

# Drivers of secondary succession rates across temperate latitudes of the Eastern USA: climate, soils, and species pools

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**Abstract** Climate change is widely expected to induce large shifts in the geographic distribution of plant communities, but early successional ecosystems may be less sensitive to broad-scale climatic trends because they are driven by interactions between species that are only indirectly related to temperature and rainfall. Building on a biogeographic analysis of secondary succession rates across the Eastern Deciduous Forest (EDF) of North America, we describe an experimental study designed to quantify the relative extent to which climate, soil properties, and geographic species pools drive variation in woody colonization rates of old fields across the EDF. Using a network of five sites of varying soil fertility spanning a latitudinal gradient from central New York to northern Florida, we added seeds of nine woody pioneer species to recently tilled old fields and monitored first-year growth and survivorship. Results suggest seedlings of southern woody pioneer species are better able to quickly establish in fields after abandonment, regardless of climate regime. Sites of lower soil fertility also exhibited faster rates of seedling growth, likely due to the slower development of the successional herbaceous community. We suggest that

climate plays a relatively minor role in community dynamics at the onset of secondary succession, and that site edaphic conditions are a stronger determinant of the rate at which ecosystems develop to a woody-dominated state. More experimental research is necessary to determine the nature of the herbaceous–woody competitive interface and its sensitivity to environmental conditions.

**Keywords** Climate change · Old field succession · Tree–herb competition · Biogeography · Species pool

## Introduction

Abandoned crop- and pasturelands across the Eastern Deciduous Forest (EDF) of North America transition from annual and perennial herbs and grasses to various states of woody dominance in a pattern that has been well described for over a century (Clements 1916; Oosting 1942; Keever 1950; Bazzaz 1968; Meiners et al. 2002). Although the trajectory is the same across the EDF, the time required for woody species to achieve dominance varies on the order of decades (Abel 1941; Bard 1952; Bazzaz 1968). In the Northeast USA, for example, fields can persist as herbaceous assemblages (often dominated by *Solidago* spp.) for more than a half-century (Mellinger and McNaughton 1975), whereas fields in the Southeast typically transition to closed pine stands in less than a decade (Oosting 1942; Keever 1950). Given this transition from an herbaceous- to woody-dominated community is a key threshold for various aspects of ecosystem functioning (Inouye et al. 1987; Haddad et al. 2001; Breshears 2006; Galang et al. 2007), understanding the causes of this geographic variation in the rate of secondary succession is of key importance to the management of EDF ecosystems, particularly given

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anticipated shifts in climate and land use across the region (Brown et al. 2005).

In a synthesis of secondary succession rates from 30 studies across the EDF over the past century, Wright and Fridley (2010) documented a clear latitudinal pattern, where the time after field abandonment required to reach 10 and 50% woody cover increased 5- to 10-fold from the southern Piedmont to the northern EDF boundary. This latitudinal pattern was associated with climatic variation (particularly temperature regime), broad-scale variation in soil fertility, which is generally higher in the glaciated soils of the Northeast (von Englen 1914), and differences in the species pools of both herbaceous and woody pioneer species between regions. From these associations, Wright and Fridley (2010) proposed a model of secondary succession rates based on the intensity of competition between herbaceous and woody species. In this model, fields of the Northeast may favor herbaceous persistence as a result of several non-exclusive processes: (1) more fertile Northern soils promote nutrient-demanding, fast-growing herbs that competitively suppress woody seedlings (Grime 2001); (2) cooler temperatures impede the apical development of woody seedlings, regardless of herbaceous competition (Norby et al. 2003); or (3) early successional species pools of the Northeast include woody species of inherently slower growth rate (e.g., no yellow pines) or herbs of inherently greater competitive ability (e.g., clonal species). However, because all three of these factors—climate, soil properties associated with fertility, and species pools—vary regionally across the EDF, at best only weak inferences could be made about which of these factors is the most important driver of successional rates in old field ecosystems.

