UNIVERSIDADE FEDERAL DE MINAS GERAIS
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
Departamento de Botânica
Programa de Pós-Graduação em Biologia Vegetal

VANESSA PONTARA

VARIAÇÕES ESPAÇO-TEMPORAIS NO CRESCIMENTO DE *Dalbergia nigra* (Vell.) Allemão ex Benth

Tese apresentada ao Programa de Pós-Graduação em Biologia Vegetal do Departamento de Botânica do Instituto de Ciências Biológicas da Universidade Federal de Minas Gerais, como requisito parcial à obtenção do título de Doutor em Biologia Vegetal.

Área de Concentração: Fisiologia vegetal

BELO HORIZONTE – MG

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Orientador: Prof. Dr. José Pires de Lemos Filho
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SUMÁRIO

RESUMO GERAL

Dalbergia nigra é uma arbórea endêmica da Floresta Atlântica, que ocorre no leste do Brasil. Produz madeira valiosa, mas este recurso foi altamente explorado que é a causa da classificação como vulnerável. Neste estudo, foi investigado os mecanismos que determinam a abundância, distribuição e crescimento de uma população de *D. nigra* em um fragmento da Mata Atlântica. No primeiro capítulo, usamos métodos dendroecologia para testar a hipótese de que a variação na posição topográfica, estaria relacionada com o crescimento radial de *Dalbergia nigra* em condições uniformes de clima e irradiância. O alto teor de alumínio, baixa fertilidade e umidade do solo presente na parte alta do fragmento ocasionou menor crescimento de árvores de *D. nigra*. No segundo capítulo, determinamos se a topografia e a variação em fina escala de disponibilidade de recursos podem resultar em diferentes taxas de mortalidade e de crescimento em plântulas de *D. nigra*. A topografia influenciou a taxa de sobrevivência e crescimento de plântulas e de indivíduos jovens de *D. nigra*, com maior crescimento e recrutamento na parte baixa do fragmento. Além disso, a taxa de sobrevivência e crescimento de plântulas foram menores na estação seca do que na estação chuvosa. Assim, a sensibilidade à seca sazonal na fase de plântulas pode ser fortemente dependente da umidade local. No capítulo 3, examinamos se há variação no incremento radial de *D. nigra* entre diferentes classes de diâmetro e como a densidade da madeira varia em relação a fatores abióticos como fertilidade e umidade do solo. Precipitação foi a variável medida mais forte implicados no crescimento de *D. nigra*, independentemente do tamanho da classe. Os fatores edáficos também foram determinantes no crescimento e na densidade da madeira de *D. nigra*. O efeito da heterogeneidade de fatores abióticos em um pequeno fragmento de Mata Atlântica ofereceu condições distintas que resultaram em maior ou menor sucesso no recrutamento e crescimento dos indivíduos de *D. nigra* de acordo com sua distribuição no mosaico de recursos.

Palavras-chave: *Dalbergia nigra*, topografia, dendrômetros, recrutamento, sazonalidade, fertilidade do solo, umidade do solo.

INTRODUÇÃO GERAL

Dalbergia nigra (Vell.) Allemão ex Benth. (Figura 1) é uma espécie considerada endêmica da Floresta Atlântica ocorrente nos estados do Rio de Janeiro à Bahia, extendendo para o interior de São Paulo e Minas Gerais (Carvalho 1997, Oliveira-Filho 2006). Ocupa a Floresta Estacional Semidecidual das Terras Baixa e Submontana, Floresta Estacional Semidecidual Baixo-Montana e Floresta Estacional Semidecidual Alto-Montana (Oliveira-Filho 2006). As flores são pequenas (0,9-1,0 cm), subsésseis e corola papilionóide creme (Bortoluzzi et al. 2004). O fruto é um legume samaróide, elíptico, subcoriáceo, verde quando imaturo e vináceo quando maduro; possui 1-3 sementes, com núcleo semnífero central e ala marginal (Bortoluzzi et al. 2004). O fruto seco, indeiscente, plano e comprido é adaptado à dispersão anemocórica (Barroso et al. 1999). Floresce nos meses de setembro a outubro e a maturação ocorre entre novembro e dezembro (Carvalho 1994). A espécie não floresce anualmente o que a caracteriza como supra-anual, produzindo flores e frutos em intervalos de dois a três anos que variam entre si quanto ao número de sementes produzidas (Angel & Martins 2005). Classificada como madeira de lei, a espécie é conhecida como jacarandá-da-bahia, cabiúna, cabiúna-rachada, cabiúna-do-mato, caviúna, jacarandá- caviúna, jacarandá-preto, jacarandá-roxo, palisandre e jacarandazinho (Carvalho 1994, Lorenzi 2000).

Sua madeira exibe coloração escura, é decorativa e apresenta grande resistência e durabilidade natural, atributos que contribuíram para que fosse mundialmente explorada para acabamento interno em construção civil e fabricação de instrumentos musicais e mobiliário de luxo (Lorenzi 1992). Foi incluída na Lista Oficial das Espécies da Flora Brasileira Ameaçadas de Extinção (IBAMA 1992, MMA 2008) e classificada como vulnerável na Lista Vermelha de Espécies Ameaçadas da União Internacional para a Conservação da Natureza e dos Recursos Naturais (IUCN 2011

Fig. 1 – Fotos de *Dalbergia nigra* (Vell.) Allemão ex Benth.: A) plântula de *Dalbergia nigra* e B) indivíduo adulto e C e D) flores e frutos e (E) aspecto do tronco

Dalbergia nigra é apropriada para se estudar a dinâmica da sucessão e recrutamento, afinal, apresenta tanto características de secundária tardia a clímax quanto caráter pioneiro, podendo ser encontrada, inclusive, em cortes de barrancos, o que a torna atrativa para manejo florestal sustentável e plantio de reposição, até o momento, inexistentes para a espécie. De fato, ela ocorre em ambientes tão distintos como o interior da mata primária densa e em formações secundárias alteradas pela ação antrópica (Lorenzi, 1992; Comunicado Técnico Embrapa 2003). Essas características parecem não se enquadrar às de uma espécie ameaçada de extinção, no entanto, a exploração desordenada de *D. nigra* fez com que ela desaparecesse de grande parte de sua distribuição original (de Carvalho 1997). Tendo isso em vista e o estado crítico de desmatamento do bioma do qual é endêmico, são prementes estudos que contribuam para a manutenção do jacarandá-da-Bahia em longo prazo.

Identificar os mecanismos que determinam a abundância e distribuição das populações de plantas e animais é um desafio central da ecologia (Coomes e Grubb 2003, Levine & Rees 2002, Osenberg et al. 2002, Turnbull et al. 2005). Os padrões espaciais de uma população de plantas em escala local são o resultado de interações bióticas e abióticas que atuam ao longo da história de vida influenciando a dispersão de sementes, distribuição de sítios seguros para a germinação e mortalidade desde a fase de plântula até a maturidade (Silvertown & Doust 1993). O fracasso de uma espécie de recrutar em um determinado local pode resultar de processos que ocorrem em praticamente qualquer fase do ciclo de vida e incluem a produção de propágulos e transporte, competição, predação e herbivoria.

O recrutamento está fortemente relacionado à produção de sementes, a existência de microssítios disponíveis para a germinação e o estabelecimento das plantas. Além disso, vários outros fatores também podem influenciar no recrutamento e crescimento de plantas como competição, predação, patógenos e herbivoria. Deste modo, o estado atual de um povoamento florestal é resultado da interação de vários processos em particular o crescimento, a mortalidade e a regeneração (Dajoz 2006).

Nesta tese me concentrei nas análises das fases iniciais do ciclo de vida de uma população de plantas de *Dalbergia nigra* e análises na fase adulta. Esta tese encontra-se distribuída em três capítulos: (i) Capítulo 1, em que examinamos se a variação da posição topográfica estaria relacionada ao crescimento radial e fenologia dos indivíduos de *Dalbergia nigra*. (ii) Capítulo 2, determinamos se variação em fina escala de disponibilidade de recursos pode resultar em diferentes taxas de mortalidade e de crescimento em indivíduos de *D. nigra*. (iii) Capítulo 3, examinamos se há variação no incremento radial de *D. nigra* entre diferentes classes de diâmetro e como a densidade da madeira varia em relação a fatores abióticos como fertilidade e umidade do solo.

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CAPÍTULO 1

Fine-scale variation in topography and seasonality determine radial growth of an endangered tree in Brazilian Atlantic Forest

Key Words: *Dalbergia nigra*, dendroecology, fertility soil, phenology, seasonal drought, soil water

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ABSTRACT

Spatio-temporal variation in soil resource availability associated with topography and seasonality may drive patterns of tree growth and phenology, but these links are poorly characterized for most tropical tree species. We use dendroecological methods to test the hypothesis that variation in topographic position is related to radial growth and phenology for individuals of the endangered tropical tree *Dalbergia nigra* under uniform conditions of climate and irradiance, and to examine effects of seasonality on plant phenology and growth periodicity. Dendrometer-based measurements of stem diameter change over 26 months and local measurements of soil nutrient and water availability were compared for 24 individuals of *D. nigra* distributed equally between summit and valley positions within a topographically heterogeneous fragment of Atlantic rain forest in southeast Brazil. Soil water and nutrient availability, and cumulative radial growth, were greater for trees in valley than summit positions. Monthly diameter increment was seasonal and positively related to monthly rainfall. *D. nigra* was seasonal in all phenophases, regardless of topographic position, and there were no differences in the frequency, timing or intensity of phenophases among topographic positions. We conclude that low soil nutrient and/or moisture availability reduce radial growth of *D. nigra* individuals growing in summit positions, while trees growing in valleys exhibit faster annual growth, but that vegetative or reproductive phenology are unaffected by fine-scale variation in topography.

INTRODUCTION

The responses of plants to resource availability is of key significance to the controls on fine-scale species distributions and the effects of a changing climate on vegetation (Liang *et al.* 2006, Niinemets 2010). For tropical trees, local variation in soil water availability, irradiance and soil nutrient status may all influence rates of tree growth (Oberhuber & Kofler 2000, Baker *et al.* 2003a) and the spatial distribution of plant populations (Clark et al. 1998, Sollins 1998, Machado *et al.* 2008, Bagchi *et al.* 2011). Even when a population of tropical trees grows under a spatially uniform precipitation regime, individual trees may show different phenological patterns and growth rates that differ in response to local heterogeneity in soil conditions (Cardoso *et al.* 2012). Hence at fine scales, factors that determine resource heterogeneity are associated with spatial variation in the structure, composition and functioning of tropical forests (Bourgeron 1983, Paoli et al. 2006, Sukri et al. 2012).

Topographic heterogeneity is a major driver of fine-scale variation in soil properties in tropical forests (Chen *et al.,* 1997; Daws et al. 2002; Fu *et al.,* 2004, Castilho *et al.* 2006, Toledo *et al.* 2011; Sukri et al. 2012). Aspect may influence radiation regimes and micro-climates at ground level in environments where cloud cover varies consistently through the day. Similarly, topography may impact soil development and influence the distribution of soil nutrient and water availability through effects on drainage and the leaching of nutrients (Brady & Weil, 2002, Luizão et al. 2004). Under these circumstances soil moisture availability is determined edaphically, not climatically (Oberhuber & Kofler 2000). Ultimately these factors may affect stand-level growth responses (Oberhuber & Kofler 2000). Thus topographic heterogeneity creates a mosaic of microhabitats (Moody & Meentemeyer 2001; Takyu *et al*. 2002), and stem diameter increment rates among individuals may respond to this variation in conditions (Baker et al. 2003b, O'Brien *et al.*

2008).

Studies have only rarely linked the fine-scale distribution of tropical tree species to differences in growth rate or phenology as potential mechanisms of topographic niche specialization (e.g. Russo et al. 2005, 2008). To contribute to perspectives on the mechanisms determining topographic niche partitioning, we determined the relationships among spatial distribution, radial growth rates and phenology for a population of *Dalbergia nigra* (Vell.) Allemão ex Benth (Papilionoideae) trees growing in a topographically heterogeneous environment in Brazilian Atlantic Forest. This species is recorded as Vulnerable on the IUCN Red List (IUCN 2013), and also provides one of the most valuable timbers in the central Atlantic Forest region. A wider understanding of the response of this species to local resource availability would contribute to action plans for species conservation and habitat restoration. We tested the hypothesis that *D. nigra* trees growing in a uniform climate would respond to the greater availability of water and nutrients in valley than high elevation sites by displaying (a) variation in vegetative and reproductive phenology between summit and valley sites and (b) higher stem increment rates when growing in valley soils.

METHODS

Study site and climate

The study was carried out in an area of semi-deciduous forest in a fragment of Atlantic rain forest in Sumidouro State Park (SSP) in the state of Minas Gerais, southeastern Brazil (19° 32' 25 S, 43° 55' 09 W). The SSP covers approximately 2000 ha and is mainly composed of Atlantic Forest and cerrado (savanna) vegetation (de Andrade 2009). The SSP was formerly used for livestock grazing and human settlements, but since the implementation of a management plan in 2010 these activities have ceased and the area is undergoing natural regeneration (Tavares, 2010). The study site for this research was a 11 ha forest fragment within the SSP that has never been subjected to logging, livestock grazing or disturbance associated with human settlements. The area is classified as having a semi-humid warm tropical seasonal climate with a dry season of 3-4 months (Nimer 1989). The average annual rainfall is 1273 mm, concentrated between October and March, and the average annual temperature is 22.5 °C. Climate data have been obtained for two years from a meteorological station approximately 27 km from the study area.

Study species

Dalbergia nigra (Vell.) Allemao ex Benth.,commonly known as Brazilian Rosewood, is a tree of the Atlantic Forest that occurs in eastern Brazil. It produces valuable timber but this resource has been over-exploited, which is the cause of the Vulnerable classification by IUCN (2013). Despite this vulnerability due to reduced population sizes, high genetic diversity was found among individuals growing in large protected reserves (Ribeiro et al. 2005, 2011)**.** The growth rate of saplings is moderate to fast and trees reach an average height of 15 - 25 m and a maximum height up to 35 m (Lorenzi 1992).

Tree selection and data collection

The 11 ha fragment selected for this study is located 50-100 m from a river and contains remnant Atlantic Forest. Within the fragment, two areas of approximately 5 ha were identified that possess contrasting topographic positions, here termed valley and summit, based on their elevation and location with respect to the river (Fig. 1). The areas were separated by a slope and differed in elevation by 20-30 m. Twelve adult (> 25 cm dbh) individuals of *D. nigra* were selected randomly in each topographic position. The minimum distance between each tree was 30 m, but most of trees in the sample were separated by 50-500 m.

