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GENDER-RELATED CLIMATE RESPONSE OF RADIAL GROWTH IN DIOECIOUS *FRAXINUS MANDSHURICA* TREES

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ABSTRACT

This paper presents an analysis of tree-ring growth patterns of male and female *Fraxinus mandshurica* trees from 1931 to 2007. The specific object was to study the response of radial growth to climate variables separately for male and female trees. The results show that the growth patterns in the two genders were similar during the mid-1950s to 1970s but different in the periods 1931–1940s and 1980–2007. In the period 1980–2007, the mean sensitivity and mean widths of the tree rings were significantly different between the genders ($p < 0.05$). The climate-growth response in female and male trees was also different. Female trees are sensitive to precipitation in November of the previous year, whereas male trees respond to mean temperature in November of the previous year. The results confirm that climatic sensitivity in male and female trees of dioecious species is different, yet this difference is not stable through time.

Keywords: tree-ring widths, dendroclimatology, dioecy, *Fraxinus mandshurica*.

INTRODUCTION

Differences in the growth of dioecious species have been described relating to climate, reproductive effort, resource allocation and physiology (Dawson and Geber 1999; Delph 1999; Obeso 2002; Bañuelos and Obeso 2004). It is observed that female trees are more sensitive to climate change (Montesinos *et al.* 2006; Xu *et al.* 2008). Factors causing gender-specific differences in the growth of plants include strategies in coping with water stress (Hill *et al.* 1996; Retuerto *et al.* 2000), water-use efficiency (Correira and Diaz Barradas 2000; Sanchez-Vilas and Retuerto 2009), and their reproductive effort (Ramp and Stephenson 1988; Nicotra 1999a, 1999b; Espírito-Santo *et al.* 2003; Nuñez *et al.* 2008). Tree growth is frequently affected by variations in climate and habitat conditions, such as precipitation, soil nutrient status, moisture availability and radiation (Tryon and Pease 1953; Adams and Kolb 2004; Benedict and Frelich 2008). Gender-specific response within the same environment could explain some of the unexplained differences in the growth of individual trees (Retuerto *et al.* 2000).

Manchurian ash (*Fraxinus mandshurica*) is a valuable broad-leaved tree species with good timber quality and beautiful wood texture. The species is native to northeastern China, northern Korea, the Far East of Russia and northern Japan. In China, it occurs predominantly in the Xiaoxing'anling and Changbai Mountains. Contrary to other species of the genus *Fraxinus*, *F. mandshurica* is strictly dioecious. Its flowers appear before the leaves in April and fruits are visible after litter fall in October. Thus, male and female trees can be identified quite easily (Zhan *et al.* 2005). The Manchurian ash represents an important component of Changbai Mountains ecosystems. Knowledge regarding the response of male and female trees to climate change is of importance for better management of the forest.

Soil moisture and late frost relating to specific terrain conditions have been identified as the growth-limiting factors for *F. mandshurica* (Su *et al.* 2003). The growth of *F. mandshurica* shows significant sensitivity to variations in climate (Zhang *et al.* 2007). Yet, little is known about

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the effects of climate on radial growth separately for male and female trees of this dioecious species. The main goals of the present study were (1) to detect whether radial growth for male and female trees of the Manchurian ash differ, and (2) to identify the pattern of climate-growth responses in male and female trees under the same terrain condition.

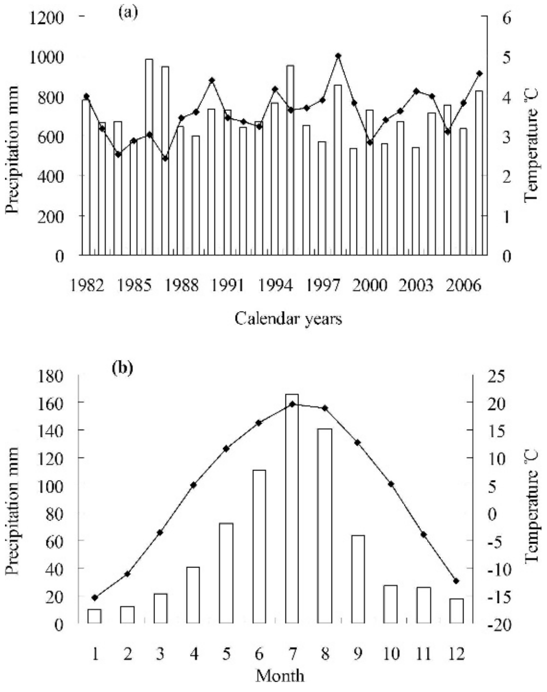

Figure 1. Distribution of mean annual precipitation and temperature (a) and monthly values (b) during the period 1982–2007 at the Changbaishan Forest Ecosystems Research Station. Lines refer to temperature, bars to precipitation.

