A dendro-ecological study of forest overstorey productivity following the invasion of the non-indigenous shrub *Lonicera maackii*

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Abstract
Question: Will a non-indigenous, invasive, understorey shrub, such as *Lonicera maackii* (Amur honeysuckle) have an impact on the productivity of overstorey trees in hardwood forests?
Location: Trees from 12 invaded and four non-invaded sites were sampled in hardwood forests of southwestern Ohio, US.
Methods: Changes in radial and basal area tree growth in the ten years prior to *L. maackii* invasion vs. ten years after invasion were examined using dendrochronological techniques. Intervention analysis was used to detect growth changes 25 years prior to and 25 years following invasion, and estimates of load impacts for *L. maackii* population and biomass were also calculated.
Results: We found that the rate of radial and basal area growth of overstorey trees was reduced significantly in eleven out of twelve invaded sites. Non-invaded sites did not exhibit this consistent pattern of reduced growth. For invaded vs. non-invaded sites, the mean basal area growth was reduced by 15.8%, and the overall rate of basal area growth was reduced by 53.1%. Intervention analysis revealed that the first significant growth reductions were 6.25 ± 1.24 (mean ± SE) years after invasion with the greatest frequency of negative growth changes occurring 20 years after invasion. In invaded stands, 41% of trees experienced negative growth changes. In terms of invasive load estimates per 1000 *L. maackii* individuals, radial tree growth was reduced by 0.56 mm.a^{-1}, and basal area growth was reduced by 0.74 cm^2.a^{-1}. Given these findings, significant economic losses could occur in hardwood forests of Ohio.
Conclusions: To our knowledge, this is the first study using dendrochronological techniques to investigate the impact of a non-indigenous, understorey plant on overstorey tree growth. Active management will likely be needed to maintain forest productivity in *L. maackii* impacted landscapes.

Keywords: Carbon sequestration; Competition; Dendrochronology; Invasive species; Ohio; Weed.

Abbreviations: MANOVA = Multivariate Analysis of Variance; RANOVA = Repeated Measures Analysis of Variance; PCQ = Point-Centered Quarter; RI = Radial Increment; BAI = Basal Area Increment.

Nomenclature: Gleason & Cronquist (1991) for vascular plants.

Introduction

Due to human activity, the earth is experiencing large environmental changes at an unprecedented rate. The human population is roughly 250% greater than it was in 1950 (Cohen 2003), and an estimated 17-fold increase in global commerce occurred between 1965 and 1990 (Anon. 1994). One result of human activity is that previously isolated, invasive species have been transplanted across barriers and established in new environments (Mack 2001). The ecological and economic tolls of this global transfer are considerable. Invasive species are ranked as the second-greatest cause of losses in biodiversity (Enserink 1999), and total U.S. monetary losses are estimated to exceed 120 billion USD per year (Pimentel et al. 2005).

Important advances have been made in the field of invasive species ecology; however, progress is sorely needed in the development of sound decision-making strategies (Richardson 2004). A substantial portion of conservation budgets is spent on control and eradication (D'Antonio & Meyerson 2002), but the majority of invasive species may not, in fact, cause significant negative impacts (Williamson 1996). Therefore, it becomes increasingly important as the first step in land management strategies to demonstrate clearly that an invasive plant is indeed having negative impacts (McCarthy 1997).

Invasive species impacts occur at a variety of scales including alterations to genetics, populations, community composition, and rare or sensitive species (Byers et al. 2002). A problem with impacts reported at these levels is that they may include random spatial, temporal, or species-specific variation (Parker et al. 1999). Relative to studies at other biological levels, investigations at ecosystem levels may at times be a more appropriate way to study inferred impacts because ecosystem level studies allow changes to be measured for a potentially larger number of species over greater spatio-temporal scales (Edwards 1988).

Ecosystem level impacts of invasive plants include (1) being different in resource acquisition vs. natives; (2)

altering the trophic structure of an ecosystem; (3) causing an altered disturbance regime (Parker et al. 1999). Well known examples of ecosystem level changes include alterations in the availability of nitrogen by *Myrica faya* (Vitousek et al. 1987), modifications to trophic interactions by introduced animals in Hawai'i (Stone 1985), and changes in the fire disturbance cycle by grasses (D'Antonio & Vitousek 1992).

A fourth type of ecosystem alteration includes changes in productivity (Ehrenfeld 2003). While there are numerous studies examining changes in productivity following non-native invasion, few studies examine changes in woody plant productivity (Robles & Chapin 1995). Non-native woody plants are encountered much less frequently, but they may have a more profound impact on community structure than herbaceous plants (Marco & Paez 2000).

We are not aware of published studies that investigate changes in overstorey tree productivity following invasion by a non-indigenous understorey plant. This is an interesting ecological question because quite often competition is assumed to be one sided with larger plants negatively influencing smaller plants, not *vice versa* (Weiner 1990). Numerous studies, however, suggest that smaller plants can negatively affect larger species including shrubs (Peterson et al. 1988), smaller trees (Yoshida & Kamitani 1998), herbaceous perennials (Dunbar & Facelli 1999), and grasses (Elliott & White 1987). Many examples in the silvicultural literature exist of strategies to reduce native inter-plant competition (Smith et al. 1997), and these include thinning practices, which have been shown to increase the availability of water and soil nutrients and the productivity of remaining trees (Cole & Newton 1986). Moreover, understorey thinning, which involves the removal of the lower strata has been shown to increase canopy tree radial growth (Nyland 2002). Invading plants in a lower forest stratum could, then, very likely impact the productivity of overstorey forest trees. We, therefore, wanted to investigate similar potential patterns of competition between the overstorey trees and *Lonicera maackii* (Amur honeysuckle), an aggressively-invading understorey shrub.

Lonicera maackii has a negative impact on eastern deciduous hardwood forests at a variety of biological levels including impacts on individual herb growth (Miller & Gorchov 2004), seedling growth and fecundity (Gorchov & Trisel 2003; Hartman & McCarthy 2004; Miller & Gorchov 2004), tree densities and seed bank and bud bank levels (Collier et al. 2002), and community composition (Hutchinson & Vankat 1997). Furthermore, these impacts may be widespread as *L. maackii* can effectively expand in range via avian dispersal (Ingold & Craycraft 1983) and has been reported in 24 states in the eastern US (Trisel 1997) and Ontario, Canada (Pringle

1973). We wanted to test the ability of *L. maackii* to impact tree productivity via tree-ring analysis considering its potential for negative above- and below-ground competitive effects (Gorchov & Trisel 2003) and successful establishment of dense populations of rapidly growing individuals (Deering & Vankat 1999). Finally, dendrochronology has been shown to be useful as a long-term indicator of tree stress and overall tree health because stem growth is one of the last prioritizations for resource allocation in trees (Fritts & Swetnam 1989).