A band dendrometer (DB20 EMS, Czech Republic) was installed on each of the 24 individuals selected for study in August 2010 at a stem height of approximately 1.5 m. Outer bark was removed before the dendrometers were installed. Monthly measurements began three months after the dendrometers were installed, to allow them to stabilize, and continued for 24 months. Thus the time series for analysis comprises the interval from November 2010 to December 2012. To minimize the influence of diurnal fluctuations in tree girth due to changes in tree water status (Kozlowzki 1972), all measurements were performed during the morning (08h 00 to 10h 00). Data on the increase in trunk circumference were analyzed in relation to environmental variables, including rainfall, temperature, topography and soil fertility. Meteorological data were obtained from the nearest Instituto Nacional de Metereologia (INMET) station, at Sete Lagoas, 27 km from the study site. Crown light exposure was estimated on individual trees by assigning a crown illumination (CI) index on a scale of 5 (crown fully exposed) to 1 (crown fully shaded) to each tree following Clark and Clark (1992). Among the sample of trees, 20 were assigned a CI of 5 (emergent crown), and the remaining four trees were assigned a CI of 4 (full overhead light on > 90% of the crown).

Vegetative and reproductive phenology was assessed simultaneously with the dendrometer band readings. Using binoculars, the proportions of the crown occupied by leaves and reproductive structures were estimated visually in four categories that summed to 100 %: leaves and reproductive structures absent, presence of buds of leaves, presence of mature leaves, presence of flowers and/or fruit. Phenology was evaluated monthly using a semi-quantitative method that scores each phenophase on the five-point scale: 0 = absence of the phenophase; 1 = 1-25% of the crown occupied by the phenophase; 2 = 26-

50%; 3 = 51-75%; and 4 = 76-100% (Fournier 1974).

Soil nutrient and moisture availability measurements

Soil samples (0-20 cm depth) were collected at five randomly selected locations in both the summit and valley areas. Each sample was made up of five bulked subsamples, collected at random locations within a radius of 20 m, and homogenized to form one composite sample. The textural and chemical analyzes of the samples were conducted at the Instituto Mineiro de Agropecuária (IMA), Brazil. Analysis of soil texture was conducted using the pipette method (Claydon, 1989). Soil acidity in distilled water was measured with a pH meter. Total N was determined using the wet oxidation (Kjeldahl) method, which converts organic N to ammonium (NH_4^+) for colometric measurement. Total organic C was determined by the calorimetric method. The determination of available phosphorus was conducted using the Mehlich 1 method (Nelson et al., 1953) and measured by molecular absorption. K and Na were extracted by the Mehlich 1 method (Nelson et al., 1953) and measured by flame photometry. Ca and Mg were also measured by atomic absorption spectrophotometry after extraction with a concentrated 1N KCl solution. Cations were extracted in a 1 M KCl solution at the unbuffered pH of the soil (EMBRAPA, 1997). Exchangeable Al and H+Al were extracted with 1 $mol_c\ L^{-1}$ KCl, cation exchange resin and buffer SMP, respectively. Volumetric soil water content at 10 cm depth was measured at 50 randomly selected locations in each topographic position using the Field Scout TDR 100 soil moisture meter (Spectrum technologies, USA). The measurements were performed at the end of the wet season (first half of April) and end of dry season (first half of September) of each year in 2011 and 2012. The measurements were all made on one day.

Statistical analysis

The effects of initial diameter at breast height (DBH), crown light exposure (CLI) and topographic position (summit vs valley) on cumulative radial increment per tree summed over two years were examined using a linear model equivalent to an analysis of co-variance, with initial DBH as a continuous covariate and CLI and topographic position as categorical variables. A t test was used to determine whether there were significance differences in mean cumulative radial increment and soil fertility across topographic position. We then explored whether stem diameter increment had a seasonal rhythm using linear mixed-effects (LME) models fitted to the monthly radial diameter increment data from individuals growing on the summit and in the valley separately. These models had mean monthly temperature and rainfall as continuous fixed effects and tree as a random effect. LME was implemented using the nlme v.3 package (Pinheiro et al. 2009) for R version 3.0.2 (R Development Core Team, 2013).

We used principal components analysis (PCA) to describe major gradients in soil chemical and physical properties using a set of 19 variables (see Table 1 for a list of the soil variables recorded in each plot). To construct the data-set for this analysis the PC scores for each sampling location was extracted from the PCA and growth rates for each tree were paired with the PC score for the closest location. We selected the closest sample site to each tree and use the data from there. Linear model analysis was used to test for the effects of the PCA resultant component (PC1 and PC2) on cumulative radial increment for each topographic position. We also used the linear model analysis to evaluate the relationship between the dependent variable of tree growth on the independent variable of soil moisture across all seasons.

To determine the mean date and synchrony of phenophases we used circular statistics based on the Fournier score per tree using the software ORIANA (Kovach 2006). In this approach to analysis, the annual cycle is represented by a circle, and data for events are transformed to the angles (in radians) reflecting dates throughout the year. For each phenophase, the mean vector (mean angle) was obtained, and its significance was tested using the Rayleigh test (Zar 1996). The difference in the mean vector between summit and valley sites was determined using the Watson–Williams test (Zar 1996). The length of the mean vector, which ranged from 0 (complete asynchrony of individuals) to 1 (complete synchrony), was also determined for each phenophase.

RESULTS

Climatic and seasonal differences

Total annual rainfall was 1318 mm during the first year (October 2010 to September 2011) of the study and 1176 mm during the second year (Oct. 2012to September 2013) (Fig. 2a). The mean air temperature during the first year was 23 ^{o}C and the second year 22 ^{o}C. There was a marked dry season from April to October, with these six months having 20 mm of rainfall in the first year and 90 mm in the second year (Fig. 2a). During the wet season from November to March mean monthly rainfall was 235 mm in 2010/2011 and 267 mm in 2011/2012 (Fig. 2a). Although there was a great variation in seasonal rainfall during the year, there was little variation in temperature with the mean air temperature during the dry season 22^{o}C (2011) and 21^{o}C (2012) and 25^{o}C (2011) and 23^{o}C (2012) during the wet season.

Differences in soil conditions between sites

There were significant differences between soil characteristics according to topographic position (Table 1). Acidity (H+Al), concentration of exchangeable Al, aluminium saturation, coarse sand and clay were significantly higher in summit soils than in those from the valley. The concentrations of Mg, P, K and silt, as well as base saturation and the sum of exchangeable bases, were all higher in the valley soils. Although the two sites experience the same rainfall, soil moisture content was consistently higher in the valley sites than the summit in both dry and wet seasons (Table 2, $P < 0.001$).

Stem radial increment

Cumulative radial growth over two years was three times greater for individuals growing in the valley (2.38 ± 0.98 mm) than on the summit (0.78 ± 0.55 mm; F= 11.03, P=0.003). In addition, the t test showed that growth also was higher in the valley than the summit in both the dry season (2011, P = 0.01; 2012, P = 0.03) and the wet season (2010/11, P = 0.05; 2011/12, P = 0.007). There were no effects of initial DBH (F = 1.09, P = 0.30) or crown exposure index (F = 0.01, P = 0.91) on cumulative radial growth, thus the higher growth rate of the individuals growing in the valley cannot be explained by differences in initial diameters between these two groups of trees.

A linear mixed effects model showed that monthly diameter increment was positively correlated to rainfall for individuals growing on the summit ($P < 0.001$) and in the valley ($P < 0.001$) during the two years of monitoring (Table 3). Thus, monthly diameter increments exhibited strong seasonality with radial growth starting at the beginning of the wet season (November), and continuing until April (Fig. 2b). However, summit individuals ceased radial increment two months before valley individuals in April 2011/2012 when the dry period started. Monthly temperature was not correlated with diameter increment ($P > 0.1$). Tree growth was related to soil moisture both at the summit and in the valley during the two years of monitoring (Table 4).

The PCA identified two main soil gradients in the study area for summit and valley (Table 5). The PC1 and PC2 were chosen to limit the number of PC axes (Fig. 5), as a result of explaining 87% of the total variance together. Among summit sites the first ordination axis (PC1) explained 62% of the variation in the data and the second axis (PC2) explained 26% of the variation in the data. The axis 1 was positively correlated with base saturation, Mg, TEB, ECE, Ca and ph and negatively with Al^{3+}, $Al^{3+}+H^{+}$, P and m. The second axis (PC2) was positively related with clay and K and negatively correlated with silt, coarse sand, fine sand, organic c and N. Similarly, there were two main axes of variation in the soil properties data among valley sites, which explained 87% of the total variation in the data. PC1 contributed to 45% of the variation was positively associated with fine sand and negatively with silt, organic c, N, Ca, TEB, CEC and ECE and PC2 which contributed to 41% was positively associated with clay, coarse sand, m, P, K, CEC and negatively with fine sand, base saturation, pH in water and Mg (Table 5, Fig. 3). A linear model showed which there were no relationship between values of the first principal component and cumulative radial growth with last measure made at the end of the last wet season in the valley and summit population, but there were significant relationship between the second principal component and cumulative radial increment on the valley (Fig. 4). However, there was no relationship between PC2 and growth tree summit (Fig. 4).

Phenology

The monitored trees did not flower during the study period. The production of leaf buds, presence of leaves and periods of deciduousness were all distributed non-randomly throughout the year (Rayleigh tests, $P < 0.001$) and their timing was similar for trees growing in summit and valley positions in all cases (Watson-Williams tests, $P > 0.5$; Table 6). As expected, the deciduous period corresponded to the dry season, and new leaf buds appeared at the beginning of the wet season (end of October and beginning of November).

DISCUSSION

Stem increment and precipitation

In this study we characterized the determinants of temporal and spatial variation in growth rates of *Dalbergia nigra* trees over a two-year period. In both valley and summit positions, tree growth rates declined to zero during the dry seasons, which provides strong evidence that low water availability during the dry season limits the growth of *D. nigra*. Previous studies on seasonal performance conducted in the tropical forest have revealed that dry-season conditions are an important driver of growth for populations of plants (Baker et al 2002, Rossato et al 2009, Toledo et al 2012). Baker et al 2002 reported that trees better supplied with water in valley positions tended to shrink less the effect of topographic position on dry season diameter change. In some instances we observed shrinkage of the trunk during the dry season months, especially for individuals growing on the summit. Negative increments during the dry season in tropical trees corresponds to shrinkage of the stem due to water loss before wood growth recommences at the beginning of the new wet season (Worbes 1999). Shrinkage and swelling of tree stems are induced by the development of water potential gradients between the phloem and the conducting xylem, producing water fluxes between these two tissues (Dobbs & Scott 1971; Molz & Klepper 1972). The reversible contraction and dilation of cells, mainly in the secondary phloem and cambial cells, associated with changes in stem water and temperature, results in short-term fluctuations in stem diameter (Kozlowski *et al.,* 1991). Thus, seasonal decreases in stem diameter are caused by water loss from elastic storage elements such as the phloem, cambium and sapwood parenchyma (Holbrook 1995). The higher frequency and greater magnitude of negative growth increments for trees in the summit positions suggests that these sites are associated with lower values of dry season soil moisture availability than adjacent valley sites. Similar results have been reported for trees growing across topographic moisture gradients in southern Ohio (Anning et al 2013).

Topography and soil fertility

Soil moisture and nutrient availability were greater in valley than summit sites, and either set of factors may have contributed to differences in radial growth of adult *D. nigra* trees during the wet seasons. Topography has a significant effect on the soil water regime in seasonal tropical forests (Oliveira-Filho *et al.* 1998; Daws *et al.* 2002, Baker *et al.* 2003b) and is an influential factor in the distribution of soil nutrients and other components of soil fertility (Baker *et al.* 2003b; Luizão *et al*. 2004). Thus trees growing under uniform climatic conditions may respond quite differently to seasonal or longer-term changes in rainfall depending on the interaction of topography and nutrient and water availability (Oberhuber & Kofler 2000, Johnson & Miller 2006). In valley sites, growth rate during the wet season was correlated with soil moisture content and a general soil fertility gradient associated with increasing base saturation and higher sand content, which suggests that fine-scale soil properties uncorrelated with topography may also contribute to growth rate during periods of high rainfall when soil water availability might be expected to be non-limiting.

Seasonal climatic changes influence tree physiology as well as chemical and biological processes in forest soils (Collignon 2012). In these ecosystems lack of water may result in a decrease in nutrient uptake by roots and in the movement of these nutrients to shoots (Bradford and Hsiao 1982), and act as an obstacle to microbial activity (Sardans 2006). These changes directly affect soil characteristics (e.g., pH, organic matter composition and inorganic ion concentration) and impact on availability and forms of Al in soils (Collignon 2012), because a decrease in soil water content during seasonal droughts can increase Al to toxic levels for the tree growth (Schier and McQuattie 2000). The low content of base cations, especially calcium (Ca), and high Al concentrations, may affect root growth and the absorption of water and nutrients by plants, which are often sufficient to cause a reduction in the yields of agricultural crops on acid soils (Sumner et al. 1986; Marsh and Grove 1992; Tang et al. 2003). The greater Al concentration and Al saturation in soils on the summit than in the valley was an important difference defining soils in the two topographic positions. The effects of high soil Al concentrations on tropical tree growth are not well explored but Al toxicity is known to affect many metabolic and physiological processes that may result in a reduction in tree growth (Schier & McQuattie 2000, Slugenova *et al*. 2011).

Phenology

Topography did not influence vegetative phenology of *D. nigra*. Although elevation may be a primary factor characterizing topography-mediated patterns of plant phenology (Bolstad *et al.* 1998, Hwang *et al.* 2011), the difference in elevation between summit and valley positions at our study site was insufficient to induce an observable response.

In our study, radial increment has a strong temporal association with individual phenology and rainfall seasonality, in agreement with other studies (Borchert 1991, 1999; Silva *et al.* 2002, Marcati *et al.* 2008, O'Brien *et al.* 2008, Rossatto *et al.* 2009, Toledo *et al.* 2012, Cardoso *et al*. 2012). As expected, leaf deciduousness occurred at the onset of the dry season, which reflects the evidence that water shortage is a proximal cue for leaf shedding (Borchert 2002). The association of leaf fall with the drier months suggests that reduction of canopy size is a water conservation mechanism that allows plants to minimize transpiration area (Boyer 1970, Morellato *et al.* 2000, Marques & Oliveira 2004, Cardoso *et al*. 2012, Toledo *et al*. 2012).

In common with this strategy, *Dalbergia nigra* avoids water stress during the dry season by shedding leaves, and this phenomenon is coupled with a pause or decrease in radial increment. A similar relationship between girth increment and phenology has been widely reported for trees growing in seasonal tropical environments elsewhere (Lisi *et al.* 2008, O'Brien *et al.* 2008, Cardoso *et al.* 2012, Toledo *et al.* 2012).

CONCLUSION

Adult *Dalbergia nigra* trees showed zero or negative mean monthly growth rate during the dry season and positive growth during the wet season. For trees growing under the same climatic conditions, radial growth rates of trees growing in a valley site were greater than those on a summit position. The high concentration of Al and low soil fertility at the summit may cause the lower radial growth of *D. nigra* when the soils are fully hydrated during the wet season. In addition, the wet (growing) season is shorter on summits because the sites drain more quickly at the beginning of the dry season. This suggests that the higher growth rates in the valley site are strongly dependent on the soil moisture content and fine-scale soil nutrient availability. Understanding the relationship between topographic position, soil fertility and soil moisture is important for predicting the effects of future habitat alterations and climate change on tree growth, and is therefore relevant to conservation polices for endangered species such as *D. nigra*. In addition these interactions provide insights for species-site matching in programmes that attempt to rehabilitate areas with native vegetation.

