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PLASTICIDADE DE ATRIBUTOS FISIOLÓGICOS E EFICIÊNCIA ENERGÉTICA EM ESPÉCIES DE PLANTAS NUMA CRONOSEQUÊNCIA DE FLORESTA TROPICAL SECA: ESTÁDIO SUCESSIONAL x DISPONIBILIDADE HÍDRICA

Recife
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Orientador: Prof. Dr. Mauro Guida dos Santos

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“PLASTICIDADE DE ATRIBUTOS FISIOLÓGICOS E EFICIÊNCIA ENERGÉTICA EM ESPÉCIES DE PLANTAS NUMA CRONOSEQUÊNCIA DE FLORESTA TROPICAL SECA: ESTÁDIO SUCESSIONAL X DISPONIBILIDADE HÍDRICA”.

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RESUMO

Para o estabelecimento de populações vegetais em ambientes que são heterogêneos no tempo e no espaço, como florestas que passam por processo de regeneração natural, é fundamental a capacidade de apresentar respostas plásticas em atributos funcionais foliares em resposta às variações ambientais. Plantas pioneiras apresentam estratégias ecofisiológicas distintas de plantas de estádios sucessionais tardios, ocupando posições opostas no espectro de economia foliar. No entanto algumas plantas conseguem se estabelecer, ao mesmo tempo, em áreas em diferentes momentos do processo sucessional. Dessa forma, o presente trabalho teve como objetivo avaliar a variação nos atributos funcionais de três espécies de diferentes hábitos, numa cronosequência (inicial (22 anos), intermediária (44 anos), e tardia (+ 60 anos)) de floresta tropical sazonalmente seca em três estações chuvosas consecutivas. As espécies selecionadas foram: *Poincianella pyramidalis* (Tul.) L.P. Queiroz (Fabaceae), arbórea; *Hyptis suaveolens* (L.) Poit. (Lamiaceae), herbácea; e *Sida galheirensis* Ulbr. (Malvaceae), subarbustiva. As duas primeiras são encontradas nos três estádios sucessionais, e a última apenas nos estádios inicial e tardio. Todas as coletas foram realizadas no período chuvoso, no mês de abril, entre os anos de 2012 e 2015. Foram mensuradas as trocas gasosas, o potencial hídrico foliar, o conteúdo e a eficiência no uso dos nutrientes, a área foliar específica, o conteúdo de compostos fenólicos, o custo de construção foliar e o tempo de compensação. As respostas ecofisiológicas das plantas foram influenciadas tanto pelo estádio sucessional quanto pela precipitação entre os anos. De um modo geral, as plantas do estádio tardio apresentaram maiores taxas de trocas gasosas, potencial hídrico, eficiência no uso dos nutrientes e investimento em defesa, especialmente em 2014, o ano mais chuvoso. Além disso, um maior custo de construção foliar e um menor tempo de compensação foram observados nas plantas da área tardia, evidenciando que em áreas preservadas as plantas são mais eficientes no uso da energia. No entanto a variação nos atributos foliares foi mais intensa entre os anos de coleta. Dentre os atributos funcionais, o potencial hídrico apresentou a maior capacidade de aclimatação à variação ambiental, seguido da eficiência no uso dos nutrientes e da área foliar específica. O atributo com a menor capacidade de resposta plástica foi o custo de construção foliar. No entanto esse atributo foi mostrou-se como um dos mais importantes na classificação das plantas de acordo com o estádio sucessional. Os resultados mostram que a água é o principal filtro ambiental que coordena as respostas ecofisiológicas na floresta tropical sazonalmente seca brasileira. No entanto as diferentes espécies captam e utilizam a água disponível de forma distinta, evidenciando uma diferenciação de nicho com relação ao uso da água. A variação nos atributos funcionais em função do estádio sucessional sugere que as espécies analisadas têm a capacidade de ajustar o seu espectro de economia foliar, utilizando-se de estratégia de captação ou de conservação de recursos de acordo com as exigências do ambiente.

Palavras-chave: Custo de construção foliar. Sucessão ecológica. Espectro de economia foliar. Fotossíntese. Ecofisiologia.

ABSTRACT

For establishing plant populations in environments that are heterogeneous in time and space, as forests that pass through natural regeneration process, it is essential the ability to present plastic responses in leaf functional traits in response to environmental variations. Pioneer plants have different ecophysiological strategies in comparison plants of late successional stages, occupying opposite positions in the leaf economics spectrum. However some plants can be established, at the same time, in areas at different stages in succession process. Thus, this study aimed to evaluate the changes in the functional attributes of three species of different habits, in a chronosequence (early (22 years), intermediate (44 years) and late (+ 60 years)) of a seasonally tropical dry forest in three consecutive rainy seasons. The species selected were: *Poincianella pyramidali*s (Tul.) L.P. Queiroz (Fabaceae), a tree; *Hyptis Suaveolens* (L.) Poit. (Lamiaceae), a herb; and *Sida galheirensis* Ulbr. (Malvaceae), a subshrub. The first two are found in the three successional stages, and the last one only in the early and late stages. All samples were collected in the rainy season, in April, between the years 2012 and 2015. The gas exchange, leaf water potential, the content and the nutrient use efficiencies, specific leaf area, the content of phenolics, the leaf construction cost and payback time, were measured. Ecophysiological responses of plants were influenced both by the successional stage as the rainfall between years. In general, plants from late stage had higher rates of gas exchange, leaf water potential, nutrients use efficiency and investment in defense, especially in 2014, the wettest year. Furthermore, a higher leaf construction cost and a shorter payback time were observed in late area, showing that, in preserved areas, plants are more efficient in energy use. However the variation in leaf traits was more intense between the years of collection. Among the functional traits, the water potential presented the highest acclimatization capacity to environmental variation, followed by the nutrient use efficiencies and specific leaf area. The leaf trait with the lowest plastic response was the leaf construction cost. However, this trait was one of the most important in classifying the plants according to successional stage. The results showed that water is the main environmental filter that coordinates the ecophysiological responses in the Brazilian seasonally tropical dry forest. However the different species capture and utilize the available water separately, showing a niche differentiation related to water use. The variation in functional traits as a function of the succession stages, suggests that the species in this study have the ability to adjust its leaf economics spectrum economy, by using a resource capture or a conservative strategy according to the requirements of the environment.

Keywords: Leaf construction cost. Ecological succession. Leaf economics spectrum. Photosynthesis. Ecophysiology.

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1. APRESENTAÇÃO

A capacidade de apresentar respostas plásticas em atributos funcionais-chave em resposta à variações ambientais, é fundamental para o estabelecimento e sobrevivência das populações vegetais em ambientes que são heterogêneos no tempo e no espaço, como os ecossistemas florestais (GRATANI, 2014). As variações ambientais impõem às plantas diferentes forças de seleção que, até certo ponto, definem quais espécies são capazes de sobreviver e manter sua performance ecofisiológica frente às novas condições do ambiente (POORTER, 2009). Dessa forma, a análise da variação nos atributos funcionais de plantas submetidas à diferentes condições ambientais vem se mostrando como uma importante ferramenta no entendimento da funcionalidade de populações e comunidades vegetais (CHAI et al. 2015).

A relação entre os atributos funcionais foliares e o balanço de carbono na planta é conhecida como espectro de economia foliar, e reflete a forma como a planta investe os fotoassimilados produzidos através do processo fotossintético (EDWARDS et al. 2014). De um modo geral duas estratégias de investimento podem ser identificadas em populações vegetais: uma baseada na captação de recursos, apresentada por plantas que apresentam rápido crescimento e são tolerantes à intensa luminosidade; e outra de conservação de recursos, apresentada por plantas de crescimento lento e tolerantes à sombra (REICH et al. 2003). Dentro os atributos funcionais que compõem o espectro de economia foliar, o custo de construção foliar é um dos mais importantes, pois determina a quantidade de glicose gasta pela planta na produção das folhas (WILLIAMS et al. 1987). Assim, o custo de construção foliar associado ao tempo de compensação dos gastos na produção das folhas, pode fornecer dados interessantes acerca da eficiência no uso da energia nas plantas (POORTER et al. 2006).

Apesar das florestas tropicais sazonalmente secas comporem cerca de 42% das florestas tropicais do mundo (MILES et al. 2006), ainda há um grande déficit de conhecimento sobre os processos ecológicos nesses ecossistemas, principalmente os relacionados à sucessão ecológica. No Brasil a floresta tropical sazonalmente seca é representada pela Caatinga, onde, segundo Cabral, Sampaio e Almeida-Cortez (2013), 80% de suas florestas são sucessionais. Nesse sentido, a análise de atributos de espécies vegetais características de diferentes momentos do processo de regeneração natural vem se mostrando interessante na determinação da dinâmica do processo sucessional (LIU et al. 2012).

Plantas pioneiras, características de estádios sucessionais iniciais apresentam maiores taxas de trocas gasosas, maior área foliar específica, maiores taxas de crescimento e um menor custo de construção foliar e tempo de compensação, quando comparadas com plantas características de estádios tardios (ZHU et al. 2013). De uma maneira geral, as primeiras utilizam da estratégia de captação, e as plantas secundárias utilizam da estratégia de conservação de recursos, ou seja, elas estão em lados opostos do espectro de economia foliar. Os trabalhos que focam nas comparações de estratégias de aquisição e utilização de recursos em plantas estabelecidas em áreas que passam por processo de regeneração natural comparam as estratégias utilizadas por plantas pioneiras com as estratégias utilizadas por plantas de estádios sucessionais tardios (ZHU et al. 2013; NAVAS et al. 2010). No entanto algumas plantas apresentam a capacidade de se estabelecer, ao mesmo tempo, em mais de um estádio no processo de regeneração natural (CABRAL; SAMPAIO; ALMEIDA-CORTEZ, 2013). Dessa forma, os resultados originados por esse trabalho de tese serão os primeiros, até onde temos conhecimento, a apresentar comparações entre atributos funcionais de uma mesma planta em áreas em diferentes períodos do processo de regeneração natural, e em anos com diferentes índices pluviométricos, gerando dados acerca da capacidade de aclimatação dessas plantas a diferentes condições ambientais, tanto no tempo quanto no espaço.

Assim, este trabalho pretende entender que estratégias plantas de diferentes hábitos utilizam para poder se estabelecer em diferentes estádios sucessionais numa cronosequência de floresta tropical sazonalmente seca, e quais atributos funcionais foliares apresentam maior capacidade de ajuste às condições abióticas características de cada estádio de sucessão. Para tanto, pretendemos testar as seguintes hipóteses: (i) plantas em estádios sucessionais tardios apresentarão maior custo de construção foliar e maior eficiência no uso da energia que plantas em estádios iniciais; (ii) as respostas dos atributos foliares à disponibilidade hídrica serão mais intensas que as respostas ao estádio sucessional; (iii) os atributos funcionais com maior capacidade de aclimatação serão os relacionados à utilização da água.

2. FUNDAMENTAÇÃO TEÓRICA

2.1 Floresta Tropical Sazonal Seca

As florestas tropicais sazonais secas (FTSS) compreendem 42% das florestas tropicais do mundo, compreendendo áreas na América do Sul, América Central, Austrália, Índia, Sudeste da Ásia, Caribe, e dois cinturões paralelos na África (MILES et al. 2006). É classificado como um dos biomas mais importantes do mundo ou, segundo Pennington, Lavin e Oliveira-Filho (2009), uma metacomunidade de abrangência global. A temperatura média das FTSS é de 25°C, com precipitação anual variando de 700 mm a 2000 mm, com pelo menos três meses secos no ano (SANCHEZ-AZOFEIFA et al. 2005). No entanto, esses valores são médias globais, variando fortemente em toda a região neotropical (ESPÍRITO-SANTO et al. 2008). A vegetação é principalmente decídua, com aproximadamente 90% das árvores perdendo suas folhas na estação seca (NASCIMENTO; FAGG; FAGG, 2007). Atualmente, muitas FTSS são consideradas *hotspots* devido seus níveis significativos de riqueza e endemismos (SANTOS, J. C. et al. 2011).

No Brasil, a FTSS é representada pela Caatinga, uma das maiores áreas de floresta seca do mundo (MILES et al. 2006). O ecossistema da Caatinga ocupa uma área de aproximadamente 735.000 km^2, extendendo-se pelos Estados do Piauí, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, Bahia e o norte de Minas Gerais (SANTOS, M. G. et al. 2014; SILVA; ALBUQUERQUE, 2005). É caracterizada por uma estação seca longa, de 7 a 11 meses no ano, e pela irregularidade das chuvas, que variam entre 240 mm a 700 mm (LUCENA et al. 2008; PRADO, 2003). A vegetação é composta por um mosaico de plantas de porte arbustivo-arbóreo e manchas de floresta seca (LEAL et al. 2005). É uma das florestas sazonais secas mais populosas do mundo, sendo explorada para produção agrícola e criação de animais, as principais causas de perda de habitat nesse ecossistema (PORTILLO-QUINTERO; SANCHEZ-AZOFEIFA, 2010). Apesar de grande parte de seu território estar ameaçado pelas atividades agropecuárias, a Caatinga possui poucas Unidades de Conservação, principalmente devido a limitadas políticas de conservação desse ecossistema por parte dos governos locais (ESPÍRITO-SANTO et al. 2009).

A água é o principal filtro ambiental que influencia a estrutura e a distribuição da comunidade vegetal em FTSS (LEBRIJA-TREJOS et al. 2011). A água é fundamental para o processo fotossintético, sendo a doadora de elétrons na etapa fotoquímica

(BLOCH; HOFFMANN; MÄRLÄNDER, 2006); é essencial na mobilidade de nutrientes do solo para a planta, e dos fotossintatos da folha para os órgãos dreno (DURAND; GONZALEZ-DUGO; GASTAL, 2010); e atua como solvente ideal para várias reações bioquímicas que ocorrem nas células vegetais. Dessa forma, a capacidade de captação e a eficiência no uso da água são fatores importantes que coordenam atributos morfo-fisiológicos e fenológicos de plantas característica de FTSS (LIMA et al. 2012).

Três principais estratégias são utilizadas pelas plantas de FTSS para lidar com o déficit hídrico sazonal, característico desse tipo de ecossistema: evitação, tolerância e escape (SOUZA et al. 2015). A estratégia de evitação é utilizada por plantas decíduas, que perdem as folhas nos meses mais secos do ano, escapando, dessa forma, dos efeitos negativos da deficiência hídrica na sua performance ecofisiológica. Já a tolerância, é encontrada em plantas perenes, que mantém suas folhas mesmo durante a estação seca (TOMLINSON et al. 2013). A estratégia de escape é utilizada por plantas anuais, como várias herbáceas da Caatinga, que completam seu curto ciclo de vida no período chuvoso do ano, escapando das consequências do déficit hídrico (COSTA; ARAÚJO; LIMA-VERDE, 2007) As plantas decíduas apresentam maior capacidade fotossintética e, consequentemente, maior taxa de crescimento na estação chuvosa, que plantas perenes. Por outro lado, as plantas perenes apresentam atributos funcionais relacionados com a minimização da cavitação dos vasos do xilema, como uma maior densidade de madeira, e diminuição das taxas de perda de água por transpiração, como uma menor área foliar (LIMA et al. 2012; KURSAR et al. 2009). Dessa forma, fica claro que a água é o fator abiótico limitante da funcionalidade das FTSS.

De acordo com o Painel Intergovernamental sobre Mudanças Climáticas (AR4 IPCC 2007), as florestas tropicais sazonalmente secas irão sofrer com o aumento da aridez, da temperatura média, e da diminuição das chuvas até 2050. Segundo algumas previsões as FTSS, como a Caatinga, irão apresentar mortalidade de espécies arbóreas e alterações no comportamento ecofisiológico das plantas. No entanto, um consenso ainda não foi alcançado no que diz respeito às alterações na performance das plantas de regiões semi-áridas quanto aos possíveis danos ocasionados pelas mudanças climáticas, já que alguns dados mostram uma certa estabilidade de FTSS ao aumento de temperatura, radiação e CO_2 atmosférico (COLLEVATTI et al. 2013; SHEFFIELD; WOOD; RODERICK, 2012). Assim, estudos que analisem aspectos ecofisiologicos de plantas de FTSS, ao longo do tempo, são importantes na determinação das respostas de atributos funcionais à variação nas condições ambientais.

2.2 Sucessão Ecológica

Sucessão ecológica é definida como um processo natural de estabelecimento e eventual substituição de espécies, de forma direcional, quando um ecossistema em sua integridade está evoluindo para um estágio clímax (WÜRTZ; ANNILA, 2010). De um modo geral, com o avanço do processo sucessional, o ecossistema torna-se mais estratificado, e as comunidades mais ricas, complexas e com maior produção de biomassa (POWERS et al. 2009).

O processo sucessão ecológica pode ser classificado em dois tipos: primário e secundário. A sucessão primária ocorre em terrenos sem vegetação prévia, ou seja, sem registro de estabelecimento de comunidades vegetais; enquanto que a sucessão secundária ocorre em áreas com uma comunidade vegetal prévia, que foi eliminada por um determinado distúrbio, seja ele ambiental, como fogo, doenças, herbivoria, ou antrópico como exploração de recursos florestais (OIKONOMAKIS; GANATSAS, 2012; UOTILA; KOUKI, 2005).

Os trabalhos sobre sucessão ecológica, de um modo geral, são realizados utilizando dois métodos de estudo. O primeiro consiste no acompanhamento do processo de regeneração natural de um determinado sítio ao longo do tempo. Porém, o tempo para obtenção e avaliação dos resultados é muito grande, tornando esse tipo de abordagem muitas vezes inviável, já que as comunidades vegetais levam anos ou mesmo décadas para passarem de um estádio sucessional para outro, até atingir a estádio clímax (WALKER et al. 2010). O segundo método envolve o uso de cronosequências, ou seja, áreas em diferentes estádios de sucessão ecológica, localizadas na mesma zona ecológica (FUKAMI; WARDLE, 2005). Com base nos dados espaciais de estrutura e composição da comunidade em cada estágio, pode-se, dessa forma, interpretar o processo de sucessão ao longo do tempo. A determinação da idade da cronosequência é realizada através de dados indiretos, como mapas geográficos, imagens de satélite, a estrutura da vegetação (área basal, cobertura da copa, densidade de indivíduos, etc.) e o histórico do uso das áreas (MORA et al. 2015; WALKER et al. 2010).

