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RESEARCH REPORT

DENDROCHONOLOGICAL POTENTIAL OF JAPANESE BARBERRY (*BERBERIS THUNBERGII*): A CASE STUDY IN THE BLACK ROCK FOREST, NEW YORK

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ABSTRACT

The deciduous forests of northeastern United States are currently experiencing an invasion of the exotic plant species Japanese barberry (*Berberis thunbergii*). This recent and rapid invasion leads to rising concern about its potential threats to native species as well as natural ecosystems, demanding a better understanding of its invasion mechanisms and potential responses to climate change. Unfortunately, few studies have been conducted to understand the influence of climate on the growth of *B. thunbergii*, largely because of the absence of long-term growth records. In this study we demonstrate growth rings of *B. thunbergii* are annually resolved and crossdatable. The first ring-width chronology of *B. thunbergii* was therefore developed using samples collected from the Black Rock Forest (BRF), New York. Climate-growth relationship analysis indicates the growth of *B. thunbergii* in the BRF is positively correlated with precipitation in prior October, current February and May–August, but is negatively correlated with current March precipitation. The growth of *B. thunbergii* is also negatively correlated with temperatures in prior winter (November–January) and current summer (June–July), but is positively correlated with current spring temperature (March–May). These dendrochronological results on *B. thunbergii*, together with further physiological studies, will improve our understanding on how the growth of this invasive species is affected by local climate dynamics, as well as the long-term invasion potential that is tied to its responses to climate change.

Keywords: Dendrochronology, *Berberis thunbergii*, Japanese barberry, Black Rock Forest, tree rings, invasive species, climate.

INTRODUCTION

Japanese barberry (*Berberis thunbergii*) is a thorny, berry-bearing shrub that forms dense thickets in forest understory (Kourtev *et al.* 1998). This species is native to Japan, but was first introduced to North America from Russia in 1875 (Steffey 1985; Silander and Klepeis 1999). Because of the eradication of common barberry (*Berberis vulgaris*) from the landscape at the beginning of the 1910s, *B. thunbergii* was suggested as a substitute for the purpose of ornamentation (Silander and Klepeis 1999). Since then it has become fully naturalized and expanded to all of New England, becoming "probably the most widely known exotic shrub in the United States" (Steffey 1985; Randall and Marinelli 1996; Ehrenfeld 1997).

B. thunbergii occurs in a wide variety of forest types, and can form dense, nearly impenetrable thickets even under closed canopies (Ehrenfeld 1999). The invasion of *B. thunbergii* acts to alter natural ecosystem properties of the invaded areas.

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An investigation performed by Kourtev *et al.* (1998) shows the pH value of soils at the invaded sites is significantly higher than that at the uninvaded sites, and the litter and organic horizons are much thinner. The invaded sites demonstrate a markedly higher nitrification rate, which can be reproduced in greenhouse studies (Kourtev *et al.* 1999, 2003; Ehrenfeld *et al.* 2001). The structure and function of soil microbial community have also been altered by the invasion (Kourtev *et al.* 2002, 2003). All the changes are potentially long-term, and are likely to promote the re-invasion of this and other exotics (Kourtev *et al.* 2003; Cassidy *et al.* 2004). Thus, the invasion of *B. thunbergii* can potentially damage the endemic ecosystem and diversity in Northeastern forests.

The vigorous growth of *B. thunbergii* is largely caused by the high initiation rate and low mortality rate of stems growing from existing root collars, high rates of seedling recruitment, and clonal spread by layering or root sucking (Ehrenfeld 1997, 1999; Silander and Klepeis 1999). Furthermore, the thorny branches of *B. thunbergii* are unpalatable to deer, so there is little mortality from browsing (Ehrenfeld 1997). These physiological characteristics to some extent explain the ability of this invasive species to rapidly produce dense, persistent populations.

