

Dendroecological analysis reveals long-term, positive effects of an introduced understory plant on canopy tree growth

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Abstract Although the introduction of non-native species can have severe ecological and economic consequences, there is increasing awareness that introduced plants can also provide valuable ecosystem services. Here, we use tree-ring data from 30 sites in the southeastern US to demonstrate that non-native *Lespedeza bicolor* has long-term, positive effects on the growth of mature *Pinus palustris* trees. Trees growing near cultivated plots planted with nitrogen-fixing *L. bicolor* have experienced on average 56 % greater annual growth than trees growing near plots planted with non-nitrogen-fixing *Secale cereale*. Moreover, this fertilization effect has persisted for 25 years, since the local introduction of *L. bicolor*. This positive effect of *L. bicolor* provides evidence that non-native species may alter the growth of overstory trees that play important ecological and economic roles in southeastern forests, and suggests that subsidies from *L. bicolor* may influence carbon sequestration and change the nature of community dynamics at habitat edges. More generally, our results illustrate that non-native nitrogen-fixing understory plants may have strong, unappreciated effects on canopy tree growth, that the effects of non-native plants may have a distinct spatial extent, and that the net effect of non-native plants depends upon the

interplay of ecological costs and benefits that may not be intuitive.

Keywords Canopy gaps · Carbon sequestration · *Lespedeza bicolor* · Longleaf pine · Nitrogen-fixation · *Pinus palustris*

Introduction

Invasive non-native plants are often recognized for their potential to compromise native biodiversity and disrupt ecosystem processes (reviewed in Ehrenfeld 2010; Simberloff 2011; Vila et al. 2011). Many of these adverse effects arise because introduced plants change the physical, chemical, and biological properties of their new environments. In many cases, non-native plants alter disturbance regimes (D'Antonio and Vitousek 1992; Brooks et al. 2004), resource dynamics (Ehrenfeld 2003; Liao et al. 2008), and trophic interactions (Orrock et al. 2008), often to the detriment of native diversity. However, there is increasing awareness that non-native species may also have positive effects on native communities and ecosystems (Stromberg et al. 2009; Schlaepfer et al. 2010; Davis et al. 2011). For example, non-native plants can provide food and shelter for native animals (Bajema et al. 2001; Sogge et al. 2008), increase structural complexity that promotes native biodiversity (Lugo 2004; Fischer et al. 2009), and contribute to ecosystem services (Pejchar and Mooney 2009).

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One possible, though unexplored, benefit of non-native plants is that they might increase the growth of native plant species that are of high ecological and economic value. Because many non-native species are nitrogen (N)-fixing plants (Richardson et al. 2000; Richardson and Rejmanek 2011), non-native N-fixing species may create localized subsidies of N, a limiting resource in many terrestrial systems (Vitousek and Walker 1989; Witkowski 1991; Liao et al. 2008). Despite evidence that non-native understory plants can reduce canopy tree growth (Hartman and McCarthy 2007; Cordell and Sandquist 2008; Rascher et al. 2011) and evidence that native N-fixing trees can have positive effects on forest productivity (Binkley 2003; Forrester et al. 2006; Kelty 2006), it remains unknown whether non-native understory plants may have the unappreciated effect of increasing rates of canopy tree growth.

In this study, we evaluate the long-term impact of an introduced understory N-fixing legume (*Lespedeza bicolor*) on the growth of mature longleaf pine trees (*Pinus palustris*), a species of ecological and economic importance in southeastern pine forests. In addition to providing habitat for many rare and threatened species (Walker 1995; Means 2006), *P. palustris* is playing an increasingly important role in elevating terrestrial carbon (C) storage (Kush et al. 2004). We collected tree core samples from 30 sites spanning 15 km in longleaf pine forests and analyzed annual tree-ring data for a 50-year period that spanned the introduction of *L. bicolor* into the study system. Using this long-term data set, we test our prediction that non-native *L. bicolor* has sustained, positive effects on annual growth rates of *P. palustris*.

