

# Estimating colonization potential of migrant tree species

INÉS IBÁÑEZ\*<sup>1</sup>, JAMES S. CLARK\*<sup>†‡</sup> and MICHAEL C. DIETZE\*<sup>2</sup>

\*University Program in Ecology, Duke University, Durham, NC 27708-90338, USA, †Nicholas School of the Environment, Duke University, Durham, NC 27708-90338, USA, ‡Department of Biology, Duke University, Durham, NC 27708-90338, USA

## Abstract

Plant populations migrating in response to climate change will have to colonize established communities. Even if a population disperses to a new region with a favorable climate, interactions with other species may prevent its establishment and further spread. The potential of these species to grow along with residents will be a critical factor controlling their response to climate change. To determine the capacity of migrating species to colonize established communities we conducted extensive long-term transplant experiments where potential tree migrant species, i.e. species within 'migration range,' were planted side by side with resident ones. Potential immigrants were selected to be representative species of their native communities. For both groups, residents and potential migrants (17 species), we compared their growth response along gradients in soil moisture and light availability. Rather than manipulate climate directly, we exploited natural microclimatic gradients and the fluctuations in climate that occurred during the 5-year experiment. Experimental results were used to estimate growth in the context of novel climate and relevant establishment factors. Results suggest that potential immigrant species had similar growth rates in the new environment than those from resident species ensuring their ability to establish in the area. However, contrary to our expectations, the soil moisture requirements for the immigrant group were similar to those of the resident species. These results could have major implications for vegetation changes under the predicted drier climate for the region. If it is the case that neither resident species nor potential migrants are able to maintain stable populations, the region may experience a decline in local biodiversity.

*Keywords:* climate change, colonization, environmental gradients, growth, hierarchical Bayes, migratory potential, seedlings, transplant, vegetation shifts

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## Introduction

Current trends in climate change are altering growing conditions for plants around the world (Watson *et al.*, 1998). In the past, plant species survived climate change through migration and adaptation (Davis & Shaw, 2001). The migratory potential of a species relied on its dispersal capabilities and on its ability to establish in the new site. If migrating populations are to track

contemporary climate change, they will often have to colonize established communities. A species' potential to colonize a new region (colonization potential) will inevitably depend on its performance relative to resident species. Although the potential to compete with residents is an important concern in the case of invasive species and has been thoroughly studied (e.g. Reinhart *et al.*, 2006), it has been overlooked as a factor controlling the capacity of native species to migrate in response to climate change (although see Prentice *et al.*, 1993; Badeck *et al.*, 2001). Studies of the latter focus on dispersal potential (will the species get there) and on climate envelopes (performance without regard to the novel set of competitors). For many species and settings, these factors could be overwhelmed by species interactions. Limited guidance comes from studies in

Correspondence: Inés Ibáñez, tel. +1 734 615 8817, fax +1 734 763 8965, e-mail: iibanez@umich.edu

<sup>1</sup>Present address: School of Natural Resources and the Environment, University of Michigan, Ann Arbor, MI 48109-1041, USA.

<sup>2</sup>Present address: Department of Plant Biology, University of Illinois, Urbana, Champaign, IL 61801, USA.

the native environment due to the differing set of interactions and abiotic conditions that prevail there. More relevant will be studies of performance relative to residents at new sites.

Although the current 'climate envelope' approach to exploring future vegetation (e.g. Fleishman *et al.*, 2001; Lasch *et al.*, 2002) provides some insight, some of the predictions could be incorrect or misleading. This method for predicting species response to climate change involves drawing an 'envelope' around the domain of climate variables where a species is found today, and then identifying regions predicted to fall within that domain under scenarios for the future. Changes in species abundances are also projected on the basis of their tolerance of the predicted climate (Iverson *et al.*, 2008). This approach does not take into consideration the fact that, even if the climate is suitable, the local community may impact establishment. These limitations are well known (see review Ibáñez *et al.*, 2006), but there have been no efforts to address them experimentally by examining establishment success in the context of novel climates, establishment factors, and new environments.

We apply an alternative method for understanding consequences of climate change, based on experimental manipulation of relevant competitive environments, climate settings, and regeneration niches. Our design stems from several well-established relationships and several assumptions (i) that canopy gaps are foci for recruitment in most forests (e.g. Runkle, 1981; Canham *et al.*, 1990; Busing & White, 1997) and, thus, must be part of the design; (ii) that future potential immigrants will be drawn from regions currently warmer (perhaps more arid) than today; and (iii) the metric for migratory potential has to be establishment success and growth relative to residents. This third assumption is based on the fact that potential immigrants must compete for resources with the local community.

Our experimental approach was designed to determine whether potential immigrants could meet or exceed growth rates of resident species along the light and soil moisture gradients that control recruitment. We conducted a long-term transplant experiment, where immigrants and residents were grown side by side. We analyzed growth with respect to key resources based on natural gradients of soil moisture and manipulation of light in experimental canopy gaps. We hypothesized (i) that resident species would be better adapted to the local environment and, as a consequence, would have higher growth rates than potential immigrants; (ii) and that potential immigrants from more xeric regions would be more tolerant to dry conditions than native species.

## Methods

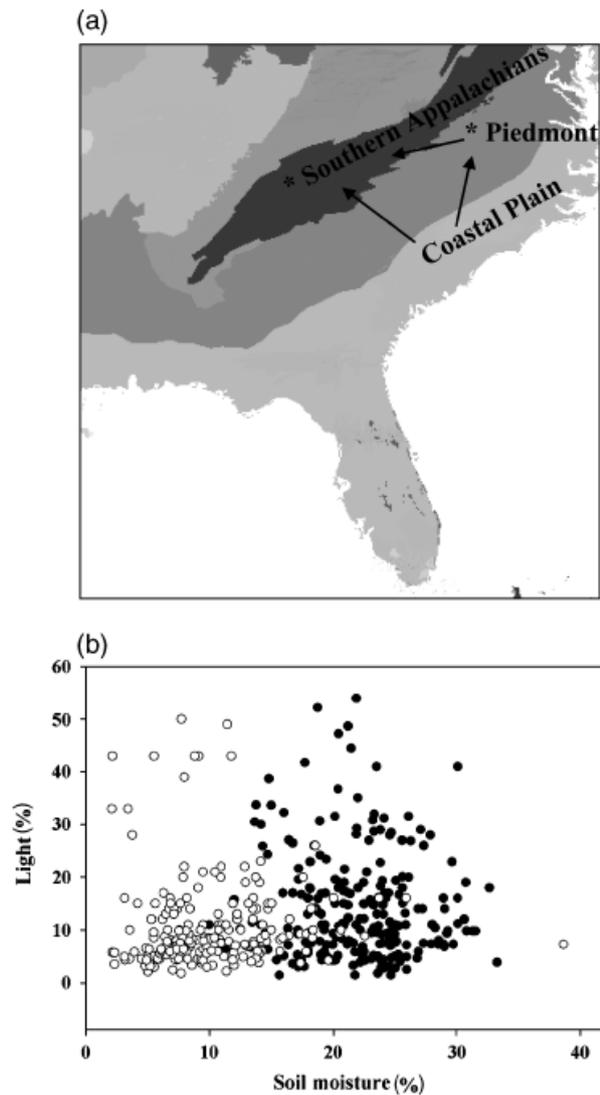
### *Rationale*

For this study, we embraced the heterogeneity inherent in the landscape and took advantage of the environmental gradients found in nature. We planted seedlings in a series of small plots spread along a diverse landscape in two regions, the North Carolina Piedmont and the Southern Appalachians. We implemented an intervention design where we created canopy openings mimicking the local disturbance regime (i.e. hurricanes) [canopy trees were pulled down with a skidder and left in place, Dietze & Clark (2008)]. Seedlings of the studied species were then planted along the canopy–canopy gap interface. Model-based inference on seedling growth was then performed on the basis of individual seedlings response to the environmental conditions they were exposed to, and from here, we estimated the overall response of the species to those environmental gradients. This type of analysis allowed us to make inference on the potential changes in the species' growth rates under the region's forecasted drier climate while they were still exposed to the full array of conditions characteristic of the sites.

