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PADRÕES DE ESPÉCIES E TIPOS FUNCIONAIS DE PLANTAS LENHOSAS EM BORDAS DE FLORESTA E CAMPO SOB INFLUÊNCIA DO FOGO

Sandra Cristina Müller

Tese apresentada ao Programa de Pós-graduação em Ecologia da Universidade
Federal do Rio Grande do Sul como um dos pré-requisitos para obtenção do
título de Doutor em Ciências – ênfase em Ecologia

Orientador: Prof. Dr. Valério DePatta Pillar

Porto Alegre, junho de 2005

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Orientador: Prof. Dr. Valério DePatta Pillar (UFRGS)
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RESUMO

Mosaicos naturais de floresta e campo são freqüentes no sul do Brasil, apesar das condições climáticas em geral serem favoráveis às formações florestais. Os campos portanto têm sido considerados um tipo de vegetação relictual de um clima mais frio e seco. Dados paleopalinológicos têm confirmado a hipótese de expansão florestal proposta por Lindman e Rambo com base em evidências fitogeográficas. Porém, fogo e pastejo têm sido utilizados no manejo dos campos, limitando o estabelecimento de árvores em áreas de campo, e parecem ser essenciais para a existência dos campos num clima úmido. Mudanças na intensidade ou freqüência do fogo ou do pastejo podem permitir o adensamento de espécies lenhosas em comunidades campestres. Todavia, os processos envolvidos são influenciados pelas condições locais e tipo de espécies pioneiras.

Esta tese aborda padrões espaciais de transição da floresta ao campo, na ausência de pastejo, porém sob diferentes condições locais relacionadas à exposição do relevo (norte, sul, sudoeste) e ao fogo. Os dados abrangem arbustos e árvores pela composição de espécies e tipos funcionais de plantas (*plant functional types*, PFTs), e variáveis do solo em bordas de floresta-campo, sob diferentes períodos de tempo transcorrido desde a última queimada nas áreas de campo. Dados sobre composição, diversidade, categoria de plantas (que rebrotam e não rebrotam) e PFTs foram analisados de acordo com o período de tempo sem fogo em dois levantamentos realizados em anos consecutivos. O objetivo desta última análise foi descrever como reagem as plantas lenhosas em áreas de campo freqüentemente queimadas, num contexto de ecótonos de floresta-campo.

O estudo foi conduzido no Morro Santana (30°03’ S, 51°07’ W, altitude máxima: 311m), Porto Alegre, RS, Brasil. A vegetação da área apresenta mosaicos de floresta-campo. Os dados foram coletados em seis pares de transecção (4,5 x 58,5 m cada) perpendiculares à borda floresta-campo. Cada transecção era composta por seis quadros grandes (LP= 20,25 m²) consecutivos na floresta e sete no campo. Em cada um dos LP, foram instalados três quadros pequenos (SPs) consecutivos, a fim de medir todos os indivíduos iguais ou maiores que 10 cm de altura. Nos LPs, o critério de inclusão foi a altura mínima de 80 cm. Uma queimada experimental foi realizada nos quadros de campo, considerando sempre uma transecção de cada par, antes da coleta dos dados.

Ao todo foram amostradas 124 espécies lenhosas de 42 famílias. Destas, 90 espécies foram amostradas nos quadros da floresta e 76 nos quadros do campo, das quais 44 foram comuns a ambas as formações (espécies típicas de borda ou pioneiras). No interior da floresta, plântulas e indivíduos jovens de árvores foram significativamente mais abundantes nos quadros próximos da borda, onde os índices de diversidade, eqüidade e riqueza também foram maiores. Os gradientes da floresta ao campo foram analisados como trajetórias de composição em um espaço de ordenação multidimensional. Diferenças nos padrões espaciais reveladas entre locais com exposição distinta foram evidenciadas. Bordas abruptas ocorreram principalmente nas transecções de exposição sul e sudoeste, enquanto transições mais graduais foram observadas no norte. As condições do solo também diferiram em relação às exposições predominantes, porém os principais parâmetros variaram conforme a distância espacial do limite da floresta. Assim, apesar dos padrões de vegetação diferirem conforme a exposição predominante, o fator mais importante na explicação dos padrões foi a distância do limite florestal, não somente *per se*, mas por todos parâmetros correlacionados que variam no gradiente.

Em relação aos dois levantamentos realizados em áreas de campo, 31 espécies arbustivas de campo e 45 florestais foram analisadas, das quais 65,8% tinham capacidade de rebrotar. A composição de espécies diferiu com o tempo após o fogo. Densidade, riqueza e diversidade foram menores nos quadros recentemente queimados, principalmente nos sítios com exposição sul. Considerando arbustos de campo, a riqueza e a densidade foram maiores nos quadros não queimados há um e dois anos do que naqueles há mais de três anos. Comparando arbustos com e sem capacidade de rebrotar, os que rebrotam tiveram sempre maior densidade. Árvores com capacidade de rebrote predominaram nas áreas com exposição norte, apresentando densidades similares, independente do tempo após o fogo. Porém, árvores sem capacidade de rebrote apresentaram maior densidade nos quadros não queimados. Diferenças na dinâmica de recrutamento de arbustos ou árvores uni- ou multi-caulinares também foram detectadas.

Nas análises com base em PFTs, foram identificados nove PFTs florestais com máxima associação com a variável distância da borda. A habilidade de rebrote foi o principal atributo de plantas florestais que colonizam áreas de campo. A diversidade de PFTs foi maior nos quadros próximos da borda que no interior da floresta. Quatro PFTs foram identificados, entre espécies lenhosas florestais e campestres, com máxima associação com o tempo decorrido após o fogo nas áreas de campo. Alguns dos principais aspectos descritos no parágrafo anterior foram corroborados. Arbustos altos com base uni-caulinar predominaram nas áreas não queimadas (3-4 anos), enquanto arbustos baixos com base multi-caulinar predominaram nas áreas recentemente queimadas (3 meses a 1 ano). PFTs florestais ocorreram nos quadros da borda ou como adultos estabelecidos no campo, não sendo afetados pelo fogo.

Com base nos principais resultados, as seguintes conclusões são possíveis:

A alta proporção de espécies com capacidade de rebrote nas áreas de campo e a alta taxa de recrutamento das demais espécies caracterizam comunidades com distúrbios freqüentes e espécies bem adaptadas. O regime de fogo com intervalos de dois a três anos não impede o adensamento de arbustos do campo, porém retarda o avanço de espécies arbóreas florestais, exceto em sítios bastante próximos a borda ou em “ilhas” protegidas do fogo intenso. PFTs lenhosos de áreas de campo, associados com os intervalos de fogo, sugerem que atributos facilmente mensurados são suficientes para avaliar a dinâmica pós-fogo em comunidades de espécies lenhosas. PFTs florestais nas áreas de campo se restringem àqueles com capacidade de rebrote, para sobreviver às queimadas recorrentes.

Com base nas estratégias das plantas, nos PFTs e no padrão espacial das espécies nas bordas de floresta-campo sob influência freqüente do fogo, nós reforçamos a presença de dois mecanismos principais como formas de expansão florestal. Um deles refere-se ao adensamento gradual de espécies arbóreas junto à borda, em áreas cujo intervalo de tempo sem fogo é maior. Outro está relacionado ao recrutamento de árvores pioneiras isoladas no campo, freqüentemente próximo de matacões, onde menor biomassa de gramíneas conduz a menor intensidade do fogo.

O fogo é portanto um fator de prevenção da expansão florestal sobre as áreas adjacentes de campo nas condições atuais de clima úmido. O presente regime de distúrbio permite a manutenção de uma elevada biodiversidade na paisagem dos morros de Porto Alegre pela co-ocorrência de ecossistemas ricos em espécies distintas (campos e florestas); a supressão de queimadas pode alterar o mosaico de tipos de hábitat, aumentando a proporção de áreas florestais.

Palavras chaves: adensamento de arbustos, capacidade de rebrote, dinâmica de expansão florestal, ecótonos de floresta-campo, espécies pioneiras, fogo, tipos funcionais, Sul do Brasil.

ABSTRACT

Patterns of species and plant functional types of woody plants at forest-grassland transitions under fire disturbance

Natural vegetation mosaics of forest and grassland are frequent in southern Brazil despite major climatic conditions suitable for forest formations. Grasslands thus have been considered vegetation relicts of a colder and drier climate period. Palaeoecolgical data have confirmed the hypothesis of forest expansion proposed by Rambo and Lindman on the basis of phytogeographical evidence. However, grazing and fire have been used for grassland management, limiting tree establishment on grassland. Therefore for grassland community existence this management should be probably essential in the present humid climate. Changes in intensity or frequency of disturbances could then enable woody species encroachment in grassland communities, but the processes are influenced by site conditions and life history of pioneer species.

This thesis is about transition patterns of forest to grassland in absence of grazing, but under different site conditions related to aspect (south, north and southwest) and time since the last burn. Data are based on shrub and tree species composition, in plant functional types (PFTs) and soil variables in forest-grassland boundaries under different elapsed time since last fire in the grassland. Additionally to gradient patterns, species composition, diversity, category (resprouter, non-sprouter) of plants and PFTs were analyzed according to time elapsed since last fire in two consecutive survey years in order to know how woody species react to fire in frequently burned grassland in grassland-forest ecotones.