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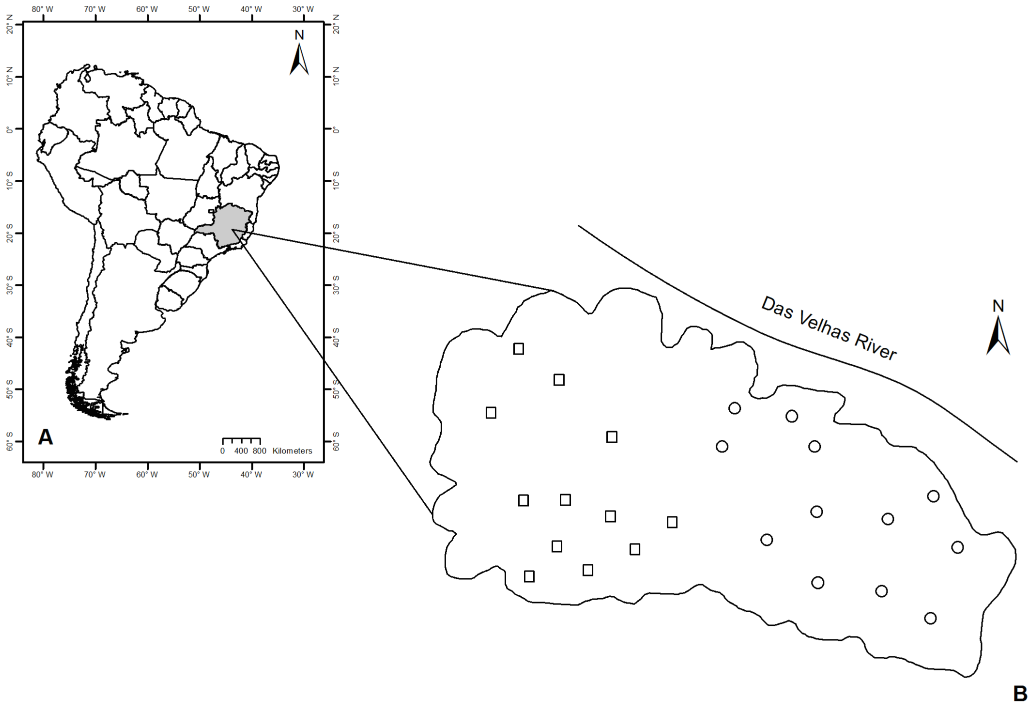

Fig. 1. (a) Map of South America with the location of the fragment of Atlantic rain forest in Sumidouro State Park (b) the locations of *Dalbergia nigra* tree (squares represent trees sampled on the summit and circules represent trees sampling in the valley).

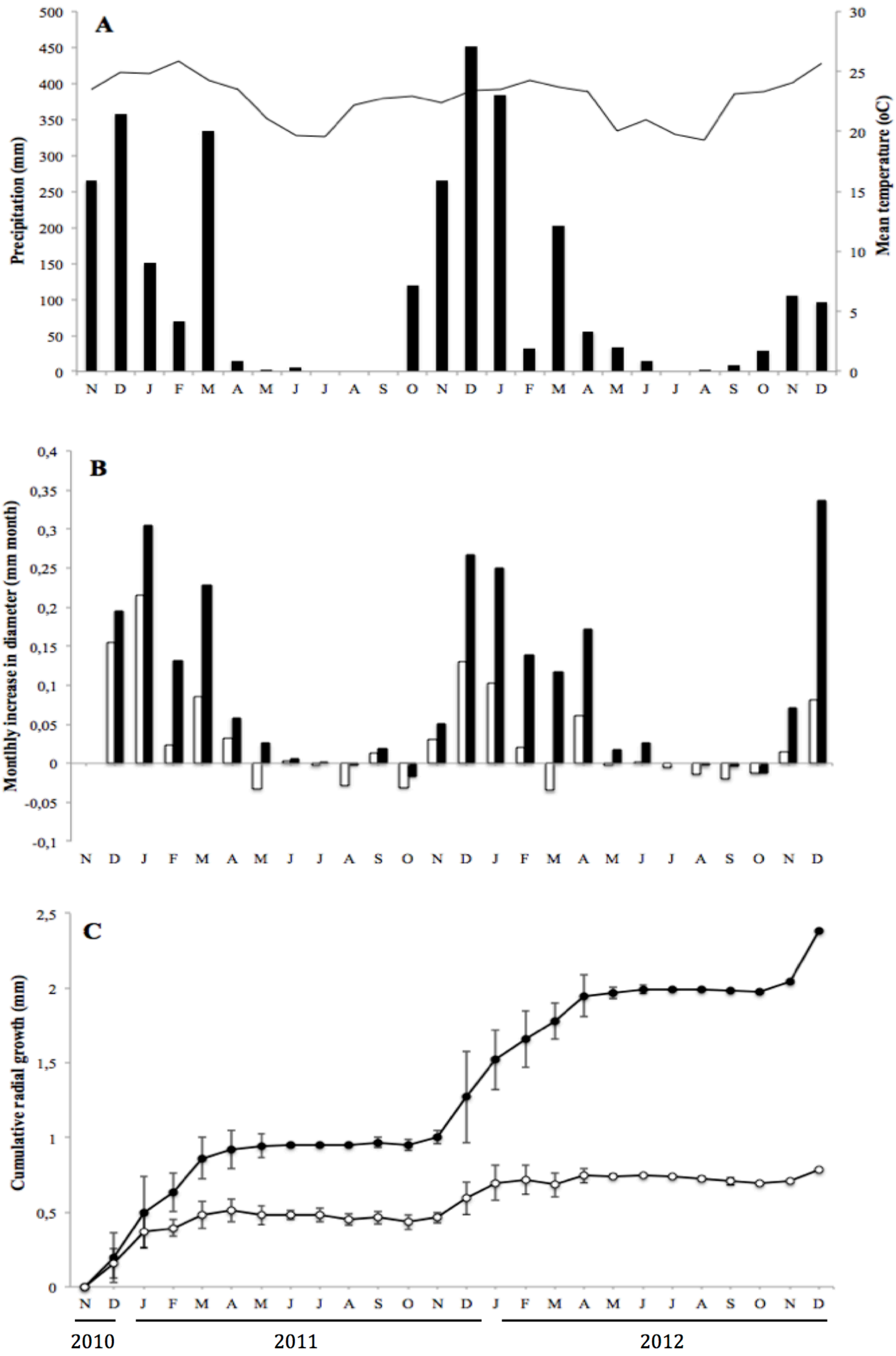

Fig. 2 a Precipitation (bars) and daily mean temperature (line). **b** Monthly diameter increment and rainfall during the study period. Bars indicate mean growth rates for valley individuals (black) and summit individuals (white). **c** Cumulative radial growth for the valley (full circle) and summit (open circle) of *D. nigra* during 24-month. The line bars represent standard errors.

Table 1. Soil physical and chemical properties (mean, standard deviation) for soil 5 - 20 cm depth beneath summit and valley positions in Atlantic Forest (P = phosphorus, K = potassium, Ca = calcium, Mg = magnesium, Al = exchangeable aluminium, V = base saturation, m = aluminium saturation). Values are mean ± SE. $^{*}P < 0.05$ / $^{**}P < 0.01$ / $^{***}P < 0.005$ (n = 10).

Variable	Summit	Valley	*P*
Clay - %	39.76 ± 10.35	22.73 ± 3.86	**
Silt - %	21.08 ± 4.93	35.55 ± 5.72	***
Coarse sand - %	6.08 ± 0.78	0.88 ± 0.59	***
Fine sand - %	33.06 ± 5.47	40.83 ± 7.75	
Base saturation %	38.15 ± 13.3	67.41 ± 4.6	***
Al saturation %	23.82 ± 15.1	0.94 ± 0.15	**
pH (H_2O)	5.18 ± 0.37	5.78 ± 0.19	*
Organic C - g/kg	41.0 ± 6.7	46.8 ± 8.2	
N - g/kg	2.0 ± 0.2	2.2 ± 0.3	
P (mg/dm^3)	1.7 ± 0.25	6.14 ± 0.79	***
K (mg/dm^3)	96 ± 19.22	46.8 ± 9.30	***
Ca ($mmol_c/dm^3$)	28.5 ± 1.06	45.6 ± 4.5	**
Mg ($mmol_c/dm^3$)	6.8 ± 1.4	11.5 ± 1.2	***
Na	0.2 ± 0.00	0.4 ± 0.00	***
Al ($mmol_c/dm^3$)	10.7 ± 0.62	0.5 ± 0.00	**
H+Al ($mmol_c/dm^3$)	63.0 ± 17.2	28.3 ± 5.0	**
Total exchangeable bases (TEB)	37.8 ± 12.1	57.33 ± 0.49	*
Cation exchange capacity (CEC)	100 ± 7.1	86.6 ± 6.1	**
Effective cation exchange capacity (t)	48.5 ± 6.4	58.9 ± 4.9	*

Table 2. Mean (± SE) soil moisture content (%) for 50 randomly selected summit and valley positions in the Sumidouro State Park, Brazil, comparing wet and dry seasons in two successive years. Values of t and df are presented for t tests comparing between topographic positions with P values indicated as follows: *** *P* < 0.001

		Topographic position				
year	Season	Summit	Valley	t	df	*P*
2011	Wet	5.48 ± 3.67	23.47 ± 5.95	-11.85	98	***
	Dry	3.74 ± 1.74	6.26 ± 2.29	-4.04	98	***
2012	Wet	4.52 ± 5.92	23.30 ± 5.28	-13.90	98	***
	Dry	1.49 ± 2.57	6.62 ± 2.64	-8.03	98	***

Table 3. Summary of ANOVA of linear mixed-effects models for tree growth and the precipitation of *Dalbergia nigra* for summit and valley habitats in a fragment of Atlantic Forest. F-statistics, and degrees of significance are reported.

	2011	2012
Summit	40.36***	21.41***
Valley	46.11***	62.31***

Table 4. Results of relationship between moisture soil and the final radial increment for each season of *Dalbergia nigra* for summit and valley habitats in a fragment of Atlantic Forest. Degrees of significance: $^{***}P < 0.001$; $^{**}P < 0.01$; $^{*}P < 0.05$.

		Topographic position			
		Summit		Valley	
year	Season	r^2	*P*	r^2	*P*
2011	Wet	0.57	0.004	0.67	0.006
	Dry	0.04	0.53	0.36	0.08
2012	Wet	0.74	0.001	0.38	0.05
	Dry	0.09	0.38	0.44	0.02

Table 5. Correlations of 18 topsoil variables (0–5 cm) and two ordination axes produced by Principal Components Analysis for summit and valley (m = aluminium saturation).

	Summit		Valley	
Variables	Axis 1	Axis 2	Axis 1	Axis 2
Clay	-0.13	0.37	-0.01	0.34
Silt	0.20	-0.28	-0.33	0.06
Coarse sand	-0.11	-0.35	-0.06	0.26
Fine sand	0.08	-0.40	0.26	-0.23
Base saturation	0.28	-0.02	-0.16	-0.31
m	-0.29	0.02	-0.07	0.31
pH in water	0.26	-0.20	-0.17	-0.29
Organic C	-0.14	-0.37	-0.32	-0.02
N	-0.15	-0.38	-0.28	-0.04
P	-0.26	-0.11	-0.01	0.36
K^+	0.18	0.33	0.13	0.32
Ca^{2+}	0.27	-0.01	-0.34	-0.01
Mg^{2+}	0.29	0.05	-0.14	-0.30
Al^{3+}	-0.28	0.03	-0.22	0.23
Al^{3+}+H^+	-0.29	0.05	0.24	0.03
Total exchangeable bases (TEB)	0.28	0.01	-0.34	-0.04
Cation exchange capacity (CEC)	-0.21	0.15	-0.24	0.25
Effective cation exchange capacity (ECE)	0.25	0.05	-0.34	-0.04

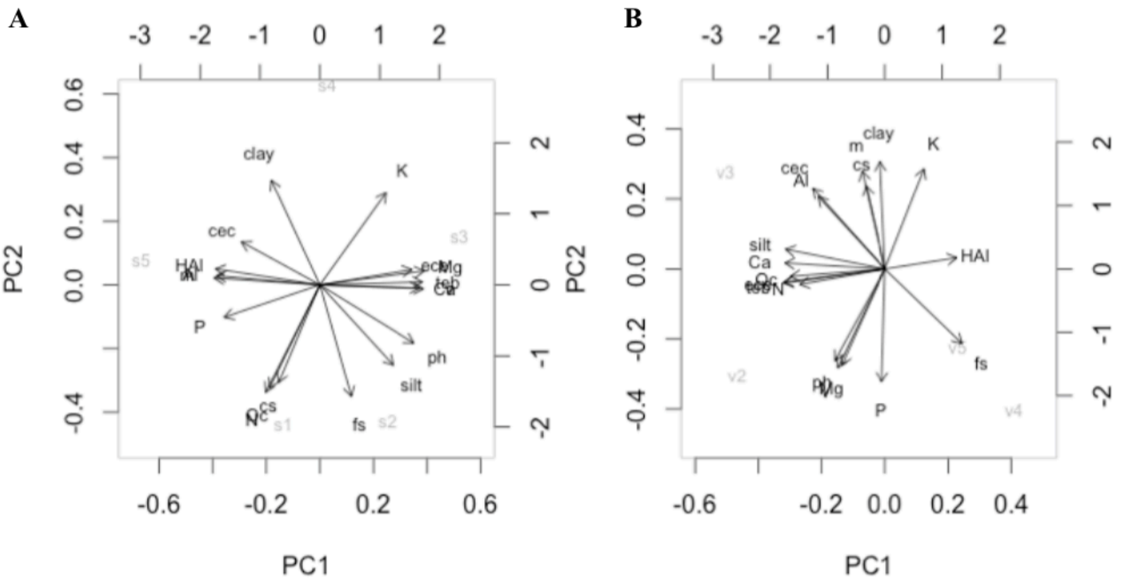

Fig 3. PCA-ordination biplot (PC1 vs PC2) of soil samples from summit (A) and valley (B) habitats in a fragment of Atlantic rain forest. (TEB = Total exchangeable bases, ECE = Effective cation exchange capacity, oc = organic c, P = phosphorus, K = potassium, Ca = calcium, Mg = magnesium, Al = exchangeable aluminium, v = base saturation, m = aluminium saturation).