MATERIALS AND METHODS

Study Area

This study was conducted just outside the Changbaishan Nature Reserve (42°19′10″N, 128°07′49″E) at an elevation of 899 m *a.s.l.* The study site is a natural secondary forest dominated by *Pinus koraiensis*, *Quercus mongolica*, *Tilia amurensis*, *Fraxinus mandshurica* and *Acer mono* in association with other subcanopy tree species. It represents the typical forest type and landscape of deciduous broad-leaved and coniferous mixed forest in Northeastern China. In order to identify the response of tree growth to climate, we used climatic records from the nearby Changbaishan Forest Ecosystems research station (42°24′N, 128°28′E; 738 m *a.s.l.*), managed by the Chinese Academy of Sciences. Records of temperature and precipitation are available for a period of 26 years from 1982 to 2007 (Figure 1).

The climate is known as continental monsoon with an average annual temperature of 3.6°C. Monthly mean temperature ranges from −15.4°C in January to 19.6°C in July. Total monthly precipitation ranges from 255 mm in January to 4299 mm in July. Average annual rainfall amounts to 707 mm. The soil is mostly a dark brown forest soil with a depth ranging from 20 to 100 cm.

Sample Selection

A permanent research plot covering an area of 200 m × 260 m was established in the study area in August 2005. Slopes are generally less than five degrees. The gender of all reproductive *F. mandshurica* individuals with diameter at breast height (dbh) greater than 5 cm was determined by observing the reproductive organs (flowers and/or fruit) through binoculars. In exceptional cases, it was necessary to climb the trees to ascertain the gender. The dbh, height and crown surface area of each tree were measured and recorded. These field observations were performed from April to October in 2005–2008. Sampling for the present study was carried out in June 2008. The trees for sampling were selected from those that have a breast height diameter exceeding 15 cm and grow in conditions without obvious competition from neighboring trees. In total, 30 female trees and 25 male trees were chosen for tree-ring analysis in the research plot. One increment core was collected on the north side at breast height (1.3 m above ground) from each of these trees. In the laboratory, the 55 core samples were dried, glued onto wooden core holders and sanded with increasingly finer grit sand paper until annual rings could be easily distinguished. Tree-ring widths of mounted cores were measured to the nearest 0.01 mm with the Lintab5 measurement system.

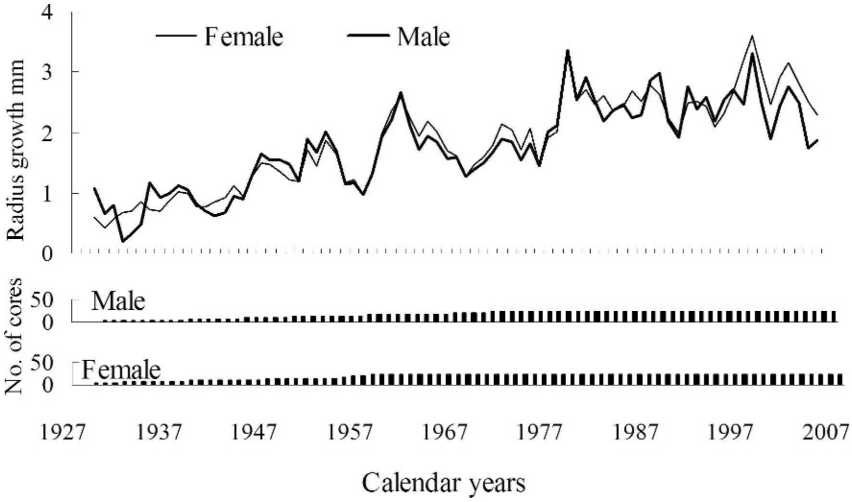

Figure 2. Comparisons of mean ring-width series between male and female *Fraxinus mandshurica* trees. The "rug"-like diagrams at the bottom show the cumulative number of cores.