The study was carried out on Morro Santana (30°03’ S, 51°07’ W, 311m a.s.l.), Porto Alegre, Rio Grande do Sul (RS), Brazil. Vegetation cover in the area is a mosaic of grassland and forests. Data were collected on six transect (each one with 4.5 by 58.5 m) pairs perpendicular to the grassland-forest limits. Each transect was composed by six contiguous large plots (LP= 20.25 m²) in the forest and seven in the grassland. Within each LP, three contiguous small plots (SPs) were set to measure all individuals with a minimal of 10 cm high, while for LPs the minimal size was 80 cm height. Before data sampling a prescribed burn was conducted in the grassland in one transect of each transect pair.

A total of 124 woody species of 42 families were sampled in the area. From this, 90 species were sampled in forest plots and 76 in grassland plots, of which 44 species were common to both forest and grassland plots (typical border or pioneer species). Inside the forest, seedlings and saplings were significantly more abundant close to the edge, where species diversity, evenness and richness were higher. Gradients from forest to grassland were analyzed as compositional trajectories in ordination space. Differences in the spatial patterns depicted between distinct site aspects were evident. Abrupt boundaries were found in south and southwest aspects, while the transition in northern transects was more gradual. Soil conditions were as well different among aspects, but in general the main features varied following spatial distance from the forest limit. Thus, despite vegetation patterns at boundaries differing according to main aspect, the most important explanatory factor was the distance from the forest limit, not just by itself, but with all correlated parameters that are changing in the gradient.

Concerning both survey years in grassland areas, 31 grassland shrubs and 45 forest species were analysed, of which 65.8% were resprouters. Species composition differed with elapsed time since fire. Density, richness and diversity were lower in recently burned plots, especially on south exposed sites. For grassland shrubs, species richness and density was higher in plots unburned for one and two years than in unburned for three years. Resprouter shrubs were always denser than non-sprouter. Resprouter trees predominated in north exposed sites, having similar density with elapsed time since fire, but non-sprouters were denser in longer unburned plots. Differences in recruitment dynamics of single- and multi-stemmed shrubs or trees were also detected.

In PFTs-based analyses, nine types of forest woody species were identified maximally associated to distance from forest limit. Resprouting ability characterized forest plants able to colonize grasslands. PFT diversity was higher in border plots than inside forest. Four PFTs of forest and grassland woody species were identified maximally associated to elapsed time since fire. At this analysis, some of the main results of the above paragraph were corroborated. Taller individuals of single-stemmed shrubs predominated in late post-fire recovery (3-4 years), while shorter multi-stemmed shrubs in recently burned areas (3 months to 1 year). PFTs of forest trees occurred in border plots or as established adults in grassland, remaining unaffected by fire.

Based on the main results, the following conclusions are possible:

The high proportion of resprouter species in burned grassland and the high recruitment rate of seeders characterize communities under frequent disturbance with well-adapted species. Fire intervals of two to three years cannot avoid shrub encroachment but retard the advance of forest species over grassland, except on sites very close to the forest border or on island patches protected from intense fire. The defined PFTs of woody plants in grassland associated to elapsed time since last fire suggests that easy-measurable traits are sufficient to evaluate post-fire community dynamics. Forest PFTs in burned grassland are restricted to those with resprouting ability to survive recurrent fire events.

Based on plant strategies, PFTs and species patterns in forest-grassland boundaries under frequent fire influence, we reinforce that two main mechanisms may promote forest expansion into the grassland. First, a gradual tree encroachment near the edge at sites where longer time since fire was observed. A second mechanism is linked to the recruitment of isolated pioneer trees within the grassland matrix, most frequently near rock outcrops, where a decrease in grass biomass leads to low-intensity fires.

Fire is thus a critical factor in preventing forest expansion over adjacent grassland areas under humid climate conditions. The current disturbance regime is maintaining high biodiversity in the study area by the co-occurrence of species rich ecosystems (grassland and forest); fire suppression can alter the mosaic of habitat types by increasing the proportion of forest.

Keywords: shrub encroachment, resprouting ability, forest expansion dinamic, forest-grassland ecotones, pioneer species, fire, plant functional types, South Brazil.

ORGANIZAÇÃO GERAL DA TESE

Esta tese foi organizada em forma de capítulos, precedidos por uma introdução geral e seguidos por uma conclusão também geral, ambas em português. Os capítulos constituem artigos independentes, elaborados e redigidos em língua inglesa, de forma a poder submetê-los para revistas especializadas na área, com circulação internacional. No início de cada capítulo, além do título, constam os demais autores do trabalho e a revista para onde se pretende submeter o artigo. A formatação geral dos capítulos foi realizada conforme as orientações de cada revista, exceto pela forma de apresentação das figuras e tabelas, as quais foram inseridas no texto, e o espaçamento entrelinhas dos títulos de figuras e tabelas e das referências bibliográficas.

INTRODUÇÃO

Padrões e processos em vegetação – uma breve introdução

Estudos de padrões em vegetação devem considerar que a percepção de um ou outro padrão é diretamente relacionada à área de abrangência em si, pois em qualquer que seja a escala podem-se encontrar variações no arranjo de plantas (Dale 1999). Diferentes padrões de arranjo espacial podem envolver desde a distribuição de indivíduos de uma ou várias espécies numa comunidade até a distribuição de comunidades ou formações distintas numa escala de paisagem, a qual pode ser local, regional ou global. Padrões de formas descontínuas da cobertura vegetal são mais facilmente observados quando envolvem comunidades que nitidamente se diferenciam na estrutura e fisionomia, como por exemplo, mosaicos de comunidades campestres e florestais. Porém, ao analisar a transição de duas formações tão distintas numa escala mais fina, pela descrição e quantificação das espécies presentes, outros padrões menos evidentes podem ser revelados, que auxiliam na geração de hipóteses sobre os mecanismos ou processos determinantes do arranjo espacial de espécies ou comunidades num contexto de dinâmica de mosaicos (*patch dynamics*, Pickett & White 1985).

A quantificação de indivíduos ou espécies de plantas num determinado momento retrata o estado atual da vegetação, porém há vários processos envolvidos no seu condicionamento, tais como dispersão, estabelecimento, crescimento, competição, reprodução, senescência e mortalidade. As relações entre vegetação e ambiente têm influência nestes processos, uma vez que ocasionam mudanças na composição florística em decorrência de características do clima (macro e microclimáticas), solo, relevo e exposição, bem como a fauna e fatores de distúrbio (*e.g.* fogo e pastejo) (Myster 1993, Usher 1981). Tendo em vista que fatores ambientais atuam de diversas formas e intensidades sobre diferentes espécies ou tipos de plantas, os processos acima mencionados podem variar de local para local, principalmente conforme a flora, a região e a história de uso e ocupação do solo. Entretanto, ocorrem convergências nos tipos de vegetação de diferentes regiões do mundo, bem como nas respostas e efeitos a determinados fatores (*e.g.* Knapp et al. 2004) e, por isso, estudos como o de padrões espaciais em mosaicos de floresta e campo, independente da região, podem auxiliar na compreensão da dinâmica dos principais processos de expansão florestal ou de resiliência e manutenção de áreas campestres (Usher 1981, Finegan 1984, Green 1989, Myster 1993). Ainda que padrões definidos pela composição e abundância de espécies possam permitir uma aproximação de como atuam tais processos, estudos de processos específicos (como a chuva de sementes e banco de sementes do solo) ou populações relevantes (espécies com comportamento ou estratégias representativas de um determinado grupo ou tipo de plantas) são fundamentais para o embasamento teórico de tais aproximações (Pijl 1972, Harper 1994, Kollmann & Poschlod 1997).

Estudos sobre padrões da vegetação no tempo têm motivado vários pesquisadores (principalmente após o clássico artigo de Watt (1947)) a buscar descrever e quantificar características das plantas numa determinada área ou região e relacioná-las com variáveis ambientais, a fim de compreender arranjos espaciais (padrões) num determinado intervalo de tempo (processos) (Peet 1991). Há, portanto, um dinamismo espacial e temporal nas comunidades vegetais, cujas características dificilmente são isoladas. Estudos temporais, de longo ou curto prazo, permitem compreender a dinâmica de plantas (indivíduos, populações, comunidades) partindo de uma condição inicial para outra, ou seja, os padrões encontrados num determinado tempo podem não ser os mesmos num outro, assim como as trajetórias percorridas em termos de características podem variar. As mudanças no tempo podem ser analisadas por aspectos da estrutura de comunidades vegetais, com enfoque na composição, riqueza e diversidade de espécies, associadas ou não à sucessão vegetacional sob condições naturais (sem interferência antrópica) ou de pós-distúrbio (natural ou antrópico) (Pickett & White 1985, Crawley 1997). Considerando a influência de variáveis externas sobre padrões e processos de comunidades vegetais num intervalo de tempo, comunidades semelhantes, sob diferentes pressões de distúrbio ou fatores, podem ser comparadas quanto ao grau de interferência de tais variáveis nos processos de desenvolvimento da vegetação.

Em relação à dinâmica temporal de comunidades vegetais, o período de coleta de dados de um pesquisador é, na maioria das vezes, limitado a um intervalo muito curto de observação, tendo em vista a “demora” na efetivação dos processos (desde a germinação até a morte) em espécies longevas. Por isso, estudos mais complexos sobre processos de dinâmica da vegetação têm sido explorados com base em dados de perfis paleopalinológicos (Orlóci 2001, Behling et al. 2004), abrangendo assim uma amplitude temporal consideravelmente maior do que com estudos de longa duração em parcelas permanentes. Outra forma de abranger uma escala temporal maior de observação é utilizar transecções ao longo de gradientes, onde se assume *a priori* a existência de séries de vegetação num gradiente com estados distintos de sucessão ou complexidade, é a substituição do tempo-por-espaço (Wildi & Schütz 2000, Orlóci 2001).