Based on the available invasive species and forestry literature, we hypothesized that *L. maackii* would reduce overstorey productivity, evidenced as a decline in tree-ring growth. Our goals were to (1) quantify and document levels of possible *L. maackii* impact on tree growth; (2) determine the timing of significant growth changes; (3) assess the sensitivity of canopy tree individuals according to factors such as site, species, shade-tolerance, size, and age differences; (4) determine the efficacy of using dendrochronological methods in assessing the impact of
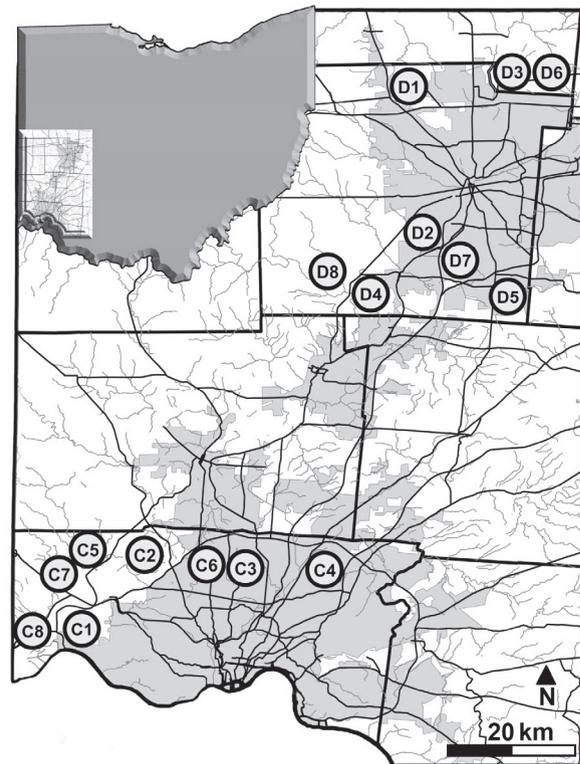
Fig. 1. Location of 16 sampled sites throughout southwest Ohio, USA (enlarged view), and site location within Ohio (map inset). Sites were in the vicinity of the cities of Dayton (D1 – D8) and Cincinnati (C1 – C8). Sites C7, C8, D7 and D8 were non-invaded, and all other sites were invaded at various times. Site codes correspond to Table 1 and Fig. 2. Grey polygons indicate urban and suburban regions. Gray lines indicate rivers and streams. Thick black lines indicate county divisions, and thin black lines designate US and state highways.

invasive species on tree growth.

Methods

Site selection and tree sampling

A total of 16 sites were sampled in the vicinity of Cincinnati and Dayton, Ohio, USA. Sites were equally divided between cities and were randomly chosen from locations on publicly-owned land. Twelve of the sixteen sites were invaded by *L. maackii*, and four of the sites had not been invaded (Fig. 1, Table 1). Within each site, we quantified vegetation using the Point-Centered Quarter (PCQ) sampling method (Krebs 1999). Fourteen PCQ points per site were sampled along two parallel 50 m transects that were positioned 50 m apart and at least 50 m from forest edges. The nearest tree to each PCQ point was cored using an increment borer, and the distances to PCQ points, species identities, and diameters at breast height (DBH) were used to compute overstorey basal area, density, and species composition.

Trees were cored only if they were canopy dominants and free from signs of physical injury, symptoms of disease, and obvious insect damage. At least twelve cores were sampled at each site ($N = 196$ trees total). Trees were measured and cored in September 2000, and *L. maackii* was sampled from June to July 2000. Satellite images (http://www.terraserver.com) from June 2000 were used to delineate forest stand boundaries and estimate stand sizes.

Lonicera maackii sampling

The time of *L. maackii* invasion was assessed by cutting one *L. maackii* shrub in each PCQ quadrant at 5 cm height and counting the annual rings ($N = 48$ stems/site). The oldest *L. maackii* at each site was identified as the time of establishment. The density of *L. maackii* was quantified by measuring the distance from PCQ points to the nearest shrub (≥ 30 cm ht) and converting distance to density (Krebs 1999). Each non-invaded site was adjacent to but not within an area invaded by *L. maackii* and was therefore likely invasible, yet not affected, by *L. maackii*.

Above-ground biomass of *L. maackii* at each site was estimated using allometric methods. Canopy height and spread, number of stems, largest stem radius, and total stem basal area were measured on randomly selected forest interior shrubs of various sizes ($N = 32$).

Table 1. Description of 16 sample invaded and non-invaded sites. Sites of C7, C8, D7, and D8 were non-invaded; all other sites were invaded with *L. maackii*. Overstorey dominants were the top three tree species in terms of density.

Site Code	Latitude, longitude	Soil type, % grade	Overstorey dominant spp.†	Overstorey basal area (m².ha⁻¹)†	Overstorey density†§	Median overstorey age †	Understorey sapling density §	*L. maackii* basal area (m².ha⁻¹)‡	*L. maackii* density ‡§	*L. maackii* biomass (kg.ha⁻¹) ‡
C1	39.19124 N, 84.71330 W	Eden silty clay loam (EcD), 15-25%	FRAM, JUNI, PRSE	31.2	343.4	65	71.4	1.8	1187.2	1127.3
C2	39.24489 N, 84.62122 W	Casco loam (EcE), 25-35%	FRAM, CACO, PRSE	26.6	682.5	40	178.6	8.2	5607.3	6438.7
C3	39.25010 N, 84.52542 W	Casco loam (EcE), 25-35 %	FRAM, JUNI, CEOC	30.3	484.3	45	1178.6	3.4	3709.1	1923.9
C4	39.28148 N, 84.38792 W	Miamian silty loam (MnC2), 2-12%	FRAM, LITU, ACSA	19.5	334.8	25	1750.0	3.0	2446.6	1429.3
C5	39.23295 N, 84.73143 W	Cincinnati silt loam (CnC2), 15-25%	ULAM, PRSE, GLTR	14.2	291.6	42	7250.0	1.6	2250.1	752.6
C6	39.27628 N, 84.53698 W	Rossmoyne silt loam (RpB2), 2-8%	FRAM, QUAL, ACSA	31.0	422.5	52	821.4	0.6	2790.9	465.9
C7	39.24444 N, 84.72742 W	Casco loam (EcE), 25-35%	FRAM, ACSA, ULRU	34.3	257.3	59	4928.6	-	-	-
C8	39.12051 N, 84.81345 W	Pate silty clay loam (PfD), 15-25%	FRAM, ACNE, ACSA	21.9	284.6	58	107.1	-	-	-
D1	39.88738 N, 84.28391 W	Miamian loam (MiB), 2-6%	FRAM, CAOV, JUNI	25.3	293.1	76	1035.7	5.2	1832.2	4253.9
D2	39.71391 N, 84.27258 W	Miamian silt loam (MiB2), 2-6%	CACO, ACSA, PRSE	30.7	278.7	108	357.1	4.3	6208.4	2687.1
D3	39.88583 N, 84.15522 W	Hennepin silt loam (HeE2), 18-25%	QURU, FRAM, ACSA	28.2	450.2	60	5892.9	0.7	3003.2	687.7
D4	39.59489 N, 84.35365 W	Hennepin silt loam (HeF2), 25-25%	FRAM, LITU, JUNI	21.3	366.8	38	6892.9	0.8	1068.9	426.8
D5	39.62081 N, 84.08420 W	†Eldean silt loam (EMC2), 6-12%	FRAM, PRSE, ACNE	18.6	509.3	23	35.7	4.3	2798.2	3749.9
D6	39.87267 N, 84.08325 W	Ross silt loam (Rs), 2-6%	FRAM, PRSE, ULAM	32.3	431.5	38	1678.6	1.7	2510.2	1240.2
D7	39.65327 N, 84.23196 W	Miamian clay loam (MiD2), 12-18%	FRAM, ACSA, JUNI	31.2	233.4	96	3607.1	-	-	-
D8	39.63585 N, 84.42258 W	Hennepin silt loam (HeE2), 12-25%	QUAL, FRAM, CAOV	35.8	255.2	63	14857.1	-	-	-
Mean	-	-		27.2	370.0	55	3165.2	3.0	2951.0	2098.7
SE	-	-		2.3	30.1	5	250.9	0.7	453.4	536.4

† Trees ≥ 10 cm diameter at breast height (DBH); ‡ *Lonicera maackii* ≥ 30 cm ht; § Density in individuals per ha. Species abbreviations as the following: *Fagus americana* (FRAM), *Juglans nigra* (JUNI), *Prunus serotina* (PRSE), *Carya ovata* (CAOV), *Celtis occidentalis* (CEOC), *Liriodendron tulipifera* (LITU), *Acer saccharum* (ACSA), *Ulmus americana* (ULAM), *Gleditsia triacanthos* (GLTR), *Quercus alba* (QUAL), *Ulmus rubra* (ULRU), *Acer negundo* (ACNE), *Carya cordiformis* (CACO), *Quercus rubra* (QURU); %< (Davis et al. 1976; Lerch et al. 1980).

