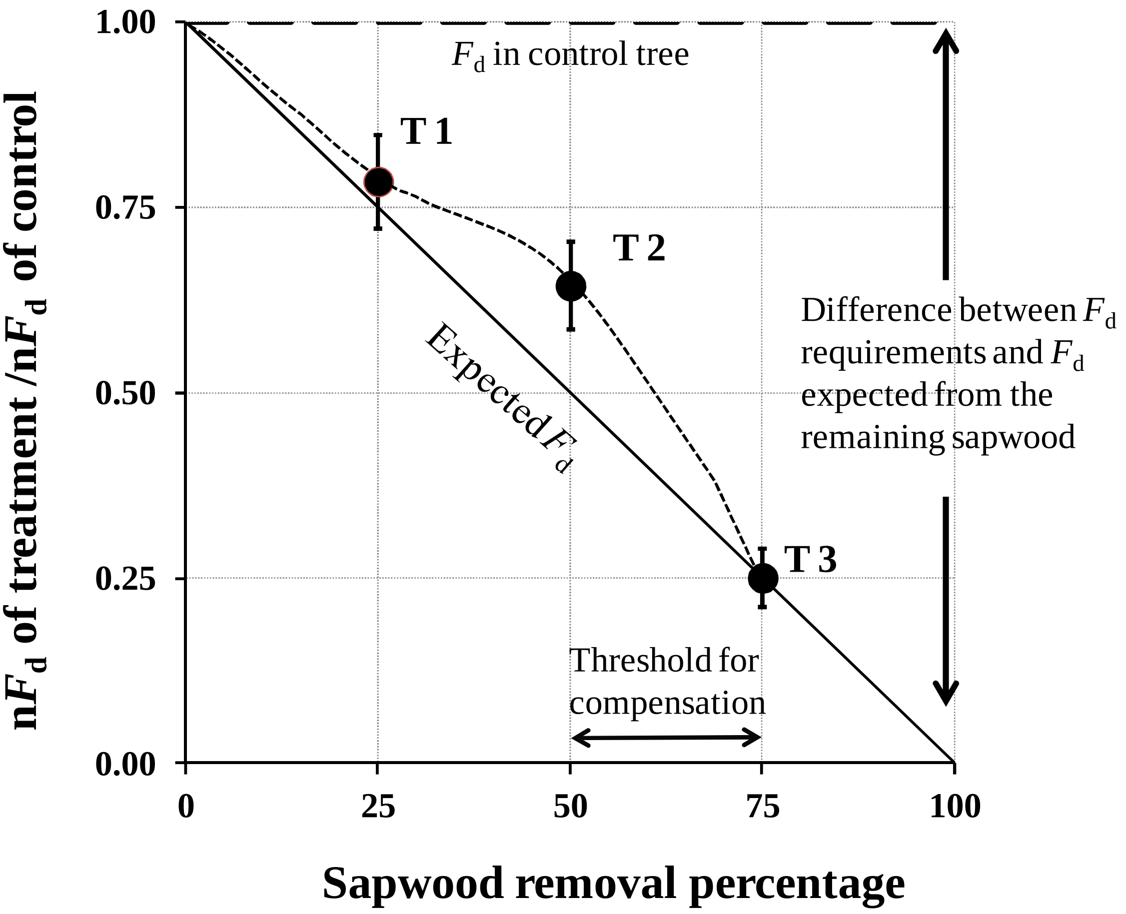

Figure 2.5 Relationship between whole-tree sap flux and the different sapwood removal percentage. Solid circles represent the ratios of averaged normalized sap flux density (nF_d) for T1, T2, and T3, respectively, in relation to the averaged nF_d for T0; thus, showing the observed whole-tree sap flux in treated trees compared with control trees. Error bars represent standard deviation of sap flux density. T1, T2, and T3 were combined by a hand-drawn curve (dashed curve) to show the trend. Stem sap flow of woody plants was estimated from the product of multiplying sap flux density by the cross sectional sapwood area of active xylem or sapwood (Köstner *et al.*, 1992). Therefore, for treated trees, post-treatment sap flux was expected to reduce in proportion to the amount of removed sapwood area (a solid line), assuming no substantial circumferential variation in sap flux density (F_d). Broken line represents the whole-tree sap flux of the control tree. Up/down arrows represent differences between the sap flux requirements of the control tree and sap flux expected from the remaining sapwood. A threshold for compensation is shown by the range of the left to right arrow. T0, control; T1, 25% of sapwood removal; T2, 50% of sapwood removal; T3, 75% of sapwood removal.