In particular, *B. thunbergii* can survive and grow in a broad range of light conditions. It is extremely shade tolerant, and can survive in as little as 1% full sun and produce berries in conditions of only 4% full sun (Silander and Klepeis 1999). *B. thunbergii* leafs out approximately one month before the overstory canopy closes, and still retains its leaves after most of the canopy leaves drop in the autumn (Silander and Klepeis 1999; Xu *et al.* 2007b). The extended leaf lifespan leads to a longer growing season and may potentially utilize more light resource. Recent study indicates that carbon uptake in early spring, when the upper canopy is still open, can contribute about 36% of total annual carbon assimilation (Xu *et al.* 2007a).

Biological invasions are gaining attention as an important element of global change and one major threat to biodiversity (Vitousek *et al.* 1997; Dukes and Mooney 1999). It is expected that biological invasions will interact with other global change components (*e.g.* climate warming) and that climate change is likely to worsen the world's invasive species problems (Dukes and Mooney 1999). However, long-term effects of climate change on the physiological performance (*e.g.* growth) of invasive plants are rarely known. As a commonly used tool to reconstruct historical climate changes from native trees, dendrochronology with invasive woody plants can provide direct evidence to link the growth rate of the invader with climate factors. The physiological characteristics of *B. thunbergii* indicate that its growth vigor is likely to be susceptible to spring weather conditions (Xu *et al.* 2007a, b), so the long-term invasion potential tends to be closely associated with climate change. Therefore, dendrochronological studies of *B. thunbergii* will not only help to understand the effect of climate change on its long-term performance in the past, but also provide essential information to predict its invasion potential under future climate conditions. In this study we developed the first ring-width chronology of *B. thunbergii* using standard methods of dendrochronology, and evaluated its relationships to climate factors (*e.g.* temperature and precipitation).

MATERIALS AND METHODS

The Black Rock Forest (BRF; 41°24′N, 74°01′W) is a 3830-acre preserve located in the Hudson Highlands of southeastern New York State, about 50 miles (80 km) north of New York City. Elevations of the forest range from 150 m to 450 m above sea level. As an oak-dominant secondary growth forest, the BRF is a typical deciduous forest in the northeastern United States in terms of forest composition, tree diversity and age (Braun 1967). Important tree species appear at the sampling site include red oak (*Quercus rubra*), chestnut oak (*Quercus prinus* L.), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), eastern hemlock (*Tsuga canadensis*), yellow birch (*Betula alleghanensis*), hickory (*Carya glabra*), and black birch (*Betula lenta*). Common understory shrubs include huckleberry (*Gaylussacia baccata*

L.), mountain laurel (*Kalmia latifolia* L.), pink azalea (*Rhododendron periclymenoides* L.), and blueberry (*Vaccinium* spp.). Japanese barberry is one of the most invasive species in the forest understory, and widely invades roadsides and previously farmed or logged areas (Barringer and Clemants 2003).

Stem cross-sections of fifteen *B. thunbergii* individuals were collected from three stands in the BRF. The three stands are located in a relatively small area, with direct distances less than one kilometer from each other. To establish the annual nature of *B. thunbergii* growth rings, seven (eight) stems were collected in the fall of 2004 (2005), respectively. All the sampled individuals grew under the closed canopy. During sampling each stem was cut as low as possible at the base of the shrub. In an attempt to extend the chronology, four of the fifteen stems were collected from dead individuals with large stem base.

Ring-width chronology of *B. thunbergii* was developed using the conventional dendrochronological techniques (Fritts 1976; Cook and Kairiukstis 1990). The fifteen cross-sections were air dried in the laboratory, and were polished with progressively fine sandpaper. All samples were carefully crossdated by visually comparing their growth ring patterns. Ring widths of crossdated samples were measured to 0.001 mm precision, and each cross-section was measured along 2-3 radii. Measurement accuracy and crossdating errors were checked using the COFECHA quality control program (Holmes 1983).

The raw ring-width series were standardized in order to remove biological growth trends that are largely attributed to tree age and size (Fritts 1976). To this end, all ring-width series were conservatively detrended using the ARSTAN program (Cook 1985) by fitting negative exponential curves or linear regression curves of any slope. Tree-ring indices were calculated as the ratio of raw measurements to the fitted curve values. All tree-ring index series were merged to develop one robust mean standard chronology that was retained for subsequent analyses.