Methods

Study system and site selection

We conducted this study at Fort Bragg, a 73,000-ha military installation located in the Sandhills region of North Carolina, USA (Sorrie et al. 2006). Throughout the study area, wildlife openings have been cultivated and maintained to manage local game populations. This program was initiated in the 1950s and currently includes approx. 1,300 plots with a combined area exceeding 400 ha (Heins et al. 2001). These plots are situated within canopy openings in mature longleaf

pine forest, wherein various non-native plant species are grown in monoculture as supplemental food sources for wildlife. As such, this system involves discrete and well-established populations of non-native plants with known introduction dates and management histories. For our study, we selected 15 wildlife openings planted with *L. bicolor* (a N-fixing legume); these plots were established ca. 1980 (Heins et al. 2001). We also selected 15 openings planted with *Secale cereale* (winter rye, a C₃ grass) to control for potential gap effects on tree growth. We determined the total area of each selected wildlife opening using aerial imagery from a Geographic Information System (GIS) database. Additionally, we accounted for potentially confounding effects arising from variation in edaphic conditions, fire history, and basal area among selected sites, as these factors have been shown to influence stand dynamics in longleaf pine forests (Kush et al. 2006). We standardized our selection of study sites based on soil type: all sites were classified as belonging to the Blaney-Gilead-Lakeland soil unit, which is noted for well-drained soils with high sand content (Wyatt 1995). To reconstruct the recent fire history of each selected site, we used GIS data that detailed annual prescribed burns and wildfire records from 1991 to 2010, noting the occurrence of dormant-versus growing-season fires. Moreover, for each focal *P. palustris* tree, we determined the total basal area of neighboring trees by measuring the dbh of all trees within a central 333-m² area.

Data collection

We used an increment borer to collect core samples from two mature *P. palustris* trees per site: we randomly selected one tree located along the margin of the wildlife opening and another tree 20–30 m beyond the margin and within the forest matrix (hereafter referred to as margin and matrix trees, respectively). At each site, margin and matrix trees were located along the same bearing radiating from the center of the wildlife opening. Because lateral root spread of mature *P. palustris* typically does not exceed 10 m (Hodgkins and Nichols 1977), focal matrix trees are unlikely to access soil resources within wildlife openings. In May 2011, a single core sample was taken on the north side of each focal tree at a height of 1.37 m.

Increment core samples were dried, mounted, and sanded according to standard dendrochronological

methods (Phipps 1985). We measured annual tree-ring widths (± 0.001 mm accuracy) using a Velmex measuring system (Velmex Inc., Bloomfield, NY) coupled with Measure J2X software (VoorTech Consulting, Holderness, NH). Tree-ring data are often detrended to remove the effects of tree age and low-frequency variation associated with stand dynamics (Fritts 1976). Determining the exact age of *P. palustris* is complicated by the fact that individuals can persist in a juvenile ‘grass stage’ for 2–15 years, during which time annual tree rings are not produced (Brockway et al. 2006). As such, knowing the duration of this ‘grass stage’ is required to accurately age individual *P. palustris* trees. Nonetheless, in our study all focal *P. palustris* trees were at least 30 years old at the time of *L. bicolor* introductions and were similar in ring-count age (mean ± 1 standard error: 78.4 ± 1.3 years old in 2010). Moreover, we truncated all tree-ring series to consider only the last 50 years of growth, thereby effectively removing potential growth trends associated with juvenile development. This approach thus eliminated the need for detrending data according to common procedures (e.g. Fritts 1976). Further, in light of our study design, detrending our tree-ring data could obscure any low-frequency variation associated with *L. bicolor* introductions (see also Hartman and McCarthy 2007; Larson et al. 2010). We converted annual tree-ring widths to basal area increments (BAI; Visser 1995). This conversion facilitates the detection of changes in radial growth patterns because increases in BAI over time are generally linear (Fritts and Swetnam 1989). For each core sample, we analyzed a 50-year period of radial growth (1960–2010), i.e. 20 years prior to and 30 years following *L. bicolor* introductions.

Data analysis

To examine differences in BAI among focal trees, we used a generalized linear mixed model (SAS Version 9.1, SAS Institute Inc., Cary, NC, USA). Plot type (*L. bicolor* vs. *S. cereale*), tree position (margin vs. matrix), and introduction status (pre- vs. post-introduction) were treated as fixed effects, whereas replicate sites were treated as a random effect. To accommodate multiple ring measurements taken on an individual tree, we modeled variance among ring measurements taken on the same tree using a first-

order autoregressive covariance structure. These plots were established ca. 1980; as such, we employed a conservative window for non-native plant introductions by analyzing radial growth from 1960 to 1975 as ‘pre-introduction’ data and radial growth from 1985 to 2010 as ‘post-introduction’ data. We used the Kenward-Rogers approximation to estimate variance components and denominator degrees of freedom, as recommended by Littell et al. (2006). Because our hypotheses allow for multiple, interactive effects, we evaluated all possible interactions in our model and used linear contrasts to further assess the nature of significant interactions among factors.