### *Field sites*

For this transplant experiment, we selected two regions of contrasting climate and soils, both with a range of natural conditions, supplemented by intervention (Fig. 1a). The Piedmont study site was located within the Blackwood division of Duke Forest, a thorough description of which can be obtained at <http://www.env.duke.edu/forest>. The Southern Appalachians location was at the Coweeta Long Term Ecological Research site, site information is available at <http://coweeta.ecology.uga.edu>. Plot locations were chosen to sample the dominant edaphic gradients in each region. At the Piedmont site, plots were selected to include several types of soils (Table 1, Fig. 1b) and expanded within a 30 ha area (Fig. 2). Soils in this region are characterized by low organic matter content and with medium to low permeability. Besides having different water holding capacities, the major distinction among soils comes from the shrink–swell potential of their clays, which ranges from low to very high (Orange County, NC Soil Survey, 1977). These differences affect plant growth because high shrink–swell potential soils provide a very hostile environment for roots. In the Southern Appalachians, plots were selected at several elevations (from 685 to 1500 m) and exposures (N–NE vs. S–SW) covering a wide range of environmental conditions (Table 1, Figs 1b and 2).

Plots were established in both locations in 2001, some designated to remain with intact canopy and others



**Fig. 1** (a) Studied locations and surrounding regions. Arrows indicate the routes of potential migration. The Southern Appalachians are dominated by oaks and northern hardwoods. In the Piedmont, successional pine and hardwood forest are the norm. And in the Coastal Plain, long leaf pine and evergreen oaks are the most common forest communities. (b) Environmental conditions sampled at each of the planting sites. Open circles indicate plots in the Piedmont, dark circles indicate plots in the Southern Appalachians.

within experimental canopy gaps. The experimental gaps were created in March 2002 with a total of four 40 m diameter (large) and four 20 m diameter (small) gaps at the Piedmont site, and six large and four small gaps at the Southern Appalachians (Fig. 2). Experimental gaps at the Piedmont site were over soils with high and low shrink–swell potential. At the Southern Appalachians site, experimental gaps were located at two elevations, 1030 and 1140 m. In 2003, four plots at the Piedmont site and eight in the Southern Appalachians

were added to increase sample sizes. We had a total of 121 plots, 5 × 5 m in size, 51 in the Southern Appalachians, and 70 in the Piedmont (Table 1).

#### *Planted species and growth measurements*

Given the geographic characteristics of our studied regions and their current and forecasted climates (Mearns *et al.*, 2003), we considered likely sources of potential immigrant species to be in the Coastal Plain and the Piedmont, respectively (Fig. 1a). This would represent a shift from low to higher latitude and from low to higher elevation. We selected the resident species (Table 2) according to their abundance in the studied sites; all were dominant species. Migrant species (Table 2) were chosen on the basis of their potential to colonize these sites, that is they are common in surrounding regions (the Coastal Plain and the Piedmont), and most are projected to increase in abundance in our study sites under 2 × carbon dioxide (CO<sub>2</sub>) scenarios of climate change (e.g. Iversen *et al.*, 2008). We avoided selecting species with very specific requirements (e.g. fire dependent or wetland species) and focused on representative functional groups, including pioneer, mid-successional, late successional. However, we are aware that their roles may shift under different environments. The Piedmont site included three potential immigrant species and the Southern Appalachians seven (Table 2).

Seeds were germinated and grown in the greenhouse for 6 weeks and then transplanted into the field early in the summer (late June). Five individuals of each species were planted in each plot in rows 25 cm apart, seedlings were also 25 cm apart within a row. We repeated the transplants (five additional individuals were planted each year) during four consecutive years, 2001–2004, totaling more than 13 000 seedlings by the end of the fourth year (Table 2). Before planting, seedling height and diameter at the base were measured. After planting, growth measurements were done in the field at the end of each growing season (late August). Height and diameter measurements were highly correlated among species ( $r$ : 0.98–0.95). In the case of diameter, measurement errors were of the same magnitude than the yearly diameter increments (not shown), as a consequence, we decided not to incorporate diameter measurements in our analyses and use height data only.

#### *Soil moisture and light data*

Soil water content (% soil moisture) was measured for the top 15 cm of soil at nearby locations around the plots (within a 5 m range) using a time domain reflectometer cable tester (Tektronic 1502B; Tektronix, Beaverton, OR, USA). We took measurements every other week during

**Table 1** Distribution of the experimental plots and site characteristics

Southern Appalachians			
Elevation (m)	Total no. of plots	Exposure N-NE	S-SW
1500	2	1 (canopy)	1 (canopy)
1170	2	1 (canopy)	1 (canopy)
1140	17	9 (5 canopy, 4 gap)	8 (4 canopy, 4 gap)
1030	25	18 (9 canopy, 9 gap)	7 (4 canopy, 3 gap)
685	2	Flat (canopy)	Flat (canopy)
Piedmont			
Soil type	No. of plots	Classification and description	
Herdon	17 (9 canopy, 8 gap)	Order: Ultisols, Suborder: Udults Organic matter: low, Permeability: moderate Available water capacity: medium Shrink swelling potential: low	
Enon	50 (25 canopy, 25 gap)	Order: Alfisols, Suborder: Udalfs Organic matter: low, Permeability: low Available water capacity: medium Shrink swelling potential: high	
Iridell	3 (canopy)	Order: Alfisols, Suborder: Udalfs Organic matter: very low, Permeability: low Available water capacity: low Shrink swelling potential: very high	

the growing season. The values used in the analysis are plots' annual means.

We estimated the proportion of full sunlight (% light) penetrating the forest canopy, from canopy hemispherical photos (Rich *et al.*, 1993; M. Dietze, unpublished results). These photos were taken in July within a 5 m range from each seedling. Hemispherical photographs were taken at 1.15 m above the ground using a Nikon F2 camera (Melville, NY, USA) with a Sigma (Ronkonkoma, NY, USA) 8 mm 180° fish-eye lens. From these photographs, the proportion of full sunlight reaching the forest floor, the global site factor (GSF), was calculated using the software package HEMIVIEW (Delta-T Devices, Cambridge, UK). The range of variation (~6%), summarized by lower and upper limits in Eqn (13) below, was derived from light values from repeated photos taken at the same time at selected locations. For eight plots in the Southern Appalachians and for four plots at the Piedmont site, light measurements were taken using a light sensor (LI-200 Pyranometer; LI-COR Inc., Lincoln, NE, USA) that measures photosynthetic active radiation (PAR). These measurements were approximated to those from the canopy photos using the following equation:

