

## Allometry and Canopy Dynamics of *Pinus rigida*, *Larix leptolepis*, and *Quercus serrata* Stands in Yangpyeong Area<sup>1)</sup>

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#### ABSTRACT

Site - specific allometric equations relating aboveground tree component biomass and leaf area to tree diameter, basal area, sapwood cross - sectional area and sapwood volume were developed using the destructive harvesting method for *Pinus rigida* Mill., *Larix leptolepis* Gordon, and *Quercus serrata* Thunb. stands in Yangpyeong, Kyonggi Province. There were significantly strong correlations between aboveground tree component biomass or leaf area and diameter at breast height (DBH), basal area, sapwood area and sapwood volume. For a similar diameter tree, the three species had a similar stem wood biomass. However, carbon allocation patterns to stem bark, foliage, branch and total aboveground biomass differed among the three species. Specific leaf area and the ratio of leaf area to sapwood cross - sectional area of the three species were significantly different. Allometric equations seemed to be related to leaf habit or leaf longevity. To elucidate the effect of leaf habit or leaf longevity on allometry and canopy characteristics clearly, more intensive studies are needed.

*Key words:* allometric equations, biomass, *Larix leptolepis*, leaf area, leaf habit, leaf longevity, *Pinus rigida*, *Quercus serrata*, sapwood, Yangpyeong

#### 요 약

경기도 양평 지역에 생육하고 있는 리기다소나무, 낙엽송, 졸참나무 임분의 지상 부위 생체량과 엽면적을 추정하기 위해 흉고직경, 흉고단면적, 변재단면적, 변재부피 등의 변수를 이용하는 회귀식을 조제하였다. 지상 부위 생체량과 엽면적은 흉고직경, 흉고단면적, 변재단면적, 변재부피 등과 각각 통계적으로 유의한 상관 관계를 보였으며, 비슷한 직경급에서 3수종 모두 유사한 수간목부 생체량을 보였다. 그러나 수피, 잎, 가지와 지상 부위 총생체량과, 단위건중량당 엽면적 그리고 엽면적:변재단면적의 비에 있어 수종 간 차이가 뚜렷하였다. 생체량과 엽면적 추정을 위한 회귀식은 대상 수종의 잎의 습성과 수명에 영향을 받는 것으로 보이며, 이들 영향을 보다 확실하게 구명하기 위해서 상세한 연구가 필요한 것으로 사료된다.

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## INTRODUCTION

*Pinus rigida* Mill.(evergreen conifer) and *Larix leptolepis* Gordon(deciduous conifer) are common conifers in the central and southern Korea. These species have been imported since early 1900s and have been planted extensively throughout the region because they have rapid early growth rates. Although numerous researchers investigated production and growth for the two species(Kim, 1971; Kim, 1976; Kim et al., 1985; Lee et al., 1985; Yim et al., 1981a,b; Yim et al., 1982), a thorough understanding of physiological and structural characteristics of growth for the two species is still needed. *Quercus serrata* Thunb.(broad-leaved deciduous tree) is native to Korea but it relatively occupies small areas compared to other *Quercus* species. Physiological and ecological processes of other *Quercus* spp. were studied intensively, however, *Q. serrata* was not focused on and the current knowledge of production and growth of the species is very limited. The three study species have different leaf habits and leaf longevities: leaf longevity ranged from 5 months for *Q. serrata* to 29 months for *P. rigida*(Y. Son, unpublished data).

Allometry, the relationship between biomass, volume or area of tree components and independent variables such as stem diameter or tree height, can be used for several purposes (Gower et al., 1987). First of all, it can be used to estimate tree component biomass or leaf area. Also it can be used to clarify the influence of biotic and abiotic factors on carbon assimilation and allocation and can be used to understand the structure and function of forest ecosystems(Chapman and Gower, 1991; Gower et al., 1992, 1993a). Developing allometric equations is expensive, time consuming and in some cases impractical, therefore, sometimes allometric equations developed from specific site and similar species are applied to various situations or even to other species(Alban and Laidly, 1982; Aldred and Alemdag, 1988). However, it should be emphasized that species-site-specific allo-

metric equations be developed because of differences in species and biotic and abiotic environmental factors(Gower et al., 1987). Furthermore, St. Clair(1993) concluded that a single regression equation could not be used to explore genetic variation in component biomass and leaf area because of family differences within a species. Also it should be noted that comparison of differences in production and growth can be studied using a common garden study, which minimize differences in environmental factors among species(Gower et al., 1993b).

