



EVELYN DA FONSECA ALECRIM BRAGION

**FUNCTIONAL GROUPS BEHAVIOUR AND
NON-STABLE NATURAL EDGES OF GALLERY
FOREST
(COMPORTAMENTO DE GRUPOS
FUNCIONAIS E BORDAS NATURAIS NÃO
ESTÁVEIS DE MATAS DE GALERIA)**

LAVRAS - MG

2016

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Tese apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Engenharia Florestal, área de concentração em Ecologia Florestal, para a obtenção do título de Doutor.

Orientador
Dr. Eduardo van den Berg

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Dr. Filipe Machado França	UFLA
Dr. Lucas del Bianco Faria	UFLA
Dr. Luiz Fernando Silva Magnago	UFLA
PhD. Robin Chazdon	UCONN
Dr. Rubens Manoel dos Santos	UFLA

Dr. Eduardo van den Berg
Orientador

**LAVRAS – MG
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A Deus, por me permitir estudar as belezas da natureza,
Dedico

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“There is no leaf of the forest, or lowly blade of grass, but has its ministry. Every tree and shrub and leaf pours forth that element of life without which neither man nor animal could live; and man and animal, in turn, minister to the life of tree and shrub and leaf. The flowers breathe fragrance and unfold their beauty in blessing to the world. The sun sheds its light to gladden a thousand worlds. The ocean, itself the source of all our springs and fountains, receives the streams from every land, but takes to give. The mists ascending from its bosom fall in showers to water the earth, that it may bring forth and bud.”

Desire of the Ages, pg. 20

GENERAL ABSTRACT

Gallery forests possess natural edges between forest and grasslands, offering a unique opportunity to examine how species performance varies across natural environmental gradients and to study forest expansion into grasslands and the effect of positive interaction on this expansion. Here we asked whether demographic rates of tree functional groups varied with distance to the edge, whether we could explain differences in plant strategies through functional traits and which traits increase growth and allow survival. We also asked whether gallery forests are expanding into grasslands and whether a facilitation process fosters forest expansion. Also, we examined whether there is a change from positive to negative interactions in these short gradients as a consequence of the change in microclimate. For this purpose, we examine mortality and recruitment for 30 species existing in the first few meters (10 m) of natural edges of 8 different gallery forests, and use demographic data from 5 annual inventories (2009 - 2013). The shade-tolerant group had the lowest mortality rates and basal area loss while both pioneer and light-demanding species had similar behavior for these rates. There was no difference between groups for recruitment the rates and basal area gain. Distance from the edge differentially affected the functional groups in terms of survival and growth. Survival of the pioneer group was enhanced near the edge, but for the light-demanding and shade-tolerant, survival increased toward the forest interior. All groups had higher growth in the grassland and reduced growth in the edge. Those differences in behavior could be explained by differences in functional traits. A great part of the species in natural edges have an acquisitive strategy. Growth was enhanced by acquisitive traits. However, mortality selected both strategies, but in distinct zones of the edge. We found forest expanding over grasslands with the pioneer species having the spearhead role, followed by the light-demanding species and, lastly, by the shade-tolerant in a clear succession process, that could suggest a facilitation process. However, the presence of facilitators did not foster forest expansion since the more facilitators, the less forest expansion. Also, there were no changes from positive to negative interactions, but even in the grassland presence of neighbors reduced survival. Our results showed how strong and sharp the edge gradient is and how the functional groups had growth and survival differentially affected by it. Although we did not find evidence of facilitation, negative interactions do not completely suppress expansion, since there was expansion in most of the sites.

Keywords: Environmental gradient. Functional groups. Dynamic. Cerrado. Positive interactions

RESUMO GERAL

Matas de galeria possuindo bordas naturais com campos limpos apresentam uma oportunidade única de estudar a performance de espécies através do gradiente ambiental natural, a expansão florestal sobre os campos e o efeito das interações positivas nessa expansão. Nesta tese, nós perguntamos se as taxas demográficas de grupos funcionais variaram com a distância da borda, se as diferenças em estratégias dos grupos funcionais podem ser explicadas através de características funcionais e quais características aumentam o crescimento e permitem a sobrevivência. Nós também questionamos se as matas de galeria estão expandindo e se processos de facilitação promovem a expansão florestal. Também examinamos se há uma mudança de interações positivas para negativas no curto gradiente como consequência da mudança em microclima. Para isso, nós acompanhamos a mortalidade e recrutamento de 30 espécies presentes nos primeiros metros (10 m) de bordas naturais em 8 matas de galeria, e usamos dados demográficos de 5 inventários anuais (2009 – 2013). O grupo tolerante à sombra possuiu a menor taxa de mortalidade e perda de área basal. Não houve diferenças quanto às taxas de recrutamento e ganho em área basal. A distância da borda influenciou os grupos funcionais de maneira diferente em termos de crescimento e sobrevivência. A sobrevivência de pioneiras foi aumentada perto da borda, enquanto para os outros grupos a sobrevivência aumenta em direção ao interior. Todos os grupos cresceram mais no campo do que na borda. As diferenças em comportamento puderam ser explicadas através de características funcionais, sendo que a maior parte das espécies possui uma estratégia aquisitiva. O crescimento foi favorecido por características aquisitivas de recurso, no entanto mortalidade selecionada as duas estratégias, mas em áreas distintas da borda. A floresta expandiu sobre os campos com as espécies pioneiras sendo as primeiras, seguidas das exigentes de luz e tolerantes à sombra, o que poderia sugerir um processo de facilitação. No entanto, os primeiros colonizadores não promoveram a expansão florestal, já que quanto maior a sua abundância, menor a expansão florestal. Ainda, não há mudança de interações positivas para negativas, mas até mesmo no campo a presença de vizinhos diminui a sobrevivência. Nossos resultados mostram o quanto o gradiente das bordas é curto e forte, e como isso afeta de forma diferenciada os grupos funcionais. Embora nós não tenhamos encontrado evidências de facilitação, as interações negativas não suprimem a expansão florestal.

Palavras – chave: Gradiente ambiental. Grupos funcionais. Dinâmica. Cerrado.

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1 GENERAL INTRODUCTION

Gallery forest that are forestry corridors along stream and river basins (RIBEIRO; WALTER, 2001). Boundaries between gallery forest and grasslands are one of the few examples of sharp natural old edges, this being one amazing opportunity for studying how plant populations and communities behave. Those boundaries are intriguing since they occur between very distinct vegetation types coexisting under a common climate. (WHITTAKER, 1975; BOND, 2005; BOND, 2005). Besides the sharp gradient with the open grassland, gallery forests also have a strong internal gradient from the streamside toward the edge. Light, soil moisture and nutrients vary along a gradient reflecting in a clear turnover of species from the stream towards grassland (KELLMAN; TACKABERRY; RIGG, 1998; ROSSATO; HOFFMANN; FRANCO, 2009; VAN DEN BERG; OLIVEIRA-FILHO, 1999). However, those factors can not satisfactorily explain the sharp feature of the edges. This feature is better explained by the frequent fire events that take place in the grasslands and eventually affect the edge, however, extinguishing there (VAN DEN BERG; OLIVEIRA-FILHO, 1999; 2000; VAN DEN BERG; SANTOS 2004; FELFILI, 1998; ROSSATO; HOFFMANN; FRANCO, 2009).

Forest and grassland exist as alternative stable states (GRAY; BOND 2015; STAVER; ARCHIBALD; LEVIN, 2011a,b), therefore limits between them could be shifting. Several studies date forest expansion starting around 3000 – 4000 YBP (BOWMAN; WALSH; MILNE, 2001; DESJARDINS et al., 1996; HOPKINS 1992; KERSHAW, 1992; SANAIOTTI et al., 2002; SCHWARTZ et al., 1996; SILVA et al., 2008). One of the main constraints to forest expansion is fire, that kills woody seedlings and samplings and topkills adults because of their lack of protective thick bark (HOFFMANN et al., 2009; ONDEI et al., 2015). Therefore, under frequent fires, forest expansion is

unlikely, but when fire is suppressed gallery forest can expand into open areas (RATTER, 1992). On the other hand, grasses are favored by frequent burn since they benefit from the created open spaces and recover faster than trees after fire events. Their presence even enhances the likelihood of burning due to their high flammability, creating positive feedback between grassland and fire.

Given all constraints and stressful conditions for forest species establishment in open areas, it is probable that forest expansion works as a succession process where a facilitation process dominates (CLEMENTS, 1916; CONNELL; SLATYER, 1977; GRIME, 1977) with an initial occupation of the grassland area by colonizer species, smoothing the harsh grassland conditions, followed by other species. As succession carries on and harsh conditions in grasslands turn more suitable for forest species, the importance of positive interactions probably decline, increasing the importance of competition and other negative interactions. The gradient from grassland to forest could be therefore in different stages of succession, when environmental stress is higher in the grassland in lower in the forest. According to the stress-gradient hypothesis in a gradient like this, interactions can change from facilitation (harsh environment) to competition (BERTNESS; CALLAWAY, 1994; CALLAWAY; WALKER, 1997).

Light is an abundant resource at natural edges, and one of the most recognized tradeoffs in terms of plant strategies is the resource acquisition vs. conservation (also known as fast-slow) (REICH, 2014) which is connected with the capacity to exploit environments that are rich or poor in resources (GRIME et al., 1997). Thus, shade-tolerance or intolerance would be the consequence of this tradeoff between high growth in productive (high light) conditions and high survival in low light conditions (BAZZAZ et al., 1983; DAVIES, 2001; DENSLOW, 1980, 1987; HARTSHORN, 1980). Because functional traits are related to plant strategies, this tradeoff can be investigated using functional traits

that are advantageous in high-light environment versus low-light environments (REICH, 2014). The relationship between functional traits and plant strategies have been tested for forest environments (FORGIARINI et al., 2015; POORTER et al., 2003), where gap openings are the main cause of light increase.

Yet, such forest gaps are transitory (SWAINE; WHITMORE, 1988) and few studies have explored the relationship between functional traits and plant strategies within natural edges, where the high light incidence is constantly present.

Several studies have investigated which factors are driving those boundaries between gallery forest and open areas (KELLMAN; TACKABERRY; RIGG, 1998; ROSSATO; HOFFMANN; FRANCO, 2009; VAN DEN BERG; OLIVEIRA-FILHO, 1999), how or if such forest-grassland limits change temporally (BURROWS; COMPTON; HOFFMANN, 1998; DUSSART; LERNER; PEINETTI, 1998; PALMER; ROOYEN, 1998; SCHWARTZ et al., 1996; SILVA et al., 2008), the role of soils (GRAY; BOND, 2015), constraints to tree establishment (HOFFMANN; ORTHEN; FRANCO, 2004), the role of facilitators in seedling establishment (HOFFMANN, 1996; KELLMAN, 1985; KELLMAN; MIYANISHI, 1982), and what community structure and species composition are like in those edges (COELHO et al., in prep., KELLMAN; TACKABERRY; RIGG, 1998). However, we lack understanding of how plants behave after the seedling stage, and if facilitators are really helping plants achieve adulthood and forest expansion. In addition, we also do not know how the environment gradient affect plant interactions. To understand how natural edges work it is necessary to examine how species performance varies across those natural environmental gradients, exploring how functional traits are related to species success or failure in this environment, since functional traits depict plant strategies (ADLER et al., 2014; FORGIARINI et al., 2015; GRIME; HODGSON; HUNT, 1988; WILSON;

HODGSON., 1999). Our understanding regarding those questions is limited in part because the large number of species present in the forests hinders generalization. Variation among functional groups in behavior across edges, however, can capture the complexity of specie response to environmental heterogeneity (DIAZ; CABIDO, 1997) and provide some insights into the processes that determine species distribution across the marked environmental gradients that occur in these forests.

I conceived this thesis considering the need to better understand the relationship between natural environment gradients, demographic rates, plant strategies and performance, functional traits and plants interactions. In the first paper, I aimed to answer how the environmental gradient affects survival and growth of different functional groups, which are the plant strategies in natural edges and how different functional traits mirror plant strategies. In the second paper, I aimed to answer whether gallery forests are expanding and, if they are, how the functional groups behave in such expansion; and also whether facilitation fosters forest expansion.

2 THEORETICAL REVIEW

2.1 Gallery forest

In the Brazilian savanna, known as *cerrado*, around 33% of plant diversity is within gallery forests (RIBEIRO; WALTER, 2001), that are forestry corridors along stream and river basins. They correspond to 5% of the cerrado territory (RIBEIRO; WALTER, 2001) representing the greatest biodiversity per area in the cerrado biome (MENDONÇA et al., 1998). Gallery forests can have boundaries with savannas and open environments, such as grasslands (RODRIGUES, 2000).

Gallery forest are a refuge for forest species in an open area environment, interfacing with many other types of vegetation like rainforest, mesophytic forest and open areas, so their high biodiversity is due to all the different floristic influences that to which they are subjected (MARIMON; FELFILI; LIMA, 2002; OLIVEIRA-FILHO; RATTER, 1995; PINTO; OLIVEIRA-FILHO, 1999; SILVA JÚNIOR et al., 1998).

They are buffer zones protecting the headwaters, controlling erosion and filtering chemicals (FELFILI, 1994; 1995a). Gallery forests are also important as a source of resources and shelter for fauna (REDFORD; FONSECA, 1986). Because of all the services provided by them, they are protected by Brazilian law, although it does not totally prevent deforestation (FELFILI, 1997).

Gallery forests are also subjected to natural perturbation because they are narrow corridors with a large perimeter of contact between them and open vegetation. This narrow, dissected shape makes them particularly susceptible to the high rates of anthropogenic burning in the adjacent savannas and grasslands (KELLMAN; MEAVE, 1997). They are also subjected to higher wind speeds.

Thus, plant species present in the gallery edges should be resistant to environmental stress (MEAVE et al., 1991).