Tree core measurement

Tree cores were dried, mounted on wooden blocks, and sanded using standard dendrochronological procedures (Phipps 1985). Radial increment was measured to the nearest 0.01 mm using an Olympus SZ40 dissecting scope (40 ×), VELMEX unislide measuring device (VELMEX Inc., Bloomfield, NY), ACU-RITE linear encoder (ACU-RITE Inc., Jamestown, NY), and Quick-Check digital readout device (Metronics Inc., Bedfore, NH) connected to a microcomputer. The MEDIR computer program Version 2.1 from the International Tree-Ring Data Bank Program Library (IRTDB) was used during measuring (Krusic et al. 1997). A master chronology was created for each site to represent the common growth pattern for all trees because it has the effect of removing (averaging) small-scale, within-site disturbances as well as competition trends of individual trees (Cook et al. 1990). Crossdating of tree rings was conducted by the use of skeleton plotting and with the COFECHA program (Grissino-Mayer 2001). Only cores that could be confidently cross-dated were statistically analysed. Tree age was calculated by counting annual rings and using a concentric ring pith estimator where tree centre was not entirely reached during coring (Applequist 1958).

Data analysis

To test for differences in overstorey canopy composition, similarity values were generated using Sørensen's index, and clustering was performed via the beta-flexible algorithm (β = –0.2). The multivariate response permutation procedure (MRPP) was used to test for compositional differences between invaded and non-invaded sites (McCune & Medford 1997).

For most analyses we analysed a 20-year period of the tree ring series, 10 years prior to (PRE) and 10 years following (POST) *L. maackii* invasion. Normally, the process of detrending removes low frequency growth changes such as those resulting from stand maturation (Fritts 1976); however, using a relatively short 20-year portion of the series eliminated the need to detrend as this would have removed the hypothesized low-frequency growth changes following *L. maackii* invasion (Stokes & Smiley 1968). Furthermore, we plotted the tree-ring growth across time and no age-related, reverse-J pattern was apparent (Phipps 1982). We also plotted precipitation, temperature, and Palmer Drought Severity Index (PDSI) from 1949 to 2000 to visualize any notable climate changes occurred during that period (National Climate Data Centre and National Oceanic and Atmospheric Administration, Anon. 2002).

Both annual radial increment (RI) and basal area increment (BAI) were used as growth indicators for each tree ring series (Visser 1995). BAI was used in addition to RI because BAI often allows growth shifts to be detected more easily because BAI often shows a positive, linear trend through time (Fritts & Swetnam 1989). Standardized measures for RI and BAI were computed by dividing annual growth by each series' mean growth through the 20-year period and were used for all statistical analyses. Standardized data has advantages over raw data by removing differences in individual tree productivity and rescaling each series so that it has a mean equal to one and stable variance (Fritts 1976).

To compare changes in the rate of growth, the RI and BAI slope was estimated from regressions of tree series data for each of the PRE and POST invasion periods. Mean RI and BAI growth was also estimated separately for both PRE and POST periods. Because non-invaded plots had no actual time of *L. maackii* establishment, we compared analyses using three PRE and POST periods throughout the non-invaded series and found that using different times did not affect the significance of the results. Differences in PRE vs. POST slope for standardized RI and BAI were calculated and will be subsequently referred to as RI_{SLOPE} and BAI_{SLOPE}, respectively. Likewise, differences in PRE vs. POST mean growth for standardized RI and BAI were computed and will be referred to as RI_{MEAN} and BAI_{MEAN}, respectively.

A three-way MANOVA was used to determine which explanatory factor variables might best explain response variable differences, specifically PRE vs. POST mean growth (RI_{MEAN} and BAI_{MEAN}) and PRE vs. POST rates of growth (RI_{SLOPE} and BAI_{SLOPE}; (Scheiner 1993). Factor variables included (1) cities; (2) sites nested within city; (3) shade-tolerance; (4) tree size, and all multi-way interactions. All MANOVA tests involving cities (Dayton vs. Cincinnati) were not significantly different ($P \geq 0.25$); therefore, cities was dropped as a factor from subsequent analyses. Site remained in the analysis and was used to test whether location had a significant effect on PRE vs. POST tree growth. Shade-tolerance tested whether early- vs. late-successional trees grew differently in PRE vs. POST time periods. Trees were classified as being either tolerant to shade or intolerant (Baker 1949; Burns & Honkala 1990). The intolerant group included trees with intermediate shade tolerance. Tree size tested whether small trees (10-35 cm DBH) vs. large trees (> 35 cm DBH) grew differently in PRE vs. POST periods. Site was treated as a random effect, and all other predictor factors were fixed effects (Table 2).

Testing species differences in mean growth (RI_{MEAN} and BAI_{MEAN}) and rate of growth (RI_{SLOPE} and BAI_{S-}

Table 2. Three-way and two-way MANOVA and follow-up ANOVA results for growth differences for pre- versus post-invasion periods (ten years prior to invasion vs. ten years post-invasion, respectively). The statistically significant differences ($P < 0.05$) for follow-up ANOVAs were the following: A = RI_{MEAN}; B = RI_{SLOPE}; C = BAI_{MEAN}; D = BAI_{SLOPE}.

Predictor variables	Wilks' λ	F-value	Num df	Den df	P-value	Response variables in follow-up ANOVA
Three-way MANOVA						
Site	0.269	3.47	44	373	< 0.001	A, B, C, D
Shade-tolerance	0.993	0.18	4	97	0.949	n.s.
Size	0.193	2.16	4	97	0.048	A, B, C, D
Site × shade-tolerance	0.646	1.13	40	370	0.279	n.s.
Site × size	0.799	1.13	20	23	0.315	n.s.
Two-way MANOVA						
Species	0.454	1.63	80	590	< 0.001	C
Invasion	0.757	11.97	4	149	< 0.001	C
Species × invasion	0.214	2.72	12	152	0.002	C

$_{LOPE}$) in pooled invaded and non-invaded sites was accomplished using a two-way MANOVA. Individual species differences at each site could not be assessed due to inadequate representation of species at each site; therefore, cores from sites were pooled to test species × invasion status (invaded vs. non-invaded; Table 2). For both two- and three-way MANOVAs, assumptions of equal variances and multivariate normal distributions of residuals were tested and satisfied prior to analyses (Scheiner 1993). Tree size was significantly predicted by tree age ($P = 0.01$), which violates the assumption that predictors are independent (Tabachnick & Fidell 2001); therefore, tree size was used as a surrogate for tree age.

Following both two-way and three-way MANOVAs, subsequent univariate F-tests were conducted to determine significant predictor variables. Bonferroni multiple comparison procedures were used to detect significant differences among groups. Orthogonal contrasts were performed to test between invaded vs. non-invaded sites for differences in rate of growth and mean growth. Paired t-tests were employed to determine significant PRE vs. POST slope and mean growth differences following Bonferroni corrections. Percent changes in mean growth and rate of growth were computed for all PRE vs. POST-invasion periods. Density and biomass invasive load effects of *L. maackii* were assessed by regressing the changes in radial and basal area growth (PRE vs. most recent ten years) against the density and biomass of *L. maackii* at sites.