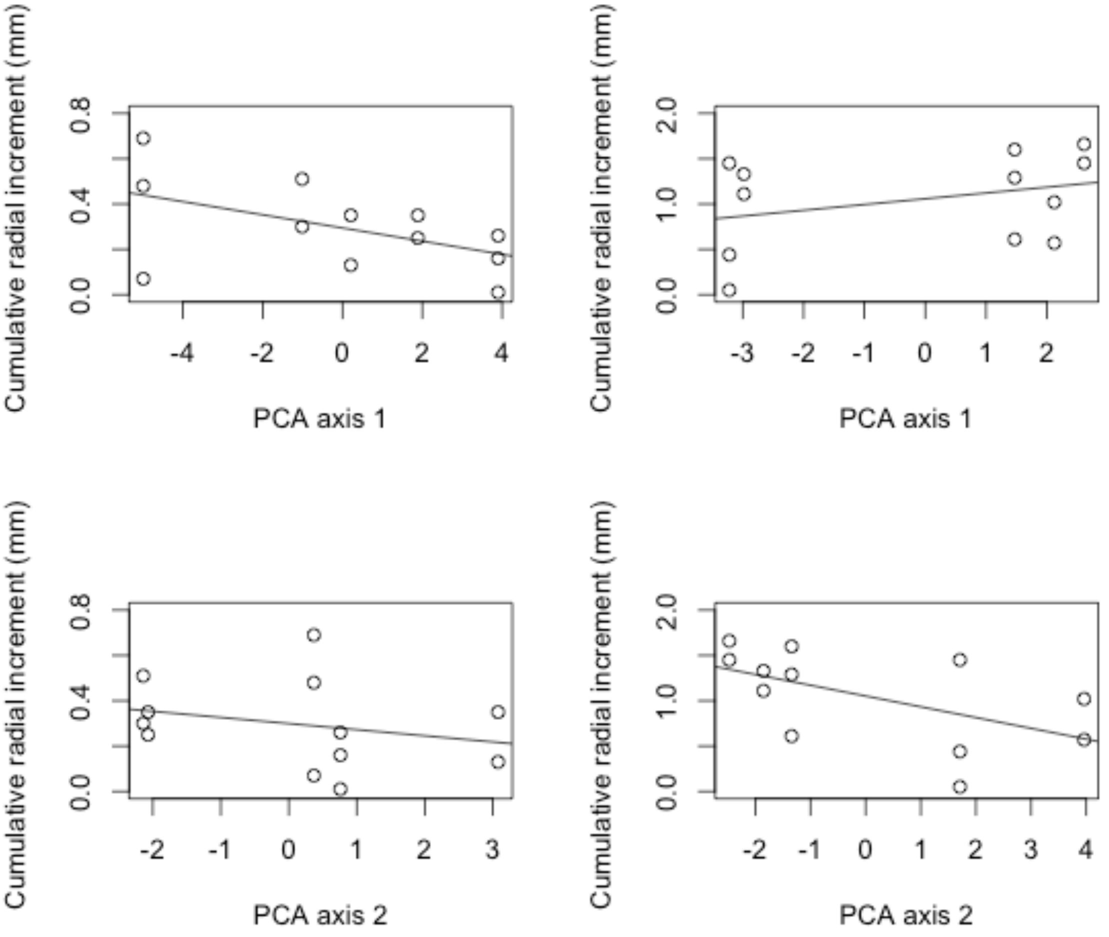

Fig 4. Relationship between PCA axis 1 and axis 2 with last measure made at the end of the last wet season for each tree for summit and valley habitats in a fragment of Atlantic rain forest. A) Summit (PCA axis 1, r^2= 0.25, *F*= 3.50 *P*= 0.09 and PCA axis 2, r^2= 0.06, *F*= 0.71, *P*= 0.41) (B) Valley (PCA axis 1, r^2= 0.10, *F*= 1.20 *P*= 0.29 and PCA axis 2, r^2= 0.31, *F*= 4.53, *P*= 0.05).

Table 6. Circular phenology results for summit and valley of *D. nigra.* All mean angles (u) are significant according to the Rayleigh test ($P < 0.05$)

Phenophase	Topography position	Mean Vector (μ)	Length of Mean Vector (r)	Watson-Williams test (F)	P value	Rayleigh test (P)
Deciduousness	Summit	255.7°	0.89	0.339	0.566	0.001
	Valley	243.0°	0.70			0.001
Bud	Summit	285.0°	0.98	0.079	0.782	0.001
	Valley	301.0°	0.97			0.001
Mature leaves	Summit	80.3°	0.18	0.273	0.607	0.001
	Valley	80.0°	0.23			0.001

Mean Vector value (μ) is the average angle of each phenophase for each topographic position, length of Mean Vector represent the synchrony of each phenophase, Watson-Williams test was used to compare the Mean Vector value between the two topographic positions.

CAPÍTULO 2

Seasonal and fine-scale spatial variation in water availability drive of the threatened tree from the Atlantic Forest

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ABSTRACT

Understanding how seasonal and spatial variation in water availability on threatened species is important for developing successful conservation strategies. We evaluated the fine-scale mortality and growth rate of *Dalbergia nigra* from an area of Atlantic rain forest during the dry and wet season in two topographic positions. We hypothesized that differential *D. nigra* performance across habitats would be lower in the dry season compared to the wet season, due to limited soil water availability. We conducted censuses of *D. nigra* distributed in the summit and valley positions. Tree performance was assessed in relation to variation in percentage of canopy openness, soil fertility, water availability and density of *D. nigra*. Linear mixed effect model was used to test for independent effects of abiotic factors and density on mortality and growth rate of *D. nigra*. The survival and growth rate was lower in the dry than in the wet season and lower in summit than in valley. Density dependence was found to act only on the seedling < 1 cm DAS. The survival of plants increased with size class. Measures of edaphic and abiotic factors differed significantly between topographic positions, but did not relationship between soil gradients with mortality, growth rates and density within of summit and valley. The results of LME showed that mortality rates of *D. nigra* with DAS ≤ 1cm and DAS > 1 ≤ 5 cm increases with the decreases of moisture soil for summit but to valley there was no significant correlation. For size class with DAS > 5 ≤ 11.8 cm there was no correlations of mortality rate with biotic and abiotic factors analyzed. Tree growth was related to soil moisture and percentage of canopy openness to class with DAS > 1 ≤ 5 cm and > 5 ≤ 11.8 cm both at the summit and in the valley during the two years of monitoring. However, to class size with DAS ≤ 1cm there was correlation only to percentage canopy openness. Ours results suggest that seasonal and spatial variation in water availability alter the dynamic and spatial distribution of *D. nigra*.

Key Words: *Dalbergia nigra*, seasonal drought, soil water, growth, mortality rate

INTRODUCTION

Interactions of spatial and temporal variation in environmental conditions are important for driving plant population dynamics. Spatial variation in plant population dynamics has been related to abiotic factors such as nutrient availability (Gotelli & Ellison 2002; Brys et al. 2005; Dahlgren & Ehrlén 2009; Toledo 2011), water availability (Casper 1996; Eckstein 2005; Schleuning et al. 2008; Comita & Engelbrecht 2009, Toräng et al. 2010), and light (Chazdon & Kabakoff 1996, Lee et al. 1996, Nicotra & Chazdon 1999, Montgomery & Chazdon 2002). Particularly water availability is of special relevancy because has the capacity to cause extreme vegetation changes (Allen & Breshears 1998; Hanson & Weltzin 2000) and is factor that determines establishment and growth of seedlings (Condit et al. 1995; Veenendaal et al. 1995; Gerhardt, 1996; Engelbrecht et al. 2005).

However, other factors affect seedling survival to the sapling stage. A range of studies has shown that biotic interactions are often of fundamental importance to plant population dynamics, such as density that may have a negative impact on seedling survival (Augspurger & Kelly 1984, Clark & Clark 1984, Queenborough et al. 2007), juvenile growth and survival (Hubbell et al. 1990, Condit et al. 1992), and adult growth, survival and fecundity (Hubbell et al. 1990, Alvarez-Buylla 1994, Gilbert et al. 1994).

Although mortality is sometimes greatest in locally dry landscape positions (Oberhuber, 2001; Dobbertin et al. 2005; Worrall et al. 2008), microsite variability may interact with density-dependent processes such as competition, or facilitation to produce complex spatial patterns of mortality at the stand and forest scale (Fensham & Holman, 1999; Lloret et al. 2004). Greater mortality can occur, for example, on more favorable sites, where higher tree density drives increased competition for water or elevated insect activity (Guarin & Taylor, 2005; Greenwood & Weisberg, 2008; Fensham et al. 2009;

Horner et al. 2009; Klos et al. 2009). In addition, population dynamics may vary substantially among populations and years within the same plant species (e.g. Pascarella & Horvitz 1998; Warton & Wardle 2003; Jongejans & de Kroon 2005) and this variation may be related to changes in population density. Thus, knowledge of dynamics in natural populations and an understanding of the factors involved in recruitment in relation to microsite types that are conducive to seedling establishment is an important consideration in reclamation and is essential in implementing conservation strategies (Conte et al. 2003, Elmarsdottir et al. 2003).

Here we examine how seasonal and spatial variation in water availability in two topographic positions drive mortality and growth of a natural population of *Dalbergia nigra*, a threatened and endemic species from the Atlantic Forest. The fine-scale variation in resource availability may also be the result of differential mortality and growth rate of *D. nigra*. Four hypotheses were formulated: (1) *D. nigra* trees show differential density along of two different topographic positions; (2) the degree of density of *D. nigra* is sufficient to regulate populations at observed densities (3) Survival and growth would be lower in the dry season compared to the wet season, due to limited soil water availability (4) soil fertility do not have a strong effect on the population dynamics as compared to the soil water availability

METHODS

Study site

The study was carried out in an area of semi-deciduous forest in a fragment of Atlantic rain forest in Sumidouro State Park (SSP) in the state of Minas Gerais, southeastern Brazil (19° 32 '25.82" S, 43° 55' 09.79"W) (Fig. 1). The SSP covers approximately 2000 ha and is mainly composed of Atlantic rain forest and Cerrado (savanna) vegetation (de Andrade 2009). The SSP was formerly used for livestock grazing and human settlements, but since the implementation of a management plan in 2010 these activities have ceased and the area is undergoing natural regeneration (Tavares 2010).

The area is classified as having a semi-humid warm tropical seasonal climate with a pronounced dry season of 3-4 months (Nimer 1989). The average annual rainfall is 1273 mm, concentrated between October and March, and the average annual temperature is 22.5 °C. Climate data have been obtained for two years from a meteorological station approximately 27 km from the study area. The 11 ha fragment selected for this study is located 50-100 m from a river and contains remnant Atlantic rain forest (Fig. 1). Within the fragment two areas of approximately 5 ha were identified possessing contrasting topographic positions, here termed valley and summit, based on their elevation. The areas were separated by a slope and differed in elevation by 10 -15 m.

Study species

Dalbergia nigra (Vell.) Allemão ex Benth. (Fabaceae-Papilionoideae), commonly known as Brazilian rosewood, is an endemic species of the Atlantic Forest that occurs in eastern Brazil. It produces valuable timber but this resource has been over-exploited, and the species is listed as Vulnerable by IUCN (2011) and international trade of its timber has been prohibited since 1992 (CITES 1992). Despite this vulnerability due to reduced population sizes, a high genetic diversity was found among individuals growing in large protected reserves (Ribeiro et al. 2005, 2011). The pollen is likely dispersed by bees (R. A. Ribeiro, personal communication) and their seeds are dispersed by the wind (Carvalho 1994).

Spatial distribution and recruitment

Within the fragment of the Atlantic Forest, where *D. nigra* is abundant, we monitored of established seedling of *D. nigra* to compare demographic rates (growth, mortality, and recruitment rates) between two topographic positions.

***Plots* -** We conducted censuses of *D. nigra* in an area randomly allocated of ten plots of 50 x 20 m, in which five plots were located at summit and five plots at valley (Fig. 1). All plants ≥ 1 cm of DAS (diameter at soil level) were marked with coloured toothpicks and their spatial distribution within of plot annotated.

Subplots - Ten circular subplots with a radius of one meter were distributed systematically within each plot of 50 x 20 m (Fig. 1). All seedling (< 1 cm DAS) of *D. nigra* were tagged inside the circular plots with a numbered label.

Censuses of these plots were conducted in October/2010 when the first census was carried out when plots were established, February/March 2011/2012 (end rainfall season) and September 2011/2012 (end dry season). In each census, we classified seedling as alive or dead, measured DAS, counted numbers of leaves < 50 leaves, height and occurrence of herbivory noted. *D. nigra* plants analyzed were defined as dead by the absence of leaves, sap and loss of bark. Also classified as dead were those trees that disappeared and those whose stems had broken or had no sap below the point of measurement.

According to the results from experimental plantings with the species condensed by Carvalho (1994), individuals with diameter at breast height (DBH) ≥ 11.8 cm are potentially reproductive. Considering this study, we separated our sampling in four size classes: one including individuals with DAS ≤ 1 cm, which are predominantly seedlings (Fig. 3a), a second class with individuals with DAS ≥ 1.1 ≤ 5.0 cm and a third class with DAS ≥ 5.1 ≤ 11.8 cm which are predominantly saplings, and a fourth class including individuals with DBH ≥ 11.8 cm, which are predominantly adults (Fig. 3b). The last class was not analyzed in this study.

We calculed mortality rates as $M = 1- (N_0 / N_1)^{1/t}$,where N_0 and N were numbers of individuals alive at the start and end of the survey period, respectively (Sheil et al. 1995).

Relative growth rate (RGR) for diameter at soil level were calculated for each season using the following equation (Kramer et al. 1979): $RGR = (\ln X_2 - \ln X_1] / \Delta t)$, where X_1 and X_2 denote variables measured at the time of the first and second assessments, respectively and Δt is the time interval between the two measurements. We examined RGR for all individuals alive of seedlings and saplings during the entire study period.

Seedling survival was analyzed over two census intervals, the dry-season interval and the wet-season interval. We combined observations of survival across two dry seasons in the analysis for the dry-season interval and across two wet seasons in the analysis for the wet-season interval.

Abiotic factors

We defined the abiotic factors using three environmental variables at each seedling plot: light (canopy openness), soil texture and fertility and soil water content. .

Soil Analysis - Soil samples (0-20 cm depth) were collected at five randomly selected locations in both the summit and valley areas. Each sample was made up of five bulked subsamples, collected at a random location within a radius of 20 m, and homogenized to form one composite sample. The textural and chemical analyzes of the samples were conducted at the Instituto Mineiro de Agropecuária (IMA). Analysis of soil texture was conducted using the pipette method (Claydon, 1989). Soil acidity in distilled H_2O was measured with a pH meter. Total N was determined using the wet oxidation (Kjeldahl) method, which converts organic N to ammonium (NH_4^+) for colorimetric measurement. Total organic C was determined by the calorimetric method. The determination of available phosphorus was conducted using the Mehlich 1 method (Nelson et al., 1953) and measured by calorimetric method. K and Na were extracted by the Mehlich 1 method (Nelson et al., 1953) and measured by flame photometry. Ca and Mg were measured by atomic absorption spectrophotometry after extraction with a concentrated 1N KCl solution. Cations were extracted in a 1 M KCl solution at unbuffered pH of the soil (EMBRAPA, 1997).