The objectives of this study were to (1) develop and compare allometric equations for biomass and leaf area and (2) examine canopy characteristics such as relationship between leaf biomass or leaf area and sapwood cross-sectional area or sapwood volume for the three species on similar sites in Yangpyeong, Kyonggi Province. Species-site-specific allometric regression equations for biomass and leaf area were not available for the area in the literature. We hypothesized that there will be differences in allometry and canopy characteristics among the three study species. This hypothesis is based on earlier studies which reported that leaf habit and leaf longevity influence physiological and structural characteristics of tree species(Son and Gower, 1992; Gower et al., 1993b).

## MATERIAL AND METHODS

### Study site

The study was conducted at the Kungol area in the Korea University Experimental Forest in Yangpyeong, Kyonggi Province. The experimental forest contains 558ha of natural and plantation forests. The study area was dominated by the natural *Pinus densiflora* Sieb. et Zucc., *Quercus* spp. such as *Q. variabilis* Bl., *Q. mongolica* Fisch. and *Q. acutissima* Carruth. forests before harvesting(Y. Son, unpublished data). For this study we selected one natural stand of *Q. serrata* and two plantations of *P. rigida* and *L. leptolepis*. *P. rigida* and *L. leptolepis* were artificially planted on the similar soil type and microclimate in the late 1950s after

the natural oak forest was clearly harvested. *Q. serrata* was naturally regenerated after the *P. densiflora* stand was harvested in the mid 1970s(M.J. Kim, personal communication).

The main understory vegetation in the *P. rigida* stand included *Q. mongolica*, *Q. serrata*, *Q. acutissima*, and *Rhus trichocarpa* Miq. In the *L. leptolepis* stand *Q. aliena* Bl., *Q. mongolica*, *Corylus heterophylla* Fisch., and *Symplocos chinensis* for. *pilosa* Ohwi were found. Characteristic understory species in the *Q. serrata* stand were *Q. aliena*, *R. trichocarpa* and *Lindera obtusiloba* Bl. Mean January and July temperatures of the last 10 years were  $-7.9^{\circ}\text{C}$  and  $24.1^{\circ}\text{C}$ , respectively(KMA, 1984-1993) and the average annual precipitation of the last 10 years was 1,365 mm(KMA, 1984-1993). The soils were classified as slightly dry brown forest soil(Chung, 1986).

#### Field and laboratory work

We established three  $15\text{m} \times 15\text{m}$  plots for *L. leptolepis* and *Q. serrata* and four  $15\text{m} \times 15\text{m}$  plots for *P. rigida*(total 10 plots) in the study area in June 1993, and the corners were permanently marked. At the same time all trees within plots were measured but only the trees greater than 2cm diameter at breast height(DBH) were tagged and DBH were recorded. Some of select physiographic and stand structural characteristics were summarized in Table 1. Distance among plots within a species was at least 10m to ensure proper buffer zones. *P. rigida* and *L. leptolepis* stands were 100m apart, and *Q. serrata* stand was at most 500m away from the two plantations. The elevation of the three stands did not differ by more than 20m.

There are many different techniques to develop allometric equations(Catchpole and Wheeler,

1992).

We decided to use destructive analysis method for this study because of its accuracy, while the major disadvantage of the method is the very high cost compared to other techniques. In August 1993, 10 dominant and codominant trees from each species(total 30 trees) were randomly sampled outside the plots and destructively harvested to develop site-specific regression equations. Trees representing the full diameter range for the three species were sampled by 2 cm diameter classes. The probability of a tree from a given diameter class for dimension analysis was proportional to the diameter frequency within plots.