Results

Site characteristics

Among selected sites, *L. bicolor* plots were generally smaller than *S. cereale* plots (0.16 ± 0.01 ha vs. 0.27 ± 0.03 ha, respectively; $t = -3.41$, $P = 0.004$); however, plot size was not correlated with mean annual growth rates of margin trees at *L. bicolor* ($r = 0.21$, $P = 0.46$) or at *S. cereale* ($r = -0.12$, $P = 0.68$) sites. Based on transformed aspect values, as recommended by Beers et al. (1966), margin tree locations (relative to forest edge aspect) were similar between *L. bicolor* and *S. cereale* sites ($t = -0.98$, $P = 0.34$). The ring-count age of focal *P. palustris* was also similar between plot types ($F_{1,56} = 1.4$, $P = 0.23$) and tree locations ($F_{1,56} = 1.6$, $P = 0.22$), as determined by counting annual growth rings and using a pith locator on off-center core samples (Applequist 1958). Fire-return intervals were similar between *L. bicolor* and *S. cereale* sites (3.33 ± 0.17 years vs. 3.68 ± 0.18 years, respectively; $t = -1.47$, $P = 0.15$), and for both plot types, the majority of burns occurred during the growing season (87.2 ± 4.2 % vs. 84.1 ± 4.1 %, respectively; $t = 0.53$, $P = 0.60$). Patterns of basal area were also similar between *L. bicolor* and *S. cereale* sites. Specifically, total basal area was greater in the neighborhood of focal margin trees than matrix trees for each plot type (*L. bicolor*: 0.87 ± 0.07 m² vs. 0.69 ± 0.07 m², respectively; *S. cereale*: 0.69 ± 0.04 m² vs. 0.65 ± 0.06 m², respectively; main effect of tree location: $F_{1,56} = 6.3$, $P = 0.015$; plot type \times tree location: $F_{1,56} = 0.1$, $P = 0.81$).

Radial growth of *Pinus palustris*

Pinus palustris grew faster when adjacent to *L. bicolor* plots (significant plot type \times tree location \times plant introduction interaction: Table 1; Fig. 1), averaging a 56 % increase in annual radial growth (Fig. 2). Prior to non-native plant introductions, annual growth rates were independent of plot type and tree position (linear contrast: $F_{3,59.8} = 0.8$, $P = 0.50$). Following introductions, margin trees grew faster than matrix trees at *L. bicolor* sites (linear contrasts: $F_{1,42.3} = 19.0$, $P < 0.001$) but not at *S. cereale* sites ($F_{1,42.3} = 0.5$, $P = 0.50$). Analysis of tree ring intervals revealed similar trends (Table 1; Fig. 3).

Discussion

Our results illustrate that the introduction of a non-native understory plant can have long-term, positive effects on the growth of a valuable timber tree species: fertilization effects of non-native *L. bicolor*, averaged over a 25-year period, increased annual radial growth of mature *P. palustris* trees by 56 % (Fig. 2). To place this in context, chemical fertilizer is often used to increase wood volume in southeastern pine forests (Morris et al. 1992; Dickens et al. 2003), and application of fertilizer at an annual rate of 200 lb N ac^{-1} for the first 9 years of stand development resulted in an 8 % increase in tree diameter after 15 years of growth (Lewis 1977). Although fertilization effects of *L. bicolor* were relatively localized, our results suggest that the long-term, positive effects of this non-native

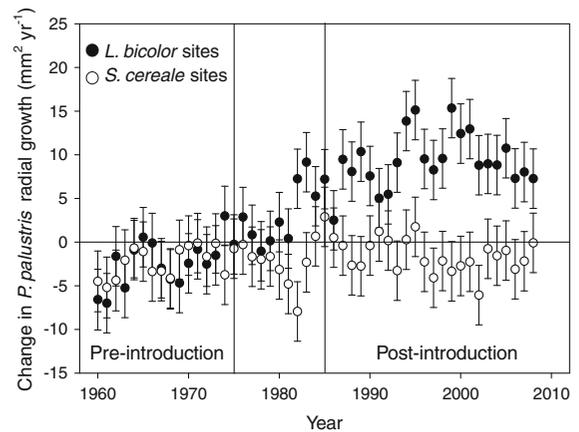


Fig. 1 Annual radial growth changes of mature *P. palustris* trees near plots of non-native *L. bicolor* (a nitrogen-fixing legume) and non-native *S. cereale* (a C_3 grass). Margin tree responses are expressed as annual differences between margin and matrix tree BAI measures per site, a standardization that controls for environmental heterogeneity among sites and facilitates the detection of changes in radial growth patterns. As such, values greater than zero signify an increase in margin tree growth relative to matrix tree growth. Non-native species were introduced ca. 1980. Data represent means \pm 1 standard error

species on neighbor productivity may greatly exceed those of chemical fertilizer application, both in magnitude and in duration.