Water soil content - We quantified soil water availability, volumetric soil water content at 10 cm depth was measured at 100 subplot (50 in each topographic position), using the FIELD SCOUT TDR 100 soil moisture meter (Spectrum technologies, USA). The measurements were performed at the end of the rainy season (first half of April) and end of dry season (first half of September) of each year in 2011 and 2012.

Canopy openness - In each censuses of seedling, a hemispherical photograph was taken from the center of each circular subplot. Photographs were taken 1.30 m above the ground, in uniformly overcast conditions in the early morning or late afternoon, using a fish-eye lens (Nikon FC-E9) and a Nikon E5400 digital camera. Images were analysed using a Gap Light Analyzer 2.0 (http://www.rem.sfu.ca/forestry/) to calculate percentage canopy openness.

Data analysis

Principal Components Analysis (PCA) - We used PCA as the ordination method to describe major gradients in the soil, using a subset of 19 variables (see Table 1 for a list of the soil variables recorded in each plot). Linear model analysis was used to test for the effects of the first PCA resultant component (PC1) on tree mortality rates, RGR and density for each topographic position. The PCA was utilized to determine whether soil variation within each topographic position contributes to variation in mortality and growth rate. We used principal components analysis (PCA) to reduce the dimensionality of the 19 topsoil variables. Since moisture soil and the soil fertility gradient (PC1) were strongly correlated ($r^2 = 0.84$; $P < 0.001$), they were not included in the same model. We used only moisture soil in a model to determine if alone could explain the spatial variation in tree mortality and RGR.

The differences in the moisture soil and canopy openness between different topographic positions were tested with t-tests. The paired t- test was performed to examine the RGR and mortality rate in different topographic positions during the dry and rainy season. Linear mixed-effects (LME) models implemented using the nlme v.3 package (Pinheiro et al. 2009) for R version 3.0.2 (R Development Core Team 2013) to evaluate the relationship between dependents variables as growth rate and mortality rate on independents variables (canopy openness, soil nutrient concentrations, water availability and density of *D. nigra*). All LME models used plots nested within sites as random effects.

RESULTS

Seasonality

Total annual rainfall during the first year (Oct. 2010-Sep. 2011) of the study was 1.318 mm and during the second year of the study (Oct. 2011-Sep. 2012) was 1.176 mm (Fig. 2). The mean air temperature during the first year was 23.04^{o}C and the second year 22.23^{o}C. There was a marked dry season from April to October, with 6 months having less than 50 mm of rainfall, with a mean dry season rainfall of 20.12 mm in 2011 and 20.14 mm in 2012. During the wet season from November to March there was a mean rainfall of 235.16 mm in 2010-2011 and 267.38 mm in 2011-2012 (Fig. 2). Although there was a great variation in seasonal rainfall during the year, there was little variation in temperature with the mean air temperature during the dry season 21.68^{o}C (2011) and 21.39^{o}C (2012) and 24.67^{o}C (2010-2011) and 23.47^{o}C (2011-2012) during the wet season.

***Edaphic and environmental variation* -** Soil variables varied widely among topographic position (Table 1). Summit soil that has a higher content of clay and coarse sand is more acidic and concentrations of H+ Al, Al^{3+}, with higher values of aluminium saturation. The concentrations of Mg^{2+}, P, K, the values of the SB, v% and silt were higher in the valley.

The ordination analysis revealed two main soil gradients in the study area for summit and valley (Table 2). The first ordination axis (PC1) explained 60% of the variation and the second axis (PC2), which explained 26% of the variation in the dataset in summit. There were two main variation axis in valley, in total, explained 96% of the data set variability. PC1 contributed to 58% of the variance and PC2 contributed to 38% (Table 2). Although the two sites experience the similar climatic variations, there was clear difference in the soil water availability among the two topographies. Soil water availability at summit was consistently lower than at valley, both in the dry and the wet season (Table 3, $P < 0.001$). Percent of canopy openness was significantly higher at summit than valley only in the first dry (Table 3).

Density – There was not significantly variation in abundance among *D. nigra* plants with DAS ≤ 1cm at summit and valley (Fig. 3a, $P > 0.05$). However, there was a high degree of variation in abundance of individuals of *D. nigra* with DAS ≥ 1 cm with 3 orders of magnitude higher in valley than summit (Fig. 3b, $P < 0.01$).

Mortality – The best-fit model for survival included season, topographic position and density of *D. nigra* individuals. Seedling mortality peaked during drought season, being drought the most important cause of mortality (Fig 4). The survival was lower in the dry than in the wet season and lower in summit than in valley of all size class (Fig 4, $P < 0.05$). The survival of plants increased with size class. Mortality of adult was rare during the period of study, only two adult of *D. nigra* died.

Growth - Relative growth rates of *D. nigra* were significantly lower in the dry season than in the wet season. In addition, negative values of the relative growth rates of *D. nigra* individuals were significantly higher in plots on the valley than in plots on the summit during the dry season of all size class (Fig. 4).

Correlations with biotic and abiotic factors **-** Measures of edaphic and environmental variables differed significantly between sites, but soil gradients showed no significant within-site topographic variation. There was no relationship between soil gradients with mortality, growth rates and density within of summit and valley (Table 4). Thus, the magnitude of differences in soil gradients between summit and valley has created a stronger contrast in these factors between than within sites. The results of LME showed that the mortality rate *D. nigra* plants ≤ 1 cm was significantly related to density to both topographic positions, but there was no significant correlation with others size class. The mortality rates of *D. nigra* with DAS ≤ 1cm and DAS > 1 ≤ 5 cm increases with the decreases of moisture soil for summit (Table 5) but to valley there was no significant correlation. For size class with DAS > 5 ≤ 11.8 cm there was no correlations of mortality rate with biotic and abiotic factors analyzed. Tree growth was related to soil moisture and percentage of canopy openness to class with DAS > 1 ≤ 5 cm and > 5 ≤ 11.8 cm both at the summit and in the valley during the two years of monitoring (Table 5). However, to class size with DAS ≤ 1cm there was correlation only to percentage canopy openness.

DISCUSSION

We found strong evidence that spatial and temporal variation in soil water availability more than soil nutrients drive population dynamics of *D. nigra*. As we had hypothesized, seedling survival and growth rates were lower in the dry season than in the wet season, indicating that dry-season conditions were strongly limiting performance compared to wet-season conditions. In all wet season, growth rate increased during the wettest period of the year, suggesting that the maximum growth rates occur when soil humidity is the highest.

Seasonal environmental changes in tropical forests mainly involve rainfall and consequently soil moisture (Comita & Engelbrecht 2009). Soil moisture is frequently recognized as the most important resource affecting vegetation structure and organization in different ecosystems (e.g., Rodrigues-Iturbe et al. 2001). Previous studies on seasonal performance conducted in the tropical forest have revealed that dry-season conditions are an important driver of establishment and growth of seedling throughout the seasonal tropics (Condit et al. 1995; Veenendaal et al. 1995; Gerhardt 1996; Engelbrecht et al., 2005, Lewis & Tanner 2000, McLaren & Mc Donald 2003, Bunker & Carson 2005, Comita & Engelbrecht 2009, Philip et al. 2010). Engelbrecht et al. (2007) reported that seedling drought sensitivity was associated with the spatial distribution of species and the water stress gradient in Panamanian forests on local and regional scales. Comita & Engelbrecht (2009) also found lower growth and higher mortality in the dry season relative to the wet season in a seasonal forest in Panama. Our study suggests that the drought also affects the mortality rate of *D. nigra* plants.

As we described soil moisture become a limiting factor for *D. nigra* growth during dry periods. Ours results also demonstrates that there is a significant variation in RGR and mortality over both temporal and spatial scales. Specifically, growth and survival of *D. nigra* was greater in valley compared to summit. According to Comita & Engelbrecht 2009, the effect of the dry season should be especially pronounced in habitats that retain less moisture. Thus, the difference between stand-level mortality and growth rate during the dry season may be determined by the balance between the soil moisture in each topographic position. In addition, the high associations of *D. nigra* density with topography at each site suggests that differences in soil water availability alone may be sufficient to limit distributions.

This study has clearly quantified the impact of density on the survival of *D. nigra*. The supply of resources (light, water and nutrients) availables typically differ between individuals and change through time, as a result of competition with other plants and differences in environmental conditions (such as soil nutrient availability) (Binkley et al 2010). It would appear, however, that density also affects only the survival of the smallest size class. Some authors have described that density-dependent survival tends to be prevalent among species at the seedling stage (Harms et al. 2000; Hille Ris Lambers et al. 2002, Clark & Beckage 2002; Comita & Hubbell 2009; Chen et al. 2010; Comita et al. 2010). Coomes et al. (2003) claimed that competition determines mortality of trees with dbh < 18 cm, and exogenous disturbances affect mortality of trees with dbh >18 cm. Similar factors are driving mortality of trees above the size limit suggested by Coomes et al. (2003) since similar relationships of mortality with soil and topography were found in all size classes with dbh < 20 cm. The conspecific responses to density also have been reported by Matos et al 1999, where the pattern of recruitment is related to the density of adult palms, and mortality amongst both seedlings and juveniles increases with the total density of plants.

Grime (1977) has argued that competition is intense in productive sites, where the potential for rapid growth allows rapid pre-emption of resources, but decreases in intensity and importance in less productive (‘stressed’) sites. The fine-scale variation in resource availability may be the result of differential mortality of plants in two topographic positions. The effect of the dry season was especially pronounced in summit, where retained less moisture soil than valley.

Measures of edaphic variables differed significantly between topographic positions, but did not correlated with mortality and growth rate within valley and summit. Thus, the magnitude of differences in soil nutrient concentrations between summit and valley has created a stronger contrast in these factors between than within sites. The distribution of resources within valley and summit may be too shallow to facilitate a high degree of fine-scale mortality and growth rate, or that larger sample sizes are required to detect them. In general, the effects of fertility are easier to detect when there is large amplitude of nutrient variation (Phillips et al. 2004; Quesada et al. 2009).

However, some studies have shown that soil fertility and topography influence the mortality and growth of plants. Oberhuber & Kofler (2000) found that topographic influences on growth of *Pinus sylvestris* L. According to Toledo et al (2011), soil fertility was the most important predictor of tree mortality in a study in a tropical forest. In contrast, in a study in a lowland dipterocarp forest did not find a clear relationship between edaphic conditions and increased mortality during the drought or pre-drought periods (Itoh et al 2012). Soil fertility may affect tree mortality indirectly because light-demanding and fast-growing pioneer species are favored under higher nutrient supply (Lawrence, 2003; Ferry et al. 2010). Thus, light may have a stronger influence on plant growth. Some authors have described that light is a major factors limiting plant growth and seedling survivorship in tropical rain forest, notably in the understorey (Chazdon & Kabakoff 1996, Lee et al. 1996, Nicotra & Chazdon 1999).

CONCLUSION

Data in our study support the hypothesis that seasonal and temporal variation in soil water influence mortality and growth rate of *D. nigra*. In addition, this study demonstrates intraspecific variation in tree mortality and growth rate in two topographic positions. Thus, sensitivity to seasonal drought at the seedling and sapling stage could be strongly dependent on the moisture local.

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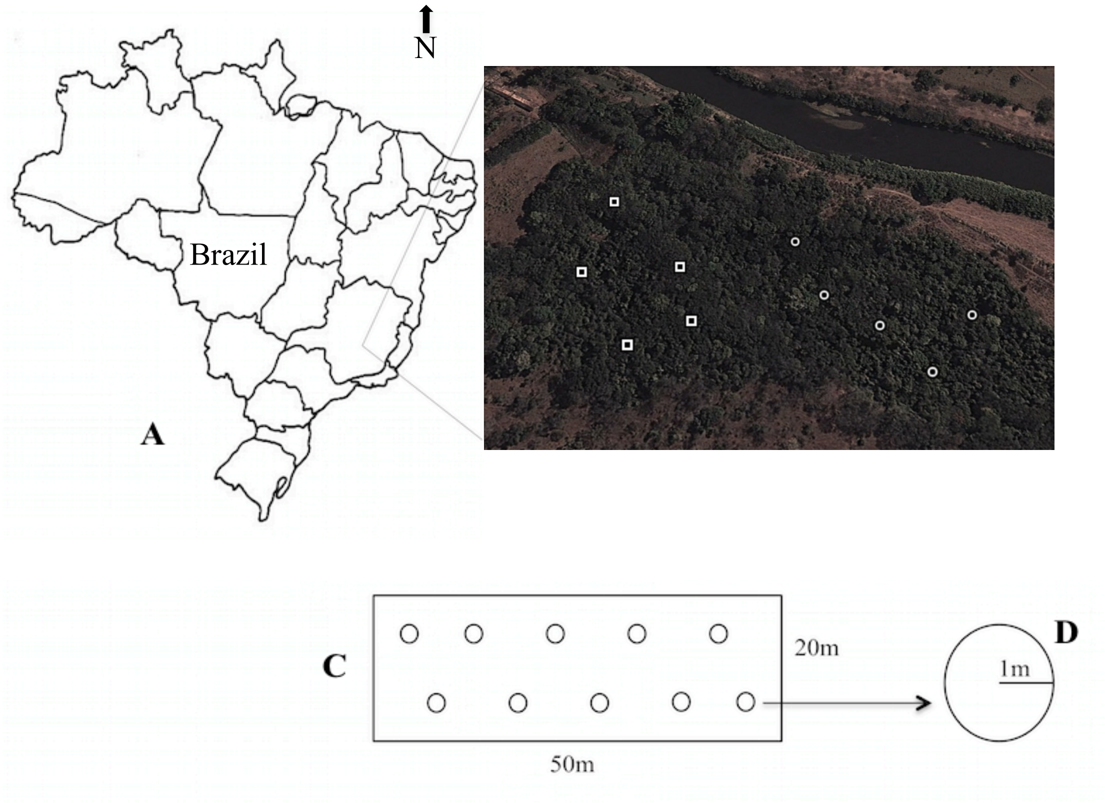

Fig. 1. (a) Map of Brazil with the locations of fragment of Atlantic rain forest in Sumidouro State Park (b) the locations of plots (square summit, circulo valley) (c) Plots with subplots distributed systematically within each plot of 50 x 20 m (d) circular plot