Boundaries between gallery forest and grasslands are one of the few examples of sharp natural old edges. Several studies have been conducted aiming to better understand the floristics and dynamics of gallery forests (BATTILANI; SCREMIN-DIAS; SOUZA, 2005; VAN DEN BERG; OLIVEIRA-FILHO, 1999; 2000; VAN DEN BERG; SANTOS, 2004; BUOSI; FELFILI, 2004; DIETZSCH et al., 2006; FELFILI, 1994; 1995a, 1995b; FELFILI et al., 2002; LOPES; SCHIAVINI, 2007; MARIMON et al., 2003; OLIVEIRA-FILHO et al., 2007; OLIVEIRA; FELFILI, 2005; 2006; OLIVEIRA-FILHO; RATTER, 1995; OLIVEIRA-FILHO; RATTER; SHEPERD, 1990; PINTO; HAY, 2005; RODRIGUES; NAVE, 2000; SILVA JÚNIOR et al., 1998), however, we lack studies aiming to specifically understand the natural few meters of the edge.

2.2 Grassland and forest boundaries

Different vegetation types and their location around the world should be subject to climate control, where temperature and rain fall determine vegetation structure patterns (WHITTAKER, 1975). However, savannas and forest can grow in the same climate and, often, in the same soils, even though they are very distinctive vegetation types (WHITTAKER, 1975; BOND, 2005; BOND; WOODWARD; MIDGLEY, 2005). In this context, there is one of the few examples of sharp natural old edges: the boundaries between grasslands and gallery forests.

Besides the sharp gradient with the open grassland, gallery forests also have a strong internal gradient from the streamside toward the edge. Light, soil moisture and nutrients vary along gradients, reflecting in a clear turnover of

species from the stream towards grassland (KELLMAN; TACKABERRY; RIGG, 1998; ROSSATTO; HOFFMANN; FRANCO, 2009; VAN DEN BERG; OLIVEIRA-FILHO, 1999). However, those factors can not satisfactorily explain the sharp feature of the edges. This feature is better explained by the frequent fire events that take place in the grasslands and eventually affect the edge, however, extinguishing there (VAN DEN BERG; OLIVEIRA-FILHO, 1999; 2000; VAN DEN BERG; SANTOS, 2004; FELFILI, 1998; ROSSATTO; HOFFMANN; FRANCO, 2009).

It is possible that the gallery forests are expanding into grassland areas. Several studies conducted around the world have shown past and recent expansions of forest into open ecosystems (BOWMAN; WALSH; MILNE, 2001; DESJARDINS et al., 1996; HOPKINS, 1992; KERSHAW, 1992; SANAIOTTI et al., 2002; SCHWARTZ et al., 1996; SILVA et al., 2008). SILVA et al., (2008) suggested that gallery forest in Brazil started to expand around 3000-4000 YBP and continue to do so. They also suggest that expansion was limited by fire, since soil nutrient differences between vegetation types are not prominent. Their conclusions are supported by other studies finding that soils do not drive changes in vegetation types, but they are responders (GRAY; BOND, 2015). Thus, boundaries between grasslands and gallery forest are important models presenting important lessons about feedback between vegetation type and fire activity under a common climate (MURPHY; BOWMAN, 2012), where fire is a main constraint to forest expansion (HOFFMANN; ORTHEN; FRANCO, 2004; HOFFMANN et al., 2009).

The oldest register of fire in the cerrado is from 32,000 YBP (LEDRU, 1993), a period that is previous to human presence in the region (11,000-12,000 YBP, COOKE, 1998; PROUS, 1992), although man presence in Brazil is older than 30.000. However, mankind changed fire event frequency for at least 10.000, since they used fire for hunting, stimulation of fruit production,

undesirable species control, and tribal war (COUTINHO, 1990a). Currently, humans burn natural areas to transform them into crop fields or planted pasture (MIRANDA; BUSTAMANTE; MIRANDA, 2002), consequently they change the natural fire regime (season and frequency of burning) with consequences for the vegetation structure and composition (MIRANDA; BUSTAMANTE; MIRANDA, 2002). The fire in the cerrado is a surface fire (MIRANDA; BUSTAMANTE; MIRANDA, 2002), burning the herbaceous layer, which is 94% of the fuels consumed during the fires.

When fire is absent, forest expansion is a gradual process involving growth of existing trees and recruitment of new ones, however forest species face several constraints when establishing in the grasslands (BOND, 2008; HOFFMANN; ORTHEN; FRANCO, 2004). They are limited by microclimate, such as high light leading to high temperature and drought stress, and are also limited by low nutrient availability, frequent fire and competition with grasses (HOFFMANN; ORTHEN; FRANCO, 2004). Thus, the forest expansion rate will be determined by tree establishment, survival and growth under those constraints. Although those constraints lead to some limitations on forest species (BOWMAN, PANTON, 1993; HOFFMANN; ORTHEN; FRANCO, 2004), the increase in recruitment after fire suppression (SAN JOSÉ; FARIÑAS, 1991; GEIGER et al., 2011) suggest that fire is the main factor limiting expansion, so the rate of forest retreat is probably determined by fire frequency and intensity (HOFFMANN; ORTHEN; FRANCO, 2004).

Open areas are favored by fire events because grasses are highly flammable and may burn at intervals of 1-3 years (HOFFMANN et al., 2009). Also, grasses benefit from the open spaces after a fire event and they additionally recover from burning faster than trees (BAUDENA et al., 2015). On the other hand, forest species are fire sensitive because they lack a protective thick bark (HOFFMANN et al., 2009; ONDEI et al., 2015). In high fire

frequency, seedlings and saplings of wood plants suffer topkill (i.e. loss of above-ground biomass) or death. Because of frequent fire, saplings can be suppressed for decades, resulting in a demographic bottleneck, also known as “fire - trap” (BELL, 1984). In this context, recruitment into adulthood will only be possible during fire-free intervals long enough to allow saplings to reach a size at which they are no longer susceptible to topkill (BOND; MIDGLEY, 2000)

When fire frequency is high, forest species fall into the fire-trap and do not contribute to an increase in canopy cover leading to an open canopy, which benefits grasses and increases fire frequency. Grasslands and forest are therefore, alternative stable states maintained by feedback between fire and vegetation (WILSON; AGNEW, 1992; SCHEFFER; CARPENTER, 2003; WARMAN; MOLES, 2009; STAVER; ARCHIBALD; LEVIN, 2011a, 2011b; HIROTA et al., 2011; HENNENBERG et al., 2006; BECKAGE; PLATT; GROSS, 2009; HOFFMANN et al., 2009).

During fire-free periods, forest species can establish in grasslands and, if the periods are long enough, can lead to an increase in tree cover and a decrease in flammability due to a cooler and moister understory, which are unsuitable for grasses (UHL; KAUFFMAN, 1990; RAY; NEPSTAD; MOUTINHO, 2005), leading to a greater reduction in fire intensity, flame length and rate of spread (HOFFMAN et al., 2011).

It is probable that boundaries between forest and grassland are undergoing major changes, with forest expansion into open areas in response to the increase in atmospheric CO₂ and mean annual precipitation (BANFAI; BOWMAN, 2006; BOWMAN; MURPHY; BANFAI, 2010), which enhance plant growth (DRAKE; GONZÁLEZ-MELER, 1997; LEWIS et al., 2009) by increasing photosynthetic efficiency, in particular at the seedling and sapling stage (BOND; MIDGLEY, 2000; LLOYD; FARQUHAR, 2008), and

resprouting ability (HOFFMANN et al., 2000). An enhanced growth should allow woody species an easier escape from the fire-trap, favoring forest expansion (BOWMAN; MURPHY; BANFAI, 2010).

2.3 Positive interactions

For a long time the importance of a positive relation among plants had been neglected in community ecology (CALLAWAY; WALKER, 1997) and traditional models for plant interactions have emphasized competition where plants compete for limiting resources, such as light, space, water and nutrients. However, recently a large body of evidence for the importance of interspecific positive interactions has accumulated (HUNTER; AARSEN, 1988; BERTNESS; CALLAWAY, 1994; CALLAWAY, 1995; CALLAWAY; WALKER, 1997; BROOKER; CALLAGHAN, 1998). Callaway (1995) states that although neighbors may compete with one another for resources, they also can provide benefits, like shade, higher nutrient levels, more available moisture, soil oxygenation, protection from herbivores, a more favorable soil microflora, shared resources via mycorrhizae and increased pollinator visits, resulting in interactions that can be positive for at least one of the species involved.

The majority of facilitation research over the last two decades has been motivated by the 'stress-gradient hypothesis' (SGH), that predicts that the relative incidence of facilitation and competition will vary inversely across gradients of physical stress or ecosystem productivity (BERTNESS; CALLAWAY, 1994). The basic idea of the SGH is that facilitation 'should be particularly common in communities developing under high physical stress and in communities with high consumer pressure' and 'where the physical environment is relatively benign and consumer pressure is less severe, positive interactions should be rare; as a result, competitive interactions should be the dominant structuring forces' (BERTNESS; CALLAWAY, 1994).

Given all constraints and stressful conditions for forest species establishment in open areas, it is probable that forest expansion works as succession process where a facilitation process dominates with an initial occupation of the grassland area by colonizer species, smoothing the harsh grassland conditions, followed by other species. In the grassland, where environmental conditions are harsh, it is probable that after the first trees establish in the grassland they can facilitate new ones, acting as facilitators (HOFFMANN, 1996; KELLMAN, 1985; KELLMAN; MIYANISHI, 1982). Facilitators provide shade preventing lethal temperatures and increasing soil moisture (PUGNAIRE; VALLADARES, 2007). They also provide nutrient enrichment by litter (HUNTER; AARSEEN, 1988). Therefore, they allow higher establishment and growth of forest species in open areas. As succession goes by and harsh conditions in grasslands turn more suitable for forest species, the importance of positive interactions probably decline, increasing the importance of competition and other negative interactions. The gradient from grassland to forest could be, therefore, in different stages of succession, when environmental stress is higher in the grassland and lower in the forest. According to the stress-gradient hypothesis in a gradient like this, interactions can change from facilitation (harsh environment) to competition (BERTNESS; CALLAWAY, 1994; CALLAWAY; WALKER, 1997).

2.4 Plants strategies and Functional traits

One of the most recognized tradeoffs in terms of plant strategies is the resource acquisition vs. conservation (also known as fast-slow) (REICH, 2014) which is connected to the capacity to exploit environments that are rich or poor in resources (GRIME et al., 1997). Thus, shade-tolerance or intolerance would be the consequence of this tradeoff between high growth in productive (high light) conditions and high survival in low light conditions (BAZZAZ et al.,

1983; DAVIES, 2001; DENSLOW, 1980, 1987; HARTSHORN, 1980). Swaine and Whitmore (1988) described two extremes of a continuum of strategies in a tropical forest environment, where light is a key resource affecting ecological and physiological processes (TURTON; FREIBURGER, 1997). One group is composed of species that need direct light incidence to germinate, establish and grow, having fast growth but also a short life span. The other is made up of species that can germinate, establish and grow under a closed canopy. Although such classifications have been considered as over simplified for a rather continuous gradient of strategies (ALVAREZ- BUYLLA; MARTINEZ-RAMOS, 1992; BAKER; BURSLEM; SWAINE, 2003), their value is undeniable, allowing pooling species together in ecologically meaningful groups (VANCLAY, 1994; CONDIT; HUBBELL; FOSTER, 1996; VAN DEN BERG; CHAZDON; CORRÊA, 2012).

Because functional traits are related to plant strategies, differences in environment exploration can be investigated using functional traits that are advantageous in high-light environments versus in low-light environments (REICH, 2014). The specific leaf area (SLA, the ratio of leaf area to leaf dry mass) and leaf dry matter content (LDMC, the ratio of leaf dry mass to fresh mass) are morphological traits measured at the leaf level that are supposed to mirror the fast-slow tradeoff, wherein species with a fast strategy have high SLA and low LDMC and species with a slow strategy have low SLA and high LDMC (POORTER; GARNIER, 1999). Wood density (WD) is also related to the fast-slow tradeoff, wherein a low WD is associated to high growth and fast resource acquisition. On the other hand, a high WD is related to slow growth but high survival (PÉREZ-HARGUINDEGUY et al., 2013). Allometric traits are also important in this tradeoff, since resource investment in crown shape and height is linked to plant strategy (HORN, 1971; POORTER et al., 2003). Shade-intolerant species are expected to have slender stems and deeper crowns as result

of their investment in vertical growth (HORN, 1971; POORTER et al., 2003). Overall, shade-intolerant species, as resource acquisition strategists, are expected to have high SLA, low LDMC, low wood density, high growth rates, high mortality, slender stems and deep crowns.

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SECOND PART

**PAPER 1 - SHARP DIFFERENTIATION ON THE PERFORMANCE OF
PLANT FUNCTIONAL GROUPS ACROSS AN ABRUPT
ENVIRONMENT GRADIENT IN NATURAL EDGES**

ABSTRACT

Gallery forests within grasslands present natural edges with open environments and offer a unique opportunity to examine how species performances vary across these natural environmental gradients and contribute to the distribution of species in the forest. This task, however, has been hampered by the high species diversity of these ecosystems. Here we asked whether demographic rates of tree functional groups varied with distance to the edge, whether we could explain differences in plant strategies and performance through functional traits and which traits increase growth and which are allowing the survival in natural edges. For this purpose, we examine mortality and recruitment for 30 species existing in the first 10 meters of natural edges of eight different gallery forests, and use demographic data from five annual inventories (2009 - 2013). We aimed to explain differences in strategies and performance of functional groups through functional traits, so we defined a priori plant strategies using functional groups classification based on light requirements for germination and establishment, classifying them in three functional groups, light-demanding, pioneer and shade-tolerant. The shade-tolerant group had the lowest mortality rates and basal area loss while both pioneer and light-demanding species had similar behavior for these rates. There was no difference between groups for recruitment and basal area gainrates. Distance from the edge differentially affected the functional groups in terms of survival and growth. Survival of the pioneer group was enhanced near the edge, but for the light-demanding and shade-tolerant, survival increased toward the forest interior. All groups had higher growth in the grassland and reduced growth in the edge. Those differences in behavior could be explained by differences in functional traits. The majority of the species in natural edges have an acquisitive strategy, with higher SLA, lower LDMC, lighter WD, higher growth, deeper crowns and less slender stems. Growth was enhanced by acquisitive traits. However, mortality selected both strategies, but in distinct zones of the edge. Our results showed how strong and sharp the edge gradient is and how the functional groups had growth and survival differentially affected by it.