Em comparação com florestas maduras, florestas em estádio inicial de sucessão, apresentam maior temperatura do ar e do solo, maior déficit de pressão vapor, e menor umidade relativa do ar e conteúdo de água no solo (PINEDA-GARCÍA; PAZ;

MEINZER, 2012). Dessa forma, é esperado que a diferença no micro habitat de cada estádio sucessional seja determinante na seleção de espécies que consigam se estabelecer na área. Áreas em estádios iniciais de sucessão irão selecionar espécies como “estratégias de captação de recursos”, que crescem em taxas elevadas e que necessitam de uma quantidade maior de luz; já os estádios sucessionais mais avançados serão dominados por espécies com “estratégias de conservação de recursos”, que apresentam crescimento lento e são tolerantes à sombra (SCHÖNBECK et al. 2015; REICH et al. 2003).

Áreas que passam por processos de sucessão ecológica vêm se tornando cada vez mais comuns em FTSS (SANTOS et al. 2014; QUESADA et al. 2009). No Brasil essa situação é ainda mais crítica já que, devido a ações antrópicas, 80% das florestas secas são sucessionais, e 40% dessas florestas são mantidas em estádio inicial de regeneração (CABRAL; SAMPAIO; ALMEIDA-CORTEZ, 2013). No entanto, muito do que se conhece acerca de sucessão ecológica é a partir de dados obtidos em estudos com florestas úmidas. Um levantamento realizado no ISI Web of Science, de 1900 a 2009, por artigos contendo os termos “sucessão” e “trópicos” retornou um resultado de 463 artigos em florestas úmidas contra apenas 60 artigos em florestas secas (QUESADA et al. 2009). Já nos últimos 50 anos uma busca com os termos “Floresta Tropical Seca” e “sucessão” retornou 25 artigos, sendo apenas um na Caatinga, evidenciando o déficit de conhecimento acerca das FTSS brasileiras.

2.3 Aclimatação

Como as condições do micro habitat de cada estádio sucessional não são constantes no tempo e no espaço, as plantas necessitam ajustar seus atributos funcionais para conseguir sobreviver às novas condições do ambiente, especialmente aquelas que conseguem se estabelecer em mais de um estádio sucessional. Blom e Voesenek (1996) descrevem três estratégias principais utilizadas pelas plantas para lidar com a variabilidade ambiental: (i) restringir a distribuição da espécie apenas para áreas favoráveis; (ii) desenvolver uma elevada plasticidade nos atributos morfológicos e fisiológicos; (iii) desenvolver interações mutualísticas com outras espécies.

Tradicionalmente o termo plasticidade é utilizado quando a resposta ao ambiente envolve atributos morfológicos, e é denominado aclimatação quando envolve atributos fisiológicos (ZUNZUNEGUI et al. 2009). Segundo Gratani, Covone e Larcher (2006), a variação nos atributos morfológicos e anatômicos em resposta ao ambiente é de longo prazo, de menor intensidade e mais conservativa, a fim de se evitar grandes gastos em estruturas muito custosas do ponto de vista energético. Desse modo, a aclimatação de variáveis fisiológicas, principalmente aquelas relacionadas à aquisição de carbono, são essenciais para as respostas de curto prazo à variação ambiental.

Ecossistemas florestais são caracterizados por grandes flutuações ambientais, e desvios continuados de qualquer fator ambiental para além dos limites das condições ótimas são considerados estressantes para as plantas (NIINEMETS, 2010). O mesmo acontece com o processo de regeneração natural. As condições ambientais de um sítio em estádio tardio de sucessão são estressantes para plantas pioneiras, que não toleram ambientes sombreados por exemplo (NAVAS et al. 2003). Além disso, as variações no ambiente raramente envolvem um único fator abiótico, forçando as plantas a se aclimatarem às novas condições em vários níveis, desde a morfo-anatomia foliar, fenologia e fisiologia (AVALOS; MULKEY, 2014). Segundo Zunzunegui et al. (2011), cada espécie apresenta um *trade-off* entre os níveis de ajuste, permitindo diferentes padrões de aclimatação.

Nas FTSS, a incidência de vários agentes estressores em conjunto como, por exemplo, déficit hídrico, excesso de luminosidade, altas temperaturas e herbivoria, disparam respostas ecofisiológicas coordenadas nas plantas, resultando em diferentes estratégias funcionais (VALLADARES et al. 2004). As plantas decíduas perdem suas folhas nos meses mais secos do ano, como estratégia de economia de água (KUSHWAHA et al. 2010). Já as plantas perenes, mantém suas folhas, mas ajustam sua fisiologia, podendo diminuir sua abertura estomática e o potencial hídrico, aumentando a eficiência no uso da água, depositando uma camada mais espessa de cera epicuticular, entre tantos outros em vários níveis (FIGUEIREDO et al. 2015). Dessa forma, a análise da aclimatação de atributos funcionais é uma importante ferramenta para a determinação da capacidade de ajuste das plantas à variação ambiental.

2.4 Atributos funcionais

Pode-se definir atributo funcional como uma característica da planta, seja ela morfológica, fisiológica ou fenológica, que influencia fortemente a performance do organismo, e/ou o *fitness* do indivíduo como um todo (McGILL et al. 2006; REICH et al. 2003). Para determinação da capacidade de aclimatação das plantas, e a função das populações em ambientes sob mudança, é importante analisar a relação entre o conjunto dos atributos funcionais foliares e o balanço de carbono. Essa relação é conhecida como espectro de economia foliar e reflete os *trade-offs* entre a aquisição e a utilização de recursos pelas plantas (EDWARDS et al. 2014).

As condições de um determinado ambiente podem ser consideradas como filtros, que selecionam quais indivíduos possuem respostas específicas em atributos funcionais-chave necessários para se estabelecer e sobreviver na comunidade (VIOLLE et al. 2007). Dessa forma, diferentes tipos de atributos-resposta foram identificados em populações vegetais submetidas a diferentes tipos de filtros ambientais. Por exemplo, a massa foliar específica e o conteúdo de nitrogênio foliar são atributos-resposta relacionados à altitude (READ et al. 2014); já a taxa de crescimento relativo de plântulas, forma de crescimento e tamanho do ramo são respostas ao fogo (LAVOREL; GARNIER, 2002). No caso de áreas que passam por regeneração natural em FTSS, as taxas de trocas gasosas, a área foliar específica e o investimento em carbono são atributos-resposta fundamentais para o entendimento do processo de sucessão ecológica (LOHBECK et al. 2013; NAVAS et al. 2003).

Dentre os atributos relacionados com o balanço de carbono, um dos mais importantes é o custo de construção foliar, que é definido como a quantidade de glicose necessária para prover esqueletos de carbono, poder redutor na forma de NADPH e energia para a síntese de compostos orgânicos (WILLIAMS et al. 1987). De um modo geral, plantas com um menor custo de construção foliar apresentam maiores taxas de crescimento, já que o custo necessário para a produção das folhas é baixo (ZHU et al. 2013). Em contrapartida, plantas que apresentam maior custo de construção foliar investem mais em metabólitos relacionados à defesa, como compostos fenólicos, que são mais custosos em termos energéticos (WESTOBY et al. 2002). Além do custo de construção os benefícios do investimento devem ser considerados. O tempo de compensação de gastos, ou seja, o tempo que a planta necessita realizar fotossíntese para poder suprir os gastos com a produção das folhas, é fundamental para entendermos o espectro de economia da planta (KARAGATZIDES; ELLISON, 2009). Dessa forma, avaliar tanto o custo de construção como o tempo de compensação nos fornece dados importantes sobre a eficiência no uso da energia das espécies vegetais (POORTER et al. 2006).

De um ponto de vista funcional, plantas pioneiras, características de estádios sucessionais iniciais, apresentam maiores taxas de trocas gasosas, maior área foliar específica, taxas mais rápidas de *turnover* de folhas e um menor custo de construção foliar, o que leva a um crescimento mais acelerado, em comparação com plantas de estádios sucessionais tardios (ZHU et al. 2013). Para as plantas pioneiras, um rápido crescimento é mais importante do que sobrevivência de longo prazo, pois essas plantas não conseguem manter sua performance ecofisiológica em ambientes mais sombreados (POORTER; BONGERS, 2006). Já as plantas de estádios tardios apresentam comportamento oposto, com menor taxa de crescimento e um maior investimento em metabólitos de defesa, evidenciado por um maior custo de construção foliar, já que a maior diversidade de espécies vegetais em florestas maduras aumenta a competição por recursos e o ataque de herbívoros (EBELING et al. 2014). No entanto, algumas espécies vegetais pioneiras conseguem se estabelecer e manter sua performance em áreas mais avançadas no processo de regeneração natural, apresentando uma interessante capacidade de aclimatação às diferentes condições ambientais a que são submetidas (CABRAL; SAMPAIO; ALMEIDA-CORTEZ, 2013). Atualmente, os trabalhos sobre plasticidade de atributos ou capacidade de aclimatação de plantas focam nas comparações entre plantas pioneiras e secundárias. Dados acerca da plasticidade de atributos funcionais da espécie arbórea *Poincianella pyramidalis* em diferentes estádios sucessionais podem ser encontrados em Falcão et al. (2015), que é parte integrante deste projeto de tese. No entanto, este tipo de abordagem é recente, sendo ainda bastante deficitário o conhecimento acerca das estratégias utilizadas por outras espécies com diferentes histórias de vida.

2.5 Espécies Vegetais

O principal critério de seleção das espécies modelo desse estudo foi a capacidade que algumas espécies vegetais tem de conseguir se estabelecer, ao mesmo tempo, em áreas em diferentes estádios do processo de regeneração natural (CABRAL; SAMPAIO; ALMEIDA-CORTEZ, 2013). Assim, seria possível mensurar a capacidade de aclimatação de cada espécie, através da comparação dos valores de seus atributos funcionais entre os diferentes estádios de uma cronosequência de FTSS. Além disso, a escolha de espécies com diferentes hábitos nos forneceria informações acerca da estratégia ecofisiológica utilizada por essas espécies para manter sua perfomance em campo. Dessa forma, foram selecionadas três espécies modelo: *Poincianella pyramidalis* (Tul.) L.P. Queiroz, *Hyptis suaveolens* (L.) Poit., e *Sida galheirensis* Ulbr.

Poincianella pyramidalis (Tul.) L.P. Queiroz é uma espécie arbórea, pioneira e endêmica da Caatinga, pertencente à família Fabaceae (MAIA, 2004). Sua distribuição ocorre ao longo de todo o domínio da Caatinga, e possui utilidade como lenha, forragem, uso medicinal e veterinário, e em restaurações florestais (SILVA, L. B. et al. 2009). Os indivíduos apresentam altura média de 4 a 6 metros, com tronco de cor cinza claro. Possui folhas bipinadas, com 5 a 11 folíolos alternos ou opostos, e flores amarelas dispostas em racimos curtos e possui alta densidade de madeira (LIMA et al. 2012; MAIA, 2004). É breve-decídua, ou seja, perde as folhas por um ou dois meses no ano, geralmente a partir de Setembro ou Outubro (AMORIM; SAMPAIO; ARAÚJO, 2009).

Hyptis suaveolens (L.) Poit. é uma herbácea ereta, anual, pioneira, pertencente à família Lamiaceae. É nativa da América tropical, mas atualmente pode ser encontrada em regiões tropicais e subtropicais ao redor do mundo, devido ao seu grande potencial como espécie invasora de ecossistemas naturais (ISLAM et al. 2014; PADALIA; KUDRAT; SHARMA, 2013). Possui poucos ramos laterais, caule quadrangular, e suas folhas apresentam elevada densidade de tricomas glandulares, armazenando vários metabólitos secundários nessas estruturas (MARTINS; POLO, 2009; SILVA, A. F. et al. 2003). Esses metabólitos formam um óleo essencial amplamente estudado devido sua utilização como fonte de vários constituintes farmacológicos e industriais (NAYAK et al. 2010).

Sida galheirensis Ulbr. é uma espécie subarbustiva perene, pioneira, nativa e endêmica do Brasil. Apresenta caule ereto, com base lenhosa e ramos cilíndricos revestidos por uma extensa pubescência. Possui folhas simples com limbo lanceolado ou ovalado, e flores de coloração amarelo-ouro, com manchas avermelhadas na base (MOREIRA; BRAGANÇA, 2011). Essa espécie é bastante utilizada na medicina popular, sendo utilizada como antiinflamatório, analgésico e seqüestrador de radicais livres (SILVA, D. A. et al. 2006; FRANZOTTI et al. 2000). Ocorre principalmente em áreas antropizadas (AMORIM, B. S. et al. 2009).

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ARTIGO I

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Phenotypic plasticity and ecophysiological strategies in a tropical dry forest chronosequence: a study case with *Poincianella pyramidalis*

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Abbreviations:

Intrinsic water use efficiency (IWUE); leaf construction cost per unit mass (CC_{mass}); leaf construction cost per unit area (CC_{area}); leaf water potential (ψ_l); maximum net CO_2 assimilation (A_{max}); Specific leaf areas (SLA); Stomatal conductance (g_s); Soil moisture (SM); transpiration rate (E); tropical dry forest (TDF)

Abstract

The plasticity of functional attributes is an important strategy for the acclimation and establishment of plants in areas that undergo natural regeneration. The irregular rainfall of the Brazilian tropical dry forest is an important environmental filter for the determination of the set of species that can successfully establish in different stages of the regeneration process and influences the plant acclimation responses to the environmental conditions at each stage of ecological succession. In order to test the hypothesis that pioneer plants which can establish themselves, at the same time, in areas at different stages of regeneration have high phenotypic plasticity, we investigated the endemic tree species *Poincianella pyramidalis* Tull., which can be found in all stages of the regeneration process in the Brazilian tropical dry forest. Three areas were selected at different successional stages (early, intermediate and late), and the functional attributes of water status, gas exchange, leaf nutrients, specific leaf area, leaf construction costs and payback time were assessed. In the three successional stages all individuals had similar age. Measurements were taken in April, for two consecutive years, a dry and a wet. The evaluated parameters in this study showed changes according to successional stage. The highest leaf water potential was found in the late stage in the rainy year and lowest in the dry year. This behavior may be related, in addition to soil water availability, to a stronger competition for resources in these areas. Gas exchange and nutrient use efficiency were higher in 2013 and in the late successional stage, which exhibited higher soil moisture, a lower vapor pressure deficit and higher nutrient mobilization. There were no differences in the construction cost per unit mass between the stages, but differences in specific leaf area led to changes in cost per area. The payback time was shorter in the wettest year. For the driest year, the late stage showed greater energy use efficiency. The results show that the phenotypic plasticity of *P.*

pyramidalis' attributes varies according to the successional stage. However, the strongest differences are observed between years, demonstrating that water is the main factor that coordinates the functional changes and confers its ability to acclimatize.

Keywords: leaf construction cost; natural regeneration; pioneer species; photosynthesis; semiarid

1. Introduction

Functional traits are important proxies of plant response to environmental conditions (Violle et al. 2007). These conditions impose different selection forces in plants and controls, to some extent, intra-specific differences in functional traits (Poorter, 2009). The ability to adjust the expression of various phenotypes according to environmental conditions is known as phenotypic plasticity (Nicotra et al. 2010). In previously and currently disturbed environmental succession areas, plasticity can lead to partially adapted phenotypes, thereby accelerating the adaptive and evolutionary processes of the plant species (Lande, 2009).

Environmental succession, which is caused by changes in the environment, results in mosaics of areas at different stages of natural regeneration. These areas are becoming more common in tropical dry forests, which are mainly located in South America, mainly due to the strong anthropization (Quesada et al. 2009; Santos et al. 2011; Lopes et al. 2012; Santos et al. 2014). According to Cabral et al. (2013), 80% of Brazilian tropical dry forests are successional, and 40% are maintained in initial stage of regeneration.

Generally, a structural perspective is used to study the process of natural regeneration, like the species composition of each successional stage. However, from a functional standpoint, the ecosystem recovers its functionality even before full floristic restoration to preconditions (Guariguata and Ostertag, 2001). Thus, the study of the functional attributes of key plant species involved in regeneration processes in these ecosystems is of fundamental importance (Griscom et al. 2009).

Because the conditions of successional forest habitats are not constant in time and space, the assessment of ecophysiological processes (particularly those related to carbon investment) is important to the understanding of how plants are able to adapt and establish themselves. The acquisition of carbon by plants is determined by multiple functional attributes, such as net photosynthesis, leaf nitrogen concentrations and specific leaf area (Shipley and Almeida-Cortez, 2003; Poorter et al. 2006). Plants invest photoassimilates in the construction of leaves and other parts, in nutrient acquisition and metabolism maintenance (Wright et al. 2004). The relationship between the acquisition and use of acquired resources is known as the leaf economics spectrum, and it directly influences plant growth rates (Marino et al. 2010; Edwards et al. 2014).

The leaf construction cost is defined as the amount of glucose necessary to construct carbon skeletons, reducing power in the form of NADPH and energy for organic compound synthesis and it is indirectly related to plant growth rates (Williams et al. 1987). For plants with low leaf construction costs, energy investment in building a new leaf, rather than in strategies to maintain the old leaves, is more biochemically and structurally economical (Poorter and Bongers, 2006; Zhu et al. 2013). On the other hand, plants with high leaf construction costs can invest their resources in defense metabolites, which are costly in terms of energy (Westoby et al. 2002). Thus, the construction cost, associated with payback time (i.e., the time required by the plant to offset the expenses of leaf construction through the photosynthetic process), provides us with an important measure of the energy use efficiency (Poorter et al. 2006).

Studies to date have not reached a consensus regarding which attribute, or set of attributes, are able to provide plants with significant phenotypic plasticity. The plasticity of traits in relation to phenology, flowering time, seed longevity, is well documented (St. Clair and Howe, 2007; Morin et al. 2009; Kochanek et al. 2010). However, some studies point higher indexes of phenotypic plasticity in physiological traits such as maximum CO_2 assimilation, dark respiration and maximum quantum efficiency of photosystem II, in detriment of structural traits (Valladares et al. 2000; Koehn et al.

2010). It is clear that variations in functional attributes depend on the plant species, the choice of the attributes to be analyzed and the environment to which the plants are subjected. Furthermore, most studies on plasticity and succession involve the assessment of pioneer plants compared with later-stage plants, since plant species exhibit different ecophysiological responses when they are analyzed during different successional stages (Navas et al. 2003; Navas et al. 2010; Zhu et al. 2013). However, some pioneer plants are able to establish, at the same time, in areas in different stages of succession.

Thus, this study attempts to elucidate the functional traits that allow plants to maintain their performances throughout the succession process by evaluating the ecophysiological and functional attributes of a pioneer and endemic tree species in a tropical dry forest, in areas that are under different periods of regeneration.