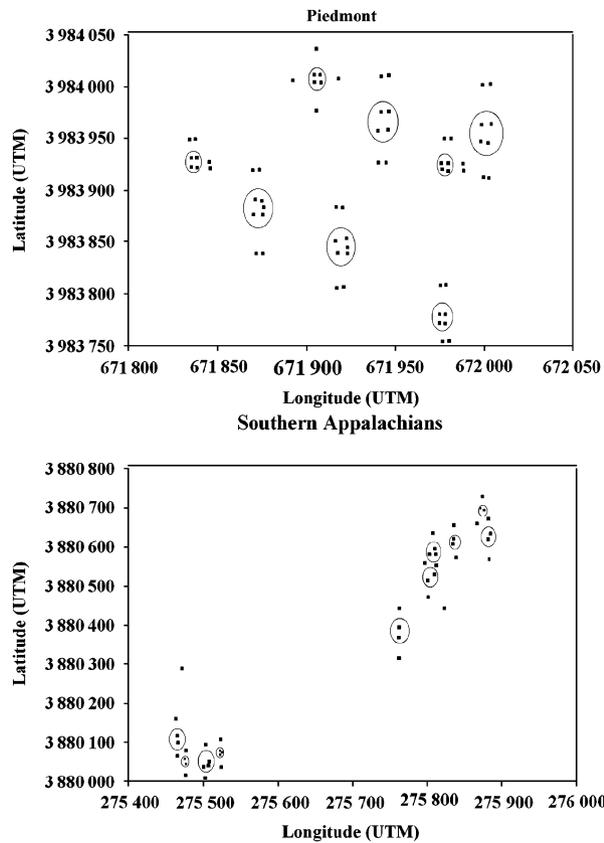
$$\% \text{ full light} = 0.088 \text{ PAR} + 6.11 (R^2 : 0.35).$$

This equation was formulated from combined light data, canopy photos and PAR sensor measurements,

taken at the same time in a series of sample locations. Because of the variability associated to the light data (in particular the measurements taken with the second method), we did not incorporate these values directly into our analyses. Instead we treated light as a latent variable that had to be estimated as part of the overall model (see 'Light model') (Berkson, 1950; Clark *et al.*, 2003).

#### *Model of seedling growth*

As stated above, the analysis of our data was performed at the individual seedling level. Instead of comparing the plots' mean responses with varying resources (ANOVA) we assessed individual seedling performance to a gradient of environmental variables. We then estimated the overall response, and its variability, of each species to varying conditions. The strength of this analysis resides on the fact that once we obtained such information, we were able to make inferences on how these species may respond to future climate scenarios. The environmental gradients sampled in this study (e.g. soil moisture) included those climate scenarios predicted for this region for the next few decades (Mearns *et al.*, 2003; Christensen *et al.*, 2007, Fig. 1b), our measurements of soil moisture included soil water content values below 5%. Therefore, these predictions of plant's



**Fig. 2** Experimental setup at each of our two study sites (shown at different scales). Circles indicate the location of the gaps and squares point at the location of the plots. Four plots at the Piedmont site and six in the Southern Appalachians fall outside the area represented in the graphs.

performance under a future climate were generated for plants still exposed to the whole set of other environmental conditions intrinsic to our sites (e.g. type of soils, herbivores, pathogens), that is we accounted for the overall environmental conditions (e.g. climate and site characteristics, plants would be exposed to). We believe this approach makes our forecasts more reliable than the traditional correlative approaches (e.g. climate envelopes).

Growth, the annual increment ( $\text{cm yr}^{-1}$ ) on seedling height in plot  $p$  for seedling  $i$  at year  $t$ , was defined as the difference in height ( $h$ , cm) between year  $t$  and year  $t-1$

$$H_{pit} = h_{pit} - h_{pit-1}.$$

We modeled growth as a saturating function of light ( $L$ ) and soil moisture content ( $M$ ) (Fig. 3), a well-established approach for this type of analysis (Pacala *et al.*, 1994; Clark *et al.*, 2003; Kobe, 2006; Mohan *et al.*, 2007). Because we did not find an effect of extreme temperatures on seedling survival in previous analyses

of the data (Ibáñez *et al.*, 2008), we opted to exclude it from the growth analyses as temperature would have mainly affected growth through soil water availability, and we directly measured that. We explored several variations of growth models (Table 3). All the models assume a positive response in growth to increasing resource levels. Submodels A and B include the additive response to light and soil moisture, and the addition of a plot random effect in B differentiates between the two models. The other three submodels combine the effect of the two resources. In submodel C, the parameter,  $g$ , the maximum growth rate, is fixed. For the other two models, D and E, there is a random individual effect  $g_i$ . Submodels D and E differ in that E has an autoregressive, AR(1), error term, to allow for possibility that growth rates are correlated from year to year, beyond annual differences taken up in fixed effects.

Plant size at the time of planting and plant age were variables included in previous analyses of seedling survival (Ibáñez *et al.*, 2008) and on preliminary analyses of seedling growth (not shown). For these two variables, results did not show a significant effect on survival or growth, and as a consequence, we opted for excluding them from the growth analyses.

We provide additional detail for submodel D, which best described the data (see ‘Model selection, predicted growth, and random effects’ for more detail). In this submodel, the response curve is defined by five parameters (Fig. 3): the asymptote  $g$ , the minimum resource requirements for growth ( $l_0$  and  $m_0$ ), and the half saturation constants ( $\theta_L$  and  $\theta_M$ ). The asymptote represents the maximum growth rate, having a random effect for individuals,  $g_i$ , with mean  $\mu$ , which is explicit for each species. This hierarchical framework admits uncertainty at several stages increasing the flexibility of the model (Lavine *et al.*, 2002; Clark, 2005). Height increment ( $H_{pit}$ ) for seedling  $i$ , in plot  $p$  in year  $t$ , is a function of its maximum growth rate,  $g_{pi}$ , a combination of the light  $L_{pt}$  and soil  $M_{pt}$  effects, and Gaussian error,  $\varepsilon_{pit}$

$$H_{pit} = g_{pi}L_{pt}M_{pt} + \varepsilon_{pit}, \tag{1}$$

$$\varepsilon_{pit} \sim \text{Normal}(0, \tau^{-1}), \quad \tau \sim \text{Gamma}(1.25, 5). \tag{2}$$

The likelihood is:

$$P(H_{pit}) = \prod_{p=1}^P \prod_{i=1}^{N_p} \prod_{t=1}^{t_n} \text{Normal}(H_{pit} | g_{pi}L_{pt}M_{pt}, \tau^{-1}). \tag{3}$$

Random effects on  $g$ , the maximum growth rate for each plant, were lognormal (growth can only be positive), with a gamma precision

**Table 2** Species planted (native or potential migrant), years, locations, seedling light and soil moisture requirements\*, and growth rates\*