Here we report a field study designed to determine whether the rate of woody colonization of old fields across the EDF is driven more by site differences in climate, soil fertility, or the species identity of woody seedlings common to successional ecosystems in the Northeast and Southeast USA. Using an experimental network of five sites from central New York to northern Florida that showed large variation in climate and soil properties, we monitored the growth and first-year survival of nine sown woody pioneer species at each site. We were particularly

interested in testing the following hypotheses about mechanisms that may drive the latitudinal pattern of secondary succession rates across the EDF:

1. *Species pool hypothesis*: Woody pioneers that are common to southern and mid-latitude old fields—including *Diospyros virginiana*, *Liquidambar styraciflua*, *Pinus taeda*, and *Prunus angustifolia*—have inherently greater growth rates than those species typical of northern fields, including *Acer negundo*, *Cornus racemosa*, *Fraxinus americana*, *Juniperus virginiana*, and *Prunus serotina*.
2. *Climate hypothesis*: Woody pioneer species, regardless of provenance, grow faster or have higher seedling survivorship in warmer climates.
3. *Soil hypothesis*: Soil properties related to fertility (nutrient availability, water retention) drive woody pioneer growth or survival rates more than climate regime, regardless of species identity.

## Methods

### Research locations

We established five experimental sites located in old fields spanning the near-northern to southernmost extent of the EDF, from Syracuse, NY, USA to Tallahassee, FL, USA (Table 1). Except for the Syracuse site, sites were located within ecological research stations with well-studied successional dynamics. An additional southern site at the Savannah River Ecology Laboratory near Aiken, GA, exhibited very poor seedling recruitment and was excluded from the present analysis. Each site was tilled in the summer of 2008 prior to fall planting to remove existing vegetation (with the exception of rhizome fragments of *Rubus* spp. at some locations) and fenced to exclude deer and small mammal herbivory. Successional communities were allowed to develop naturally at each site; no attempt was made to weed surrounding vegetation. Herbaceous communities were well developed at most sites by the summer of 2009 but varied significantly in composition between sites (Table S1, Electronic supplementary material, ESM).

**Table 1** Five experimental locations spanning the EDF

Site	Research station	Location	Latitude
SYR	Syracuse Field Research Plots	Syracuse, NY, USA	43°20'
IES	Cary Institute of Ecosystem Studies	Millbrook, NY, USA	41°47'
HMF	Hutcheson Memorial Forest	New Brunswick, NJ, USA	40°30'
DKE	Duke Forest	Durham, NC, USA	36°00'
FLA	Tall Timbers Research Station	Tallahassee, FL, USA	30°40'

## Seed sources

Seeds for focal species were obtained through commercial sources. Where possible we obtained seeds of both northern and southern provenances for each species (northern sources from Pennsylvania, North Dakota, Montana, and Missouri; southern sources from Louisiana and Georgia). Seeds for *C. racemosa* could only be obtained from a northern source and seeds of *P. taeda* and *A. negundo* only from a southern source. Seed provenances for each species were identical across experimental locations. Although the performance of seed provenances within species was monitored, we detected no significant provenance patterns and so here report performance at the species-level only.

## Experimental design, planting, and measurements

At each site we established experimental units of 60 × 60 cm arrayed in a grid, each separated by 1-m walkways on one side and 40 cm between adjacent plots on the remaining sides. Seed provenances of each species were sown into their own experimental units and replicated randomly within three blocks, giving a total of 45 experimental units per site (two provenances per species for six species, plus three sole provenances for the remaining three species, all replicated three times). For each experimental unit we broadcast 100 seeds in October 2008 and another 100 seeds in May 2009. October 2008 seeds were dry-sown without pretreatment, and May 2009 seeds were stratified in the laboratory in the preceding winter according to known dormancy requirements (Baskin and Baskin 2000).

Each site was visited in May 2009, October 2009, and May 2010 to monitor seedling performance. At each visit all seedlings present in each experimental unit were measured for height and mapped to quadrants to facilitate the tracking of individual survivorship. Height data analyzed here are for spring 2010 (after one full growing season); survivorship data include those individuals germinating in 2009 that were still alive in May 2010.

## Climate and soil data

Daily min and max temperature and rainfall data for 2009 were collected at all five sites. Temperature data were collected with aspirated digital temperature sensors located at ca. 1 m height and rainfall was collected with self-tipping tip-bucket sensors of 2 mm resolution (HOBO data logging rain gauge, Onset Computer Corporation, Pocasset, MA, USA). In two cases temperature records were incomplete and replaced with daily data from weather stations within 10 km (data retrieved at <http://www.ncdc.noaa.gov>, National Climate Data Center, Asheville, NC, USA). From daily temperature and rainfall data we derived

14 climate summary variables for each site, including min, max, and mean annual temperature; total annual, spring (March–May), summer (June–Aug), and growing season (days above 10°C) rainfall; growing degree-days (10°C base) starting from 1 January or 1 March; frost-free days (days above 0°C); potential evapotranspiration (PET, monthly Thornthwaite method), summed annually and over the summer months; and summer and annual water balance, calculated as the difference between rainfall and PET.