2. Material and Methods

2.1. Study area and plant material

The study was conducted in the month of April during the years 2012 and 2013, in a chronosequence of three successional stages of a seasonally tropical dry forest (TDF), Caatinga, in Tamanduá Farm (06°59'13" to 07°00'14" S and 37°18'08" to 37°20'38" W), located in the Santa Terezinha municipality, Paraíba, Brazil. The study area is at an average altitude of 240 meters and contains the shallow and low-fertility soil type Leptosols (Embrapa, 1997). The mean temperature and annual rainfall of the city are 32.8°C and 600 mm (Fig. 1). In 2012 and 2013, the cumulative rainfall levels up to April were 257 mm and 338 mm, respectively. Rainfall was recorded monthly at a meteorological station that was installed in the study area. In April, the rainfall levels totaled 35 mm in 2012 and 84 mm in 2013, which amounted to a difference of 140%

between the years. The environmental data from 2012 and 2013 are presented in Table 1.

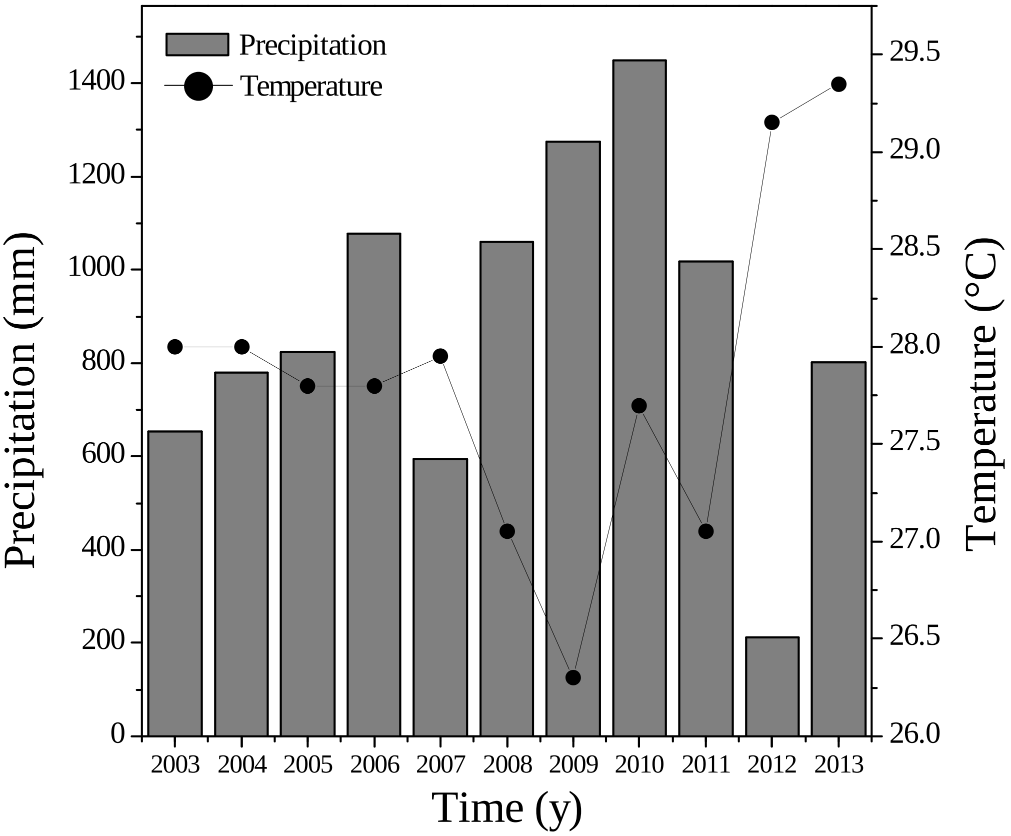

Fig. 1. Time series of annual rainfall (mm) and mean annual temperature (°C) overthe past ten years in the Santa Terezinha municipality, Paraíba, Brazil.

Table 1. Rainfall, average temperature, soil moisture and vapor pressure deficit in April of 2012 and 2013 in three different successional stages. Santa Terezinha, Paraíba, Brazil.

Stage	Year	Precipitation (mm)	Temperature (°C)	Soil Moisture (%)	Vapor Pressure Deficit (kPa)
Early	2012	35	32.6	2.15	1.50
	2013	84	32.1	11.07	1.69
Intermediate	2012	35	32	1.86	2.38
	2013	84	30.6	11.88	1.15
Late	2012	35	29.2	1.25	1.63
	2013	84	28.5	12.80	0.70

Each successional stage was represented by an area. The area in early succession is in natural regeneration for 21 years, and the intermediate area is in succession for 43 years. The early successional area was submitted to clearcutting in 1965 for cotton planting, and in 1970 the cotton plantation was replaced for *Cenchrus ciliaris* L. (buffel grass) and used by cattle for pasture before being abandoned in 1992. The intermediate successional area was also submitted to a clearcutting in 1965 for cotton planting, however was abandoned in 1970. There is no registry of clearcutting in late successional area or major disturbances since 1950 (Freitas et al. 2012; Silva et al.2012).

Fertilizer was not applied to any of the areas, and in 2007, they were all surrounded with barbed wire to prevent the entry of cattle, goats and sheep. In each area, a 50 x 20m plot was delimited with a 5 m edge on all four sides. The chemical and physical properties of the soil surface layers were presented in Freitas et al. (2012).

In a phytosociological survey of tree species made in the study area, Cabral et al. (2013) have identified 6 species and 3 families in the early stage of regeneration, 15 species and 10 families in the intermediate stage, and 21 species and 12 families in the late stage, with predominance of the Fabaceae family in the three areas. The average density was 0.083 individuals m^{-2} in the early stage, 0.113 individuals m^{-2} in the intermediate stage, and 0.093 individuals m^{-2} in the late successional stage. The shoot biomass was 29.9 Mg ha^{-1} in the early stage of succession, 37.5 Mg ha^{-1} in the intermediate stage and 49.4 Mg ha^{-1} in late stage.

The plant species that was used in this study was *Poincianella pyramidalis* Tull. (Fabaceae), which is a native pioneer and endemic tree species that is highly representative of the Brazilian TDF. According to Valladares et al. (2007), to avoid conclusions concerning to an age-dependent phenotypic variation in leaf traits, we selected plants with the same age in all successional stages. To determine the age of the plants, the diameters moving method described by Scolforo et al. (2008) was used, through linear regressions as a function of diameter at breast height (DBH). The results showed that all individuals, in the three successional stages, had an average age of 21 years. Despite being a pioneer species, *P. pyramidalis* can also be found colonizing intermediate and late areas during the natural regeneration process.

2.2. Leaf water potential and soil moisture

The leaf water potential (ψ_l) was determined according to Scholander et al. (1964) using a Scholander´s pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA, USA). The measurements were performed during the predawn (05:00) on fully expanded and undamaged leaves off our individuals from the three successional stages. Soil moisture (SM) was obtained at a depth of 30 cm at five sites from each area using a soil moisture meter (HFM 2030, Falker, Porto Alegre, BR).

2.3. Gas Exchange

Gas exchange measurements were performed using an infra-red gas analyzer (LCi, ADC Bioscientific, Hoddeston, UK). All evaluations were performed on fully expanded and undamaged leaves from four individuals on sunny and cloudless days in the morning (07:30). This measurement time was determined following the construction of a gas exchange daily curve in the field (data not shown), for which the saturating photosynthetic radiation that was experienced by *P. pyramidalis* in its natural conditions in the study areas (1500 µmol m^{-2} s^{-1}) was observed. Stomatal conductance (g_s), maximum net CO_2 assimilation (A_{max}) and transpiration rates (E) were measured at each of the successional stages. The intrinsic water use efficiency (IWUE) was determined by the ratio between net CO_2 assimilation and stomatal conductance.

2.4. Leaf contents and nutrient use efficiency

For the quantification of nutrients (nitrogen, phosphorus and potassium), approximately 30 *P. pyramidalis* leaves from four individuals were collected, dried in a forced air oven at 60°C for 72 hours and ground in an industrial blender. They were then digested in an acid solution (H_2SO_4) in a digester block at 350°C to obtain plant extracts, and the total N content was determined from an extract titration with HCl after the addition of boric acid and a colored indicator (Thomas et al. 1967). The phosphorus content was determined spectrophotometrically (Spectrophotometer 600S, FEMTO, São Paulo, BR) according to Murphy and Ryley (1962) using a concentration curve for phosphorus. The K content was determined by flame photometry (DM-62, Digimed, São Paulo, BR) using a solution of 5 ppm K as a standard (Silva, 2009). Photosynthetic nutrient use efficiency was determined by the ratio of maximum CO_2 assimilation (A_{max}) and the leaf content of each nutrient.

2.5 Leaf construction costs and payback time

Thirty healthy and fully expanded leaves from four individuals were collected in the three successional stages. The leaves were scanned, and their areas were determined using the program Image - Pro Plus 4.5 (Media Cybernetics, Inc., Rockville, US). After determining the leaves areas, the leaves were dried in a forced air oven at 60°C for 72 hours and weighed on a precision balance (HR-200, AND, Tokyo, JP). Specific leaf areas (SLA) were determined by the ratios between leaf areas and dry masses (cm2 g-1).

To obtain the ash contents (g Kg^{-1}), 1 g of dry matter was weighed on a precision balance and then placed in a muffle, where it remained at 500°C for 6 h. The ash contents were determined by the pre- and post-muffle weight differences (Li et al. 2011).

The calorific values (ΔHc KJ g^{-1}) were obtained by the combustion of 500 mg of dry matter in a calorimeter (C200, IKA, Heitersheim, DE) according to Villar and Merino (2001). The results were determined by the formula: ΔHc = calories / (1-ash). The leaf construction cost per unit mass (g $glucoseg^{-1}$) was calculated using the results of the ash, nitrogen concentration and ΔHc according to Williams et al. (1987): CC_{mass} = [(0.06968 ΔHc - 0.065) (1 - ash) + 7.5 (kN / 14.0067)] / GE, where k is the state of the oxidation of nitrogen (+5 to -3 for nitrate and ammonium), and GE is the growth efficiency that is estimated to be 0.87 (Penning de Vrieset al.1974). The leaf construction cost per unit area (g glucose m^{-2}) was calculated as the ratio between CC_{mass} and SLA.

The payback time was calculated from the ratio between the leaf construction cost (CC_{mass}) and the maximum CO_2 assimilation value, which were both expressed per unit mass (Navas et al. 2003). The results were expressed in days, considering a 12-hour period to be a day, relative to the photoperiod.

2.6. Statistical analysis

The criterion for selection of plants to be analyzed was the same age. The selected plants were marked to make sure that the measurements were performed in the same individuals in the two consecutive years. Data were subjected to factorial ANOVA, with two independent factors: the successional stage and the year. Significant differences were compared by the Student Newmna-Keul´s test at a 5% probability. The statistical software used was the STATISTICA 8.0 (Statsoft Inc., Tulsa, USA).

3. Results

3.1. Water Potential

The higher leaf water potential was observed in the plants located in the late area in 2013, the most wet year ($P<0.05$), and the lower in the same area in 2012, the most dry year (Fig. 2). The difference was about 13-fold between the years in the late area. The leaf water potential was higher in all areas in 2013 when compared with 2012. However the greatest differences in water potential were observed in 2012, with the initial area showing values 93% higher than the late area ($P<0.05$), an opposite pattern to that found in the wettest year.

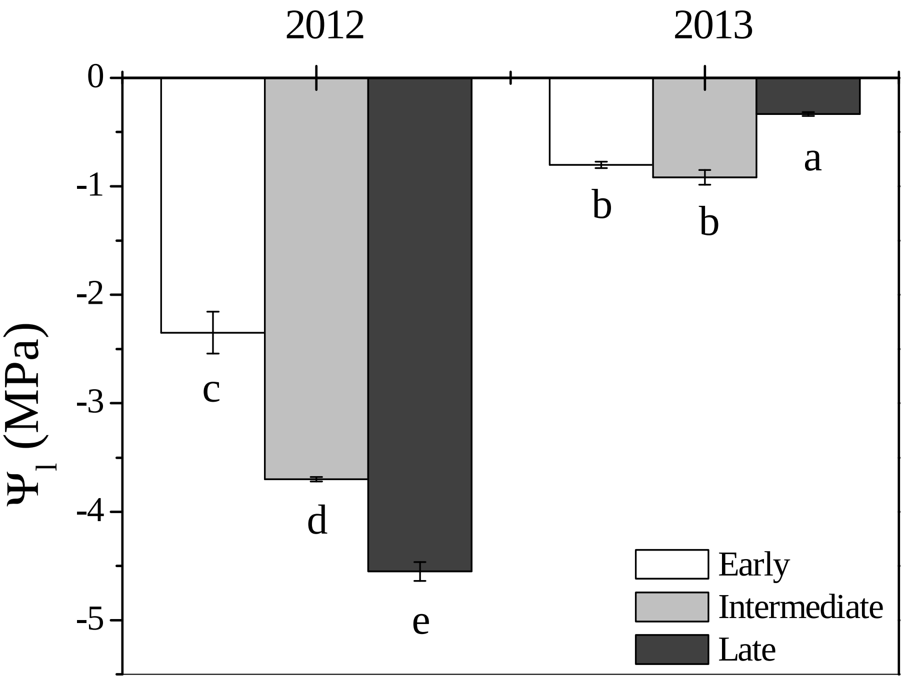

Fig. 2. Leaf water potential of *P. pyramidalis* in three different successional stages over two consecutive years. Bars ± SE with the same letter are not significantly different by Student Newman-Keul´s test (5%), n = 4.

3.2. Photosynthetic capacity

The stomatal conductance was higher in the plants of the late area in 2013, and the lower value was found in the initial and intermediate areas in 2012 (P <0.05), a 4.5-fold difference (Fig. 03A). When we observe the years separately, 2013 showed the greatest values for all successional stages when compared to the driest year (P <0.05).

The maximum net CO_2 assimilation rate followed the decrease or increase in stomatal conductance (Fig. 3B). The plants in the late area in 2013 showed the greatest A_{max}, with values 3.5-fold higher, in average, than those observed in all areas in 2012, which showed the lower values and did not differed significantly between them (P>0.05).

There were no differences in transpiration rates among successional stages in 2012 and 2013 ($P > 0.05$) (Fig. 3C). The transpiration rate was higher in 2013 than in 2012 ($P < 0.05$). The largest increase over the years was observed at the intermediate stage, with rates that were 17-fold higher compared with those that were measured in 2012 ($P < 0.05$).

The intrinsic water use efficiency (IWUE) was greater in the plants located in the initial area in 2012 ($P < 0.05$), a value 63% higher, in average, than those found in all areas in 2013 (Fig. 3D). It is important to note that the greatest difference was observed between the initial and the late areas in 2012, the driest year, with a difference of 137% ($P < 0.05$).

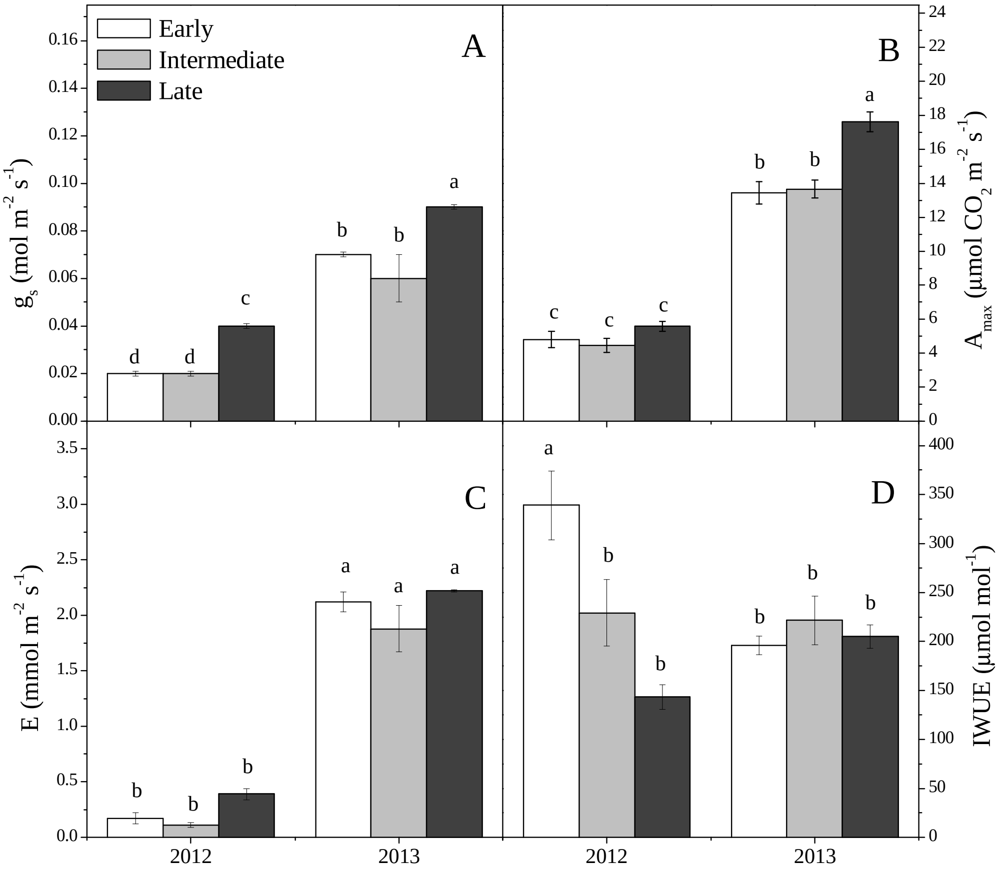

Fig. 3. Gas exchange of *P. pyramidalis* in three different successional stages over two consecutive years. (A) stomatal conductance; (B) maximum net CO_2 assimilation; (C) transpiration; (D) intrinsic water use efficiency. Bars ± SE with the same letter are not significantly different by Student Newman-Keul´s test (5%), n = 4.

3.3. Changes in contents and nutrient use efficiencies

The greatest values of leaf N concentration were observed in all successional stages in 2013, when compared to 2012 ($P < 0.05$). The lower N content was observed in the late area in 2012, with a difference of 31%, in average, between the successional stages in 2013 (Table 2). The photosynthetic nitrogen use efficiencies were significantly higher in the late stage in 2013, when compared to all other areas in the two years ($P < 0.05$).

The leaf P concentration did not differ between the stages in 2012 or 2013 ($P>0.05$). In 2012, the leaves contained, in average, 2-fold more phosphorus than in 2013 ($P<0.05$). The plants in the late stage showed a photosynthetic P use efficiency7-fold higher than all successional stages in 2012 ($P<0.05$), which showed the lower P use efficiency.