Our work suggests that when wildlife openings planted with *L. bicolor* occur in high density within N-limited landscapes, as in our study system, these non-native plants could provide a valuable service by reducing the demand for anthropogenic N inputs, a significant concern in terrestrial ecosystems (Vitousek

Table 1 Results of separate repeated-measures ANOVAs testing the effects of introduction status (pre-introduction vs. post-introduction), tree location (margin vs. matrix), and plot type (*L. bicolor* vs. *S. cereale*) on measures of *P. palustris* radial growth

Source	Basal area increment			Tree-ring width		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Introduction status (I)	1,31.7	18.0	<0.001	1,28	19.1	<0.001
Tree location (T)	1,40.1	0.3	0.60	1,28.2	13.7	<0.001
Plot type (P)	1,77.1	0.3	0.62	1,28	0.9	0.35
P \times T	1,40.1	3.2	0.08	1,28.2	0.7	0.42
T \times I	1,1169	98.4	<0.001	1,1169	5.3	0.02
P \times I	1,31.7	1.7	0.21	1,28	0.8	0.37
P \times T \times I	1,1169	73.5	<0.001	1,1169	46.2	<0.001

These non-native species were introduced to wildlife openings ca. 1980, and thus we provide a conservative classification of pre-introduction (1960–1975) and post-introduction (1985–2010) growth responses of *P. palustris*. Significant *P* values in bold

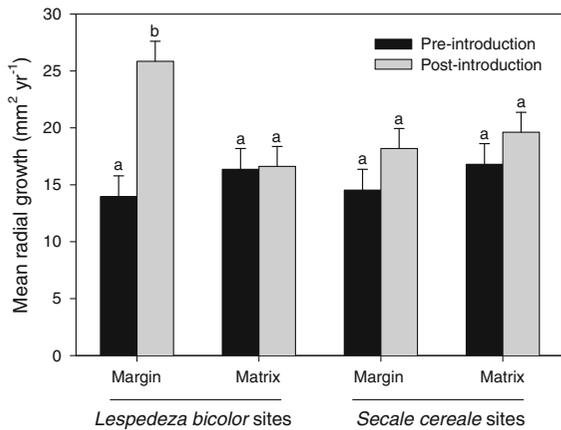


Fig. 2 Mean radial growth of *P. palustris* during the pre-introduction (1960–1975) and post-introduction (1985–2010) periods of non-native *L. bicolor* and *S. cereale* within wildlife openings. Margin trees were located along the margins of wildlife openings, whereas matrix trees were located within the forest matrix 20–30 m beyond these margins. Data represent means \pm 1 standard error. Different letters above bars denote significant differences between means

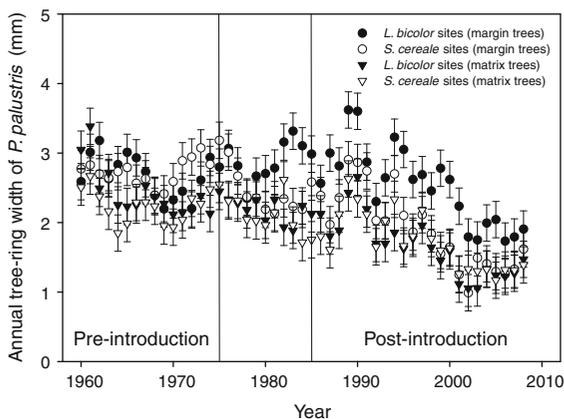


Fig. 3 Annual tree-ring widths of margin and matrix trees associated with non-native *L. bicolor* (a nitrogen-fixing legume) and *S. cereale* (a C_3 grass) plots. Margin trees were located along the margins of wildlife openings, whereas matrix trees were located within the forest matrix 20–30 m beyond these margins. Non-native species were introduced ca. 1980. Data represent means \pm 1 standard error

et al. 1997). The benefits of N produced in situ have long been recognized, as the importance of planting N-fixing trees as sources of N has been shown in many mixed-species forest plantations (Binkley et al. 1992; Binkley 2003; Forrester et al. 2006; Kelty 2006). Our work illustrates that a non-native understory plant can also serve this function. Moreover, unlike the N-fixing trees that have previously been studied (e.g. *Alnus*,

Acacia, and *Albizia* spp.), *L. bicolor* is a shrub <3 m in height; as such, this N-fixing species is less likely to compete with and constrain the production of mature timber trees, as has been documented in mixed-species forest plantations (e.g. Binkley 2003).