Assim como se utiliza a espécie como unidade básica na descrição de padrões e processos, outras formas de categorização de plantas podem ser empregadas na descrição dos mesmos padrões ou processos (Orlóci et al. 2002). A utilização de formas de vida, grupos com estratégias diferentes (normalmente contrastantes) e tipos funcionais de plantas têm permitido que floras diferentes possam ser comparadas quanto aos padrões e processos em tipos de vegetação, por vezes, muito semelhantes pelos aspectos fisionômico-estruturais e funcionais (Noble & Slatyer 1980, Pillar & Orlóci 1993, Pausas 1999, Díaz et al. 2004).

A vegetação no Rio Grande do Sul – um enfoque nos mosaicos de floresta-campo

Na paisagem do Rio Grande do Sul são freqüentes as formações campestres entremeadas por florestas, formando mosaicos de vegetação natural. Na porção mais meridional do estado predomina a formação campestre, o *Pampa* gaúcho, e o contato com florestas ocorre principalmente em ambientes ripários. Na região do planalto a formação de mosaicos é mais proeminente, sendo as florestas com Araucária (Floresta Ombrófila Mista, segundo Teixeira et al. 1986) sempre descritas em conjunto com áreas de campos, não havendo distinção evidente de variáveis ambientais a justificar tais padrões de transição, freqüentemente, abrupta (Rambo 1956, Klein 1975). Na região da Serra do Sudeste (Escudo Cristalino Sul-Rio-Grandense) os mosaicos também ocorrem, porém as florestas são em geral menos exuberantes (Jurinitz & Jarenkow 2003), sendo consideradas pela classificação da vegetação brasileira como Floresta Estacional Semidecidual (Teixeira et al. 1986). As áreas de campo nessa região variam desde formações abertas (campos limpos) até áreas conhecidas como *vassourais* de *Baccharis* spp. e *Dodonaea viscosa* e "matinhas subarborescentes" (Rambo 1956).

Quanto à classificação dos campos no sul do Brasil, não há consenso entre as diversas terminologias utilizadas (Marchiori 2002), sendo ora denominados savana, ora estepes, e subdivididos em classes conforme aspectos fisionômicos de maior ou menor presença de arbustos e árvores (Veloso & Góes-Filho 1982, Teixeira et al. 1986, Leite &

Klein 1990, Leite 2002). Descrições locais apontam para diferenças florístico-fisionômicas conforme a região do estado (Lindman 1906, Rambo 1956, Boldrini 1997), denominando-os amplamente como Campos, por vezes subdivididos e adjetivados segundo algum componente dominante (p.ex.: Campo limpo, Campo sujo, Campo paleáceo).

Quanto às formações florestais, além das já mencionadas Floresta com Araucária e Floresta Estacional Semidecidual, a Floresta Estacional Decidual e Floresta Ombrófila Densa (Mata Atlântica), também ocorrem no Rio Grande do Sul (Fig. 1). A primeira situa-se no oeste (principalmente no vale do rio Uruguai) e no centro do estado (encosta sul da Serra Geral), e a segunda se restringe a um faixa estreita no nordeste do estado. Estas áreas florestais constituem as principais rotas migratórias de elementos florísticos oriundos das florestas estacionais da bacia do rio Paraná e do corredor tropical atlântico (Rambo 1961, Jarenkow 1994, Jarenkow & Waechter 2001, Waechter 2002, Waechter & Jarenkow 2003). O encontro dessas duas correntes é o principal fator responsável pelo caráter semidecidual das florestas das encostas orientais da Serra do Sudeste e do Vale do rio dos Sinos (Jarenkow & Waechter 2001, Jurinitz & Jarenkow 2003).

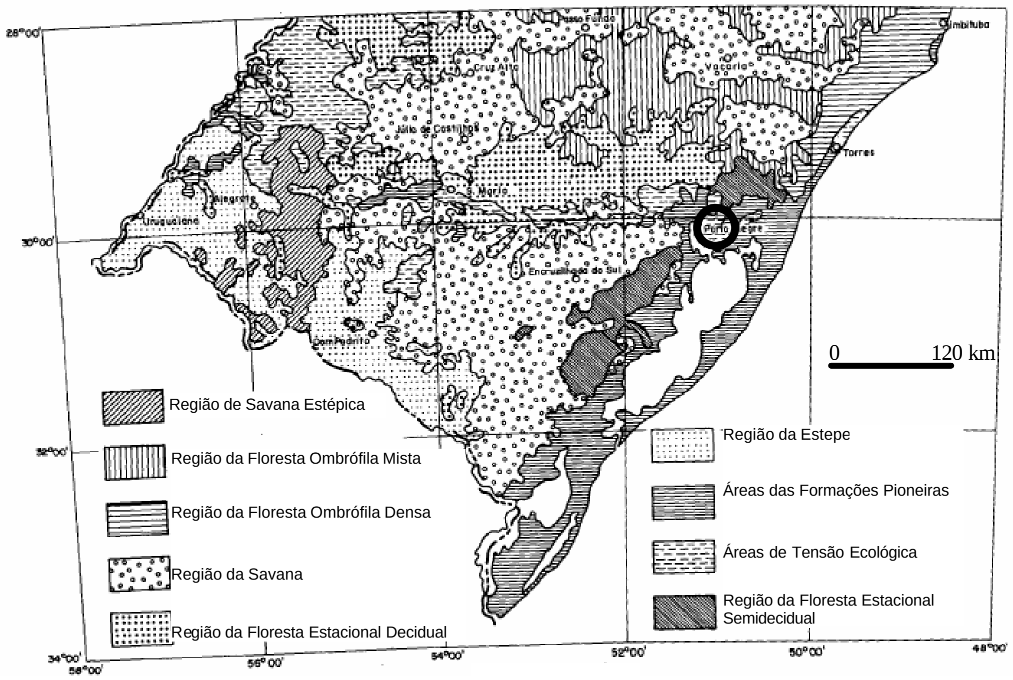

Figura 1. Mapa de distribuição da vegetação natural segundo dados do projeto RADAMBRASIL (Teixeira et al. 1986). Somente as legendas foram reeditadas, a fim de tornar legível, o restante é original. O círculo indica a região de Porto Alegre, área de abrangência deste estudo.

De modo geral, o clima no Rio Grande do Sul corresponde ao subtropical úmido, sem uma estação seca bem definida, pois há uniformidade na pluviosidade ao longo do ano. A precipitação média anual varia de 1250 a 2500 mm, conforme as diferentes regiões do estado, assim como ocorrem variações no regime térmico (Moreno 1961, Nimer 1990) e há probabilidade de déficit hídrico em algumas regiões no sul e sudoeste do estado (Pillar & Quadros 1997). Segundo a classificação de Köppen, são identificados o tipo Cfa (subtropical úmido) e o tipo Cfb (temperado úmido), sendo o primeiro predominante no estado e o segundo presente nas porções mais altas do planalto e em parte da Serra do Sudeste (Moreno 1961, Nimer 1990). Ambos os tipos climáticos estão inseridos numa condição macroclimática que é favorável à formação de florestas (Walter 1986).

A presença de campos naturais em áreas adjacentes a florestas tem instigado estudiosos da vegetação desde as primeiras descrições sobre a cobertura vegetal do estado, ainda antes da grande expansão agrícola (Lindman 1906, Rambo 1954, 1956). Já naquela época, os autores conjeturavam que a ocorrência de vegetação campestre na região da floresta com Araucária, onde não há déficit hídrico, estava relacionada a um tipo vegetação relictual, remanescente de um período climático mais seco e frio, e que a floresta estaria em plena expansão, pois além do corrente clima úmido, não havia limitações edáficas. Tais conjecturas vêm sendo confirmadas por estudos paleopalinológicos que indicam o processo de expansão das florestas e de retração dos campos (Behling 1998, 2001; Ledru et al. 1998, Behling et al. 2004), sendo a manutenção dos campos até os dias atuais em grande parte devida à ação do fogo e do pastejo (Pillar & Quadros 1997, Pillar 2003, Behling et al. 2004). Segundo os últimos autores, a expansão da floresta com Araucária começou a ficar mais evidente a partir de 4000 anos antes do presente (A.P.), quando o clima tornou-se mais úmido, havendo uma aceleração maior no processo de expansão sobre os campos nos últimos 1000 anos A.P. Atualmente, estudos locais sobre padrões e processos em áreas de ecótono de floresta-campo têm convergido para conclusões semelhantes, demonstrando a *recorrência* da tendência de expansão florestal em áreas excluídas de fogo e pastejo (Oliveira 2003, Machado 2004, Oliveira & Pillar 2004, Duarte et al. *submetido*).

A região dos morros de Porto Alegre

A região de Porto Alegre, área de abrangência deste estudo, compreende a porção mais nordeste da Serra do Sudeste e tem sido descrita como Área de Tensão Ecológica (Teixeira et al. 1986), uma vez que comporta e recebe a influência de várias formações vegetacionais distintas (Fig. 1). O núcleo desta região é formado por uma cadeia de morros graníticos, com formas suavemente arredondadas (altitude máxima 311 m) que emergem de uma planície aluvial, e cujas áreas de topo e encosta norte apresentam-se principalmente cobertas por campos e matas ciliares que acompanham arroios ou nascentes, enquanto na maior parte das encostas meridionais predominam as florestas. Descrições sobre a flora e os principais tipos vegetacionais podem ser obtidas principalmente em Rambo (1954), Aguiar et al. (1986) e Brack et al. (1998 e citações bibliográficas).