The leaf K concentration was, in average, 4-fold higher in all successional stages in 2012 when compared to 2013 ($P<0.05$). The photosynthetic potassium use efficiency was greater in the plants of the late stage in 2013, and was always higher than 2012 for all successional stages ($P<0.05$).

The N:P ratio was higher in 2013 in all successional stages when compared to 2012, with a difference of 152%, in average ($P<0.05$).

Table 2. Leaf content, nitrogen, phosphorous and potassium photosynthetic use efficiency, and N: P ratio of *P. pyramidalis* in three different successional stages in two consecutive years. Averages ± SE followed by the same letter are not significantly different by Student Newman-Keul's test (5%), n = 4.

Stage	Year	N		P		K		N:P
		[N] g.Kg^{-1}	PNUE (µmol C mmol N)	[P] g Kg^{-1}	PPUE (µmol C mmol P)	[K] g Kg^{-1}	PKUE (µmol C mmol K)	Ratio
Early	2012	20.3 ± 0.3 bc	69.8 ± 2.7 c	3.9 ± 0.5 a	863.6 ± 168.7 c	8.9 ± 0.7 a	447.5 ± 29.7 c	6.4 ± 0.9 b
	2013	26.2 ± 1.3 a	118.9 ± 1.9 b	1.6 ± 0.1 b	4280.9 ± 366.1b	1.9 ± 0.07 b	4926.5 ± 448.2 b	16.2 ± 1.5 a
Intermediate	2012	23.0 ± 0.8 b	40.4 ± 2.6 c	4.0 ± 0.2 a	513.5 ± 37.8 a	10.8 ± 1.2 a	251.2 ± 39.0 c	5.7 ± 0.1 b
	2013	26.3 ± 1.0a	129.2 ± 3.5b	1.6 ± 0.04 b	4700.1 ± 353.2b	2.4 ± 0.2 b	3922.8 ± 369.5 b	16.4 ± 1.1 a
Late	2012	19,4 ± 1.3 c	57.7 ± 4.3 c	3.1 ± 0.5 a	798.9 ± 139.2 c	7.2 ± 1.5 a	446.7 ± 89.6 c	6.2 ± 0.9 b
	2013	25.3 ± 0.5 a	189.5 ± 3.7a	1.8 ± 0.1 b	5783.7 ± 485.6a	1.9 ± 0.2 b	7795.7 ± 828.4 a	13.8 ± 1.3 a

3.4. Specific leaf area and energy costs

The SLA was higher in 2013 than in 2012 ($P < 0.05$) with the exception of the initial stage. In 2013, the specific leaf area (SLA) was higher in the initial and late stage in 2013 ($P < 0.05$), and lower in the late stage in 2012, a difference of 84%.

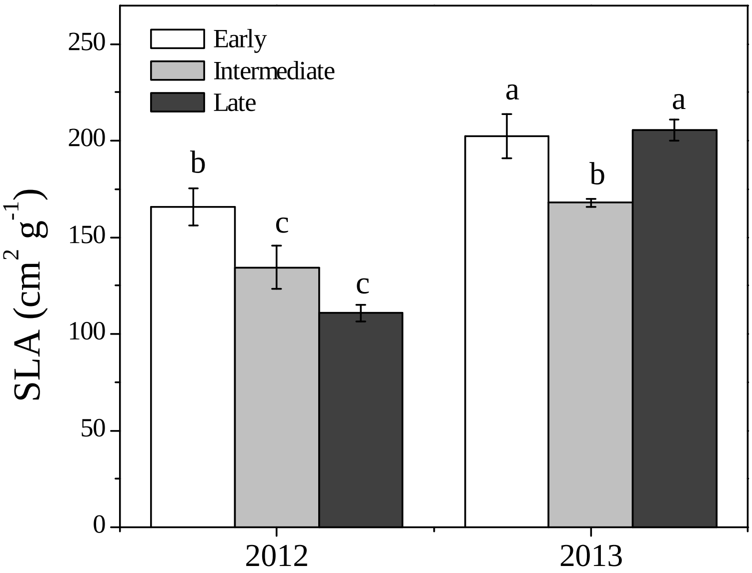

Fig. 4. Specific leaf area of *P. pyramidalis* in three different successional stages over two consecutive years. Bars ± SE with the same letter are not significantly different by Student Newman-Keul´s test (5%), n = 4.

No differences were observed in leaf construction costs per unit dry mass among successional stages in either 2012 or 2013 ($P>0.05$) (Fig. 5A). However, the values were, in average, 9% higher in all successional stages in 2013 when compared to 2012 ($P<0.05$). As construction costs per mass, the leaf construction cost per unit area did not differ between successional stages in 2012 or 2013 ($P>0.05$) (Fig. 5B) but, contrary to what occurred in construction costs per mass, the values were 32% higher in all stages in 2012 ($P<0.05$).

The higher payback times were observed in the initial and intermediate areas in 2012, and the lower in initial and late areas in 2013, a difference of 50% (*P* <0.05).

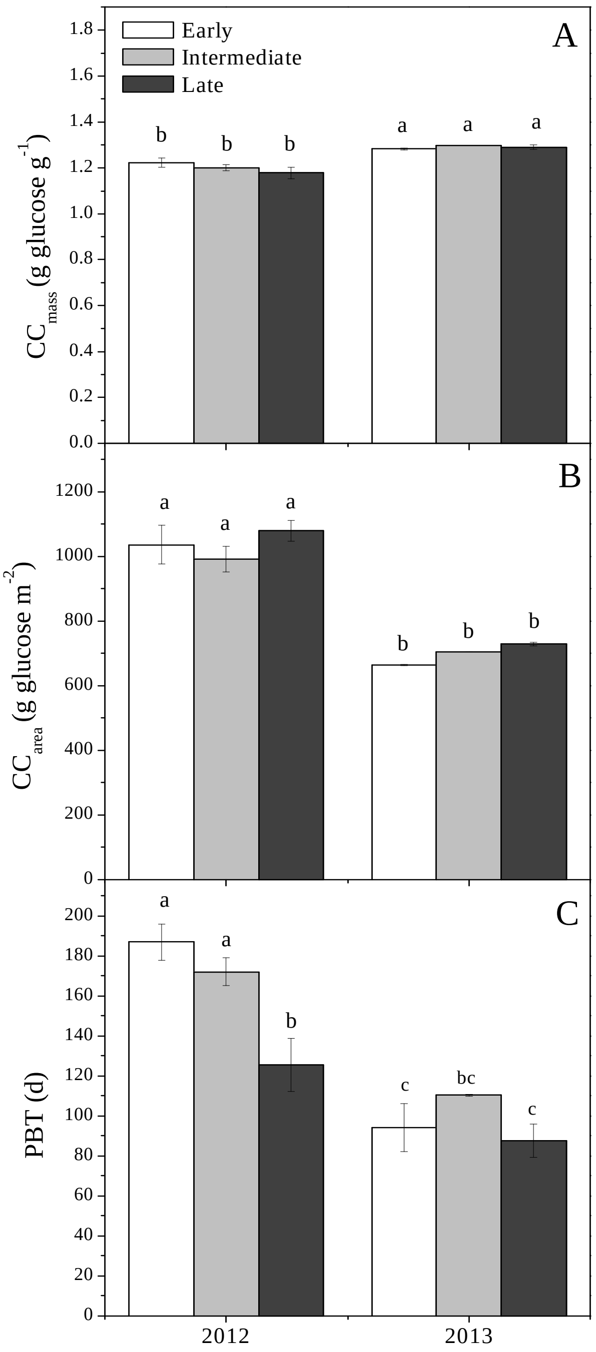

Fig. 5. Leaf construction cost of *P. pyramidalis* in three different successional stages over two consecutive years. (A) construction cost per unit of dry mass; (B) construction cost per unit of leaf area; (C) payback

time. Bars ± SE with the same letter are not significantly different by Student Newman-Keul´s test (5%), n = 4.

4. Discussion

4.1. Water status and gas exchange: alterations in response to successional stage and water availability

Our dataset shows that *P. pyramidalis* responds quickly to small changes in the environment, such as variations in annual rainfall and VPD, and the differences between micro-habitats that are formed at each successional stage, showing great plasticity in response to changing environmental conditions in time and space. The most striking differences, however, were found among the dry (2012) and wet (2013) years, confirming that the main environmental filter limiting the photosynthetic performance and growth of this species was water availability.

The leaf water potential was higher in all areas during the rainy year compared with the dry year. Furthermore, we expected the water potential of *P. pyramidalis* in the late stage to be greater than those in other stages in the two years of the study. There is a gradient of desiccation risk along the successional process, with late areas having greater soil water availability and lower temperatures and VPD, which would lead to higher water potentials of the plants in conserved areas (Lebrija-Trejoset al. 2011; Pineda-Garcia et al. 2013). Such behavior was observed in the wet year but not in the dry year, with the late-stage plants exhibiting low water potentials compared with of the intermediate and initial stages. It is possible that not only the environmental conditions but the floristic compositions of the plant community of the area itself played an important role in the water status of *P. pyramidalis*. In the studied area, the late stage of regeneration had the highest species richness and plants with greater heights, circumferences at breast height and shoot biomasses (Cabral et al. 2013). Higher and more developed plants are more efficient competitors for resources, such as water and nutrients (Falster and Westoby, 2005). Thus, plants from the late stage of regeneration show more developed root systems that were able to deeply penetrate soil layers in search of water. In the driest year of 2012, the late-stage plants most likely quickly exhausted the available water supply from the soil compared with those of the intermediate and initial stages, leading to a more negative water potential.

The good hydration status of the plants in 2013 allowed them to much more efficiently photosynthesize compared with those from 2012, and they also exhibited higher rates of gas exchange, mainly in the late stage at which the soil moisture levels were higher and VPD was lower. When *P. pyramidalis* reaches a water potential of between -2 and -5 MPa in the dry year, gas exchange rates are altered, leading to reductions in g_s, and consequently, in CO_2 assimilation. The plants maintained low water potentials during this period and a low and similar assimilation rates between successional stages, indicating that even after reaching extremely negative predawn values, the plants did not reach the wilting point, which would be expected in plants with high drought tolerance (Bartlett et al. 2012). Apparently, the reduced water potential was the main strategy that was used by the plant to decrease desiccation and maintain basal rates of photosynthesis. Because the shoot:root ratio is high in trees, a reduction in transpiration via greater stomatal closure prevents excessive water loss in cases of low water availability and protects the hydraulic architecture of the plant, even under conditions of low leaf water potential (Brodribb and Holbrook, 2003; Rivas et al. 2013). The maintenance of photosynthesis even under a very restrictive water regime is a common characteristic of native deciduous plants in TDF, that need to accumulate energy during the short periods of the year when they possess leaves, while concurrently conserving as much water as possible (Souza et al. 2010; Santos et al. 2014).

Aside from the higher stomatal conductance that was observed in the late successional stage, the gas exchange rates in 2012 did not differ between the different successional stages because the plants maintained only basal rates of photosynthesis due to the severe water restrictions. The IWUE, however, showed contrasting patterns, being highest at the early stage and lowest at the late stage, possibly due the g_s values that were presented by plants in this area in association with the lower leaf water potential and low soil moisture levels.

An opposite pattern of higher IWUE in late stages has often been reported in works studies that have been performed in humid tropical or subtropical forests, which is where ecological succession research is most frequently performed (Quesada et al. 2009; Pineda-García et al. 2013; Zhu et al. 2013). The patterns and processes governing ecological interactions in addition to the establishment and performance of the species along the successional process differ between wet and dry forests, which are particularly due to the environmental filters that confer the strongest affects, including light in rainforests and water in dry areas (Vieira and Scariot, 2006; Hennenberg et al. 2008; Lebrija-Trejos et al. 2011).

4.2. Mobilization and photosynthetic nutrient limitation

Plants that colonize tropical forests in early secondary succession show low foliar nutrient contents, which increase due to their accumulation in the soil over time (Boeger et al. 2005; Davidson et al. 2007). The foliar concentrations of N, P and K, in general, did not differ between the stages in the same year in this work despite the analysis of soil from areas presenting trends of increases in some nutrients, particularly P and organic carbon, along the successional process (Freitas et al. 2012). In addition to availability in the soil, the water status of the plant is a key factor in the mobilization of nutrients from the soil to the leaves (Durand et al.2010). Drought adversely affects the acquisition, assimilation and allocation of nutrients among plant organs (Gonzalez-Dugo et al. 2012). Thus, when the *P. pyramidalis* plants presented lower water potentials and leaf nutrient contents in 2012, detrimental effects on metabolic processes were observed.

Because basal rates of photosynthesis were observed in *P. pyramidalis* in 2012, the lowest leaf N concentration was associated with low N use efficiency, indicating that little nitrogen was being mobilized to the photosynthetic process in the form of proteins, especially Rubisco (Zhu et al. 2012). In addition, the accumulation of P and K in the leaf, and low use efficiency by the plants, demonstrated that molecules, such as ATP and NADPH, were produced or consumed in small quantities, and key enzymes for photosynthesis ceased to function (Soleimanzadeh et al. 2010). These data are corroborated by the N:P ratios, which indicated that photosynthesis was limited in the driest year by the amount of nitrogen in the leaves (Koerselman and Meuleman, 1996). In 2013, the greatest water potentials and high photosynthetic rates of *P. pyramidalis* in association to the increased availability of N caused the N use efficiency to be higher compared with that of2012, especially in the late stage, and photosynthesis was limited due to phosphorus leaf concentrations.

4.3. Leaf construction costs and leaf energy use efficiency

Specific leaf area is a key functional trait that may allow for the understanding of the ecophysiological behaviors of plants because it directly influences the photosynthetic capacity and resources use efficiency, such as light, water and nutrients (Shipley et al.

2005; Nouvellon et al. 2010). In general, specific leaf area tend to be higher in plants that colonize areas that are at the early successional stage, where the investment in growth is more important than the investment in attributes that allow for the long-term persistence of plants, such as the production of defense compounds (Zhu et al. 2013). This behavior was observed by *P. pyramidalis* in 2012, which was the driest year. It is interesting to note that although there were differences in specific leaf area, leaf photosynthetic rates were similar in all successional stages. The intraspecific variation in several functional attributes, including specific leaf area and photosynthesis, has been demonstrated to occur along gradients of water availability (Martínez-Vilalta et al. 2009). This can be observed mainly in the initial stage of succession, which had a higher specific leaf area compared with those of the other stages, especially in 2012. Because the photosynthetic rates of *P. pyramidalis* were much higher in 2013, it is possible that the water was the determining factor in controlling this attribute because the initial stage in 2012 was associated with higher leaf water potential and increased IWUE.

During the process of natural regeneration, pioneer species, such as *P. pyramidalis*, have high rates of growth and survival, and these characteristics may be associated with low leaf construction costs; i.e., these plants require less energy and use it more efficiently for the production of biomass than those of the late successional stages (Liu et al. 2013; Martinez-Garza et al. 2013). Our results did not indicate any differences in the investment of carbon per unit mass among the three successional stages. However, in the wettest year, the plants spent more energy on biomass production. This greater amount of energy expenditure in the wettest year was likely directed toward the production of larger amounts of structural carbohydrates, such as cellulose, hemicellulose and pectin, as can be observed in association with higher specific leaf area, which are cheaper to the plants from an energy perspective (Poorter et al. 2006).

The major differences in leaf construction costs were observed when this parameter was expressed per unit area. This is due to differences in specific leaf area. Plants that have high specific leaf areas have higher leaf N contents, suggesting that most of the energy is used for protein synthesis, mainly in the form of Rubisco, which contributes to higher photosynthetic rates (Villar and Merino, 2001) as was observed in *P. pyramidalis* in 2013 to occur mainly in the late stage, when water availability was higher. Not only the leaf construction costs but also the benefits of the investment must be determined (Karagatzides and Ellison, 2009). Thus, payback time can be used as a measure of energy use efficiency, reflecting the energetic benefits for the plant (Poorter et al. 2006). The payback time, and consequently leaf turnover, was, in general, lower in all three stages in 2013 compared with 2012, possibly due to the high rates of photosynthesis and low leaf construction costs per unit area that were observed. According to Kikuzawa (1991), leaf longevity decreases with increased photosynthetic rates, and increases with increased leaf construction costs (Shipley et al. 2006), which was supported by this work. It should be noted that in 2012, the late-stage plants showed the lowest payback time despite their low rates of photosynthesis. It is possible that these plants produced smaller leaves as a strategy to decrease the time that was required to recoup the costs of leaf construction (Poorter et al. 2006) as can be observed by the alterations in specific leaf area. These results show the importance of the preserved areas conservation in the Brazilian TDF because the lates tage plants were demonstrated to use energy that was acquired from photosynthesis more efficiently, even with the basal rates of photosynthesis and lower water potential that occurred in the dry year.

From the results that are presented here, we conclude that *P. pyramidalis* has a high plasticity of its functional attributes, and consequently, a high capacity for acclimation to environmental changes by altering its physiological mechanisms to survive, even at the expense of productivity and biomass generation. It is also clear that the main limiting factor that shaped the ecophysiological response of this species was water restriction, and attributes that were related to the uptake of water and the maintenance of water status were the main contributors to this high capacity for acclimation. Our results suggest that in studies of TDF leaf water potential, gas exchange and payback time must be maintained among the attributes that are evaluated. Future studies should also include hydraulic conductivity to better characterize the ability of the plant to transport water. Due to its ability to adapt, without major damage, to very contrasting environmental conditions, which is demonstrated by its successful establishment indifferent stages of succession, the *P. pyramidalis* can be considered to be important species in the management and reforestation of degraded areas.

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Figure legends

Fig. 1. Time series of annual rainfall (mm) and mean annual temperature (°C) over the past ten years in the Santa Terezinha municipality, Paraíba, Brazil.

Fig. 2. Leaf water potential of *P. pyramidalis* in three different successional stages over two consecutive years. Bars ± SE with the same letter are not significantly different by Student Newman-Keul´s test (5%), n = 4.

Fig. 3. Gas exchange of *P. pyramidalis* in three different successional stages over two consecutive years. (A) stomatal conductance; (B) maximum net CO_2 assimilation; (C) transpiration; (D) intrinsic water use efficiency. Bars ± SE with the same letter are not significantly different by Student Newman-Keul´s test (5%), n = 4.

Fig. 4. Specific leaf area of *P. pyramidalis* in three different successional stages over two consecutive years. Bars ± SE with the same letter are not significantly different by Student Newman-Keul´s test (5%), n = 4.