Southeastern pine forests are increasingly recognized for playing an important role in elevating terrestrial C storage (Kush et al. 2004; Zhao et al. 2010), particularly since much of the landscape that was once used for agriculture has been converted to pine plantations (Hedman et al. 2000). *P. palustris*, in particular, has many traits that are favorable for sequestering C under changing environmental conditions; for example, *P. palustris* is a long-lived species with a low mortality rate, high specific gravity, and high tolerance to fire, pests, and pathogens (Kush et al. 2004, 2006). Considering the widespread establishment of wildlife openings currently planted with *L. bicolor* throughout N-limited pine forests in the southeastern US, our results indicate that a significant potential may exist for this non-native N-fixing species to promote forest C sequestration. Moreover, because non-native species may be more resilient than native species to global environmental change (Hellmann et al. 2008), the potential ecological value of non-native plants such as N-fixing *L. bicolor* may increase in the future (Schlaepfer et al. 2010).

In addition to documenting the strong effect of *L. bicolor* on adjacent overstory tree growth, our work captures the spatial extent of this localized nutrient subsidy: the positive effect of *L. bicolor* on *P. palustris* growth is spatially confined to a margin (<25 m) surrounding each wildlife opening. This distance is consistent with the root foraging extent of mature *P. palustris*, which is generally <10 m (Hodgkins and Nichols 1977). Because the direct benefits of *L. bicolor* fertilization on neighbor productivity occur near the margins of wildlife openings, our findings suggest that the N subsidies provided by *L. bicolor* may also alter biological interactions at habitat edges (Ries et al. 2004; Prevedello and Vieira 2009; Watling et al. 2011). For example, differences in litter input caused by N fertilization may alter the persistence of native plant species by changing microsites available for seedling establishment. Similarly, although establishment of invasive fire ants (*Solenopsis invicta*) in southeastern forests may be facilitated by canopy openings (Stiles and Jones 1998), it is unknown

whether changes in edge structure or productivity caused by *L. bicolor* affect the likelihood of *S. invicta* establishment. An important implication of the spatial extent revealed in our study is that it provides a direct way to mitigate the strength of *L. bicolor* effects by manipulating the size and shape of wildlife openings: long and linear openings (i.e. shapes that maximize the amount of patch perimeter relative to patch area) will maximize the amount of forest area that receives N subsidies from *L. bicolor*.

Although we document 25 years of elevated *P. palustris* growth in the presence of N-fixing *L. bicolor*, the strength of this fertilization effect did vary over time. Notably, the effect of *L. bicolor* begins to wane in the late-1990s (Fig. 1), a trend that could arise through several possible mechanisms, including differential N allocation as trees age as well as interactions between climatic factors (e.g. temperature and precipitation) and N allocation. Although studies have indeed shown that tree age and climatic variation can profoundly affect *P. palustris* growth rates (e.g. Kush et al. 2006; Bhuta et al. 2009; Henderson and Grissino-Mayer 2009), the manner in which these factors influence mature tree growth responses to N subsidies remains poorly understood.

Conclusions

Non-native plant introductions can have substantial negative ecological and economic impacts (Mack et al. 2000; Pimentel et al. 2000; Vila et al. 2011). While the possible negative effects of non-native plants will continue to be important to characterize, a key conclusion of our work is that non-native understory plants may benefit native systems in some instances, and that these positive effects may be revealed by members of the ecological community that may be unlikely to benefit at first glance. Future work that examines longer-term changes in soil N availability and other potential effects of the nutrient subsidies provided by non-native legume species will be important for understanding the balance of ecological costs and benefits of introduced N-fixing species. Moreover, future work evaluating interactions between non-native plant-mediated N subsidies and other drivers of tree growth (e.g. variation in precipitation and temperature) will be essential for understanding the dynamics of canopy tree growth in the context of introduced understory plants.

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