Climate-growth relationships of *B. thunbergii* were investigated by calculating Pearson's correlations between the chronology and monthly climate data from nearby weather stations. The correlations were calculated using the PCREG program (E. Cook, personal communication), and were verified by PRECON (Fritts *et al.* 1991) and DENDROCLIM2002 (Biondi and Waikul 2004). The climate data were obtained from two stations. Monthly total precipitation records were obtained from the BRF station, which is located in the same forest and spans from 1850–2004. As monthly temperature records at the BRF station are not available until 1996, we used monthly mean temperature records at West Point (41°23′N, 73°58′W) instead. The West Point station is just a few miles southeast to the BRF, and its data span the period 1824–2005.

RESULTS AND DISCUSSION

Annual growth rings produced by trees or shrubs are one of the best natural proxies to reconstruct past climate and to investigate climate-growth relationships for many species (Fritts 1976; Cook and Kairiukstis 1990). Until today there have been more than 1100 tree and shrub species employed in tree-ring research (Dendrochronology species database (http://www.wsl.ch/dbdendro/species/), Grissino-Mayer 1993). However, there have been no dendrochronological studies on *B. thunbergii* reported in the published literature. This paper reports the first dendrochronological study of *B. thunbergii*, which is representative for early leafing understory shrubs in the northeastern United States.

B. thunbergii samples from the BRF displayed very clear ring patterns, with all rings well distinct from each other. During crossdating, no sign of false or missing rings was observed. The samples collected in 2004 and 2005 showed only one ring formed in between, directly confirming the formation of annual growth rings. Ring-width measurements indicate very good crossmatching both within and between the tree-ring sequences of *B. thunbergii* (Figure 1). For instance, growth rings formed in 1978, 1983, 1993, and 1999 are considerably narrow, whereas those formed in 1981, 1990, 1994, and 1996 are fairly wide. This ring-width pattern is also reflected in the standard chronology (Figure 2A). COFECHA results fur-