Keywords: Gradient. Pioneer. Light-demanding. Shade-tolerant. Gallery forest. Dynamic.

1 INTRODUCTION

A gallery forest is narrow strip of forest growing alongside small streams within the Cerrado biome. Gallery forest edges with natural grasslands are an amazing opportunity for studying how plant populations and communities behave in old forest edges. Besides the sharp gradient with the open grassland, gallery forests also have a strong internal gradient from the streamside toward the edge. Light, soil moisture and nutrients vary along the gradient reflecting in a clear turnover of species from the stream towards grassland (KELLMAN; TACKABERRY; RIGG, 1998; ROSSATO; HOFFMANN; FRANCO, 2009; VAN DEN BERG; OLIVEIRA-FILHO, 1999). However, those factors can not satisfactorily explain the sharp feature of the edges. This feature is better explained by the frequent fire events that take place in the grasslands and eventually affect the forest- grassland edge, however, extinguishing there (VAN DEN BERG; OLIVEIRA-FILHO, 1999; 2000; VAN DEN BERG; SANTOS 2004; FELFILI 1998; ROSSATO; HOFFMANN; FRANCO, 2009).

Several issues have been investigated along the years, as to which factors are responsible for those boundaries (KELLMAN; TACKABERRY; RIGG, 1998; ROSSATO; HOFFMANN; FRANCO, 2009; VAN DEN BERG; OLIVEIRA-FILHO, 1999), how or if the forest-grassland temporally limits change (BURROWS; COMPTON; HOFFMANN, 1998; DUSSART; LERNER; PEINETTI, 1998; PALMER; ROOYEN, 1998; SCHWARTZ et al., 1996; SILVA et al., 2008) and the nature of the community structure and species composition in those edges (Coelho et al., in prep., KELLMAN; TACKABERRY; RIGG, 1998). On the other hand, to understand how natural edges work it is necessary to examine how species performance varies across those natural environmental gradients, exploring plant strategies and related

functional traits associated to species success or failure in these environments (ADLER et al., 2014; FORGIARINI et al., 2015; GRIME; HODGSON; HUNT, 1988; WILSON; HODGSON, 1999). Our knowledge regarding those questions is limited in part because the large number of species present in the forests hinders generalization. However, approaching this complexity by using functional groups and evaluating how their responses vary across edges possibly can capture the main facets of this complex relationship between plant behavior and environmental variation (DIAZ; CABIDO 1997) and provide insights into the processes that determine species distributions across the sharp environmental gradients, such as that one existing between grassland and gallery forest.

One of the most recognized tradeoffs in terms of plant strategies is the resource acquisition vs. conservation (also known as fast-slow; i.e. rates of resource acquisition and processing) (REICH, 2014), which is connected with the capacity to exploit environments that are rich or poor in resources (GRIME et al., 1997). Thus, shade-tolerance or intolerance would be the consequence of this tradeoff between high growth in productive (high light) conditions and high survival in low light conditions (BAZZAZ, 1983; DAVIES 2001; DENSLOW 1980; 1987; HARTSHORN, 1980). Swaine and Whitmore (1988) described two extremes of a continuum of strategies in a tropical forest environment, where light is a key resource affecting ecological and physiological processes (TURTON; FREIBURGER, 1997). One group is composed of species that need direct light incidence to germinate, establish and grow, having fast growth but also a short life span. The other is made up of species that can germinate, establish and grow under a closed canopy and low light conditions. Although classifications as this one have been considered over simplified for a rather continuous gradient of strategies (ALVAREZ- BUYLLA; MARTINEZ-RAMOS, 1992; BAKER; BURSLEM; SWAINE, 2003), their value is undeniable, allowing pooling species together in ecologically meaningful groups

(VANCLAY, 1994; CONDIT; HUBBELL; FOSTER, 1996; VAN DEN BERG; CHAZDON; CORRÊA, 2012).

Because functional traits are related to plant strategies, differences in environmental exploration can be investigated using functional traits that are advantageous in a high-light environment versus low-light (REICH, 2014). The specific leaf area (SLA, the ratio of leaf area to leaf dry mass) and leaf dry matter content (LDMC, the ratio of leaf dry mass to fresh mass) are morphological traits measured at the leaf level that are supposed to mirror the fast-slow tradeoff, wherein species with fast strategy have high SLA and low LDMC and species with a slow strategy have low SLA and high LDMC (POORTER; GARNIER 1999). Wood density (WD) is also related to the fast-slow tradeoff, wherein a low WD is associated to high growth and fast resource acquisition. On the other hand, a high WD is related to slow growth but high survival (PÉREZ-HARGUINDEGUY et al., 2013). Allometric traits are also important in this tradeoff, since resource investment in crown shape and height is linked to plant strategy (HORN, 1971; POORTER et al., 2003). Shade-intolerant species are expected to have slender stems and deeper crowns as a result of their investment in vertical growth (HORN, 1971; POORTER et al., 2003). Overall, shade-intolerant species, as resource acquisition strategists, are expected to have high SLA, low LDMC, low wood density, high growth rates, high mortality, slender stems and deep crowns. Nevertheless, the relationship between functional traits and plant strategies have been tested for forest environments (FORGIARINI et al., 2015; POORTER et al., 2003), where gap openings are the main cause of light increase. However, forest gaps are transitory (SWAINE; WHITMORE, 1988), unlike forest edges where high light incidence is rather permanent.

Considering the need for better understanding of the relationship between the natural environment gradient, demographic rates, strategies and

performances of plants and functional traits we aimed to answer the following questions:

1) Are the demographic rates different between functional groups? Overall, we expected a higher annual mortality, recruitment and basal area change for the pioneer group, compared to the other groups, as a result of their investment in fast growth, which may also result in higher mortality.

2) How do environmental gradients affect survival and growth of different functional groups? We expected pioneers to perform better (high survival and growth) in the immediate edge with the surrounding grassland, where light conditions are likely to be more favorable. Shade-tolerant species must be more successful towards the interior of the plots, where the canopy is more developed and shade is greater, and light-demanding species would occupy an intermediate position between both groups;

3) Could we explain differences in functional group strategies and performance through functional traits? We expected that pioneer groups will have a set of traits and behaviors that distinguish them from the non-pioneers, such as higher SLA, lower LDMC, lighter wood density, higher growth rates, higher mortality, slender stems and deeper crowns;

4) Which traits increase growth and which allow the survival in natural edges? We expected that the high light and disturbed environment in the edges will act as an environmental filter selecting traits related to the acquisition strategy, like fast growth, high SLA and high stem slenderness. On the other hand, we expect low LDMC, low WD and crown format in these conditions

2 METHODS

Study Sites – A gallery forest is narrow strip of forest growing alongside small streams within the Cerrado biome. We studied 8 sites where the gallery forest had boundaries with natural grasslands in the south of Minas Gerais State,

Brazil (Figure 1). The sites are located in a disjunction of the Cerrado biome, within distribution area of seasonal semi-deciduous rainforests in southeastern Brazil (Brazilian Institute of Geography and Statistics-Instituto Brasileiro de Geografia e Estatística – IBGE, 2004). The climate is Cwa according to the Köppen climate classification, temperate and rainy (mesothermic) with dry winters and rainy summers (DANTAS; CARVALHO; FERREIRA, 2007). Elevation varies from 850 m to approximately 1500 m a.s.l.

We chose sites that had natural boundaries with native grasslands and which lacked obvious anthropogenic impacts such as logging, undergrowth clearing, clear cutting, or evidence of recent fires, and.

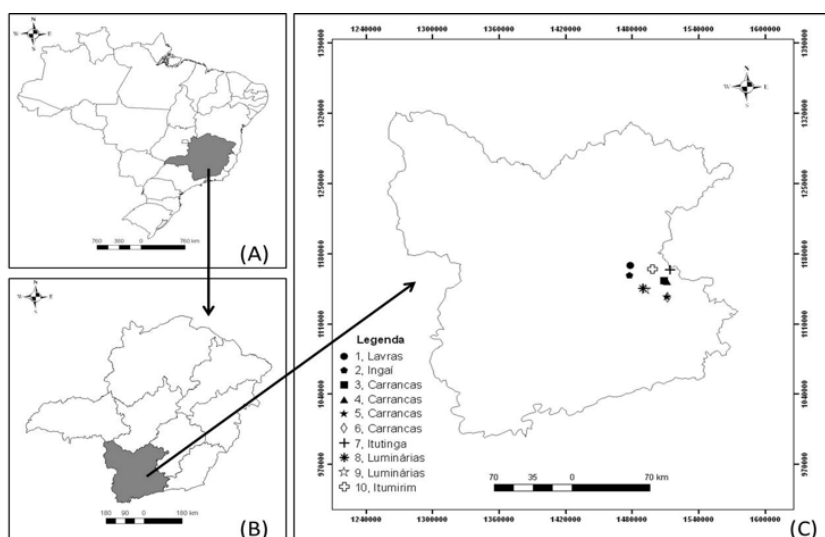


Figure 1 Geographical location of the studied sites.

Sampling – In 2009, we established three permanent plots (15 m × 20 m; 300 m²) in each of the 8 sites respecting a 10 m minimum distance between plots within a site. We laid out the plots with their wider side parallel to the forest

edge, including 5 m of grassland and 10 m of forest (Figure 2). We identified, mapped, and measured height and DBH of all individuals with diameter at breast height (DBH) ≥ 1 cm. In the present study, we worked with all species with 50 or more sampled individuals across sites corresponding to 30 species (Table 1).

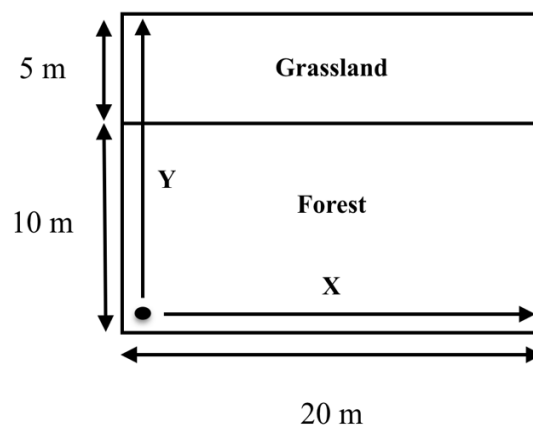


Figure 2 Sketch of how plots were assembled with 5 m of grassland and 10 m of forest's edge. X is the distance parallel to the upper limit of the plot as measured from the corner, Y is the distance of the individual from the upper limit of the plot.

Since 2009, we have carried out five annual inventories (2009 to 2013). In each inventory we measured and re-measured all alive individuals and verified all dead ones. The recruits, i.e., the new individuals meeting the inclusion criterion (DBH ≥ 1 cm), were identified and mapped, and had their height and DBH recorded.

Functional traits –We collected young totally expanded and healthy leaves without evidence of herbivory or pathogens. We randomly selected five individuals of each species, following the recommendations of Pérez-Harguindeguy et al. (2013). We collected 5 leaves from each plant and we

measured leaf thickness using a digital micrometer and then weighed and scanned them. After measurements, the leaves were dried during 72 h at 60 °C and weighed again.

For wood density analysis, we collected samples of each species, following the recommendations of Pérez-Harguindeguy et al. (2013). In order to ensure the homogeneous distribution of water before calculating the green volume, we placed samples in containers with water for thirty minutes and then the volume was measured through the method of water displacement. After such procedure, samples were dried until constant weight and were then weighed (PÉREZ-HARGUINDEGUY et al., 2013).

Based on the measurements described above, we obtained the following traits: specific leaf area (SLA, $\text{mm}^2 \text{mg}^{-1}$); leaf dry mass content (LDMC, %) and wood specific gravity (g.cm^{-3}).

Allometric traits – For allometric measurements we randomly selected 25 trees of each species within plots. We measured total height (Ht), height of the first bifurcation (Hb), height of the first leaves from the ground (HL), crown diameter (CD) in two perpendicular directions, stem diameter at breast height (DBH at 1.3 m from the ground), stem diameter at 10% of the height. Using these measures, we calculated the following indices: crown format (CF), calculated as the ratio of tree crown width to crown depth (crown depth was calculated as the difference between tree height and height of the first leaves); stem slenderness (RTH), calculated as the ratio of tree height to tree CBH (circumference at breast height).

Plant strategies – Functional groups can be defined as a group of different species that respond in a similar way to a set of environmental factors (GOURLET-FLEURY et al., 2005), in other words, a group of species with a similar strategy. We defined a priori plant strategies using functional groups classification based on light requirements for germination and establishment:

pioneer (fast growth – acquisition strategy) and non-pioneer (slow growth – conservative strategy) (SWAINE; WHITMORE, 1988). Pioneers (P) were those species whose seeds only germinate in sites with direct light at the ground level for at least part of the day. Their germination is triggered by an increase in red light or soil temperature fluctuation and their seedlings also require direct light for establishment and growth. On the other hand, non-pioneers germinate and their seedlings establish under the canopy without direct light (SWAINE; WHITMORE, 1988). We subdivided this last group into two others: light-demanding species (L), which demand more solar radiation for growth and have faster growth; and shade-tolerant species (S), which require very little light and grow slowly (SWAINE; WHITMORE 1988). We based our classification on studies developed in the same region (NUNES et al., 2003; OLIVEIRA-FILHO et al., 1994A, 1994B; OLIVEIRA-FILHO; MELLO; SCOLFORO, 1997; PEREIRA et al., 2010; PINTO; HAY, 2005). We recognize the existence of other classifications and approaches to classify functional groups, however, we believe that the classification proposed by Swaine and Whitmore is suitable for our analysis, since it is based on light requirements, which is a major defining environmental condition for natural edges. We used the Kruskal-Wallis test to seek for differences in functional and allometric traits between groups.