Soil cores were collected at the three northern sites during the last week of September 2008 ( $N = 3$  for SYR, 5 for IES, and 7 for HMF), at the southernmost FLA site during the last week of June 2008 ( $N = 12$ ), and at the DKE site in early April 2008 ( $N = 20$ ). Cores were 2 cm wide and 10 cm deep below the litter layer. Cores were transported to the laboratory for chemical and textural analysis; see the ESM for details of each assay. Measurements for each sample included nitrogen (extractable nitrate and ammonium, total inorganic N, N mineralization rate), % organic matter, pH, Mehlich III extractable phosphate, Ca, Mg, and K, and % clay, sand, and silt.

## Analysis

Major sources of climate and soil variation between sites from the above soil and climate data were extracted with principal components analysis (PCA) conducted separately for the described climate (14 variables) and soil (13) data. Axis 1 of each PCA was used as a predictor variable for site-based regressions of height and survivorship.

The nine focal species were split into two groups on the basis of whether they predominate in northern or southern ENA successional communities (Wright and Fridley 2010, Table 2 therein). The northern group included *Acer negundo*, *Cornus racemosa*, *Fraxinus americana*, *Juniperus virginiana*, and *Prunus serotina*, and the southern group included *Liquidambar styraciflua*, *Pinus taeda*, and *Prunus angustifolia*. *Diospyros virginiana* is dominant in succession at mid-latitudes (between Georgia and Missouri; Wright and Fridley 2010); its inclusion in either group did not qualitatively influence our regression results so results below include it as a southern species.

Height data for all species were right-skewed and were log-transformed for analysis. Because inherent growth rates varied by species, and this level of variation dominated height variation at the within-site scale, we first fit mean height data from each plot to an ANOVA model using species as the sole predictor variable. Residuals from this model were then analyzed at the between-site scale using a mixed effects model (the ‘lmer’ function in the *lme4* library for R; Bates and Maechler 2009), with ‘site’ as a random effect and fixed effects of primary climate and

soil axes and the species pool grouping variable, including two- and three-way interactions. Because of the between-species standardization of heights resulting from the initial ANOVA, species group could not have a main effect in this second between-site model, but its inclusion did allow us to address species-level interactions with climate or soil variables. We assessed the significance of model terms by comparing the maximal and reduced candidate models using Akaike weights based on model  $AIC_c$  values from maximum likelihood estimates (Burnham and Anderson 2002). As a guide to assessing the relative importance of climate and soil variables for the best-fit model, we calculated standardized model coefficients by standardizing climate and soil variables by subtracting their mean and dividing by their standard deviation before model fitting. An analogous model comparison procedure was performed to determine individual species height responses to climate and soils, using separate models for each species including main effects of primary climate and soil axes and two-way interactions. For the species-level models we report coefficients of only the best-fit models as assessed via  $AIC_c$ .

Survivorship data were calculated as the total number of 2009 germinants surviving to May 2010. We used a mixed effects, generalized linear model (GLM) framework appropriate for proportion data (the ‘lmer’ function in R with a logit link and binomial error), and survival data were weighted by the total number of germinants for each species–site combination. A random effect accounted for within-site correlations. As for the height response variable, the significance of model factors was determined via  $AIC_c$  of maximal and reduced models and coefficients were fitted via maximum likelihood. Standardized coefficients

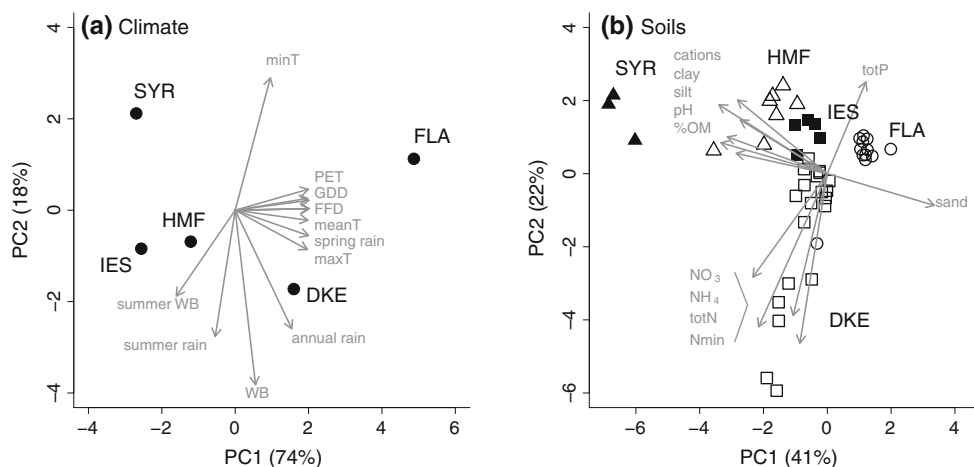
were calculated as for the height model. This approach was repeated for survivorship data for each species separately, with reported coefficients for  $AIC_c$ -determined best-fit models. All analyses were performed in R version 2.10.0 (R Development Core Team 2010).