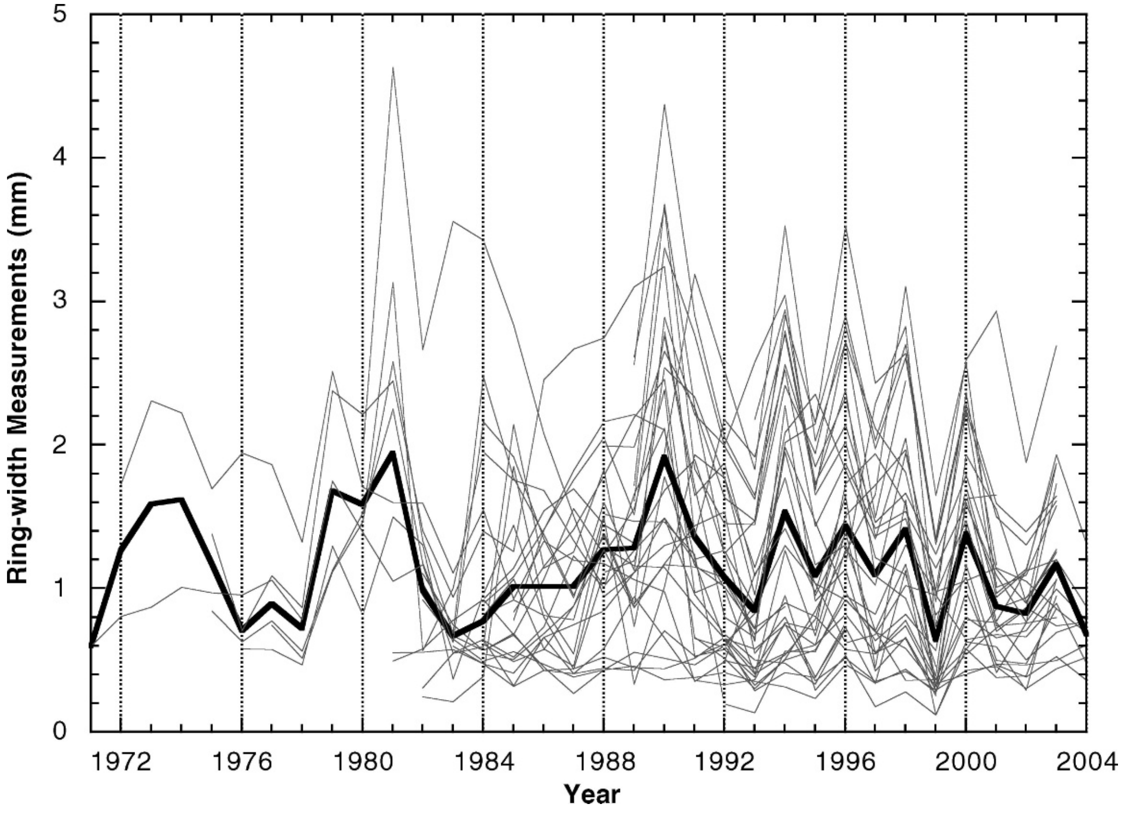

Figure 1. Ring-width measurements of *B. thunbergii* from the BRF. The bold line indicates the mean value for each year.

ther demonstrate the mean correlation of all 36 radii from 15 cross-sections with the master series is fairly high (r = 0.52), indicating good cross-dating among the cores. Therefore, the above evidence from multiple sources together suggests growth rings of *B. thunbergii* can be successfully crossdated, and this species can be employed in dendrochronological studies.

The mean value of all ring-width measurements is 1.21 mm, indicating a fairly low radial growth rate of *B. thunbergii* in the BRF, as expected for an understory species. The ring-width sequences were used to develop the first chronology of *B. thunbergii* (Figure 2A). The chronology spans only 34 years (1971–2004), apparently too short for dendroclimatic reconstruction. However, the values of standard deviation (0.22) and mean sensitivity (0.29) are moderately high (Table 1), suggesting strong year-to-year growth variations that are likely caused by climate variations. The extremely low first-order autocorrelation (−0.19) of the chronology agrees well with the fact that *B. thunbergii* is a shallow rooted shrub (Kourtev *et al.* 2002), suggesting annual growth of *B. thunbergii* more likely reflects climatic conditions in the current biological year. Based on these observations we consider the *B. thunbergii* chronology is valid for exploring its relationships with climate factors.

Although the number of replicates earlier than 1976 was very limited (< 5), most of the ring series (except one) demonstrate very similar variability during 1975–1980 (Figure 1). In addition, a scatter plot of tree rings and climate data (*e.g.* June precipitation) shows the outliers are mostly in the 1980s instead of late 1970s, justifying the feasibility of using tree-ring data back into the late 1970s for climate-growth relationship analysis. Therefore, climate-growth relationships of *B. thunbergii* were analyzed for the period of 1975–2004 (30 years) when there are at least four sample replicates (Figure 2B). The analyses were performed over a biological year from prior October