As áreas de campo são geralmente descritas como um tipo de flora insular, tanto pela forma como compõem a paisagem e pela analogia com a história geológica dos morros (durante a primeira grande transgressão marinha, a região dos morros de Porto Alegre configurava-se como uma ilha (Menegat et al. 1998)), quanto por características fitogeográficas de muitas espécies presentes (Rambo 1954, Porto et al. 1998). Fundamentados principalmente nestes argumentos, os campos dos morros de Porto Alegre têm sido considerados como uma vegetação relictual de períodos cujo clima era mais seco e frio, de maneira similar aos campos da região do Planalto. A alta diversidade de espécies na vegetação dos campos corrobora com a origem natural destas áreas, apresentando padrões diferenciados conforme o tipo de declividade e exposição predominante, bem como em relação ao impacto do fogo (Boldrini et al. 1998, Overbeck et al. no prelo).

As florestas podem ser consideradas como inseridas na área de abrangência da Floresta Estacional Semidecidual (Fig. 1). Porém, tendo em vista a proximidade e a influência dos corredores florestais oriundos do oeste e do norte do estado, uma classificação definitiva torna-se bastante subjetiva. Desta forma, os estudos em áreas de floresta na região dos morros de Porto Alegre têm se referido à composição de espécies predominantes como elementos tropicais tipicamente pluvais ou sazonais. Até o momento, a maior participação no componente arbóreo parece ser de espécies tropicais pluviais oriundas da corrente atlântica (Rambo 1954, Mohr 1995, Brack et al. 1998, Forneck 2001), embora estudos especificamente voltados para tal tema sejam necessários. De qualquer modo, essas áreas estão inseridas no domínio Mata Atlântica, se considerada a definição *lato sensu*, conforme a proposta que abrange a formação de Floresta Ombrófila Densa e ecossistemas associados (Morellato & Haddad 2000, Oliveira-Filho & Fontes 2000).

A denominação de "Área de tensão ecológica" para a região de Porto Alegre realmente condiz com um espaço geográfico relativamente pequeno onde há o encontro de diferentes tipos de formação vegetacional em distintas proporções de contato. O paralelo 30°S da região de Porto Alegre parece representar uma transição florística e vegetacional na América do Sul, sendo um "limite" de distribuição tanto para táxons oriundos dos trópicos (Provícia Atlântica e Paranaense) quanto das zonas mais temperadas (Província Pampeana), uma vez que é considerado a linha central dos subtrópicos (Cabrera & Willink 1980, Waechter 2002).

Em zonas de contato de um ou mais tipos de vegetação contrastantes, como é o caso das áreas de ecótono de floresta-campo na região de Porto Alegre, a dinâmica de troca entre comunidades distintas é muito intensa. Considerando as condições climáticas atuais de um clima subtropical úmido, sem estação seca pronunciada (pluviosidade média anual: 1400 mm), temperaturas amenas ao longo do ano (média anual: 19°C), com raros eventos de geada (média anual: 6 dias), e a tendência de avanço florestal sobre as comunidades de campo no Sul do Brasil, as áreas de ecótono da presente região parecem ideais para a realização de tais estudos sobre dinâmica de padrões e processos em comunidades vegetais.

Principais fatores que influenciam no processo

Como fatores do processo, consideramos aqueles relacionados à dinâmica de expansão de espécies florestais sobre as comunidades campestres, bem como à dinâmica de adensamento de espécies arbustivas, comumente presentes nas áreas de campo, que por sua vez acabam por determinar os atuais padrões de mosaico de floresta-campo, com maior ou menor intensidade.

As interações que ocorrem entre comunidades campestres e arbóreas vão desde diferenças no microclima junto à borda até os processos populacionais que envolvem o avanço de espécies de ambas as comunidades (Longman & Jeník 1992, Kollmann & Poschlod 1997, Gehlhausen et al. 2000), por meio de processos abióticos e bióticos que atuam ao longo do gradiente sucessional (Myster 1993). Os diásporos (unidade de dispersão) tendem a se mover em ambas as direções da borda, formando um fluxo contínuo, a *chuva de sementes*, que é fortemente determinante das populações potenciais da comunidade vegetal (Harper 1994), sendo a estrutura da vegetação e a forma de dispersão das espécies fatores que afetam os padrões de deposição das sementes (Willson & Crome 1989). Além do fluxo de chegada de sementes de comunidades locais ou adjacentes, há aquelas que já se encontram presentes no local, no *banco de sementes do solo* (Parker et al. 1989). Considera-se que espécies pioneiras geralmente apresentam sementes que permanecem num estado de dormência no solo, prontas para iniciar os processos de germinação momentos após a ocorrência de algum distúrbio ou evento natural que venha favorecer o sucesso da colonização (Garwood 1989, Harper 1994, Baskin & Baskin 1998).

Mesmo que ocorra a disponibilidade de sementes no local ou proximidades, que haja agentes dispersores e que as condições climáticas sejam favoráveis ao avanço de espécies florestais no campo, a habilidade das espécies em germinar, estabelecer e recrutar envolve aspectos bastante complexos que relacionam intensidade luminosa, umidade, temperatura, disponibilidade de nutrientes, cobertura e competição de espécies, densidade e tipo de serapilheira, danos mecânicos, predação e herbivoria (Hopkins 1992, Longman & Jeník 1992, Bell et al. 1993, Myster 1993, Holl 1999). Diferenças sutis, inerentes à fisiologia da espécie, igualmente combinadas com a heterogeneidade de ambientes numa escala apropriada de tempo e espaço são fatores suficientes para gerar diferenças na forma de estabelecimento das espécies (Myster 1993, Harper 1994) e conseqüentes padrões de sucessão ou dinâmica nas comunidades vegetais.

A presença de estratos distintos na fisionomia de áreas abertas sujeitas à colonização por espécies florestais (como é o caso dos campos das regiões do planalto e do sudeste do Rio Grande do Sul) formados por espécies arbustivas/arbóreas pode favorecer as taxas de colonização de outras espécies também lenhosas, geralmente, zoocóricas. A heterogeneidade da matriz campestre, a busca por refúgio, alimento ou simplesmente um lugar para pouso (no caso de aves) são alguns dos aspectos que atraem agentes dispersores (Jackson 1993, Vieira et al. 1994, Holl 1998, Hovestadt et al. 1999). Além do fator de atratividade destas espécies/indivíduos no campo, a sua presença também pode vir a facilitar os estádios subseqüentes à dispersão, promovendo condições microclimáticas menos hostis para o estabelecimento de plântulas e menor competição com o estrato inferior de gramíneas (Li & Wilson 1998, Holl 2002, Hoffmann et al. 2004). Além da heterogeneidade vertical, pequenas variações locais no espaço horizontal podem influenciar no padrão de colonização de espécies lenhosas em áreas predominantemente campestres, tais como oscilações no relevo, variações edáficas localizadas e presença de murunduns (p.ex.: cupinzeiros abandonados) (Furley 1992, 1999, Hochberg et al. 1994, Cabral et al. 2003).

Outros fatores, extrínsecos às espécies e ao ambiente natural, porém que exercem influência nos processos e/ou padrões supracitados, estão normalmente relacionados com eventos de distúrbio e a história de uso e ocupação do solo. Entre os fatores de distúrbio, destacam-se o pastejo e o fogo, na maioria das vezes atuando como variáveis indissociáveis (Langevelde et al. 2003), pois áreas com vegetação aberta são mundialmente utilizadas como pastagens naturais e o fogo tem sido uma constante, seja por eventos naturais ou antropogênicos. Uma série de interações relacionadas ao balanço de espécies herbáceas (gramíneas) e lenhosas (árvores) em vegetação de savanas deve ser considerada (Green 1989, Scholes & Archer 1997). Tais interações envolvem desde aspectos relacionados à biologia das espécies até a influência de fatores de distúrbios, o que levou os autores a concluírem que não podem ser preditas por modelos simples, pois incluem elementos de competição e facilitação que variam no tempo e no espaço de modo complexo, principalmente onde condições ou fatores não previsíveis (distúrbios) ocorrem. Uma maior previsibilidade ocorre na ausência de distúrbios e em condições de clima úmido, pois há uma tendência de constante adensamento de indivíduos e espécies arbóreas até a formação de uma vegetação arbórea densa (Scholes & Archer 1997).

Ao longo deste trabalho, a área do presente estudo será por diversas vezes comparada com regiões de savana de outras partes do mundo ou do Brasil (cerrados – savanas neotropicais). Apesar das críticas em se utilizar o termo savana para outras regiões que não as tropicais (Leite 2002, Marchiori 2002), a referência tem sido feita não apenas para as áreas de campos subtropicais do Sul do Brasil (Teixeira et al. 1986) como também para regiões temperadas (Archer et al. 2001), levando em consideração características puramente fisionômicas. A caracterização de savanas envolve a presença de um estrato baixo mais ou menos contínuo, dominado principalmente por gramíneas, com indivíduos lenhosos distribuídos de forma mais ou menos esparsa, sem formar um dossel contínuo. Com base nesta caracterização e tendo em vista o atual processo de expansão das florestas sobre áreas de campo nativo no sul do Brasil, assim como a estrutura de mosaicos de comunidades florestais e campestres (com e sem indivíduos lenhosos), considera-se que as áreas de campo sujeitas à “invasão” de espécies lenhosas sob o impacto do fogo apresentam processos similares aos observados em comunidades de savana. Portanto, grande parte do embasamento teórico e da discussão da tese será comparativa a trabalhos sobre savanas, estepes ou escrubes (*shrublands*), principalmente quando relacionados ao fogo e espécies lenhosas.