Data Analysis

In order to assign each individual tree ring with its exact year of formation, the tree-ring series were crossdated by matching the patterns of wide and narrow rings among samples. The results of crossdating were quality-checked using the program COFECHA (Holmes 1983, see http://www.ltrr.arizona.edu/pub/dpl/). The cores that could not be crossdated were excluded from further analysis. Finally, 25 cores from male trees and 25 cores from female trees were successfully crossdated.

A one-way analysis of variance (ANOVA) was carried out to evaluate the effects of gender (male and female) on tree-ring widths. When the interaction term was significant, comparisons with a Bonferroni *post hoc* test was performed to isolate these differences whenever one was detected. Tree-ring widths were square-root transformed $x' = x^{1/2}$ to meet the normality assumptions required in the ANOVA. A Kolmogorov-Smirnov test (which is a form of minimum distance estimation used to determine if two datasets differ significantly) and paired t-test was used to assess differences between male and female trees.

The growth trends in tree-ring series were removed by a fixed 32-year cubic spline using the ARSTAN software (Grissino-Mayer and Fritts 1997). Residual chronology (RES) was selected for climate-growth response analysis because the series autocorrelation was removed. The relationships between ring-width index chronologies and the climate variables were evaluated using response-function analysis and tested by Pearson's product-moment correlation coefficients. One thousand bootstrapped samples were used to compute response coefficients and to test their significance at the 0.05 level. Climate variables used in the response-function analysis include monthly mean temperature and total precipitation from August of the previous year to August of the current year of growth. The analysis was performed using the program DENDROCLIM2002 (Biondi and Waikul 2004).

RESULTS

Pattern in Tree-Ring Width Growth

The average tree-ring widths series of two genders were shown in Figure 2. A Kolmogorov-Smirnov test showed that growth patterns in the two genders were similar during the mid-1950s to 1970s but significantly different in the periods 1931–1940s and 1980–2007 ($p < 0.05$).

The mean ring widths of both female and male trees reached a maximum in the year 1980 (Figure 2). The ring widths of two genders were compared for the period after 1980 (Table 1). Results of the paired t-test show that, in the period

Table 1. Characteristics of the tree-ring widths for the period 1980–2007 for male and female trees of *Fraxinus mandshurica*.

	Mean Width (mm)		Mean Sensitivity		Standard Deviation	
	Female	Male	Female	Male	Female	Male
1980–2007	2.4	2.52	0.18	0.13	0.66	0.60

1980–2007, the ring widths of males were significantly greater than that of the females ($p < 0.05$). The mean sensitivity and the standard deviation of the mean ring widths are both greater in the females (Table 1). This indicates that females are more sensitive to change in climate and carry more climate information (Fritts 1976). These results reveal the differential growth rate between males and females during the period 1980–2007 and that elevated temperatures may induce males to express a greater increase in radial growth.

The main descriptive characteristics of the common interval analysis of the tree-ring width residual chronologies are presented in Table 2. The common intervals for the males (1968–2007) and females (1966–2007) span almost the same period. The mean correlations and the expressed population signal (EPS) are greater than the threshold values 0.40 and 0.85 proposed by Wigley *et al.* (1984). This indicates that the chronologies represent the population signal rather precisely. The high SNR value emphasizes the feasibility in analyzing the response of chronologies to climate for both male and female trees. Female trees have higher mean sensitivity and SNR than those of the male trees.

Table 2. Descriptive statistics of the common interval analysis of tree-ring width residual chronologies for *Fraxinus mandshurica* trees.

Chronology Statistics	Female (1935 to 2007)	Male (1931 to 2007)
No. of cores	25	25
Mean sensitivity	0.195	0.184
Standard deviation	0.176	0.169
First order autocorrelation	0.049	0.069
Mean correlations among all cores	0.52	0.49
Expressed population signal (EPS)	0.95	0.93
Signal-to-noise ratio (SNR)	20.33	13.04
Variance in first eigenvector (%)[a]	54.6	52.47

[a] The variance in the first eigenvector is the percentage of the common variance among tree-ring series explained by the first principal component.

