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A DISSERTATION FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

**Effects of Leaf Area Change on Transpiration and
Productivity of 50-year-old *Pinus koraiensis*
Stands in Mt. Taehwa**

엽면적 변화가 50년생 태화산 잣나무림의
증산 및 생산성에 미치는 영향

BY
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DEPARTMENT OF FOREST SCIENCES
GRADUATE SCHOOL
SEOUL NATIONAL UNIVERSITY

AUGUST 2014

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ABSTRACT

Forests play an important role as a conduit connecting biosphere and atmosphere, providing important feedback controls on the water and carbon balance of the entire earth system. In other words, forest water and carbon uses, uptake and release of water and carbon by forest, are important to understand how lithosphere, atmosphere and biosphere interact for sustainability of earth system especially under the substantial changes by natural disturbances as well as human management. To enhance the understanding of ecosystem responses to such changes, I tried to quantify the effect of leaf area changes on water and carbon balance, more specifically, transpiration and productivity of 50-year-old *Pinus koraiensis* stand.

For leaf area changes, I conducted two different approaches. First, I performed the defoliation of individual trees, which mimics the reduction of leaf area by insect, herbivore, environmental stress or pruning, by removing 30 and 60% of branches. Second, I conducted the leaf area reduction by 20 and 40% thinning, which is the most common forest management practice to improve the quality of timber production and sustainable forest management.

To evaluate the effect of leaf area changes on water and carbon at tree and stand level, transpiration, which was measured with Granier-type heat dissipation sensor, and growth measured with dendroband were compared at different treatments. In addition, canopy carbon net assimilation was

estimated using Canopy Conductance Constrained Carbon Assimilation model.

I found 1) thirty percent artificial defoliation treatment decreased water stress of individual tree and increased leaf hydraulic conductance, resulted in the compensation of transpiration at the tree level. However, 60% defoliation treatment was not able to compensate the leaf area loss with the increase of hydraulic conductivity and resulted in the decrease of tree-level transpiration. Canopy carbon assimilation in 30% defoliation treatment showed no change due to the compensation of transpiration, however, those of 60% defoliation treatments decreased. This implied that the mild defoliation event can be overcome by the enhanced physiological processes of *Pinus koraiensis*, due to less water stress and better light environment. However, severe defoliation was not able to easily recover in transpiration and productivity.

2) In thinning experiment, there was the increase of precipitation throughfall at thinned plots, which resulted in the increase of soil water content and sapflux density, and leaf- and tree-level transpiration. However, stand transpiration decreased ~30 % and 50 % at 20 % (mild-thinned) and 40 % (heavy-thinned) plots, respectively. Therefore, unlike transpiration compensation with mild defoliation of individual tree, thinning decreased stand transpiration even at the mild density (e.g., 20 %). However, thinning treatment enhanced the DBH increment at the tree level in both intensities. The enhanced diameter growth at the tree level also increased stand net

primary production at light-thinned plots without statistical significance. Therefore, water use efficiency increased with thinning treatments.

My study quantified the transpiration and productivity and carbon assimilation of *Pinus koraiensis* plantation in Mt. Taehwa under various leaf area indices with different treatments. Leaf reduction at different levels, tree and stand, respond differently in water and carbon relations. At the tree level, transpiration was compensated at the mild defoliation, but transpiration decreased with thinning treatment. Photosynthesis increased in both treatments due to less water stress and better light environment. Consequently, water-use-efficiency enhanced with in both treatments. As a result, my study provided insight for water and carbon use of *Pinus koraiensis* plantations for forest ecosystem management.

Keywords : *Pinus koraiensis*, leaf area change, artificial defoliation, thinning, transpiration, productivity, sap flux

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ACRONYMS

<i>A_{net}</i>	Net carbon assimilation ($\mu\text{mol C m}^{-2} \text{ leaf s}^{-1}$)
<i>C_a</i>	Ambient air CO ₂ concentration (ppm)
<i>C_i</i>	Intercellular CO ₂ concentration of leaf (ppm)
DBH	Diameter at breast height (1.4 m) (cm)
<i>E</i>	Transpiration (mm)
<i>E_L</i>	Transpiration per unit leaf area ($\text{mmol m}^{-2} \text{ s}^{-1}$)
<i>g_c</i>	Leaf canopy conductance ($\text{mmol leaf}^{-2} \text{ s}^{-1}$)
<i>g_s</i>	Leaf stomatal conductance ($\text{mmol leaf}^{-2} \text{ s}^{-1}$)
<i>G_C</i>	Sap flux scaled canopy conductance ($\text{mmol leaf}^{-2} \text{ s}^{-1}$)
GPP	Gross primary production (g C gr^{-2})
<i>J_{max}</i>	Light saturated rate of electron transport ($\mu\text{mol leaf}^{-2} \text{ s}^{-1}$)
LA	Tree leaf area ($\text{m}^2 \text{ tree}^{-1}$)
LAI	Leaf area index
<i>P_{net}</i>	Net photosynthetic rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
<i>Q</i>	Photosynthetic photon flux density ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)
SA	Sapwood area per unit ground area ($\text{m}^2 \text{ mgr}^{-2}$)
<i>T</i>	Air temperature ($^{\circ}\text{C}$)
<i>J_s</i>	Sap flux density ($\text{mmol m}^{-2} \text{ s}^{-1}$)
<i>V_{cmax}</i>	Maximum Rubisco capacity per unit leaf area ($\mu\text{mol CO}_2$ $\text{leaf}^{-2} \text{ s}^{-1}$)
WUE	Water use efficiency
SWC	Soil water Content (%)
RH	Relative humidity in the air (%)
<i>D</i>	Vapor pressure deficit in the air (kPa)
<i>z</i>	Height from the ground (m)

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CHAPTER 1. INTRODUCTION

1.1. General introduction

Forests connects atmosphere and geosphere with biosphere, providing the regulative feedback controls on the water and carbon balance of the entire earth's ecosystem (Bonan, 2008; Ceulemans and Mousseau, 1994). In other words, the uptake and release of forest water and carbon are important for understanding of ecosystem function (Ainsworth et al., 2002). It is well known that water and carbon usage by forest can be affected by various environmental and biological factors, and the quantification of water and carbon use change by these factors are frequently studied (Sellers et al., 1997).

The impact of environmental and biological variables on water and carbon use depends on tree leaf area (Vertessy et al., 1995), the stomatal behavior (Whitehead, 1998), forest structure (Anderson-Teixeira et al., 2013; Forrester et al., 2013b), tree species (Grossiord et al., 2013) and ages of tree (de Souza et al., 2013). Among those various variables, understanding how tree leaf area change affects water and carbon use of forests is crucial for managing forest ecosystem especially for high quality timber harvesting under sustainable forest management (White et al., 1998).

Leaf area change including defoliation and thinning can alter crown architecture and stand structure (Forrester et al., 2012). Leaf area change can influence microclimatic variables such as light penetration (Forrester et al.,

2013a), temperature (Jonsson and Sigurdsson, 2010), vapor pressure deficit (Rambo and North, 2009) and wind speed (Ma et al., 2010).

Change of each variable can affect the water use at different scales of leaves, trees and stands (Wullschleger et al., 2000). Water use of trees is driven by environmental variables, including vapor pressure deficit (Oren et al., 1999), net radiation (Zotz et al., 1998), wind speed (Li et al., 2013), temperature (Van Herk et al., 2011) and availability of soil water within the rooting zone (Chang et al., 2014).

The impact of these variables on the amount of water transpired depends on tree leaf area (Vertessy et al., 1995) and the stomatal behavior of the tree species (Hogg and Hurdle, 1997). Therefore understanding how tree leaf area change affects water use of forests is crucial for managing water fluxes in forests and for making efficient use of water in relation with wood production.

Forests play an important role in the climate system, providing important feedback to the level of carbon dioxide in the atmosphere (Bonan, 2008). Temperate forests in Korea can act as a carbon sinks due to several factors such as rising atmospheric CO₂ concentration and warming temperature (Li et al., 2010). Forests comprise the largest carbon pool of all terrestrial ecosystems and the annual gross exchange of CO₂ between forests and the atmosphere exceeds the anthropogenic release of CO₂ due to combustion of fossil fuels (Goodale et al., 2002).

Attempting to reduce the rate at which atmospheric CO₂ increase, the Kyoto Protocol has transformed CO₂ emissions and sinks into valuable trading commodities (Choi et al., 2008). The size of the carbon sink in forest ecosystems and the contribution of different processes under the current atmospheric CO₂ concentration are still uncertain (Schimel et al., 2001).

To reduce uncertainties of water and carbon balances, studies often combine different approaches and methodologies to estimate water and carbon fluxes into and out of forest ecosystem (Hasenauer et al., 2012). The degree of confidence in these estimates is high when different methods produce similar results, thereby closing water and carbon budget for an ecosystem (Gielen et al., 2010).

Physiological and biophysical models of transpiration, net canopy assimilation and respiration by trees can be compared to water and carbon balances estimated by eddy covariance, biomass-based estimates of NPP and chamber based estimates of respiration (Richardson et al., 2006; Richardson et al., 2010; Wayson et al., 2006). Interestingly, the degree of closure in the carbon balance varies considerably among studies (Loescher et al., 2006).

In Korea, forests cover two thirds of the land area and include large areas of plantation. Plantations of the evergreen conifer which is the most common plantation species in Korea and Evergreen conifer forest occupy about 40.5% of the total forested area (Korea Forest Services, 2011). Therefore, quantification of water and carbon budgets of evergreen conifer

forest including plantation is essential for understanding the functions of Korean forests. But about the forest of Korea relatively few studies have been performed to determine energy, water and carbon exchanges (Joo et al., 2012; Kang et al., 2009; Kwon et al., 2009).

In this study at the Mt. Taehwa site, the annual values of major components of the water and carbon balance were examined, especially emphasizing on transpiration and productivity of a *Pinus koraiensis* stands continuously since 2011. Presenting the annual amount and variation in precipitation, throughfall, soil water content, runoff, transpiration and evapotranspiration clarifies the water flux and all of these variables are related to carbon balances too.

Our understanding of the effects of using land for *Pinus koraiensis* stands on carbon dynamics could also be improved by process model based on attempts to estimate water and carbon fluxes in these stands.

As mentioned above, forests are experiencing diverse leaf area changes. The reaction for these changes are classified as level of trees and stands differently. Defoliation, that is the leaf area change as level of trees could change leaf area without change in microclimate and water supply. Thinning, that is the leaf change as level of stands, could result in decrease of stand density with major change in light and water supply. Therefore, in my study, I tried to quantify the effect of leaf area changes resulted from defoliation and thinning on transpiration and productivity of 50-year-old

Pinus Koraiensis stand seperatly.

The objectives of this study are to understand change of water and carbon fluxes especially transpiration and productivity of *Pinus koraiensis* stands in Mt. Taehwa to different intensity of artificial defoliation and thinning in annual based changes and to test the hypothesis that the different intensity of thinning can improve or decrease water use and carbon assimilation.

From the results, water and carbon use of *Pinus koraiensis* stands in Mt. Taehwa can be quantified and understand what would be the main variables infecting water and carbon use when leaf area changes. In addition, more detail information for transpiration and growth of *Pinus koraiensis* plantation provide background for managing tools for forest ecosystem management.

1.2. Literature reviews

1.2.1. Transpiration of forest plantation

As a consequence of the climate change, forestry practices and land use change, alteration in ecosystem water balances are expected to occur and there are increasing needs for information about forest water use (Ward et al., 2013). Such changes in the timing and the amount of rainfall entering and leaving the system can change both the net primary productivity and decomposition, having thus also a feedback effect on the climate change itself (MacKay et al., 2012). Water budget studies can provide baseline data on which carbon and chemical element cycling studies can be based (Schafer et al., 2002).

The amount and seasonal variation in the availability of water of forests is one of the key elements determining the typical biological processes, such as growth and survival, and species composition of the site (McLaughlin et al., 2013). Depending on the location of the ecosystem, the key issue may be excess or shortage of water, either occasionally or continuously (Goulden et al., 2012). Water relations belong to the most important physiological processes in plants, because water is often a growth limiting (Larcher, 2003).

In principle the composition of a water balance of forest ecosystem is simple but in practice this can be a very complicated task to carry out for a given area, and due to this complex studies of the water balances where all

components of the water balance are hard to measured (Wullschleger et al., 1998a). Recently number of comprehensive reviews on the water use in forest plantation were written over the last decades (Vanclay, 2009; Whitehead and Beadle, 2004).

The general equation of a water balance of forest catchment is as follows:

$$P + I = ET + R + dW$$

where P = precipitation, I = inflow, ET = evapotranspiration, R = runoff, and dW = changes in water storages retained into the soil matrix and in the ground water (Ilvesniemi et al., 2010).

Precipitation includes all forms of atmospheric moisture. It can fall on the leaf and be evaporated (interception), run down the stem to the ground (stemflow) or fall between the crowns of trees to the ground (throughfall). Interception and subsequent evaporation is the greatest cause of water loss of precipitation and the leaf area are important factor in interception loss (Alavi et al., 2001). Leaf and stem surface roughness, architecture, and geometric shape control both leaf drip and stemflow (Xiao et al., 2000).

During photosynthesis, plants transpire water. Transpiration rates are often used as an indicator of stomata closure. Direct evaporation from the soil and transpiration from the plants is collectively called evapotranspiration. Transpiration is by far the largest water flux from Earth's continents, representing 80 to 90 per cent of terrestrial evapotranspiration (Jasechko et al.,

2013). These days, the number of sites where the evapotranspiration is measured continuously by eddy-covariance method, has increased rapidly (Williams et al., 2009).

In water balance studies, it would be important that all these component should be measured independently, and with proper precision (Caldato and Schumacher, 2013). Often one or more of the measurements of the component fluxes are either very uncertain, inaccurate or not measured at all and estimated with models or with a subtraction method. Also, climatic conditions occur quite randomly during different years and the variation between years in the amount and in the timing of the precipitation, evapotranspiration and outflow can be covered if the measurements are continuous and the measurement period is long.

In water balance of the forest ecosystem, transpiration of trees is a fundamental component in relation with its importance of forests. The effects of leaf microclimate on stomatal regulation of transpiration are well described, although the underlying mechanisms are not completely understood (Buckley, 2005). Measurement of transpiration provides access to the canopy conductance of the forest, a key parameter in water and carbon exchange models, since the water and carbon fluxes are tightly linked by their common way through the stomata (Moren et al., 2001). In general transpiration by temperate forests is relatively uniform (Roberts, 1983). Subsequent study showed that broad-leaved forests use more available energy

for transpiration than do coniferous stands (Komatsu, 2005). Also, variation in annual water use by temperate broad-leaved forests can be large, even within small regions (Roberts and Rosier, 2006).

Many efforts have been made to quantify water fluxes in forest ecosystems (Verstraeten et al., 2005). A common problem for water and carbon models working on the scale from adult trees to the ecosystem, is the need for large calibration and validation datasets. The growing availability of eddy covariance data provides the opportunity to compare the models with long-term data. However, eddy covariance assesses the total water vapor flux, which contains not only transpiration by the trees, but also soil and canopy evaporation and understory transpiration. In contrast, sap flow measurements allow the calibration and testing of models of transpiration only.

Sap flow techniques provide a mean at the tree level to estimate forest stand transpiration (Granier et al., 1996; Köstner et al., 1998; Lu et al., 2004). Sap flow rates of trees scaled to forest canopy transpiration are used to compare tree transpiration in relation to water vapor flux from the forest floor and to total water vapor flux measured above the forest canopy (Wilson et al., 2001). Where measurements of transpiration by individual branches or whole plants are required, sap flow methods hold important advantages over other techniques (Ewers et al., 2007). Sap flow methods are easily automated, so continuous records of plant water use with high time resolution can be obtained. Plant chambers can be used to measure transpiration by

whole plants, including even large trees, but they are not very portable and, critically, they alter the microclimate of the plant, whereas sap flow methods can be used anywhere with very little disturbance to the site (Wullschleger et al., 1998b).

Both water balances and micrometeorology can provide estimates of evapotranspiration, which includes soil evaporation and plant water use, while sap flow techniques measure transpiration alone. Therefore sap flow methods are a useful tool in studies of the water or energy budgets of land surfaces, as they can be used to partition evapotranspiration between plant and soil evaporation and to divide estimates of transpiration among the component species of plant mixtures.