Intervention detection was used to quantitatively evaluate the significance and timing of mean BAI growth changes for a 50-year time interval spanning 25 years before and 25 years after *L. maackii* infestation in invaded sites and from 1949 to 2000 in non-invaded sites. Time-series models were constructed using maximum likelihood estimates for each tree series (Box & Jenkins 1970), and growth changes were detected by identifying outliers as statistically significant changes in growth pat-

terns (i.e., step interventions; Downing & McLaughlin 1990). Methods of Box & Tiao (1975) were used to estimate possible interventions and allow for detection of changes in tree growth in 5-year increments, as well as, tests for changes in levels of tree growth before and after invasion (Box & Tiao 1975, eq. 5.2, variables ϖ_{02} anannd ϖ_{03}, respectively). Frequencies of positive and negative step interventions through time were analyzed using a repeated measures multivariate analysis of variance (RMANOVA (Von Ende 1993). Positive and negative intervention frequencies were the response variables, and invasion status (i.e., invaded vs. non-invaded) was tested as the between-subject factor. Time was the repeated (i.e., within-subject) factor. Adjustments for unequal within-subject covariances were made using Huynh-Feldt corrections to create more stringent F-values (Crowder & Hand 1990). Follow-up repeated measures analyses of variance (RANOVA) tests were conducted, and Bonferroni post tests were utilized to discern between significant within- and among-subject factors (Von Ende 1993). A similar RMANOVA test and following RANOVAs were also conducted using magnitude, intensity, and duration of positive and negative interventions through time as response variables (for calculations see caption for Fig. 3). Invasion status was the between-subject factor, and time was the within-subject factor.

All statistical analyses were performed using the SAS statistical program Version 9.1 using the PROC GLM statement except the density and biomass load effects and rate of growth estimates (i.e., slope), which were made using the PROC REG statement (Anon. 2001). All tests were performed using standardized values; however, raw means ± 1 SE are reported. Tests were considered significant when $P < 0.05$.

Results

Lonicera maackii characteristics

Sites experienced a range of *L. maackii* invasion times and infestation levels. Sites were initially invaded 12 to 26 years before sampling. The mean density of *L. maackii* was 2951.0 plants per ha, which was only slightly less than the mean tree sapling density of 3165.2 plants per ha. On a per ha basis, mean *L. maackii* basal area was nearly one tenth of overstorey tree basal area (Table 1). Basal area was the best predictor of adult *L. maackii* biomass [weight per individual (kg) = basal area (in cm^2 units) $\times 0.907 + 0.147$, $R^2 = 0.91$]. Mean honeysuckle plant density was positively predicted by honeysuckle age ($R^2 = 0.22$; $P = 0.04$) as was honeysuckle biomass per ha ($R^2 = 0.67$; $P < 0.001$). There was also a significant, positive relationship between honeysuckle biomass at each site and honeysuckle density ($R^2 = 0.33$; $P = 0.02$), but there was no significant difference between the two cities in terms of honeysuckle age, density, or biomass (all $P \geq 0.31$).

Forest stand characteristics

Forest stands were generally even-aged. Individual sites were significantly different from each other in terms of overstorey tree age, density, and basal area, but invaded sites were not significantly different from non-invaded sites (all $P \geq 0.14$; Table 1). Sites were not visibly different in terms of disturbance history. Mean forest stand size was 112.9 ± 20.27 ha. Canopy composition at sites exhibited no pattern of grouping related to invasion according to beta-flexible clustering and MRPP analyses ($P = 0.83$). Tree species at sites were composed mainly of *Fraxinus americana* (34.4%) and a mixture of moderately common species (5 - 10% each species) including *Liriodendron tulipifera*, *Acer saccharum*, *Acer negundo*, *Juglans nigra*, *Quercus alba*, *Celtis occidentalis*, and several uncommon species (< 5%) such as *Carya cordiformis*, *C. ovata*, *Prunus serotina*, *Q. rubra*, *Q. prinus*, *Ulmus americana*, *Gleditsia triacanthos*, *Catalpa speciosa*, *Ulmus rubra*, *Aesculus glabra*, *Gymnocladus dioicus*, *Nyssa sylvatica*, *Maclura pomifera*, *Fraxinus quadrangulata*, and *Tilia americana* (Table 1).
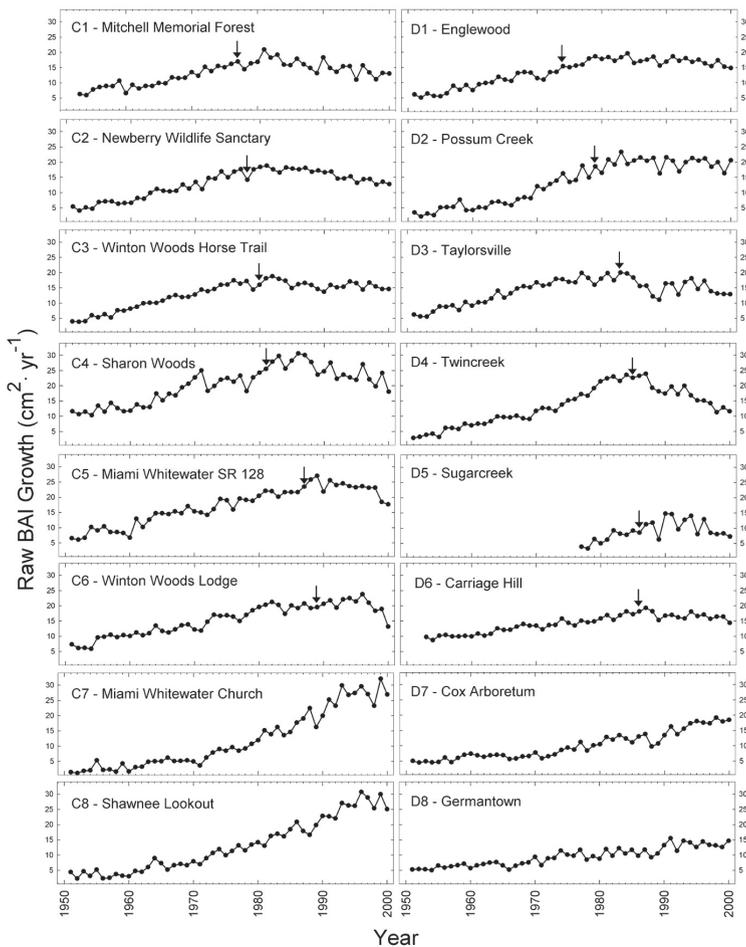
Fig. 2. Master chronology for each site indicating raw mean basal area index (BAI) growth for all cored trees each site (≥ 10 cm DBH) vs. time. Panels **C1** - **C8** represent trees from Cincinnati and vicinity, and panels **D1** - **D8** represent trees from Dayton and vicinity. Panels **C7**, **C8**, **D7** and **D8** designate tree-ring growth from non-invaded sites, and all others are from invaded sites. Arrows indicate the time of initial *Lonicera maackii* invasion.

Table 3. Means of PRE vs. POST periods in invaded and non-invaded tree-ring series and t-test results. RI slope is measured in measured in mm $\times$ a^{-2} units; BAI slope is measured in cm^2 $\times$ a^{-2}; RI mean is measured in mm.a^{-1}; BAI mean is measured in cm^2.a^{-1}. Significance values are reported after Bonferroni corrections.

Invasion status	Variable	PRE	POST	% change	P-value
Invaded	RI slope	0.05 ± 0.01	–0.01 ± 0.01	–80%	0.05*
Non-invaded	RI slope	0.07 ± 0.01	0.08 ± 0.02	+14%	0.13
Invaded	BAI slope	1.10 ± 0.08	-0.39 ± 0.05	-65%	0.01*
Non-invaded	BAI slope	1.14 ± 0.10	1.38 ± 0.06	+21%	0.07
Invaded	RI mean	2.70 ± 0.06	1.81 ± 0.55	–33%	0.01*
Non-invaded	RI mean	2.68 ± 0.04	2.75 ± 0.64	+03%	0.23
Invaded	BAI mean	12.89 ± 1.11	13.53 ± 1.06	+05%	0.20
Non-invaded	BAI mean	12.57 ± 1.08	15.13 ± 1.03	+20%	0.03*

Changes in tree growth following invasion

Tree-ring analysis indicated significant growth changes following *L. maackii* invasion. The most pronounced changes were in the rates of tree growth. Three-way MANOVA and follow-up ANOVAs indicated that sites were significantly different in terms of radial (RI$_{SLOPE}$) and basal area growth rates (BAI$_{SLOPE}$; $P <$ 0.001; Table 2; Fig. 2). Paired t-tests indicated that all invaded sites except site D6 had significantly reduced RI and BAI rates of growth from PRE to POST periods ($P \leq 0.05$), and no significant differences ($P \geq 0.07$) were found for non-invaded sites in RI$_{SLOPE}$ and BAI$_{SLOPE}$ (Table 3). Orthogonal contrasts for both RI$_{SLOPE}$ and BAI$_{SLOPE}$ showed that pooled non-invaded sites were greater than pooled invaded sites. The rate of radial growth in invaded sites was 58.02% less than non-invaded sites (reduced 0.04 mm.a^{-2}), and the rate of BAI growth was 53.13% less in invaded vs. non-invaded sites (reduced 0.27 cm^2.a^{-2}; Table 3).