Nos campos sulinos, a utilização do fogo tem sido uma ferramenta de manejo muito freqüente entre os pecuaristas, empregada com o objetivo principal de “limpar” o campo, ou seja, manter a estrutura de Campo Limpo, sem espécies arbustivas (Boldrini 1997). Estudos paleopalinológicos recentes sugerem, com base na proporção de partículas de carvão, que o fogo era raro nos períodos glaciais, tornando-se mais freqüente a partir de 7400 anos antes do presente (Behling et al. 2004) na região do Planalto Sul-Brasileiro ou desde o início do Holoceno na região mais a oeste no vale do rio Ibicuí (Behling et al. 2005). Independente da origem das queimadas, o fato é que elas “acompanham” a vegetação campestre desde um longo período histórico, em diferentes partes do mundo (Bond & van Wilgen 1996). O papel do fogo como fator determinante ou mantenedor das formações campestres abertas foi recentemente rediscutido no trabalho de Bond et al. (2003). As evidências sobre a influência do fogo na distribuição das formações campestres no mundo revelaram que grande parte das áreas atualmente cobertas por campos e savanas seriam formações predominantemente arbóreas, caso não houvesse queimadas. Vários aspectos sobre a influência do fogo em espécies lenhosas serão analisados e discutidos nos capítulos desta tese, não sendo, portanto, abordados aqui na introdução. Aspectos da influência em comunidades de espécies herbáceas do campo foram abordados no trabalho de tese de Gerhard Overbeck, desenvolvido num período concomitante e na mesma área de estudo da presente tese (Overbeck et al. no prelo, Overbeck et al. submetido-b, a, Overbeck & Pfadenhauer submetido).

OBJETIVO GERAL E DIVISÃO DOS CAPÍTULOS

Esta tese tem como objetivo geral avaliar os atuais padrões espaciais de espécies lenhosas em mosaicos de floresta-campo, considerando aspectos relacionados com processos de expansão florestal no gradiente de transição floresta-campo e adensamento de arbustos em áreas de campo freqüentemente queimadas. O trabalho foi desenvolvido na região dos morros de Porto Alegre (morro Santana), onde se conjetura que haja uma tendência natural de expansão florestal sobre as áreas de campo e de que o atual padrão de mosaicos tem sido consideravelmente determinado pelo uso freqüente do fogo.

A abordagem deste tema foi dividida em três capítulos com enfoques distintos:

1) Com enfoque nas espécies lenhosas (arbustivas e arbóreas) ao longo de gradientes de floresta-campo, objetivou-se descrever os diferentes padrões do componente lenhoso da vegetação em relação às variáveis do solo, exposição predominante e eventos de fogo. (**1° capítulo:** *Woody species patterns at forest-grassland boundaries in southern Brazil*)
2) Com enfoque nas espécies lenhosas (arbustivas e arbóreas) em áreas de campo, objetivou-se descrever a dinâmica e os padrões de densidade e estratégias de colonização ou permanência das espécies em áreas submetidas à queima, com diferentes intervalos de tempo após o fogo. (**2º capítulo**: *Woody vegetation dynamics in burned subtropical grassland in a forest-grassland mosaic*)
3) Com enfoque em tipos funcionais de plantas (PFT) de espécies arbóreas ao longo de gradientes floresta-campo e PFT de espécies arbustivas e arbóreas em áreas de campo, objetivou-se avaliar quais os grupos (tipos) de plantas que propriamente avançam da floresta sobre o campo e quais conseguem permanecer no campo em diferentes intervalos de tempo após o fogo. (**3º capítulo:** *Plant functional types of woody species related to fire disturbance in forest-grassland ecotones*).

LOCALIZAÇÃO E DELINEAMENTO AMOSTRAL

O morro Santana apresenta uma área de cerca de 1.000 hectares, dos quais aproximadamente 60% pertencem à Universidade Federal do Rio Grande do Sul (UFRGS).

Assim como os demais morros graníticos da região, ele está inserido na malha urbana de Porto Alegre. Processos de expansão ocorrem também dos centros urbanos sobre as áreas naturais e estes têm sido crescentes e rápidos, principalmente nos entornos dos morros de Porto Alegre (Adelmann & Zellhuber 2004). Considerando que a maior parte da área do morro Santana é de propriedade da UFRGS, situando-se no complexo do Campus do Vale, as áreas naturais apresentam-se relativamente bem preservadas e a expansão ilegal dos assentamentos urbanos adjacentes se mantém mais estável do que em outros locais com situação semelhante. De qualquer maneira, urge a necessidade de medidas mais rígidas e eficazes no que tange à conservação destas áreas naturais. Desde 1989 se cogita a criação de uma reserva natural para a área do morro Santana pertencente à UFRGS, porém vários acontecimentos têm até o momento dificultado a realização de tal intento (Dossiê do Morro Santana, agosto 2003).

Ainda em relação ao morro Santana, cabe ressaltar o convênio de cooperação internacional Brasil-Alemanha (UFRGS e TUM – Universidade Técnica de Munique), financiado via Projeto ProBral pela Capes/Brasil e pelo DAAD/Alemanha, que de sobremaneira contribuiu para a realização deste e de outros trabalhos de conclusão de curso, dissertações e doutorados na área do morro Santana ou abrangendo outros morros da região (Porto 2004).

Nesta tese, o delineamento amostral seguiu o seguinte esquema:

- Foram escolhidas três áreas distintas de transição floresta-campo. A distinção foi principalmente em decorrência de diferenças fisionômicas do componente lenhoso nas áreas de campo. Essas mesmas áreas foram distinguidas quanto à estrutura fisionômica no trabalho de Sebastian Klebe (Klebe 2003, Klebe et al. 2003).
- Em cada uma das áreas foram instalados dois pares de transecções em gradientes de floresta-campo. De modo geral, estas áreas também foram distintas quanto à exposição predominante no morro. Assim, dois pares de transecções foram localizados no topo-sul (T1/T7; T2/T8)[1]; dois no topo-sudoeste (T3/T9; T4/T10), e dois em exposição predominante norte (T5/T11; T6/T12) (Fig. 2). O objetivo dos pares foi ter áreas com vegetação afim, para posterior realização de uma queimada experimental numa transecção do par, mantendo a outra sem fogo. As transecções em cada par distavam aproximadamente 5 m uma da outra, sendo a vegetação do par considerada homogênea nos principais caracteres (fisionomia e densidade de lenhosas, profundidade do solo no campo). Cada transecção tinha 31,5 m no campo e 27 m na floresta, sendo subdividida em

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[1] As transecções de 1 a 6 tinham sido designadas a não queimarem, enquanto a seqüência de transecções de 7 a 12 corresponde aos seus respectivos pares. No texto abaixo seguem explicações sobre a queima experimental.

quadros grandes (*large plots*= LP) de 4,5 x 4,5 m distribuídos de forma consecutiva. Estes por sua vez foram subsequentemente subdivididos em quadros pequenos (*small plots*= SP) de 1,5 x 1,5 m (Fig. 3). O limite entre a floresta e o campo foi definido pela presença (ausência) do último indivíduo arbóreo florestal adulto. Este esquema de transecções com parcelas consecutivas e em diferentes tamanhos segue modelos similares adotados em outros trabalhos desenvolvidos no Laboratório de Ecologia Quantitativa da UFRGS (e.g. Oliveira 2003, Machado 2004, Sosinski Jr. & Pillar 2004), uma vez que permite diferentes aproximações de escala, pela junção (*pool*) de quadros consecutivos, mostrando-se bastante efetivo na análise de padrões na vegetação.