Demographic Rates – We calculated annual mortality rates (M), recruitment (R) and net change (Ch_N) rates in terms of individuals, and loss (L), gain (G) and net change (Ch_{BA}) of basal area for each site and species. We calculated M, R, L and G following Sheil, Jennings and Savill, (2000):

$$M = \left\{ 1 - \left[\frac{(N_0 - N_m)}{N_0} \right]^{\frac{1}{t}} \right\} \times 100 ; \quad (1)$$

$$R = \left[1 - \left(1 - \frac{N_r}{N_t} \right)^{\frac{1}{t}} \right] \times 100 ; \quad (2)$$

$$P = \left\{ 1 - \left[\frac{(BA_0 - BA_m - BA_d)}{BA_0} \right]^{\frac{1}{t}} \right\} \times 100 ; \quad (3)$$

$$G = \left\{ 1 - \left[1 - \left(\frac{BA_r + BA_g}{BA_t} \right) \right]^{\frac{1}{t}} \right\} \times 100; \quad (4)$$

where t is the time between censuses in years (precisely 1 year in the present case); N_0 and N_t are the initial and final individual tree counts, respectively; N_m and N_r are the number of dead trees and recruits, respectively; BA_0 and BA_t are the initial and final tree basal areas, respectively; BA_m is the basal area of dead trees; BA_r is the basal area of recruits; and BA_d and BA_g are the decrease (due to trunk break or partial loss) and increase in the basal area of surviving trees, respectively.

We calculated Ch_N and Ch_{BA} using the following equations (KORNING; BALSLEV, 1994):

$$Ch_N = \left[\left(\frac{N_t}{N_0} \right)^{\frac{1}{t} - 1} \right] \times 100 ; \quad (5)$$

$$Ch_{BA} = \left[\left(\frac{BA_t}{BA_0} \right)^{\frac{1}{t} - 1} \right] \times 100 . \quad (6)$$

Finally, we calculated those rates for each functional group separately within each site.

Effect of environmental gradient and size on survival and growth – To examine how annual growth (Gr , $\% \cdot \text{year}^{-1}$) and survival (S) change with distance from the edge and with the size of individuals we fitted Bayesian models, in which the growth and survival probability were a function of the size of the individual and distance Y (Figure 2). The growth model takes the form:

$$Gr_j = \rho + \delta_i * dist_j + \sigma_i * size_j \quad (7)$$

Growth was calculated as:

$$Gr = \left(\frac{(DBH_f - DBH_i)}{DBH_i} \right)^{1/5} \quad (8)$$

Survival was modelled as a logistic:

$$\text{logit}(S_j) = \alpha + \beta_i * \text{dist}_j + \theta_i * \text{size}_j \quad (9)$$

Rather than fit separate models for each functional group, we included a second level (parameter β) in the hierarchical model for each parameter in Equations 1 and 2. For instance, Parameter β for functional group i in Eq. 2 is modelled as:

$$\beta_i = \text{normal}(\mu_i, \tau_i) \quad (10)$$

For each model we calculated the predicted values and the credible intervals for the four following distances: in grassland (upper limit of plot), edge (5 m from upper limit), 5 m from edge (10m from upper limit) and 10 m from edge (15 m from upper limit).

Functional traits and survival – To answer which functional and allometric traits affected growth (annual growth rate, % yr⁻¹) and survival at edges we fitted Bayesian models and we modeled mortality as a Binomial process and growth as a Gaussian process.

$$\text{logit}(S) = \varepsilon + \varphi_1 x_1 + \dots + \varphi_n x_n \quad (11)$$

$$Gr = \psi + \omega_1 x_1 + \dots + \omega_n x_n \quad (12)$$

we used the predictors: SLA, LDMC, stem slenderness, crown format and Relative Growth Rate (RGR), for survival and SLA, LDMC, stem slenderness and crown format for growth. RGR as calculated as:

$$RGR = \frac{\ln\left(\frac{DBH_i}{DBH_f}\right)}{(t_f - t_i)(DBH_i)} \quad (13)$$

where DBH_i and DBH_f are the initial and final DBH, respectively. t_i and t_f are the initial and final years, respectively.

We obtained posterior distributions of parameters of both models using the Markov Chain Monte Carlo (MCMC) method. We monitored convergence by running three different chains with different start values. From the posterior distribution we computed the mean and credible intervals (CI) for all parameters and the significance of parameters was assessed by a 95% CI, and, for evaluating discrepancy, we calculated Bayesian p-value (GELMAN; MENG; STERN, 1996).

For all analyses, we used the R software, version 3.1.1. For the Bayesian models, we used the RJAGS package (PLUMMER, 2014). For the Kruskal-Wallis tests, we used the *Agricolae* package (MENDIBURU, 2014).

3 RESULTS

Demographic rates and functional groups – The recruitment and basal area gain rates were equal for all groups and only mortality and basal area loss were lower for shade-tolerant group (Table 2 and 3).

For the majority, the recruitment was higher than mortality, leading to a positive net change rate (Table 2). When considering gain and loss of basal area rates, gain was higher than loss for all the functional groups, also leading to positive net change rates. The recruitment rates were higher than mortality rates for 2011-2012 and 2013-2014 and lower than mortality for 2010-2011 and 2012-2013 (Table 2). Despite the two periods with negative net change rate in terms of individuals, the net change in basal area was negative only in 2012-2013 (Table 3), as the surviving individuals gained enough basal area to compensate for the loss in terms of basal area related to mortality.

Since negative rates could be a consequence of fires that took place during both periods, we recalculated the rates, removing sites that burned: Site 9 (2010-2011) and Site 8 (2012-2013). The exclusion of Site 9 for the 2010-2011 period did not lead to recruitment higher than mortality or a positive net rate change in number of individuals, but there was a decrease in mortality (from 4.79 % year⁻¹ to 3.67% year⁻¹) and an increase in the net change rate for number of individuals (from -1.56% year⁻¹ to 0.00 % year⁻¹). However, the basal area loss rate (11.09 % year⁻¹) continued to be higher than the gain rate (7.75 % year⁻¹) and the net change rate continued to be negative (-1.34 % year⁻¹). For the 2012-2013 period, removing Site 8 led to higher recruitment than mortality (M = 3.21 % year⁻¹; R = 5.71 % year⁻¹) and to a positive net change rate in number of individuals (2.66 % year⁻¹). For basal area, all rates continued positive (L = 6.10 year⁻¹; G = 10.93 year⁻¹; Ch_{BA} = 5.35 year⁻¹).

Growth, environmental gradient and size – The Gaussian model for growth based on size and distance had a good fit for all groups, since p-values were close to 0.50 (p-value (P)=0.50; p-value (L)= 0.49; p-value (S)=0.50). Size and distance had a negative effect on growth for all the groups (Figure 3). Pioneers had the highest growth, and shade-tolerant had the lowest (Figure 4). There was a decline in growth from grassland toward the interior for all groups (Figure 4). Although the effect of size was negative, its effect was much weaker than the distance effect (Figure 3 and 4).

Probability of survival, environmental gradient and size – The binomial model for survival had a good fit with Bayesian p-value of 0.49. Size had a positive effect on survival of pioneer and light-demanding groups but had a non-significant effect on survival of shade-tolerant species. Distance had a positive effect on survival of light-demanding and shade-tolerant species, but a negative effect on pioneer group survival (Figure 3). In grasslands and edges the pioneer group had highest survival regardless of size, however, deeper inside the forest

(10 m), light-demanding and shade-tolerant species had higher survival (Figure 5).

Differences in strategies between functional groups – The functional groups had different strategies to survive at the edges (Table 4). Pioneers had higher rates of growth, SLA, intermediate LDMC and lower stem slenderness than light-demanding and shade-tolerant species. Light-demanding species had lower LDMC than the other groups and did not differ from shade-tolerant species in SLA and stem slenderness. Crown form and WD did not differ among the groups.

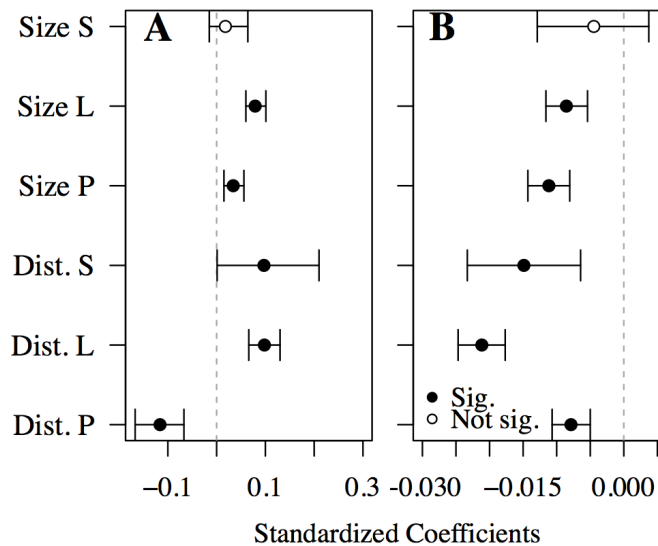


Figure 3 Credible interval (95%) for survival parameters (A) and growth model parameters (B). Values that do not overlap zero are significant. P: Pioneer; L: Light-demanding; S: Shade-tolerant; Dist.: Distance.

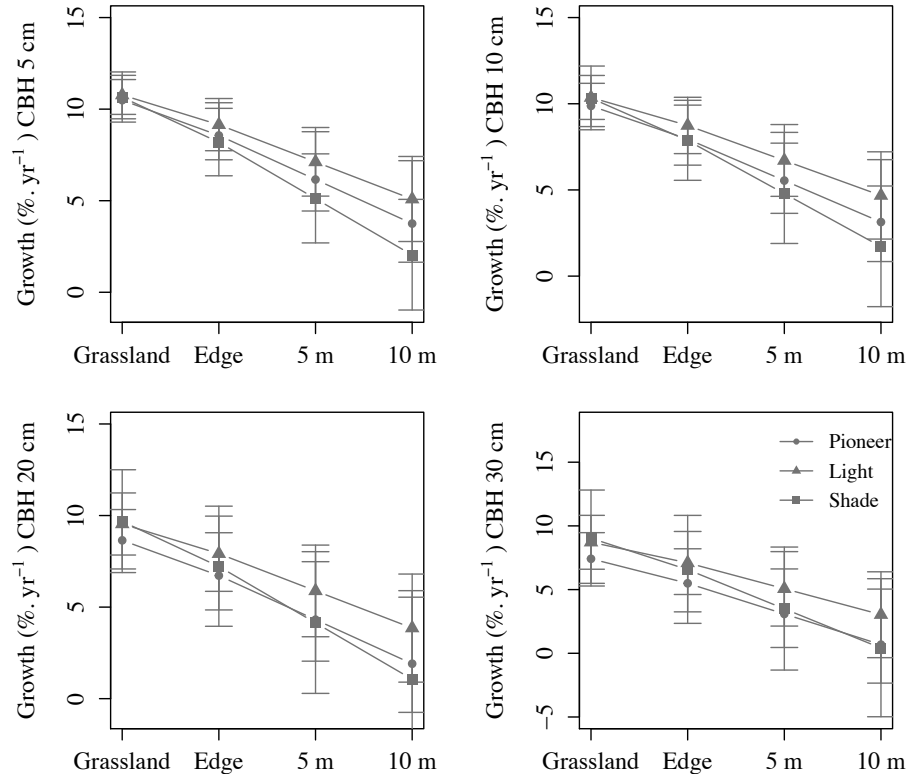


Figure 4 Predicted growth values and credible intervals (95%) for each functional group in four distances: grassland (upper limit of plot), edge (5 m from upper limit), 5 m from edge (10m from upper limit) and 10 m from edge (15 m from upper limit).

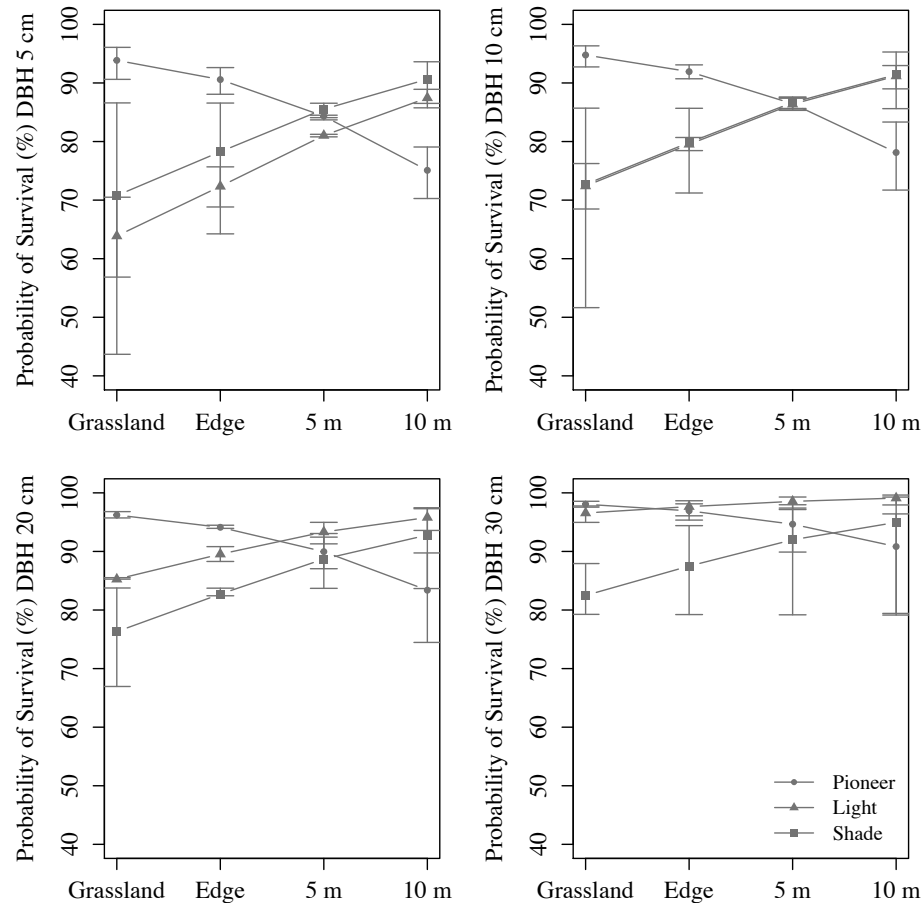


Figure 5 Predicted survival probability values and their credible intervals (95%) for each functional group in four distances: grassland (upper limit of plot), edge (5 m from upper limit), 5 m from edge (10m from upper limit) and 10 m from edge (15 m from upper limit).