Three-way MANOVA and follow-up univariate F-tests revealed that sites were significantly different from PRE to POST periods for mean radial (RI$_{MEAN}$) and mean basal area (BAI$_{MEAN}$) growth (Fig. 2; Table 2). Paired t-tests demonstrated that all non-invaded sites experienced significant increases in basal area growth (BAI$_{MEAN}$) across time ($P <$ 0.001), while invaded sites showed a variety of patterns of growth including significant increases, decreases, and non-significant differences (Fig. 2). The mean radial growth (RI$_{MEAN}$) was reduced from PRE to POST periods for invaded sites (P = 0.01), but for non-invaded sites, differences were not significant ($P =$ 0.23; Table 3). According to orthogonal contrasts for PRE to POST periods, pooled non-invaded sites had significantly greater mean BAI growth than pooled invaded sites ($P =$ 0.03; Table 2), and RI growth in non-invaded sites was reduced but not significantly ($P =$ 0.10). Two-way MANOVA and post tests indicated that four species grew differently depending on whether they were from invaded or non-invaded sites (species $\times$ invasion significant interaction; Table 2). *Liriodendron tulipifera* grew better than *Acer saccharum* in invaded sites in terms of BAI$_{MEAN}$, and *Juglans nigra* grew better than *Fraxinus americana* in non-invaded sites (Table 2). Tree size was significant; however, no difference of PRE vs. POST growth between shade tolerant and intolerant species was exhibited (Table 2). Trees with DBH > 35 cm had significantly greater PRE to POST growth relative to smaller trees in terms of RI$_{SLOPE}$, BAI$_{SLOPE}$, RI$_{MEAN}$, and BAI$_{MEAN}$, and this pattern was consistent across all sites, regardless of invasion status (site $\times$ size interaction n.s.; Table 2). The mean radial growth in invaded sites was 17.44% less than non-invaded sites (reduced 0.64 mm.a^{-1}), and the mean BAI growth was 15.80% less in invaded vs. non-invaded sites (reduced 1.97 cm^2.a^{-1}; Table 3).

For assessment of the *L. maackii* population and biomass load effects, we found significant or nearly significant negative relationships between mean radial and mean basal area tree growth and *L. maackii* population size and *L. maackii* biomass (All $P \leq 0.07$; Table 4).

Table 4. Change in invaded overstorey tree growth from PRE to POST periods as predicted by regressing productivity against *L. maackii* density and *L. maackii* biomass.

Tree stem productivity variable	Infestation metric	Difference in pre vs post growth ± SE	R^2; P-value
RI mean	Per 1000 *L. maackii* individuals	-0.56 ± 0.10 mm $\times$ a^{-1}	R^2 = 0.69; P < 0.001
BAI mean	Per 1000 *L. maackii* individuals	-0.74 ± 0.42 cm^2 $\times$ a^{-1}	R^2 = 0.34; P = 0.073
RI mean	Per 1000 *L. maackii* kg biomass	-0.79 ± 0.11 mm $\times$ a^{-1}	R^2 = 0.57; P < 0.001
BAI mean	Per 1000 *L. maackii* kg biomass	-1.04 ± 0.43 cm^2 $\times$ a^{-1}	R^2 = 0.46; P = 0.047
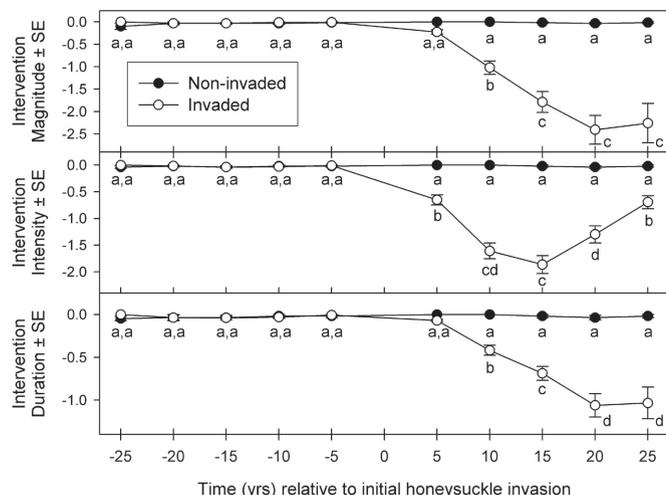
Fig. 3. Magnitude, intensity, and duration of interventions relative to time of initial invasion (time = 0). Significant differences of values within panels ($P < 0.05$) are given by different lowercase letters. Values among times for non-invaded trees were all nonsignificant. Intervention magnitude, intensity, and duration were calculated using the methods of Gray et al. (2004). Magnitude was calculated by subtracting the long-term mean from each 5-year interval growth value within a series and summing these values over the series period. Intensity was calculated by taking the ratio of the magnitude and duration and was calculated as the average magnitude per intervention. Duration was the mean number of consecutive significant interventions for the series period.

Intervention analysis

The RMANOVA and RANOVA tests on the frequency of interventions found a significant interaction of invasion status × time (results not shown). *Post hoc* comparisons found that invaded and non-invaded sites were not significantly different through time in terms of the frequency of positive interventions ($P = 0.34$; 3.15% ± 1.78 of trees with positive interventions). For the within-subject time variable, the frequency of interventions in invaded sites was significantly different in the 5 -10 year period following *L. maackii* invasion and increased in a linear fashion until the period when the greatest number of negative interventions was measured, 20 years after invasion. In post-invasion periods, a substantial proportion of the trees were experiencing negative interventions (41.50%), but no significant positive interventions (i.e., releases in other trees' growth) were detected at invaded sites.

The first significant growth reductions were detected 6.25 ± 1.24 years after invasion, and the timing of growth reductions was fairly consistent with 66% of first negative interventions (2 SD) occurring four to eight years after invasion. The RMANOVA and succeeding RANOVAs involving the magnitude, intensity, and duration of negative interventions found that the invasion status (invaded vs. non-invaded) × time interaction was significant. These intervention variables were not significantly different through time in non-invaded sites ($P > 0.10$), but in invaded sites, these variables were significantly different depending on time period (Fig. 3).

Discussion

While tree-ring chronologies represent simultaneous responses to several growth factors (Schweingruber 1996), our results indicate that a pattern of reduced, sustained tree growth following *Lonicera maackii* invasion was among the strongest signals in our tree-ring chronologies. This signal permitted the timing and quantification of invasive impact and lends strong support to *L. maackii* having strong negative influence on the growth and productivity of canopy trees.

An important aspect of forest research is to attempt to predict the productivity of a site based on biotic and abiotic attributes. In Ohio's deciduous hardwood forests, studies have found a number of site factors that affect tree growth such as parent material, topographic position, and soil classification including surface soil depth, texture, and drainage (Carmean 1965; Anderson & Vankat 1978). Indeed, we did also find significant differences in productivity among sites; however, we found that site was relatively unimportant compared to *L. maackii* invasion status. Non-invaded stands did not show patterns of significant growth reductions throughout tree-ring chronologies, while 11 out of 12 invaded sites showed consistent patterns of significant radial and basal area growth rate decline in the ten years following invasion.