Destructive analysis was conducted using minor modifications of procedures outlined by Gower et al.(1987) and Son et al.(1993). In brief, trees were cut at the soil surface and breast height(BH) and base of live crown(BLC) were marked on the stem. Live crown length was divided into three positions(upper, middle, and lower) and two representative live branches from each canopy position were selected, weighed, and taken to the laboratory to calculate the ratio of foliage and woody part and moisture content. All the other branches were detached from the stem and weighed. The stem was sectioned into every 2 m and at BH and BLC, and weighed. A 5 cm thick disk was removed from the base of each stem section, BH and BLC, weighed and moved to the laboratory to calculate the ratio of bark and wood mass and moisture content. The ratio of stem bark and stem wood of each disk was used to compute stem bark and stem wood mass for the section, and these were summed to calculate total stem bark and stem wood mass.

For understory vegetation all trees and shrubs

**Table 1.** Physiographic and stand structural characteristics for the three study stands.

Species	Aspect	Slope (%)	Age(yr) <sup>a)</sup>		DBH(cm)		Basal area (m <sup>2</sup> /ha)	No. of trees/ha
			mean	range	mean	range		
<i>Pinus rigida</i>	NW	18-23	37.7	37-39	23.6	18.2-32.7	64.8	667
<i>Larix leptolepis</i>	NW	15-19	36.0	36-36	24.0	17.6-30.0	55.5	548
<i>Quercus serrata</i>	SE	28-32	22.9	18-32	14.6	4.9-26.1	29.2	682

<sup>a)</sup> Based on 10 harvested trees from each species

with less than 2cm DBH and grasses were clipped at the ground level from two 1m $\times$ 1m quadrates within each plot, dried in an oven at 70 °C and weighed (Turner et al., 1992). Under-story biomass comprised less than 2% of the total aboveground biomass for the three species (J.S. Kim, unpublished data).

In the laboratory, each tissue type was dried in an oven at 70 °C to a constant mass and weighed. The ratios of fresh and dry weights of each tree component were used to calculate biomass of each component. The branches were separated into foliage (current and >1 year old foliage for *P. rigida*, and total foliage for *L. leptolepis* and *Q. serrata*) and woody part. Before drying subsamples of foliage were saved for specific leaf area (SLA, fresh foliage area/dry mass, cm<sup>2</sup>/g) measurement. Leaf areas of 50–150 foliage subsamples from three canopy positions were measured using a Delta-T Area Meter<sup>®</sup> and SLA was calculated. Total one-sided leaf area of each tree was calculated by multiplying the foliage biomass and SLA of unweighted mean of three canopy positions. Stem disks were also used to measure sapwood cross-sectional area. Sapwood was easily differentiated from heartwood by color for *L. leptolepis* and *Q. serrata*. However, O-anisidine hydrochloride+10% sodium nitrite solution were sprayed to delineate the boundary between sapwood and heartwood for *P. rigida* (AWPA, 1990). The sapwood image was traced into clear acetate, cut out, and sprayed with black paint and the area was measured using the Delta-T Area Meter<sup>®</sup> (Son et al., 1993). Sapwood volume was estimated using sapwood cross sectional area and stem length (Chapman and Gower, 1991).

### Statistical analysis

Allometric equations were prepared relating aboveground tree component biomass (total above-ground, stem wood, stem bark, branch, current foliage, old foliage, and total foliage) or leaf area (Y) to DBH, basal area, sapwood cross-sectional area at BH and BLC or sapwood volume (X) using a log-log (base e and base 10) transformation to correct nonhomogeneous variance

of biomass or leaf area. To correct bias in log-transformed allometric equations Sprugel's (1983) correction factors were used. An analysis of covariance was used to test for equality of slopes and intercepts of the regression equations among species (Zar, 1983). If species effects were significant, multiple comparison tests were used to compare the slopes or intercepts (Zar, 1983). Values of biomass, leaf area, SLA, sapwood cross-sectional area and the ratio of leaf area to sapwood cross-sectional area were analyzed using the analysis of variance to find species difference. Regression analysis was also used to relate canopy characteristics to leaf longevity. For two species comparison a t-test was used. All statistical analyses were conducted using SAS (1988).