Effect of functional traits on growth and survival - Both the binomial and Gaussian model had a good fit with p-value of 0.51 and 0.50, respectively. LDMC, crown format and stem slenderness were significant for growth (Figure 6). Species with small LDMC, deeper crown and slimmer stem grew faster. RGR, SLA and LDMC were significant for survival (Figure 6). Species with

higher RGR and LDMC and lower SLA and wood density have a higher survival probability.

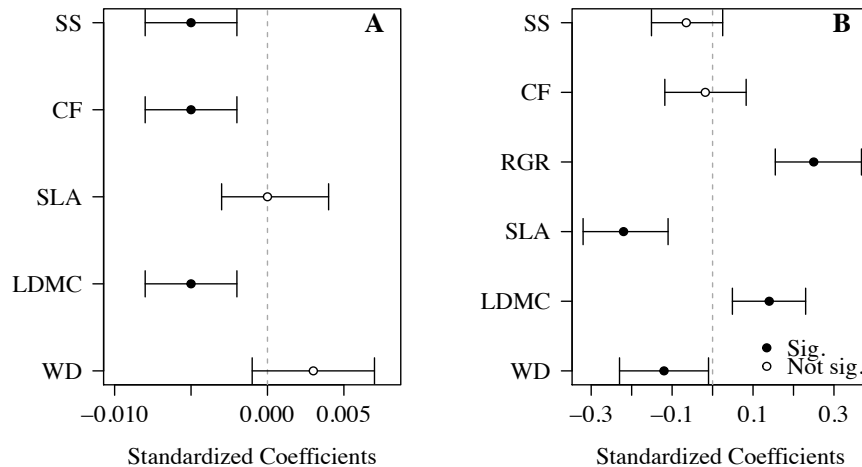


Figure 6 Credible intervals (95%) for growth model parameters (A) and for survival model parameters (B). Values that do not overlap zero are significant. SS: Stem slenderness; CF: Crown format; SLA: Specific leaf area; LDMC: Leaf dry matter content; WD: Wood density; RGR: Relative Growth Rate.

4 DISCUSSION

We assessed how the environmental gradient in gallery forest edges affects the dynamic rates of different functional groups classified based on their light requirements. We also investigated how different plant strategies, evaluated by functional traits, lead to different performances in natural edges. Our results showed how strong and sharp the edge gradient is and how functional groups had their growth and survival differentially affected by it. Shade-intolerant species were favored by grassland proximity and shade-tolerant species were favored by canopy closure. Functional traits explained differences in behaviour

between groups with different resource use. A large part of the species in natural edges have an acquisition strategy and growth was enhanced by those traits. However, mortality selected both strategies, but in distinct zones of the edges, i.e. groups with an acquisition strategy have a higher survival by the edge, while groups with a conservative strategy survive more toward the interior.

Differences in demographic rates - We expected shade-tolerant species to have lower mortality, recruitment and basal area gain. However, they only had lower mortality leading to a lower basal area loss. This is strong evidence that despite the high levels of light in the edges, due to vertical and lateral gaps (VAN DEN BERG; SANTOS, 2003), the light gradient is abrupt, allowing coexistence of light-demanding and shade-tolerant species in these 10 m wide plots. Actually, we found that although the shade-tolerant species have lower number of individuals than the pioneer and light-demanding groups, they gained individuals, basal area and even had a lower mortality and basal area loss than the other groups. Therefore, regardless of all disturbances that take place at natural edges and their environmental conditions, shade-tolerant species are thriving well in the gallery forest edges, even increasing in number and biomass because of the sharp environmental gradient, which allows shade-tolerant to survive a few meters inside the forest.

For all groups we found mortality rates lower than recruitment and a positive net change rate in terms of number of individuals and basal area. We also found a higher gain than loss, although, for years when there were fires, we found higher mortality and basal area losses. The increase in number of individuals and basal area in forest edges (positive rates of vegetation change in terms of number of individuals and basal area) confirm the expansion of the forests towards the surrounding natural grasslands, a trend found by several authors (BURROWS; COMPTON; HOFFMANN, 1998; DUSSART; LERNER; PEINETTI, 1998; PALMER; ROOYEN 1998; SCHWARTZ et al., 1996;

SILVA et al., 2008). However, after a fire event, the number of individuals in Site 8 grassland reduced and some studies have shown that in the savanna-forest boundary, forest can expand and retreat as a consequence of disturbances (HOPKINS, 1992; WOODWARD; DIAMENT,1991). Fire suppression is therefore important for recruitment in the grassland, since fire seems to be the most important constraint to forest expansion in Brazil (HOFFMANN et al., 2009).

Environmental gradient effect on survival and growth - Pioneer species had a higher survival probability closer to the edge, whereas the survival of climax species (whether shade tolerant or not) increased with increasing distance from the immediate edge. In addition, the survival of pioneer and light-demanding species depends on their DBH, whereas shade-tolerant species survival is only affected by the distance to the edge. The height of shade-tolerant species is less variable than the height of the other groups since they are species commonly restricted to the understory of gallery forests. This contributes to the non-detection of a plant-size effect on their survival, if any effect actually exists.

All groups grew faster in the grasslands. Pioneer species need light to germinate and grow so they benefit from the permanent gap condition found in the edge, however this permanent gap condition only exists in the first few meters, leading to a higher mortality risk and lower number of individuals toward the interior probably due to shading. For the pioneer species, light is, therefore, the most important factor for their survival, regardless of the disturbances and harsh microclimatic environments occurring at the forest edge. On the other hand, although climax species also benefit from the higher luminosity leading to higher growth toward the grassland, the harsher conditions there have a price in terms of survival. In addition to the high light conditions in the immediate edge, there are also microclimatic differences, such as lower humidity and higher temperature variations (MURCIA, 1995). We did find soil

moisture differences between grassland and forest during the dry season (BRAGION, in prep.), that is a limiting factor because of drought stress (SCHOLLES; ARCHER 1997). These environmental conditions handicap climax species (LAURANCE; PERES, 2006), increasing mortality and reducing the number of individuals in grassland and first meters of edge. Therefore, for climax species, the unsuitable microclimatic conditions in the exposed edge is the most important factor for their survival, although, for the surviving trees, the growth is favored by higher light availability.

Differences in strategies between functional groups – Even though we worked with subjective groups, we found significant similarities within groups and differences in strategies among the groups. SLA and LDMC are markers of position in the fundamental tradeoff between acquiring or conserving resources (GARNIER et al., 2001), and we found differences between groups, with pioneer species with higher SLA and lower LDMC (acquiring strategy) and shade-tolerant species with lower SLA and higher LDMC (conservative strategy).

Groups had a different spatial distribution at the edges and are affected by the edge in different ways. Pioneer species were favored in the most exposed section of the edge while shade-tolerant species were favored in the opposite side deeper inside the forest, with the light-demanding group in an intermediary situation. Those differences in behavior can be explained by functional traits. Pioneer species are favored in the most exposed section of the edge because they have a strategy focused on acquiring resources, resulting in low investment in traits related to endurance and longevity (ALVAREZ-BUYLLA; MARTINEZ-RAMOS, 1992). Their leaves with high SLA and low LDMC are productive (POORTER; VAN DER WERF, 1998; VAN DER WERF et al., 1998) allowing them to have higher growth and to grow more than climax species in a more productive environment, such as the immediate edge. On the other hand, shade-

tolerant species have low SLA and higher LDMC, features that favor efficiency in resource use and, consequently, survival and longevity, being more advantageous toward the interior, when light is scarce. Their investment in resource conservation mirrors their slower growth rates more than pioneer species. Light-demanding species in turn have intermediate traits which reflect in their intermediate growth and intermediate response to the edge.

Normally, pioneer species are associated with investment in height, having slender stems (POORTER et al., 2003). On the contrary, we found pioneer species to be the less slender group. This is a consequence of environmental conditions at the front of the edge, where pioneers are found. In a closed forest condition pioneer species colonize gaps (SWAINE; WHITMORE 1988), and although those gaps receive a high levels of light, they form a more enclosed environment than natural edges, with light coming predominantly from the top. Under this condition investment in height improves survival and further growth. However, in natural edges, the lateral light incidence is permanent implying in no need for height growth. Besides this, the higher wind exposure of the edges could lead to higher damage for taller trees. Therefore, in natural edges, due to the environmental conditions, pioneers have a less slender trunk than climax species.

Functional traits and growth - We found that some functional and allometric traits enhance growth. In the edges, species with deeper crowns, instead of wider, grew more. A crown shape that can boost light interception is crucial and given that in edges light reaches the forest not only vertically but also laterally, deeper crowns allows a better interception of lateral light promoting higher growth. The crown shape is also linked with successional position (HORN, 1971) and because early-successional species (thus pioneers and light-demanding) are fast-growing species with low investment in wood they can not bear wide crowns. Shade-intolerant species are multilayer, with

narrow crowns and several branches disposed along those layers (HORN, 1971). However, self-shading in deeper crown pays off only in high light environments, such as natural edges.

Our results support the acquisition-conservation tradeoff (DIAZ et al., 2004; WRIGHT et al., 2004) where it is expected that species with the strategy of a rapid production of biomass, i.e. high growth rates, will have low LDMC. In natural edges, species with low LDMC grow more. LDMC is a functional marker of plant strategy and low LDMC is linked to shade-intolerant species and its also linked to productive and often highly disturbed environments (PÉREZ-HARGUINDEGUY et al., 2013), such as natural edges. We expected that growth would have a positive relationship with stem slenderness, but we found the opposite, less slender stems grew more. This could be a consequence of how RGR is measured, since it is based on the trunk diameter increment. However, we also found that pioneer species have less slender trunks and also have higher growth. Therefore, having a less slender stem can be an advantageous trait in natural edges for the reasons put forth previously.

Functional traits and survival - Climate, disturbance and site productivity act as consecutive environmental filters that select certain traits (WOODWARD; DIAMANT 1991). In natural edges, a high productive environment, due to the high light incidence, environmental filters are expected to select traits associated with resource acquisition. However, we found species with traits of both strategies, acquisition and conservation. Survival is enhanced by lower SLA and higher LDMC, both features of shade-tolerant species and of conservation strategy. Survival is also enhanced by higher growth and lower WD, features of shade-intolerant species and of an acquisition strategy. We found that probability of survival varies with distance from the edge and among the functional groups. As mentioned before, pioneer species have a higher survival probability closer to the edge, whereas the survival of climax species (whether

shade tolerant or not) increased with increasing distance from the edge. So, in this short gradient, both strategies are selected but in distinct zones of the edge. The same effect was not observed for growth because all groups grow less toward the interior, thus the effect of the gradient on growth did not change with functional group.

Synthesis - Our study showed the nature of strong and sharp gradients of natural edges in gallery forests, where in a few meters, canopy coverage changes completely. Growth and survival of groups with different light use strategies varied differentially and strongly along the sharp gradient of only 10 m studied here. Shade-intolerant species were favored by grassland proximity and shade-tolerant species were favored by canopy closure. Those differences in behavior can be explained by differences in functional traits. A large part of the species in natural edges have an acquisitive strategy, with higher SLA, lower LDMC, lighter WD, higher growth, deeper crowns and less stem slenderness. Growth was enhanced by acquisitive traits. However, mortality selected both strategies, but in distinct zones of the edge. We encourage further studies focusing on the mechanisms behind forest expansion as to if/how pioneer species facilitate non-pioneer establishment; and the long-term effect of fire as a forest expansion suppressor.

Table 1 Species with more than 50 individuals ordered by their numbers (N) followed by their functional group (FG): P=pioneer, L= light-demanding, S= shade-tolerant.

Species	N	FG
<i>Myrsine umbellata</i> Mart.	652	L
<i>Eremanthus erythropappus</i> (DC.) MacLeish	619	P
<i>Myrcia splendens</i> (Sw.) DC.	498	L
<i>Psychotria vellosiana</i> Benth.	397	L
<i>Miconia chartacea</i> Triana	223	L
<i>Vismia guianensis</i> (Aubl.) Pers.	214	P
<i>Hyptidendron asperrimum</i> (Epling) Harley	211	L
<i>Leandra scabra</i> DC.	209	P
<i>Protium spruceanum</i> (Benth.) Engl.	207	L
<i>Pera glabrata</i> (Schott) Poepp. ex Baill.	179	L
<i>Casearia sylvestris</i> Sw.	175	P
<i>Vochysia tucanorum</i> Mart.	164	L
<i>Calyptranthes brasiliensis</i> Spreng.	150	S
<i>Clethra scabra</i> Pers.	143	L
<i>Daphnopsis fasciculata</i> (Meisn.) Neuling	134	L
<i>Miconia pepericarpa</i> DC.	121	P
<i>Tapirira obtusa</i> (Benth.) J.D.Mitch.	107	L
<i>Myrcia venulosa</i> DC.	99	L
<i>Faramea latifolia</i> (Cham. & Schltdl.) DC.	91	L
<i>Miconia paulensis</i> Naudin	90	P
<i>Protium widgrenii</i> Engl.	85	L
<i>Casearia decandra</i> Jacq.	82	S
<i>Calyptranthes clusiifolia</i> O.Berg	78	S
<i>Miconia theaezans</i> (Bonpl.) Cogn.	77	L
<i>Myrsine guianensis</i> (Aubl.) Kuntze	70	P
<i>Alchornea triplinervia</i> (Spreng.) Müll.Arg.	65	L
<i>Siphoneugena reitzii</i> D.Legrand	63	L
<i>Copaifera langsdorffii</i> Desf.	57	S
<i>Myrcia tomentosa</i> (Aubl.) DC.	51	L

Table 2 Dynamic rates in number of individuals for light-demanding, pioneer and shade-tolerant groups in natural forest edges of gallery forests, from 2009 to 2013. Values followed by the same letter are not significantly different according to an LSD test.