Species	Piedmont		Southern Appalachians	
	Native	Potential migrant	Native	Potential migrant
<i>Acer barbatum</i> (Acba) N: 109 ID Light: shade intolerant Soils: moist well drained Growth: moderate to fast				2002, 2004
<i>Acer rubrum</i> (Acru) N: 556 ID Light: shade intolerant Soils: moist Growth: moderate to fast	2002, 2003, 2004		2002, 2004	
<i>Acer saccharum</i> (Acsa) N: 270 ID Light: very shade tolerant Soils: moist well drained Growth: slow	2004		2001, 2004	
<i>Carya glabra</i> (Cagl) N: 432 D Light: sun to partial shade Soils: tolerant to dry soils Growth: slow	2001, 2002, 2003, 2004		2002	
<i>Carya illinoensis</i> (Cail) N: 228 D Light: shade tolerant Soils: well-drained Growth: rapid		2002		2003, 2004
<i>Fagus grandifolia</i> (Fagr) N: 287 D Light: shade tolerant Soils: moist well drained Growth: slow	2001, 2003		2001	
<i>Liquidambar styraciflua</i> (List) N: 723 ID Light: sun to partial shade Soils: drought intolerant Growth: moderate to rapid	2001			2001, 2002, 2003, 2004
<i>Liriodendron tulipifera</i> (Litu) N: 683 ID Light: shade intolerant Soils: drought intolerant Growth: rapid	2001		2001, 2002, 2003, 2004	
<i>Magnolia grandiflora</i> (Magr) N: 112 ID Light: sun to partial shade Soils: well-drained Growth: slow to moderate		2002, 2004		2004
<i>Pinus rigida</i> (Piri) N: 353 D Light: shade intolerant Soils: drought intolerant Growth: moderate			2001, 2003	
<i>Pinus taeda</i> (Pita) N: 1268 ID Light: sun to partial shade Soils: drought intolerant Growth: rapid	2001, 2002			2001, 2002, 2003, 2004
<i>Quercus alba</i> (Qual) N: 257 D Light: sun Soils: drought tolerant Growth: moderate	2002, 2004		2002	
<i>Quercus falcata</i> (Qufa) N: 677 D Light: sun	2001, 2003			2001, 2004

*Continued*

Table 2. (Contd.)

Species	Piedmont		Southern Appalachians	
	Native	Potential migrant	Native	Potential migrant
Soils: tolerates poor dry soils Growth: moderate				
<i>Quercus phellos</i> (Quph) N: 1020 D Light: tolerant to shade Soils: moist well-drained Growth: moderate	2001, 2002			2001, 2002, 2003, 2004
<i>Quercus prinus</i> (Qupr) N: 176 D Light: sun Soils: tolerates poor dry soils Growth: slow to moderate			2002	
<i>Quercus rubra</i> (Quru) N: 1198 D Light: sun to partial shade Soils: well drained Growth: moderate	2001, 2002, 2003, 2004		2001, 2002, 2003, 2004	
<i>Quercus virginiana</i> (Quvi) N: 273 D Light: sun Soils: moist, tolerates compacted clay Growth: slow to moderate		2001, 2002, 2003, 2004		

N, number of individuals included in the analysis; D, determinate growth; ID, indeterminate growth.

\*www.na.fs.fed.us/spfo/pubs/silvics-manual, www.ces.ncsu.edu/dpets/hort

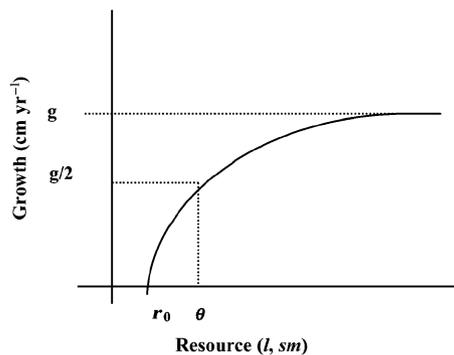


Fig. 3 Growth response to increasing resource availability: *l*, light; *sm*, soil moisture;  $r_0$ , minimum value of the resource at which growth starts;  $\theta_R$ , half saturation constant; and *g*, maximum growth increment.

$$\ln(g_{pi}) \sim \text{Normal}(\mu, \tau_g^{-1}). \quad (4)$$

and priors

$$\mu \sim N(r, 4), \quad \tau_g \sim \text{Gamma}(0.07, 0.2). \quad (5)$$

To maintain parameter estimates within realistic values, we constrained their prior parameters but still allowed for large variability; this would reflect the fact that plants do not have unlimited growth rates although

Table 3 Submodels tested

Submodel	Model description
Submodel A	$\ln(H_{pit}) = \alpha_1 L_{pt} + \alpha_2 M_{pt} + \epsilon_{pit}$ linear response, only fixed effects
Submodel B	$\ln(H_{pit}) = \alpha_1 L_{pt} + \alpha_2 M_{pt} + \gamma_p + \epsilon_{pit}$ linear response, plot random effects added
Submodel C	$H_{pit} = g L_{pt} M_{pt} + \epsilon_{pit}$ asymptotic response, all individuals have same maximum growth rate parameter
Submodel D	$H_{pit} = g_{pi} L_{pt} M_{pt} + \epsilon_{pit}$ asymptotic response, each individual has its own maximum growth rate parameter
Submodel E	$H_{pit} = g_{pi} L_{pt} M_{pt} + \epsilon_{pit}$ $\epsilon_{pit} \sim \text{Normal}(\rho \epsilon_{pit-1}, \tau_\epsilon^{-1})$ asymptotic response, autoregressive error

they may greatly differ in how much the species can grow in a particular year. The priors for  $\mu$ , the maximum growth rate associated with each species, are specified as a mean equal to *r*, the maximum growth rate observed for each species, and a variance of 4 (the range of variation on maximum growth rates [ln] observed). Precision terms ( $\tau_g$  and  $\tau$ ) were also assigned priors that

constrained these parameters within the realistic range that is observed in the data. These choices of prior parameter values ensure that predicted growth rates fall within realistic ranges while still allowing for large variability.

The effects of light on growth are modeled following a well-established relationship (e.g. Pacala *et al.*, 1994; Clark *et al.*, 2003):

$$L_{pt} = \frac{l_{pt} - l_0}{\theta_L + l_{pt}}, \quad (6)$$

where  $l_{pt}$  is the estimated light level at plot,  $p$ , and year,  $t$  (see 'Light model');  $l_0$  is the minimum value of light for growth; and  $\theta_L$ , the half saturation constant, describes the shape of the light response curve. For species with determinate growth (Table 2), where the growth increment in year  $t$  depends on resources stored in year  $t-1$  (Kozlowski & Ward, 1957), the light observations for year  $t$  were taken in year  $t-1$  (i.e.  $l_{pt-1}$ ).

Effects of soil moisture have a similar form,

$$M_{pt} = \frac{m_{pt} - m_0}{\theta_M + m_{pt}}, \quad (7)$$

where  $m_{pt}$  is soil moisture at plot,  $p$ , and year,  $t$ ;  $m_0$  represents the minimum percent soil moisture at which that species can grow; and  $\theta_M$  specifies the moisture level at which each species reaches 50% of maximum growth. To incorporate uncertainty in the soil moisture observations (soil moisture can be highly heterogeneous even at small scales), values included in the analysis ( $m_{pt}$ ) were sampled from a normal distribution,

$$m_{pt} \sim \text{Normal}(\text{Soilm}_{pt}, \text{varSoilm}), \quad (8)$$

with mean value  $\text{Soilm}_{pt}$ , this is the observed soil moisture, and variance  $\text{varSoilm}$ , which had fixed value of 10, this value represents the average variance among measurements taken in the same plot at the same time. As for light data, height increments of species with determinate growth were analyzed using soil moisture from the previous year,  $m_{pt-1}$ .