## Results

### Variation of soils and climate across sites

Variables related to site temperature regime explained 74% of the total variation in climate variables across sites, with PC1 site scores closely related to latitude (Fig. 1a). A secondary climate axis explaining 18% of the total variation reflected differences in site water balance, including annual rainfall, but also involved winter minimum temperatures (Fig. 1a). Remaining PC axes explained only 8% of the total variation in climate parameters among sites (Table S2, ESM).

The primary axis of edaphic variation among sites was related to soil texture, cation concentration, and organic matter, explaining 41% of the total variation in soil characteristics (Fig. 1b). Organic matter, pH, and cation availability were highest at the northernmost SYR site, with the other four sites following out rough order of latitude as soil particle size increased to the southernmost FLA site. A secondary axis, explaining 22% of total soil variation, involved opposing gradients of soil N and P within soil samples of only one site, DKE (Fig. 1b). PC axes 3–5 explained 13, 9, and 6% of total soil variation across samples, respectively (Table S3, ESM). The Pearson



**Fig. 1** Principal component biplots of **a** 14 climate variables and **b** 13 soil variables measured across five experimental locations (*black labels*, abbreviations follow Table 1). Axis labels include the total variance explained by the first two components. Climate variables were estimated at the site level and soil variables were measured in 3–5 locations for the northern sites (*filled triangles* SYR, *filled*

*squares* IES, *open triangles* HMF) and 12 (FLA, *open circles*) and 20 (DKE, *open squares*) locations for the southern sites. Climate variables shown include min, max, and mean annual temperature, annual and seasonal water balance (WB) and precipitation, growing degree-days (GDD), frost-free days (FFD), and potential evapotranspiration (PET). Soil variables are described in the text

**Table 2** Model comparison results for seedling height and survivorship in response to site climate regime (climate PC axis 1; *CLIM*), soil regime (soils PC axis 1, *SOIL*), and a categorical variable for northern or southern species group (*SPP*)

Model	<i>k</i>	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	<i>w</i>	<i>R</i> <sup>2</sup>
<b>Seedling height</b>					
CLIM + SOIL + CLIM:SOIL	6	75.31	0.00	0.82	0.24
CLIM + SOIL + SPP + CLIM:SOIL + CLIM:SPP + SOIL:SPP + CLIM:SOIL:SPP	10	80.48	5.16	0.06	0.26
SOIL	4	81.30	5.99	0.04	0.25
SOIL + SPP + SOIL:SPP	6	82.64	7.32	0.02	0.26
CLIM	4	83.12	7.81	0.02	0.25
CLIM + SOIL	5	83.16	7.85	0.02	0.25
CLIM + SOIL + SPP + SOIL:SPP	7	84.62	9.31	0.01	0.26
CLIM + SPP + CLIM:SPP	6	85.25	9.94	0.01	0.26
CLIM + SOIL + SPP + CLIM:SPP	7	85.35	10.04	0.01	0.26
<b>Seedling survival</b>					
CLIM + SOIL + SPP + CLIM:SOIL + CLIM:SPP + SOIL:SPP + CLIM:SOIL:SPP	9	838.96	0.00	1.00	0.44
CLIM + SPP + CLIM:SPP	5	857.92	18.96	0.00	0.43
SOIL + SPP + SOIL:SPP	5	871.73	32.76	0.00	0.44
CLIM + SOIL + CLIM:SOIL	5	923.99	85.02	0.00	0.40
CLIM + SOIL	4	928.42	89.46	0.00	0.40
CLIM	3	934.42	95.45	0.00	0.40
SPP	3	935.63	96.67	0.00	0.40
SOIL	3	935.76	96.79	0.00	0.40
SPP + CLIM	4	936.15	97.18	0.00	0.40
SPP + SOIL	4	937.54	98.57	0.00	0.40

Seedling height data were modeled as residuals from a species-only model; the species pool term is for addressing interactions only. Survivorship data were modeled with binomial error. All models include an overall intercept and random site effect

*k* number of estimated parameters, *AIC<sub>c</sub>* small-sample Akaike Information Criterion, Δ*AIC<sub>c</sub>* differences of *AIC<sub>c</sub>* from the best model, *w* Akaike weight indicating the weight of evidence in favor of the best model compared to the rest, *R*<sup>2</sup> explained deviance

correlation of primary climate and soil PCA axes across sites was  $r = 0.69$ .