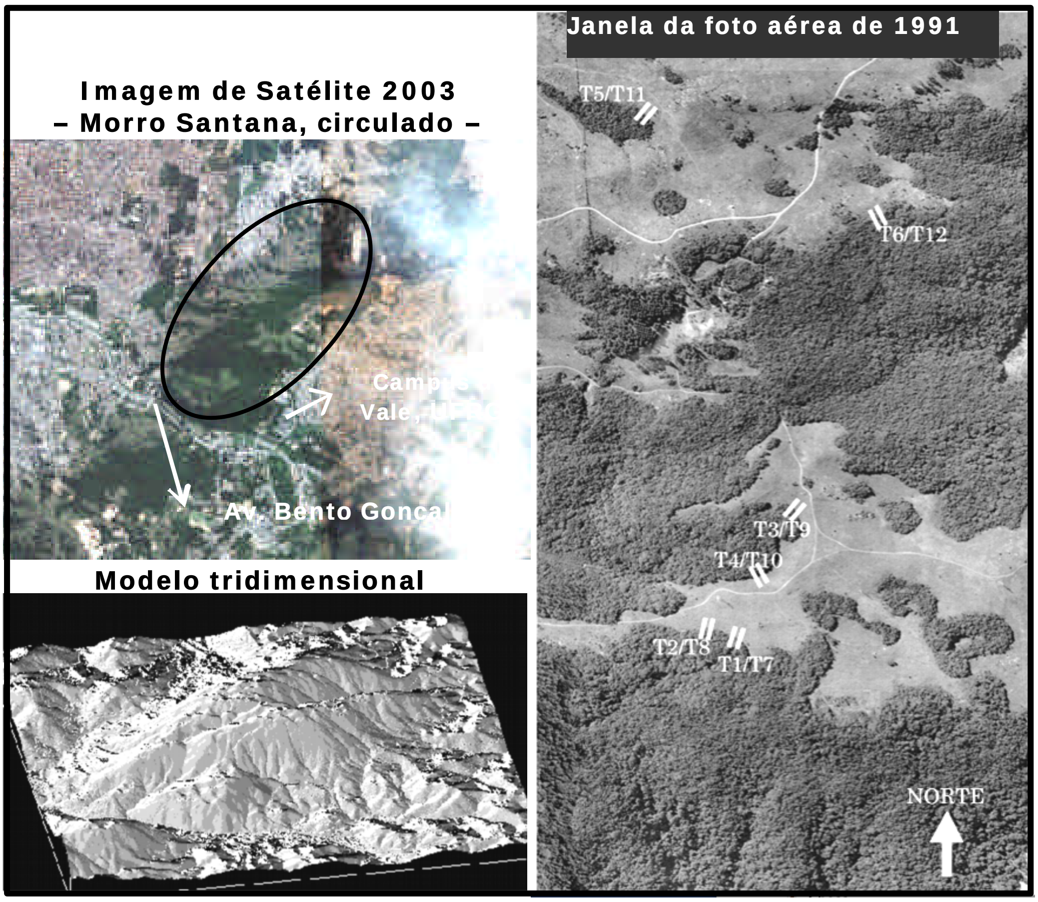

Figura 2: Imagem de satélite *Quickbird* de junho de 2003 sobre a área do morro Santana (gentilmente cedida pelo Prof. Heinrich Hasenack do laboratório de Geoprocessamento da UFRGS), o modelo tridimensional da área do morro (Laboratório de Ecologia de Paisagem, Dossiê do Morro Santana 2003) e uma janela de foto aérea de 1991 (gentilmente cedida por Wolfram Adelmann), detalhando a área central do presente estudo. As imagens estão voltadas para o norte. Na foto aérea, temos a posição aproximada dos 6 pares de transecção utilizados na amostragem da vegetação deste presente estudo.

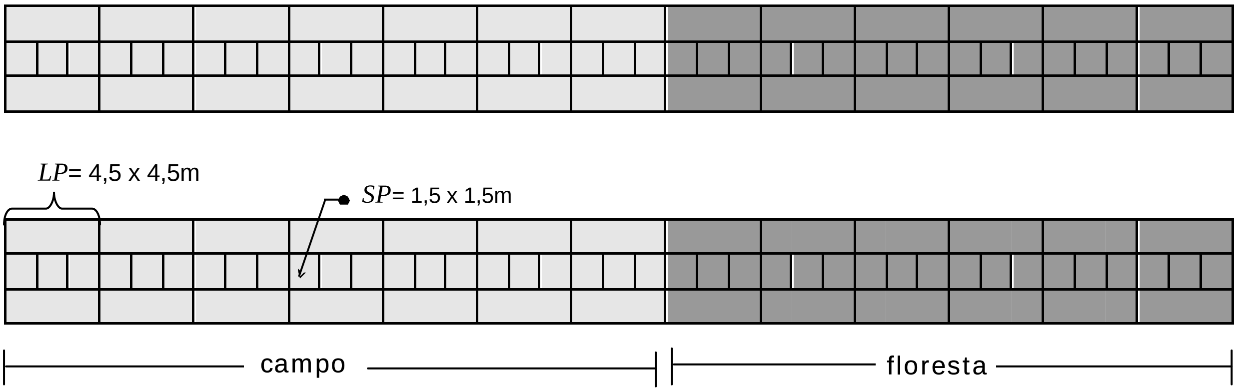

Figura 3. Esquema geral de cada par de transecção, conforme a disposição e o tamanho dos quadros no campo e na floresta. *LP*= quadros grandes; *SP*= quadros pequenos. No total foram seis pares de transecção.

- Uma transecção de cada par foi destinada para realização de uma queimada experimental. O procedimento foi realizado em outubro de 2002, em conjunto com outros trabalhos e os detalhes se encontram descritos em Klebe (2003). Cabe salientar que somente a porção da transecção relativa ao campo foi queimada. O fogo normalmente pára na beira da floresta propriamente dita pela ausência de biomassa seca de gramíneas (principal fonte de combustão). Verões extremamente secos, como neste ano de 2005, em que o fogo chegou a penetrar dois a três metros borda adentro em alguns locais, são eventos raros.

- Apesar do plano inicial, em dois pares de transecção (T3/9 e T4/10) a queimada não foi bem sucedida, simplesmente por que não havia biomassa seca o suficiente no momento do experimento. A falta de biomassa seca nestas áreas de campo ocorreu em decorrência de uma queimada no local 10 meses antes, em janeiro do mesmo ano (2002). Os demais pares onde foi efetivada a queima experimental em uma das transecções, as áreas de campo não queimavam há pelo menos três anos (conforme informações da equipe de guardas da universidade, que circula no local freqüentemente).

- O levantamento nas parcelas da floresta foi realizado de maio a setembro de 2003, enquanto a vegetação das parcelas de campo foi amostrada em dois levantamentos. O primeiro foi três meses após o experimento de queima (janeiro e fevereiro de 2003) e o segundo foi aproximadamente um ano após o experimento (novembro e dezembro de 2003).

- Para cada tamanho de quadro, foram considerados critérios distintos para a inclusão dos indivíduos e alguns parâmetros mensurados também diferiram. Na Tabela 1 há um esquema com os diferentes critérios e medidas, bem como o período do levantamento e o capítulo da tese onde foram empregados os respectivos dados.

Tabela 1: Na primeira parte, os quadros em relação ao tamanho, quantidade, critério de inclusão dos indivíduos lenhosos e itens mensurados no campo. Na segunda parte, a relação dos quadros, dos parâmetros utilizados, o tamanho e a quantidade de quadros amostrados na floresta e no campo, bem como a relação dos critérios de inclusão e dos parâmetros mensurados em cada tipo de quadro.

Quadro	**Critério inclusão**	**Itens mensurados**	**Outras observações**
“grande”: LP (20.25m^2) 72: floresta 84: campo *	indivíduos = 80cm de altura	- altura total; altura do fuste (primeira ramificação); diâmetro da base do caule; dois diâmetros de copa e identificação da espécie	- base multicaulinar (sim ou não) - variáveis da parcela (% solo descoberto, rochas, gramíneas, herbáceas, lianas)
“pequeno”: SP (2.25m^2) 216: floresta 254: campo *	indivíduos = 10cm de altura	- altura total; altura do fuste (primeira ramificação); diâmetro da base do caule; % de cobertura aérea da sp no quadro (escala decimal)[#] e identificação da espécie	- base multicaulinar (sim ou não) - variáveis da parcela (% solo descoberto, rochas, gramíneas, herbáceas, lianas); - medidas dos atributos para definição dos tipos funcionais de plantas (Tab. 1; cap. 3) sempre que havia variação entre indivíduos da mesma espécie, ou se repetia a cada três SP.

	Quadros	**Parâmetros empregados**	**Levantamentos utilizados**
Capítulo 1	LP e SP	LP: cobertura basal, cobertura da copa (projeção), densidade e diâmetros basais, altura total; SP: % de cobertura (escala).	Quadros da floresta e 2°levantamento dos quadros do campo
Capítulo 2	LP e SP	LP e SP: densidade, cobertura basal, altura, “base multicaulinar”, variáveis da parcela; LP: cobertura da copa (projeção), SP: % de cobertura (escala).	Somente quadros do campo; 1º e 2º levantamento.
Capítulo 3	SP	Performance utilizada na matriz W: Análise gradiente floresta-campo – espécies florestais: densidade Análise influência fogo nos quadros campo – espécies florestais e de campo: cobertura basal - além de todos os dados dos atributos (veja acima em *outras observações*)	Quadros da floresta e do campo (1º e 2º levantamentos na análise da influência do fogo; 2º levantamento na análise do gradiente)

* nas áreas de campo houve dois levantamentos, nos mesmos quadros (LP e SP). O primeiro foi em janeiro-fevereiro/2003 e o segundo em novembro-dezembro/2003.

[#] escala conforme (Londo 1976): 0.1= <1%; 0.4= 1-5%; 1= 5-10%; 2= 10-20%; e assim sucessivamente.

PRIMEIRO CAPÍTULO

WOODY SPECIES PATTERNS AT FOREST-GRASSLAND BOUNDARIES IN SOUTHERN BRAZIL [*]

Trabalho realizado em conjunto com:

Gerhard E. Overbeck, Jörg Pfadenhauer e Valério DePatta Pillar

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[*] Trabalho submetido à revista BIOTROPICA. A formatação está conforme as orientações da revista, exceto pela posição das figuras no texto, pelo alinhamento e o espaçamento entre linhas.

ABSTRACT

Vegetation mosaics of grassland/savanna-forest can be found in tropical and subtropical regions of the world, as in southern Brazil, where climate conditions are suitable for forest. Changes in intensity or frequency of disturbances could enable woody species encroachment in grassland communities; however the processes are related to site conditions and life history of pioneer species. In this paper, we study transition patterns of forest to grassland in the absence of grazing, but under different site conditions related to aspect (landscape position) and time since the last burn. Data are based on shrub and tree species composition and soil variables in forest-grassland boundaries. We found 119 woody species of 42 families. Gradients from forest to grassland were analyzed as compositional trajectories in ordination space and differences in the spatial patterns depicted between distinct site aspects. Inside the forest, seedlings and saplings were significantly more abundant close to the edge, where species diversity, evenness and richness were higher, than to the center. Two main mechanisms may promote forest expansion into the grassland. First, a gradual tree encroachment near the edge was observed at sites with longer time since fire. A second mechanism is linked to the recruitment of isolated pioneer trees within the grassland matrix, most frequently near rock outcrops, where a decrease in grass biomass leads to low-intensity fires. Despite vegetation patterns at boundaries differing according to aspect, the most important explanatory factor was the distance from the forest limit, not just by itself, but with all correlated parameters that are changing in the gradient.