Species identity is another important factor in predicting tree productivity (Desplanque et al. 1999) as well as the interaction of species and site (Orwig & Abrams 1997). We did indeed find differences among species performance, and despite the fact that we were not able to test the interaction of species × site due to inadequate representation of species at all sites, our finding of *Liriodendron tulipifera* having better growth through time than *Acer saccharum* in invaded sites, and in non-invaded sites *Juglans nigra* growing better than

Fraxinus americana was intriguing and warrants further investigation of species-specific responses to *L. maackii* invasion.

Although non-native shrubs are well known for their negative impacts, both native and non-native shrub species can reduce cover beneath them that can negatively impact other plant species (Hobbs & Atkins 1991). Unlike *L. maackii*, native shrubs in Ohio, however, historically did not dominate forest understories (Braun 1916). Presently, *L. maackii* can occur in great abundance with 100% coverage estimated at some sites (Luken et al. 1997), and in this sense, *L. maackii* may be taking advantage of a previously unfilled midstory stratum, i.e. taking advantage of a 'niche opportunity' (see Shea & Chesson 2002). Furthermore, Luken (1988) estimated *L. maackii* biomass production to be nearly equal to that of entire forests! Thus, exotic shrubs in great abundance may be more likely than native shrubs to be detrimental to indigenous plant communities (Collier et al. 2002).

To our knowledge, no previous study has used dendrochronological methods to investigate changes in overstorey tree productivity following the invasion of a non-indigenous species. This type of growth reduction is possible given that numerous studies have indicated growth releases following removal of native species including native shrubs (McClay 1955; Chang et al. 1996), small hardwood trees (Grano 1970; Strong & Erdmann 2000), grasses (Gakis et al. 2004), bamboo (Takahashi et al. 2003), and understorey woody plant strata (Fujimori 2001).

Although we studied the patterns of tree growth over time and not the mechanism of action, interference competition is a likely explanation for reduced tree growth. In dense forests, 'overtopping' is a classic example of asymetrical resource pre-emption due to light interception (Schwinning & Weiner 1998), but it may not be the mode of competition in our study. Below-ground interference may be a more plausible type of competition to explain reductions in tree growth following *L. maackii* invasion due to the differential stratification of *L. maackii* and trees. When competition is primarily for soil resources, it is often independent of plant size (Casper & Jackson 1997). What may be important for competing plants in addition to size is the availability of critical nutrients, effect of plant density, efficiency of nutrient uptake, and conversion to biomass (Schwinning 1996). *L. maackii* has been associated with reduced pH and soil moisture in invaded sites (C. Keiffer pers. comm. 2000). Photosynthetic activity and chemical inhibition may also be factors associated with *L. maackii* competition since it has an extended leaf phenology (Trisel 1997), and allelopathic effects have been reported for *L. maackii* and two other congeners (Norby & Kozlowski 1980; Trisel 1997; Skulman et al. 2004).

The observed changes in tree growth patterns were not likely associated with responses to shifts in climate as we saw no apparent large-scale changes in precipitation, temperature, or Palmer Drought Severity Index during the period of 1949 - 2000 (National Climate Data Centre and National Oceanic and Atmospheric Administration, Anon. 2002). Pollution was also an unlikely cause of growth change during this time period because pollution-related declines in tree growth in the Ohio River Valley were already being detected previous to the beginning of our chronologies (McClenahen & Dochinger 1985). It is possible that the decline could be associated with human or other-caused perturbations that we are not aware of, as invasion is often correlated with disturbance (Pickett 1989). Measured tree growth could be different than site productivity, and stress-induced changes in growth could cause differential allocation of resources to roots or branches. Therefore, overall tree or site productivity may be different than our measured stem growth. It is normal for large groups of trees to die or exhibit growth declines in response to aging as well as environmental stresses (Mueller-Dombois 1987); however, the asynchronous pattern of initial invasion among sites, but parallel temporal pattern of decline within sites following *L. maackii* invasion is evidence that leads more toward causation, and away from correlation, of invasion-associated declines. Growth reductions were not likely associated with differences in forest age or density because these invaded and non-invaded stands were not significantly different in these attributes. Furthermore, no reverse j-shaped decline in tree growth was detected in non-invaded stands, indicating that tree growth had not declined due to stand maturation. Finally, measured trees were canopy dominants which do not succumb as quickly to inter-tree competition as suppressed or midstory individuals (Winget & Kozlowski 1965).

Growth reductions associated with *L. maackii* does have the potential to be quite costly because this shrub seems to be impacting the productivity of overstorey trees, a resource with great ecological and economic value. We showed strong evidence for growth reductions in overstorey hardwood trees when *L. maackii* occurs in the understorey. Ca. 16% reduction in basal area growth was observed at invaded vs. non-invaded sites. Obviously productivity of trees will vary as a function of the level of understorey infestation, relative growth rates, and composition of overstorey trees, all of which depend on local site conditions. The value of forested sites will vary in terms of their ability to provide timber and non-timber products, habitat, and provide ecosystem services including sequester carbon (see Panshin 1980); nevertheless, the presented data should command the attention of forest managers to consider the impact of invasive understorey species on overstorey tree productivity.

In the future, it will be important to understand the long-term effects of *L. maackii* on the dynamics and species composition of invaded forests. Although our data suggest that *L. maackii* is able to successfully compete with canopy trees, as a shrub, *L. maackii* does not possess the ability to ascend into their canopy position. Even so, *L. maackii* could have strong ecological effects on communities as it has already shown ability to negatively alter the abundance of the native seed and bud bank (Collier et al. 2002), seedling growth and survival (Gorchov & Trisel 2003; Hartman & McCarthy 2004), saplings (KMH pers. obs.), and tree growth as reported in our study. It will, therefore, be important to understand *L. maackii*'s effect on the long-term dynamics of forests and possible threshold levels whereby *L. maackii* may cause negative impacts on communities. For instance, a dense *L. maackii* shrub layer may have the ability to have the impacts that other lower forest strata have demonstrated, which is act as an ecological filter in directing canopy tree regeneration (George & Bazzaz 1999; Gorchov & Trisel 2003). *Lonicera maackii* may be able to impact long-term inter-individual or interspecific performance, which could influence long-term canopy accession, species composition, and successional trajectories (see Grime 2001). Although, evidence for L. *maackii*'s pervasive impact makes it important to limit its further spread, a great deal is still unknown regarding *L. maackii* including its mechanisms of impact and the restoration potential of invaded forests. Understanding these aspects will be essential to maintaining sustainable forests.

References

Anon. 1994. *World resources: 1994-1995*. Oxford University Press, New York, NY, US.

Anon. 2001. SAS / STAT user's guide, version 5.0. SAS Institute, Cary, NC, US.

Anon. 2002. *CLIMVIS information: selection criteria for displaying period of record*. URL: http://www5.ncdc. noaa. gov/cgi-bin/climatenormals/climatenormals.pl/ National Climate Data Center and National Oceanic and Atmospheric Administration, Washington, US.

Anderson, D.S. & Vankat, J.L. 1978. Ordination studies in Abner's Hollow, a south-central Ohio deciduous forest. *Bot. Gaz.* 139: 241-248.

Applequist, M.B. 1958. A simple pith locator for use with off-center increment cores. *J. For.* 56: 141.

Baker, F.S. 1949. A revised tolerance table. *J. For.* 47: 179-181.

Box, G.E.P. & Jenkins, G.M. 1970. *Time series analysis: forecasting and control*. Holden-Day, Inc., San Francisco, CA, US.