#### Seedling growth responses to climate and soils

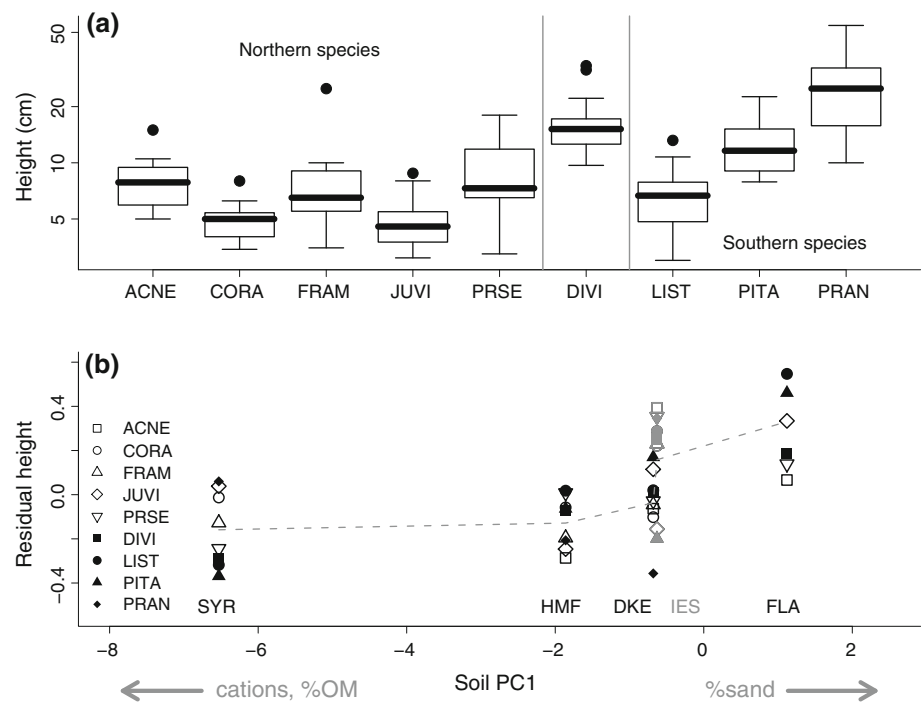
Height differences between species explained 67% of the overall variance in seedling height across all plots and sites (Fig. 2; ANOVA species effect  $F = 29.0$  on 8,153 degrees of freedom (DF),  $P < 0.001$ ). Northern species had generally slower growth rates than southern species (Fig. 2); ‘species pool’ was a significant predictor of heights in a simple one-way ANOVA ( $F = 76.8$  on 1,160 DF,  $P < 0.001$ ; with *D. virginiana* in the northern category,  $F = 22.7$ ,  $P < 0.001$ ). Residual variation in seedling height across sites was influenced by both soil and climate factors and their interaction, as supported by *AIC<sub>c</sub>* values of the full model compared to other candidate models (Akaike weight of 0.82, Table 2). Standardized coefficients of the soil and climate axes indicated the primary soil axis has a stronger influence on seedling height than climate regime (Table 3). Seedlings on soils more typical of the south grew faster than those on more fertile northern soils,

and this did not vary with species group (Fig. 2). There was also a small but significant interaction of climate and soil; seedlings in warmer (more positive climate PCA axis 1) sites on southern soil types grew faster. The soil effect was nonlinear, however, due to the significantly higher growth responses of all species at the FLA site (Fig. 2), which was both the warmest site and had the poorest soils.