Fig. 5. Leaf construction cost of *P. pyramidalis* in three different successional stages over two consecutive years. (A) construction cost per unit of dry mass; (B) construction cost per unit of leaf area; (C) payback time. Bars ± SE with the same letter are not significantly different by Student Newman-Keul´s test (5%), n = 4.

MANUSCRITO I

Submetido ao periódico *Plant Biology*

WATER RELATIONS AND ENERGETIC EFFICIENCY OF THREE SPECIES FROM A SEASONAL TROPICAL DRY FOREST CHRONOSEQUENCE

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ABSTRACT

1. Pioneer species have different ecophysiological responses to secondary species. However, some pioneer plants may settle in other successional stages, and the strategies used by them are not yet fully understood.
2. In order to investigate the acclimation response of plants established in areas going through different successional stages, we measured gas exchange, water potential, nutrient use efficiency, specific leaf area, phenolics content, leaf construction cost and payback time of *Poincianella pyramidalis* (tree), *Hyptis suaveolens* (herb) and *Sida galheirensis* (subshrub) in a chronosequence (early, intermediate and late) of a seasonally tropical dry forest in three different rainy seasons.
3. The late stage plants showed, in general, high water potential and gas exchange rates, which were influenced by the nutrient use efficiency and N:P ratio. The construction cost was also higher in the late stage due to high phenolics in the herbaceous and subshrub species, and long-lived leaves in the tree species, but payback time was higher only in *S. galheirensis.* From all traits, water potential, nutrient use efficiency and specific leaf area had the highest acclimation capacity.
4. The results show that the analyzed species have the ability to adjust their leaf economics spectrum according to the regeneration time of the forest and environmental conditions. The most markedly results were related to rainfall regime, since the water is the main environmental filter that coordinates ecophysiological responses in seasonally tropical dry forests. For their acclimation capacity, these species can be important agents in the recovery and conservation of forest landscapes programs.

INTRODUCTION

The evaluation of the ecophysiological performance of plant species may produce very important results that help to understand the future scenario of tropical dry forests related to global and regional climate change forecasts (IPCC 2007; Comita & Engelbrecht 2009; Santos *et al*. 2014). The ability to show plastic responses in key functional traits, depending on the variation in environmental conditions, is essential to the establishment and reproductive success of plants in environments that are heterogeneous in time and space (Gratani 2014). This heterogeneity is accentuated in areas undergoing natural regeneration processes that influences the resources availability according to the gradual replacement of species, and selects plants that are able to adjust their traits to new environmental conditions (Lu *et al*. 2015).

Areas undergoing ecological succession processes are becoming increasingly common in Seasonally Dry Tropical Forests (SDTF) (Espírito-Santo *et al*. 2009). In Brazil, which has one of the largest dry forest areas in the world, approximately 80% of its SDTF are successional (Miles *et al*. 2006; Cabral *et al*. 2013). Moreover, the extreme rainfall irregularity of this ecosystem directly affects the ecophysiological performance of plant populations, since water is the main limiting factor to growth and biomass production in SDTF (Santos *et al*. 2014).

Plants can use carbon acquired by the photosynthetic process in the production of leaves, nutrient acquisition, metabolism maintenance or re-investing it in leaves (Wright *et al*. 2004). The change in some foliar key traits, i.e., specific leaf area, maximum CO_2 assimilation rate and leaf nutrient content, is relevant to the identification of plant responses to environmental conditions (Westoby & Wright 2006). The relationship between leaf traits and carbon balance in plants is fundamental to understand the function of populations in environments undergoing changes. This relation is known as leaf economics spectrum and reflects the trade-offs between the acquisition and the use of resources by plants (Edwards *et al*. 2014).

Changes in leaf traits take place at various levels, both morphological and physiological, and provide the adjustment capacity needed for the species to maintain its performance after the environment change event (Avalos & Mulkey 2014). However, Gratani *et al*. (2006) suggest that variations in physiological attributes are faster and more intense, especially under stress conditions. Thus, parameters of photosynthetic metabolism, water relations, capture and efficiency in the use of nutrients are important factors in determining the acclimation capacity of plant species.

From a functional point of view, pioneer plants, characteristic from areas in early stages of natural regeneration, are different from late-stage plants. These have higher gas exchange rates, higher specific leaf area, higher growth rates and lower investment in leaf production (Zhu *et al*. 2013). This lower investment is evidenced by a lower leaf construction cost, that is, a lower expenditure of glucose and reducing power in the form of NADPH in the production of leaves (Williams *et al*. 1987), and a shorter payback time due to higher rates of photosynthesis (Kikuzawa *et al*. 2013).

The studies involving functional responses and ecological succession, in general, focus on the differences between pioneer and late plants (Navas *et al*. 2010; Zhu *et al*. 2013). However, in the Brazilian SDTF, some pioneer plant species have the ability to establish themselves, at the same time, in more advanced areas of the natural regeneration process, adjusting their functional traits in response to the biotic and abiotic conditions of each successional stage (Cabral *et al*. 2013; Falcão *et al*. 2015).

It is known that plants with different habits show different ecophysiological responses when exposed to the same environmental filters (Pimentel *et al*. 2004; Shi *et al*. 2015). In a meta-analysis performed with global data of gas exchange and water status, in drought conditions, Yan *et al*. (2016) found that herbaceous species had lower CO_2 assimilation rates, stomatal conductance, transpiration and water potential than trees and shrub species. According to Marino *et al*. (2010) gas exchange is part of the leaf economics spectrum and influence parameters such as the leaf construction cost and payback time. Thus, species with different habits may have different strategies of survival and energy investment throughout the natural regeneration process. Such data are important in determining the ecophysiological responses of different functional groups over time.

The aim of this study was to identify how three plant species from different habits adjust their leaf functional traits in response to the successional stage in three consecutive rainy seasons in a chronosequence of SDTF. Our hypotheses were (i) the leaf construction cost will be higher in plants established in late areas, independent of the growth habit. Furthermore, they will have a higher payback time; (ii) the responses of physiological traits are more marked between rainy seasons than successional stages.

MATERIALS & METHODS

Study area, growth conditions and plant material

The study was conducted in a chronosequence of a Seasonally Dry Tropical Forest in the Brazilian Northeast (06°59'13" to 07°00'14" S and 37°18'08" to 37°20'38" W). The area has an average altitude of 240 m and a Lithic Neosol soil (EMBRAPA 1997). The temperature and annual rainfall are, in average, 32.8°C and 600 mm, respectively. All samples were collected in April, considered the peak of the rainy season in three consecutive years, from 2013 to 2015. A historic series covering the last ten years, regarding annual rainfall data, annual temperature average and accumulated rainfall until the month of April, is shown in Figure 1, as well water balance in the study area from January to April of the three years of collection.

The chronosequence used in this work was represented by three areas at different stages of natural regeneration: early, intermediate and late (Freitas *et al*. 2012). Different successional stages were determined according to the vegetation structure and the land use history. The early successional area suffered a clearcutting and was cultivated with cotton from 1965 until 1970, moment when the culture was replaced by *Chencrus ciliaris* L. (buffel grass) and used for cattle pasture until 1992. Since then, the area was not cultivated, thus being in natural regeneration for 23 years. The intermediate area also suffered a clearcutting in 1965 to cultivate cotton then left in regeneration since 1970. Regarding the late area, there was no clear-cut logging or other human intervention since 1950. There was no increase of fertilizer in soil since the areas were left under regeneration. In each area, a plot of 20 x 50 m, with a 5 meter edge on all sides, was enclosed and surrounded with barbed wire to prevent the entry of animals. There were no differences in soil physical-chemical characteristics in the three successional stages (Freitas *et al*. 2012). In each plot, at least four individuals of each species were selected for the measurements. The tree species richness is higher in the late successional stage. It had 21 species and 12 families, followed by 15 species and 10 families in the intermediate area and 6 species and 3 families in the early area. The shoot biomass production was 49.4 Mg ha^{-1} in the late stage, 37.5 Mg ha^{-1} in the intermediate stage and 29.9 Mg ha^{-1} in the early stage of succession. More details on tree phytosociology can be found in Cabral *et al*. (2013).

In this study, we used three plant species, native to and pioneer from the Brazilian SDTF, with different habits and phenological characteristics occurring simultaneously in at least more than one successional stage. The species selected were *Poincianella* *pyramidalis* (Tul.) L.P. Queiroz (Fabacaeae), a deciduous tree found in the three successional stages; *Hyptis suaveolens* (L.) Poit. (Lamiaceae), an annual herb found in the three successive stages, and only in the intermediate stage in 2015; and *Sida galheirensis* Ulbr. (Malvaceae), a perennial subshrub found in the early and late stages of succession. Data of *P. pyramidalis* in 2013 can be found in Falcão *et al.* (2015); it occurred in the same study area. Since the rainfall was significantly different between 2013 and 2015, we decided to use this species on this study. However, the data were not the same since we used other individuals to calculate the means of leaf traits and perform the statistics.

Only plants with the same age and size were selected in this study to avoid conclusions regarding age-dependent variations in leaf functional traits (Valladares *et al.* 2007). The age of *P. pyramidalis* was determined by the diameters moving method using a linear regression according to the annual increase in diameter at breast height (DBH) (Scolforo *et al.* 2008). According to this method, individuals at average age of 22 years were selected in the three successional stages. The standardization of *S. galheirensis* was performed according to plant size and DBH. Because it is an annual species, all *H. suaveolens* individuals had the same age in the three areas. The individuals of *P. pyramidalis* and *S. galheirensis* were marked. The measurements of *H. suaveolens* were made on individuals that appeared in the same spot of ground in the three consecutive years.

Leaf and soil water status

The leaf water potential (Ψ_l) was measured according to Scholander *et al.* (1964) using a pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA, USA). The measurements were performed on fully expanded, non-senescent and free of damage leaves, in the predawn (05:00), in the three successional stages. Soil moisture

(SM) was measured at five points of each plot at a depth of 30 cm using a soil moisture meter (HFM 2030 Falker, Porto Alegre, BR).

Gas exchange

Gas exchange were measured in fully expanded leaves, but not senescent and free from damage, on sunny and cloudless days from 07:30 to 08:30 in the three consecutive years using an infrared gas analyzer (LC-pro, ADC Bioscientific, Hoddeston, UK). The time of measurement was determined by designing a daily curve of gas exchange for the three species in the three successional stages (data not shown). For the daily curves we used expanded, non-senescent and healthy leaves, and the measures were performed hourly, from pre-dawn to sunset, with the gas analyzer calibrated with the photon flux observed at the moment of each measurement. The time considered was when solar radiation was saturating for the photosynthetic process at ambient CO_2 concentration (1,500 µmol m^{-2} s^{-1}). Thus, the CO_2 assimilation was the maximum assimilation rate (A_{max}) for these species under field conditions (Pérez-Harguindeguy *et al*. 2013). Measurements of stomatal conductance (g_s), net CO_2 assimilation (A_{max}) and transpiration rate (E) were made. From this data, we calculated water use efficiency (WUE (A/E)). Soil moisture data, air temperature and vapor pressure deficit, at the moment of measurements, are presented in Table 1.

Nutrient use efficiency and phenolic compounds

Ten to twenty leaves of each individual were collected, scanned, weighed, dried in a forced ventilation oven at 60°C for 72 hours and ground in a mill. The dried material was used to determine leaf nitrogen, phosphorus and potassium concentrations, phenolics, specific leaf area and leaf construction cost.

About 250 mg of dry material was digested in an acid solution (H_2SO_4) in the digester block at 350°C to obtain the plant extracts. The nitrogen concentration was determined by titration with an HCl solution containing boric acid and an indicator dye according to Thomas *et al*. (1967). The phosphorus concentration was obtained spectrophotometrically (600S spectrophotometer, FEMTO, California, USA) according to Murphy & Riley (1962). The leaf potassium concentration was obtained by flame photometry (DM-62, Digimed, Sao Paulo, BR) as described by Silva (1999). The use efficiency of each nutrient was obtained by the ratio between the A_{max} and its respective leaf content. The Nitrogen:Phosphorus ratio was also calculated.

Approximately 20 mg of dry plant material were used to determine total phenolics. The extract was obtained by mid-boiling the material in 80% methanol and the reaction was performed using a 10% Folin-Ciocalteu reagent according to Amorim *et al*. (2008). The results were obtained by interpolation of the samples' absorbance against a calibration curve designed with tannic acid (0.1 mg ml^{-1}) in a spectrophotometer (Genesys 10S UVVIS, Thermo Scientific, Waltham, USA) calibrated at a wavelength of 760 nm.

Specific leaf area and leaf construction cost

The leaf area of each species, in the three successional stages, was measured using the images obtained from the scanned leaves using the Image-Pro Plus 4.5 software (Media Cybernetics, Inc., Rockville, US). The specific leaf area (SLA) was determined by the ratio between leaf area and leaf dry weight (m^2 kg^{-1}).

The leaf construction cost was calculated from the ash content, nitrogen concentration and heat combustion of dry material. To determine ash, 500 mg of dried material were weighed and placed in a muffle at 500°C for 6 hours. The ash content was obtained by the difference between the pre and post-muffle weight according to Li *et al*. (2011). The heat combustion was determined by setting fire to 300 mg of dry material in a calorimeter (C2000, IKA, Heitersheim, DE) according to Villar & Merino (2001).

Leaf construction cost (g glucose g^{-1} DM) was obtained by the formula described by Williams *et al.* (1987): $CC = [(\Delta Hc\ 0.06968 - 0.065)\ (Ash - 1) + 7.5\ (kN / 14.0067)] / GE$, where k is nitrogen oxidation state and GE is growth efficiency, which is estimated at 0.87 (Penning de Vries *et al.* 1974). In this work, we considered that the nitrogen oxidation in our study area was to nitrate ($k = +5$), as this is the main source of nitrogen for higher plants in the field (Villar & Merino 2001).

Payback time was calculated as a measurement of efficiency in the use of the energy obtained by photosynthesis. The results were obtained by the ratio between CC and A_{max}. They were expressed in days, considering twelve hours as a day unit, related to the average time of light in the study area.

Statistical analysis

Regarding to comparisons of the leaf traits between the successional stages, the data were submitted to One-Way ANOVA with the successional stage as independent variable. Means were compared using the Student Newman-Keul's test (5%), when appropriate. For comparisons between the years, in the same area, the data were submitted to a Repeated-Measures ANOVA, and the means were compared using the Student Newman-Keul's test (5%), when appropriate. To certify the degree of plastic response of leaf traits, depending on the successional stage, for each trait of the three species we calculated the coefficient of variation (%) considering as more plastic the trait with the highest CV value. A general value of plastic response was obtained by averaging the coefficients of variation of all leaf traits of each species in the three successional stages. The statistical software used was the STATISTICA 8.0 (Statsoft Inc., Tulsa, USA). To assess whether measured functional traits were decisive in the classification of plants as belonging to the initial, intermediate or late stage, a Principal Component Analysis (PCA) was performed for each species. Data were standardized by range to equalize the difference among traits units. All attributes were included in the PCAs, but only those that had the highest correlations with the axes 1 and 2 were used for designing graphs. *H. suaveolens* data in 2015 were not included in PCA because it was only able to settle in the intermediate area that year. The software used was Fitopac 2.1 (Sheperd 2010).

RESULTS

Climatic conditions of the study site

The climate irregularity of the Brazilian SDTF is illustrated in the time series of precipitation and temperature (Fig. 1). Most of the rainfalls occurred until April, the month of collection. However, rainfall is very irregular. Some years are very rainy, as it was the case for 2008 to 2011, and preceded and/or followed by very dry years. In our collection period (2013-2015), the irregularity of rainfall and temperature was noteworthy. The annual rainfall values were 562 mm, 1,001 mm and 400 mm for the years 2013, 2014 and 2015, respectively. In those years, over 70% of rains occurred until April (Fig. 1A). This difference in rainfall was accompanied by soil moisture. In the wettest year (2014) the soil moisture in the areas at the moment of data collection was higher than in the other years (Table 1). Furthermore, the water balance in 2014 showed that there was an excess of water in the soil and that there were deficits in 2013 and 2015 (Fig. 1B). The air temperature was lower in the late stage area in the three years of collection, which led to a lower vapor pressure deficit followed by the intermediate and early stages.

Leaf water status

The leaf water potential in *P. pyramidalis* was 60% higher in the late stage of succession than in the early and intermediate areas in 2013, ($p < 0.05$) (Fig. 2A). There were no differences between the stages in 2014, which showed the greatest Ψ_l values for the early and intermediate stages, -0.40 and -0.46 MPa, respectively. In 2015, there was a decrease in Ψ_l values in all stages in comparison to the other years, with the late stage showing 30.6% lower Ψ_l than the early and intermediate stages, on average ($p < 0.05$).

In 2013, the highest Ψ_l value for *H. suaveolens* in (Fig. 2B) was observed in the plants of the late stage of succession, with the plants showing values 66% and 45 % higher than those of the early and intermediate stages, respectively ($p < 0.05$). In the rainiest year, Ψ_l did not differ among successional stages in any species, showing values of -0.10 MPa, on average, the greatest Ψ_l observed in all species and years of collection. In 2015, the plants of intermediate stage showed Ψ_l of -1.44 MPa.

For *S. galheirensis*, there was no difference in Ψ_l among the successional stages, with plants showing Ψ_l of -1.8 MPa, on average (Fig. 2C). In the driest years, the Ψ_l was 31% and 54% higher in the plants of the late stage than the early stage, in 2013 and 2015 respectively ($p < 0.05$).

When the data were analyzed between years in the same area, the three species showed a similar pattern of response in the early stage of succession, with a higher Ψ_l 2014, followed by 2013 and 2015. *S. galheirensis* showed the same pattern in the late stage. The tree species *P. pyramidalis* showed similar Ψ_l in 2013 and 2015 in the intermediate stage, and *H. suaveolens* in the late stage of succession in 2013 and 2014 ($p > 0.05$).

Gas exchange

P. pyramidalis had higher g_s values in late stage in all years when compared to the early and intermediate stages ($p < 0.05$) (Fig. 2D), with the highest g_s value observed in 2015 (15.8 $\mu mol.m^{-2}.s^{-1}$). Nevertheless, A_{max} did not completely follow the changes in

g_s (Fig. 2G). In 2013, A_{max} was 27% higher in the late stage if compared to the others. There was no difference among successional stages in 2014 ($p > 0.05$). Between years in the same area, there was a reduction in g_s and A_{max} in the early stage from 2014 to 2015, and an increase in g_s in the intermediate and late stages, with increase by A_{max} only in the first ($p < 0.05$).