## RESULTS AND DISCUSSION

### Allometric relations

Regression equations relating aboveground, stem wood, stem bark, branch and foliage biomass and leaf area to DBH, basal area, sapwood cross-sectional area and sapwood volume were given in Table 2. In general, allometric equations for biomass and leaf area were better for *Q. serrata* than for *P. rigida* and *L. leptolepis*. The developed regression equations for *Q. serrata* should be cautiously interpreted due to the wide range of age and DBH (Table 1). The log-log transformation with base e did not consistently decrease standard error of estimate, therefore, we did not present equations using base e transformation here. Variation in DBH, basal area, sapwood cross-sectional area and sapwood volume explained between 44% and 98% of the variation in biomass of the tree components, and between 48% and 96% in leaf area, respectively.

Slope and intercept coefficients for stem wood biomass were not significantly different ( $p > 0.05$ ) among *P. rigida*, *L. leptolepis*, and *Q. serrata* (Table 2). This suggested that, for a similar diameter tree, the three species had a similar stem wood biomass. Based on this study, *Q. serrata* appeared to a viable candidate for stem

**Table 2.** Regression equations for estimating aboveground tree component biomass and leaf area for *P. rigida*, *L. leptolepis* and *Q. serrata* in Yangpyeong, Kyonggi Province<sup>a)</sup>. Slope or intercept coefficients for a biomass component and leaf area of the three species followed by the same letter are not significantly different ( $p > 0.05$ ). Intercepts were not tested if slopes were significantly different.

Component	a	b	S <sup>2</sup> <sub>y,x</sub>	r <sup>2</sup>	p	CF <sup>b)</sup>
<i>P. rigida</i>						
Biomass						
total aboveground						
DBH	-0.783a	2.245a	0.004	0.891	0.0001	1.002
stem wood						
DBH	-0.929a	2.237a	0.007	0.835	0.0002	1.003
stem bark						
DBH	-1.859	2.238a	0.004	0.905	0.0001	1.002
branch <sup>c)</sup>						
DBH	-1.832a	2.433a	0.015	0.726	0.0018	1.007
foliage (current)						
DBH	-1.570a	1.615	0.022	0.442	0.0359	1.011
foliage (>1year)						
DBH	-3.005	2.740	0.008	0.856	0.0001	1.004
foliage (total)						
DBH	-2.155a	2.307a	0.009	0.785	0.0006	1.005
basal area	1.246	1.092	0.006	0.869	0.0001	1.003
sapwood area at BH	0.965	1.269	0.006	0.869	0.0001	1.003
sapwood area at BLC	2.059	0.865	0.021	0.538	0.0157	1.010
sapwood volume	4.729	1.205	0.003	0.924	0.0001	1.002
Leaf area						
DBH	-1.647a	2.275a	0.007	0.828	0.0003	1.004
basal area	-1.182	1.049	0.005	0.870	0.0001	1.003
sapwood area at BH	-1.452	1.219	0.005	0.871	0.0001	1.003
sapwood area at BLC	-0.399	0.830	0.019	0.538	0.0158	1.010
sapwood volume	2.163	1.152	0.004	0.915	0.0001	1.002
<i>L. leptolepis</i>						
Biomass						
total aboveground						
DBH	-0.726a	2.234a	0.004	0.903	0.0001	1.002
stem wood						
DBH	-0.891a	2.258a	0.004	0.898	0.0001	1.002
stem bark						
DBH	-1.045	1.627b	0.006	0.733	0.0016	1.003
branch <sup>c)</sup>						
DBH	-1.851a	2.478a	0.019	0.673	0.0037	1.010
foliage						
DBH	-2.568b	2.363a	0.008	0.824	0.0003	1.004

Table 2. continued.