Modeling  $L$  and  $M$  as in Eqns (6) and (7) assumes asymptotic growth response to increasing resource availability. Minimum resources required for growth,  $l_0$  and  $m_0$ , have priors,

$$l_0 \sim \text{Uniform}(0, 10), \quad (9)$$

$$m_0 \sim \text{Uniform}(0, 10), \quad (10)$$

that span the lowest values we observed for locations supporting seedlings. The half saturation constants,  $\theta_L$ , and  $\theta_M$ , are also assigned uniform priors that cover the range of light and soil moisture values we recorded,

$$\theta_L \sim \text{Uniform}(0, 55), \quad (11)$$

$$\theta_M \sim \text{Uniform}(0, 40). \quad (12)$$

### Light model

Our GSF and PAR light measurements are only a coarse approximation of the light levels to which each seedling was exposed (see 'Soil moisture and light data'). We incorporated this uncertainty by treating the true light level as a latent state to be estimated (Clark *et al.*, 2003; Mohan *et al.*, 2007). The  $l_{pt}$  was assigned a uniform prior limited by the range of variability we observed in the data:

$$l_{pt} \sim \text{Uniform}(\text{Lower}L_{pt}, \text{Upper}L_{pt}). \quad (13)$$

The lower and upper limits for the light estimates come from the variability observed among canopy photos taken at the same locations and times each year (see 'Methods'). The full model was then:

posterior

$$p(\theta_L, \theta_M, l_0, m_0, l, g, \mu, \tau_g, \tau | H, \text{Lower}L, \text{Upper}L, m) =$$

$$\prod_{p=1}^P \prod_{i=1}^N \prod_{t=1}^{t_2(p)} N(H_{pit} | g_i L_{pt} M_{pt}, \tau^{-1}) \quad \text{likelihood}$$

$$\times \prod_{p=1}^P \prod_{t=1}^T \text{Unif}(l_{pt} | \text{Lower}L_{pt}, \text{Upper}L_{pt}) \quad \text{priors}$$

$$\times \prod_{p=1}^P \prod_{i=1}^N N(\ln(g_{pi}) | \mu, \tau_g^{-1}) N(\mu | 0, 4)$$

$$\times \text{Unif}(l_0 | 0, 10) \text{Unif}(m_0 | 0, 10) \text{Unif}(\theta_L | 0, 50) \text{Unif}(\theta_M | 0, 40)$$

$$\times \text{Gamma}(\tau | 1.25, 5) \text{Gamma}(\tau_g | 0.07, 0.2) \quad \text{hyperpriors.}$$

### Model implementation, convergence, and model selection

We carried out Markov chain Monte Carlo simulations for several variations of the growth model (Table 3). Gibbs sampling (Geman & Geman, 1984) was performed in WINBUGS 1.4 (Lunn *et al.*, 2000). Convergence required from 1000 to 5000 iterations, and each species was run for 50 000 iterations and three chains. Posterior parameter mean values are based on postconvergence results. Model selection was based on the deviance information criterion (DIC) a commonly used approach in hierarchical model comparisons (Spiegelhalter *et al.*, 2000). DIC penalizes models based on their deviations from the data, favoring a good fit, and on the effective number of parameters,

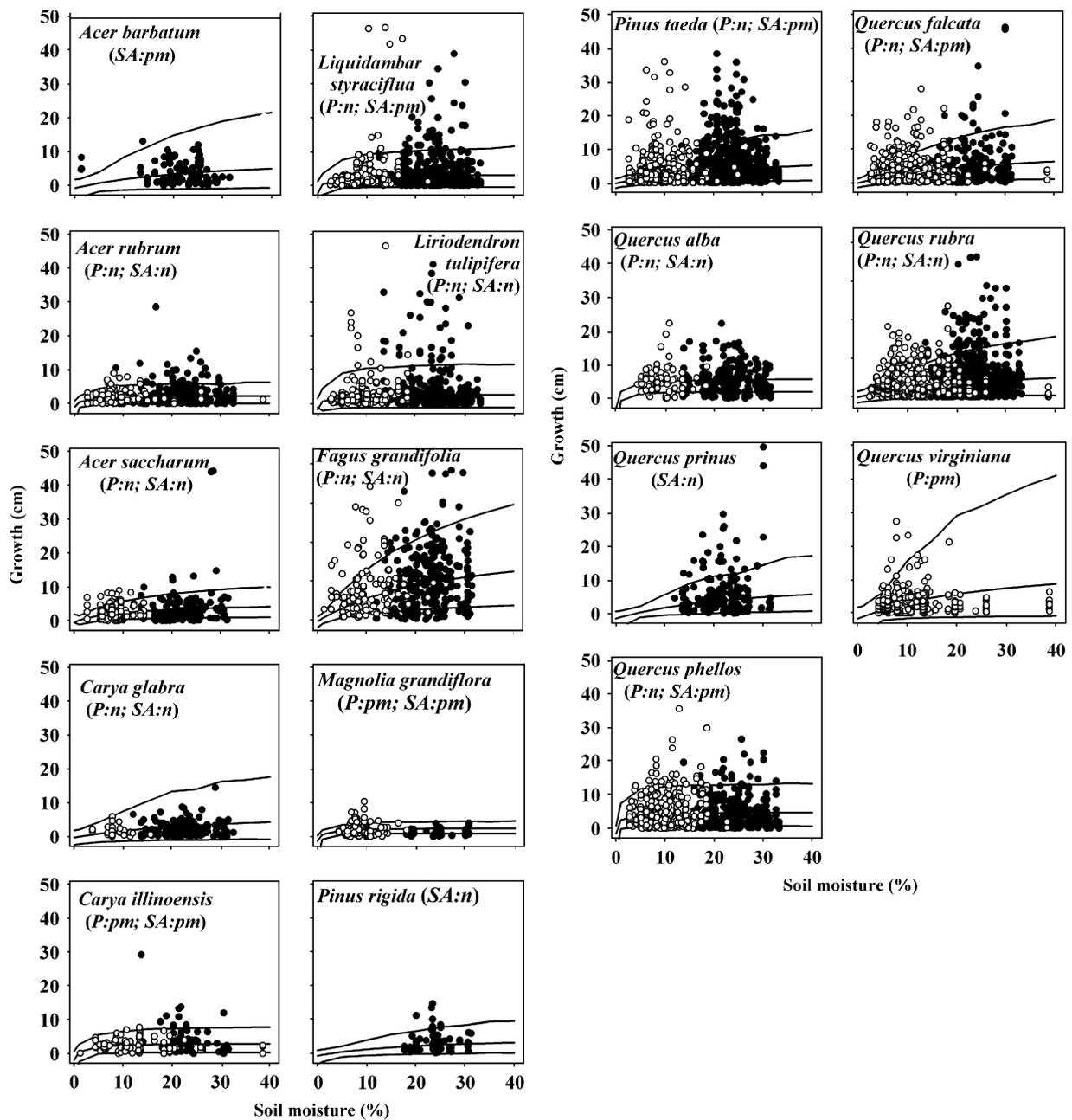


Fig. 4 Growth data (dots) for the Southern Appalachians, SA, (●), and the Piedmont, P, (○) sites and predicted growth [lines – mean and 95% prediction interval (PI)] as a function of soil moisture. n, native; pm, potential migrant.

favoring models with smaller number of parameters (Spiegelhalter *et al.*, 2000; Gelman *et al.*, 2004).

**Results**

*Model selection, predicted growth, and random effects*

Model D had the lowest DIC value (Table 3). This model includes a random individual effect in the asymptote  $g$  that allowed a better fit for the wide range of responses

we observed (Figs. 4 and 5). Given the large range of growth increments at similar resource levels (Figs. 4 and 5), predicted growth showed various degree of concordance with the observed data (Fig. 6). A diagnosis of the residuals,  $\epsilon_{pit}$ , and of the individuals random effects for the asymptote,  $g_i$  (not shown), did not reveal any patterns among the plots. That is, plots with similar characteristics, such as soil type, exposure, elevation, did not have consistent biases that would have indicated a plot effect.