#### Variation in height response to soils and climate across species

Species varied widely in their growth responses to the major axes of variation in site climate and soils (Table 4). Best-fit models assessed separately by species indicated that three of the nine species were responsive to the major temperature-based climate gradient, with the two conifers (*J. virginiana* and *P. taeda*) growing significantly faster in the warmer sites, and *P. angustifolia* growing faster in cooler sites. Four species were responsive to the main soil gradient, including the southern *P. taeda* and three broad-leaved species more common to southern old fields (*D. virginiana*, *L. styraciflua*, *P. angustifolia*). In each of these

**Fig. 2** Seedling height at the beginning of the second growing season, **a** summarized by species and **b** by the principal axis of soil variation between sites after removing main species effects. Boxplots in **a** delimit inner and outer quartiles with median as *thick horizontal line* and outliers as *points* (mean  $N = 18$ ); species are listed by region and abbreviations follow Table 3 (*Diospyros* is common to mid-latitudes). In **b** values are mean residuals of each species per site after accounting for species effects, see text for details. *X-axis values* are mean site values shown in Fig. 1. The *dashed line* connects mean residual values for each site



**Table 3** Fitted coefficients for best-fit models for overall seedling height and survivorship listed in Table 2

Seedling height	Coefficient	SE	<i>t</i>	Std coefficient
(Intercept)	0.102	0.032	3.136	−0.160
Climate	−0.022	0.014	−1.585	−0.237
Soils	0.145	0.026	5.650	0.350
Climate × soils	0.034	0.008	4.623	0.234
Seedling survival	Coefficient	SE	<i>z</i>	Std coefficient
(Intercept)	−0.636	0.180	−3.534	0.797
Species pool	0.172	0.186	0.922	0.287
Climate	0.424	0.076	5.547	1.604
Soils	−0.873	0.147	−5.947	−2.110
Climate × species pool	0.392	0.079	4.939	1.515
Soils × species pool	−0.138	0.149	−0.925	−0.285
Climate × soils	−0.099	0.044	−2.278	−0.655
Climate × soils × species pool	−0.098	0.041	−2.423	−0.650

Standardized coefficients reported in the last column are those fitted with standardized climate and soil variables (zero mean, unit variance)

cases growth was faster on poorer soils (those of lower organic matter and cation availability). For *P. angustifolia*, the soil response was enhanced in the warmer sites, as indicated by a significant climate–soil interaction (Table 4). The growth of four species (*A. negundo*, *C. racemosa*, *F. americana*, *P. serotina*) was not responsive to overall climate and soil differences, although all of these species except *P. serotina* had relatively small sample sizes (<100 germinants).

#### Seedling survivorship across sites and species

Seedling survival across sites was strongly species dependent (Fig. 3). An overall model of survivorship with respect to the major climate and soil axes, species pool, and their interactions, explained about half of the total variation in survival and included a significant three-way interaction; this maximal model was overwhelmingly supported by AIC<sub>c</sub> analysis (Table 2). As for seedling height responses,

**Table 4** Parameter estimates (with standard errors, SE) for seedling height and survivorship models analyzed at the species level

Species	Code	Region	Germinants	Seedling height model				Seedling survival model			
				Climate	Soils	Climate × soils	R <sup>2</sup>	Climate	Soils	Climate × soils	R <sup>2</sup>
<i>Acer negundo</i>	ACNE	N	72				–				–
<i>Cornus racemosa</i>	CORA	N	52				–	–1.073 (0.935)			0.48
<i>Fraxinus americana</i>	FRAM	N	46				–				
<i>Juniperus virginiana</i>	JUVI	N	486	0.057 (0.020)			0.64	0.279 (0.229)	–0.694 (0.470)		0.41
<i>Prunus serotina</i>	PRSE	N	238				–	0.580 (0.290)	–0.528 (0.290)		0.33
<i>Diospyros virginiana</i>	DIVI	N/S	227		0.063 (0.0169)		0.39				–
<i>Liquidambar styraciflua</i>	LIST	S	227		0.086 (0.017)		0.53	0.336 (0.200)			0.28
<i>Pinus taeda</i>	PITA	S	456	0.081 (0.011)	0.029 (0.012)		0.92	0.500 (0.274)			0.57
<i>Prunus angustifolia</i>	PRAN	S	327	–0.090 (0.046)	0.350 (0.080)	0.112 (0.023)	0.53	1.074 (0.390)	–2.115 (1.043)		0.90

Region describes whether the species is most common in old field succession in the Northeast or Southeast USA, followed by total number of germinants observed across sites for each species. Single-species height model coefficients for site climate regime (climate PC axis 1), soil regime (soils PC axis 1), and their interaction are listed along with explained deviance (R<sup>2</sup>). Only coefficients from best-fit models (assessed via AIC<sub>c</sub>) are listed. Seedling survival models include the same predictor variables in a binomial GLM