Component	a	b	S <sup>2</sup> <sub>y,x</sub>	r <sup>2</sup>	p	CF <sup>b)</sup>
basal area	1.211	0.944	0.011	0.752	0.0012	1.006
sapwood area at BH	1.868	0.854	0.016	0.634	0.0058	1.008
sapwood area at BLC	2.173	0.783	0.015	0.673	0.0036	1.007
sapwood volume	4.558	1.301	0.009	0.802	0.0005	1.004
Leaf area						
DBH	-1.308a	2.099a	0.007	0.800	0.0005	1.004
basal area	-0.623	0.841	0.009	0.733	0.0016	1.005
sapwood area at BH	0.153	0.671	0.019	0.481	0.0262	1.009
sapwood area at BLC	0.312	0.656	0.015	0.582	0.0102	1.008
sapwood volume	2.340	1.046	0.009	0.747	0.0012	1.005
<i>Q. serrata</i>						
Biomass						
total aboveground						
DBH	-1.543b	2.867a	0.008	0.979	0.0001	1.004
stemwood						
DBH	-1.932a	2.992a	0.021	0.957	0.0001	1.011
stembark						
DBH	-2.396	2.759a	0.019	0.953	0.0001	1.010
branch <sup>c)</sup>						
DBH	-2.038b	2.761a	0.022	0.947	0.0001	1.011
foliage						
DBH	-3.220c	3.267a	0.038	0.936	0.0001	1.019
basal area	0.324	1.449	0.034	0.943	0.0001	1.017
sapwood area at BH	0.362	1.741	0.065	0.891	0.0001	1.033
sapwood area at BLC	0.944	1.516	0.078	0.868	0.0001	1.040
sapwood volume	5.312	1.281	0.039	0.933	0.0001	1.020
Leaf area						
DBH	-1.759c	3.024a	0.021	0.957	0.0001	1.004
basal area	-1.239	1.334	0.023	0.953	0.0001	1.012
sapwood area at BH	-1.229	1.616	0.041	0.917	0.0001	1.020
sapwood area at BLC	-0.682	1.404	0.056	0.888	0.0001	1.028
sapwood volume	3.362	1.186	0.022	0.956	0.0001	1.012

<sup>a)</sup> Equations are in the form  $\log Y = a - b \log X$ , where Y is tree component biomass or leaf area(m<sup>2</sup>) and where X is diameter at breast height(DBH, cm), basal area(cm<sup>2</sup>), sapwood cross-sectional area(cm<sup>2</sup>) at breast height(BH) and base of live crown(BLC), or sapwood volume(cm<sup>3</sup>).

<sup>b)</sup> Correction factor (Sprugel, 1983).

<sup>c)</sup> Live and dead branches.

wood production in the study area. Gower et al.(1987) reported the same carbon allocation pattern to stem wood for *P. contorta* Dougl., *L. occidentalis* Nutt., and *Pseudotsuga menziesii* (Mirb.) Franco in a mixed conifer stand in U.S.A.

Carbon allocation patterns to stem bark, foliage, branch, and total aboveground biomass differed( $p < 0.05$ ) among the three species(Table 2). For trees of the same diameter, *P. rigida* and *L. leptolepis* had a significantly greater stem bark biomass than *Q. serrata*. The similar slope coefficients and significantly greater intercept coefficient for total foliage biomass of *P. rigida* versus *L. leptolepis* and *Q. serrata* suggested that for similar diameter trees *P. rigida* supported a greater total foliage biomass than *L. leptolepis* and *Q. serrata*. *P. rigida* and *L. leptolepis* had similar current foliage biomass(data not shown). These data were consistent with the previous results(Gower et al., 1987, 1993b); for trees of a similar diameter, tree species with long-lived foliage supported a greater total foliage biomass, but did not produce a greater amount of current foliage biomass, than tree species with short-lived foliage. *P. rigida* and *L. leptolepis* allocated significantly greater biomass to branch than *Q. serrata*. For a similar diameter tree, *P. rigida* and *L. leptolepis* supported a greater total aboveground biomass than *Q. serrata*.