1.2.2. Productivity of forest plantation

Widespread concern about global climate change has led to interest in reducing emissions of CO₂ through afforestation. Obviously forests play crucial roles as sinks of atmospheric CO₂ (Whitehead, 2011). The current state of, and future changes in, sink activity due to climate and land-use change are urgent issues to be investigated. In this context it is quite important to understand the consequences of environmental fluctuations and ecosystem processes, because these are fundamental to ecosystem functions with respect to determinants of global climate changes (Arneth et al., 2010).

There are many ways for performing the carbon cycling study of terrestrial ecosystems, including measurements of plant biomass (Yashiro et al., 2010), decomposition processes of soil organic matters and litterfall (Finzi et al., 2001), ecophysiological processes of plants in various functional types in various vegetation types (Landsberg and Sands, 2011), micrometeorology and atmospheric research for interpreting vegetation functions and the ecosystem scale CO₂ budget (Gu et al., 1999), remote sensing of ecosystem structure (Muraoka and Koizumi, 2009), and modeling approaches (Dufrene et al., 2005). These intensive researches from plot to regional scales have contributed to our present knowledge of the global carbon budget and its effects on the interactions between the biosphere and the climate system.

Quantification of carbon balance is essential for assessing the function of forest ecosystems. The amount of carbon sequestered by forest ecosystems can play an important role in regulating atmospheric levels of CO₂ (Hardiman et al., 2013).

Eddy covariance for assessing CO₂ flux over the canopy provide quantitative information on forest ecosystem functions. These techniques have recently been used to determine net ecosystem exchange (NEE) and to quantify the role of forests as major contributors to terrestrial carbon sinks (Kessomkiat et al., 2013).

However, NEE cannot provide information on the partitioning of sequestered carbon in terrestrial ecosystems. In addition, eddy correlation

techniques may underestimate nocturnal respiration during periods of low wind speed (Baldocchi, 2003). One comparison of eddy correlation estimates with respiration measured with a sap flow measurement revealed that nocturnal respiration could not be measured accurately on calm nights in complex forested terrain .

Studies of carbon exchange in terrestrial ecosystems, therefore, should use a combination of alternative approaches, such as biometric-based methods. Biometric-based net ecosystem production (NEP) is conceptually equivalent to the carbon sequestration rate (Clark et al., 2001). NEP estimation using biometric-based flux measurements clarifies the contributions of different biological processes to carbon sequestration in forest ecosystems. Comparison of biometric based NEP with tower flux-based NEP reveals that we can estimate carbon budgets more accurately, as well as the contributions of various biological processes to forest carbon sinks.

1.2.3. Ecophysiological studies on *Pinus koraiensis* plantation stands

Pinus koraiensis is one of the most important and valuable timber tree species in northeast China, Korea, Russia, Japan (Aizawa et al., 2012). The tree species *Pinus koraiensis* is commonly called Korean Pine. A five-leaved pine, it has a straight trunk, good wood quality and high wood productivity, and is hardy but slow growing. The timber is resistant to decay. The resin, bark and seeds also have varied uses.

It is native to eastern Asia including Korea, Manchuria, far eastern Russia, and central Japan. In the north of its range, it grows at moderate altitudes, typically 600 m to 900 m, whereas further south, it is a mountain tree, growing at 2,000 m to 2,600 m altitude in Japan. It is a large tree, reaching a mature size of 40 m to 50 m height, and 1.5 m to 2 m trunk diameter.

In South Korea, area of *Pinus koraiensis* is 230,000 ha which is 8.6 % of total area of coniferous forests (2,687,000 ha). Each areas of *Pinus densiflora*, *Larix kaempferii* and *Pinus rigida* are 1,447,000 ha (55.0%), 462,000 ha (17.2%) and 409,000 ha (15.2%) (Korea Forest Services, 2011).

Pinus koraiensis is shade tolerant species which can survive in relatively low light conditions and become major species in climax successional stage (Kwon and Lee, 2006). In Korea lots of studies dealing with *Pinus koraiensis* biomass (Kwak et al., 2010; Kwon and Lee, 2006; Li et al., 2011; Noh et al., 2010; Wang et al., 2013a; Wang et al., 2013b; Xiao Dong Li; Myong Jong YI; Mi Jeong Jeong; Yow Han Son, 2010)

Conversion of land uses, such as natural forests to artificial forests, that is plantations, changes ecosystem structure and function greatly. Of the world's total land area, 39.5 million square kilometers are forested, and 2.8% of that is under plantation (Thomas and Packham, 2007).

In Korea, forests cover two thirds of the land area and include large areas of plantation. Plantations of the evergreen conifer which is the most

common plantation species in Korea, Evergreen conifer forest occupy about 40.5% of the total forested area. Therefore, quantification of carbon budgets of evergreen conifer forest including plantations is essential for understanding the functions of Korean forests (Korea Forest Services, 2011).

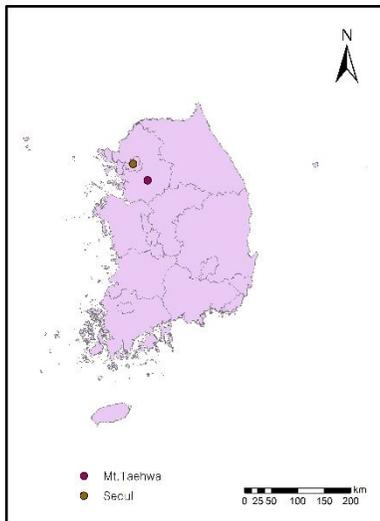
Relatively few studies were conducted about transpiration of *Pinus koraiensis* plantation recently including as followed. The photosynthesis and transpiration of *Pinus koraiensis* needles at different canopy positions and of different leaf ages were measured in the field (Huo and Wang, 2007). The stem respiration of *Pinus koraiensis* was also measured (Wang et al., 2005).

Our understanding of the effects of using land for *Pinus koraiensis* plantations on carbon dynamics could also be improved by determining the difference in carbon sequestration between plantations and natural forests. Although changes in biomass and productivity in *Pinus koraiensis* plantations have been reported, there have been little process model based on attempts to estimate water and carbon balance in these plantations.

1.3. Site description and overview of experimental design

The study was conducted at a 50-year-old *Pinus koraiensis* plantation, which is located in Mt. Taehwa Seoul National University Forest, Gwangju, Gyeonggido (37°18'19.08" N, 127°19'07.12" S), Republic of Korea (Figure 1.1 (a)). The site is located in the northeast slope of Taehwa Mountain and average altitude is 162 m. The plantation's average age was 48 years and average stand density was 433 trees ha⁻¹ (Figure 1.1 (b)).

(a)



(b)

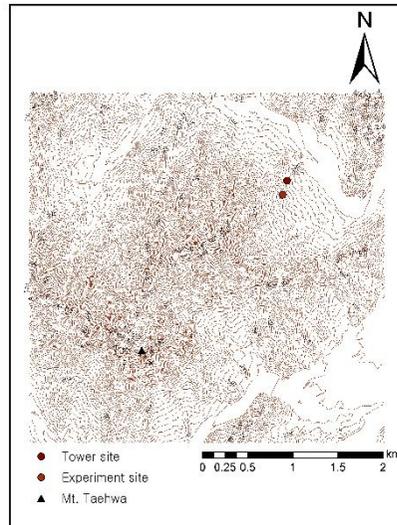


Figure 1-1 Study site of experiment located in Mt. Taehwa Seoul National University Forest, Gwangju, Gyounggido

The climate is classed as having a temperate climate with four distinct seasons, but temperature differences between the hottest part of summer and the depths of winter are extreme. The annual temperature and precipitation are respectively 11.2 °C and 1,329 mm (KMA, Icheon Meteorological Observation Station). Most of the precipitation falls in the summer monsoon period between June and September, as a part of the East Asian monsoon season.

The soil is brown forest soil which is mild acidic sandy loam. The maximum soil water content of the study site was about 31 % and maximum water holding capacity was about 65 %. The soil bulk density of the experiment site was 1.37 g cm⁻³.

Common understory species are *Rhus trichocarpa*, *Castania crenata*, *Styrax obassia* and the commonly found shrubs and herbaceous species include *Zanthoxylum schinifolium*, *Stephanandra incisa* var. *incisa*, *Symplocos chinensis* for. *pilosa*, *Staphylea bumalda* and *Oplismenus undulatifolius*. However, the proportions of these understory species to total basal area were less than 5% in all study plots, and they were not included for stand transpiration calculation.

A defoliation experiment was conducted during the growing season of 2011. 19 trees were selected within a large rectangular plot (50 X 25 m), and

each 5 trees were assigned to controls and 7 trees were assigned to two treatments groups randomly. Control trees were not trimmed. The branches of trees in the treatment groups were trimmed 30%, 60% in each whorl, respectively. To minimize the difference of microclimate and the effect of trimming on soil water conditions caused by the potentially different transpiration rate, each tree in the four treatments was randomly selected in the plots. The defoliation treatment consisted of hand removal of branches on DOY 171. At the time of defoliation treatment, two age of classes of foliage were present; the previous year's needles and current needles.

For thinning experiment, nine 20 x 20 m study plots are located at the northeast slope of Taehwa Mountain and the average altitude is 162m (Figure 1.2). Eight plots were located together and the other was located about 200 m away from the rest of plots. Ten meter buffer zones were allocated between each study plots for the prevention of interference among sites. The study site was planted in early 1960s and the first thinning was operated in 1988. Second thinning was conducted in 2000 leaving current density of 433 trees ha⁻¹.

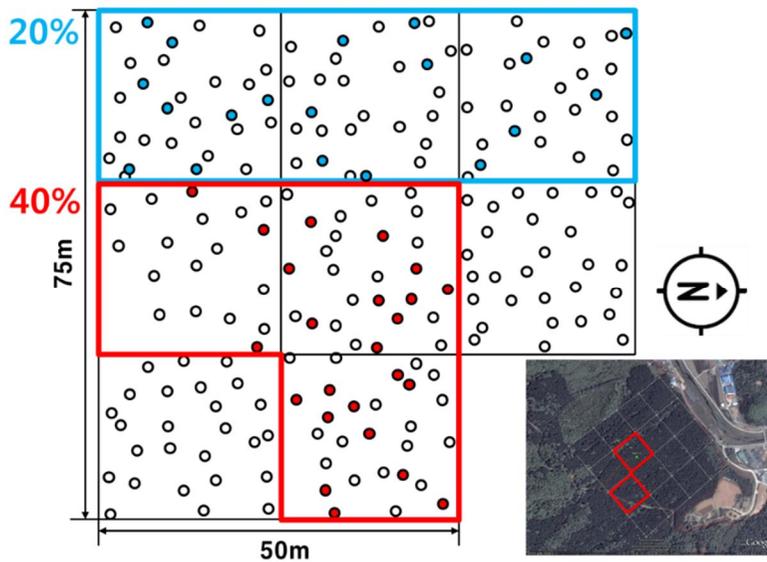


Figure 1-2 Schematic diagram of thinning experiment at *Pinus koraiensis* stand near Gwangju, Gyeongido. 20 % (3 plots encapsulated by blue box), 40 % (3 plots encapsulated by red box), control (2 plots encapsulated black box and 1 tower plot (not shown in this figure)).

CHAPTER 2. EFFECTS OF ARTIFICIAL DEFOLIATION ON TRANSPIRATION AND PRODUCTIVITY OF PINUS KORAIENSIS PLANTATION

2.1. Introduction

Forest trees are experiencing diverse disturbances including forest fire (Kulakowski et al., 2003), windstorm (DeGayner et al., 2005), insect and disease outbreak (Waller, 2013) during the life cycle and disturbances are key process in forest ecosystem dynamics (Seidl, 2011). The intensity and frequency of forest disturbances can be influenced by global change. Forest disturbances greatly alter the carbon cycle at various spatial and temporal scales. It is critical to understand disturbance regimes and their impacts on ecosystems to quantify regional and global carbon dynamics (Liu et al., 2011).

A typical result of disturbances is the decrease of growth (Hoogesteger and Karlsson, 1992; Jacquet et al., 2013; Moulinier et al., 2014). The reason for decrease of growth is that defoliation of canopy reduced the leaf area which is a source of carbohydrates. But partial defoliation of modest intensity increased carbon uptake more than would have been expected from replacement of leaf area alone (Pinkard et al., 1999; Reich et al., 1993).

Physiological responses to defoliation have been well characterized for woody species and, in general, involve the activation of multiple

compensatory mechanism that function to increase total crown photosynthesis (Eyles et al., 2009b; Lavigne et al., 2001; Quentin et al., 2010). These include compensatory photosynthesis, defined as an increase in photosynthetic rates of the remaining foliage on damaged relative to undamaged plants. Plants with defoliation events compensate the decrease of leaf area with photosynthetic up-regulation. Because leaf area decrease resulted from defoliation has no effects on change of root absorption ability, trees can compensate water demand (Quentin et al., 2012; Quentin et al., 2011; Wiley et al., 2013).

The defoliation decrease the leaf area of trees and it changes also crown microclimate (Radunz et al., 2013), photosynthetic ability (Man et al., 2013) and water relation of plants (Quentin et al., 2012). Morphological change of tree crown resulted from defoliation leads to changes in microclimate (Pataki et al., 1998), so that trees catch up the increased water demand even though the remaining leaves increase the water demand. This could be due to the increasing transpiration rate per unit leaf area as leaf area decreases. Many experiments have recorded a parallel increase in stomatal conductance in herbaceous plants with increased assimilation rate following defoliation (Gramacho et al., 2001; Hicks and Turkington, 2000; Rooney and Waller, 2001), but there are relatively few studies about tree species. Also the process of scaling carbon uptake from single leaf responses to the canopy level requires an understanding of radiation interception and the distribution

of light in the crown (Battaglia et al., 2011).

It is also recognized that plant hydraulic and ecophysiological properties are not static but evolve with plant age and growth conditions (Katul et al., 2003). The carbon and water balances are so closely related to each other. Photosynthetic parameters adjust so that the maximum biochemical demand for carbon uptake is in equilibrium with the maximum carbon gain permissible by the soil-to-root hydraulics on time scales relevant to stand development.

Several studies have been conducted to recoveries after defoliation events but many of these studies showed only short term responses to defoliation. Stepwise reduction of leaf area to quantify leaf stomata conductance during one day may have some limitations (Pataki et al., 1998). This approach did not show long term effects of defoliation and stepwise reduction of the leaf area is not a realistic pattern of defoliation resulted from insect herbivory.

Pinus koraiensis is an important plantation species in East Asia, especially in Korea. *Pinus koraiensis* is undergoing damage from herbivory including *Acantholyda posticalis posticalis* Matsumura and *Dendrolimus spectabilis* Butler (Lee, 2012). Damage of *Pinus koraiensis* induces decrease in growth and change the carbon and water balances. But most of the studies dealing with the carbon and water balances did not incorporate herbivory factor. There were few studies dealt the physiological reaction to

intensities of defoliation especially in long term scale.

The objectives of this experiment were to examine recovery of water and carbon status *Pinus koraiensis* to different intensities of artificial defoliation in order to assess long-term changes in transpiration and productivity using sap flow measurement.

2.2. Materials and methods

2.2.1. Meteorological measurements

Meteorological data were measured on 25 m walk-up tower located on the reference plot. Air Temperature (T) and relative humidity used for calculating vapor pressure deficit (D) were measured at 20 m, 5 m and 1 m heights using HMP35C (Vaisala, Helsinki, Finland). Incoming solar radiation ($W\ m^{-2}\ s^{-1}$) was measured with Li-Cor 200S (LI-COR Biosciences, USA) and Photosynthetic Active Radiation (PAR, $\mu\text{mole}\ m^{-2}\ s^{-1}$) was measured using Li-Cor 190 (LI-COR Biosciences, USA) at the top of the canopy. Above canopy precipitation was measured manually with a 10cm diameter rain gauge (Productive Alternatives Inc., Fergus Falls, Minnesota, USA) located in open space 500 m apart from study site about 9 AM every day. The rainfall fraction reaching the soil, throughfall, was determined using 3 manual rain gauge set up below the canopy. Soil water contents were measured using CS616 (Campbell Scientific, USA). Wind speed was measured with a cup anemometer (Model 03001-5, R.M. Young, Traverse City, MI).

All meteorological data were measured every 10s and half-hourly averages were stored by dataloggers (CR1000, Campbell Scientific, USA). The data gaps in environmental data were gapfilled with data from 50 m flux tower which is 50 m apart from the reference plot.