Tree-Ring Width Response to Climate Variables

Response function analysis involving the climate variables and the ring-width index chronologies, carried out with DENDROCLIM2002, show different results for the two genders (Figure 3). There is a significant negative correlation between the ring-width index chronology of male trees and November temperature in previous year ($p < 0.05$). The ring-width index chronology for females is correlated positively with the November precipitation of the previous year ($p < 0.001$). Therefore, the climatic conditions of the previous November had an effect on radial growth in both genders (Figure 3). Pearson's product-moment correlation also confirmed that the ring-width index chronology of female trees is positively correlated with total precipitation in previous November and the ring-width index chronology of male trees is negatively correlated with mean temperature in previous November (Figure 4).

DISCUSSION

To our knowledge previous dendroclimatology studies of *F. mandshurica*, which attempted to explain growth response to climate, did not pay any attention to the effect of gender. This paper presents an analysis of tree-ring growth and chronologies of male and female trees separately, and analyzes their response to climate. One result obtained from this study is the finding that growth patterns in the two genders were similar during the mid-1950s to 1970s but different in the periods 1931–1940s and 1980–2007 ($p < 0.05$). In the period 1980–2007, the ring widths of males were significantly greater than that of the females ($p < 0.05$).

Males and females of dioecious plants have different reproductive characteristics (Lloyd and Webb 1977; Lovett *et al.* 1988). A general assumption is that the cost of reproduction for females is higher than that for males (Delph 1990; Allen and Antos 1993; Cipollini and Whigham 1994). This suggests that females need greater

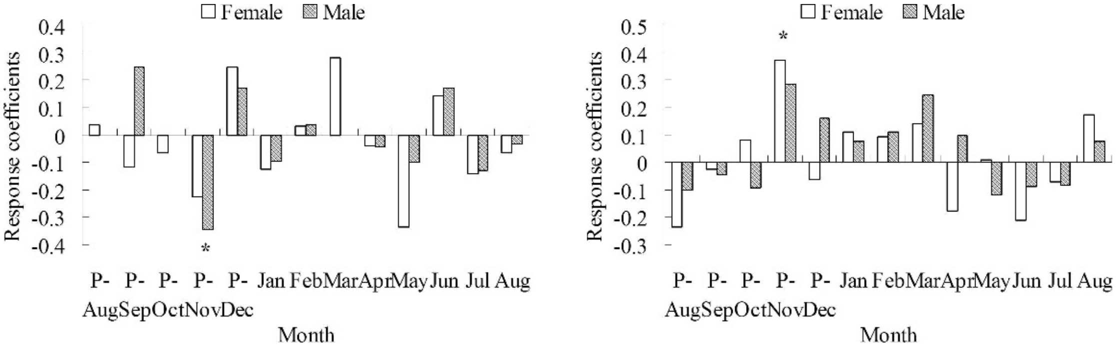

Figure 3. Response coefficients for male and female *Fraxinus mandshurica* ring-width index chronology and monthly mean temperature (left) and total precipitation (right) from August of the previous year (P-Aug) to current August (Aug). The asterisks indicate significant correlations at $p < 0.05$.

quantities of essential resources to compensate for that cost. It has also been found that female trees are more easily affected by stressful conditions than males (Bullock 1992; Guillon and Fievet 2003; Xu *et al.* 2008). The stress may be traced to physiological processes that are affected by unfavorable conditions of the climate. According to IPCC (2007), temperature has generally increased worldwide since the 1980s. Higher temperature will improve photosynthesis and thus promote the radial growth where high temperature is not growth-limiting. Male plants always showed higher activities of Chlase [chlorophyllase] (Kumar *et al.* 2006) and higher photosynthetic rate than that of females (Gehring 1994). This may be the reason that the radial growth in female and male trees of Manchurian ash is different, and it also indicates that elevated temperatures may induce males to express a greater increase in the radial growth.