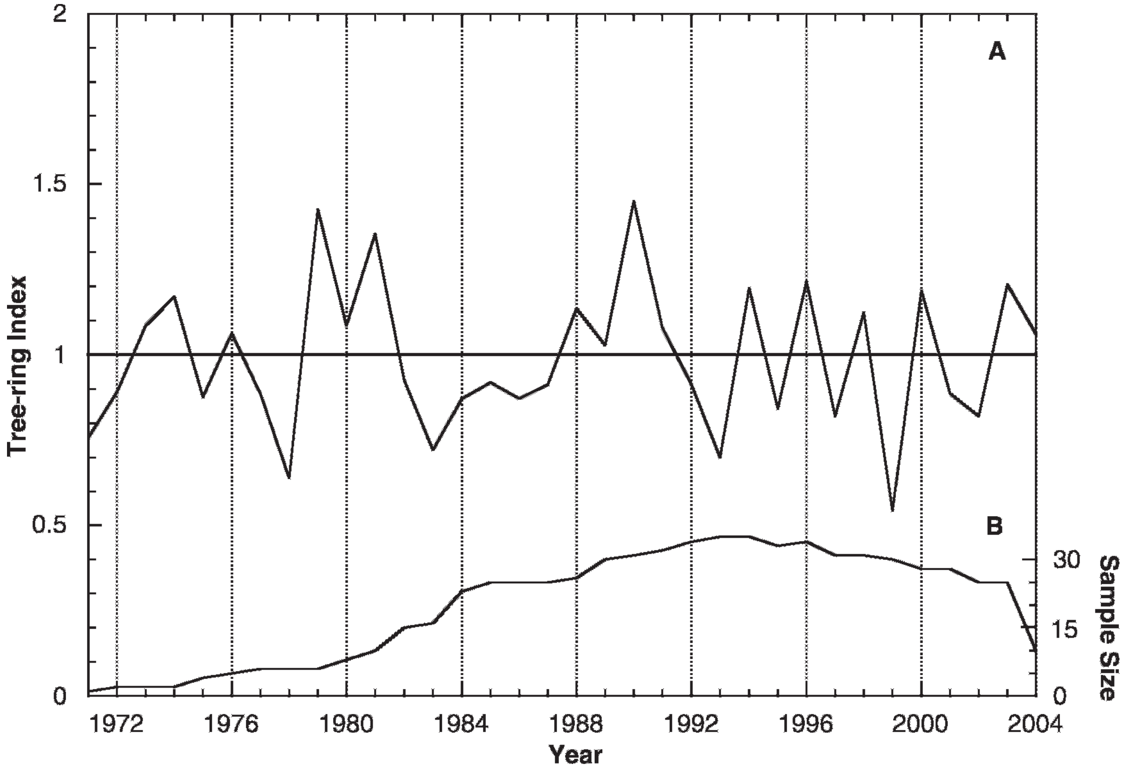

Figure 2. Standard ring-width chronology of *B. thunbergii* from the BRF (A), and its corresponding sample size (B).

to September of the current growth year. As shown in Figure 3, growth of *B. thunbergii* shows positive correlation with precipitation in prior October, current February and May–August, with correlations in prior October ($r = 0.43$) and current June ($r = 0.37$) statistically significant ($p \leq 0.05$). A significant negative correlation with precipitation was identified in current March ($r = -0.37$). Temperatures in prior winter (November–January) and current summer (June–July) are generally negatively correlated with the growth of *B. thunbergii*, with only prior December statistically significant ($r = -0.43$). Current spring temperature (March–May) correlates positively with the growth of *B. thunbergii*, especially in March (yet still statistically insignificant). The above climate-growth relationships produced by PCREG were also achieved by both PRECON and DENDROCLIM2002, although the correlation values are slightly different because of different methods employed in these programs.

Table 1. Statistics of robust mean standard chronology of *Berberis thunbergii* from the BRF.

Chronology interval (A.D.)	1971–2004
Number of shrubs (radii)	15 (36)
Mean index	0.99
Standard deviation	0.22
Skewness	0.27
Kurtosis	3.09
Mean sensitivity	0.29
First-order autocorrelation	−0.19

Before interpreting the above statistical climate-growth relationships, it is necessary to examine whether there are intercorrelations between temperature and precipitation in each month, as such intercorrelations may obscure the real climate factor that controls tree growth (Shi *et al.* 2007). Our calculation indicates no significant intercorrelations ($p \leq 0.05$) between temperature and precipitation in each month, suggesting the above statistical climate-growth relationships are able to provide information on how climate affects the growth of *B. thunbergii*.