Year	Group	N°	N°	N°	Initial Number	Final Number	Mortality (%)	Recruitment (%)	Change
2009-2010	Light	79	336	3200	3279	3536	2.41^a	9.50^a	7.84^a
2009-2010	Pioneer	19	113	1377	1396	1490	1.36^{ab}	7.58^a	6.73^a
2009-2010	Shade	4	27	337	341	364	1.17^b	7.42^a	6.74^a
2009-2010	Overall	102	476	4914	5016	5390	2.03	8.83	7.46
2010-2011	Light	182	92	3354	3536	3446	5.15^a	2.67^a	-2.55^a
2010-2011	Pioneer	68	72	1422	1490	1494	4.56^a	4.82^a	0.27^a
2010-2011	Shade	8	10	356	364	366	2.20^b	2.73^a	0.55^a
2010-2011	Overall	258	174	5132	5390	5306	4.79	3.28	-1.56
2011-2012	Light	190	292	3283	3473	3575	5.47^a	8.17^a	2.94^a
2011-2012	Pioneer	81	129	1420	1501	1549	5.40^a	8.33^a	3.20^a
2011-2012	Shade	8	39	362	370	401	2.16^b	9.73^a	8.38^a
2011-2012	Overall	279	460	5065	5344	5525	5.22	8.33	3.39
2012-2013	Light	260	216	3336	3596	3552	7.23^a	6.08^a	-1.22^a
2012-2013	Pioneer	74	65	1482	1556	1547	4.76^a	4.20^a	-0.58^a
2012-2013	Shade	10	27	391	401	418	2.49^b	6.46^a	4.24^a
2012-2013	Overall	344	308	5209	5553	5517	6.19	5.58	-0.65
2009-2013	Light	616	861	2739	3355	3600	3.98^a	5.32^a	1.42^a
2009-2013	Pioneer	209	354	1212	1421	1566	3.13^a	5.00^a	1.96^a
2009-2013	Shade	26	100	318	344	418	1.56^b	5.32^a	3.97^a
2009-2013	Overall	851	1315	4269	5120	5584	3.57	5.23	1.75

Table 3 Dynamic rates in terms of basal area for light-demanding, pioneer and shade-tolerant groups in natural forest edges of gallery forests, from 2009 to 2013. Values followed by the same letter are not significantly different according to an LSD test.

Year	Group	Dead	Recruits	Survivor	Increm.	Decrem.	Initial	Final	Loss	Gain	Change
2009-2010	Light	0.04	0.05	5.34	0.53	-0.10	4.96	5.39	2.85^a	10.88^a	8.61^a
2009-2010	Pioneer	0.01	0.02	4.49	0.50	-0.08	4.10	4.51	2.35^a	11.51^a	10.12^a
2009-2010	Shade	0.01	0.01	0.61	0.06	-0.01	0.57	0.62	3.65^a	10.70^a	7.83^a
2009-2010	Overall	0.06	0.09	10.44	1.09	-0.20	9.64	10.52	2.68	11.14	9.21
2010-2011	Light	0.13	0.02	5.22	0.34	-0.48	5.39	5.25	11.41^a	6.94^a	-2.60^a
2010-2011	Pioneer	0.09	0.02	4.44	0.37	-0.41	4.51	4.47	11.12^a	8.86^a	-0.95^a
2010-2011	Shade	0.01	0.00	0.61	0.04	-0.04	0.62	0.62	8.08^a	6.67^a	-0.29^a
2010-2011	Overall	0.23	0.05	10.26	0.75	-0.94	10.52	10.34	11.09	7.75	-1.76
2011-2012	Light	0.09	0.04	5.40	0.48	-0.28	5.25	5.45	7.03^a	9.58^a	3.82^a
2011-2012	Pioneer	0.06	0.02	4.58	0.36	-0.22	4.47	4.61	6.37^a	8.35^a	3.06^a
2011-2012	Shade	0.00	0.01	0.63	0.04	-0.02	0.62	0.63	4.67^a	6.98^a	2.43^a
2011-2012	Overall	0.15	0.07	10.61	0.88	-0.53	10.34	10.69	6.60	8.90	3.41
2012-2013	Light	0.03	0.03	5.64	0.57	-0.34	5.45	5.68	6.75^a	10.50^a	4.12^a
2012-2013	Pioneer	0.01	0.01	4.81	0.57	-0.33	4.61	4.84	7.35^a	11.94^a	5.10^a
2012-2013	Shade	0.00	0.00	0.67	0.05	-0.01	0.63	0.67	1.87^a	7.81^a	6.44^a
2012-2013	Overall	0.04	0.04	11.12	1.18	-0.68	10.69	11.19	6.72	10.96	4.68
2009-2013	Light	0.37	0.18	5.68	1.27	-0.56	4.96	5.68	4.07^a	5.74^a	2.72^a
2009-2013	Pioneer	0.33	0.12	4.85	1.22	-0.48	4.10	4.84	4.28^a	6.28^a	3.39^a
2009-2013	Shade	0.01	0.01	0.67	0.12	-0.02	0.57	0.67	1.22^b	4.33^a	3.23^a
2009-2013	Overall	0.72	0.31	11.20	2.62	-1.05	9.64	11.19	3.98	5.88	3.04

Table 4 Differences in functional and allometric traits for tree functional groups in natural edges of gallery forest. SLA: Specific Leaf Area ($\text{mm}^2 \text{mg}^{-1}$); LDMC: Leaf dry matter content (%); SS: stem slenderness (tree height/CBH); CF: Crow Format (crown width/crown depth).

	SLA	LDMC	SS	CF	WD
Pioneer	4.35 ^a	0.37 ^a	0.36 ^a	0.86 ^a	0.25 ^a
Light	3.99 ^b	0.35 ^b	0.42 ^b	0.85 ^a	0.25 ^a
Shade	3.24 ^{ab}	0.44 ^c	0.43 ^b	0.76 ^a	0.35 ^a
	$\chi^2=10.67;$ p < 0.001	$\chi^2=65.28,$ p < 0.001	$\chi^2=18.79,$ p < 0.001	$\chi^2=1.75,$ p = 0.41	$\chi^2=4.37,$ p = 0.11

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**PAPER 2 - DOES FACILITATION FOSTER GALLERY FOREST
EXPANSION INTO GRASSLANDS IN BRAZIL?**

ABSTRACT

Boundaries between gallery forest and grasslands are one of the few examples of sharp, natural old edges and they are fascinating given the very distinct vegetation type coexisting under a common climate. However, a forest could be expanding into grassland areas and this process could be fostered by positive interactions, since forest species face several environmental constraints when living in open areas, thus, after first the trees are established in grassland they can facilitate new ones. It is also probable that forest expansion works as a succession process and as succession goes by and harsh conditions in grasslands turn more suitable for forest species, the importance of positive interactions probably declines, increasing the importance of competition and other negative interactions. In order to answer whether gallery forests are expanding and whether this expansion follows a succession process with the pioneers and light – demanding taking the lead, we studied 8 sharp boundaries of gallery forests with grasslands in a five year interval (2009-2013). We classified all species with at least 50 samplings across sites in three functional groups: pioneer, light – demanding and shade – tolerant and we generated bar plots for the number of individuals in the grassland over the years. To test if forest expansion is fostered by a facilitation process we selected *E. erythroppapus*, one of the few first pioneers to establish in the grassland and should be a facilitator. We fitted a regression line expecting to find a positive relation between the abundance of facilitators and recruitment. Expecting a change from positive interactions to negative ones in the short gradient we fitted hierarchical Bayesian models expecting a positive relationship between Competition Index and survival where facilitation processes dominate (grasslands) and a negative relationship where competition processes dominate (inside the forest). We found forest expanding over grasslands with the pioneer species having the spearhead role, followed by the light-demanding species and, lastly, by the shade-tolerant in a clear succession process, what could suggest a facilitation process. However, the presence of facilitators did not foster forest expansion since the higher the number of facilitators, the lower the forest expansion. Also, there was no change from positive to negative interactions, but even in the grassland, neighbors reduced survival. Although we did not find evidence of facilitation, negative interactions do not completely suppress it, since there was expansion in most of the sites.

Key – words: positive interactions, functional groups, SGH, environmental gradient, cerrado

1 INTRODUCTION

Boundaries between gallery forest and grasslands are one of the few examples of sharp, natural, old edges. Those boundaries are intriguing since they are very distinct vegetation types coexisting under a common climate. (WHITTAKER, 1975; BOND, 2005; BOND; WOODWARD; MIDGLEY, 2005). It has been asserted that soil nutrients could explain these vegetation mosaics (FURLEY 1992; FÖLSTER; DEZZEOB; PRIESSA, 2001; GOODLAND; POLLARD, 1973; LLOYD et al., 2008; SARMIENTO, 1992), however new studies have shown that soil nutrients do not explain differences in vegetation (BOND, 2010; SILVA et al., 2008; ROSSATO; HOFFMANN; FRANCO, 2009; VAN DEN BERG; OLIVEIRA-FILHO, 1999) or even drive changes in vegetation types, but they are responders (GRAY; BOND 2015). The sharp boundaries between open ecosystems and forest are better explained by the frequent fire events that take place in the grasslands and eventually affect the forest edge, however, extinguishing there (VAN DEN BERG; OLIVEIRA-FILHO 1999, 2000; VAN DEN BERG; SANTOS 2003; FELFILI, 1998; ROSSATO; HOFFMANN; FRANCO, 2009).

It is possible that the gallery forests are expanding into grassland areas. Several studies conducted around the world have shown past and recent expansions of forest into open ecosystems (BOWMAN; WALSH; MILNE, 2001; DESJARDINS et al., 1996; HOPKINS 1992; KERSHAW, 1992; SANAIOTTI et al., 2002; SCHWARTZ et al., 1996; SILVA et al., 2008), however fire is a main constraint to forest expansion (HOFFMANN; ORTHEN; FRANCO, 2004; HOFFMANN et al., 2009). In the grassland, the grass layer enhances the likelihood of fire events due its high flammability creating a positive feedback between grassland and fire, since fire favors grasses and

hinders woody plants (BAUDENA et al., 2015). Fire kills woody seedlings and samplings and topkills adults because of their lack of protective thick bark (HOFFMANN et al., 2009; ONDEI et al., 2015). Therefore, under frequent fires, forest expansion is unlikely, but when fire is suppressed, a gallery forest can expand into open areas (Ratter, 1992). Therefore, forest and savanna exist as alternative stable states where forests are favored by suppressing fire events (GRAY; BOND 2015; STAVER; ARCHIBALD; LEVIN, 2011).

Forest species face several constraints when establishing in the grasslands (BOND, 2008; HOFFMANN; ORTHEN; FRANCO, 2004). They are limited by microclimate, such as high light leading to high temperature and drought stress. Furthermore, grasses outcompete them in this environment, mostly when as seedlings. After the first trees establish in the grassland they can facilitate new ones (HOFFMANN, 1996; KELLMAN, 1985; KELLMAN; MIYANISHI, 1982). These first colonizers provide shade preventing lethal temperatures and increasing soil moisture (PUGNAIRE; VALLADARES 2007). They also provide nutrient enrichment via their litter (HUNTER; AARSEEN, 1988). Therefore, they allow higher establishment and growth of forest species in open areas. As time goes by, more forest tree species establish in grasslands forming a more closed canopy and a more humid understory that exclude grasses and is less flammable reducing frequency and intensity of fires events (HOFFMANN et al., 2011) leading to a positive feedback between fire exclusion and forest expansion. Consequently, although constraints can reduce establishment and survival, they cannot prevent forest expansion into grasslands (BOWMAN; PANTON, 1993; HOFFMANN, 1996; HOFFMANN; ORTHEN; FRANCO, 2004).

Given all constraints and stressful conditions for forest species establishment in open areas it is probable that forest expansion works as a succession process where a facilitation process dominates (CLEMENTS, 1916;

CONNELL; SLATYER, 1977; GRIME, 1977) with an initial occupation of the grassland area by colonizer species, smoothing the harsh grassland conditions, followed by other species. As succession continues and harsh conditions in grasslands turn more suitable for forest species, the importance of positive interactions probably declines, increasing the importance of competition and other negative interactions. The gradient from grassland to forest could therefore be in different stages of succession, when environmental stress is higher in the grassland in lower in the forest. According to the stress-gradient hypothesis in a gradient like this, interactions can change from facilitation (harsh environment) to competition (BERTNESS; CALLAWAY, 1994; CALLAWAY; WALKER, 1997).

Several issues have been explored through the years regarding forest expansion into grasslands, such as if forest are expanding (Silva et al., 2008), the role of soils (GRAY; BOND 2015), constraints to tree establishment (HOFFMANN; ORTHEN; FRANCO, 2004), and the role of facilitators in seedling establishment (HOFFMANN, 1996; KELLMAN 1985; KELLMAN; MIYANISHI, 1982). However, we lack understanding of how plants behave after the seedling stage, and if first colonizers are really helping plants achieve adulthood and forest expansion. In addition, we also do not know how the environment gradient affect plants interactions. The southern mesic grasslands of Brazil are a unique opportunity to study forest expansion and the relationship between positive interactions and forest expansion. In these grasslands, at elevations above 900m a.s.l, *Eremanthus erythropappus* is a pioneer woody tree known for its capacity to colonize grasslands. They form a monodominant buffer surrounding gallery forests and prevent fire from advancing further inside the forest (OLIVEIRA-FILHO; FLUMINHAN FILHO, 1999). Possibly this species, could nurse forest tree seedlings by forming a shading canopy that increases soil moisture, reducing grasses and fire events and thus facilitating forest expansion.

Therefore, we hypothesized that over time the density of trees increases in the grassland areas close to the forest edge, following the general pattern of expansion of forest over savannas observed around the globe. We expected this expansion process to follow a path similar to that of forest succession, with an initial occupation of the grassland area by pioneer species, followed by the light-demanding and shade-tolerant species. We also hypothesized that gallery forest expansion over the grassland is fostered by a facilitation process where trees previously established on the grassland nurse new plants, so sites with higher abundance of new colonizers will have a higher expansion toward the grassland. Also, based on the stress-gradient hypothesis we believe that there is a change from positive interactions (facilitation) to negative ones (tolerance) in the short gradient from grassland to the gallery forest as a consequence of the sudden change in microclimate (Figure 1). Because of that, we expected survival to be enhanced by neighbors in the grassland and the opposite pattern deeper within the gallery forest.