No differences regarding g_s were observed for *H. suaveolens* in 2013 among successional stages ($p > 0.05$). Nevertheless, the A_{max} was 8% higher in late stage than in the other stages (Fig. 2H, K). Interestingly, in the rainy year, the lowest g_s was observed in the late stage, but A_{max} had the highest value (22.2 $\mu mol.m^{-2}.s^{-1}$). In 2015, the g_s and A_{max} from the intermediate stage were the lowest observed for this species. The response of g_s between years was similar to the A_{max} response, that is, when g_s decreased A_{max} decreased as well, with a reduction of 40% and 14% respectively ($p < 0.05$).

S. galheirensis had similar g_s and A_{max} among successional stages in 2013 and 2014. There were no differences in g_s among the successional stages in 2015, the driest year ($p > 0.05$). However, A_{max} was 24% lower in the plants of the late successional stage than in the early, with values of 10.6 $\mu mol.m^{-2}.s^{-1}$ and 13.9 $\mu mol.m^{-2}.s^{-1}$, on average, respectively ($p < 0.05$). Between years in the same stage, there was a decrease in g_s from 2014 to 2015, but the response of A_{max} was different. From 2013 to 2014 A_{max} values increased 5%, and from 2014 to 2015 decreased 41%, on average, in all stages ($p < 0.05$).

The water use efficiency in *P. pyramidalis* was high in plants in the early and late stages in 2014 (9.6 $\mu mol.mmol^{-1}$ and 9.2 $\mu mol.mmol^{-1}$) (Fig. 2J). In 2015, the plants in the early stage showed the highest WUE for this species, 75% and 18% greater than the same area in 2013 and 2104, respectively ($p < 0.05$).

The herbaceous species, *H. suaveolens*, had a WUE 22.5% higher in late stage in 2014 when compared to the other stages ($p < 0.05$) (Fig. 2K). The lowest WUE was observed in the early stage in 2014. The highest WUE values in *S. galheirensis* were in 2014 (13 µmol.mmol^{-1}, on average), without differences among the successional stages (Fig. 2L). The lowest efficiency for this species was observed in the late stage in 2013 and 2015 ($p > 0.05$). However, in 2015 the WUE values were 33% lower than those of the early stage ($p < 0.05$).

Content and nutrients use efficiency

In *P. pyramidalis*, a higher efficiency in the use of N (PNUE) was observed in the late stage in 2013 compared with the other stages, with values 60% and 45% between the early and intermediate stages, respectively ($p < 0.05$) (Table 2). The highest values of P use efficiency (PPUE) was observed in 2014, the wettest year, without differences among the successional stages ($p > 0.50$). The K use efficiency (PKUE) was higher in 2013 in all successional stages, with the late stage showing the highest value compared to the other stages (8.21 µmol C.mmol^{-1}.s^{-1}) ($p < 0.05$). The highest N:P ratio values were observed in 2014, with plants of intermediate stage showing values 30% and 32.5% higher than the early and late stages ($p < 0.05$). A similar pattern of response was observed for *H. suaveolens*. The highest PNUE was observed in the late stage of succession in 2013 (0.43 µmol C.mmol^{-1}.s^{-1}), and the highest PPUE and PKUE was observed in 2014 and 2013, respectively. The plants of the intermediate stage showed PPUE values 65% and 60% higher than the early and late stages, respectively ($p < 0.05$), and PKUE was 58% and 74% higher in the late stage than the early and intermediate stages, respectively ($p < 0.05$). As *P. pyramidalis* the N:P ratio in *H. suaveloens* was higher in the intermediate stage in 2014 (41.15) than other stages and years of collection ($p < 0.05$). *S. galheirensis* had a contrasting behavior. The PNUE was higher in the late stage, but there was no difference between the years 2013 and 2014 ($p > 0.05$). The PPUE was higher in the late stage than in the early stage, except in 2015. Finally, the PKUE use was 63% higher in the late stage in 2013 compared to the early stage ($p < 0.05$), without differences among successional stages in the other years. The N:P ratio was higher in 2014, primarily in the early successional stage ($p < 0.05$).

Specific leaf area

Specific leaf area in *P. pyramidalis* was 25% higher in the intermediate and late stages in 2013 compared to the early stage ($p > 0.05$) (Fig. 3A). There were no differences in the SLA among the successional stages in 2014 ($p > 0.05$). In 2015, the lowest SLA was observed in plants of late stage (12.2 $m^2.kg^{-1}$), a value 21% lower than the early and intermediate stages, on average ($p > 0.05$). It was observed a decrease in SLA on plants of the early and intermediate stage from 2013 to 2014, and an increase from 2014 to 2015. However, in the late stage the plants showed a reduction in SLA values only from 2013 to 2014, maintaining lower values in 2015, the driest year. In *H. suaveolens* the highest SLA was observed in the intermediate and late stages in 2013 (34.4 $m^2.kg^{-1}$ and 34.5 $m^2.kg^{-1}$), and in the early and intermediate in 2014 (25.2 $m^2.kg^{-1}$ and 26.6 $m^2.kg^{-1}$) (Fig. 3B). Between years, it was observed a reduction in SLA values in all successional stages, with the greater reduction showed by the plants of the late stage (40.5%) ($p < 0.05$). Except for 2014, when there were no differences among successional stages, the highest values for *S. galheirensis* were observed in the late stage ($p < 0.05$), a difference of 54% and 87% compared to the early stage in 2013 and 2015, respectively ($p < 0.05$) (Fig. 3C).

Phenolic compounds

In *P. pyramidalis*, the concentration of phenolic compounds in the leaves showed no differences among the successional stages regarding the year of collection ($p > 0.05$)

(Fig. 3D). However, the phenolics concentration was lower in all stages in 2015 when compared to other years, with a median decrease of 28%, 26% and 23% in the early, intermediate and late stage, respectively (p <0.05). In *H. suaveolens* the highest phenolics concentration was observed in the late stage in 2013 (25.8 g.kg^{-1}) and 2014 (36 g.kg^{-1}) (Fig. 3E). In 2013 this value was 129% higher, in median, than in the early and intermediate stages, and in 2014 was 123% and 52.5% higher than the early and intermediate stages, respectively (p <0.05). In 2015, the phenolics concentration was similar to the values of 2014 in the intermediate area (p >0.05).

The leaf concentration of phenolic compounds in *S. galheirensis* was, on average, 16% higher in late stage in all years analyzed in comparison with the early stage, without differences in the same area in different years (p >0.05) (Fig. 3F).

Leaf construction cost

There were no differences on leaf construction cost in *P. pyramidalis* in 2013 (p >0.05). Both in 2014 as in 2015, the CC was, on average, 8% higher in late stage than in other successional stages (p <0.05) (Fig. 3G). Between years in the same area, the CC of the plants of late stage in 2015 was 11.5% and 7% higher in than in 2013 and 2014, respectively (p <0.05). In *H. suaveolens*, the CC was 7.5% higher in the late stage (1.12 g.g^{-1} DM) than in the other successional stages in 2013 (Fig. 3H). There were no differences in CC among the successional stages in 2014 (p >0.05). The differences between years were observed only in the early stage, with values 5% higher in 2014 than in 2013 (p <0.05). The species *S. galheirensis* had a higher CC in the late stage in all years (Fig. 3I). These values were, on average, 6% higher than in the early stage (p <0.05). In 2014 the late stage plants showed CC 8% higher (1.19 g.g^{-1} DM) than the early stage plants, without difference between the values of 2014 and 2015.

The payback time in *P. pyramidalis* was similar among the successional stages in 2013, about 80 days on average (Fig. 3J). Both in 2014 as in 2015, the PBT was 33% and 53.5% higher in the early stage, on average, compared to the intermediate and late stages ($p < 0.05$). The highest increase in PBT was observed in the early stage plants, that showed values 46.5% higher than in 2013 and 2014 in the same area ($p < 0.05$).

In *H. suaveolens*, there were no differences in PBT among the successional stages all years (Fig. 3K). However, the highest PBT values were observed in the wettest and driest years, 2014 and 2015, respectively. These values were 21% higher, on average, than in 2013 ($p < 0.05$). For *S. galheirensis*, the PBT was 92% and 66% higher in the late stages in 2013 and 2015, respectively, when compared to the early stage values ($p < 0.05$) (Fig. 3L). In 2014, *S. galheirensis* had the lowest values, 32 days on average, without differences among successional stages ($p > 0.05$). The highest increase in PBT was observed from 2014 to 2015 in the late stage, a difference of 237%.

Coefficient of variation and PCAs

The coefficient of variation (CV) of the traits had a similar response pattern for the three species (Table 3). The highest CV was observed in leaf water potential, P and K use efficiency and specific leaf area. The difference among the responses of species occurred in the successional stage at which CVs were higher. For *P. pyramidalis*, the highest values were observed in plants in the late stage. For *H. suaveolens*, the highest values were found in the intermediate stage. For *S. galheirensis*, the highest values were observed in the early stage of succession for Ψ_l and PPUE, and in the late stage for PKUE and SLA. The smaller CV value was in leaf construction cost for all species. Both *P. pyramidalis* and *S. galheirensis* had a higher overall CV value in the late stage and *H. suaveolens* in the intermediate stage of succession.

The principal component analysis arranged *P. pyramidalis* plants in three groups related to the year of collection (Fig. 4A). As for successional stages, the variation of traits was able to separate more strongly the late stage from the others in 2013, the intermediate stage from the others in 2014 and the early stage from the others in 2015. The traits most correlated to annual variation (Axis 1) of the data were SLA and N:P ratio (R = 0.90 and R = -0.82). Regarding successional stage (Axis 2), the main traits were Ψ_l, CC and A_{max} (R = 0.91; R = 0.68 and R = 0:51).

For *H. suaveolens*, the separation of groups for both years of collection and successional stages was patent (Fig. 4B). The traits most related to the temporal variation of the data were Ψ_l, N:P ratio and g_s (R = 0.86; R = 0.61 and R = -0.91). The separation by successional stage was influenced by PNUE and CC (R = 0.85 and R = 0.78).

The principal component analysis of the traits of *S. galheirensis* could identify groups according to the year of collection. Furthermore, the separation related to successional stages was also obtained (Fig. 4C). The traits correlated with the year of collection were A_{max}, payback time and WUE (R = 0.93; R = 0.83 and R = -0.90). The spatial separation was influenced by SLA and PNUE (R = 0.84 and R = 0.71).

DISCUSSION

Our data shows that the analyzed species respond differently according to the successional which they are established, adjusting their leaf economics spectrum to the needs imposed by the environment, what directly affects the plants' growth. However, the most striking differences were observed between years of collection, that presented large variations in rainfall, VPD, water balance and soil moisture. Furthermore, the way these species use the acquired resources was influenced by the characteristics of their habit and life history.

Water status

The leaf water potential of the analyzed species was higher in the rainiest year compared to other years of collection. This was a predictable outcome, since other authors observed a seasonal variation in Ψ_l, with the plants showing higher valus of Ψ_l in the wet season (Rossato *et al*. 2013; Oliveira *et al*. 2014).A drying gradient risk is related to the forest regeneration stage, with plants at early stages of succession presenting greater risk than plants in late successional stages due to an increased solar radiation index and lower soil moisture and air humidity (Lebrija-Trejos *et al*. 2011). However, in the wettest year, the water potential was similar in the three successional stages, in all species. The water is the main factor that limits the plant growth in STDF, so the high rainfall, which led to a positive water balance in 2014, may have buffered the differences between the successional stages. In the driest years, 2013 and 2015, the plants were less hydrated in the early stage area, followed by the intermediate and late stages. Indeed, soil moisture data, in general, follow the gradient of desiccation risk, and the water potential of plants responded to this variation (Fig. 2A-C). Interestingly, in 2015, with rainfall 41% lower than in 2013, *P. pyramidalis* had a lower water potential in the late stage, even with higher soil moisture. Areas in late stage of regeneration have greater species richness, plant density, plant height, DBH and a more developed root system, which makes them better competitors for resources such as light and water (Iida *et al*. 2011). Thus, despite higher water availability, compared to the early stage, the plant community of the late stage may have consumed the soil water content faster, leading to a low water potential in *P. pyramidalis* in the driest year, as pointed by Falcão *et al*. (2015).

Unlike tree species, herbs have shallow root system (Rossato *et al*. 2013), which strongly affects the plants´ water status (Nolf *et al*. 2016). Such groups of plants have a lower water transport path due to their smaller size, and can recover faster the water transport capacity in the case of embolism when the conditions are favorable (Broddrib & Holbrook 2005; Ganthaler & Mayr 2015). In arid and semi-arid environments, often the water from rainfalls cannot reach the deeper layers of the soil, becoming available only in surface layers (Ferrante *et al*. 2014). Thus, species that in general have a more shallow root system, such as herbaceous and subshrubs, may benefit from it regarding water intake (Schenk & Jackson 2002). However, the water evaporation on superficial soil layers is high, leading to low soil moisture, which was observed in the early and in the late successional areas. In a study with four herbaceous species, of dry and humid sites, Nolf *et al*. (2016) found that these species were very vulnerable to dehydration mainly due to hydraulic conductivity loss, which can affects, stomatal conductance and photosynthesis, and may lead to tissue and leaf mortality. It may have been decisive for *H. suaveolens* failing to settle in the early and late areas in the driest year.

In general, herbaceous are more sensitive to water stress than subshrubs. Although it also has many lateral and shallow roots, species of *Sida* genus have a taproot which can reach deeper layers of the soil (Navas *et al*. 2013). Thus, a dimorphic root system is an advantage for plants in arid environments. Some authors have shown that perennial plants of dry sites, as is the case of *S. galheirensis*, are able to use the water flexibly according to its availability, because they compensate the lack of water in the shallow soil using the deeper layers´ water content (BassiriRad *et al*. 1999; Schwinning *et al*. 2002). These root characteristics may explain the fact that even with low soil moisture in 2015, *S. galheirensis* was able to establish and maintain the fitness in the early and late areas, unlike *H. suaveolens*.

The water potential was one of the more plastic traits in the three species (Table 3). Since water is the most limiting factor for plant growth in dry forests (Santos *et al*. 2014), the water availability imposes the largest selection force to plants´ establishment and development. The principal component analysis (Fig . 4) shows a marked formation of groups for the three species, related to the rainfall regime of each year of collection, with SLA, Ψ_l and WUE as the most important traits in this temporal separation of data in *P. pyramidalis*, *H. suaveolens* and *S. galheirensis*, respectively. All these traits are directly or indirectly influenced by soil water availability (Sperry *et al*. 2002; Xu *et al*. 2009). These results make clear that the ability to adjust water status to deal with changes in the environment is critical to the establishment of these species throughout the regeneration process.

Photosynthetic capacity

The gas exchange of *P. pyramidalis* responded to the annual and spatial variation of the VPD and water potential. When the water potential was high and the VPD was low, there was an increase in stomatal conductance and CO_2 assimilation. However, in 2015, the driest year, despite having very low water potential, the stomatal conductance of *P. pyramidalis* was the highest observed for this species throughout the experiment, especially in the late stage, causing it to maintain photosynthetic rates comparable to the wettest year (Fig. 2D-I). This response may have been influenced by the low PKUE (Table 2). Potassium is an important osmotic solute in plant tissues, and its accumulation provides the water potential needed to water uptake for the various metabolic processes in the cells (Arquero *et al*. 2006). Furthermore, K acts in the stomatal closure, controlling the turgor pressure in guard cells, promoting drought tolerance (Wang *et al*. 2013). In fact, the low PKUE in plants of the intermediate and late stages in 2015 denotes that K was not depleted in leaves. This, associated with a low DPV (Table 1), causes the highest stomatal conductance in the driest year in those areas. Despite having a large stomatal opening in the most preserved areas, the A_{max} was similar to other years of collection. In those areas, a low N:P ratio indicates that the photosynthesis is limited by N supply (Koerselman & Meuleman 1996). Nitrogen, in order to be part of various aspects of the photosynthetic machinery, as part of the chlorophyll molecule and Rubisco, is directly correlated with the CO_2 assimilation capacity of the plant (Goedhart *et al*. 2010). Besides that, Lima *et al*. (2012) showed that *P. pyramidalis* has high wood density, what can prevent xylem cavitation more efficiently. Consequently, they can keep their photosynthetic rates even with a low water potential and keeping a low WUE, as noted in the late successional stage in the driest year. The maintenance of CO_2 assimilation, even under low water potential conditions, is a common strategy of semi-arid species (Santos *et al*. 2014).

It is interesting that *H. suaveolens* had a greater stomatal conductance in all stages in 2013 when compared to 2014, with greater CO_2 assimilation in the late stage, even with higher soil moisture and water potential in the wettest year. In 2014 the plants presented high PNUE, so the leaf N concentration was low, but it was not limiting for this species. The high N:P ratio, in all successional stages, showed that photosynthesis was limited by P concentration in the leaves. Phosphorous directly influences the energetic balance of the plant because integrate different molecules in photosynthetic machinery (Huang *et al*. 2012). Thus, without an appropriate supply of P, the Calvin-Benson cycle is compromised, leading to low photosynthetic rates. By not having a lignified stem, herbs need a great amount of water for the maintenance of their size (Nolf *et al.* 2006). It can be observed in the late stages in 2013 and 2014 for *H. suaveolens*, which even with a high Ψ_l it presented high WUE as well, demonstrating a water saving strategy in this preserved areas. It was also observed in *S. galheirensis* in 2014. However, the photosynthetic rates were the highest for this species during the experiment, due to elevated PNUE, PPUE and PKUE. In 2015, the driest year, the combination of low soil moisture, Ψ_l, and N:P ratio led to depletion in daily A_{max} (Güswell 2004).

Some studies show that plants can adjust their nutrient levels according to the successional stage, soil type or light availability (Gleason *et al*. 2009; Gratani 2014; Falcão *et al*. 2015). In this work we can observe that nutrient use efficiencies of the studied species presented the highest levels of CV along with Ψ_l. The translocation of nutrients from the soil solution to the sink organs of the plant is dependent of water availability, so it was an expected result. This relationship is clear in environments with poor soils and where the mobility of nutrients is affected by the water availability, as in tropical dry forests (Hidaka & Kitayama 2009).