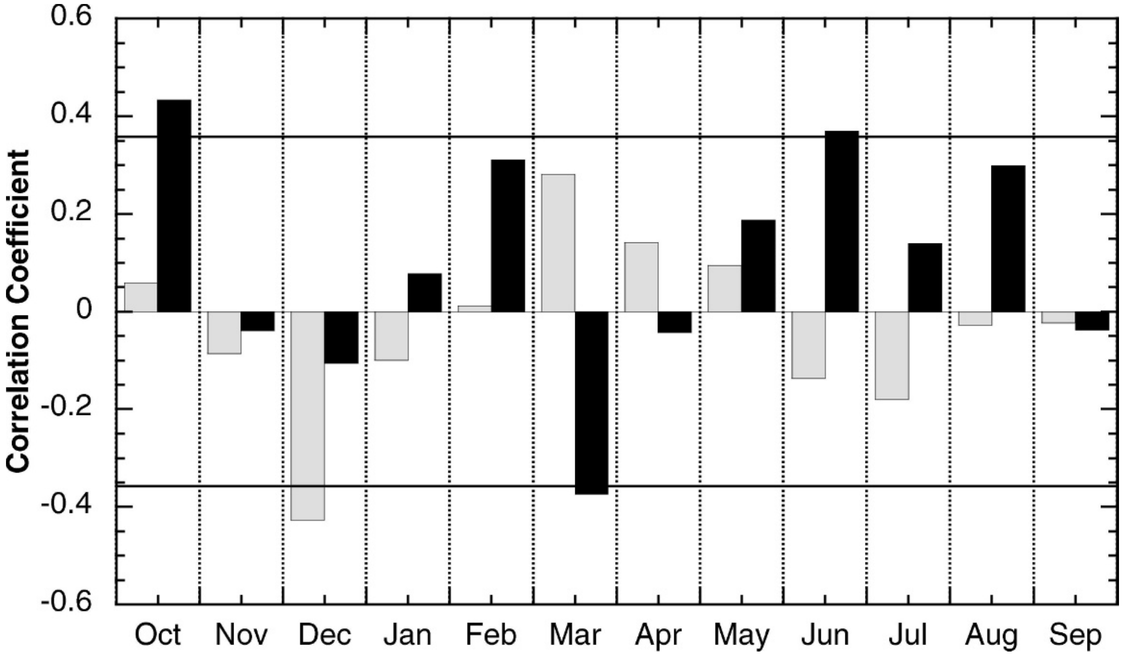

Figure 3. Correlations of *B. thunbergii* chronology with monthly precipitation (solid bars) and temperature records (light bars) in 1975–2004. The horizontal lines indicate the 95% confidence levels.

The growth of *B. thunbergii* is positively correlated with prior October precipitation. A potential mechanism for this relationship is that abundant precipitation at the end of the previous growing season acts to improve (1) the physiological activity of *B. thunbergii* in late fall, which is crucial for the translocation of nutrients and/or carbohydrates from leaves before defoliation, and (2) the soil moisture, which is likely to be preserved until next spring because the evaporation would be inhibited by the winter snow pack. These factors all tend to enhance the growth in the following year (Fritts 1976; Kozlowski *et al.* 1991). The positive response of *B. thunbergii* to prior fall precipitation is similar to that of trees (*i.e. Q. prinus* and *T. canadensis*) in the BRF (D'Arrigo *et al.* 2001). The difference is that the two tree species and *B. thunbergii* are significantly positively correlated with prior September and October precipitation, respectively. The lagged response of *B. thunbergii* may be caused by its extended leaf lifespan compared to the overstory trees (Silander and Klepeis 1999).

The growth of *B. thunbergii* correlates positively with current May–August precipitation, especially in June. In contrast, temperature in current June–July is negatively correlated with the growth of *B. thunbergii*. Therefore, the concurrence of these inverse relationships suggest both temperature and precipitation work to modulate the intensity of evapotranspiration and thus soil moisture availability in the current growing season. These relationships can be further explained by the fact that *B. thunbergii* develops shallow root systems and is thus less tolerant to moisture deficit (Kourtev *et al*. 2002). There is also a physiological explanation to this phenomenon. Normally, the early-leafing plants develop narrow xylem elements to weather late frost in early spring so that the probability of forming embolisms in the xylem is lower (Givnish 2002). Such narrow xylem elements resist cavitation but are hydraulically inefficient, making early leafing plants more vulnerable to summer drought.