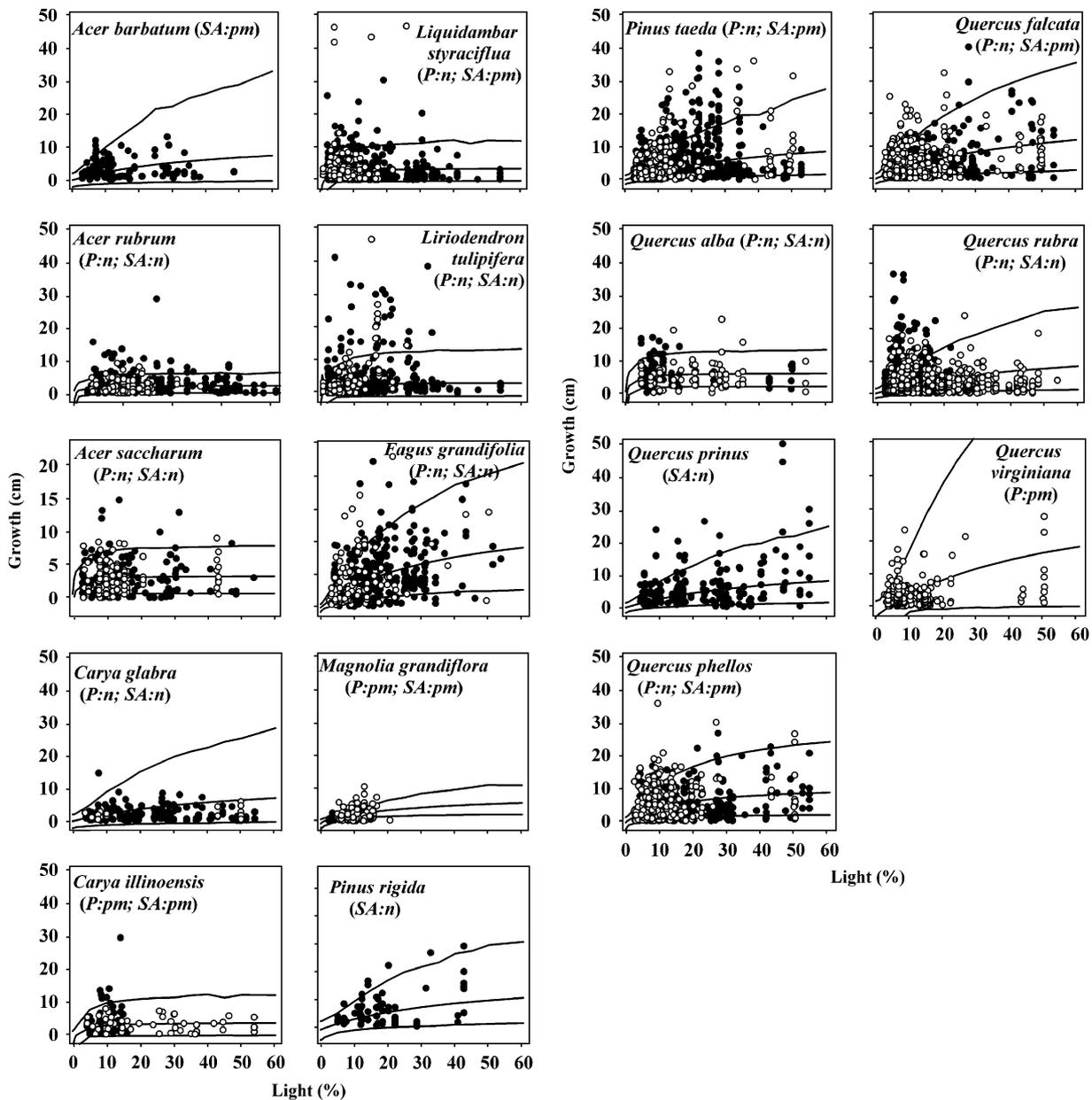


Fig. 5 Growth data (dots) for the Southern Appalachians, SA, (●), and the Piedmont, P, (○) sites. Predicted growth [lines – mean and 95% prediction interval (PI)] as a function of light levels. n, native; pm, potential migrant.

*Maximum growth rates*

The posterior means of the maximum growth rate parameter,  $\mu$ , among all the tested species ranged between 0.8 and 4.7 ( $e^{\mu}$ : 2.2–59.7 cm) (Fig. 7). Comparisons among species did not show consistent differences between residents and potential immigrant species (Fig. 7). At the species level, maximum growth capacity of potential immigrant species lies within the range of values found among native species. This applies to species planted in both the Southern Appalachians and the Piedmont.

*Growth response to soil moisture*

Percent soil moisture ranged from 8.4% to 33.2% in the Southern Appalachians sites, and from 2.1% to 38.6% at the Piedmont location (Fig. 1b), these include a degree of variation in soil water availability that would mimic predicted climate scenarios for the region (Mearns *et al.*, 2003; Christensen *et al.*, 2007). We found a wide range of variability in growth rates for any given soil moisture level (Fig. 4, dots). Mean predicted growth [mean  $\pm$  95% prediction interval (PI); Fig. 4, lines] bounds most of the data.