Leaf economics

Among the most important plant functional traits that comprise the leaf economics spectrum, specific leaf area is considered one of the most important to be measured because it directly influences the photosynthetic capacity of the plant (Nouvellon *et al*. 2010). Plants with a smaller SLA are more tolerant to drought, preventing excessive water loss by transpiration (Sánchez-Gómez *et al*. 2013). Furthermore, a lower SLA decreases the light gathering area, promoting the protection of photosystems against the production of reactive oxygen species, which cause damage to cell membranes and decrease the photosynthetic capacity of the plant (Uzilday *et al*. 2012). This was observed for *H. suaveolens* and *S. galheirensis* (Fig. 3A-C) in the driest years in the early stage of succession, following the low soil moisture and Ψ_l in this area, conditions that improved drought stress risk and led to depltetion in photosynthesis (Frosi *et al.* 2012; Oliveira *et al.* 2014). In other words, the plants' tissues were drier, so a lower SLA was a strategy to prevent excessive water loss. According to Reich *et al.* (1999), there is leaf biophysical limitations that impose the plants with low SLA that also showed low A_{max}, and this was observed in *P. pyramidalis*, which showed lower SLA and A_{max} when compared with the other species analysed despite the different growth habit.

The leaf construction cost of the three studied species was higher in the late stage than in the early and intermediate in all years analyzed (Fig. 3G-I). Chai *et al.* (2015) working with 31 species in a chronosequence of secondary forest in a semi-arid region found that species from advanced successional stages presented higher CC in comparison to early species. It is curious to verify that the leaf construction cost has the lowest plastic variation among the analyzed variables (Table 3). Indeed, the CC is a low plastic trait in many species (Poorter *et al*. 2006). However, even small variations in the CC may significantly alter the performance of the plants (Poorter & Villar 1997). The habit and life-form have an important influence on leaf economics spectrum of the plant. In a review about leaf longevity in plants, Kikuzawa & Ackerly (1999) pointed that leaf life span increases from annual herbs to deciduous trees, as well as CC, since long-lived leaves need more energy investment to maintain its structures. In fact *P. pyramidalis* showed the highest values of CC among the studied species. *H. suaveolens* and *S. galheirensis* had a high phenolics investment in the late successional stage (Fig. 3D-F). Phenolic compounds are important secondary metabolites acting, among other factors, on the UV protection of the photosynthetic machinery (Oliveira-Junior *et al*. 2013). Furthermore, phenolic compounds also act in the protection against herbivory (Fürstenberg-Hägg *et al*. 2013), especially in more preserved areas, where the greatest diversity of plant species favors a greater diversity of herbivores (Ebeling *et al*. 2014). This investment is particularly important to *H. suaveolens* because of its short life cycle, and to *S. galheirensis*, which, because it is a perennial species, serves as a food source for grazing in the dry season.

Not only the cost, but also the benefit of the investment should be considered in the leaf economics spectrum (Karagatzides & Ellison 2009). In this sense, the three species behaved differently. *P. pyramidalis* showed low PBT in the preserved areas, in the wettest and driest year, without differences between successional stages in 2013 (Fig. 3J-L). A similar result was achieved by Falcão *et al*. (2015) working with the same species. The opposite situation can be observed for *S. galheirensis* in the late area, possibly influenced by high phenolic concentration, as well as for *H. suaveolens* in the wettest year.

The principal component analysis was able to identify groups regard to successional stage in which the plants were established (Fig. 4). The formation of groups was more influenced by CC and parameters related to photosynthetic capacity such as A_{max} and PNUE, reflecting that the studied species can adjust their energetic balance according to microclimate variations of each successional stage. It is interesting to note that, despite showing a low plastic response, the CC is one of the main leaf traits grouping the plants according to the successional stage in which they are. Thus, it is a good indicator of plant strategy and classification of functional type as pioneer or as late successional species.

Our results show that the traits of *P. pyramidalis, H. suaveolens* and *S. galheirensis* in STDF are influenced by the time of regeneration and water availability. However, the variations in functional traits were markdley stronger due to water availability. The Ψ_l, PPUE, PKUE and were essential for the formation of groups related to the rainfall regime, presenting the highest plastic response of all measured leaf traits. In addition, these pioneer species showed an interesting plastic response according to the successional stage, presenting higher CC in the late stage, than in early and intermediate stages, despite the its low plastic response. This high CC may be related to the maintenance of the leaves for a longer period in *P. pyramidalis*, and the production of phenolics in *H. suaveolen* and *S. galheirensis.* The climate changes predicted for the tropical areas, in which it is possible to find STDF, increase in air temperature and decrease in annual rainfall. Under this scenario, these species can be important agents in the recovery and conservation of forest landscapes programs due to their capacity of acclimating to the different environmental conditions observed in this study.

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Table 1. Mean soil moisture, air temperature, and vapor pressure deficit, at the moment of collection, in April of three consecutive years, in a seasonally tropical dry forest chronosequence, Santa Terezinha, Paraíba, Brazil. E – early; I – intermediate; L – late.

Year	Stage	Soil Moisture (%)	Air Temperature (°C)	Vapor Pressure Deficit (KPa)
2013	E	6.66	32.70	1.71
	I	9.33	28.50	0.84
	L	9.00	27.50	0.70
2014	E	11.96	27.20	0.95
	I	12.67	28.30	1.07
	L	11.40	26.60	0.57
2015	E	3.10	27.50	0.73
	I	6.13	26.80	0.65
	L	4.56	26.50	0.53

Table 2. Efficiency in the use of Nitrogen (PNUE), Phosphorous (PPUE), Potassium (PKUE), and N:P ratio of *Poincianella pyramidalis*, *Hyptis suaveolens* and *Sida galheirensis*, in a seasonally tropical dry forest chronosequence, in three consecutive years. Lower case letters indicate comparisons between successional stages within the year. Capital letters indicate comparisons between years in the same successional stage. Average ± SE followed by the same letter, in each species, did not differ by the Student Newman-Keuls´ test (5%), *n*=4. E –early; I – intermediate; L – late. * The species could not settle in these areas that year.

Species	Year	Stage	PNUE (µmol C mol N)	PPUE (µmol C mol P)	PKUE (µmol C mol K)	N:P Ratio
P. pyramidalis	2013	E	0.11 ± 0.001 ^{Ab}	4.29 ± 0.29 ^{Bb}	5.11 ± 0.26 ^{Ab}	16.10 ± 1.07 ^{Ba}
		I	0.13 ± 0.002 ^{Ab}	4.71 ± 0.248 ^{Bb}	3.95 ± 0.26 ^{Ab}	16.93 ± 0.78 ^{Ba}
		L	0.19 ± 0.002 ^{Aa}	5.80 ± 0.43 ^{Ba}	8.21 ± 0.50 ^{Aa}	13.95 ± 0.96 ^{Bb}
	2014	E	0.11 ± 0.005 ^{Ab}	9.160 ±0. 67 ^{Aa}	1.31 ± 0.08 ^{Ba}	36.01 ± 2.78 ^{Ab}
		I	0.11 ± 0.006 ^{Ab}	10.58 ± 0.21 ^{Aa}	1.05 ± 0.04 ^{Ab}	43.54 ± 1.99 ^{Aa}
		L	0.14 ± 0.006 ^{Ba}	9.81 ± 0.21 ^{Aa}	1.09 ± 0.11 ^{Bb}	32.83 ± 0.78 ^{Ab}
	2015	E	0.10 ± 0.005 ^{Bc}	1.14 ± 0.004 ^{Cb}	1.22 ± 0.11 ^{Ba}	11.20 ± 0.11 ^{Cb}
		I	0.13 ± 0.00 ^{Ab}	1.83 ± 0.02 ^{Ca}	1.00 ± 0.08 ^{Aa}	13.61 ± 0.12 ^{Ca}
		L	0.14 ± 0.003 ^{Ba}	0.95 ± 0.04 ^{Cb}	1.05 ± 0.02 ^{Ba}	6.53 ± 0.20 ^{Cc}
H. suaveolens	2013	E	0.28 ± 0.01 ^{Ac}	14.53 ± 0.98 ^{Aa}	6.70± 0.18 ^{Ab}	23.41 ± 0.97 ^{Ba}
		I	0.35 ± 0.02 ^{Ab}	20.96 ± 1.93 ^{Ba}	6.09 ± 0.28 ^{Ab}	26.55 ± 0.62 ^{Ba}
		L	0.43 ± 0.01 ^{Aa}	18.24 ± 1.16 ^{Aa}	10.65 ± 0.51^{Aa}	18.68 ± 0.39 ^{Bb}
	2014	E	0.27 ± 0.04 ^{Ab}	19.13 ± 1.59 ^{Ab}	0.96 ± 0.06 ^{Ba}	28.72 ± 0.53 ^{Ab}
		I	0.34 ± 0.02 ^{Aa}	31.75 ± 1.60 ^{Aa}	0.80 ± 0.047 ^{a}	41.25 ± 0.91 ^{Aa}
		L	0.31 ± 0.04 ^{Bb}	20.27 ± 3.36 ^{Ab}	0.47 ± 0.034 ^{b}	28.92 ± 1.06 ^{Ab}
	2015	E*	-	-	-	-
		I	0.13 ± 0.004 ^{B}	1.42 ± 0.04 ^{C}	0.28 ± 0.009 ^{C}	10.41 ± 0.05 ^{C}
		L*	-	-	-	-
S. galheirensis	2013	E	0.17 ± 0.007 ^{Bb}	7.11 ± 0.58 ^{Ba}	3.51 ± 0.29 ^{Ab}	18.14 ± 0.69 ^{Ba}
		L	0.30 ± 0.01 ^{Aa}	8.85 ± 0.24 ^{Ba}	5.77 ± 0.37 ^{Aa}	13.18 ± 0.60 ^{Bb}
	2014	E	0.21 ± 0.008 ^{Ab}	15.78 ± 0.58 ^{Aa}	0.92 ± 0.26 ^{Ba}	30.05 ± 0.71 ^{Aa}
		L	0.28 ± 0.01 ^{Aa}	17.00 ± 1.01 ^{Aa}	0.88 ± 0.40 ^{Ba}	26.86 ± 0.74 ^{Ab}
	2015	E	0.11 ± 0.001 ^{Cb}	0.99 ± 0.03 ^{Ca}	0.27 ± 0.22 ^{Ca}	8.87 ± 0.34 ^{Ca}
		L	0.17 ± 0.004 ^{Ba}	1.15 ± 0.03 ^{Ca}	0.25 ± 0.008^{Ca}	6.52 ± 0.36 ^{Ca}

Table 3. Coefficient of variation (CV%) of leaf functional traits of *Poincianella pyramidalis*, *Hyptis suaveolens* and *Sida galheirensis*, in a seasonally tropical dry forest chronosequence, Santa Terezinha, Paraíba, Brazil.

Species	Stage	CV(%)											
		A_{max}	g_s	WUE	Ψ_l	PNUE	PPUE	PKUE	N:P Ratio	SLA	CC_{mass}	PBT	Phenols
P. pyramidalis	Early	13.65	23.24	29.51	67.39	8.39	72.53	75.18	15.05	54.81	5.12	20.86	24.76
	Intermediate	14.81	36.66	21.73	35.82	8.94	68.62	72.79	21.25	58.17	4.50	30.61	13.12
	Late	9.79	27.80	19.68	76.76	17.64	69.27	102.93	23.39	65.72	4.20	14.60	14.47
H. suaveolens	Early	21.74	14.27	15.74	58.00	22.83	26.95	80.24	21.66	12.24	3.23	22.09	16.15
	Intermediate	23.54	36.23	11.56	106.43	39.93	74.07	115.00	19.13	50.65	2.36	13.56	32.56
	Late	9.73	20.62	20.47	28.51	25.20	23.18	101.09	15.16	40.49	2.43	11.29	10.67
S. galheirensis	Early	30.38	37.02	23.00	94.05	29.44	78.06	94.96	14.96	47.93	3.59	32.89	21.25
	Late	36.53	27.31	36.27	74.91	25.61	76.06	113.07	27.02	57.41	5.56	47.10	4.25

FIGURE CAPTIONS

Fig. 1. (A) Historical series of annual precipitation (mm), accumulated rainfall from January to April (mm), accumulate rainfall from May to December (mm) and annual average air temperature (°C) over the last ten years for Santa Terezinha, Paraíba, Brazil; (B) water balance (mm) from January to April of 2013 to 2015 in the same place.

Fig. 2. Leaf water potential (A-C), stomatal conductance (D-F), maximum CO_2 assimilation rate (G-I) and water use efficiency (J-L) of *Poincianlle pyramidalis*, *Hyptis suaveolens* and *Sida galheirensis* in a seasonally tropical dry forest chronosequence in three consecutive years, Santa Terezinha, Paraíba, Brazil. Lower case letters indicate comparisons between successional stages within the year. Capital letters indicate comparisons between years in the same successional stage. Bars ± SE followed by the same letter, for each species, did not differ by the Student Newman-Keuls´ test (5%), *n*=4.

Fig. 3. Specific leaf area (A-C), phenolic compounds content (D-F), leaf construction cost (G-I) and payback time (J-L) of *Poincianlle pyramidalis*, *Hyptis suaveolens* and *Sida galheirensis* in a seasonally tropical dry forest chronosequence in three consecutive years, Santa Terezinha, Paraíba, Brazil. Lower case letters indicate comparisons between successional stages within the year. Capital letters indicate comparisons between years in the same successional stage. Bars ± SE followed by the same letter, for each species, did not differ by the Student Newman-Keuls´ test (5%), *n*=4.

Fig. 4. Principal Component Analysis of the data collected from *Poincianlle pyramidalis* (A), *Hyptis suaveolens* (B) and *Sida galheirensis* (C) in a seasonally tropical dry forest chronosequence, Santa Terezinha, Paraíba, Brazil. The vectors shown in the graphs represent the leaf traits with the highest correlations with the axis PC1 and PC2.

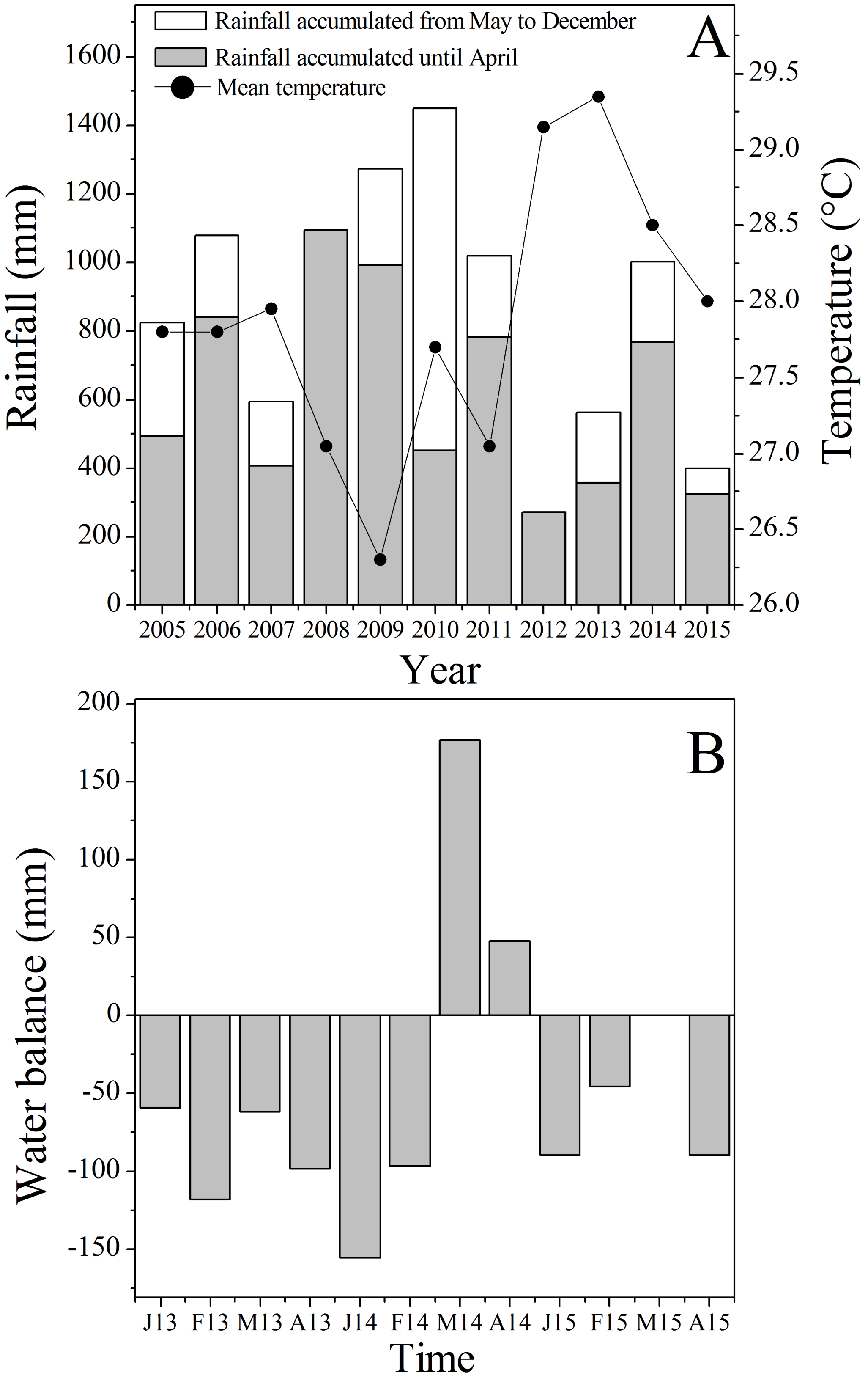
A
Rainfall accumulated from May to December
Rainfall accumulated until April
Mean temperature
Rainfall (mm)
0
200
400
600
800
1000
1200
1400
1600
Temperature (°C)
26.0
26.5
27.0
27.5
28.0
28.5
29.0
29.5
2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015
Year
B
Water balance (mm)
200
150
100
50
0
-50
-100
-150
J13 F13 M13 A13 J14 F14 M14 A14 J15 F15 M15 A15
Time

Fig. 1.