Sapwood in the woody species conducts water and nutrients from roots to leaves and stores water, nutrients and carbohydrates, therefore, it is expected that sapwood area or volume is associated with tree productivity. For example, Chapman and Gower(1991), Espinosa Bancalari et al.(1982), and Waring et al.(1977) reported strong correlations between sapwood cross-sectional area and leaf area for several coniferous and deciduous tree species. Also Ryan(1989) and de Kort(1993) reported that sapwood volume had a significant influence on tree age and size, foliage mass, and leaf area for several conifers. We found significant correlations between sapwood cross-sectional area and foliage mass or leaf area in this study(Table 2), however, the

relationships were relatively weak for *L. leptolepis* compared to *P. rigida* and *Q. serrata*. Regression equations relating foliage biomass to sapwood cross-sectional area at BH or BLC for *Q. serrata* were better than for *P. rigida* and *L. leptolepis*. Han et al.(1992) also found strong correlations between foliage biomass and sapwood cross-sectional area at BH in *Q. mongolica* stands. For *P. rigida* and *Q. serrata* sapwood cross-sectional area at BH was a better predictor of leaf area than sapwood cross-sectional area at BLC. In general, sapwood volume was a better predictor of foliage biomass and leaf area than DBH, basal area or sapwood cross-sectional area, with  $r^2$  ranging from 0.75 to 0.96(Table 2).

Although there were close relationships between foliage biomass or leaf area and sapwood area or volume, DBH seemed to serve as a better independent variable to estimate foliage biomass or leaf area because it could be measured more easily than sapwood cross-sectional area or volume. Allometric regression equations developed from this study allow foresters or researchers to estimate tree component biomass or leaf area for the three species in the area more accurately.

### Canopy characteristics

Specific leaf area(SLA) calculated from 10 destructively harvested trees of each species was presented in Table 3. Specific leaf areas of the three species were significantly different ( $p < 0.001$ ); unweighted means of SLA were 28.8  $\text{cm}^2/\text{g}$  for *P. rigida*, 83.0  $\text{cm}^2/\text{g}$  for *L. leptolepis* and 162.2  $\text{cm}^2/\text{g}$  for *Q. serrata*, respectively (Table 3). We were not aware of other studies which measured SLAs for *P. rigida*, *L. leptolepis*, and *Q. serrata*. Specific leaf area of *L. leptolepis* from this study was similar to 83.7  $\text{cm}^2/\text{g}$  of *L. occidentalis*, which has the same needle morphology(Gower et al., 1989). As there were so much variations in leaf morphology among species within a genus, it was difficult to compare SLAs of *P. rigida* and *Q. serrata* with other results. Gower et al.(1989) reported 38.7–43.4  $\text{cm}^2/\text{g}$  for *P. contorta* while Chapman

**Table 3.** Specific leaf area(SLA) by canopy position for *P. rigida*, *L. leptolepis*, and *Q. serrata* from 10 harvested trees. Standard error of the mean is in parenthesis. Unweighted mean of SLA followed by different letters are significantly different( $p < 0.05$ ).

Species	Canopy position	SLA (cm <sup>2</sup> /g)	
		mean	range
<i>P. rigida</i>	Upper	30.4(1.4)	26.2-39.4
	Middle	29.8(2.1)	24.5-45.5
	Lower	26.4(1.1)	22.3-32.7
	Unweighted mean	28.8(0.9)c	
<i>L. leptolepis</i>	Upper	76.0(5.5)	40.0-108.4
	Middle	83.6(7.7)	55.7-119.2
	Lower	89.5(15.7)	41.1-215.6
	Unweighted mean	83.0(5.9)b	
<i>Q. serrata</i>	Upper	139.2(11.2)	99.0-196.7
	Middle	162.1(11.4)	119.3-213.0
	Lower	181.2(17.1)	123.4-294.3
	Unweighted mean	162.2(12.6)a	

and Gower(1991) and Son et al.(1993) calculated 113.1 cm<sup>2</sup>/g for *Q. rubra* and 128.1 cm<sup>2</sup>/g for *Q. variabilis*, respectively.