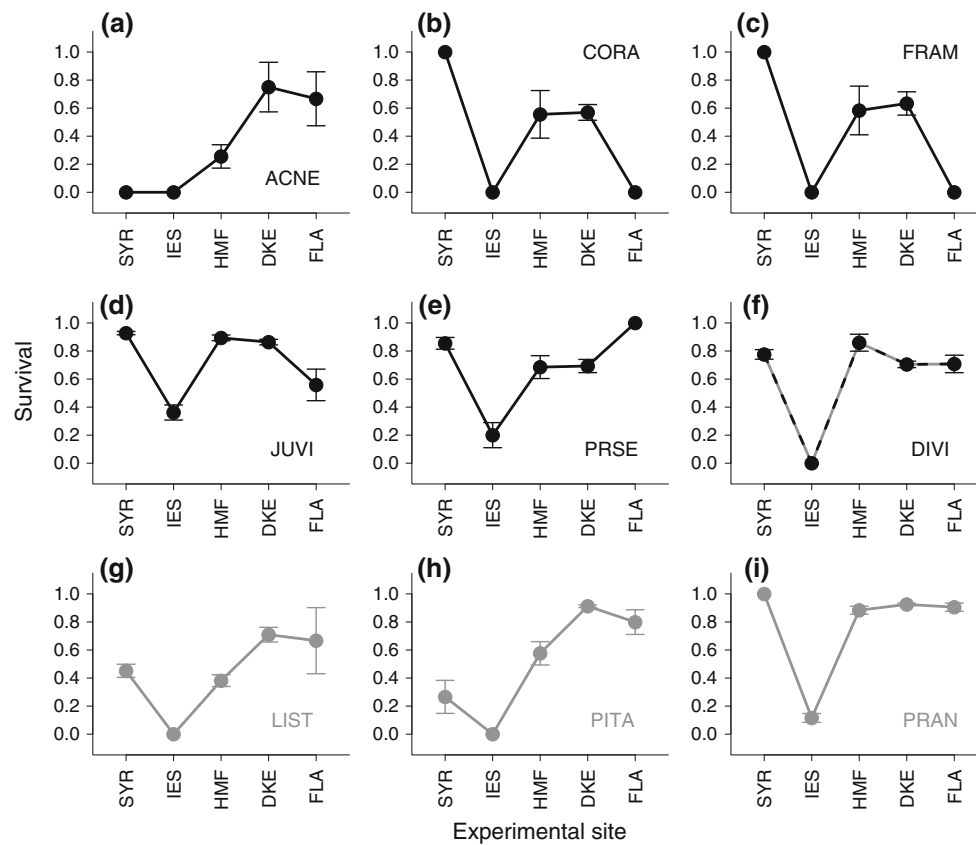
soil variation between sites was more influential on survivorship than climate regime (Table 3). Survivorship of five of the nine species significantly increased in sites of warmer climates (Table 4), but three of these plus *C. racemosa* responded positively to the finer textured soils (Table 4), an effect driven largely by high survival at the most fertile SYR site (Fig. 3). In contrast, seedling survivorship was uniformly low at the northern IES site. Latitudinal patterns in survivorship were only apparent for three species (one northern species, *A. negundo*, and two southern species, *L. styraciflua* and *P. taeda*), all of which had higher survival in southern sites (Fig. 3).

**Discussion**

Our experiment was designed to test three non-exclusive hypotheses underlying the described latitudinal gradient in secondary succession rates across the Eastern USA (Wright and Fridley 2010). By growing a common set of ‘northern’ and ‘southern’ pioneer woody species at five sites of highly variable soil texture, cation content, and organic matter across the climatic gradient of the EDF, we were able to assess the contribution of (1) species identity, (2) climate, and (3) soil properties to the first-year recruitment potential of woody seedlings invading recently tilled old fields. Although our inferences are limited to the earliest stage of

woody invasion and climate and soil effects could not be attributed to specific mechanisms, results of our study point toward species identity (growth rates of southern species) as a key driver of regional differences in the rate of woody establishment in old fields, and soil properties as a potentially more significant driver of woody establishment than mechanisms directly associated with climate.