2.2.2. Sap flux density and stand transpiration

Sap flux density was measured with thermal dissipation sensor according to Granier (Granier, 1987). The sensor consists of a heated (200 mW) and a reference probe, 20 mm long and 2 mm in diameter. The heated probe was placed 12 ~ 15 cm above the reference probe to prevent thermal interference and the distance is sufficiently small to avoid large thermal gradients in the tree trunk (Goulden and Field, 1994). Sensors were installed in the outer 20 mm of the xylem towards north and covered with a radiation shield to protect from direct radiation. Temperature difference was monitored every 30 s, and 30 min averages were stored on the logger used for storage of environmental data (CR 1000, Campbell Scientific, U.S.A). The signal was converted to sap flux density (J_S in g H₂O m⁻² sapwood s⁻¹).

Granier (1987) found that:

$$J_S = 119 \times 10^{-6} \left(\frac{\Delta T_M - \Delta T}{\Delta T} \right)^{1.231}$$

Where J_S is sap flux density (g m⁻² s⁻¹) and ΔT_M is the temperature difference when $J_S = 0$.

Xylem was divided into two parts, sapwood and heartwood, and sapwood depth is related tree size and tree age (Cermak and Nadezhdina, 1998). Sapwood was determined by water contents and visible color. For

determination of sapwood area, tree rings of forty-five trees near the experiment sites were extracted with tree ring core at the end of the experiment. Heartwood was not developed in most sample trees. Only, a few sample trees had distinct small heartwood.

The sap flux density profile in sapwood was variable temporally (Ford et al., 2004a). The sap flux density profile was affected by several environmental factors. Diurnal change in the radial profile of conifer stems have been correlated to vapor pressure deficit (Nadezhdina et al., 2002) and soil drying (Phillips et al., 1996). However, many studies reported that sap flux density profile in pine sapwood was Gaussian in shape on average. So, I thought that temporal variability of sap flux density profile how affected whole-tree water use. I calculate the mean ratio of sap flux density on mid/outer and inner/outer sap flux density. It will be very useful if the mean ratio was existed, because the mean ratio will be adapted to calculate whole-tree and stand water use. Keeping errors in stomatal conductance estimate to less than 10% using thermal dissipation sensor, estimate of stomatal conductance should be limited to condition in which $D \geq 0.6$ kPa and whole-tree water use were related with stomatal conductance strongly (Ewers and Oren, 2000). So, I applied this standard to deduce the mean sap flux density sap flux density profile.

Sap flow from multiple point data of sap flux density in sapwood was

integrated to estimate whole-tree water use. The total sap flow in xylem was calculated by summing of each conducting area (sapwood area) \times sap flux density of that point. Canopy transpiration (E_C , $\text{mm m}^{-2} \text{ ground area s}^{-1}$) was calculated by summing the transpiration of individual trees (Oren et al., 1998).

2.2.3. Growth and Photosynthesis measurement

Diameter measurements were made every 2 weeks during the growing season and monthly during the winter with dendrometer bands positioned at breast height (1.3 m). As previously mentioned the wood of *Pinus koraiensis* is sapwood. Therefore, sapwood volume and dry mass estimates were based on inside-bark diameters. Sapwood density was calculated from a relationship between stem mass and sapwood volume developed from 20 trees harvested in thinning of 2012.

Biomass production of stems and branches was estimated from species-specific allometric equations based on diameter and height at the beginning and end of each growth period (Zabek and Prescott, 2006). Then calculating the weighted mean based on the density of trees in our study relative to those in published studies. Foliage biomass production during the first growth period only was calculated by multiplying the increase in leaf area by mean leaf mass per area.

Photosynthesis was measured with a portable photosynthesis system

(LI-6400, LI-COR, Inc, USA). The measurements were made between 08:00 and 15:00 h during October 1 to 20, 2012. Photosynthesis of sun branches in the upper and lower canopy of *Pinus koraiensis* were measured using 20 m walking tower built in research site.

The response curves of net photosynthetic rate (P_N) to Photosynthetic photon flux density (PPFD) were generated by increasing irradiance at 9 interval from 0 to 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (0, 30, 60, 100, 250, 500, 1000, 1500, 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) provided by an LED light source at ambient CO_2 concentration of 400 $\mu\text{mol Mol}^{-1}$. Leaf temperature, relative humidity and leaf-to-air vapor pressure deficit in the leaf chamber was maintained at approximately 20 C, 50 % and 0.8 kPa, respectively.

The needles were allowed to acclimate each PPFD for 1 – 3 min until values of photosynthetic rate and stomatal conductance were stable. Each light-response curve was typically completed within 30 min. According to the relationship between net photosynthetic rate and PPFD, light response curves of *Pinus koraiensis* at different canopy positions were fitted by non-retangular hyperbolic model.

Modeling of actual Anet by the canopy and gross primary productivity (GPP) was based on the 4C-A scheme (Schäfer et al., 2003). 4C-A is a multi-layer canopy photosynthesis model where sap-flux-scaled total conductance constrains estimates of stomatal conductance and the aerodynamics of boundary layer conductance, and the constrained

conductance is coupled to a Farquhar-type photosynthesis model (Buckley et al., 2003; Farquhar and Wong, 1984; Farquhar et al., 1980).

Total canopy conductance was calculated from the sum of the boundary layer conductance and stomatal conductance to water vapor. The boundary layer conductance to water vapor was calculated based on the wind speed at each layer. G_c was calculated based on a simplified equation (Kelliher et al., 1992). Only the conditions of $D \geq 0.6$ kPa (~70% of the time) were used to ensure that errors in estimates of G_c remained below 10 % (Ewers and Oren, 2000). Net photosynthesis (A_{net}) integrated over an individual tree and over the entire canopy was calculated.

2.2.4. Defoliation treatment and leaf area measurement

A defoliation experiment was conducted during the growing season of 2011. 19 trees were selected within a large rectangular plot (50 X 25 m), and each 5 trees were assigned to controls and 7 trees were assigned to two treatments groups randomly. Sensors were installed on 19 in June 2011 with Granier-type sensors. Control trees were not trimmed. The branches of trees in the treatment groups were trimmed 30%, 60% in each whorl, respectively. To minimize the difference of microclimate and the effect of trimming on soil water conditions caused by the potentially different transpiration rate, each tree in the four treatments was randomly selected in the plots. The defoliation treatment consisted of hand removal of branches

on DOY 171.

In defoliation experiment, all trimmed branches were collected and branch diameter, position heights of branch and fresh weight were measured. Based on relationships derived for branches, the leaf area of each branch was estimated and summed to tree-level leaf area (LA), which was then related to the percentile of DBH represented by the four sample trees at each of the five sampling times.

51 branches were sampled to measure total leaf fresh weight of current leaves and last year leaves of each branch. All branches and leaves are dried in dry-oven until there was no change in weights and then measured. To measure specific leaf area (SLA), 10 leaves of 51 branches were scanned and leaf areas are measured.

Leaf area index (LAI) was estimated from the leaf area of the 50th percentile tree multiplied by tree density. I converted LA and LAI to biomass based on the leaf mass per area obtained from 32 oven-dried (78 C for 48 hours) leaves collected in the branches about halfway through the study.

The profiles of leaf area index were estimated in each 1-m canopy layer. Values of LAI profile and its seasonal variation were obtained from the sample trees for which branch diameter and insertion height were measured. Because LAI profile was unrelated to tree size, it was expressed relative to the total tree leaf area, normalized by height, and the product averaged for the four sample trees and employed for all trees in the plot. The

sum of the LAI profile of individual trees yielded the canopy-level LAI profile. The change of leaf area after June was estimated according to Kinerson's growth model (Kinerson et al., 1974).

Table 2-1 Experimental tree characteristics: diameter at 1.3 m (DBH), estimated sapwood area (A_{SW}), projected leaf area (A_L) and the ratio of A_{SW} to A_L for control and defoliated trees

Treatment	Tree	DBH (cm)	ASW (cm ²)	AL (m ²) pre- treatment	AL (m ²) post- treatment	ASW:AL (cm ² m ⁻²) pre- treatment	ASW:AL (cm ² m ⁻²) post- treatment
Control	1	31.5	779.3	96.1	96.1	8.11	8.11
	2	25.5	510.7	61.0	61.0	8.37	8.37
	3	24.5	471.4	56.5	56.5	8.34	8.34
	4	27.8	607.0	72.6	72.6	8.36	8.36
	5	30.0	706.9	85.7	85.7	8.25	8.25
30%	1	35.1	967.6	86.2	57.0	11.23	16.98
	2	22.6	401.1	50.0	36.3	8.02	11.05
	3	28.1	620.2	82.4	62.4	7.53	9.94
	4	26.8	564.1	78.4	59.6	7.20	9.46
	5	25.3	502.7	65.3	41.3	7.70	12.17
	6	24.5	471.4	65.3	41.0	7.22	11.50
	7	25.2	498.8	93.1	49.4	5.36	10.10
60%	1	27.3	585.3	56.0	24.3	10.45	24.09
	2	24.6	475.3	72.5	32.1	6.56	14.81
	3	27.5	594.0	45.7	18.9	13.00	31.43
	4	37.2	1086.9	180.3	50.6	6.03	21.48
	5	27.6	598.3	63.8	18.1	9.38	33.06
	6	26.3	543.3	103.8	42.2	5.23	12.87
	7	31.7	789.2	41.2	15.0	19.16	52.61

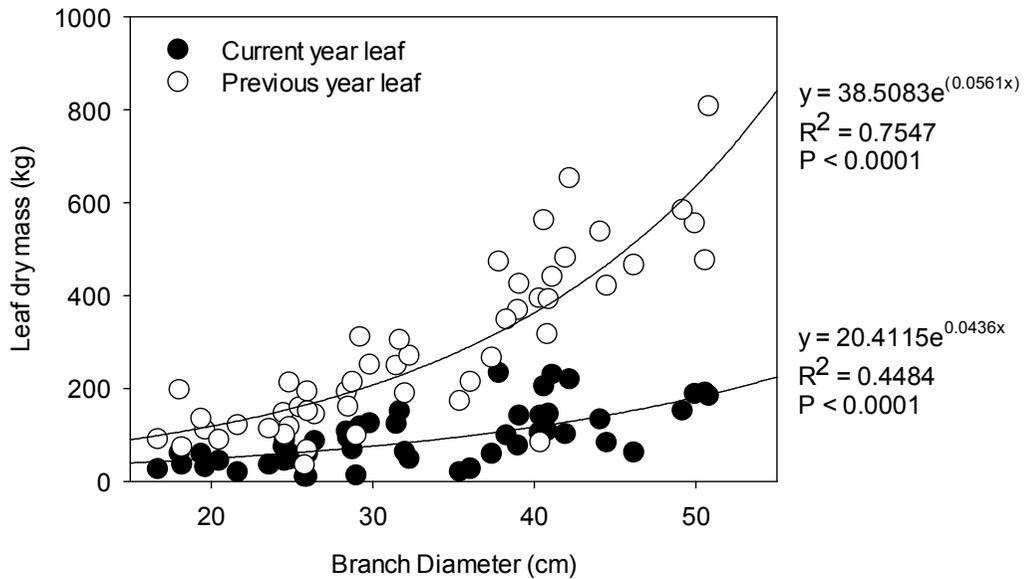


Figure 2-1 Regression of leaf dry mass (single branches) measured by destructive harvest against branch diameter. Closed circles are current year leaves and open circles are previous year leaves

2.2.5. Statistical analysis

Most of the statistical analysis was conducted with SPSS 13.0 for Windows (SPSS, USA). Values of variables between treatments were analyzed by standard ANOVA for comparing means. Regression analysis based on the measured data was used to estimate the derived parameters. Duncan's multiple range test was used for multiple comparisons (Duncan, 1955). Graphs were plotted using Sigma Plot for Windows 10.0 (SPSS, USA).

2.3. Results

2.3.1. Environments of study site

The study period was 145 to 326 day of year (182 days). Date loss was occurred between 205 and 271 day of year, because the experimental site was broken down by heavy rainfall in 205 day of year. So, environmental date was gap filled by correlation between nearest weather station data and other day data in our site.

Daily values of meteorological conditions, leaf area index increment of 2011 are shown in Figure 2-2. Except for an occasional cloudy day, the pattern of solar radiation followed the maximum sun angle, with mean daytime air temperature and vapor pressure deficit lagging maximum radiation. Maximum mean daytime daily temperature and vapor pressure deficit of 2011 were 27.4 °C and 1.49 kPa and those of 2012 were 27.5 and 1.65 kPa. LAI was 5.9 at the beginning of the study in May, rose rapidly to a maximum of 9.5 in July, and declined slowly to 6.0 by the end of the study in September (Figure 2-2 E).

In order to compare two years environments, I used the data from 168 to 293 of each years. Air temperatures showed no difference between two years ($P=0.83482$). Because there were difference between two years precipitation pattern and intensity, water regime of two years were not same. Average vapor pressure deficit of 2011 and 2012 were 0.55 and 0.70 and

significantly different ($P=0.001$). Average total incoming radiation of 2011 and 2012 were 288.8 and 327.4 and also significantly different ($P=0.039$).

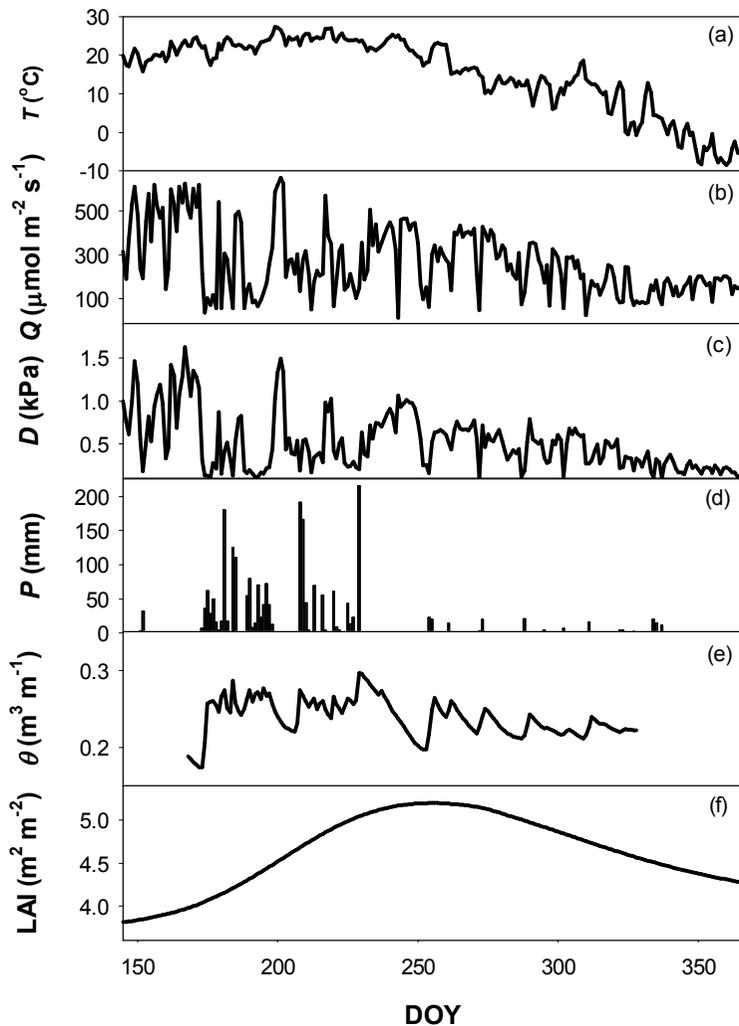


Figure 2-2 Environmental variables during 2011. (a) Daily mean air temperature (T), (b) photosynthetically active radiation (PAR), (c) vapor pressure deficit (VPD), (d) precipitation, (e) water content, (f) leaf area index.

2.3.2. Leaf area change with defoliation intensities

The leaf area profiles, before and after the defoliation treatments are shown in Figure 2-6. Each line shows the average leaf area profile for each treatment. Before the pruning, leaf area profiles were similar in all treatment. However, after the defoliation treatment, the leaf area profile move to left depending on the percentage of branch removed. Three levels of defoliation treatments were successfully carried out and the leaf area of treated trees made changed the leaf area index after defoliation treatments.