Generally, broad leaved deciduous species seemed to have higher SLAs than conifers while within coniferous species deciduous conifers (*Larix* spp.) had higher SLAs than evergreen conifers(Gower et al., 1989). There was no significant linear relationship between leaf longevity and SLA for the three species( $p > 0.1$ ). Although species with short lived foliage seemed to have large SLA to compensate for its low production efficiency and a greater initial construction cost than species with long-lived foliage from earlier studies(Gower et al., 1993b), this pattern was not clear in this study. Several earlier studies reported SLA differences among canopy positions(Chapman and Gower, 1991; Del Rio and Berg, 1979; Keane and Weetman, 1987; Waring et al., 1980), however, we did not find any significant difference in SLA among the three canopy positions within a species( $p > 0.05$ ).

Sapwood cross-sectional areas by species and tree height were presented in Table 4. Sapwood cross-sectional areas of each stem section were significantly different among species( $p < 0.001$ ) except for 11.2m and 13.2m stem sections of *P. rigida* and *L. leptolepis*. Sapwood cross-sectional

areas at the same stem section were highest for *P. rigida* followed by *L. leptolepis* and *Q. serrata*(Table 4). In general, sapwood cross-sectional area decreased from the stump to the top of trees, and this pattern was consistent with other studies(Espinosa Bancalari et al., 1987; Han et al., 1992; Ryan, 1989).

We found a significant difference in the ratio of leaf area to sapwood cross sectional area at BH and BLC among the three species( $p < 0.001$ ). Several studies also reported differences among species and between trees of the same species growing under different condition(Binkley, 1984; Espinosa Bancalari et al., 1987; Whitehead et al., 1984). The ratios of leaf area to sapwood cross-sectional area at BH and BLC were 0.12 and 0.17m<sup>2</sup>/cm<sup>2</sup> for *P. rigida*, 0.30 and 0.47m<sup>2</sup>/cm<sup>2</sup> for *L. leptolepis*, and 0.84 and 1.08m<sup>2</sup>/cm<sup>2</sup> for *Q. serrata*, respectively(Table 5). These ratios were similar to values of other conifers (0.11-0.75m<sup>2</sup>/cm<sup>2</sup>, specifically 0.11-0.38m<sup>2</sup>/cm<sup>2</sup> for *Pinus* spp.) and deciduous species(0.21-1.39m<sup>2</sup>/cm<sup>2</sup>, specifically 0.99-1.39m<sup>2</sup>/cm<sup>2</sup> for *Quercus* spp.)(Chapman and Gower, 1991; Gower et al., 1989, 1993a; Han et al., 1992; Keane and Weetman, 1987; Rodgers and Hinckley, 1979; Waring et al., 1977, 1982).

The ratio of leaf area to sapwood cross-



**Table 4.** Sapwood cross-sectional area( $\text{cm}^2$ ) change with tree height for the three study species. Standard error of the mean is in parenthesis. Values followed by the same letter within a species are not significantly different at  $p=0.05$ .

Stem position	<i>P. rigida</i>	<i>L. leptolepis</i>	<i>Q. serrata</i>
Stump	355.5(41.2)a	164.1(21.9)a	134.6(31.8)a
Breast height (1.2m)	277.9(29.4)b	141.8(17.2)a	73.7(16.1)ab
3.2m	256.0(26.8)b	133.6(13.8)abc	73.6(19.6)ab
5.2m	236.5(24.4)bc	123.3(12.8)bc	52.7(10.3)b
7.2m	200.8(22.9)bc	117.7(12.8)bcd	35.9(4.7)b
9.2m	168.3(21.8)cd	106.7(10.9)bcd	17.8(3.7)b
11.2m	119.7(16.8)de	97.6(10.2)cd	
13.2m	75.0(8.6)e	83.4(10.2)de	
15.2m		57.1(9.0)ef	
17.2m		48.5(7.0)ef	
19.2m		35.1(5.6)f	

**Table 5.** Comparison of leaf area:sapwood cross-sectional area ratios for the three species. Standard error of the mean is in parenthesis. Leaf area(LA):sapwood area(SA) ratio followed by the same letter are not significantly different at  $p=0.05$ .