Our species pool hypothesis, wherein rates of establishment of southern woody pioneers are faster due to their inherently faster growth rate, was generally supported by our study. About two-thirds of the variance in 1-year seedling heights across sites was explained by species identity, and the three fastest growing species (*D. virginiana*, *P. taeda*, and *P. angustifolia*) are endemic to the southeastern USA where woody colonization rates are the highest (Wright and Fridley 2010). Only *L. styraciflua* from the Southeast exhibited a mean growth rate as low as the five northern species, and this species is more typically old-field dominant in waterlogged soils; it is likely that mid-summer water deficits slowed the growth of *L. styraciflua* to a greater extent than the other southern species, all of which tolerate dry conditions (Radford et al. 1964). A fast seedling growth rate is a key component of woody invasion of recently abandoned fields because the more competitive and light-usurping perennial herbaceous community takes several years to establish (Oosting 1942); fields dominated by annual forbs in the first years post-abandonment are less



**Fig. 3** Seedling survival (mean proportion of germinants alive in the spring of the second season,  $\pm$ SE) across experimental sites listed from north to south for the nine focal species. Species in **g–i** are from

the southern successional group; *Diospyros* (DIVI) is intermediate. Species abbreviation is given in Table 4

able to competitively exclude woody recruits (Bazzaz 1968). Seedling growth rate of northern species may be slowed by the need to allocate carbohydrates to frost resistance mechanisms at the cost of greater investment in carbon gain (Loehle 1998).

Our results were generally not consistent with our climate hypothesis, in which the performance of both northern and southern species is enhanced in warmer climates, regardless of soil properties. Only two species—the conifers *P. taeda* and *J. virginiana*—exhibited positive growth responses to warmer climates, and these species dominate in old fields in different regions. Seedling survivorship was high for most species at the southern sites, but it was also high for the most northern site (Syracuse) with the exception of *A. negundo*, a species that is common in northern old fields (Wright and Fridley 2010), and two southern species (*L. styraciflua*, *P. taeda*) that nevertheless produced many robust seedlings by the start of the second growing season. It is possible that survival of southern species at the Syracuse site was facilitated by the consistent winter snow pack that prevents mortality due to frost damage or desiccation, despite the complete mortality of *A. negundo* seedlings from unknown causes. The very low

survival for all species at the climatologically similar IES site in Dutchess County, NY, USA is likely not directly driven by climate but competition from a robust herbaceous community; the strong IES signal likely drove most of the main climate effects in species-level models.

Our soils hypothesis encompasses both the direct effects of soil fertility on the growth rate and survival of woody seedlings in competition with more nutrient-demanding herbs (Sterner and Elser 2002), and the potential for high soil fertility to promote a particular herbaceous community that has growth characteristics associated with greater competitive abilities (Grime 2001). Secondary succession studies conducted across the EDF show a clear contrast of seral herbaceous communities across regions: in the Northeast, rapid colonization by clonal, fast-growing herbs such as *Solidago altissima* is typical except on very coarse soils, whereas southern old fields are more typically dominated by perennial bunchgrasses such as *Andropogon virginicus* (Wright and Fridley 2010), a species widely believed to be tolerant of drought and nutrient stress (Bazzaz 1968). At the same time, soils of lower C to nutrient ratios may stoichiometrically favor herbs in competition with woody seedlings of higher tissue C to nutrient



ratios (Larcher 2001; Sterner and Elser 2002; Graves et al. 2006); furthermore, the greater evaporative demands and lower water retention capacity of coarser southern soils may limit the apical growth of species with herbaceous stems via turgor loss. Although our experiment was not designed to differentiate between direct effects of soil properties on seedling growth versus indirect effects of herbaceous competitors, we were able to compare the effects of a general axis of site fertility to that of climate, and soils were a stronger predictor of seedling performance. Because seedling growth rates were highest in the sites of lowest fertility, we infer that the mechanism relates to competition between seedlings and the herbaceous community. It is not obvious why higher growth rates did not translate to higher seedling survivorship rates in low fertility sites, as coefficients for overall and species-level models indicated opposing effects of soil properties on growth and survivorship. It may be that smaller seedlings were less prone to death by water stress, particularly if they were protected in part by a more established herbaceous layer. Manipulations of the herbaceous layer across soil fertility levels are necessary to resolve the role that herbs play in regulating the latitudinal gradient of woody succession (Wright and Fridley 2010).

Although our inferences are limited to the first year of woody establishment, it is notable that climate only played a secondary role in driving seedling growth and survivorship patterns, after the primary influences of species identity and soil properties. Several species performed well despite being outside their current climate distribution, beyond both northern and southern range boundaries. Although climate, and particularly winter minimum temperatures, has likely been a key selective factor on the growth physiology of woody pioneer species (Loehle 1998), ecological factors including competition between growth forms may play a stronger role in the continual redevelopment of communities from fields to forest across mesic temperate biomes in light of global change.

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