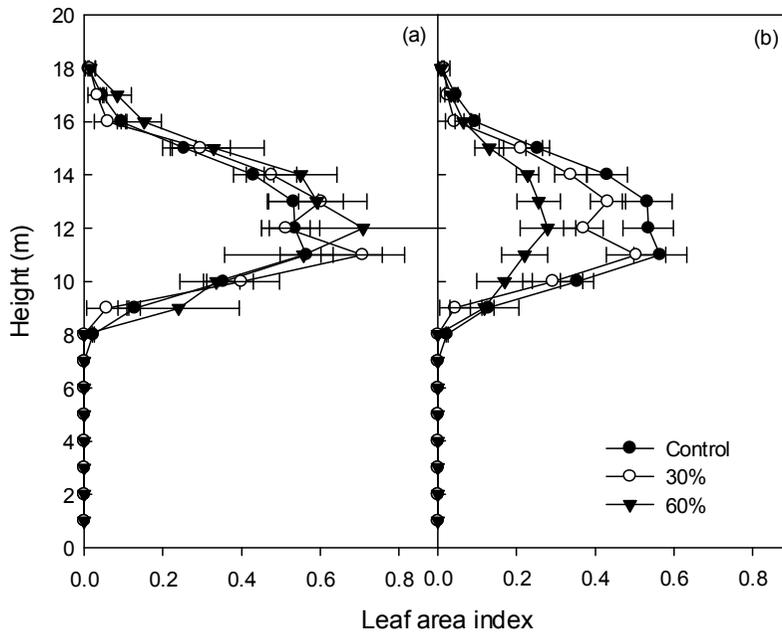


Figure 2-3 Leaf area profile (a) before and (b) after defoliation experiment. Control (black circle), 30% defoliation (light shade circle) and 60% defoliation (heavy shade triangle).

2.3.3. Sap flux density and stand transpiration

Mean daily value of sap flux density of mid and inner of *Pinus koraiensis*, is less than outer and daily pattern of sap flux density is repetitive. The maximum value of sap flux density appeared near noon. Daily mean of sap flux density of outer is most part of total sap flux density (81.8, 14.6 and 3.6%, outer, mid and inner, respectively) (Figure 2-4).

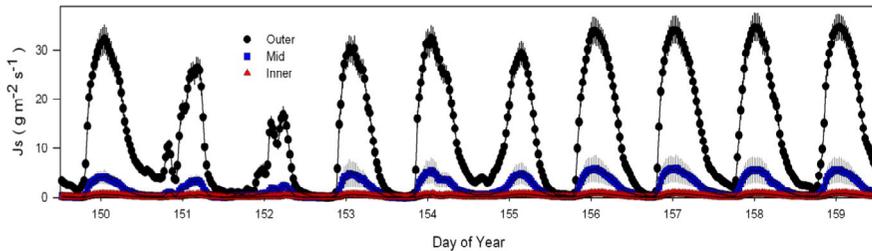


Figure 2-4 Diurnal pattern of Sap flux density of *Pinus koraiensis* stands in Gwangju, Korea

Sap flux density was decreased exponentially toward inner xylem. Almost sap flow occurred in outer part in xylem. Even, sap flux density was nearly zero which relative depth was 30%. This pattern of sap flux density in pine was reported in several studies (Ford et al., 2004a; Ford et al., 2004b; Phillips et al., 1996).

It is that there was a much lower sap flux density in the mid and the inner sapwood because the mid and inner sapwood was composed of juvenile

wood, while the outer were mature sapwood. So, low hydraulic conductivity of juvenile relative to mature sapwood is the likely cause of the reduced sap flux density with depth in the sapwood (Ford et al., 2004a; Phillips et al., 1996). Most studies reported that the peak sap flux density in sapwood was appeared between 2 and 4 cm from the cambium (Delzon et al., 2004; Mark and Crews, 1973; Nadezhdina et al., 2002; Phillips et al., 1996; Swanson, 1967a; Swanson, 1967b; Swanson, 1994).

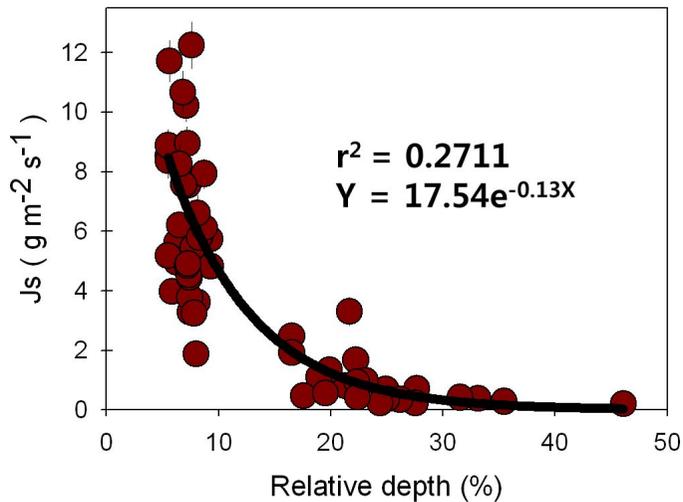


Figure 2-5 Sap flux density radial profile with relative depth of *Pinus koraiensis* plantation in Gwangju, Korea.

Scaling of sap flow to the stand level has often been carried out by first scaling flux measurements to the tree using tree circumference, tree sapwood area, or projected crown area. The apparently good relationship between a measure of tree size and tree transpiration, especially convincing when the range in tree size is large, has been used to justify calculating stand flux by combining the number of individuals per hectare in each size category with the flux density in a representative individuals. However, this may mask potentially known and accountable sources of variability in the original sap flux data.

2.3.4. Photosynthetic response

To examine the photosynthetic parameters for 4C-A model, light response curves were generated. Light responses of sun leaves and shade leaves have different response curves as light intensities went high. Figure 2-5 (a) is a graph of light intensities and stomatal conductance and figure 2-5 (b) is a graph of light intensities and net assimilation of *Pinus koriensis* leaves.

Saturating point of stomatal conductance and net assimilation of sun leaves were much higher than that of shade leaves. This means that sun leaves have higher photosynthetic potential than shade leaves.

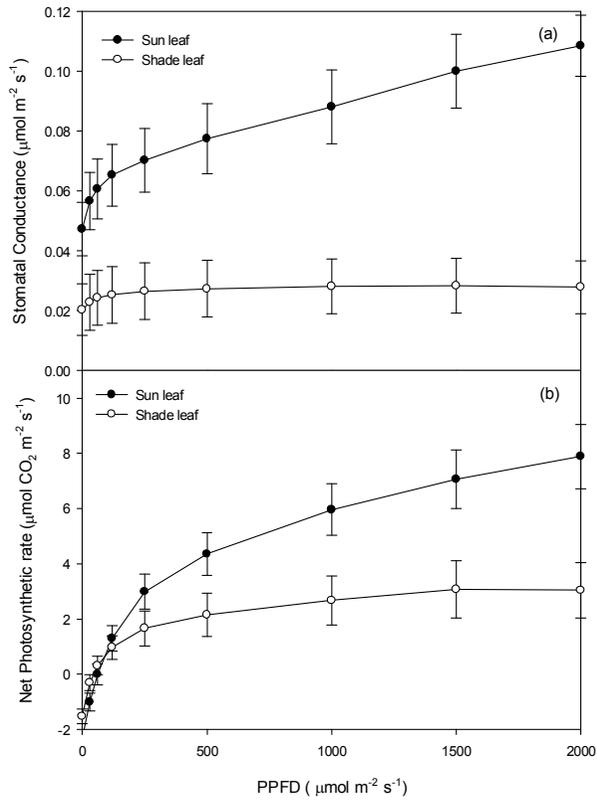


Figure 2-6 Light response curves of sun leaf and shade leaf of *Pinus koraiensis* plantation in Gwangju, Korea, (a) stomatal conductance and (b) net photosynthetic rate.

Also V_{cmax} and J_{max} were calculated with A-ci curves. Average V_{cmax} of sun leaves was $37.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ and that of shade leaves was $25 \mu\text{mol m}^{-2} \text{s}^{-1}$. Average J_{max} of sun leaves was $67.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ and that of shade leaves was $36.7 \mu\text{mol m}^{-2} \text{s}^{-1}$. These numbers also showed that the sun leaves of above canopies have better photosynthetic potentials.

The overall mean values of V_{cmax} and J_{max} for *P. koraiensis* at the field site were similar to the mean maximum values of $V_{\text{cmax}} = 36 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $J_{\text{max}} = 72 \mu\text{mol m}^{-2} \text{s}^{-1}$ for temperate forest species (Wullschleger, 1993). However, comparison of values for these parameters from the literature and in the parameters used to describe their dependence on temperature (Leuning, 2000; Medlyn et al., 2002). Linear increases in V_{cmax} and J_{max} with increased leaf nitrogen concentration on leaf area basis are common for conifer trees (Walcroft et al., 1997).

2.3.5. Sapflux density and stand transpiration

Defoliated pines showed similar sap flow per tree (J_S) to control trees, but if we consider sap flow per unit leaf area (J_L), defoliated trees showed higher sap flow per unit leaf area to defoliated trees as defoliation intensities increased. This plasticity of J_S response resulted in increase of J_L due to decrease of leaf area. Increase of J_L was higher in 60% defoliation than in 30% defoliation. During the total experiment periods, same tendency was continued. During the sunny weather with high D , decreases were enhanced. In 2011, heavy and frequent rain event after treatment provide sufficient soil water availability and there were no restriction due to drought. Low soil water availability due to summer drought decrease J_L more in defoliated trees than in control trees (Poyatos et al., 2013).

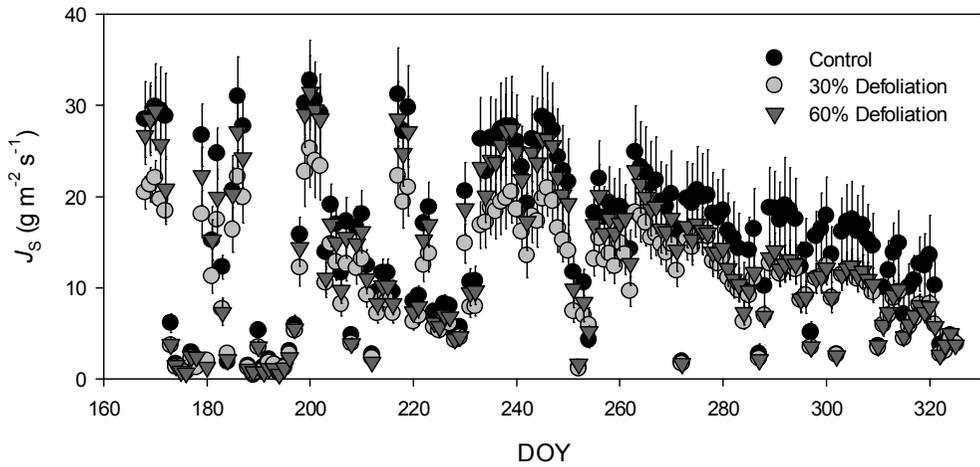
Short term responses of normalized J_s was interesting. Normalized J_s to pretreatment during treatment day (171) decreased as defoliation intensities. Compared to control trees (100.8%), 30% defoliated trees and 60% defoliated pines showed each 92.8% and 90.5% J_s . The day after treatment (172), control trees maintained 98.6% J_s but 30% defoliated trees and 60% defoliated trees showed each 87.0% and 73.2% J_s . Next day control trees decreased to 20.9% J_s due to bad weather conditions and 30% defoliated pines and 60% defoliated pines showed each 17.4 and 13.0% J_s . Rain weather conditions resulted in low J_s and gave no difference to each treatments. Only the day 183 showed significant decrease in 60% defoliation pines.

Intensities of defoliation showed different responses of J_s . In 30% defoliated pines showed no significant decrease after treatment. In 60% defoliated pines showed significant decrease of J_s shortly after treatment but after two weeks from treatment, J_s were recovered to control trees.

This result showed that in short time scales, decrease in leaf area directly related to decrease in sap flow density and transpiration. Shortly after defoliation treatment, leaf area decrease did not result in change of physiological adaptation such as change of stomatal conductance. Defoliated trees experienced a short-term decrease in water flux shortly after the application of the defoliation treatment (Quentin et al., 2011). But, as time passed, the trees showed different response patterns of sap flux density.

Decrements were recovered at the level of pre-defoliation in all treatments.

(a)



(b)

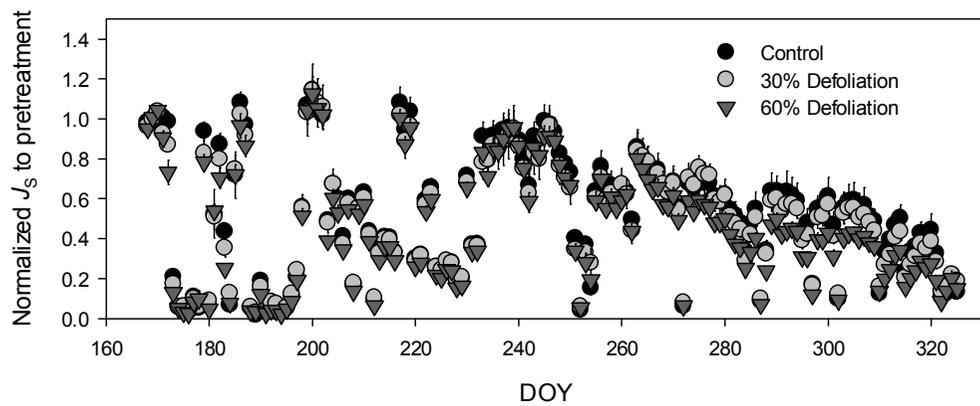


Figure 2-7 Daily mean (a) sapflux density of 0 – 20 mm sapwood area, (b) normalized sapflux density to pretreatment. Control (black circle), 30% defoliation (light shade circle) and 60% defoliation (heavy shade triangle).

Figure 2.8 is monthly average of normalized J_S to pretreatments. Sap flux densities were higher during treatments and decreased after summer. Heavy-rainy periods after treatments in early summer decreased J_S of pine trees. Tree-level water use was consistently lower in defoliated pines, but the difference was not statistically significant when averaged over monthly periods and total periods. Results from ANOVA showed normalized J_S to pretreatments during 6 months did not significantly decreased in two intensities of defoliation even though there were decreasing tendency of J_S .

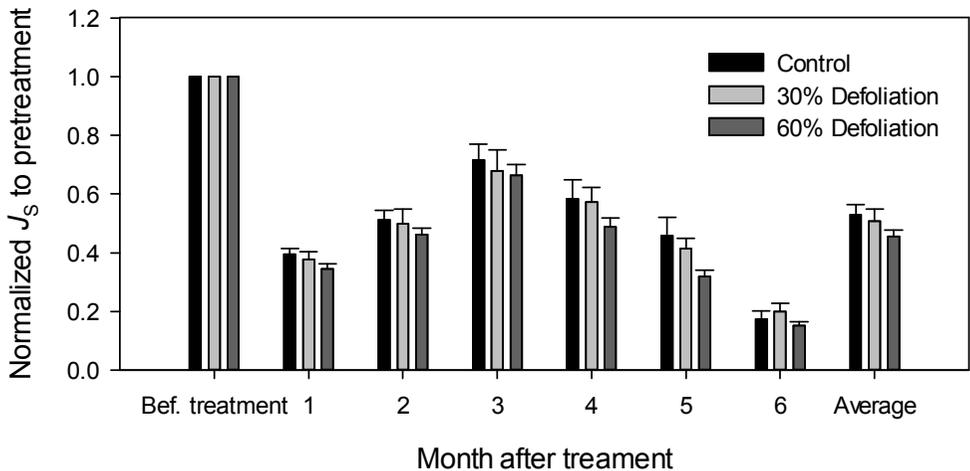


Figure 2-8 Monthly mean (a) normalized sapflux density to pretreatment. Control (black bar), 30% defoliation (light shade bar) and 60% defoliation (heavy shade bar).

2.4. Discussion

2.4.1. Relationship with environmental factors

Figure 2-9 (a) and (b) showed how the J_S respond to Q and D respectively. J_S increased with pruning at the same Q and D conditions, due to decrease of leaf area relative to root water absorption. J_S have a linear relationship with Q and non-linear relationship with D saturating in high D . There was no change in the relationship between normalized J_S and Q and D (Figure 2-9 (c) and (d)).