Prior winter temperature (November–January) is negatively correlated with the growth of *B. thunbergii*, especially in prior December (Figure 3). High temperature in prior winter enhances evaporation as well as snowpack melting, decreasing soil moisture storage (Fritts 1976). In contrast, current spring temperature (March–May) correlates positively with the growth of *B. thunbergii*, especially in March (yet still statistically insignificant). *B. thunbergii* buds open in late March, and its leaves develop in early April, approximately one month before the overstory canopy closes (Silander and Klepeis 1999; Xu *et al*. 2007a, b). The early budding and leafing of *B. thunbergii* lead to a significant spring carbon subsidy by stimulating photosynthetic carbon gain when high irradiance is available (Xu *et al.* 2007a). This physiological relationship explains the positive correlations of *B. thunbergii* with spring temperature as well as its negative correlation with March precipitation, as high March precipitation often means lower temperature and low light availability, resulting in lower growth. Interestingly, similar to the positive correlation between *B. thunbergii* growth and March temperature, significant positive correlation with March temperature has been observed for evergreen *T. canadensis* (understory tree) in the BRF and many other locations in northeastern North America, but not for deciduous *Q. prinus* (overstory tree) in the BRF (Cook and Cole 1991; D'Arrigo *et al.* 2001). Therefore, the response to spring temperature of the evergreen *T. canadensis* is similar to *B. thunbergii*, which has extended leaf lifespan in understory forests, but it is dissimilar to the late-leafing deciduous *Q. prinus*. Such similarities and discrepancies in responses of trees and/or shrubs to temperature at specific locations are worth attention in future studies.

Previous works have developed models to predict the potential distribution of invasive species in future climate change scenarios based on the climate condition in their current distribution (*e.g.* CLIMAX, Sutherst *et al*. 2004), but the physiological properties of the invader and small-scale climate dynamics are rarely incorporated in these predictive models. The results of the above climate-growth relationship analysis also provide us some hints about the potential responses of *B. thunbergii* to local climate dynamics. For instance, previous studies suggested that carbon assimilation in early spring, when the forest canopy is open, could contribute to 36% of annual leaf level carbon gain of *B. thunbergii*. Meanwhile, *B. thunbergii* also displayed the highest leaf respiration rate of the whole growing season in early spring, which can be related to active growth (Xu *et al.* 2007a, b). These physiological characteristics match the climate-growth relationship elucidated in this study well, indicating the susceptibility of the growth vigor to spring weather conditions. As shown in Figure 4, June precipitation in the vicinity of BRF has increased during the last five decades, and if such a trend continues, may benefit the growth of *B. thunbergii* as well as its competitive advantage. Meanwhile, March temperature generally increased from the 1960s to 1980s, but decreased somewhat since the 1990s. The fluctuating temperature trend may cause a complex influence on the growth and competitive ability of *B. thunbergii* in different life stages. Therefore, the changes of climate in different seasons may either benefit or inhibit the biological invasion of *B. thunbergii*, and the final effect depends on which climate factor is dominant on the growth of *B. thunbergii* as well as other co-occurring understory species. The results of this study warrant further studies to compare and contrast the dendrochronological studies of *B. thunberii* with other shrubs and overstory trees, which will gain us historical insights of whether *B. thunberii* has over-performed native competitors at long time scales, and significantly improve our knowledge to predict the invasion potential of *B. thunbergii* under future climate conditions in the northeastern US.

CONCLUSIONS

This study demonstrates the feasibility of crossdating growth rings of Japanese barberry (*B. thunbergii*). Based on the good ring-pattern matching, the first ring-with chronology of *B. thunbergii* was developed using samples collected from the Black Rock Forest, New York. Climate-growth relationship analysis indicates the growth of *B. thunbergii* in the BRF correlates positively with precipitation in prior October, current February and May–August, and negatively with current March precipitation. The growth of *B. thunbergii* correlates negatively with temperature in prior winter (November–January) and current