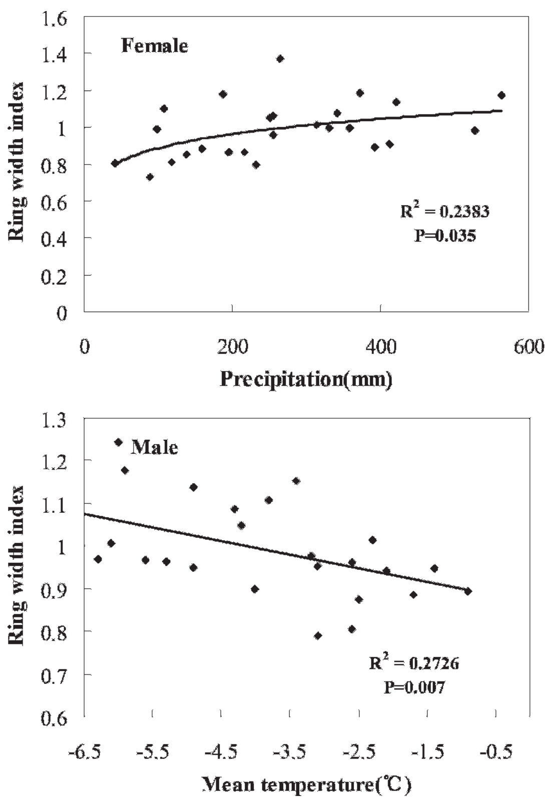

Figure 4. The correlations between ring-width indices of both genders and November total precipitation (top) and mean temperature (bottom) of the prior growth year for period 1982–2007.

The results of the response-function analysis indicate that the climatic conditions during the previous November had an effect on the radial growth in both genders (Figure 3). Temperature in November of the previous year has a significant negative correlation with the growth of males, but its correlation with the growth of females is not significant. This suggests that the climatic sensitivity is different in male and female trees. The influence of winter temperature on tree-ring growth has been reported in other studies (Jacoby and D'Arrigo 1989; Grace and Norton 1990). A common response to low or high temperature is impaired biosynthesis (Tewari and Tripathy 1999). High winter temperatures usually cause deficit in soil moisture (D'Arrigo *et al.* 2001) and loss of carbohydrates stored during the previous growing season (Cullen *et al.* 2001). They can even induce a permanent physiological shock (Kullman 1990; Oleksyn *et al.* 1998). Lower temperatures in winter are less stressful, and may contribute to improved radial growth in the following growing season. November is the beginning of the winter, and high temperatures in November may cause increasing rates of respiration, at the cost of biomass, resulting in reduced radial growth in the following growing season. Females need to allocate more biomass and nitrogen to reproduction and thereby reduce the allocation of resources to growth more than males. Thus, females are generally considered to be more sensitive to temperature (Xu *et al.* 2008) than males. However, females that were prevented from reproducing were able to re-allocate resources to growth, and produced more radial growth on average than males (Nicotra 1999a). This reallocation response may have evolved to reduce delayed costs of reproduction in females and compensate for the losses caused by the winter temperature. Thus, this may be one of the reasons why the effect of temperature on female tree growth is less significant than on male trees.

On the other hand, only female trees of Manchurian ash showed a significant response to November precipitation of the previous year. Winter precipitation has been reported as an important factor affecting radial growth of ash trees (Yasue *et al.* 1996). Greater precipitation in November indicates more snow on the forest floor during the winter months and thus increasing soil moisture during spring, which promotes radial growth during the following growing season (LaMarche 1974; Takahashi *et al.* 2003). The cost of reproduction is assumed to be higher for females than for males (Espírito-Santo *et al.* 2003). In *F. mandshurica*, flowers appear before the leaves in April and the fruits are visible after litter fall in October. Fruiting is especially costly in terms of water demand for female plants (Su 2003). During the fruiting period, instantaneous water-use efficiency was significantly lower in females than in males (Leigh *et al.* 2003) and female trees exhibited different stomatal behavior in response to changes of water availability (Ward *et al.* 2002). Thus soil moisture, which is enhanced by high winter precipitation, seems to be a major factor influencing female radial growth.

Previous studies showed that growth was positively correlated with precipitation from winter and spring in male trees but only to current spring precipitation in females (Montesinos *et al.* 2006). Female trees marginally associate with precipitation in the months preceding the growing season (Bañuelos and Obeso 2004), and December precipitation is negatively correlated with ring widths of ash trees (Yasue *et al.* 1996). This study showed a different response pattern that may be related to the species and the samples selected for study. The samples used in this study are even-aged and selected from mature forest. Usually in older communities, male plants have an ecological competitive advantage over female plants in regard to water uptake (Correira and Barradas 2000). Climatic sensitivity is assumed to decrease with increasing age (Rozas *et al.* 2009). These different findings suggested that the response of male and female trees to climate may be related to biology of the species, tree age and site topography.

The available evidence in our paper confirms that the responses of two genders to climate are significantly different, female trees being more sensitive to changes in precipitation and males being especially sensitive to the mean temperature of previous winter at least in the period after 1980. Future research on reconstruction of climate from tree rings of dioecious species should consider the gender's effect.

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