Figure 2-10 (a) and (b) showed the temporal pattern of total transpiration (E_T) after defoliation treatments. These patterns also showed in total transpiration (E_T). 30% and 60% defoliation treatment all showed no change relatively to control. Modification of tree level adaptation to defoliation made no change in E_T responses to Q and D .

But transpiration per leaf area (E_L) showed different relationship. Decreased leaf area in defoliation treatments resulted in increased E_L (Figure 2-11 (a) and (b)). The tree leaf area is an important determinant of whole-plant transpiration (Roberts, 2000). Following the removal of foliage of the upper canopy, defoliated trees had higher transpiration rates and canopy conductance than the control, non-defoliated trees, providing strong support for hydraulically mediated control of gas exchange (Meinzer and Grantz, 1990; Oren et al., 1999; Pataki et al., 1998).

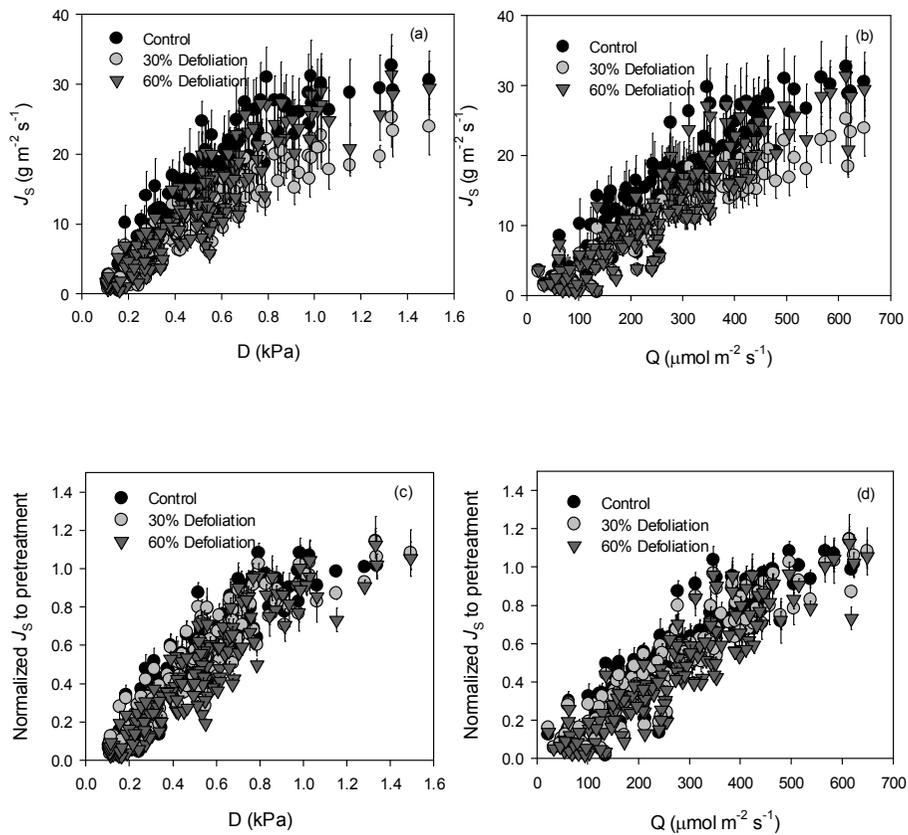


Figure 2-9 Relationship between J_s and (a) PAR, (b) VPD and between normalized J_s to pretreatment (c) PAR, (d) VPD. Control (black circle), 30% defoliation (light shade circle) and 60% defoliation (heavy shade triangle).

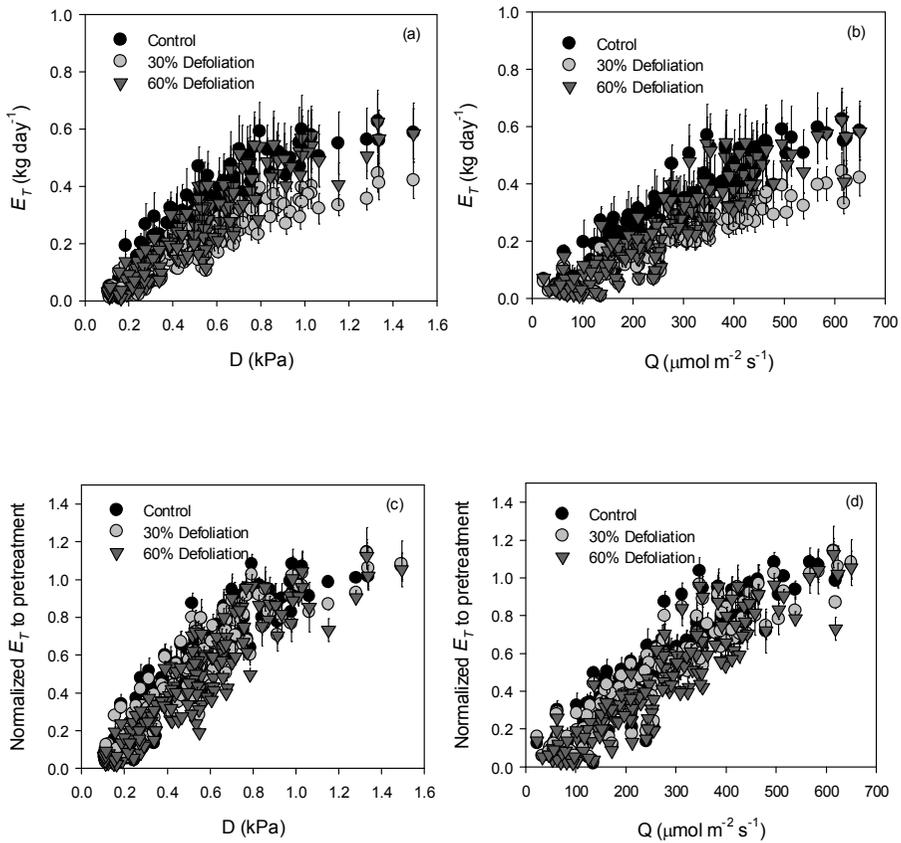


Figure 2-10 Relationship between E_T and (a) PAR, (b) VPD and between normalized E_T to pretreatment (c) PAR, (d) VPD. Control (black circle), 30% defoliation (light shade circle) and 60% defoliation (heavy shade triangle).

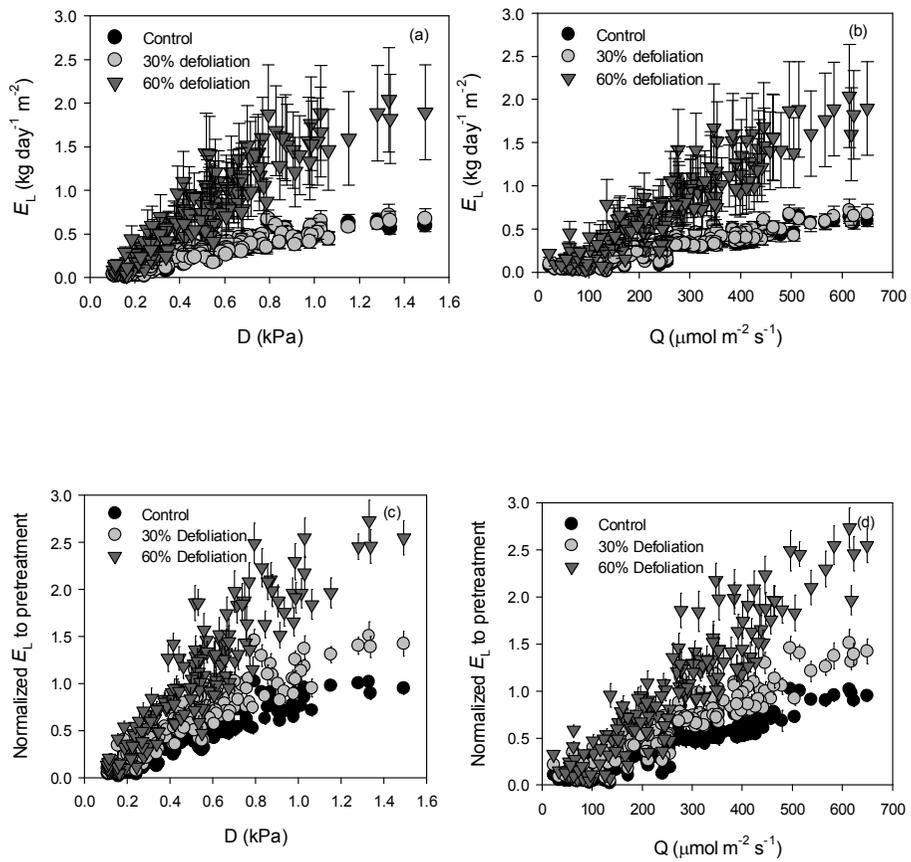


Figure 2-11 Relationship between E_L and (a) PAR, (b) VPD and between normalized E_L to pretreatment (c) PAR, (d) VPD. Control (black circle), 30% defoliation (light shade circle) and 60% defoliation (heavy shade triangle).

Soil-to-leaf hydraulic conductance of sugar cane increased in experimentally via partial defoliation (Meinzer and Grantz, 1990). Removal of 40% of plant leaf area resulted in increased leaf stomatal conductance, such that E_T on a whole-plant basis, and leaf water potential of the residual leaf area remained similar to pre-defoliation levels. Similarly examining the effect of defoliation on leaf-level CO_2 assimilation demonstrated that increased in photosynthetic rate was correlated with increased stomatal conductance throughout the tree crown (Quentin et al., 2010). Also, increased canopy conductance was observed in defoliated *Pinus taeda* trees and also attributed this to increased soil-to-leaf hydraulic conductance (Pataki et al., 1998).

In the current experiment, increased transpiration per leaf area and stomatal conductance could be attributed to increase in hydraulic conductivity. Strong correlations between the soil-to-leaf hydraulic conductance and E has been reported in a previous study (Brodribb and Holbrook, 2004). It is generally accepted that increases and decreases in hydraulic conductivity result in similar directional changes in stomatal conductance (Brodribb and Holbrook, 2004). Thus higher soil-to-leaf hydraulic conductance and the resultant increases in stomatal conductance observed provide a mechanistic insight into the commonly observed up-regulation of photosynthesis in response to defoliation, as increased hydraulic conductivity alleviates leaf water stress, permitting increased conductance to both water vapor and CO_2

(Pinkard et al., 1998; Quentin et al., 2010; Reich et al., 1993).

Although no significant differences in water use between the treatments were observed, defoliated trees experienced a short-term decrease in water flux shortly after the application of the defoliation treatment (Battaglia et al., 2011; Quentin et al., 2011). However, as the experiment progressed and leaf area recovered, rates of water use in the defoliated trees were similar to that observed in the control trees. This is a significant result, as it is often assumed that defoliation reduces transpiration (Cunningham et al., 2009), potentially having a significant impact on forest water balance. However, expected reductions in water use were offset by increases in soil-to-leaf conductance and associated increases in gas exchange, such that total volumes of water transpired remained similar in the two treatments.

At the stand scale, the control of water use may be modified considerably by the structure of the vegetation, which influences coupling with the microclimate or soil moisture, and may result in maintenance of forest transpiration (Phillips and Oren, 2001). For example, similar transpiration rates in two species of eucalyptus under conditions of similar water availability and atmospheric conditions even though the leaf area index of the *Eucalyptus nitens* stand was twice of the *Eucalyptus delegatensis* (Honeysett et al., 1992).

Perfect coupling was not valid when the leaf area index is high (White et al., 2000), as it was in this study, in the *Pinus koraiensis* stand. Despite

the considerable progress made during the last three decades in the knowledge of transpiration rate, understanding the underlying extrinsic and intrinsic regulatory mechanisms of forest water use are still incomplete.

At the canopy level, this model strongly resembles similar phenomenological models developed for *Eucalyptus nitens* and *Eucalyptus globules* at the leaf level high (White et al., 2000). Increased stomatal regulation of water use in response to increased atmospheric VPD plays an important role in conserving water and maintaining water status within limits that avoid catastrophic loss of xylem function. Transpiration of defoliated trees was not limited by stomatal closure but depended on VPD. This result suggests that defoliated trees were less sensitive to high atmospheric VPD because more water was available per unit leaf area, resulting from higher soil to leaf conductance.

2.4.2. Defoliation impact on productivity

In Figure 2-13, DBH increments of each treatment were shown. Control 1 means the trees in defoliation treatments were carried out. Defoliation treatments beside the control trees resulted in a good light environment and relatively high increased DBH increments. So I selected the trees outside of plot not influenced by defoliation treatments and made them control 2. Comparing with Control 2, there was no change in DBH increment of 30% treatments, but in 60% showed decreased DBH increments.

This result complied with net assimilations (A_{net}) of the treatments calculated by 4C-A Model (Schäfer et al., 2003) compared with control (figure are not shown). The ratio between treatment over control showed no change in 30% but similar to patterns of stand transpiration, with 60% treatments ratio were constantly decreased after defoliation treatments.

Previous studies of defoliation on the growth of young *Eucalyptus Globules* trees have shown reduced diameter and height growth (Pinkard et al., 2007; Pinkard et al., 2011a), or no significant change in diameter following partial defoliation (Eyles et al., 2009a; Eyles et al., 2009b). Also there were no significant changes in height or diameter increments following defoliation in either water-availability treatment, despite the removal of 60% of the total leaf area (Barry et al., 2012; Quentin et al., 2012).

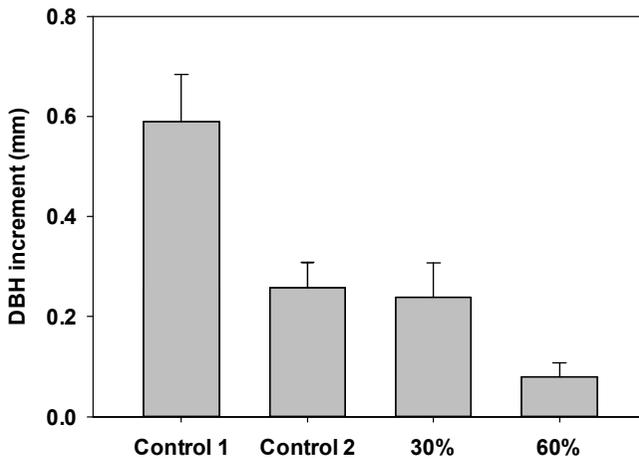


Figure 2-12 DBH increments of each treatment including control 1, control 2, 30% defoliation treatment and 60% defoliation treatment.

Studies on the interactive effects of defoliation with abiotic factors such as nutrients and water supply in *Eucalyptus Globules* have demonstrated that adequate resource availability favors the compensatory response (Pinkard et al., 2007; Pinkard et al., 2011b). Starch concentrations in coarse roots declined in response to defoliation in the irrigated treatments suggesting that aboveground growth may have been maintained by the depletion of below-ground growth may have been maintained by the depletion of below-ground carbohydrate reserves (Eyles et al., 2009a). As carbohydrates have a role in osmoregulation under drought conditions, increases in foliar carbohydrates in the no-irrigated treatments may inhibit a compensatory leaf photosynthetic response (Pinkard et al., 2011b).

2.4.3. Change in water balance and water use efficiency

For water balance, precipitation interception was higher in the control site due to the higher leaf area index, and this causes higher soil water changes on the treatment site. In both sites most of the water was lost by surface evaporation and runoff because most precipitation came down in a few heavy rain events. Transpiration accounts for only about 20 % of annual precipitation in both sites. Even though it is somewhat lower than expected, it may be due heavy precipitation regime during the summer. Drainage were also similar at both sites.