Key words: Atlantic forest; Campos; ecotone; fire; forest expansion; shrub encroachment; vegetation dynamics.

RESUMO

(Padrões de espécies lenhosas em bordas de floresta-campo no Sul do Brasil)

Mosaicos entre campo/savana e floresta podem ser encontrados em várias regiões tropicais e subtropicais, como no sul do Brasil, onde as condições climáticas são favoráveis às florestas. Mudanças na intensidade ou freqüência de distúrbios podem proporcionar um adensamento de espécies lenhosas no campo, porém os processos estão relacionados às condições locais e às características vitais das espécies pioneiras. Neste trabalho, estudaram-se os padrões de transição da floresta ao campo na ausência de pastejo, porém sob diferentes condições locais relacionadas à exposição do relevo e ao fogo. Os dados abrangem composição de espécies arbustivas e arbóreas e variáveis do solo em bordas de floresta-campo. Foram identificadas 119 espécies de 42 famílias. Foram analisados gradientes da floresta ao campo como trajetórias de composição em um espaço de ordenação multidimensional, sendo diferenças nos padrões espaciais reveladas entre locais com exposição distinta. Na floresta, plântulas e indivíduos arbóreos jovens foram significativamente mais abundantes próximos à borda, onde a diversidade, a eqüidade e a riqueza de espécies foram maiores. Dois mecanismos principais promovem a expansão florestal sobre o campo. Um deles refere-se ao adensamento gradual de espécies arbóreas junto à borda, em áreas cujo intervalo de tempo sem fogo é maior. Outro está relacionado ao recrutamento de árvores pioneiras isoladas no campo, freqüentemente próximo de matacões, onde a menor biomassa de gramíneas conduz à menor intensidade do fogo. Apesar dos padrões de vegetação diferirem conforme a exposição predominante, o fator mais importante na explicação dos padrões foi a distância do limite florestal, não somente *per se*, mas por todos parâmetros correlacionados que variam no gradiente.

INTRODUCTION

Vegetation mosaics of grassland/savanna-forest can be found in many tropical and subtropical regions of the world, such as in India (Mariotti & Peterschmitt 1994, Puyravaud *et al.* 2003), South America (Coutinho 1990, Pillar & Quadros 1997, Furley 1999), and Africa (Hovestadt *et al.* 1999, Guillet *et al.* 2001, Bond *et al.* 2003). In grassland or savanna-type communities, an increase in density of woody species in the last 50-300 yr has been observed worldwide (*e.g.* Archer 1990, Van Auken 2000, Roques *et al.* 2001, Cabral *et al.* 2003), changing the vegetation physiognomy by vegetation shifts at boundaries, shrub encroachment, or through the presence of woody patches within the grassland matrix. These vegetation changes are usually related to climatic shifts, particularly by alterations in regional precipitation during the dry season, since the capacity of species to support seasonal drought periods is considered as the most distinct feature of tropical areas with either savanna or forest (Longman & Jeník 1992, Sternberg 2001). Furthermore, changes in the intensity or frequency of disturbance, especially grazing and fire regimes, should operate improving the conditions for woody species in grassland communities, mainly in regions with absence of critical drought period (Eggers & Porto 1994, Boldrini & Eggers 1996, Pillar & Quadros 1997, Scholes & Archer 1997, Hoffmann *et al.* 2003, Langevelde *et al.* 2003).

The encroachment of woody species frequently shows a clumpy pattern (Archer *et al.* 1988, Guillet *et al.* 2001, Cabral *et al.* 2003). Therefore, wherever forest is the potential vegetation according to climatic conditions, its expansion may either begin through the development of woody species patches within the grassland matrix or follow a gradual continuum of tree colonization from the forest border into the grassland (Guillet *et al.* 2001, Puyravaud *et al.* 2003). Both forms involve seed dispersion, seedling establishment and a successful recruitment, suggesting attractiveness for seed disperser animals and presence of adequate regeneration niche conditions as principal requirements. Therefore, causes of woody species nucleation or encroachment should differ according to the local site conditions (soil, relief, vegetation structure, disturbance history and land use) as well as to life history and seed dispersal type of the initial colonizers (anemochory or zoochory) (Archer *et al.* 2001, Guillet *et al.* 2001, Cabral *et al.* 2003, Puyravaud *et al.* 2003). In the same way, different types of boundary can be observed, from abrupt straight or curvilinear with short transitions between ecosystem types, to a real gradient from one type to another (Wiens *et al.* 1985, Longman & Jeník 1992). In general, abrupt borders occur where the disturbance regime is intense, such as high fire frequency, in contrast to gradual transition under no disturbance and climatic conditions favorable to forest. Despite these general patterns, boundaries between forest and grassland may differ in their features, since environmental variables and disturbance factors are locally interacting upon the present structure.

In southern Brazil, grassland and forest cover characterize most of the basaltic plateau in the northeast and of the crystalline shield in southeastern Rio Grande do Sul state (Lindman 1906, Rambo 1956, Leite & Klein 1990). Both regions present climate conditions suitable for forest vegetation, but currently a mosaic pattern of grassland and forest predominates (Pillar & Quadros 1997, Pillar 2003). Palaeopollen studies indicate that forest expansion over grassland formations has been accelerated especially since around 1000 years before present (Behling 1998, 2001, Behling *et al.* 2004), and it has been suggested that, in the absence of disturbance, expansion is still in progress (Rambo 1954b, 1956, Klein 1975). However, the expansion process seems to be very slow at the scale of a decade (Oliveira & Pillar 2004).

Considering that fire and grazing can stabilize the present forest-grassland boundaries in southern Brazil, similarly to other subtropical and tropical regions with no or very short dry season, forest expansion may be very slow or not occur at all. In this paper, we study transition patterns of forest to grassland in absence of grazing, but under different site conditions related to aspect (landscape position) and time since the last burn. We use data on shrub and tree species composition and soil chemical and physical variables along transects across forest-grassland boundaries. Our hypothesis is that gradient patterns are related to site aspect, soil conditions and time since fire, and that associated to these patterns we should find different stages of forest expansion or woody species encroachment in the adjacent grassland.

METHODS

STUDY AREA – The study area is on Morro Santana (Santana hill) (30°03’ S, 51°07’ W, 311m a.s.l.), Porto Alegre, Rio Grande do Sul (RS), which is part of a chain of hills at the northeastern part of the South-Rio-Grandean Crystalline Shield. Natural vegetation cover is grassland (*Campos*) on the northern side and the top of the hill and, covering *ca.* 2/3 of the area, forest on the southern side and along creeks. Fire is a frequent disturbance in the grassland, with return intervals of three to five years, usually caused by local residents. The area is not grazed and the present mosaic pattern of vegetation is principally maintained by anthropogenic fire (Overbeck *et al.* in press). The region is part of an ecotone zone of grassland and different forest formations, sharing forest species with the seasonal deciduous forest of the upper Uruguay river valley and the tropical Atlantic rain forest (*stricto sensu*) (Rambo 1961, Teixeira *et al.* 1986). According to Teixeira *et al.* (1986), the site is placed on the seasonal semi-deciduous forest of the Jacuí valley, but most of the dominant species are from the Atlantic rain forest (Mohr 1995, Brack *et al.* 1998, Forneck 2001), which agrees with the Atlantic forest *lato sensu* definition (Oliveira-Filho & Fontes 2000). The grassland species stem principally from the *Pampas* province, but also from Central Brazil, under the broad influence of the Chacoan domain (Rambo 1954a). The climatic conditions around latitude 30°S, a distribution limit for many species originating from northern and southern regions (Cabrera & Willink 1980), may explain the ecotone.

The climate is Cfa according to Köppen, a subtropical humid climate without dry season along the year. Annual mean temperature is 19.5°C and annual average rainfall is 1348 mm (Nimer 1990). Frost is uncommon; annual average of six days (Moreno 1961). The soil types are typical dystrophic red-yellow argisols, developed from granite (Streck *et al.* 2002), corresponding to acrisols, alisols and umbrisols in the FAO-classification (Garcia Martinez 2005). Rounded rock outcrops are abundant on the hill.

DATA SAMPLING – The focus of the sampling was on individuals of woody species occurring on the forest-grassland gradient. Six pairs of transects were established at three different boundary types, according to visually defined vegetation physiognomy. Transects of each pair were separated by five meters. In October 2002 we carried out a controlled burn in the grassland portion of one transect in each of four transect pairs located on grassland that was unburned for three years or more. Two of these transect pairs were on north and two on top/south aspect. The other two transect pairs, on top/southwest aspect, had burned earlier in January 2002 and by the time of the experimental burn had not accumulated sufficient flammable biomass. Each transect was composed of 13 adjacent plots of 4.5 by 4.5 m (large plots – LP), seven in grassland vegetation and six in the forest. Each LP contained three small plots (SP) of 1.5 by 1.5 m at the center, forming continuous transects of 39 plots. For the LPs the inclusion criterion for sampling of woody species individuals was minimum height of 80 cm, while in the SPs, minimal height was 10 cm. All individuals were identified to the species level and their height and basal stem diameter measured. In the SPs, species cover was further estimated by a decimal scale (Londo 1976). The survey was carried out from July until September in the forest and in November/December 2003 in the grassland, *i.e.* one year after the experimental burn.