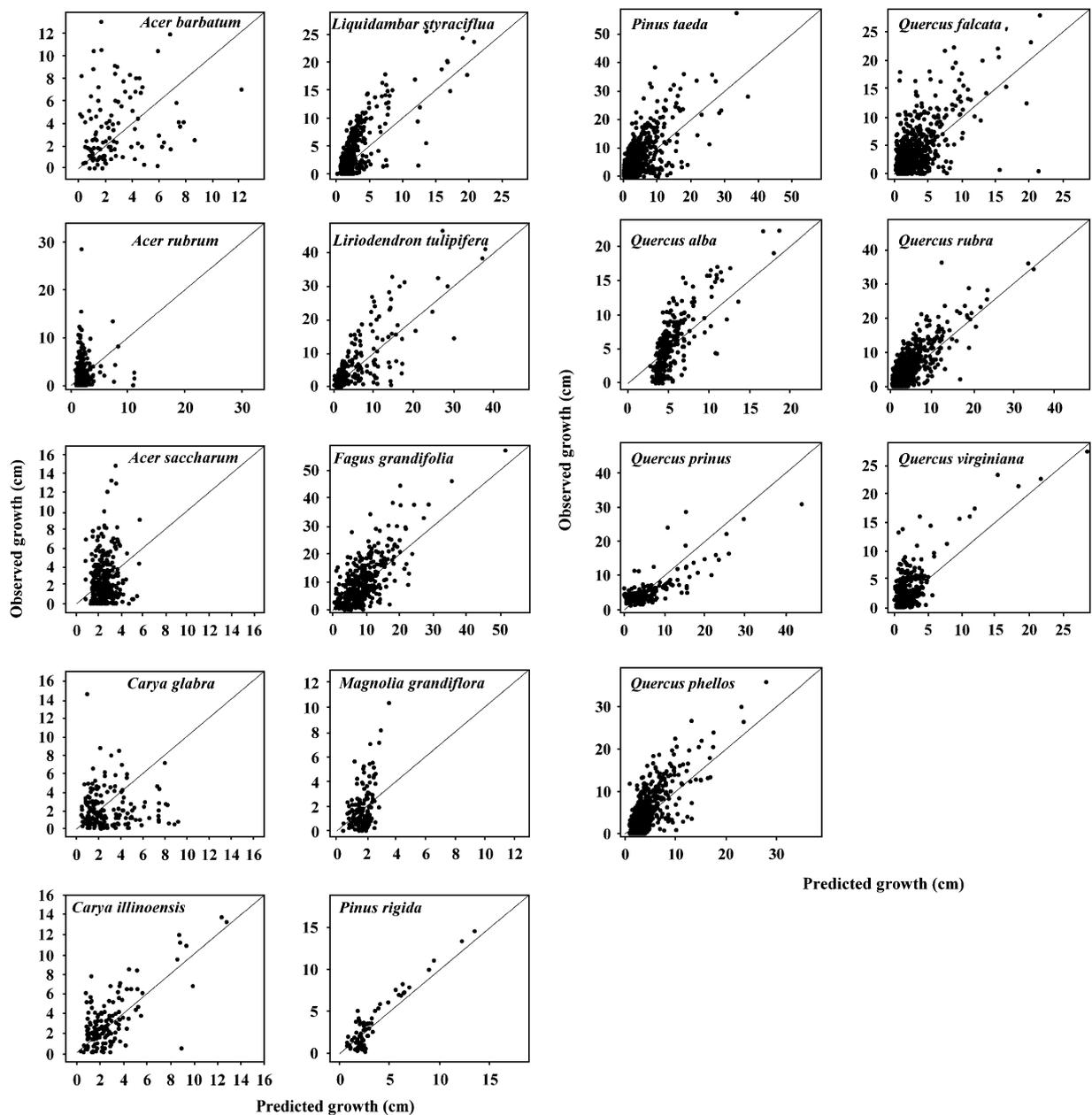


Fig. 6 Predicted vs. observed growth (dots) and 1:1 line.

The specific values for the soil moisture-related parameters (Figs. 6 and 7) do not reveal differences between the two groups of species, i.e. natives and potential migrants. All species responded favorably to higher soil moisture levels, and potential migrant did not seem to perform better than natives under drier conditions, as we had expected.

#### Growth response to light

Seedlings were exposed to natural range of light values found in forest communities. Percent light varied be-

tween 1.4% and 53.9% in the Southern Appalachian plots, and from 1.2% to 49.8% at the Piedmont sites (Fig. 1b). Growth data along the light level gradient is presented in Fig. 4. As with soil moisture, there is a wide range of variability on growth rates at similar irradiance levels (Fig. 5, dots). Again, the mean predicted growth (mean  $\pm$  95% PI; Fig. 5, lines) covers most of the data, but still leaves some of the most extreme values out of the 95% PI.

The specific values for the light level-related parameters did not differentiate between shade tolerant and shade intolerant species. The minimum level of light

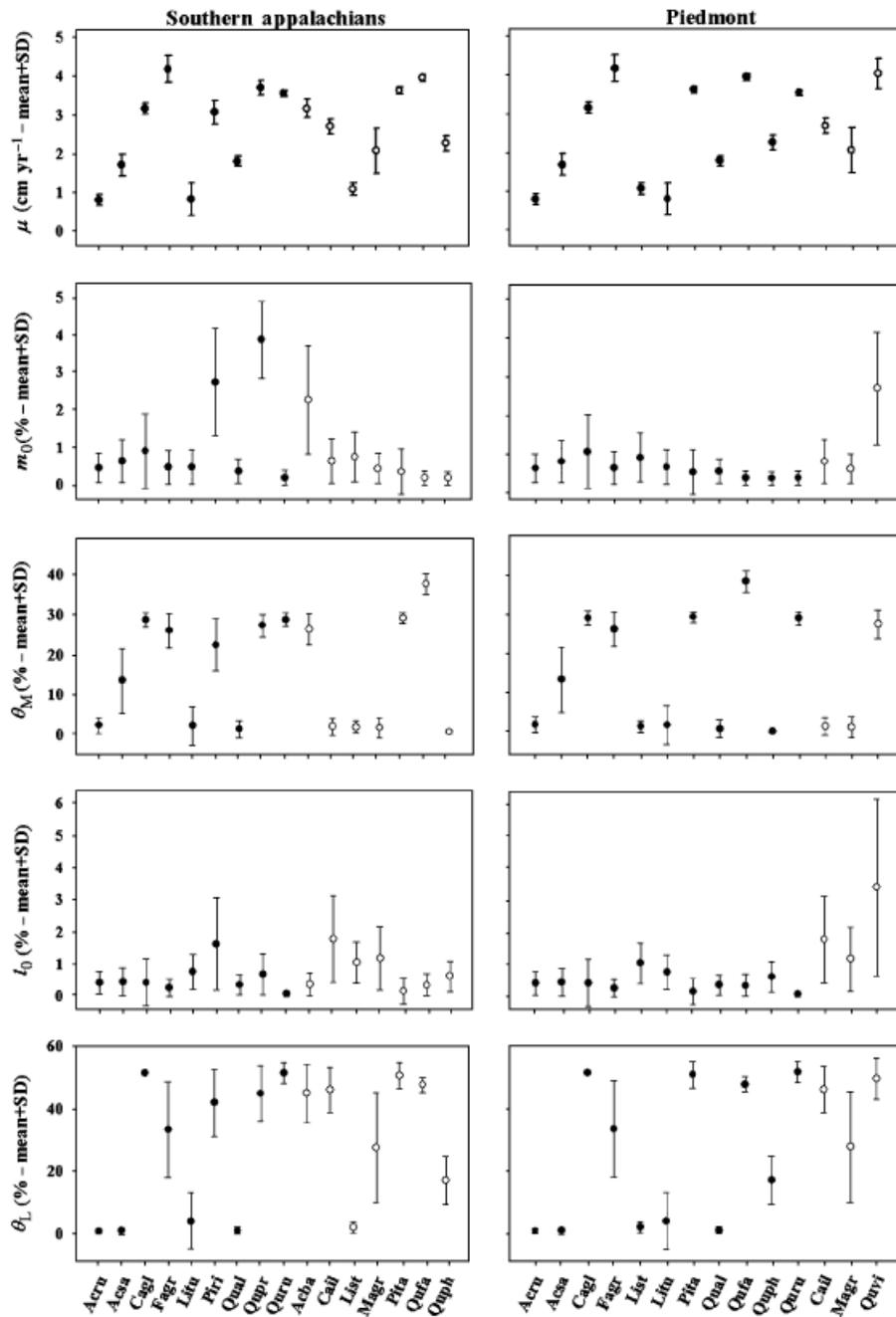


Fig. 7 Growth related parameter posterior means ( $\pm$  SD) for each species, (●) local species, (○) potential migrants.

required for each species to start growth was similar among most species (Fig. 7).

**Discussion**

By comparing long-term growth rates between resident and potential migrant species, we examined whether potential migrants could compete with the resident community when introduced. Experimental manipulations of canopy gaps, together with a range of light, soil

moisture conditions, and parent material, allowed us to assess the potential for long-term success. The years of study included some of the most arid conditions on record and are thus relevant for climate change scenarios (Ibáñez *et al.*, 2007; as of 2005, six of the 10 highest recorded mean July temperatures for the region had occurred in the previous 15 years). Our results provide two major conclusions. First, growth rates for potential immigrant species were comparable with those of local species, showing no general advantage in any of the

environmental combinations included in our study. Under the current climate and local conditions (e.g., predators, herbivores, pests, etc.), the potential colonizers we tested could grow along native species once established, showing obvious migratory potential, but not necessarily at the expense of resident species. Second, the minimum soil moisture requirements for the potential migrants were similar to those of the local species. These results could have major implications for vegetation changes under the predicted drier climate for the region, if seedlings cannot sustain growth rates high enough to develop into adult trees, the establishment of viable populations may not be possible. If local species decrease in abundance and potential migrants are not able to establish in sufficient numbers, the region may see recruitment impacts for both resident and newly immigrating species.