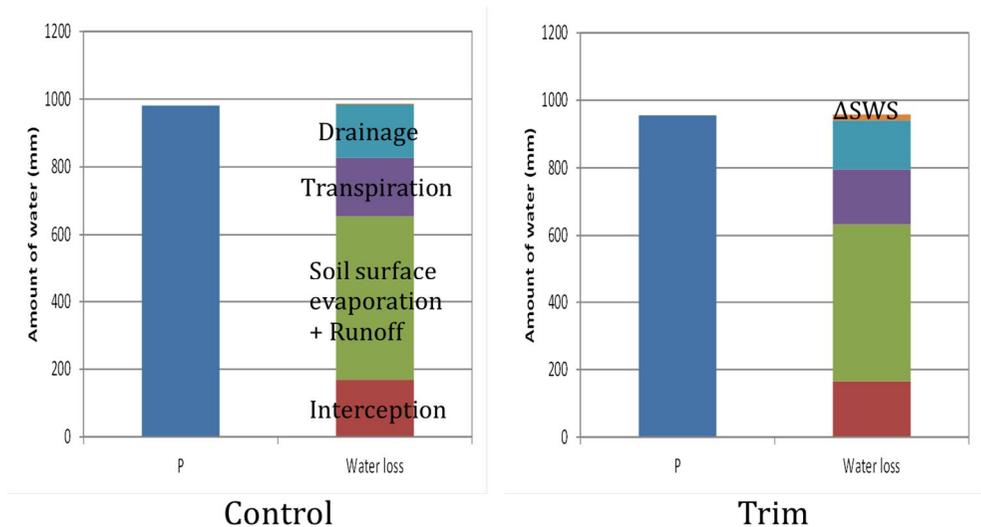


Figure 2-13 Change of water balance between control and trim treatment

Water use efficiency (WUE) of 30% defoliation treatment decreased compared with control (Figure 2-13). ΔC^{13} and WUE has reversed relationship (Li et al., 2007). ΔC^{13} of leaves of each treatment also showed increases in 30% defoliation treatment. In 60% WUE were complemented by the improved light conditions and decreased water use.

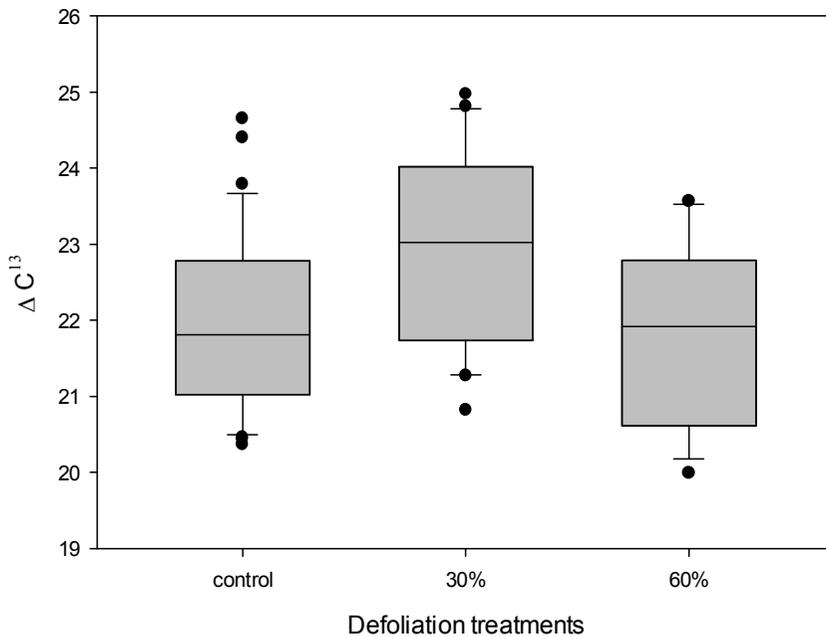


Figure 2-14 Change of ΔC^{13} of leaves of defoliation treatments

Tolerance to herbivore damage can be defined as a plant's capacity to compensate for the lost leaf area and thereby maintain rates of growth at a level similar to those present pre-defoliation. A single defoliation event removing the upper half of the crown will likely have little effect on mature

trees when resources are not limited. Numerous studies have found that a range of tree species can compensate for partial defoliation (Bassman and Dickmann, 1982; Eyles et al., 2009a).

2.5. Conclusions

The effects of tree level defoliation on transpiration and productivity were examined by removing branches along the canopy at 30 and 60% intensities. Thirty percent defoliation treatment, which is considered as the mild defoliation, decreased water stress and increased hydraulic conductance. The enhanced hydraulic conductance compensated the decrease of leaf area and was able to transpire about the same amount of water from individual tree. However, in 60% defoliation, severe defoliation treatment, the decrease of leaf area exceeded the limits of compensation and resulted in decreased transpiration of individual tree.

Similar pattern were also shown in net assimilation and diameter growth. Net assimilations of 30% defoliated trees showed no changes compared to control trees, but those of 60% defoliated trees were substantially decreased. In 30% defoliation, ratio over control was maintained over time, thus the carbon sequestration was also maintained in 30% intensities. These results mean that the mild defoliation event could be overcome by the enhanced physiological processes of *P. koraiensis*, but more severe defoliation such as 60% loss of leaf area resulted in decreased carbon uptake at least for 5 months.

Understanding of the controls on plant water use is an important consideration for managing plantations and their associated impacts on water

balance. Defoliation agents such as insects can significantly affect plantation productivity, but their effects on the plantation water use still remain poorly understood. This study has shown that the experimental manipulation of plant canopies can be a useful tool for tree-level response research and provided strong support for hydraulic controls of carbon uptake in plant canopies.

CHAPTER 3. THE EFFECTS OF THINNING INTENSITIES ON TRANSPIRATION AND PRODUCTIVITY OF PINUS KORAIENSIS PLANTATION

3.1. Introduction

Interactions between forests and atmosphere affects the regional and global climate in various ways including physically and biogeochemically (Bonan, 2008). Forest changes the albedo of land surface and energy partitioning into latent and sensible heat flux (Mansuy et al., 2013; O'Halloran et al., 2012). They also changes atmospheric chemical composition through photosynthesis, respiration, emission of volatile organic compounds and so on (Reimann et al., 2007). However, natural disturbance or anthropogenic interferences including forest management practices could change these interactions and their effects on climate change substantially. Among various forest management practices, thinning is the most widely conducted to produce more valuable and large-diameter timber by reducing the competition among remaining trees, risk of natural fire, and maintaining healthy forest (Lee, 2012).

Thinning affects the microclimate of forest, such as light and wind, and these micro-environmental changes alter the growth and water use and distribution of forest. The effect of thinning on tree and forest stand growth

has been widely conducted around the world. In addition, the effect of thinning on forest water use is getting more attention especially under worldwide changes of precipitation pattern due to climate change and increasing water shortage due to the increase of human populations and their water demand (Vanclay, 2009). To sum up, thinning effects can be various depending on location, stand structure and age, and thinning conditions. In addition, these thinning effects are not proportional to thinning intensities (Olivar et al., 2014; Stogsdill et al., 1992). Thinning stimulates the individual tree growth at mild intensity, but hampers the growth at heavy intensity. On the other hand, in some species, thinning effects are proportional to thinning intensities. The effects of thinning intensities need to be investigated more (da Silva et al., 2012).

In general, thinning is normally conducted 3 times before clear-cut harvesting (Lee, 2012). Depending on the tree species and aimed timber quality, first thinning is conducted at 18 – 20 years after afforestation, second thinning is carried out at 12 – 15 years after first thinning, and final thinning is conducted at 15 – 20 years after the second thinning. Annually 5% of total forested area is thinned and thinned area is increasing with maturing of forest plantation (Lee, 2012).

Pinus koraiensis is one of main species in East Asia resulting in one of most population species for forest restoration in the region. More than 4 million *Pinus koraiensis* trees are planted since 1970s, which is the 2nd

largest planting area in coniferous species. The main purpose of *Pinus koraiensis* plantation is making profit from various sources such as seed, pulp, and timber. The species planted national widely in 1970s and large area of *Pinus koraiensis* forest is about time for final thinning treatment. In Korea, lots of researches have been conducted on *Pinus koraiensis*, but most of the studies are about properties as a timber and the effects of thinning on growth of *Pinus koraiensis* are barely conducted despite of plenty of thinning history. In addition, the effects of thinning on transpiration have not been investigated in Korea. These thinning effects on forest water use have less-focused worldwide, although there are a few studies existed.

Thus, the objectives of this study are (1) to quantify the effect of thinning intensities on individual tree and stand water use of *Pinus koraiensis* stand, (2) to evaluate the effect on growth of remaining trees and stand net primary productivity, and (3) to understand the changes of forest water use and carbon gain by thinning.

3.2. Material and methods

3.2.1. Thinning treatment

In March 2012, the third thinning were conducted prior to the beginning of new growth. The thinning treatments were conducted with two intensities, which were decided by remaining stand density, which were about 430, 350 and 270 trees per hectare for control, mild-thinned and heavy-thinned plots, respectively. As results of thinning treatment about 20 and 40% of trees were harvested using motor saws from randomly selected 3 plots for mild- and heavy-thinned treatments, respectively. Trees for thinning was selected with three criteria, small DBH, short distance to neighboring trees and previous treatment like defoliation in Chapter 2. The harvested trees were removed carefully from the sites by hands to minimize the disturbances such as soil compaction and damages to remaining trees. Only 2 control plots were assigned in this site due to restriction of topography. Another control plot, which is considered as reference plot, were assigned to north of this site where tower measurement system were set up.

3.2.2. Diameter growth and Net Primary Production estimation

In 2011, diameter at breast height (DBH) of all trees > 2 cm in DBH were measured and hand-made stainless steel dendrobands were installed at breast heights in all study plot. Dendroband recording was conducted at 2

weeks intervals during the growing season and monthly intervals during the winter resulting 13 measurements during 2012.

The diameter growth of individual trees was converted into the Net Primary Production (NPP, $\text{g C m}^{-2} \text{ yr}^{-1}$) using the site and species specific allometric equations for needle, branch and stem and root biomass production was estimated (Ryu et al., 2014).

3.2.3. Leaf area profile and leaf area index

Leaf area indices (LAI) of the study plots were estimated using site and species specific the allometric equations and seasonal leaf variation similar to previous research (Kinerson et al., 1974). The allometric equations for needle biomass were developed from pruned branches in 2011 (Chapter 2) and thinned trees in 2012 (Chapter 3), the LAI was calculated by multiplying needle biomass with specific leaf area (SLA, $\text{m}^2 \text{ g}^{-1}$). SLA was calculated by measuring area of over 48 hours oven-dried leaves using scanner. In addition, LAI of stand was validated twice using estimates by a plant canopy analyzer (LAI-2200, Li-Cor Inc., Lincoln, NE, U.S.A). The measurements were conducted at 5 fixed points (four corners and the center) per plot.

3.2.4. Gap-filling of missing data

Major gaps occurred in June to July due to frequently power failures by heavy rains during monsoon. In addition, minor gaps occurred by sensor breakage. The average gap ratio of individual sap flux sensors to the total number of measurement was $10 \pm$ %. The single tree gaps were filled using the regression analysis with other trees in the same plot. Data of 10 days before and after the gaps was used, and the tree with the highest correlation was selected as the reference. The average correlation coefficient was 0.98 and the minimum correlation coefficient was 0.91. Major gaps, where no sap flux data was available, were gap-filled using the relationship between sap flux density and environmental variables such as PAR, air temperature and VPD. The correlation was developed with 10 day data before and after gaps. The average correlation coefficient was 0.78 and minimum coefficient was 0.64. These gap-filled data was not used in sap flux density comparison, but only used in total stand transpiration estimates.

3.2.5. Statistical analysis

For comparison of sap flux density, growth and productivity among different treatments, ANOVA test was conducted on daily averaged sap flux density, diameter increment and NPP with SPSS 13.0 (SPSS, USA). Regression analysis based on the measured data was used to estimate the derived parameters. Duncan's multiple range test was used for multiple comparisons (Duncan, 1955). Graphs were plotted using Sigma Plot 10.0

(SPSS, USA).

3.3. Results

3.3.1. Meteorological conditions

Figure 3-1 shows daily average air temperature, PAR, VPD during the study period. In 2012, mean air temperature and total precipitation of study area was 10.7 °C and 1484.2 mm, respectively. VPD and rain events were closely related. About 70% of total rainfall occurred on July and August and most of intensive rainfall event also occurred this period due to summer monsoon, which caused data gaps by power failure. The high frequency of rainfall event during summer time caused the reduction of PAR and VPD. On the other hand, air temperature was highest on summer time. These seasonal dynamics made interesting combination of environmental conditions. Before summer heavy rainfall, it showed high VPD, PAR, and low soil moisture contents with relatively low air temperature. Heavy rainfall in July recharged the soil moisture to the field capacity, then study plots showed similar environment but with higher soil moisture.

Soil moisture changes of each treatment have been shown in Figure 3-2. Volumetric soil water content at 0 - 30 cm was about 4 % higher in control plot than thinned plots. This differences in soil water content showed daily fluctuation, but were maintained throughout the growing season. However, after thinning treatment soil moisture content of 40 % treatment was increased to that of 20 % treatment, due to the increase throughfall at

heavy-thinned plots.

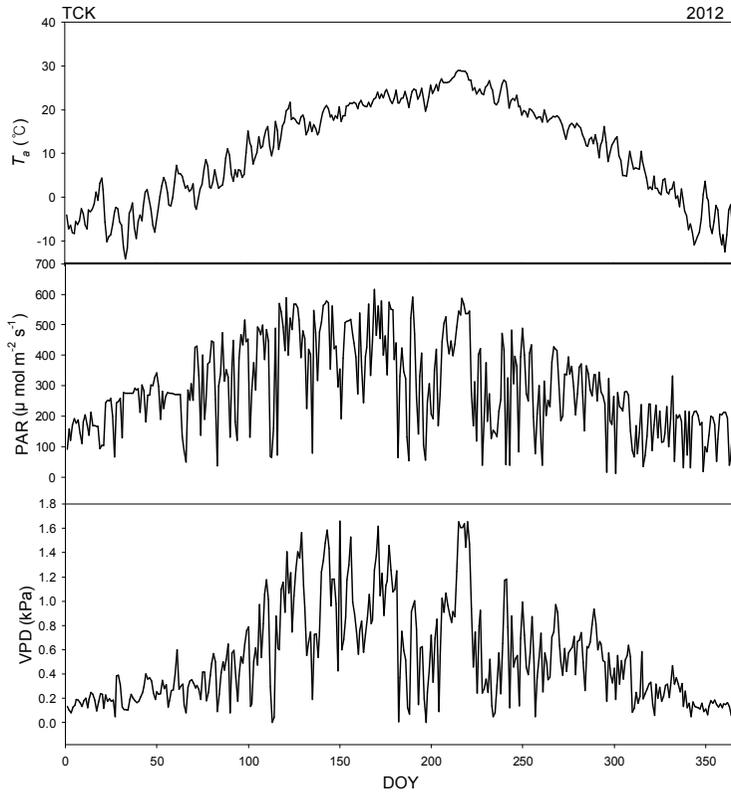


Figure 3-1 Environmental variables during 2012. Daily mean air temperature (T), photosynthetically active radiation (Q), and vapor pressure deficit (D)

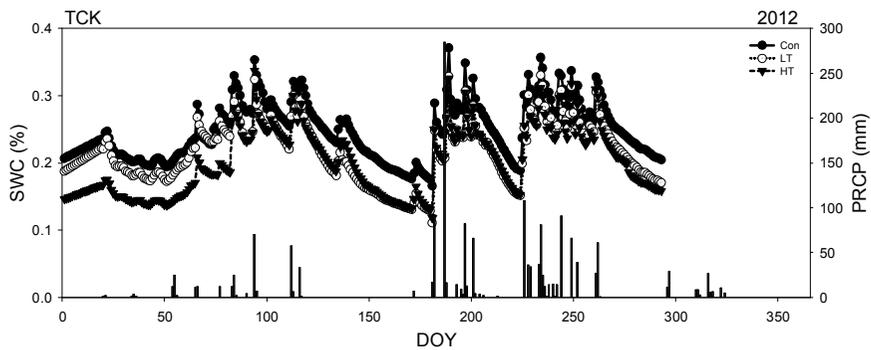


Figure 3-2 Daily total precipitation (bars) and soil water content (SWC) at 0-30 cm in the control (filled circle), mild-thinning (open circle), and heavy-thinning (reverse filled triangle) stands showing \pm S.E.

3.3.2. Leaf area change

Figure 3.4 shows projected annual LAI patterns of each treatment, which was estimated from species and site allometric equations (Ryu et al., 2014) and projected and validated with LAI-2200 measurement (Kinerson and Fritsche, 1971). The thinning treatment initially reduced the leaf area index of the stand by $0.54 \pm \text{m}^2 \text{m}^{-2}$ at the mild-thinned plots and by $0.87 \pm \text{m}^2 \text{m}^{-2}$ at heavy-thinned plots on average (Table 3-1 and Figure 3-3).

Table 3-1 Description of the thinning treatments at *Pinus koraiensis* stand near Gwangju, Gyeongido.