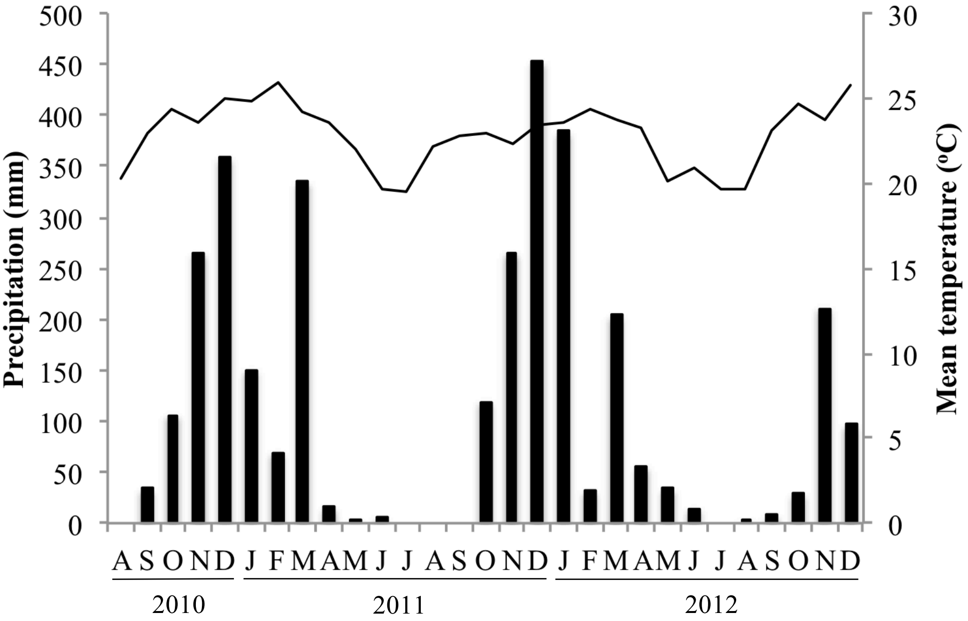

Fig. 2. Precipitation (bars) and daily mean temperature (line)

Table 1. Soil physical and chemical properties for soil 0 - 20 cm beneath summit and valley in Atlantic Forest (OM = organic matter, P = phosphorus, K = potassium, Ca = calcium, Mg = magnesium, Al = exchangeable aluminium, V = base saturation, m = aluminium saturation. BS= base sum). Values are mean ± SE. **P* < 0.05 / ***P* < 0.01 / ****P* < 0.005 (n = 10)

Variable	Summit	Valley	*P*
Clay - %	39.76 ± 10.35	22.73 ± 3.86	**
Silt - %	21.08 ± 4.93	35.55 ± 5.72	***
Coarse sand - %	6.08 ± 0.78	0.88 ± 0.59	***
Fine sand - %	33.06 ± 5.47	40.83 ± 7.75	
V%	38.15 ± 13.3	67.41 ± 4.6	***
m%	23.82 ± 15.1	0.94 ± 0.15	**
pH (H_2O)	5.18 ± 0.37	5.78 ± 0.19	*
OM - dag/kg	4.10 ± 0.67	4.68 ± 0.82	
N - dag/kg	0.2 ± 0.02	0.22 ± 0.03	
P (mg/dm^3)	1.7 ± 0.25	6.14 ± 0.79	***
K (mg/dm^3)	96 ± 19.22	46.8 ± 9.30	***
Ca^{2+} (cmol. carga/dm^3)	2.85 ± 1.06	4.56 ± 0.45	**
Mg^{2+} (cmol. carga/dm^3)	0.68 ± 0.14	1.15 ± 0.12	***
Na^{2+}	0.02 ± 0.00	0.04 ± 0.00	***
Al^{3+} (cmol. carga/dm^3)	1.07 ± 0.62	0.05 ± 0.00	**
H+Al (cmol. carga/dm^3)	6.30 ± 1.72	2.83 ± 0.50	**
Total exchangeable bases (TEB)	3.78 ± 1.21	5.73 ± 0.49	*
Cation exchange capacity (CEC)	10.09 ± 0.71	8.66 ± 0.61	**
Effective cation exchange capacity (t)	4.85 ± 0.64	5.89 ± 0.49	*

Table 2. Correlations of 19 topsoil variables (0–20 cm) and two ordination axes produced by Principal Components Analysis for summit and valley

	summit		valley	
Variables	Axis 1	Axis 2	Axis 1	Axis 2
Clay	-0.12	0.38	-0.30	-0.06
Silt	0.19	-0.30	-0.04	-0.60
Coarse sand	-0.11	-0.31	-0.04	-0.01
Fine sand	0.07	-0.39	0.38	0.68
v	0.28	-0.02	0.37	-0.19
m	-0.29	0.04	-0.01	-0.00
pH in water	0.25	-0.21	0.01	-0.00
Organic C	-0.14	-0.35	0.00	-0.07
N	-0.15	-0.36	0.00	-0.00
P	-0.26	-0.09	0.06	0.00
K^+	0.18	0.29	-0.77	0.31
Ca^{2+}	0.27	-0.01	0.00	-0.04
Mg^{2+}	0.28	0.02	0.00	-0.00
Na^{2+}	0.16	0.22	0	0
Al^{3+}	-0.28	0.04	-0.00	-0.00
$Al^{3+}+H^+$	-0.28	0.07	-0.04	0.00
Total exchangeable bases (TEB) SB	0.28	0.00	0.00	-0.05
Cation exchange capacity (CEC) T	-0.206	0.18	-0.03	-0.05
Effective cation exchange capacity t	0.26	0.05	0.00	-0.05

Table 3. Moisture soil (%) and % canopy openess results for summit and valley. Values are mean ± SE

Season		Topographic position				
Moisture soil		Summit	Valley	t	df	*P*
2011	Wet	5.48 ± 3.67	23.47 ± 5.95	-11.85	98	***
	Dry	3.74 ± 1.74	6.26 ± 2.29	-4.04	98	***
2012	Wet	4.52 ± 5.92	23.30 ± 5.28	-13.90	98	***
	Dry	1.49 ± 2.57	6.62 ± 2.64	-8.03	98	***
% Canopy openess		Summit	Valley			
2011	Wet	14.90 ± 2.51	14.23 ± 2.54	1.32	98	
	Dry	17.89 ± 2.01	15.22 ± 1.18	6.39	98	***
2012	Wet	16.99 ± 4.82	16.59 ± 2.61	0.51	98	
	Dry	21.52 ± 3.48	21.64 ± 2.29	-0.18	98	

Table 4. Results of linear model relating soil (PC1) with growth and mortality rate of *Dalbergia nigra* at the end of the last rainy season

< 1 cm	**PC1**	
Mortalidade rate	**r^2**	***P***
Summit	0.07	0.64
Valley	0.78	0.04
Growth rate	**r^2**	***P***
Summit	0.62	0.10
Valley	0.11	0.58
< 1.1 > 5 cm	**PC1**	
Mortalidade rate	**r^2**	***P***
Summit	0.32	0.31
Valley	0.28	0.35
Growth rate	**r^2**	***P***
Summit	0.48	0.19
Valley	0.18	0.46
< 5.1 > 11.8 cm	**PC1**	
Mortalidade rate	**r^2**	***P***
Summit	0.48	0.18
Valley	0.72	0.06
Growth rate	**r^2**	***P***
Summit	0.38	0.26
Valley	0.05	0.70

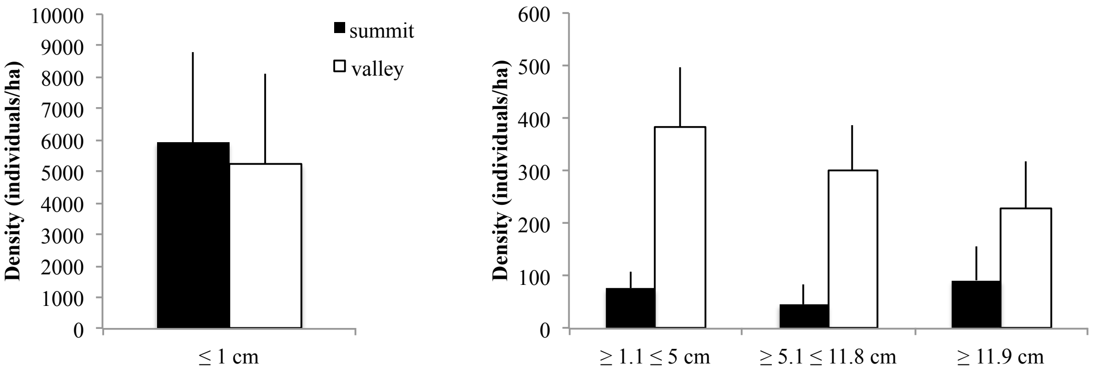

Fig. 3. *Dalbergia nigra* individuals density sampled within plots along two topographic positions (summit= 5 plots; valley = 5 plots). Tree density was calculated as the total number of trees recorded per 0.1 ha plot and converted to individuals/ha

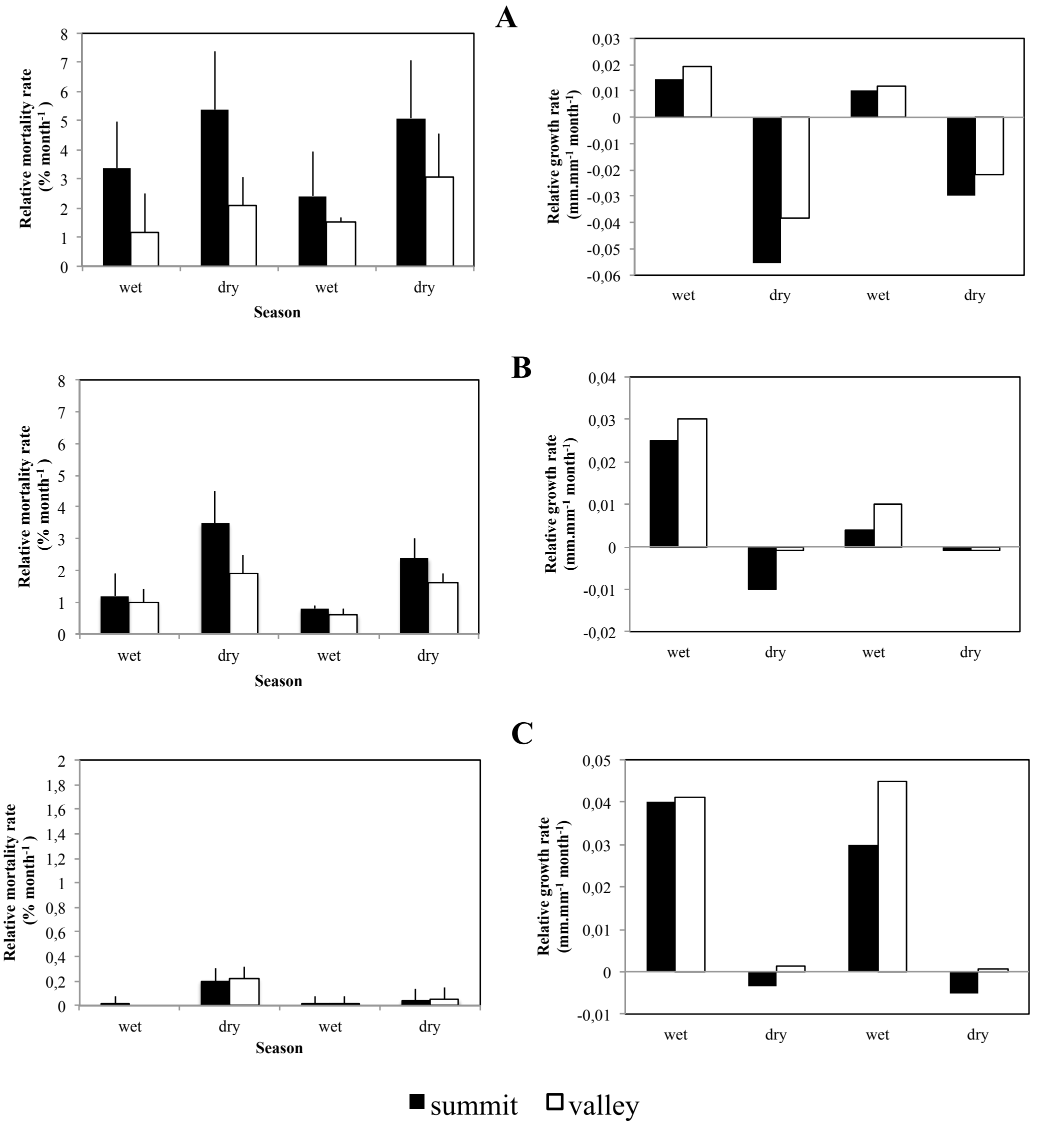

Fig. 4. Relative mortality rate (left) and relative growth rate (right) of *Dalbergia nigra* in the dry and wet season in summit and valley habitats in a fragment of Atlantic rain forest. (A) individual with DAS < 1 cm (B) DAS >1.1 < 5 cm (C) DAS >5.1 < 11.8 cm

Table 5. Summary of ANOVA of linear mixed-effects models relating mortality and growth rate of *Dalbergia nigra* with canopy openness, moisture soil and density for summit and valley in three DAS size class in four census intervals. F-statistics, and degrees of significance are reported. Degrees of significance: $^{***}P < 0.001$; $^{**}P < 0.01$; $^{*}P < 0.05$

	Summit				**Valley**			
≥ 1 cm	**2011**		**2012**		**2011**		**2012**	
Mortality rate	**Wet**	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**
Canopy openess	2.47	1.86	0.44	0.01	0.13	1.52	0.70	1.32
Moisture soil	14.81*	13.87*	14.01*	0.64	0.07	0.75	0.75	0.09
Density	13.08*	13.08*	51.74***	62.08***	23.59*	11.33*	20.11*	32.67*
Growth rate								
Canopy openess	0.03	9.88*	16.32*	2.02	6.60	1.25	9.98*	9.78*
Moisture soil	0.00	1.04	0.09	0.70	0.03	1.05	1.68	0.02
Density	1.22	1.25	0.20	1.34	0.0	0.90	0.15	0.91

≥ 1.1 ≤ 5cm	**Summit**				**Valley**			
	2011		**2012**		**2011**		**2012**	
Mortality rate	**Wet**	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**
Canopy openess	1.71	1.98	0.67	0.53	1.02	2.12	1.01	0.17
Moisture soil	10.01*	31.09*	21.72*	28.56*	13.02*	31.23*	4.45	30.92*
Density	4.22	1.20	1.36	6.06	2.67	3.04	2.04	3.01
Growth rate								
Canopy openess	12.02*	2.17	3.67	0.37	9.98*	1.25	1.01	4.25
Moisture soil	18.02*	10.02*	22.32*	9.88*	1.23	13.08*	1.68	12.88*
Density	0.02	0.8	0.0	0.33	0.45	0.00	0.92	0.04

≥ 5.1 ≥ 11.8	**Summit**				**Valley**			
	2011		**2012**		**2011**		**2012**	
Mortality rate	**Wet**	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**
Canopy openess	0.29	0.41	0	0.12	0.98	0.01	1.32	0.00
Moisture soil	1.22	0.02	0.21	0.39	0.44	0.12	0.64	0.66
Density	0.32	0.09	0.00	0.05	1.21	0.00	0.44	0.22
Growth rate								
Canopy openess	0.34	2.23	0.12	0.37	2.23	1.12	2.02	2.05
Moisture soil	14.01*	22.02*	3.32	14.08*	11.12*	15.21*	1.68	3.88
Density	0.34	0.01	0.20	0.00	0.03	0.14	0.15	1.25

CAPÍTULO 3

Effects of ecological factors on growth and wood density across diameter size classes of *Dalbergia nigra* (Vellozo) Freire Allemão ex Bentham a threatened tree from the Atlantic Rain Forest

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ABSTRACT

Dendroecological methods were used to determine how annual radial growth of *Dalbergia nigra* varies between different size classes and how wood density of *D. nigra* varies in response to soil characteristics and crown illumination. We recorded the monthly diameter growth of 48 tree for 24 months using dendrometer bands. Crown light exposure (CI), wood density, fertility and soil moisture were avaluated. The growth of *D. nigra* increased with increased of DBH. The size classes differed in radial growth increment at the end monitoring of *D. nigra* trees. The results showed that the monthly diameter increment was positively correlated to rainfall and CI for all the size class. There was no relationship between wood density with radial increment, DBH and crown illumination. However, a negative linear relationship between soil and wood density was observed. We conclude that the precipitation was the strongest measured variable implicated in *D. nigra* growth, regardless of class size. The effect of heterogeneity of abiotic factors provides distinct condictions that affect the growth and wood density of *D. nigra* according their distribuition.