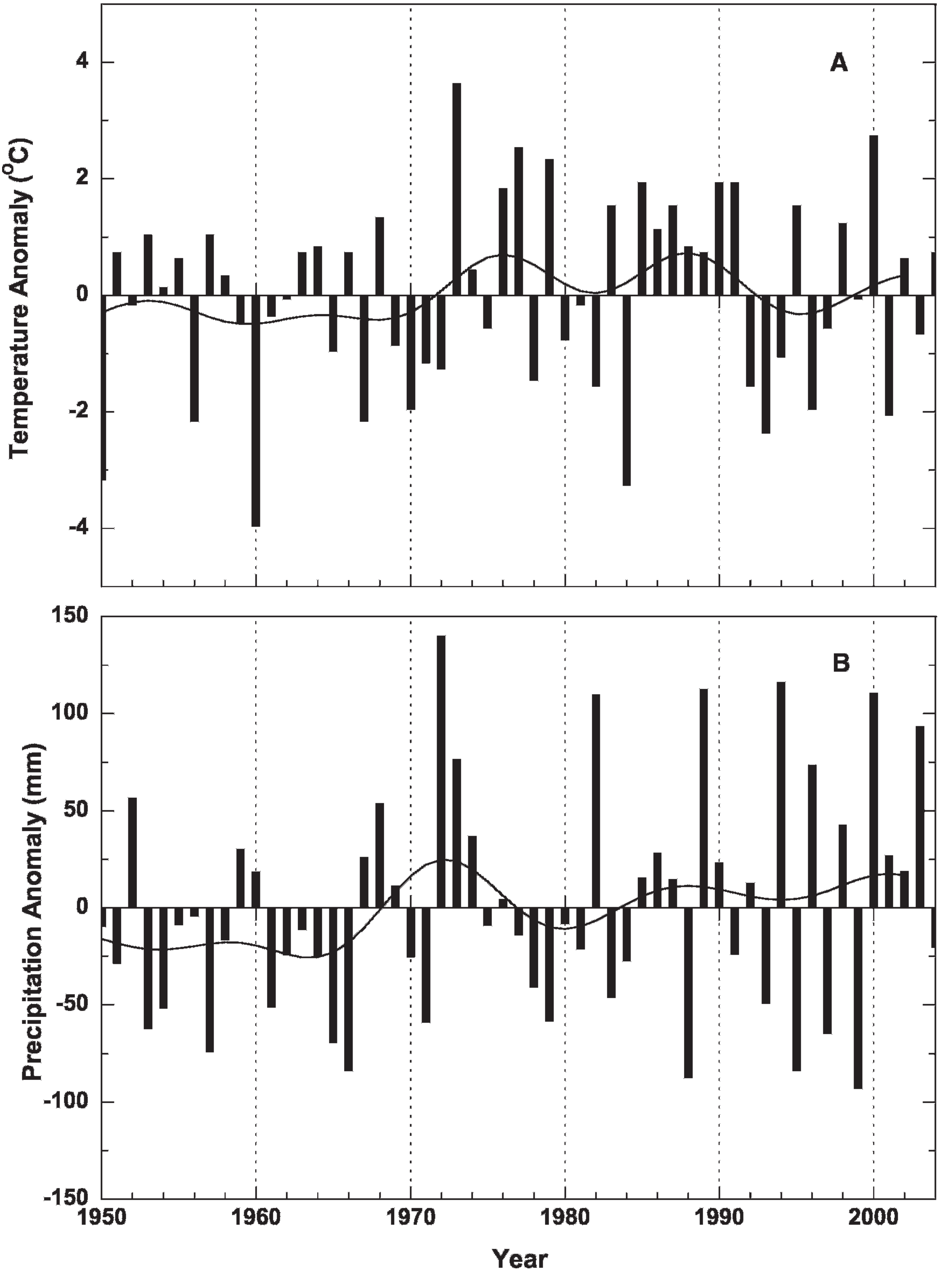

Figure 4. Anomalies of March temperature (A) and June precipitation (B) during 1950–2004 (relative to their mean, respectively) in the BRF, New York. The smooth curve indicates a 5-year moving average.

summer (June–July), but positively correlates with current spring temperature (March–May).

Admittedly, the chronology of *B. thunbergii* developed from the BRF is somewhat short by dendroclimatic standards. Longer chronologies may be obtained by sampling large shrubs in the BRF and other locations in the northeastern North America or around the globe. Although the *B. thunbergii* chronologies may be not ideal for dendroclimatic reconstructions, they surely will improve our understanding on how the growth of this invasive species is affected by local climate dynamics, so as to provide some clues on mechanisms of successful invasion associated with physiological properties and climate change.

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