Parameter	Control		20%		40%	
Mean DBH (cm)	29.37±5.4		27.8±7.4		29.23±5.0	
Mean Height (m)	16.3±1.1		16.1±1.1		16.3±1.0	
Basal Area (m ² ha ⁻¹)	31.7±1.0		28.4±3.7		26.0±1.9	
Age (year)	50		50		50	
Density (tree ha ⁻¹)	448±31		320±0		240±0	
LAI (m ² m ⁻²)	before	After	before	after	before	after
	3.85	3.84	3.37	2.83	3.15	2.28

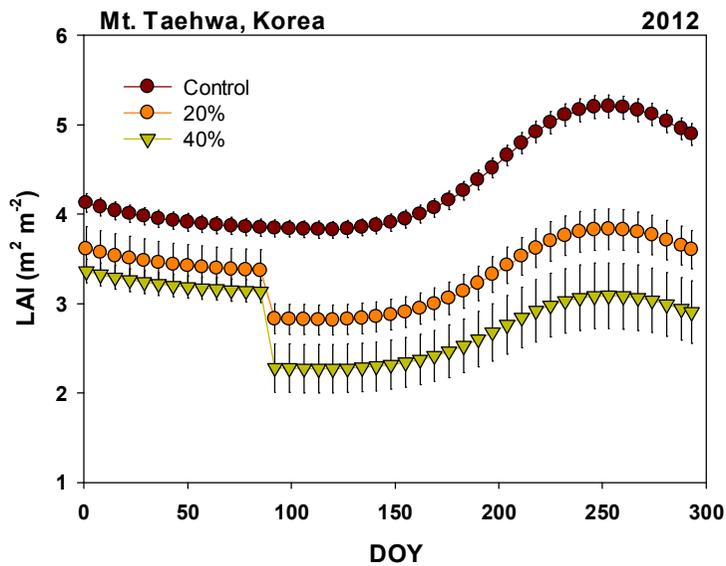


Figure 3-3 Annual pattern of leaf area index of thinning treatments at the *Pinus koraiensis* stand near Gwangju, Gyeongido: unthinned treatment (red circle); 20% treatment (orange circle); 40% treatment (green triangle). Error bars are 1 standard error (n=3).

3.3.3. Sap flux density and transpiration

There was little difference in sapflux density among different thinning intensities (Figure 3-55 (a)). On average, sapflux density of mild-thinned and heavy-thinned plot were 6.7% and 2.4% higher than control plot, but the differences were never significant due to large variation within treatments. Daily sapflux density showed high fluctuation due to large variation in environmental conditions. The seasonal pattern of sapflux density showed similar trends regardless of thinning treatment.

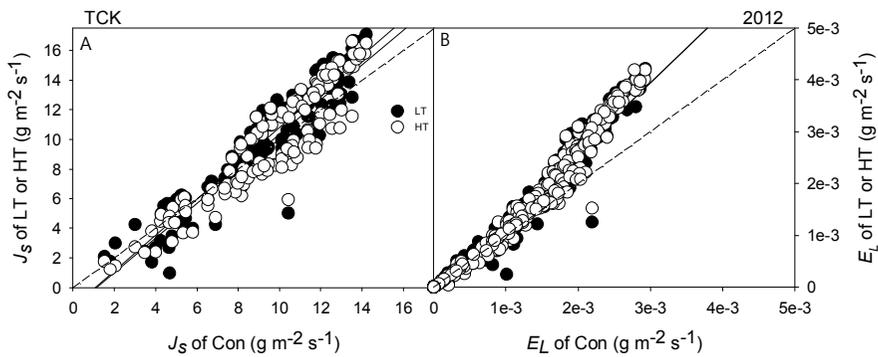


Figure 3-4 The relationship between (a) sap flux density and (b) leaf-level transpiration of control to mild-thinning (filled circle) and heavy-thinning (open circle) stands. Lines indicate linear regressions and r^2 , statistical significant of the regression line (p) are also shown. Dotted line indicates 1:1 line.

On the other hand, leaf level transpiration showed significant difference between mild- and heavy-thinned plots and control plots (Figure 3-5 (b)). Leaf-level transpiration of thinned plots was higher than control plot throughout the growing season, but there was no difference between heavy and mild- thinning treatment. The differences were most significant in summer time, when leaf-level transpiration was highest (Figure 3-6). It also showed variation with time. After thinning treatment, the differences were increased until late of May. The differences decreased gradually until beginning of summer monsoon. After heavy rainfall events, the differences were consistent with minor daily fluctuations.

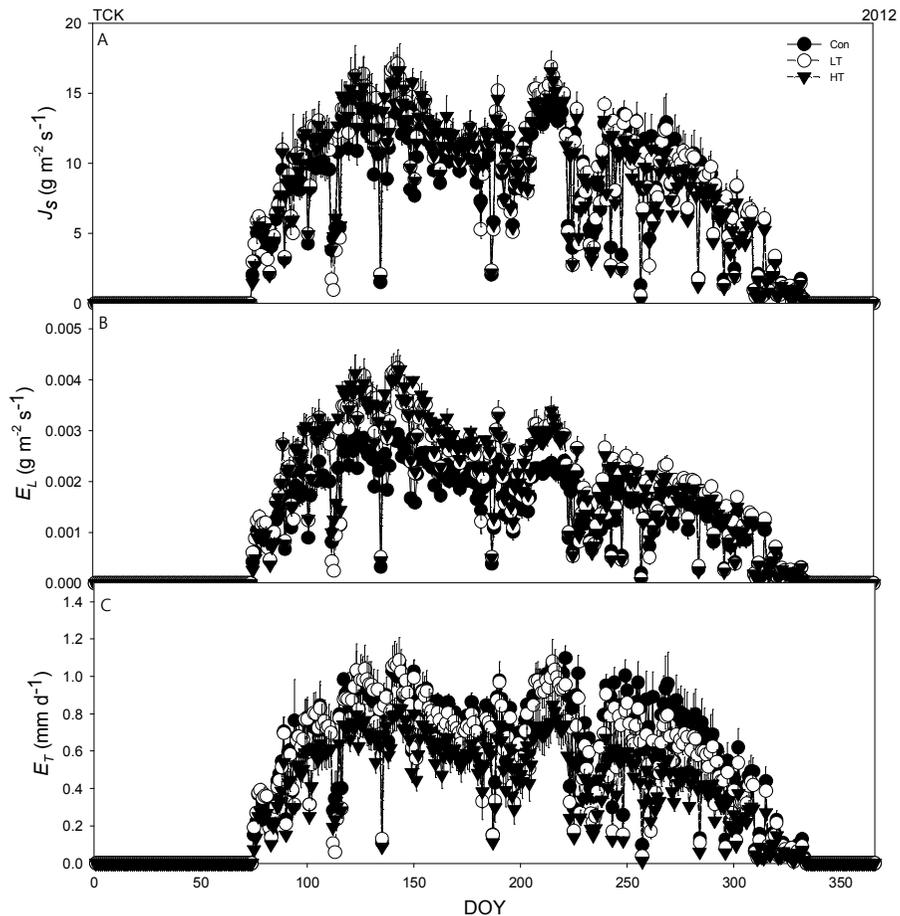


Figure 3-5 Daily mean (a) sapflux density of 0 – 20 mm sapwood area, (b) leaf level transpiration (E_L), and (c) daily stand transpiration of control (filled circle), mild-thinning (open circle) and heavy-thinning (reverse filled triangle) stands. Statistical differences between thinning treatment stands are shown in the bottom of each graph. The letters indicate Duncan grouping at $P < 0.05$ by ANOVA.

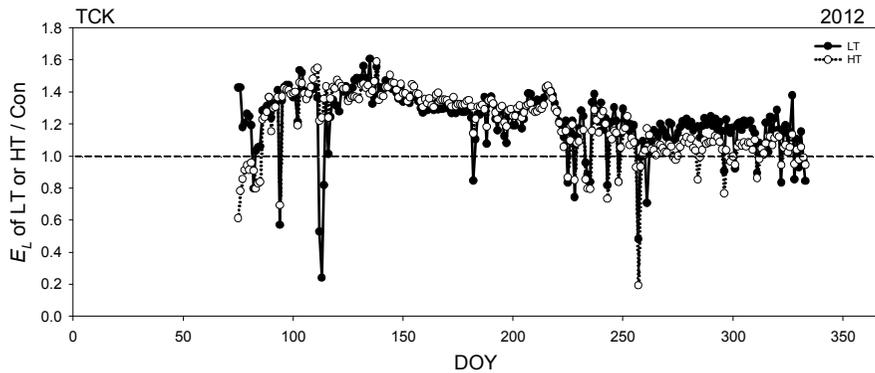


Figure 3-6 Quotient between leaf-level transpiration of control and mild-thinning (filled circle) and heavy-thinning (open circle) stands. Dotted line indicates 1:1 line.

Even though leaf-level transpiration was higher in thinned plots, stand transpiration was higher in control plot due to large sapwood conducting area and leaf area (Figure 3-5 (c)). Maximum daily transpiration reached Annual stand transpiration was 166.4 ± 23.5 mm for control plot, 152.4 ± 26.9 mm for mild-thinned plot, and 116.8 ± 26.8 mm for heavy-thinned plot. The difference in stand transpiration also showed temporal variation like leaf-level transpiration.

3.3.4. Effects of thinning intensities on diameter growth and stand productivity

Absolute diameter growth and relative growth rate were highest in heavy-thinned plot (3.85 ± 0.33 mm and $1.28 \pm 0.23\%$) and lowest in control plot (2.42 ± 0.81 mm and $0.83 \pm 0.30\%$). Light-thinned plot (3.23 ± 0.75 mm and $1.03 \pm 0.21\%$) showed medium growth rate, but the differences were only significant between heavy-thinned and control plots (Figure 3-7 9 (a)). The differences in absolute growth were larger than the differences in relative growth due to high initial average DBH of heavy and mild-thinned plot. That means that improved mild conditions and reduced resources needs unlimit the restriction of growth in thinned plots.

Annual growth pattern showed similar trends among thinning intensity treatment (Figure 3-7 (b)). Trees in heavy thinned plot showed higher growth rate from the beginning of growing season, and this trends continued throughout the whole growing period, and trees in mild-thinned plot showed medium growth rate. Individual biomass increment was also highest in heavy-thinned plot, and lowest in control plot, and the difference between heavy-thinned and control plots was only significant. Light-thinned plot showed medium growth rates, but the difference with control or heavy-thinned plot was not significant.

This increase of individual tree growth by thinning resulted in increase

of stand net primary productivity of thinned stand even though the stand density were reduced by thinning, but the differences were not significant. (Figure 3-8).

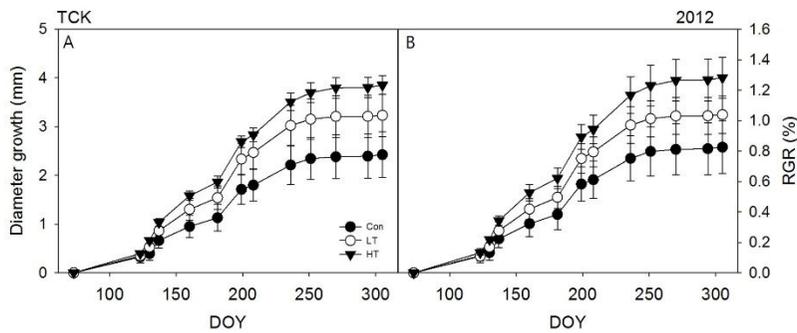


Figure 3-7 Seasonal pattern of (a) mean diameter growth and (b) relative growth rate of control (filled circle), mild-thinning (open circle) and heavy-thinning (reverse filled triangle).

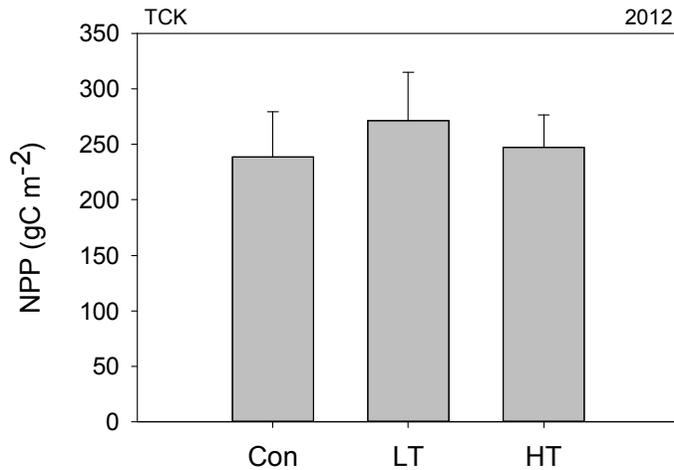


Figure 3-8 The annual net primary productivity (NPP) of control, mild-thinning, and heavy-thinning stands. There was no statistical difference between thinning treatments.

Thinning reduced stand transpiration without the decrease of stand net primary productivity, which caused increase of stand level water use efficiency. This tendency was much significant on heavy-thinned plot, and water use efficiency of heavy-thinned plot ($2.13 \pm 0.15 \text{ g C kg H}_2\text{O}^{-1}$) was 43% higher than control plot ($1.49 \pm 0.65 \text{ g C kg H}_2\text{O}^{-1}$). Variations within treatment were much higher in control plot ($CV = 0.43$) than mild-thinned ($CV = 0.11$) and heavy-thinned ($CV = 0.07$) plots. The relationship between stand transpiration and NPP showed a distinct difference between control plot and thinned plots. In the heavy and mild-thinned plots, stand transpiration was positively correlated with NPP, but the relationship was opposite in control plot (Figure 3-9).

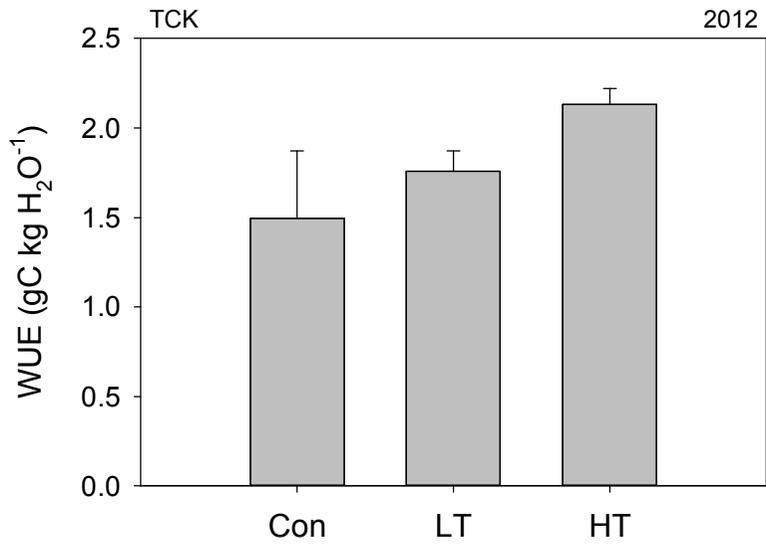


Figure 3-9 The stand level water use efficiency (WUE) of control, mild-thinning, and heavy thinning stands. The letters above bars indicate the Duncan grouping by two-way ANOVA ($p < 0.05$).

3.4. Discussion

3.4.1. Temporal pattern of sap flux density

After thinning treatment, sap flux density was increased on both thinning intensities initially. On average thinning increase the sap flux density ca. 8.7% on mild-thinned stand, and 4.1% on heavy-thinned stand, but in the first two months sap flux density increased ca. 14.6% and 13.4% on mild and heavy-thinned stand, respectively. In addition, the differences between control and two thinning stands were also increasing.

These initial increment of sap flux density could be explained by changes of light environment. Thinning created more gaps, and remaining trees can utilize more light source, especially on the lower and shaded leaves. This improved light environment induces the more leaf level transpiration under little limitation by soil water. These trends were more significant on leaf-level transpiration. This initial increase of sap flux density was contradict with other studies which reported post-thinning stress or “thinning shock” (DeBell et al., 2002; Harrington and Reukema, 1983).

The increase of sap flux reached its maximum just before new leaves came out, since then it decreased gradually or stayed at the similar ratio to control plots up to the beginning of monsoon (Figure 3-5 and 3-6). After monsoon, the increase of J_s at thinned plots were deteriorated especially at the heavy-thinned plots. However, these reduction in J_s increment could be

explain as the increase of J_s at the control plots as the water status at the control plots became favorable due to monsoon.