Key Words: dendroecology, seasonal drought, soil water, fertility soil, growth

INTRODUCTION

Growth rates and wood density of tropical tree species vary widely between species and in response to resource availability (e.g. light, soil moisture, nutrients) and individual condition (e.g. size, vigor) (Dalling et al 2004, Herault et al 2010). Such variations make it difficult to elucidate the weather effects on tree diameter growth and variation in wood density, especially in natural forest stand having trees of various sizes and diverse species (Nabestima et al 2010). Trees of smaller diameter classes are typically aged in demographic studies (i.e., dendroecology), but there have been few attempts to examine how interannual variations in radial growth–climate relationships may differ between trees of different diameter size classes (Piutti and Cescatti, 1997; Cescatti and Piutti, 1998; Meyer and Braker, 2001). Acording to Carrer and Urbinati (2004) the growth in response to the weather is independent of tree size. However, recent theoretical and ecophysiological studies suggest that functional processes strongly coupled to tree growth are closely associated with their size (Hubbard et al., 1999; Midgley, 2003; McDowell et al., 2005; Nabeshima and Hiura, 2007) rather than with their age (Mencuccini et al., 2005; Matsuzaki et al., 2005; Bond et al., 2007).

Dominant trees are supposed to be more climatically sensitive than smaller crown classes, because they are less affected by competition from neighbouring trees (Phipps 1982). Therefore, they are supposed to be more climatically sensitive than smaller crown classes (e.g. Phipps 1982). For example, after drought and frost, Liu & Muller (1993) observed greater growth reductions in dominant and codominant crown classes of several deciduous tree species than in intermediate and suppressed trees. In contrast, smaller trees have fewer resources available owing to greater competition and may react to unfavourable weather periods sooner and more severely than dominant trees (Abrams & Mosteller 1995). The inconsistencies between different observations may indicate that relative growth reactions of trees belonging to different crown classes may be dependent on local site and stand conditions, as well as tree species (Makinen et al 2002).

The relationship between radial growth pattern and wood density profile requires further investigation for different growing conditions and tree ages. Nevertheless, few studies have focused on the issue of interaction among site condition, growth of tree between size classes and wood density. Thus, the objectives of this study focusing a threatened species from Atlantic Rain Forest, Brazil, *Dalbergia nigra* are: (a) to determine how their annual radial growth as a response to climatic factors varies between different size classes of diameter breast height (DBH) (b) how wood density of *D. nigra* varies in response to soil characteristics and crown illumination.

METHODS

Study site and climate

The study was carried out in an area of semi-deciduous forest in a fragment of Atlantic rain forest in Sumidouro State Park (SSP) in the state of Minas Gerais, southeastern Brazil (19° 32' 25 S, 43° 55' 09 W). The SSP covers approximately 2000 ha and is mainly composed of Atlantic Forest and cerrado (savanna) vegetation (de Andrade 2009). The SSP was formerly used for livestock grazing and human settlements, but since the implementation of a management plan in 2010 these activities have ceased and the area is undergoing natural regeneration (Tavares, 2010). The study site for this research was a 11 ha forest fragment within the SSP that has never been subjected to logging, livestock grazing or disturbance associated with human settlements. The area is classified as having a semi-humid warm tropical seasonal climate with a dry season of 3-4 months (Nimer 1989). The average annual rainfall is 1273 mm, concentrated between October and March, and the average annual temperature is 22.5 °C. Climate data have been obtained for two years from a meteorological station approximately 27 km from the study area.

Study species

Dalbergia nigra (Vell.) Allemao ex Benth.,commonly known as Brazilian Rosewood, is a tree of the Atlantic Forest that occurs in eastern Brazil. It produces valuable timber but this resource has been over-exploited, which is the cause of the Vulnerable classification by IUCN (2013). Despite this vulnerability due to reduced population sizes, high genetic diversity was found among individuals growing in large protected reserves (Ribeiro et al. 2005, 2011)**.** The growth rate of saplings is moderate to fast and trees reach an average height of 15 - 25 m and a maximum height up to 35 m (Lorenzi 1992).

Soil fertility and moisture measurements

Soil samples (0-20 cm depth) were collected at ten randomly selected locations in the fragment. Each sample was made up of five bulked subsamples, collected at a random location within a radius of 20 m, and homogenized to form one composite sample. The textural and chemical analyzes of the samples were conducted at the Instituto Mineiro de Agropecuária (IMA), Brazil. Analysis of soil texture was conducted using the pipette method (Claydon, 1989). Soil acidity in distilled water was measured with a pH meter. Total N was determined using the wet oxidation (Kjeldahl) method, which converts organic N to ammonium (NH_4^+) for colometric measurement. Total organic C was determined by the calorimetric method. The determination of available phosphorus was conducted using the Mehlich 1 method (Nelson et al., 1953) and measured by molecular absorption. K and Na were extracted by the Mehlich 1 method (Nelson et al., 1953) and measured by flame photometry. Ca and Mg were also measured by atomic absorption spectrophotometry after extraction with a concentrated 1N KCl solution. Cations were extracted in a 1 M KCl solution at the unbuffered pH of the soil (EMBRAPA, 1997). Exchangeable Al and H+Al were extracted with 1 $\mathrm{mol_c}\ \mathrm{L}^{-1}$ KCl, cation exchange resin and buffer SMP, respectively. Volumetric soil water content at 10 cm depth was measured at 50 randomly selected locations in each topographic position using the FIELD SCOUT TDR 100 soil moisture meter (Spectrum technologies, USA). The measurements were performed at the end of the rainy season (first half of April) and end of dry season (first half of September) of each year in 2011 and 2012. The measurements were all made on one day.

Tree selection and data collection

Over a 2-year period, basal area growth measurements were taken monthly on *D. nigra* tree to observe radial growth increment and capture growth patterns throughout rainy and dry seasons. A band dendrometer (DB20 EMS, Czech Republic) was installed on each of the 48 individuals selected for study in August 2010 at a stem height of approximately 1.5 m above ground level. Trees were grouped into five size classes (Table 1). Excessive outer bark were removed before the dendrometers were installed. Monthly measurements began three months after the dendrometers were installed, to allow them to stabilize, and continued for 24 months. Thus the time series for analysis comprises the interval from November 2010 to December 2012. To minimize the influence of diurnal fluctuations in tree girth due to changes in tree water status (Kozlowzki 1972), all measurements were performed during the morning (08h 00 to 10h 00). Data on the increase in trunk circumference were analyzed in relation to environmental variables, rainfall, temperature, and soil fertility. Meteorological data were obtained from the nearest INMET station, at

Sete Lagoas, Minas Gerais State, 27 km from the study site.

Crown light exposure was estimated on individual trees by assigning a crown illumination (CI) index on a scale of 5 (crown fully exposed) to 1 (crown fully shaded) to each tree following Clark and Clark (1992).

Calculation of the Basal Area Increment (BAI) - We used basal area increment (BAI) to describe growth patterns between different size class of *D. nigra* because this variable removes the variation in growth attributable to increasing stem circumference and captures changes in growth better than linear measures such as tree-ring width (Biondi and Qeadan, 2008). BAI was calculated as follows:

$BAI = \pi\ (R^2_t - R^2_{t-1})$,

where R_t and R_{t-1} are the stem radius in years t and t-1.

Wood density measurements - We collected randomly 15 radial wood strips oriented from pith to bark and positioned at DBH (1.3 m above ground level) by using non-destructive methods, including sampling with Pressler increment borers (core diameter 5.15 mm) and a motorized extractor (core diameter 18 mm). These samples were cut to 2 mm along ray, and air dried at 12% moisture content. The samples were scanned at right angles to the fibre direction in a Quintek Qtrs-01x scanning x-ray micro-densitometer and tree ring analyser (Quintek measurement systems, knoxville, tn).

Statistical analysis - We used Principal Components Analysis (PCA) as the ordination method to describe major gradients in the soil, using a subset of 19 variables (see Table 2 for a list of the soil variables). Linear model analysis was used to test for the effects of the first PCA resultant component (PC1) on radial growth increment and wood density. The PCA was utilized to determine whether soil variation contributes to variation in wood density and growth tree. We used principal components analysis (PCA) to reduce the dimensionality of the 19 topsoil variables. Since moisture soil and the soil fertility gradient (PC1) were strongly correlated ($r^2 = 0.84$; $P < 0.001$), they were not included in the same model. We also used the linear model analysis to evaluate the relationship between the dependent variable of tree growth on the independent variable of soil moisture across all seasons and wood density.

RESULTS

Seasonality - Total annual rainfall was 1318 mm during the first year (October 2010 to September 2011) of the study and 1176 mm during the second year (Oct. 2012to September 2013) (Fig. 1a). The mean air temperature during the first year was 23 ^{o}C and the second year 22 ^{o}C. There was a marked dry season from April to October, with these six months having 20 mm of rainfall in the first year and 90 mm in the second year (Fig. 2a). During the wet season from November to March mean monthly rainfall was 235 mm in 2010/2011 and 267 mm in 2011/2012 (Fig. 1a). Although there was a great variation in seasonal rainfall during the year, there was little variation in temperature with the mean air temperature during the dry season 22^{o}C (2011) and 21^{o}C (2012) and 25^{o}C (2011) and 23^{o}C (2012) during the wet season.

Soil - The PCA identified two main variation components, which, in total, explained 89.2% of the data set variability (Table 2). Axis I contributed to 78.8% of the total variation. This axis was positively correlated with base saturation, pH in water, P, Ca, Mg, Na and total exchangeable bases. The second axis (PC2), explained 10.4% of the variation and was positively associated with K^+ and negatively with organic C and N.

Growth - The associations between BAI and DBH were positive for *D. nigra* at the end of two years of monitoring (Fig 2) and the radial increment of *D. nigra* also increased with size class (Fig. 1b). The size classes differed significantly in radial growth increment at the end monitoring of *D. nigra* tree (one-way ANOVA, $P < 0.001$). Of all trees, radial growth increment of individuals < 15 DBH were the lowest and the radial growth increment of size class 5 was greatest than other class juveniles (Fig.1b). The results of LME showed that the monthly diameter increment was positively correlated to rainfall for all size classes (Table 3), with radial growth starting at the beginning of the wet season (November), and continuing until April (Fig. 1b). Each year, the radial increment decreased during the dry season (May until October), and the growth was re-activated after the first rains (November). For all the size class, a significant linear relationship between radial increment and crown illumination index (CI) was observed (Fig. 3).

Woody density – The average wood density was 0.86 ± 0.04 g/cm^3. There was no relationship between wood density with radial increment (Fig. 4, $r^2 = 0.10$, $P > 0.05$), DBH ($r^2 = 0.06$, $P > 0.05$) and crown illumination ($r^2 = 0.16$, $P > 0.05$). However, a negative linear relationship between PC1 and soil moisture with wood density was observed (Fig. 5).

DISCUSSION

Radial growth

Our results suggest that the growth of BAI of *D. nigra* tree increased with DBH. Clark and Clark (1996) reported decreasing basal area increment rates with increasing diameter for very large trees of five emergent species in Costa Rica. Unlike, Kohyama et al. (2003) analyzed the relationship between tree size and growth rate and found that as the diameter increases the diameter growth rate decreases.

The radial growth response to the weather of *D. nigra* is independent of tree size. Although the classes size presented a similar pattern of seasonality of radial growth, our results suggest a higher radial variation with increase of DBH, where the growth was more explicit with increased of size classes. Toledo et al. (2012), observed a reduced radial growth or even shrinking of the trunk during the months the drought periods, for *Plathymenia reticulata* trees growing in the same region. According to Chhin et al. (2008), trees of all diameter classes generally responded to climate in the same way.

The resulting delayed growth responses to climatic factors, such as monthly temperature and precipitation, have been repeatedly reported by dendrochronological studies (e.g., Yasue et al., 1996). These results demonstrate the influence of precipitation on the rhythm of the cambium and thus its corresponding seasonal effect on the growth tree of species from tropical semi-deciduous forests. The widespread nature of relatively reduced growth during dry season indicates that one or more common environmental factors strongly influenced diameter growth rates during this period (Nath et al. 2006). The effects of tree size, age, and growth rate are frequently mixed and, in practice, they are difficult to separate unequivocally in field studies of tree populations (Martínez-Vilalta et al. 2012).

Among the environmental factors that influence tropical plants, light availability is likely to be the resource most frequently limiting growth, survival and reproduction (Chazdon et al. 1996). Light availability is widely believed to be one of the most important environmental factors driving growth of tropical rainforest trees (Denslow 1987, King et al. 2005). Our findings support this emphasis on light resources. All size classes grew faster at higher light availability. However, we suggest that other factors considerably contribute to shaping tree growth. Greatest growth was observed in soils rich in Mg, P, V% and silt and where higher moisture was found. The effect of heterogeneity of abiotic factors in a small fragment of Atlantic Forest provides distinct conditions that result in greater or lesser growth of individuals according to their distribution in the mosaic of resources.

Wood density – Highest wood density was found in site with Al concentration and the m% (aluminium saturation). High wood density is characteristic of slowly growing species, such as those found in the understory (Falster & Westoby, 2005), in dry soils (Hacke & Sperry, 2001; Ackerly, 2004), or in nutrient-poor soils (Muller- Landau, 2004) and those with more shrub-like growth forms (Ackerly, 2004a). However, wood density differs among species as well as among individuals from the same species as a result of tree age and edaphic conditions (Baker et al. 2004, Muller-Landau 2004). The strong positive correlation between soil water deficit and wood density can be attributed to a reduction in tracheid enlargement and an associated increase in the proportion of the various ring segments made up of cell walls (Muller-Landau 2004, Chave et al. 2006, Bouriard et al 2005).