In the following sections, we explore the performance of potential migrant species relative to locals, based on their maximum growth rates and on their response to soil moisture and light gradients.

*Will potential migrant species have competitive growth rates with respect to local species?*

Even if climate is suitable for an immigrant species, local conditions may limit invasion potential. We examined the growth of potential immigrant species in the context of the novel conditions presented by the full biotic and abiotic influences at our sites over a period of 5 years with varying environmental conditions, i.e. soil water availability and light. The pertinent question here is not whether a species can grow and survive, but rather how it performs relative to residents. We hypothesized that local species, adapted to local conditions, could have an advantage over potential immigrants and would then show higher maximum growth rates. However, climate during the last decade has been more arid than most years when the current populations established (two of our sampled years, 2002 and 2005, are within the 15 warmest seasons ever recorded). This increased aridity could have shifted the advantage to species derived from warmer climates.

The potential immigrant species included in our study did not have consistently higher or lower growth rates than did those of local species. This was the case in both the Piedmont and in the Southern Appalachians. Given the size and duration of the experiment, these results suggest that immigrants would perform, as well as residents, but not necessarily better.

Within the resident and potential immigrant groups, we expected to see clear differences between species traditionally considered to be slow growing and those classified as fast growers or pioneer species (Table 2).

This turned out not to be the case: *Fagus grandifolia* and most of the oak species, *Quercus*, which are slow or medium growers, had the highest maximum growth rates, whereas *Liquidambar styraciflua* and *Liriodendron tulipifera*, both fast growing species, showed low growth. We note that seedlings from all planted species were exposed to a range of light and soil moisture values. One possible explanation for the high growth rates among the supposedly slow growers is a delay in ontogeny due to their large seed size (Niinemets, 2006). Initial growth is correlated to leaf area, which in turn is correlated with seed size (Farmer, 1980). Here, seedlings of some shade tolerant species, or slow growers, have large initial size due to large seeds, and thus could have high growth rates initially, but slow thereafter (Sack & Grubb, 2001; Niinemets, 2006). Whitmore & Brown (1996) observed that 40 months after gap creation, the tallest seedlings belonged to the group of shade tolerant species derived from the seedling bank. But after 53 months, faster growing shade intolerants had surpassed the shade tolerants. In our case, seedling age ranged between 15 and 51 months at the time of the last measurements, and canopy gaps had been in place for 41 months. In this case, the length of the experiment may not have been long enough to discriminate among species with different growth responses to the variety of microhabitats we exposed them to, although it still gives us information on these species' early response to the varying environment. In addition, the response to those environmental gradients may also shift at later stages of the plant's lifespan.

*What are the performances of potential migrants and resident species along the soil moisture and light gradients?*

We hypothesized that potential immigrant species from xeric regions could be more tolerant of dry conditions than native species. According to this hypothesis, we were expecting potential immigrants to have lower minimum soil moisture requirements and lower half saturation constants than those of the local species. However, posterior means for this parameters,  $m_0$  and  $\theta_M$ , were similar for species from both groups. As a consequence, we can assume that they would not have a clear advantage in these regions. Even if competitive interactions change with climate, our results do not show clear potential for these immigrant species when growing conditions become more arid (Mearns *et al.*, 2003; Christensen *et al.*, 2007). These results suggest the need for longer term studies to allow for more variation in climate and a clearer assessment of cumulative effects on growth and survival.

Canopy gap succession is considered essential to the maintenance of forest diversity (Rees *et al.*, 2001). Light levels under the canopy of most eastern US forests are below 1% of full sunlight (Canham, 1988a, b). However, practically all tree species present in these areas need higher light levels to grow to the canopy status (Barden, 1980; Canham, 1989). Disturbances that create canopy gaps generate opportunities for invasions by altering biotic and abiotic barriers, and by providing suitable microsites for the recruitment of new species (Johnstone, 1986; Rejmanek, 1989; Horvitz *et al.*, 1998).

We expected that growth response to light conditions for both immigrants and residents would depend on differences in shade tolerance. Instead we found that shade intolerant species (e.g. *L. styraciflua*, *L. tulipifera*) had minimum light requirements similar to those of shade tolerant species (e.g. *Acer saccharum*, *F. grandifolia*, *Quercus rubra*). Studies on *L. tulipifera* have shown that seedlings can achieve maximum photosynthetic efficiency at relatively low light levels, 3–10% (Renshaw & Warren, 1958; Olson, 1969). Low light compensation points among shade intolerant species could also be explained by the fact that shade intolerant species commonly leaf out early in the season (Struik, 1965; Bain & Attridge, 1988). These species would therefore begin their photosynthesis and carbon storage for growth before the canopy foliage is out. And again, tolerance to low light levels may shift in later stages.

In general, both groups of species, natives and potential migrants, would benefit from growing in a canopy gap, where light resources are high, if soil water availability levels are still sufficient for growth.

### Limitations

Many other environmental variables that affect seedling growth rates are not included as specific covariates in this study. Parent material and nutrient status can have a large effect on plant performance (e.g. Grime, 1977; Tilman, 1982; Latham, 1992; Sher & Marshall, 2003). In our work, major differences on environmental conditions associated with the plots seemed to be mainly related to soil water availability and light conditions, and we incorporated these variables in the analysis. Previous studies indicate that species interactions will be altered by increasing concentrations of atmospheric CO<sub>2</sub> (Poorter, 1993, 1998; Hattenschwiler & Korner, 2000, 2003; Hattenschwiler, 2001). The effects of elevated CO<sub>2</sub> may be driven directly by a rising concentration of the photosynthetic substrate, and indirectly by increasing the plant's efficiency in water used (Pearcy & Björkman, 1983). There is limited field knowledge of tree species differences in CO<sub>2</sub> response (Ellsworth *et al.*, 2004; Saxe & Kerstiens, 2005; Mohan *et al.*, 2007;

Sefcik *et al.*, 2007). Extensive studies on grasses and herbs (Craine *et al.*, 2003; Ellsworth *et al.*, 2004) confirm differential response to increasing atmospheric CO<sub>2</sub> among species. Our study cannot exclude the possibility of important climate/CO<sub>2</sub> interactions on migratory potential.

### Conclusions

Vegetation models predict biome shifts in the Southeast USA as a consequence of climate change (Bachelet *et al.*, 2001; Hansen *et al.*, 2001; Iverson *et al.*, 2008). Migrating populations will have to invade established communities, and their success in colonizing a new region will depend on their performance relative to resident species. Local species will likewise be affected by the changing climate: some species will increase in abundance, others may go regionally extinct, changing the interactions among species.

Under conditions that included a broad range of spatio-temporal variation in the important variable of soil moisture, we found that growth rates of potential immigrants species were comparable with those of the native species. This result indicates potential to perform, as well as resident species, but not necessarily better. Because of the large range of conditions included in the study (e.g. soil types and soil associated microorganisms, herbivores, pests, etc.) as well as limited evidence for combinations of settings that would clearly favor residents or immigrants, we question the value of simple climate correlations as the basis for predicting future biodiversity. Although we expected potential immigrants to be more resistant and/or more resilient to low soil moisture conditions than residents, we found similar responses for both. The implications of these findings could have large repercussions for future communities. If local species decrease in abundance and potential migrants are not able to establish in sufficient numbers, the region will experience considerable decline in its biodiversity.

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