2.5 Conclusions

I examined variation in the whole-tree sap flux of *Q. serrata* stems after 3 levels of sapwood removal, which simulated vessel dysfunction due to JOW. Our results showed that the 3 levels of treatments caused significant reduction in whole-tree sap flux. Twenty-five percent and 50% treated trees showed significant sap flux compensation, whereas 75% treated trees showed no compensatory effects at all. The threshold for showing compensation ranged between 50% and 75% of vessel dysfunction, but was probably closer to 75%, because the observed whole-tree sap flux of T3 (75% treated tree) did not differ to the sap flux expected from the remaining sapwood. To my knowledge, this study is the first to identify the whole-tree sap flux compensatory effect in treated but surviving trees. Compensatory radial growth in the untreated direction was detected in 25% treated trees, which caused the compensation in whole-tree sap flux. Increased sap flow ascent in the inner xylem may also contribute to this phenomenon. The physiological mechanisms supporting the compensatory effect could not be fully assessed; however, the present study reveals how infested, but surviving, *Q. serrata* trees control the magnitude of whole-tree transpiration. This information will be useful in better understanding watershed-scale hydrology in forests disturbed by JOW.

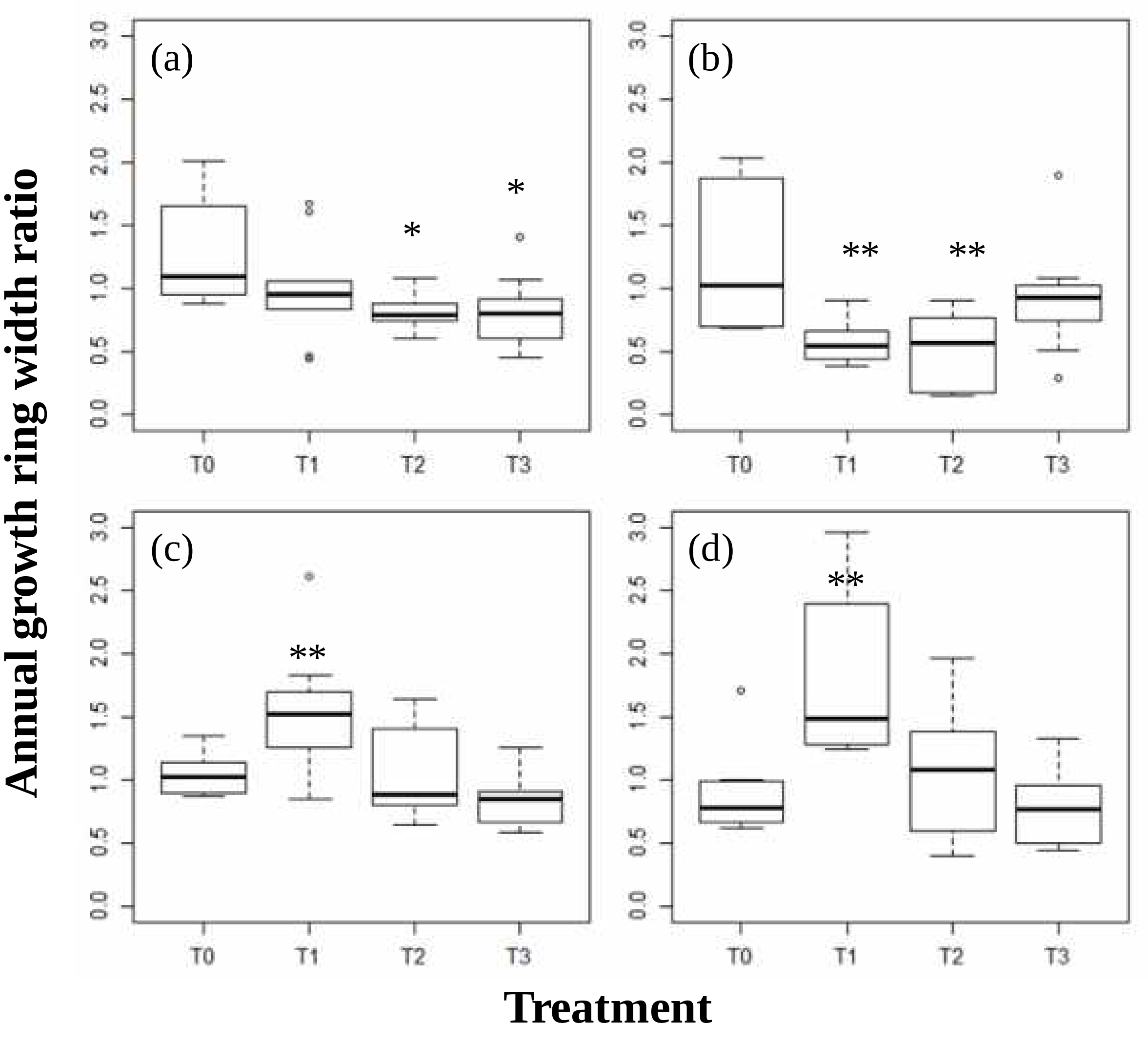

Figure 2.5 Trunk radial growth after sapwood removal for treated (north) and untreated (south) directions. Ratios for radial growth in 2013 are shown for 2014 and 2015. (a) North, 2014; (b) North, 2015; (c) South, 2014; (d) South 2015. Top bar, maximum; lower bar, minimum; top of a box, third quartile; bottom of the box, first quartile; middle thick bar in the box, median. T0, control; T1, 25% of sapwood removal; T2, 50% of sapwood removal; T3, 75% of sapwood removal. To examine the influence of treatment type on the width of annual growth rings, a linear model (LM) was used, in which "growth ring width ratio" was a response variable, "treatment (T0, T1, T2, and T3)" was an explanatory variable; p-value < 0.05 is considered significant (**p* < 0.05; *****p* < 0.01).**