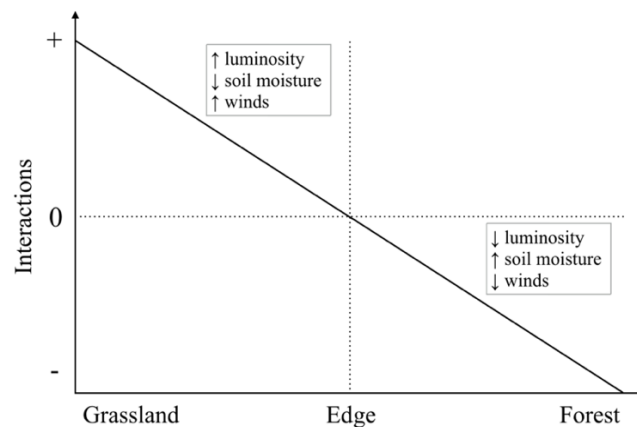


Figure 1 Interaction among plants can be context depend. In a stressful environment such as grasslands, neighbors can provide shelter whose benefits can overlap resource depletion. However, when stress declines toward the forest interior the benefits of shelter decreases and the ability to explore shared resources becomes more important.

2 METHODS

Study Sites – We studied 8 gallery forests with natural edges with grasslands in the south of Minas Gerais State, Brazil (**Figure 2**). The vegetation of the region is a disjunction of the Cerrado biome, inserted within the seasonal semi-deciduous rainforests distribution area of southeastern Brazil (Brazilian Institute of Geography and Statistics-Instituto Brasileiro de Geografia e Estatística – IBGE, 2004). The climate is Cwa according to the Köppen climate classification, temperate and rainy (mesothermic) with dry winters and rainy summers, and subtropical (DANTAS; CARVALHO; FERREIRA, 2007). Elevation varies from 850 m to approximately 1500 m a.s.l.

We chose sites lacking obvious anthropogenic impacts such as logging, undergrowth clearing, clear cutting, or evidence of recent fires, and that had natural edges with native grasslands.

Vegetation sampling – In 2009, we established three permanent plots (15 m × 20 m; 300 m²) in each of the 8 sites respecting a 10 m minimum distance between plots within a site. We laid out the plots with their wider side parallel to the forest edge, including 5 m of grassland and 10 m of forest (Figure 2). We identified, mapped, and measured height and DBH of all individuals with diameter at breast height (DBH) ≥ 1 cm.

Since 2009, we have carried out five annual inventories (2009 to 2013). In each inventory we measured and re-measured all alive individuals and verified all dead ones. The recruits, i.e., the new individuals meeting the inclusion criterion (DBH ≥ 1 cm), were identified and mapped, and had their height and DBH recorded. We identified the recognizable species during the fieldwork, or by collecting samples and comparing them to identified specimens

in an herbarium (ESAL Herbarium of the Federal University of Lavras) or consulting the literature and specialists.

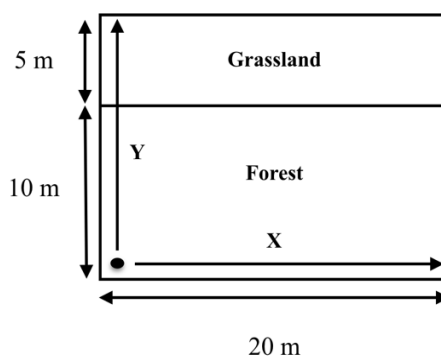


Figure 2 Sketch of how plots were assembled with 5 m of grassland and 10 m of forest edge. X is the distance parallel to the upper limit of the plot as measured from the corner, Y is the distance of the individual from the upper limit of the plot.

Mapping of individuals – We mapped all individuals within the plots. For each individual we measured the distance between the rooting point and two corners of the plot, using an ultrasound distance measuring instrument (Haglöf DME 201 Cruiser). We transformed the distances into coordinates (X and Y) using the Pythagorean equation, where X is the distance parallel to the upper boundary of the plot as measured from the corner, Y is the distance of the individual from the upper limit of the plot (Figure 2).

Expansion of gallery forest over time – We established the plots including 5 meters of grasslands so we could follow expansion or retraction of the forest. To test if there was an initial occupation of the grassland area by pioneer species, followed by light-demanding and shade tolerant species, we generated bar plots for number of individuals for each functional group in the grassland over the years. We also calculated recruitment and mortality rates, following Sheil, Jennings and Savill (2000):

$$M = \left\{ 1 - \left[\frac{(N_o - N_m)}{N_o} \right]^{\frac{1}{t}} \right\}^{\frac{1}{t}} \times 100 ; \quad (1)$$

$$R = \left[1 - \left(1 - \frac{N_r}{N_t} \right)^{\frac{1}{t}} \right] \times 100 ; \quad (2)$$

where N_o are the initial count of individual trees, N_r is the number of recruits and N_t is the final counts of individual trees.

For this analysis, we used all species with at least 50 samplings across sites (Table 1). We defined functional groups using a classification based on light requirements for germination and establishment (SWAINE; WHITMORE, 1988) and studies in the same region (NUNES et al., 2003; OLIVEIRA-FILHO et al., 1994a, 1994b, 1997; OLIVEIRA-FILHO, MELLO, SCOLFORO, 1997; PEREIRA et al., 2010; PINTO; HAY, 2005). Pioneers (P) were those species whose seeds only germinate in sites with direct light at ground level for at least part of the day. Their germination is triggered by an increase in red light or soil temperature fluctuation and their seedlings require direct light for establishment and growth. In contrast, non-pioneers germinate and their seedlings establish under the canopy without direct light. We subdivided this non-pioneer group into two: light-demanding species (L), which demand more solar radiation for growth and have fast growth; and shade-tolerant species (S), which require very little light and grow slowly. We recognize the existence of other classifications and approaches to classify functional groups, however, we believe that the classification proposed by Swaine and Whitmore (1988) is suitable for our analysis, since it is based on light requirements, which is a major defining environmental condition for natural edges.

Facilitation and forest expansion – We hypothesized that forest expansion is governed by facilitation process. For this, we selected *E. erythropappus* as a model species, since it is the first pioneer to establish in the grassland and it is the only species with significant number of individuals

establishing in the grassland. It should be a facilitator providing protection against the environmental stress for new plants. We fitted a regression line expecting to find a positive relation between the abundance of *E. erythroppapus* and recruitment (%.year⁻¹). We calculated recruitment (R) following Sheil, Jennings and Savill (2000), as described above.

Interactions and survival – We hypothesized based on the SGH that there is a change from positive interactions to negative ones in the short gradient from grassland to the gallery forest. In this analysis we select all species with more than 50 samplings across sites that had dead individuals in the grassland, edge and forest (Table 2).

We expected a positive relationship between Competition Index (see below) and survival where facilitation processes dominate (grasslands) and a negative relationship where competition processes dominate (inside the forest). We computed the competition index as (HEGYI, 1974):

$$CI_i = \sum_{j=1}^{N_i} \left(\frac{dbh_j}{dbh_i} \right) \left(\frac{1}{D_{ji}} \right), \text{ for } i \neq j \quad (3)$$

where CI_i is the competition index for the subject tree i , dbh_j is the diameter of the competitor tree j , dbh_i is the diameter of the subject tree and D_{ji} is the distance between subject tree i and competitor tree j , and N_i the number of competitor trees per subject tree i .

Survival was modelled as a logistic model:

$$\text{logit}(S_i) = \alpha + \beta_i * CI \quad ; \quad (4)$$

where S_i is the probability of survival for each environment, G is the annual growth (yr⁻¹) and α and β were parameters. Rather than fit separate models for each environment (grassland, edge and forest, Figure 4), we used a second level in the hierarchical model for β parameter in Equation 1. Parameter β for environment i in Eq. 1 is modelled as:

$$\beta_i = \text{normal}(\mu_i, \tau_i)$$

We obtained posterior distributions of parameters using the Markov Chain Monte Carlo (MCMC) method. We monitored convergence by running three different chains with different start values. From the posterior distribution we computed the mean and credible intervals (CI) for all parameters and the significance of parameters was assessed by a 95% C.I., and, for evaluating discrepancy, we calculated Bayesian p-value (GELMAN; MENG; STERN, 1996).

Light and Soil Moisture data – We hypothesized that there is a change from positive interactions to negative interactions in the short gradient from grassland to the gallery forest as a consequence of the change in the microclimate. To test differences in microclimate we measured light and soil moisture. We measured the canopy cover with a Lemmon convex spherical densitometer, facing north, south, east and west, 1 m above the ground every one meter from the top to the bottom of the plot.

We collected soil for surface moisture measurements under two contrasting conditions: the rainy season (January and February) and the dry season (August and September). In each round of sampling, we collected two soil samples covering 0-20 cm of depth, one within the forest (10 m inside) and one within the grassland (5 m from the edge), and placed them in hermetically sealed containers. We measured soil moisture as the difference between the initial weight of the sample and the final weight following oven drying at 110°C until constant weight. The differences between the wet and dry weights of the soil samples were used to calculate the soil moisture percentages for each plot. The normality of the data distribution was checked graphically, and then a two-way ANOVA was used to compare the data. We investigated possible differences between grassland and forest during the rainy and dry seasons and between seasons within each of the two environments for 3 years: 2011; 2013 and 2014. For all analyses, we used the R software, version 3.1.1. For the

Bayesian models, we used the RJAGS package (PLUMMER, 2014).

3 RESULTS

Expansion of gallery forest over time –We found recruitment higher than mortality for all sites (Table 3). When we first assembled the plots we included 5 m of grassland and found a few saplings and trees, most of them were pioneers, a few light-demanding and no shade-tolerant species. The increase of the number of trees in the grassland since 2009 follows a clear pattern: first there was a rise in the number of pioneers followed by a rise in the light-demanding and finally a rise in the shade-tolerant species (Figure 3). Site 8 was burned in 2012 leading to a decrease in the number of individuals in the grassland in 2013.

Facilitation and forest expansion – We expected a positive relation between recruitment and abundance of *E. erythropappus*. However, there is a negative relation ($y = 54.45 - 1.13x$, $R^2 = 0.32$, $p = 0.02$, Figure 4) between variables suggesting that facilitators are not promoting forest expansion.

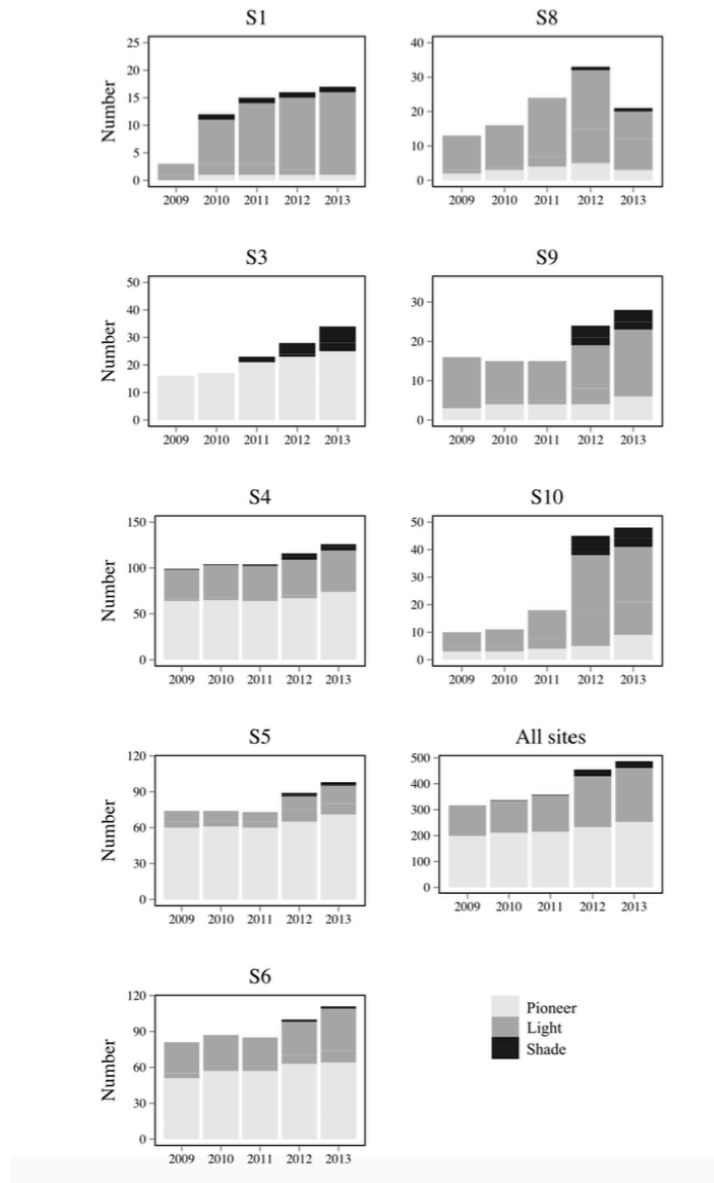


Figure 3 Number of recruits in grassland year by year for each site and for all sites.

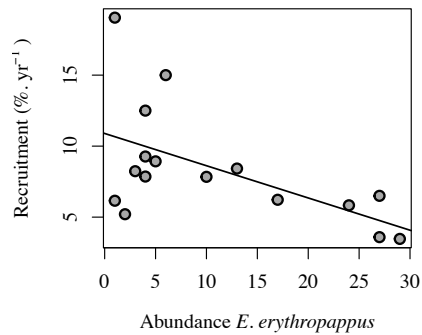


Figure 4 Relationship between *E. erythropappus* abundance and recruitment. Regression line shows a negative relation between variables suggesting that *E. erythropappus* is not promoting forest expansion.

Plant interactions and survival – The binomial model for survival had a good fit, since the p-value was close to 0.50 (p-value = 0.52). Interactions do not change from positive to negative across the environmental gradient, since all parameters were negative (Figure 5). Therefore, probability of survival decreases with the increase of CI in all environments (Figure 6).