3.4.2. Reaction of transpiration with soil water and environmental condition

The differences in transpiration per leaf area between control and thinned stands increase with the decrease of soil water content (Figure 3-10). In addition, the increase of transpiration was greater at the heavy-thinned plots than mild-thinned plots, which implying the water stress was greater at the control than thinned plots.

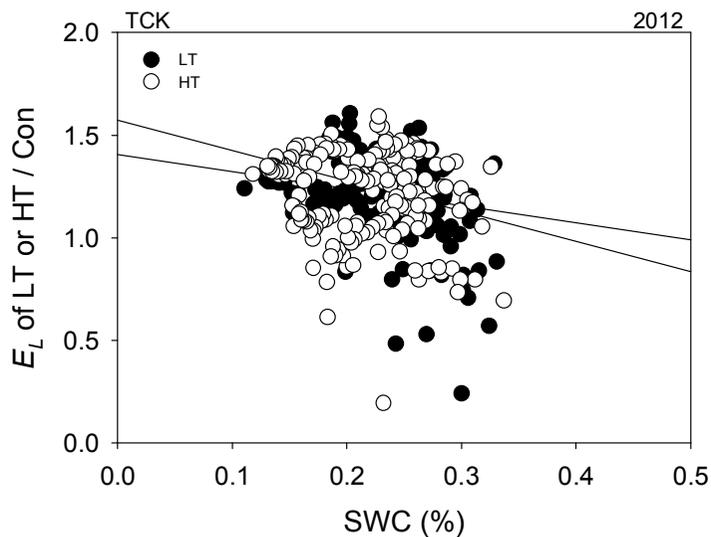


Figure 3-10 The effects of volumetric soil water content (SWC) on the ratio between leaf-level transpiration of mild-thinning (filled circle) and heavy-thinning (open circle) to control stands. Lines showing linear regressions and r^2 and p-value are also shown.

The differences in transpiration per unit leaf area between control and thinned plots also increased as potential evapotranspiration increased (Figure 3-11). In other words, as the demand of transpiration increased the ratio between thinned plots and control plots increased, which support the increase of water availability under severe conditions.

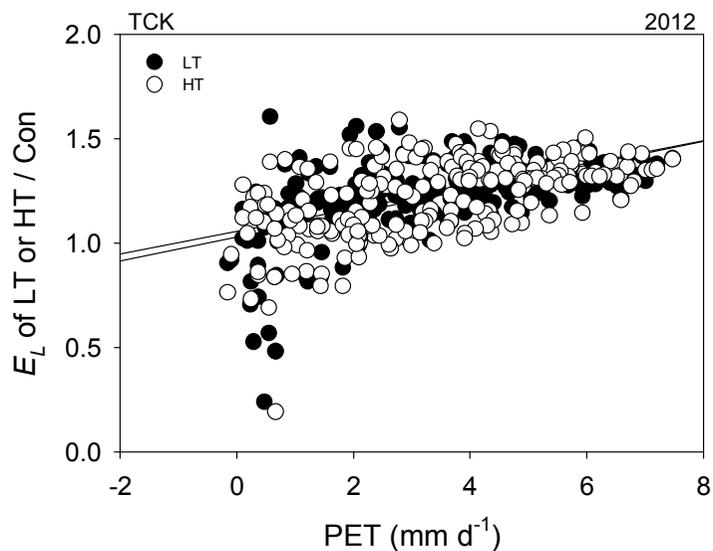


Figure 3-11 The relationship between potential evapotranspiration (PET) and the ration between leaf-level transpiration of mild-thinning (filled circle) and heavy-thinning (open circle) to control stands. Lines showing linear regressions and r^2 and p-value are also shown.

However, at the stand level, transpiration of stands of *Chamaecyparis obtusa* was reduced in direct proportion to the reduction of basal area (Morikawa et al., 1986), and similar results from *Quercus petraea* stands were found (Breda et al., 1995). In the latter study, transpiration on the thinned plot returned to the same level as that on the reference plot in the second year after thinning. A reduction of transpiration (relative to the reference plot) by more than 40% after a thinning in a mixed Scots pine/Norway spruce stand was reported when basal area was reduced by 24% (Lagergren et al., 2008). A reduction of transpiration after thinning by ca. 24% in a Scots pine plantation was modeled (basal area reduced by 34%) (Sturm et al., 1998).

On the other hand, with Douglas fir (*Pseudotsuga menziesii*) (Black et al., 1980) and Loblolly pine (*Pinus taeda*) (Stogsdill et al., 1992), there was little or no effect of thinning on stand transpiration, compared to an unthinned stand during dry conditions. It was also found no effect of thinning on total transpiration in boreal *Pinus sylvestris* (Vesala et al., 2005).

The effects of thinning on transpiration have also been theoretically analyzed (Whitehead et al., 1984). An interesting feature of their analysis of thinning is that it is thought to reduce the vulnerability of drought as the interception and competition for water will decrease, which has also been shown in field studies (Aussenac and Granier, 1988).

The relative increase of soil water content at the thinned plot are also shown at Figure 3-2, especially at heavy-thinned plots. Throughfall of 40%

thinning intensities are significantly higher than control but that of 20% are not higher than control. In 40% thinning intensities thinning practices made open spaces and low LAI let more rain come to ground directly relative to control.

As a major component of the water balance in both plots, evaporation from the stand canopy on the thinned plot was dramatically reduced due to decreased stand density. The lower values of evaporation on thinned plot were associated with its reduction in LAI. However, the reduction in leaf area also allowed greater amounts of solar radiation and water to reach the soil surface, allowing higher surface evaporation after thinning. Therefore, soil surface evaporation might have increased. This response is in accordance with earlier report that soil evaporation was greater in a thinned stand of ponderosa pines (Simonin et al., 2007).

3.4.3. Increase of individual growth by thinning

Thinning induced the increment of individual tree growth, and this is much significant at heavy-thinning stand (Figure 3-8). The reduction of competition alleviates the available soil water and nutrients and irradiative energy input for remaining trees. Constant final yield (Weiner and Freckleton, 2010) and self-thinning (Thoranisorn et al., 1990) emphasize the increase of individual tree growth as the reduction of competition. The

increase of individual tree growth not only can supply high quality timber production, but also provide efficient, low-cost ways to increase biodiversity and variability of ecosystem (Puettmann and Tappeiner, 2014).

3.4.4. The effects of thinning intensities on stand water use efficiency

The increase of individual tree growth and decrease of stand transpiration increased WUE (Figure 3-9). Figure 3-12 shows the relationship between stand transpiration and NPP, as expected NPP increased with stand transpiration at mild- and heavy-thinned plots. In addition, heavy-thinned plots showed higher NPP at the same transpiration than mild-thinned plots. Unlike thinned plots, control plots showed a negative relationship between transpiration and NPP.

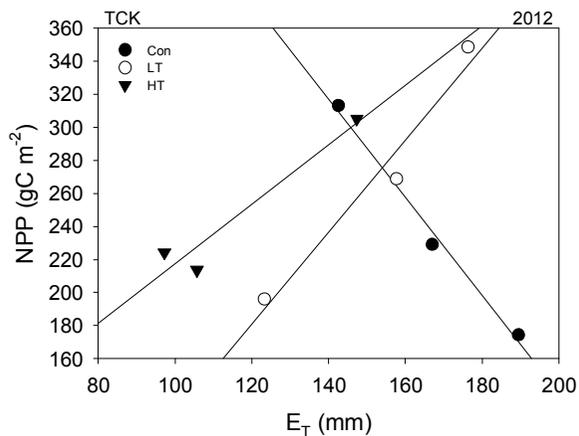


Figure 3-12 The relationship between annual stand transpiration (E_T) and net primary productivity of control (filled circle), mild-thinning (open circle), and heavy-thinning (reverse filled triangle). Lines showing linear regressions and

r^2 and p-value are also shown.

3.5. Conclusions

The effect of thinning, the most common forest practice, has been studied in many studies. However, those studies are mainly focused on forest management aspects including timber quality improvement. With the increased attention to water and carbon especially due to climate change, I studied how the change of leaf area by thinning at different intensities (20 % and 40 %) influenced water use, growth, productivity and water use efficiency of Korean pine trees and stands.

Thinning relieved water stress to the remaining trees by increasing throughfall, soil water content and reducing competition among trees. Less water stress increased transpiration and led to increase of productivity and growth at the tree level. However, stand transpiration decreased ~30 % and 50 % at 20 % (mild-thinned) and 40% (heavy-) thinned plots, respectively. But, these reductions in stand transpiration with thinning only reduced the stand productivities at high intensities. In contrast, NPP of 20 % thinned plots was higher than controls plots, even though it was not significant.

My study showed the different stand responses on transpiration and productivity according to thinning intensities. Long term monitoring and analysis on all components of water and carbon balance are necessary to improve our understanding on the effects of thinning and better ecosystem management.

CHAPTER 4. OVERALL CONCLUSIONS

Leaf area index, which is considered as a proxy of ecosystem productivity and biomass, could change significantly due to various disturbances at different scales and intensities. Understanding the change of forest water use and productivity due to environmental disturbances resulted in leaf area change is important for ecosystem management. Therefore, the effects of tree level defoliation and stand level thinning on transpiration and productivity at tree- and stand-level were evaluated based on continuous field measurements using Granier type sap flux sensors with different leaf area conditions.

At the tree-level, my study has shown that up to 50% of defoliation resulted in the compensated transpiration due to higher soil-to-leaf conductance which led to the increased G_C and E in defoliated trees compared to control trees. These compensated transpiration also caused positive effects on tree level photosynthesis and growth due to the better light environment and less competition for water at individual tree level. Consequently, it increased stand level productivity and water use efficiency. These results support the strong hydraulic control on gas exchange in plant canopies.

At the stand level, my study quantified changes of water balance components such as precipitation throughfall, canopy evaporation and

especially emphasizing stand transpiration at different thinning intensities. Thinning released water stress to the remaining trees by increasing throughfall, soil water content and reducing competition for water. Less water stress increased transpiration and led to the increase of productivity and growth at the tree level. However unlike tree level defoliation, thinning reduced the stand transpiration even at mild intensity at least for short terms like a year which was our experiment duration. However, enhanced individual tree growth stimulated the stand productivity at mild intensity without significance.

In summary, my work improved the quantification of transpiration, productivity and carbon assimilation of *Pinus koraiensis* plantation in Mt. Taehwa with different treatments, which created the change of leaf area. My research emphasized on the different responses following the reduction at different levels, tree and stand. At the tree level, transpiration was able to continue to utilize about the same amount of water at mild defoliation. Thinning treatment even increased leaf and tree level transpiration, but it could not keep up at the stand-level transpiration. For carbon, photosynthesis increased in both treatments due to less water stress and better light environment. Consequently, water use efficiency enhanced with defoliation and thinning treatments. As a result, my study provided the effect of tree and stand level leaf area change on water and carbon use of *Pinus koraiensis* plantation for more productive and sustainable forest management.

However there are several limitations in generalizing my outcomes for forest management. 1) Even though my experiment lasted more than 5 months with continuous measurements of transpiration in each treatment, at the aspect of forest management 5 months is a short period enough especially considering that timber production usually takes more than 70 years. Therefore, further monitoring of our treatments are necessary to see the long term effect of defoliation and thinning. 2) Defoliation treatments, which I conducted by pruning branches evenly along canopy depth and from all directions, are not similar to natural disturbances and forest management practice in many aspects, even though we tried to mimic insects or disease outbreak or pruning. 3) The treatment area was much smaller than usual forest practice or disturbances. Thinning and disturbance commonly occur at the scales of several hectares or larger. However, our treatment was conducted about a hectare size, which also include measurement replications.

With such above mentioned limitations, my research is only a small step to understand the effects of leaf area changes on transpiration and productivity at different scales and intensities. However, my study has shown the experimental manipulation of plant canopies can be a useful tool for the elucidation of water and carbon relations and responses to leaf area changes at tree and stand scales. As future researches, I will extend my research scopes to entire water and carbon balance and continue to see the long term effects on both balances. Thorough analysis on all components of

water and carbon balance will improve our knowledge for better forest management.

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ABSTRACT IN KOREAN

엽면적 변화가 50년생 태화산 잣나무림의 증산 및 생산성에 미치는 영향

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산림은 전 지구 수분과 탄소 수지 균형에 있어 육상생태계와 대기권을 연결하는 교두보 역할을 하고 있다. 다시 말해, 산림의 수분과 탄소 이용에 대한 이해는 전 지구 생태계의 역할을 이해하는 데 있어 중요한 요소 중 하나이다. 산림의 수분과 탄소의 이용은 다양한 생물학적인 요소, 특히 산림 엽면적의 변화에 의해 영향을 받는데, 이러한 엽면적 변화에 따른 산림의 수분과 탄소 수지 변화에 대한 정량화는 최근 많은 관심을 받고 있다. 따라서 본 연구는 50년생 잣나무 (*Pinus koraiensis*) 임분에서 엽면적의 변화가 산림의 수분과 탄소 이용에 미치는 영향을 파악하기 위해서 실시하였다.

엽면적 변화를 위한 두 가지 방법을 적용하였다. 먼저, 개체목마다 30%와 60%의 엽면적을 감소시켰는데, 이것은 병해충, 환경 스트레스 또는 가지치기에 의한 엽면적 감소를 모의한 것이다. 다음으로 임분의 생산성과 지속 가능한 산림 경영을 위해 가장 일반적으로 실시하는 간벌을 통해 엽면적을 20%와 40% 감소시켰다.

엽면적 변화가 산림의 수분 및 탄소 수지 변화에 미치는 영향에 대해 알아보기 위해, Granier-type의 수액속 센서를 이용하여 임분의 증산량을 측정하였고, 임분 생산량 측정을 위해 덴드로밴드를 이용하였다. 이와 더불어 4C-A 모델을 이용하여 임분의 광합성을 계산하였다. 본 연구의 결과는 다음과 같다.

1) 30 %의 엽면적을 감소시킨 개체에서 수분 스트레스 감소와 잎의 수리전도도 증가로 인해 잎 손실에 의한 증산을 보완하였다. 하지만 60 %를 감소시킨 개체에서는 수분 스트레스 감소와 잎의 수리전도도 증가가 잎 손실에 의한 증산을 보완하지 못했다. 수관의 탄소 흡수도 30 %를 감소시킨 개체에서는 변화가 없었지만, 60 %를 감소시킨 개체에서는 감소를 보였다. 이러한 결과는 30 % 엽면적 감소는 수분 스트레스의 감소와 개선된 광 환경의 결과로 그 손실이 보완되지만, 60 % 엽면적 감소는 증산과 생산성의 보완이 이루어지지 못한다는 것을 의미한다. 이를 통해 심한 엽면적 감소는 증산과 생산성에 있어서 쉽게 회복하지 못함을 확인할 수 있었다.

2) 간별로 인해 임상으로 유입되는 강우의 양이 증가하였고, 이에 따라 토양 수분, 수액속과 잎 단위에서의 증산이 증가하였다. 그러나, 임분의 증산량은 20 %와 40 % 간별 처리에서 각각 ~30 %와 ~50 %씩 감소하였다. 따라서, 개체목에는 30 % 엽면적 감소가 증산의 감소로 연결되지 않았지만, 간별에 의한 20 % 엽면적 감소는 증산의 감소로 이어졌다. 하지만 간별에 의한 20 % 엽면적 감소는 개체목 단위에서 흉고직경 성장을 강화했고, 또한 순일차생산의 증가를 유발했고, 결과적으로 수분이용효율이 증가하였다.

본 연구는 태화산 잣나무 임분에서 다양한 엽면적의 감소에서 증산량과 생산, 그리고 탄소 축적을 정량화하였다. 엽면적

감소가 임분의 수분 및 탄소 관계의 미치는 영향은 개체목과 임분 단위에서 각각 다르게 나타났다. 개체 단위에서 30 %의 엽면적 감소로 인한 증산의 손실은 없었지만, 임분 단위에서 20 %의 엽면적 감소는 증산의 손실을 가져왔다. 하지만 광합성을 개선된 광환경에 의해 모든 단위에서 증가하였다. 결과적으로 수분이용효율은 간벌에 의해서는 증가하였지만, 개체 단위에서는 감소하였다. 본 연구를 통해서 얻어진 잣나무 조림지에서의 수분과 탄소의 이용에 대한 자료는 생태적 관리를 위한 통찰을 제공한다.

* 주요어 : 잣나무, 엽면적 변화, 인위적 탈엽, 간벌, 증산, 생산성, 수액속

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