CHAPTER 5: OVERALL CONCLUSION

This research focused on influences of ambrosia beetle (*P.quercivorus*) attacks on evapotranspiration in a secondary warm-temperate forest. Even though the study was conducted in three different spatiotemporal scales in Central Japan, findings could be applicable for beetle-infested warm-temperate forested catchments throughout the world. The findings of this research would be important for broadening scientific understanding of hydrological alteration by JOW and lead to improve pre and post-disturbance watershed management decisions. Therefore, this chapter will not repeat the individual conclusions drawn by each experiment, but it will describe the broader aspect of the overall findings which will be important for drawing the future research directions in the similar field of studies.

Recent ambrosia beetle outbreak in family Fagaceae trees dominated forested watersheds in Japan demonstrates the importance of insect induces disturbances in changing forest structure and ecosystem services (Kuroda and Yamada, 1996; Ito and Yamada, 1998; Kamata *et al*., 2002; Hata *et al*., 2014). The wide spread of JOW in Japanese islands is expected to be accelerated as a result of global warming (Kamata *et al*., 2002; Sanguansub, 2012). The mass mortality of oak tree results in loss of canopy cover and thus directly alters E, T, and canopy I in the hydrologic cycle. As indirect effects of tree mortality, alteration of the watershed hydrologic processes such as infiltration, percolation, runoff, and stream discharge can be highlighted. The potential alteration of ETI by JOW finally may change the catchment water budget and hydrological processors. Therefore, estimation of changes in ETI following the JOW is important for assessing the water balance of the infested catchments. However, studies on ETI changes related to the JOW have not been reported so far. Therefore, the objective of this study was to evaluate the changes of ETI in *Q. serrata* dominated forested catchments before and after JOW infestation. Experiments were conducted in three different spatiotemporal scales at AKRF in a warm-temperate secondary forest in Central Japan.