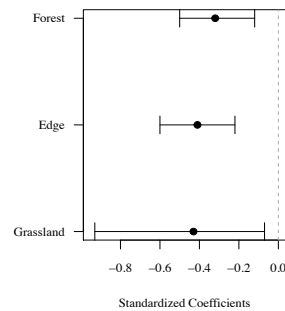


Figure 5 Credible interval (95%) for parameters of survival model. Values that do not overlap zero are significant.

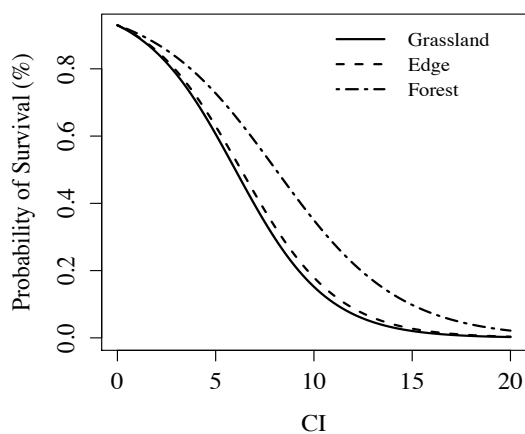


Figure 6 Probability of survival for trees with $DBH \geq 1$ cm in grassland, edge and gallery forest as function of the Competition Index (CI). There was no change from positive to negative interactions, in all environments neighbors reduce the probability of survival.

Light and Soil Moisture – The canopy coverage increased towards the forest interior, however after 7 m from the edge it stabilized around 85-90% (Figure 7). In 2010, the only difference in soil moisture is between edge and grassland during dry season. In 2012, there was no difference between edge and grassland in the wet season, so grasslands are drier than edges during the dry season. In 2013; there is no difference between seasons for each environment, however edges are moister than grasslands in the wet and dry season (Table 4).

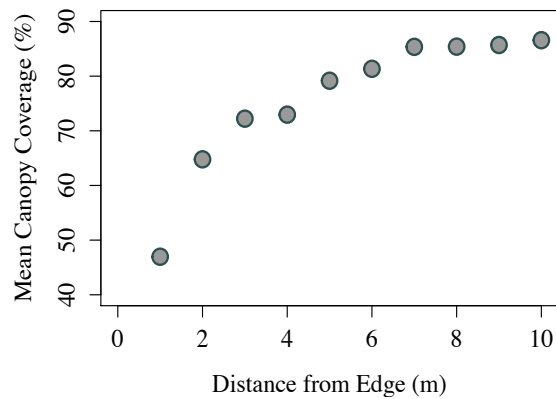


Figure 7 Mean canopy coverage (%) for 8 gallery forests in Brazil.

4 DISCUSSION

We examined if forest expansion over grassland is fostered by a facilitation process. We assessed whether gallery forests are expanding into grasslands and whether there is a facilitation process, where first colonizers facilitate the recruitment fostering forest expansion. Also, based on the stress gradient hypothesis (SGH), we examined whether there is a change from positive to negative interactions in the short gradient from grassland to gallery forest as a consequence of the change in microclimate. We found forest expanding over grasslands, with recruitment rates higher than mortality. We also found the pioneer species having the spearhead role, followed by the light-demanding species and, lastly, by the shade-tolerant in a clear succession process, that could suggest a facilitation process. However, the presence of facilitators did not foster forest expansion since the more facilitators, the less the forest expansion. Also, there was no change from positive to negative interactions, but even in the grassland neighbors reduced survival. Although we did not find first colonizers acting as facilitators, negative interactions do not completely suppress it, since there was expansion in most of the sites.

The increases in number of individuals indicate forests expansion into surrounding natural grasslands, a trend found by several authors (BOWMAN; WALSH; MILNE, 2001; DESJARDINS et al., 1996; HOPKINS, 1992; KERSHAW, 1992; SANAIOTTI et al., 2002; SCHWARTZ et al., 1996; SILVA et al., 2008). In addition, the behavior of the studied functional groups denotes that the expansion front is in a continual succession process with pioneer and light-demanding species taking the lead, followed by shade-tolerant species. Such a sequence of occupation has been previously observed in the Congo (SCHWARTZ et al., 1996) and the Ivory Coast (HENNEMBERG et al., 2006), where the line of forest expansion towards the savanna was dominated by pioneer species, followed by shade-tolerant species after the pioneer species had formed a forest canopy.

However, after a fire event, the number of individuals in Site 8 grassland decreased. Fire suppresses forest expansion by topkill (i.e. loss of above-ground biomass) and mortality (HOFFMANN; ORTHEN; FRANCO, 2004). In our study we could not differentiate between topkill and mortality, but both processes can lead to reduction of the number of trees, stalling or even reverting forest expansion. During this study period, only in three sites the grasslands burned (Sites 8, 9 and 10), but in Site 9 fire did not cause death in the grassland and on Site 10 the fire extinguished before reaching the plots. Considering that open areas normally burn at 1-3 year intervals (HOFFMANN; ORTHEN; FRANCO, 2004), fires in our sites seem much less frequent, at least for the studied period. These longer intervals are possibly allowing gallery forests in the southern gallery forest to expand over their surrounding grassland (see also BOND; MIDGLEY, 2000). Fire suppression could therefore be important for recruitment in the grassland, since fire seems to be the more important constraint to forest expansion in Brazil (HOFFMANN et al., 2009).

Although forest expansion behaves similar to a succession process that could suggest a facilitation process, our hypothesis of the first colonizer favoring forest expansion was not confirmed, since forest expansion was negative in relation to *E. erythropappus* abundance. Several studies have shown the importance of isolated trees in open areas in providing shade, preventing lethal temperatures and increasing soil moisture (PUGNAIRE; VALLADARES, 2007), so seedlings die less and grow more (HOFFMANN; 1996; KELLMAN; 1985; KELLMAN; MIYANISHI, 1982). However, if the same effect occurred for older plants we expected to observed a positive relationship between abundance and recruitment, which did not occur. Therefore, for older plants the positive effect of protection is exchanged for the negative effect of resource sharing.

In this context, it is important to consider the lifespan of the colonizer, since *E. erythropappus* is a long lifespan pioneer. Previous studies (HENNEMBERG et al., 2006; SCHWARTZ et al., 1996) and our data showed that forest expansion starts with shade intolerant species, which mostly have a short lifespan. Thus, it is probable that they act as facilitators, but given their short lifespan, they die fast releasing space and resources sooner than *E. erythropappus*, allowing the plants initially favored by the nurse trees to reach adulthood. Therefore, although a long lived colonizer could still favor seedling establishment, they probably do not favor their continuity up to adulthood leading to lower recruitment rates when they are more abundant.

Changes in microclimate can affect how plants interact with each other (BERTNESS; CALLAWAY, 1994; CALLAWAY; WALKER, 1997). Boundaries studied here between grasslands and forest are very sharp and in few meters the conditions change from a completely open area to a closed forest. Our light measurements showed that the major changes in canopy cover occur in the first 5-7 meters of edge. We believed that these differences in light would lead to

finding differences in soil moisture, even for the rainy season (December to February), however we found differences in soil moisture only during the dry season. Therefore, in these wet conditions (mean annual rain fall 1517 ± 168 mm) soil moisture in grassland is a limiting factor for forest expansion during the dry season, resulting in plant drought stress (SCHOLES; ARCHER, 1997).

We hypothesized, based on the stress-gradient hypothesis, that differences in microclimate would lead to changes from positive interactions in the grassland to negative interactions in the forest (BERTNESS; CALLAWAY, 1994; CALLAWAY; WALKER, 1997). However, our results do not support this idea, since there was no change from positive interactions to negative as a response to changes in microclimate, on the contrary neighbors had negative impact even in the grassland, where neighbors could shelter seedlings and young trees against environment stress. Given that boundaries between gallery forest are old, species living there were probable selected by environmental filters that prioritized traits related to endurance, so they are shade intolerant species that thrive well under high light, low soil moisture and high speed winds. However, shade intolerant species seems not to be so good in sharing resources, such as nutrients and water and in fact, savannas occur in nutrient-poor soils (KELLMAN 1984; HOFFMANN et al., 2009; LEHMANN et al., 2011). Therefore, the positive effect of environmental protection in grasslands is not strong enough to overlap the negative effect of resource sharing.

It is important to consider that even with no positive interactions in the grassland, there was forest expansion, and even for sites when *E. erythroppapus* reduced recruitment the most, recruitment rates were still pretty impressive, with an expansion of 20% in 5 years. This suggests that while negative interactions could delay forest expansion, they could not prevent it and that species establishing and surviving on grasslands are surviving due their great competition ability in this environment.

Our hypothesis that facilitation fosters forest expansion was not validated. Although forest expansion behaves similar to a succession process suggesting a facilitation process, our hypothesis of facilitators favoring forest expansion was not confirmed, since recruitment was negative in relation to facilitator abundance. Given that *E. erythroppapus* is a long lifespan pioneer, it is probable that short lifespan pioneers could facilitate forest expansion, since they would die faster releasing space and resources, but this requires further study. Also, there were no changes from positive to negative interactions along microclimate gradient, and even in the grassland, neighbors reduced survival. While facilitators can increase seedlings growth and survival, as plants grow the positive affect of protection is possibly exchanged for a negative effect of resource sharing. Likewise, the positive effect of environmental protection in grasslands is not strong enough to overlap the negative effect of resource sharing. Although we did not find first colonizers and the presence of neighbors facilitating forest expansion, they do not completely suppress it, since there was expansion in most of the sites, suggesting that plants establishing in grasslands are good competitors. On the other hand, fire seems to be much more restrictive to forest expansion than negative interactions, causing reduction in the number of trees on the grassland.

Table 1 Species that had more than 50 samplings across sites in 8 gallery forests, ordered by their number of individuals (N) followed by functional group (EG): P=pioneer, L= light-demanding, S= shade-tolerant.

Species	N	FG
<i>Myrsine umbellata</i> Mart.	652	L
<i>Eremanthus erythropappus</i> (DC.) MacLeish	619	P
<i>Myrcia splendens</i> (Sw.) DC.	498	L
<i>Psychotria vellosiana</i> Benth.	397	L
<i>Miconia chartacea</i> Triana	223	L
<i>Vismia guianensis</i> (Aubl.) Pers.	214	P
<i>Hyptidendron asperrimum</i> (Epling) Harley	211	L
<i>Leandra scabra</i> DC.	209	P
<i>Protium spruceanum</i> (Benth.) Engl.	207	L
<i>Pera glabrata</i> (Schott) Poepp. ex Baill.	179	L
<i>Casearia sylvestris</i> Sw.	175	P
<i>Vochysia tucanorum</i> Mart.	164	L
<i>Calyptranthes brasiliensis</i> Spreng.	150	S
<i>Clethra scabra</i> Pers.	143	L
<i>Daphnopsis fasciculata</i> (Meisn.) Nevling	134	L
<i>Miconia pepericarpa</i> DC.	121	P
<i>Tapirira obtusa</i> (Benth.) J.D.Mitch.	107	L
<i>Myrcia venulosa</i> DC.	99	L
<i>Faramea latifolia</i> (Cham. & Schltdl.) DC.	91	L
<i>Miconia paulensis</i> Naudin	90	P
<i>Protium widgrenii</i> Engl.	85	L
<i>Casearia decandra</i> Jacq.	82	S
<i>Calyptranthes clusiifolia</i> O.Berg	78	S
<i>Miconia theaezans</i> (Bonpl.) Cogn.	77	L
<i>Myrsine guianensis</i> (Aubl.) Kuntze	70	P
<i>Alchornea triplinervia</i> (Spreng.) Müll.Arg.	65	L
<i>Siphoneugena reitzii</i> D.Legrand	63	L
<i>Copaifera langsdorffii</i> Desf.	57	S
<i>Myrcia tomentosa</i> (Aubl.) DC.	51	L

Table 2 Species that had more than 50 samplings across sites in 8 gallery forests and had dead samples in the grassland, edge and forest.

Species	N	FG
<i>Myrsine umbellata</i> Mart.	652	L
<i>Eremanthus erythropappus</i> (DC.) MacLeish	619	P
<i>Vismia guianensis</i> (Aubl.) Pers.	214	P
<i>Hyptidendron asperrimum</i> (Epling) Harley	211	L
<i>Pera glabrata</i> (Schott) Poepp. ex Baill.	179	L
<i>Miconia pepericarpa</i> DC.	121	P
<i>Myrcia venulosa</i> DC.	99	L
<i>Miconia theaezans</i> (Bonpl.) Cogn.	77	L

Table 3 Recruitment and mortality in grasslands surrounding gallery forests in Brazil during 5 years.

Site	Recruitment (%. yr ⁻¹)	Mortality (%. yr ⁻¹)
S10P1	11.18	3.41
S10P2	16.80	2.14
S10P3	0.00	0.00
S1P1	8.33	2.86
S1P2	5.95	0.53
S3P1	19.09	0.00
S3P2	8.42	0.00
S3P3	12.50	0.00
S4P1	11.03	3.89
S4P2	3.71	1.33
S4P3	7.18	2.67
S5P1	4.92	4.56
S5P2	9.09	0.36
S5P3	8.89	1.38
S6P1	8.41	1.35
S6P2	6.83	2.92
S6P3	6.84	1.00
S8P1	20.00	0.00
S8P2	11.67	1.54
S8P3	16.47	5.83
S9P1	13.33	2.86
S9P2	16.36	0.00
S9P3	20.00	0.00
Overall	8.95	1.93

Table 4 Soil moisture differences between seasons and different environments for 2010, 2012 and 2013 according to Two-way ANOVA and Tukey test.

2010					
Season					
Environment		Wet	Dry	F value	p
	Edge	12.04	13.00	45.93	0.83
	Grassland	11.11	8.84		
	F value	20.84			
p	0.84	0.002			
2012					
Season					
Environment		Wet	Dry	F value	p
	Edge	18.12	12.25	45.93	< 0.001
	Grassland	14.23	8.00		
	F value	20.84			
p	0.013	< 0.001			
2013					
Season					
Environment		Wet	Dry	F value	p
	Edge	16.05	16.03	45.93	0.99
	Grassland	11.47	10.92		
	F value	20.84			
p	0.007	<0.001			

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