Box, G.E.P. & Tiao, G.C. 1975. Intervention analysis with applications to economic and environmental problems. *J. Am. Stat. Assoc.* 70: 70-79.

Braun, E.L. 1916. *The physiographic ecology of the Cincinnati region*. The Ohio State University, Columbus, OH, US.

Burns, R.M. & Honkala, B.H. (Tech. Coords.) 1990. *Silvics of North America: Vol. 2, Hardwoods. Agricultural Handbook 654*. U.S.D.A. Forest Service, Washington, DC, US.

Byers, J.E., Reichard, S., Randall, J.M., Parker, I.M., Smith, C.S., Lonsdale W.M., Atkinson, I.A.E., Seasted, T.R., Williamson, M., Chornesky, E. & Hayes, D. 2002. Directing research to reduce the impacts of nonindigenous species. *Conserv. Biol.* 16: 630-640.

Carmean, W.H. 1965. Black oak site quality in relation to soil and topography in southeastern Ohio. *Soil Sci. Soc. Am. Proc.* 29: 308-312.

Casper, B.B. & Jackson, R.B. 1997. Plant competition underground. *Annu. Rev. Ecol. Syst.* 28: 545-570.

Chang S.X., Weetman G.F. & Preston C.M. 1996. Understory competition effect on tree growth and biomass allocation on a coastal old-growth forest cutover site in British Columbia. *For. Ecol. Manage.* 83: 1-11.

Cohen, J.E. 2003. Human population: the next half century. *Science* 302: 1172-1175.

Cole, E.C. & Newton, M. 1986. Nutrient, moisture, and light relations in 5-year-old Douglas-fir plantations under variable competition. *Can. J. Forest Res.* 16: 727-732.

Collier, M.H., Vankat, J.L. & Hughes, M.R. 2002. Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. *Am. Midl. Nat.* 147: 60-71.

Cook, E., Shiyatov, S. & Mazepa, V. 1990. Estimation of the mean chronology. In: Cook E.R. & Kairiukstis L.A. (eds.) *Methods of dendrochronology: applications in the environmental sciences*, pp. 123-132. Kluwer Academic Publishers, Dordrecht, NL.

Crowder, M.J. & Hand, D.J. 1990. *Analysis of repeated measures*. Chapman and Hall, London, UK.

D'Antonio, C. & Meyerson, L.A. 2002. Exotic plant species as problems and solutions in ecological restoration: a synthesis. *Restor. Ecol.* 10: 703-713.

D'Antonio, C.M. & Vitousek, P.M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* 23: 63-87.

Davis, P.E., Lerch, L., Tornes, L., Steiger, J., Smeck, N., Andrus, H., Trimmer, J. & Bottrell, G. 1976. *Soil survey of Montgomery County, Ohio*. U.S.D.A. Soil Conservation Service, Washington, DC, US.

Deering, R.H. & Vankat, J.L. 1999. Forest colonization and developmental growth of the invasive shrub *Lonicera maackii*. *Am. Midl. Nat.* 141: 43-40.

Desplanque, C., Rolland, C. & Schweingruber, F.H. 1999. Influence of species and abiotic factors on extreme tree

ring modulation: *Picea abies* and *Abies alba* in Tarentaise and Maurienne (French Alps). *Trees Struct. Funct.* 13: 218-227.

Dickinson, M.B., Putz, F.E. & Canham, C.D. 1993. Canopy gap closure in thickets of the clonal shrub, *Cornus racemosa*. *J. Torrey Bot. Soc*. 120: 439-444.

Downing, D.J. & McLaughlin, S.B. 1990. Detecting shifts in radial growth by use of intervention detection. In Cook, E.R. & Kairiukstis, L.A. (eds.) *Methods of dendrochronology: applications in the environmental sciences*, pp. 259-271. Kluwer Academic Publishers, Dordrecht, NE.

Dunbar, K.R. & Facelli, J.M. 1999. The impact of a novel invasive species, *Orbea variegata* (African carrion flower), on the chenopod shrublands of South Australia. *J. Arid Environ*. 41: 37-48.

Edwards, K.R. 1988. A critique of the general approach to invasive plant species. In: Starfinger U., Edwards K., Kowarik, I. & Williamson, M. (eds.) *Plant invasion: ecological mechanisms and human responses*, pp. 85-94. Backhuys Publishers, Leiden, NL.

Ehrenfeld, J.G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosyst*. 6: 503-523.

Elliott, K.J. & White, A.S. 1987. Competitive effects of various grasses and forbs on ponderosa pine seedlings. *For. Sci*. 33: 356-366.

Enserink, M. 1999. Biological invaders sweeping in. *Science* 285: 1834-1836.

Fritts, H.C. 1976. *Tree rings and climate*. Academic Press, New York, NY, US.

Fritts, H.C. & Swetnam, T.W. 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. *Adv. Ecol. Res*. 19: 111-188.

Fujimori, T. 2001. *Ecological and silvicultural strategies for sustainable forest management*. Elsevier, Tokyo, JP.

Gakis, S., Mantzanas, K., Alifragis, D., Papanastasis, V.P., Papaioannou, A., Seilopoulos, D. & Platis, P. 2004. Effects of understorey vegetation on tree establishment and growth in a silvopastoral system in northern Greece. *Agrof. Systems*. 60: 149-157.

George, L.O. & Bazzaz, F.A. 1999. The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. *Ecology*. 80: 833-845.

Gleason, H.A. & Cronquist, A. 1991. *Manual of vascular plants of Northeastern United States and Adjacent Canada*. 2nd. ed. New York Botanical Garden, New York, US.

Gorchov, D.L. & Trisel, D.E. 2003. Competitive effects of the invasive shrub, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae), on the growth and survival of native tree seedlings. *Plant Ecol*. 166: 13-24.

Grano, C.X. 1970. *Small hardwoods reduce growth of pine overstorey*. S. For. Expt. Station., Research Paper SO-55. New Orleans, LA, US.

Gray, S., Graumlich, L.J., Betancourt, J.L. & Pederson, G.T. 2004. A tree-ring based reconstruction of the Atlantic Multidecadal Oscillation since 1567 A.D. *Geophys. Res. Lett*. 31: Article No. L12205.

Grime, J.P. 2001. *Plant strategies, vegetation processes, and ecosystem properties*. John Wiley & Sons, West Sussex, UK.

Grissino-Mayer, H.D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Res*. 57: 205-221.

Hartman, K.M. & McCarthy, B.C. 2004. Restoration of a forest understory after the removal of an invasive shrub, Amur honeysuckle (*Lonicera maackii*). *Restoration Ecol*. 12: 154-165.

Hobbs, R.J. & Atkins, L. 1991. Interactions between annuals and woody perennials in a western Australian nature preserve. *J. Veg. Sci*. 2: 743-654.

Hutchinson, T.F. & Vankat, J.L. 1997. Invasibility and effects of Amur honeysuckle in southwestern Ohio forests. *Conserv. Biol*. 11: 1117-1124.

Ingold, J.L. & Craycraft, M.J. 1983. Avian frugivory on honeysuckle (*Lonicera*) in southwestern Ohio in fall. *Ohio J. Sci*. 83: 256-258.

Krebs, C.J. 1999. *Ecological methodology*. 2nd. ed. Benjamin/Cummings, Menlo Park, CA, US.

Krusic, P.J., Holmes, R.L. & King, J.C. 1997. The international tree-ring data bank program library version 2.1 user's manual. In: Grissino-Mayer, H.D., Holmes, R.L. & Fritts, H.C. (eds.) *MEDIR Version 1.13 measurement program*, pp. 18-20. Laboratory of Tree-Ring Research, University of Arizona, Tucson, AZ, US.

Lerch, N.K., Hale, W.F. & Lemaster, D.D. 1980. *Soil Survey of Hamilton County, Ohio*. U.S. Dept. of Agric., Soil Conserv. Serv., Washington, DC, US.