As a canopy dominant, transpiration of oak trees plays a key role in the hydrological cycle. However, oak trees infested with JOW may show changes in transpiration even if they are still alive. Partial sapwood removal (25%, 50%, and 75%) experiment simulating the JOW showed that whole-tree sap flux was significantly reduced in all treatments. However, 25% and 50% treated trees showed significant F_d compensation, whereas 75% treated trees showed significantly smaller whole-tree sap flux than the value expected from the treatment. This study is the first to identify the whole-tree sap flux compensatory effect in infested but surviving trees. It was identified that the threshold for showing compensation ranged between 50% and 75% of sapwood damage, but was closer to 75% since the observed whole-tree sap flux of 75% treated tree did not differ to the sap flux expected from the remaining sapwood. Compensatory radial growth in the untreated direction was detected in 25% treated trees, which caused the compensation in whole-tree sap flux. Increased sap flow ascent in the inner xylem may also contribute to this phenomenon. Girdling treatments were applied for top canopy oak trees to simulate oak mortality effect on stand scale. Before and after applying the treatment, F_d measurements for the first growing season were conducted for surrounded vegetation in 3 treatment groups and one control group. Some test trees (not all) showed higher F_ds at two different timing; (1) day following the treatment and (2) 10 days following the treatment (after the canopy wilting of treated oak). In individual tree level, the increased F_d following the treatment was significantly ($p < 0.05$) greater than the that of before treatment condition. However, in stand-scale the increased F_ds were not significant ($p > 0.05$). The result implies that, no significant T increases in neighboring trees for offsetting the transpiration reduction by oak tree die-off. In deciduous trees, stomatal conductance is constant from summer to autumn due to constant stomatal density and chlorophyll concentration (Ito *et al*., 2008). Therefore, it can be assumed that deciduous trees could not show higher transpiration in same growth season with respective resource release by oak tree die-off. Even though, evergreens produce new leaves throughout the year, it didn’t show significant transpiration increase following the treatment. It can speculate that timing could be a limiting factor for evergreen trees for adjusting tree hydraulic architecture for increasing their transpiration (Andrade *et al*., 1998; Traver *et al*., 2010). Therefore, reduction of ETI could be anticipated in JOW infested watersheds. Following the JOW, stand BA of *Q. serrata* trees decreased to 50%, 49% compared to the 2007 level by 29% and 33% tree mortality rates in NC and SC respectively. Before and after the JOW, daily ETI rates of NC, and SC watersheds were determined using SPWB method. At the same time, a simple model was developed to determine ETI (ETI_MD) based on the hydrological and climatological parameters. Comparison of long-term (7 years) observed and calculated ETI data showed that 6% to 21% of annual ETI reduction in SC and NC, respectively. Moreover, results showed that ETI reduction is closely related with BA reduction rather than tree mortality rate. Results suggest that T reduction by dead oak tree have not been compensated by increases of T by surrounding vegetation in spite of resource release by oak tree die-off. This information will be useful in better understanding the watershed-scale hydrology in forests disturbed by JOW

In contrary to my hypothesis (Chapter 1), results suggest that T reduction by dead oak trees have not been compensated by increased T of surrounding trees with time (year) progression in spite of resource releases by oak tree die-off. As suggested by sapwood removal experiment, even though infested trees similar to the healthy trees, actual T could hinder owing to the internal sapwood damage. On the other hand, results from the oak tree girdling experiment showed that there were no significant T increases in surrounded trees in same growth season following the oak mortality. In addition, watershed scale long-term ETI analyses confirmed that T increases of surrounded vegetation was not significant enough to offset the ETI losses by the death of oak trees. Therefore, now it is clear that, significant ETI reduction is anticipated following a mass attack of *P. quercivorus*. The results provide a validated conclusion for the hypothesis “watersheds receiving more than ~500 mm of annual precipitation decreases in ETI from a loss of overstory T and I (Adams *et al*., 2012). In spite of the same rate of tree mortality, larger difference in ETI reduction was observed in studied watersheds. Percentage reduction of stand BA covered by *Q. serrata* may be more important for determining ETI reduction.

In summary, results of this study provide some insight into evaluation of JOW impact on forest ETI in three different scales; (1) reduction of T in individual tree scale in infested but surviving trees, (2) in stand scale there was no significant T increase from surrounded vegetation to offset the T reduction from death of infested oak trees, (3) and finally lead to reduction of ETI in watershed scale in JOW infested warm-temperate forests. As observed, hydrological consequence of beetle-infested forests will likely to depend on the level of sapwood damage in an individual tree, the percentage of BA reduction due to tree die-off, and transpiration response of neighboring vegetation. This information will be useful in better understanding watershed-scale hydrology in forests disturbed by JOW

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