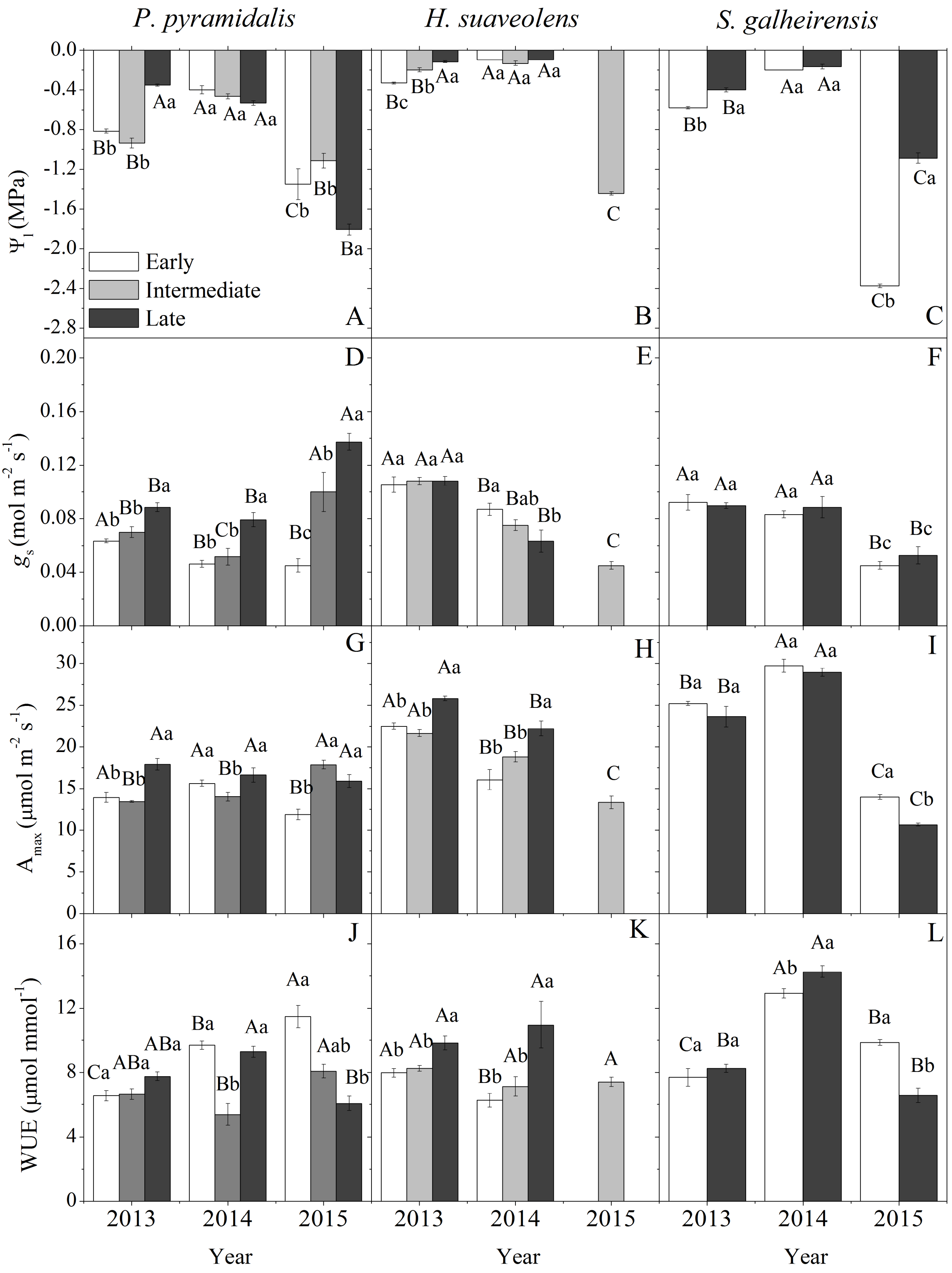
P. pyramidalis
H. suaveolens
S. galheirensis
Ψ_l (MPa)
0.0
-0.4
-0.8
-1.2
-1.6
-2.0
-2.4
-2.8
Early
Intermediate
Late
Bb
Bb
Aa
Aa
Aa
Aa
Cb
Bb
Ba
A
Bc
Bb
Aa
Aa
Aa
Aa
C
B
Bb
Ba
Aa
Aa
Cb
Ca
C
g_s (mol m^-2 s^-1)
0.20
0.16
0.12
0.08
0.04
0.00
Ab
Bb
Ba
Bb
Cb
Ba
Bc
Ab
Aa
D
Aa
Aa
Aa
Ba
Bab
Bb
C
E
Aa
Aa
Aa
Aa
Bc
Bc
F
A_max (μmol m^-2 s^-1)
30
25
20
15
10
5
0
Ab
Bb
Aa
Aa
Bb
Aa
Bb
Aa
Aa
G
Ab
Ab
Aa
Bb
Bb
Ba
C
H
Ba
Ba
Aa
Aa
Ca
Cb
I
WUE (μmol mmol^-1)
16
12
8
4
0
Ca
ABa
ABa
Ba
Bb
Aa
Aa
Aab
Bb
J
Ab
Ab
Aa
Bb
Ab
Aa
A
K
Ca
Ba
Ab
Aa
Ba
Bb
L
2013
2014
2015
Year

Fig. 2.

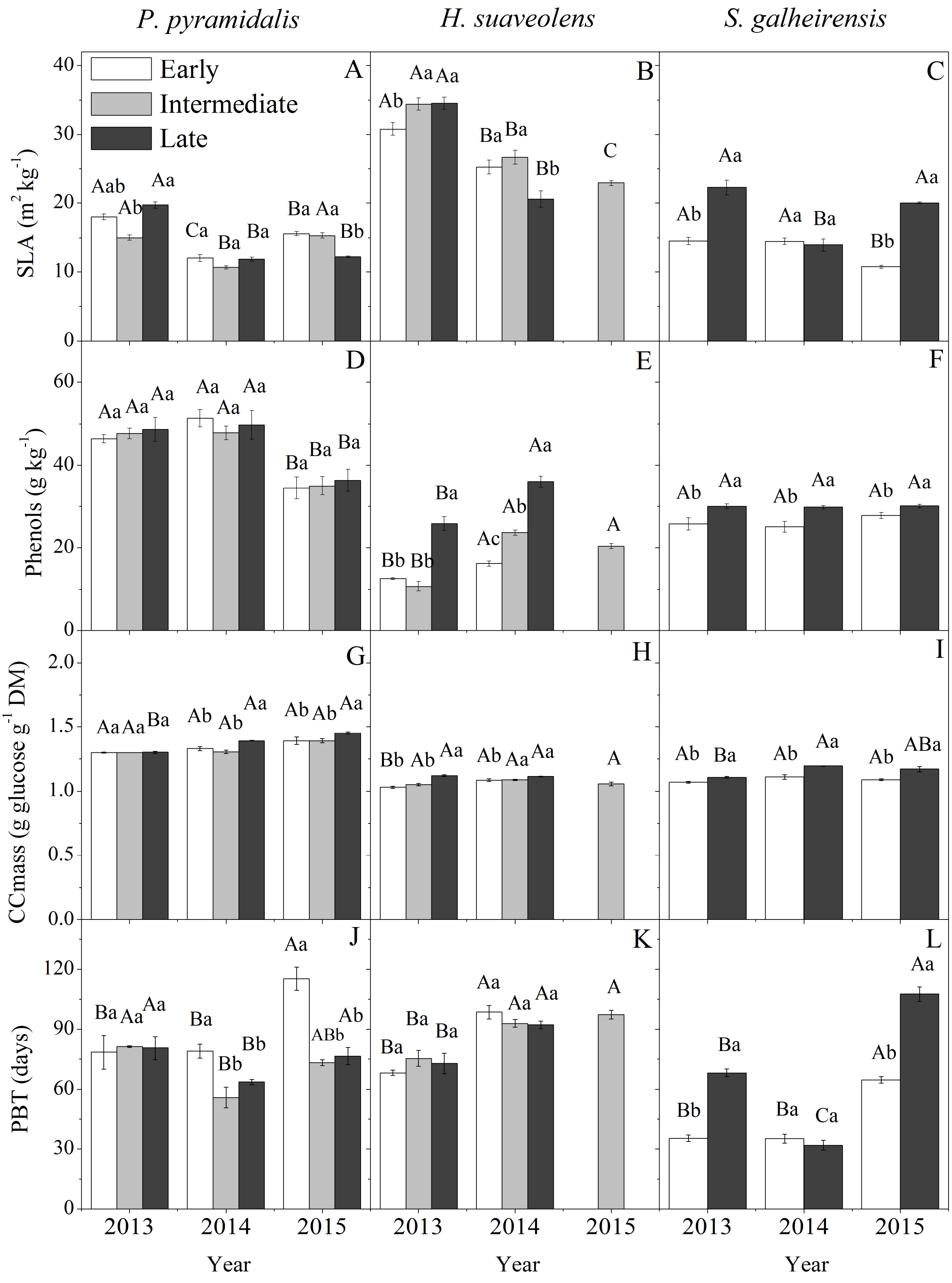
P. pyramidalis
H. suaveolens
S. galheirensis
Early
Intermediate
Late
SLA (m^2 kg^{-1})
Phenols (g kg^{-1})
CCmass (g glucose g^{-1} DM)
PBT (days)
A
B
C
D
E
F
G
H
I
J
K
L
2013
2014
2015
Year

Fig. 3.

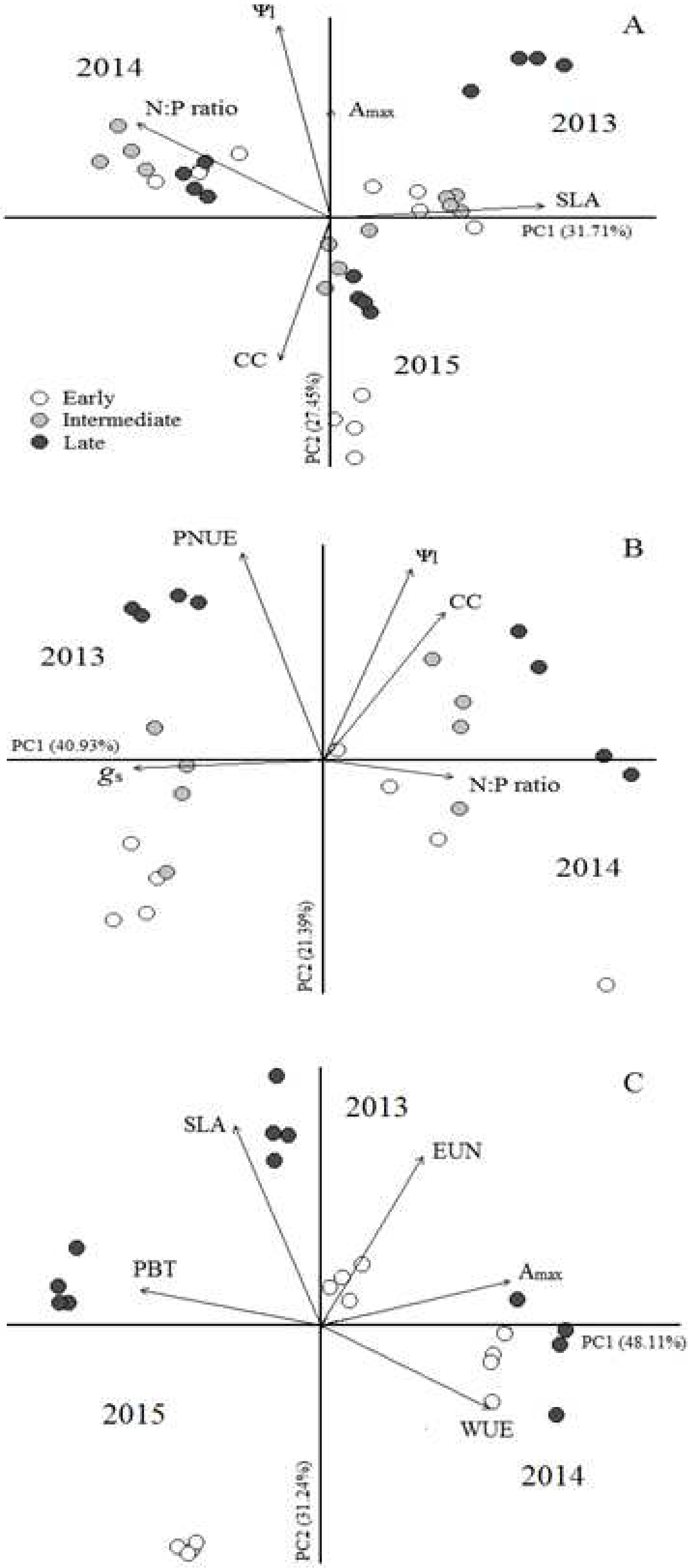
Ψl
A
2014
N:P ratio
Amax
2013
SLA
PC1 (31.71%)
CC
2015
○ Early
● Intermediate
● Late
PC2 (27.45%)
PNUE
Ψl
B
CC
2013
PC1 (40.93%)
gs
N:P ratio
2014
PC2 (21.39%)
C
SLA
2013
EUN
PBT
Amax
PC1 (48.11%)
2015
WUE
2014
PC2 (31.24%)

Fig. 4.

4. CONCLUSÕES

- As plantas do estádio tardio apresentaram maiores taxas de trocas gasosas, potencial hídrico, eficiência no uso dos nutrientes. Além disso, apresentam maior custo de construção foliar associado a um menor tempo de compensação, o que indica que essas plantas de utilizam a energia de forma mais eficiente em áreas preservadas.

- As plantas do estádio tardio, por apresentarem maior assimilação de carbono, investem na produção de compostos fenólicos, metabólitos secundários relacionados à proteção contra radiação UV e herbivoria.

- O regime hídrico influencia fortemente os valores dos atributos funcionais das espécies estudadas.

- Dentre os atributos funcionais mensurados, aqueles relacionados à água apresentaram maior capacidade de aclimatação, principalmente o potencial hídrico, que foi o atributo mais plástico dentre os analisados.

- As espécies estudadas captam e utilizam a água de forma distinta. *Poincianella pyramidalis* altera sua área foliar específica, que é diretamente influenciada pela disponibilidade hídrica; *Hyptis suaveolens* apresenta os maiores potenciais hídricos, ou seja uma maior capacidade de captação de água; por fim *Sida galheirensis* é mais eficiente no uso água.

- Apesar de apresentar a menor resposta plástica, o custo de construção foliar é um dos principais determinantes na classificação das espécies em função do estádio sucessional.

- As plantas da área tardia apresentaram maior capacidade de aclimatação, evidenciando a importância da preservação e recuperação de áreas degradadas.

ANEXOS

(Normas dos Periódicos)

FOREST ECOLOGY AND MANAGEMENT

Science to Sustain the World's Forests

AUTHOR INFORMATION PACK

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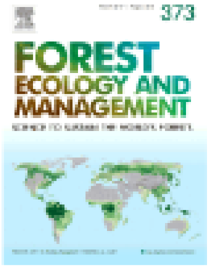

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DESCRIPTION

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2. Novel ideas or approaches to important challenges in forest ecology and management;
3. Studies that address a population of interest beyond the scale of single research sites (see the editorial), Three key points in the design of forest experiments, Forest Ecology and Management 255 (2008) 2022-2023);
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The Journal receives more submissions than we can publish, so authors should demonstrate a clear link with forest ecology and management. For example, papers dealing with remote sensing are acceptable with a strong link between ecology and management, but not if the main thrust is technological and methodological. Similarly, papers dealing with molecular biology and genetics may be more appropriate in specialized journals, depending on their emphasis.

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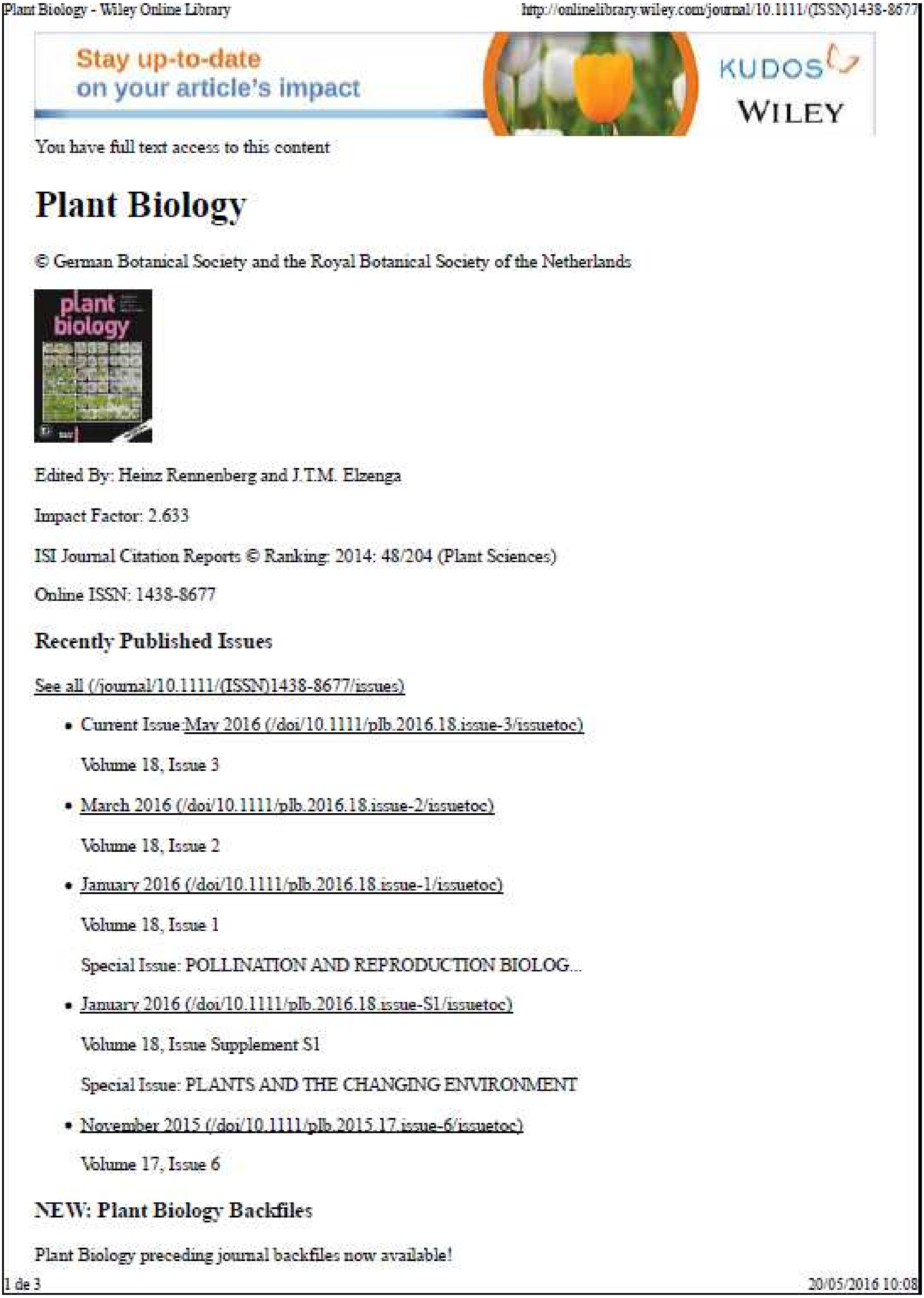

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