Luken, J.O. 1988. Population structure and biomass allocation of the naturalized shrub *Lonicera maackii* (Rupr.) Maxim. in forest and open habitats. *Am. Midl. Nat*. 119: 258-267.

Luken, J.O., Kuddes, L.M. & Tholemeier, T.C. 1997. Response of understory species to gap formation and soil disturbance in *Lonicera maackii* thickets. *Restor. Ecol*. 5: 229-235.

Mack, R.N. 2001. Motivations and consequences of the human dispersal of plants. In: McNeely, J.A. (eds.) *The great reshuffling: human dimensions of alien species*, pp. 23-34. IUCN, Cambridge, UK.

Marco, D.E. & Paez, S.A. 2000. Invasion of *Gleditsia triacanthos* in *Lithraea ternifolia* Montane forests of central Argentina. *Environ. Manage*. 26: 409-419.

McCarthy, B.C. 1997. Response of a forest understory to experimental removal of an invasive nonindigenous plant (*Alliaria petiolata*, Brassicaceae). In: Luken J.O. & Thieret J.W. (eds.) *Assessment and management of plant invasions*, pp. 117-130. Springer-Verlag, New York, NY, US.

McClay, T.A. 1955. *Loblolly pine growth as effected by removal of understory hardwoods and shrubs*. U.S. Dept. of Agric. For. Serv., Asheville, NC, US.

McClenahen, J.R. & Dochinger, L.S. 1985. Tree ring response of white oak to climate and air pollution near the Ohio River Valley. *J. Environ. Qual*. 14: 274-280.

McCune, B. & Medford, M.J. 1997. *Pc-Ord. Multivariate analysis of ecological data, Version 3.0*. MJM Software Design, Gleneden Beach, OR, US.

Miller, K.E. & Gorchov, D.L. 2004. The invasive shrub, *Lonicera maackii*, reduced growth and fecundity of perennial forest herbs. *Oecolologia* 139: 359-375.

Mueller-Dombois, D. 1987. Natural dieback in forests. *BioSci*. 37: 575-583.

Norby, R.J. & Kozlowski, T.T. 1980. Allelopathic potential of ground cover species on *Pinus resinosa* seedlings. *Plant Soil*. 57: 363-374.

Nyland, R.D. 2002. *Silviculture: concepts and applications*. 2nd. ed. McGraw-Hill, New York, NY, US.

Orwig, D.A. & Abrams, M.D. 1997. Variation in radial growth responses to drought among species, site, and canopy strata. *Trees-Struct. Funct*. 11: 474-484.

Panshin, A.J. 1980. Textbook of wood technology: structure, identification, properties, and uses of the commercial woods of the United States and Canada. 4th ed. McGraw-Hill, New York, NY, US.

Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E. & Goldwasser, L. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biol. Invasions*. 1: 3-19.

Peterson, T.D., Newton, M. & Zedaker, S.M. 1988. Influence of *Ceanothus velutinus* and associated forbs on the water stress and stemwood production of Douglas-fir. *For. Sci*. 34: 333-343.

Phipps, R.L. 1982. Comments on interpretation of climatic information from tree rings, eastern North America. *Tree-ring Bull*. 42: 11-22.

Phipps, R.L. 1985. *Collecting, preparing, crossdating, and measuring tree increment cores*. U.S. Geological Survey, Water Service Investigation Report 85-4148.

Pickett, S.T.A. 1989. Space-for-time substitution as an alternative to long-term studies. In Likens, G.E. (ed.) *Long-term studies in ecology: approaches and alternatives*, pp. 20-70. Springer-Verlag, New York, NY, US.

Pimentel, D., Zuniga, R. & Morrison, D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol. Econom*. 52: 273-288.

Pringle, J.S. 1973. *Lonicera maackii* (Caprifoliaceae) adventive in Ontario. *Can. Field-Nat*. 87: 54-55.

Richardson, D.M. 2004. Plant invasion ecology – dispatches from the front line. *Divers. Distribut*. 10: 315-319.

Robles, M. & Chapin, F.S., III. 1995. Comparison of the influence of two exotic communities on ecosystem processes in the Berkeley Hills. *Madroño* 42: 349-357.

Scheiner, S.M. 1993. MANOVA: multiple response variables and multispecies interactions. In: Scheiner S.M. & Gurevitch J. (eds.) *Design and analysis of ecological experiments*, pp. 94-112. Chapman and Hall, New York, NY, US.

Schweingruber, F.H. 1996. *Tree rings and environment: dendrochronology*. Swiss Federal Institute for Forest, Snow, and Landscape Research, Vienna, AT.

Schwinning, S. 1996. Decomposition analysis of competitive symmetry and size structure dynamics. *Ann. Bot*. 77: 47-57.

Schwinning, S. & Weiner, J. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* 113: 447-455.

Shea, K. & Chesson, P. 2002. Community ecology theory as a framework for biological invasions. *Trends Ecol. Evolut*. 17: 170-176.

Skulman, B.W., Mattice, J.D., Cain, M.D. & Gbur, E.E. 2004. Evidence for allelopathic interference of Japanese honeysuckle (*Lonicera japonica*) to loblolly and shortleaf pine regeneration. *Weed Sci*. 52: 433-439.

Smith, D.M., Larson, B.C., Kelty, M.J. & Ashton, P.M.S. 1997. *The practice of silviculture: applied forest ecology*. 9th ed. John Wiley & Sons, New York, NY, US.

Stokes, M.A. & Smiley, T.L. 1968. *An introduction to tree ring dating*. University of Chicago Press, Chicago, IL, US.

Stone, C.P. 1985. Alien animals in Hawaii's native ecosystems: towards controlling the adverse effects of introduced vertebrates. In: Scott J.M. (ed.) *Hawaii's terrestrial ecosystems: preservation and managment*, pp. 251-297. Cooperative National Park Resources Studies Unit, University of Hawaii, Honolulu, HI, US.

Strong, T.F. & Erdmann, G.G. 2000. Effects of residual stand density on growth and volume production in even-aged red maple stands. *Can. J. For. Res*. 30: 372-378.

Tabachnick, B.G. & Fidell, L.S. 2001. *Using multivariate statistics*. 4th ed. Allyn & Bacon, Needham Heights, MA, US.

Takahashi, K., Uemura, S., Suzuki, J.I. & Hara, T. 2003. Effects of understory dwarf bamboo on soil water and the growth of overstorey trees in a dense secondary *Betula ermanii* forest, northern Japan. *Ecol. Res*. 18: 767-774.

Trisel, D.E. 1997. *The invasive shrub, Lonicera maackii (Rupr.) Herder (Caprifoliaceae) factors leading to its success and its effect on native species*. Dissertation, Miami University, Department of Botany, Oxford, OH, US.

Visser, H. 1995. Note on the relation between ring widths and basal area increments. *For. Sci*. 41: 297-304.

Vitousek, P.M., Walker, L.R., Whiteaker, L.D., Mueller-Dombois, D. & Matson, P.A. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawai'i. *Science* 238: 802-804.

Von Ende, C.N. 1993. Repeated-measures analysis: growth and other time-dependent measures. In: Scheiner S.M. & Gurevitch J. (eds.) *Design and analysis of ecological experiments*, pp. 113-137. Chapman and Hall, New York, NY, US.

Weiner, J. 1990. Asymmetric competition in plant populations. *Trends Ecol. Evol*. 5: 360-364.

Williamson, M. 1996. *Biological invasions*. Chapman & Hall, London, UK.

Winget, C.H. & Kozlowski, T.T. 1965. Seasonal basal area growth as an expression of competition in northern hardwoods. *Ecology*. 46: 786-793.

Yoshida, T. & Kamitani, T. 1998. Effects of crown release on basal area growth rates of some broad-leaved tree species with different shade-tolerance. *J. For. Res*. 3: 181-184.