Toledo et al 2012, reported a negative relationship between radial growth and wood density for *Plathymenia reticulata* in forest ecotype, which was not observed for the Cerrado ecotype. We also did not observed relationship between growth trees of *D. nigra* with wood density. The relationship between radial growth pattern and wood density profile requires further investigation on more trees. Additionally, growth of trees has frequently been associated with abiotic factors (Oberhuber & Kofler 2000, Baker et al 2003, Cardoso et al 2012) that may also influence wood density of tree.

CONCLUSION

Precipitation was the strongest measured variable implicated in *D. nigra* growth, regardless of class size. The effect of heterogeneity of abiotic factors provides distinct conditions that result in greatest growth of individuals according to their distribution. In sum, with the exclusion of water availability, we suggest that light and soil fertility are the major factors limiting plant. However, wood density was not correlated with light, but was strongly correlated with moisture and soil fertility.

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Table 1. The size classification of *Dalbergia nigra*, as defined by diameter of breast at soil level (DBH)

	DBH (cm)		
Size class	**Minimum**	**Maximum**	**no. tree**
1	9	15	10
2	15.1	21	9
3	21.1	27	9
4	27.1	33	11
5	33.1	…	9

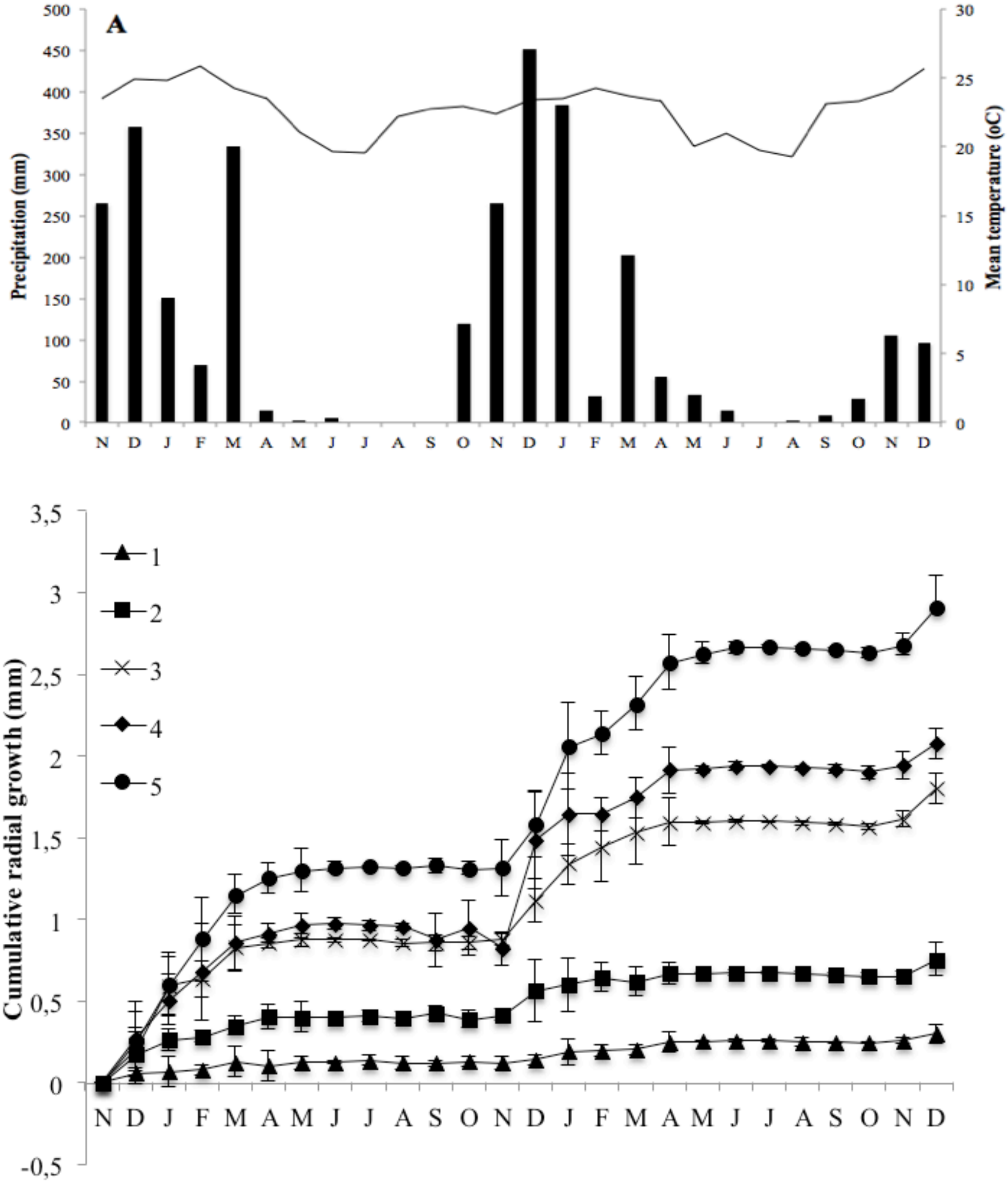

Fig. 1 a Precipitation (bars) and daily mean temperature (line). **b** Cumulative radial growth for size class individuals *Dalbergia nigra*. Size class 1 (≥ 9 < 15 cm), 2 (≥ 15.1 < 21 cm), 3 (≥ 21.1 < 27 cm), 4 (≥ 27.1 < 33 cm) and 5 (≥ 33.1 cm DBH). The line bars represent standard errors

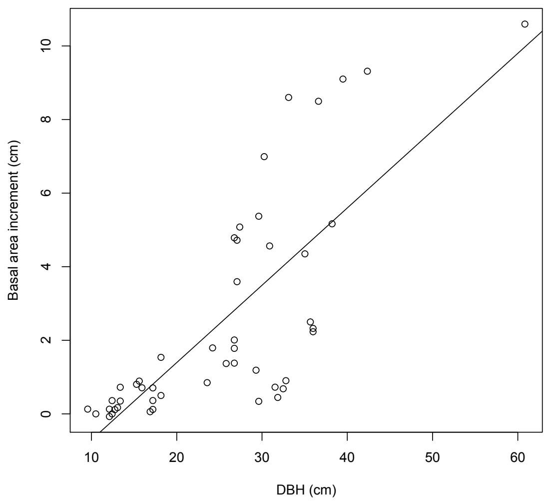

Fig. 2 Linear regression between Basal area increment (BAI) and Diameter breast height (DBH) at the end of two years of monitoring of *Dalbergia nigra*.

Table 2. Correlations of 19 topsoil variables (5 – 20 cm) and two ordination axes produced by Principal Components Analysis (P = phosphorus, K = potassium, Ca = calcium, Mg = magnesium, Al = exchangeable aluminium, V = base saturation, m = aluminium saturation) (n = 10).

Variables	Axis 1	Axis 2
Clay	-0.23	0.10
Silt	0.23	-0.17
Coarse sand	-0.23	-0.01
Fine sand	0.15	0.05
V%	0.26	0.10
m%	-0.25	-0.19
pH in water	0.25	0.00
Organic C	0.09	-0.58
N	0.09	-0.59
P	0.23	-0.12
K^+	-0.19	0.32
Ca^{2+}	0.24	0.09
Mg^{2+}	0.26	0.01
Na^{2+}	0.23	0.07
Al^{3+}	-0.25	-0.17
$Al^{3+}+H^+$	-0.26	-0.12
Total exchangeable bases (TEB)	0.25	0.10
Cation exchange capacity (CEC)	-0.22	-0.12
Effective cation exchange capacity	0.23	0.02

Table 3. Summary of ANOVA of linear mixed-effects models for tree growth and the precipitation of different size class of *Dalbergia nigra* in a fragment of Atlantic rain forest. F-statistics, and degrees of significance are reported

Size class	**F**	***P***
1	16.54	< 0.001
2	21.53	< 0.001
3	66.14	< 0.001
4	34.27	< 0.001
5	71.12	< 0.001

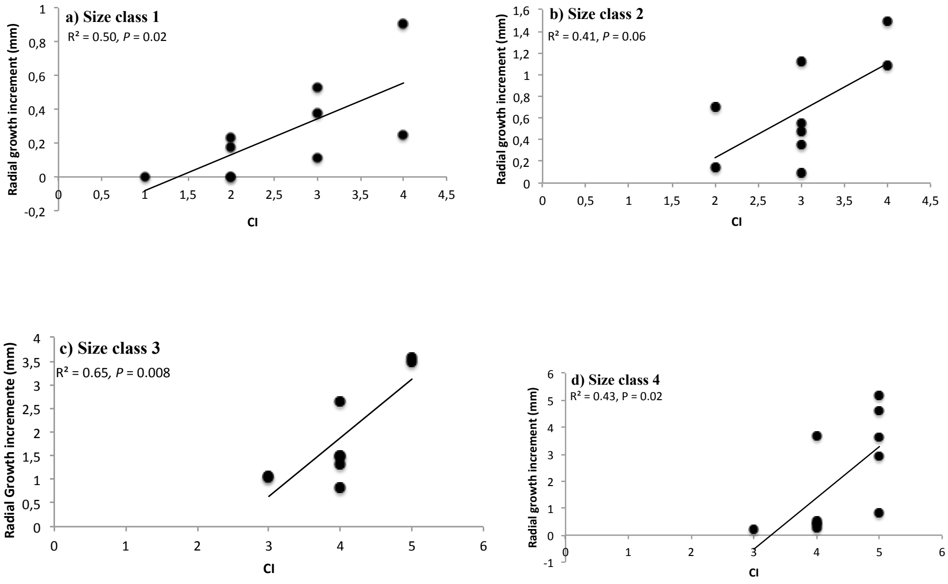

Fig. 3 Linear regression between crown illumination (CI) and radial growth increment in different size classes at the end of two years of monitoring of *Dalbergia nigra*

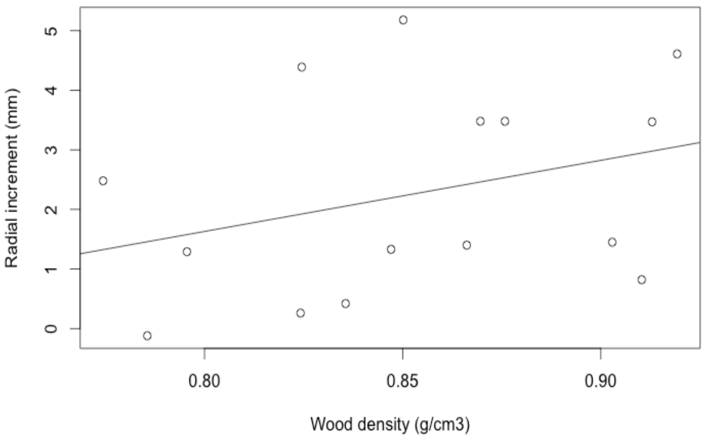

Fig. 4 Linear regression between the wood density and radial increment at the end of two years of monitoring ($r^2 = 0.11$, $P > 0.05$) of *Dalbergia nigra*

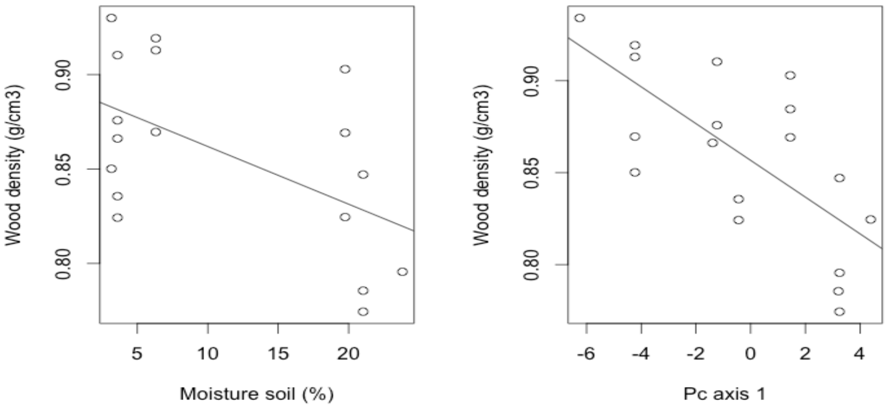

Fig. 5 Linear regression between moisture soil during the wet season and wood density (left) ($r^2 = 0.30$; $P < 0.05$) and linear regression between PC1 and wood density (right) ($r^2 = 0.47$; $P < 0.001$) of *Dalbergia nigra*

CONSIDERAÇÕES FINAIS

Dalbergia nigra é uma espécie ameaçada de extinção que fornece uma das madeiras mais valiosas na região central da Mata Atlântica, portanto, uma compreensão mais ampla da resposta desta espécie com a disponibilidade de recursos locais contribuirá para planos de ação para a conservação da espécie e restauração de habitat. Há pouco conhecimento sobre o efeito de variáveis abióticas no recrutamento e crescimento de *D. nigra*. Identificar os principais mecanismos que determinam a abundância, distribuição e crescimento de *D. nigra* foi o desafio do nosso estudo. Com base nos resultados podemos concluir que indivíduos de *D. nigra* podem ser encontrados desde locais íngremes até locais como no interior da mata com pouca luminosidade. No entanto, diversos fatores bióticos e abióticos influenciam no crescimento e recrutamento desta espécie. Deste modo, concluímos que:

- Sob condições ambientais semelhantes indivíduos adultos de *D. nigra* apresentaram variação no crescimento em diferentes posições topográficas. O alto teor de alumínio, baixa fertilidade e umidade do solo presente na parte alta do fragmento ocasionou menor crescimento de árvores de *D. nigra*.

- A variação em escala fina na disponibilidade de recursos também pode ser o resultado da mortalidade diferencial e taxa de crescimento de plântulas de *D. nigra* no fragmento. Indivíduos de *D. nigra* apresentaram diferentes densidades ao longo das duas posições topográficas, o que também influenciou a taxa de sobrevivência e crescimento de plântulas e de indivíduos jovens de *D. nigra*, com maior crescimento e recrutamento na parte baixa do fragmento. Além disso, a taxa de sobrevivência de plântulas e crescimento foram maiores durante o período mais chuvoso do ano, o que sugere que as taxa de crescimento máxima ocorre quando a umidade do solo é mais alta.

- Independente da classe de diâmetro de indivíduos de *D. nigra*, precipitação foi a variável mais forte implicado em todos os nossos modelos de crescimento. No entanto, com a exclusão da disponibilidade de água, sugerimos que a disponibilidade de luz e fertilidade do solo são os principais fatores que limitam o crescimento de *D. nigra* em todas as classes de diâmetro.

- Os fatores edáficos também foram determinantes na densidade da madeira de *D. nigra*.

Apesar do nosso estudo ser realizado em um pequeno fragmento da Floresta Atlântica, a variação sazonal e espacial da disponibilidade de água, resultaram em mortalidade e crescimento diferencial de *D. nigra* através do fragmento. Deste modo, o efeito da heterogeneidade de fatores abióticos ofereceu condições distintas que resultam em maior ou menor sucesso dos indivíduos de *D. nigra* de acordo com sua distribuição no mosaico de condições edáficas, notadamente a umidade do solo.