Species	LA:SA BH ( $\text{m}^2/\text{cm}^2$ )	LA:SA BLC ( $\text{m}^2/\text{cm}^2$ )
<i>P. rigida</i>	0.12(0.01)b	0.17(0.01)c
<i>L. leptolepis</i>	0.30(0.04)b	0.47(0.06)b
<i>Q. serrata</i>	0.84(0.16)a	1.08(0.17)a

sectional area appeared to be higher for deciduous species(especially *Quercus* spp.) than for conifers(Chapman and Gower, 1991; but see Waring et al., 1982). The high ratio for *Quercus* spp. corroborated an earlier study that concluded that the xylem structures of the species were different from other species. Our observed ratios of leaf area to sapwood cross-sectional area for the three species supported the previous conclusion that species having small ratios yielded large water storage capacities to avoid damage from drought and inhabited dry environments(Chapman and Gower, 1991; Gower et al., 1987; Ryan, 1989; Waring et al., 1982); therefore, *Q. serrata* requires more moist sites to survive than *L. leptolepis* and *P. rigida*. However, we did not find a significant linear relationship between leaf longevity and the ratios

of leaf area to sapwood cross-sectional area at BH and BLC( $p>0.1$ ).

The range of the ratios of leaf area to sapwood cross-sectional area for individual trees was greater for *Q. serrata*(0.18–1.98 $\text{m}^2/\text{cm}^2$  at BH and 0.24–1.98 $\text{m}^2/\text{cm}^2$  at BLC) than for *P. rigida*(0.08–0.15 $\text{m}^2/\text{cm}^2$  at BH and 0.09–0.25 $\text{m}^2/\text{cm}^2$  at BLC) and *L. leptolepis*(0.19–0.62 at BH and 0.28–0.94 $\text{m}^2/\text{cm}^2$  at BLC) because of high variations in foliage biomass and SLA in *Q. serrata*.

The ratios of leaf area to sapwood cross-sectional area at BLC were significantly( $p<0.001$ ) greater than those of leaf area to sapwood cross-sectional area at BH for all three species. This pattern was consistent with the results from other studies(Chapman and Gower, 1991; Espinosa Bancalari et al., 1987; Gower et al., 1989, 1993a).

The ratio between sapwood volume and total leaf area was significantly different for the three species( $p<0.001$ ), and the ratios were 0.009 $\text{m}^3/\text{m}^2$  for *P. rigida*, 0.010 $\text{m}^3/\text{m}^2$  for *L. leptolepis*, and 0.001 $\text{m}^3/\text{m}^2$  for *Q. serrata*, respectively. Conifers had a higher ratio than broad-leaved deciduous species. It was reported that the ratio between sapwood volume and leaf area increased with tree size and differed among species(Chapman and Gower, 1991; de Kort, 1993; Ryan, 1989). And large trees had more sapwood volume per

leaf area than small trees and would store more water, nutrients, and carbohydrates to avoid drought (Ryan, 1989; but see Chapman and Gower, 1991). It appeared that *Q. serrata* had lower water storage capacity than *P. rigida* and *L. leptolepis*. However, it was not possible to directly correlate data from the present study to the previous studies which had the same range of tree size for the different species and therefore to conclude the relationship between the ratio and physiological characteristics. We had different ranges in tree size for the three study species (Table 1).

Due to the limited number of tree species in this study, it was difficult to determine the exact form of relationship between canopy characteristics and leaf longevity. Therefore, we chose to use a simple linear form. Although we did not find any significant linear relationships between canopy characteristics and leaf longevity, more intensive studies with large number of tree species having different leaf habits and longevities are needed to elucidate the influence of leaf habit or longevity on canopy structure and function.

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