A composed soil sample of the first 10 cm was taken in all LPs with a Pürkhauer drill, and maximum soil depth was measured (maximal possible drill depth: one meter). Chemical and textural parameters were analyzed by the Soil Analysis Laboratory of the Faculty of Agronomy, UFRGS, Porto Alegre, following the methodology described in (Tedesco *et al.* 1995). The parameters we used for the further analyses of vegetation data were soil depth, pH, contents of available phosphorus (P; in mg L^{-1}; Mehlich I) and potassium (K; in mg L^{-1}; Mehlich I), contents of exchangeable aluminium (Al; in $cmol_C$ L^{-1}), calcium (Ca; in $cmol_C$ L^{-1}) and magnesium (Mg; in $cmol_C$ L^{-1}), cation exchange capacity (CEC; in $cmol_C$ L^{-1}; at pH = 7.0), potential Al saturation (Al_{sat}; in % of CEC), potential acidity (Al+H; in $cmol_C$ cm^{-3}), potential bases saturation (BS_{sat}; in % of CEC), organic matter (OM), and fractions (%) of gravel, clay, silt, fine and thick sand.

DATA ANALYSIS – Vegetation patterns were examined by exploratory multivariate analyses, using cover values of each species for SPs and the abundance/cover value of each species, given by the sum of relative crown and stem covers (% of plot covering) divided by two plus the relative density of the species in the plot for LPs, giving same weight to cover and density. The methods used were cluster by minimum variance and ordination by principal coordinates analysis, both based on chord distances between plots (Podani 2000). Interpretation was aided by methods of bootstrap resampling for evaluating group partition sharpness and significance of ordination dimensions (Pillar 1999a, b). Trajectories connecting the plots in the same transect were drawn in the ordination diagrams in order to reveal any spatial trend related to the forest-grassland transition. All analyses were carried out using the application programs *MULTIV* and *SYNCSA* (Pillar 2004a, b). Grassland and forest communities were also described by density, frequency and cover parameters (Mueller-Dombois & Ellenberg 1974), as well as the importance value index, which is a composed value given by the sum of these relative parameter values divided by three.

For LPs analyses, only 62 of the grassland plots were used, since the other plots did not present any woody individuals higher than 80 cm. Thus, together with the forest plots, we had a total of 134 LPs for the grassland-forest pattern analysis. Further, forest plots were analyzed separately to examine spatial gradients from the last plot inside the forest to the border (limit plot between grassland and forest, which was defined by the last adult tree), using species density. The correlation of vegetation patterns and distance from the forest limit was evaluated by congruence analysis (Pillar & Orlóci 1993). For the forest data, plots in all transects were additionally compared by analysis of variance with randomization testing (Pillar & Orlóci 1996) in order to examine differences in community structure along the edge gradient, using tree density in different diameter classes, Shannon diversity (based on natural logarithm, nats), evenness (Pielou 1969), and species richness as parameters. Thousand iterations were used in randomization testing.

For SPs, we first analysed the data with the original plot-size (1.5 by 1.5m) in order to find spatial patterns in the forest-grassland transects. Similar trajectories in the ordination space were identified visually, resulting to definition of three trajectory types. Transects in each type were pooled. Pooled transects were described by the average species cover values for each of the 39 plots. Then, with these data (3 x 39 plots) we performed a cluster analysis in order to identify sharp groups of plots and typical species composition. Additionally, to reveal forest expansion, individuals of tree species were categorized by size classes (height) along the forest-grassland gradient. The classes were individuals less than 30 cm of height (class 1); between 30 and 79 cm high (class 2), with or higher than 80 cm but less than 5 cm of basal diameter (class 3), or else (class 4).

Groups of plots according to aspect and distance from the forest-grassland limit were compared regarding soil variables by using multivariate analysis of variance with randomization testing (Pillar 2004a), based on Euclidean distance between sampling units with previous normalization of variables (Podani 2000). Congruency between soil and vegetation data matrices was analysed for LPs and SPs, by calculating a matrix correlation between vegetation composition dissimilarities and environmental dissimilarities. The congruency value is similar to a Mantel test (Legendre & Fortin 1989, Legendre & Legendre 1998) but a ranking of the environmental variables (soil parameters, depth and distance) was performed to find a subset of variables maximizing the correlation with the vegetation (Pillar & Orlóci 1993). The same method was also applied to find environmental variable subsets better correlated with the vegetation patterns depicted in ordination diagrams.

RESULTS

SPECIES COMPOSITION

A total of 119 woody species from 42 families was sampled (Appendix 1). The forest plots presented 90 species, 70 genera and 40 families and the grassland plots 72 species, 52 genera and 29 families. In the grassland, 28 species were exclusive, *i.e.* 44 species occurred in both formations. Shannon diversity (H') for total area of LPs was 3.41 and 3.34 for forest and grassland areas, respectively, and 3.37 and 2.62 for SPs. Considering different criteria for inclusion of woody individuals in forest plots, we found 62 species (H'= 2.96) using 5 cm of diameter criterion or 41 species (H'= 2.53) using the 10 cm criterion. In the forest, Myrtaceae was the most diversified family (16 species), followed by Lauraceae (7), Rubiaceae (7), Euphorbiaceae (5), Meliaceae and Salicaceae (4). Considering the importance value index (IVI), the families Nyctaginaceae and Moraceae stood out because of high density and frequency of *Guapira opposita* and large individuals of *Ficus organensis*, respectively. In grassland, Asteraceae alone added up to 51 percent of the IVI's values, also being the richest in species (18). Myrtaceae, Sapindaceae, Euphorbiaceae, Symplocaceae and Myrsinaceae added together 32.6 percent of IVI. These families, in contrast to the Asteraceae, which are mostly grassland shrubs, represent also forest species that can colonize grassland. In the grassland, the Asteraceae stood out with *Baccharis cognata*, *Eupatorium ligulaefolium*, *Porophyllum lanceolatum*, *Heterothalamus psiadioides*, *Vernonia nudiflora* and *Baccharis patens*, which together with *Dodonaea viscosa*, *Symplocos uniflora* and *Myrcia palustris* add up to 52.5 percent of total IVI.

FOREST-GRASSLAND GRADIENT PATTERN

Ordination results of data from the large plots (Fig. 1) showed a gradient from grassland (at the right portion of the diagram) to the forest and some clear differences between north and south/southwest sides became obvious, despite the weak explanation of the axes. At sites with south or southwest aspect, typical grassland shrubs, mostly members of the Asteraceae, locally denominated "*vassouras*" (brooms), had high importance in the grassland. We observed that the majority of these shrubs (*e.g. B. cognata*, *E. ligulaefolium*, *P. lanceolatum* and *B. patens*) were resprouters, *i.e.*, shoots reappear quickly after fire. Non-sprouter species such as *D. viscosa*, *H. psiadioides*, *Baccharis dracunculifolia* as well as resprouters such as

S. uniflora and *Mimosa parvipinna* were more abundant on northern grassland sites and at the border.

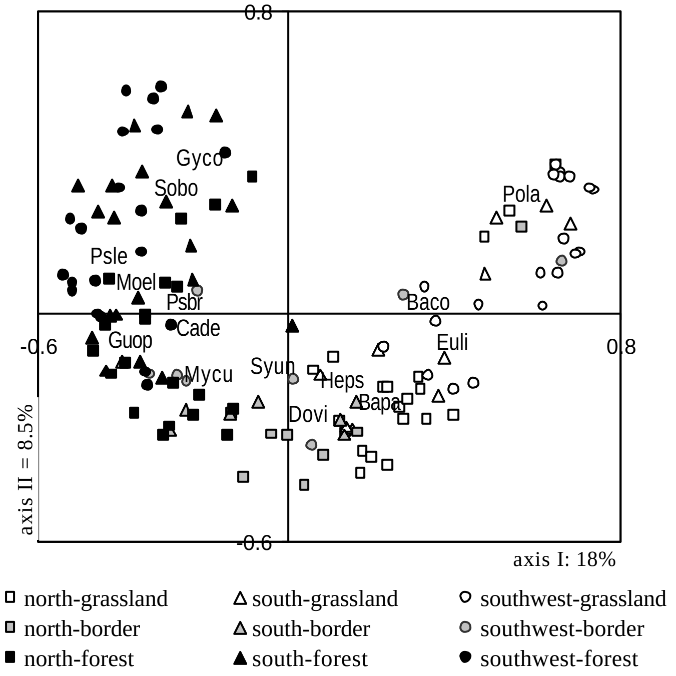

Figure 1. Ordination diagram of large plots based on the abudance/cover value of species. The method was Principal Coordinates Analysis (PCoA), with chord distance between sampling units. All plots are identified by the aspect of transects and according to grassland or forest ambient, and the two LPs at the limit between forest and grassland as border. Taxa are shown on diagram in positions proportional to the correlation level with the ordination axes (see the taxa's code in Appendix 1).

Considering forest plots, species more representative of the Atlantic rain forest were found mainly on the south exposed part of the survey area (*Mollinedia elegans*, *Psychotria leiocarpa, P. brachyceras*), while the species present in border plots on the north and south side (*G. opposita, Trichillia elegans, Myrciaria cuspidata, Casearia decandra,* further by *Lithrea brasiliensis*, *Maytenus cassineformis*, *Myrsine guianensis* and *Sebastiania serrata)* have broader geographical distribution, being common in subxerophytic and riparian forests in the region (Brack *et al.* 1998). The congruence analysis indicated that distance from forest maximized the correlation between vegetation and environmental variation, with a correlation coefficient of 0.52. None of the soil variables improved the correlation with the vegetation composition data.

Concerning only forest plots, a change in species composition from the border to the plot furthest inside the forest could be verified (Fig. 2). This trend was confirmed by the congruency between vegetation forest composition and the spatial distance from the border, which gave a correlation coefficient of 0.36. Most plots near the border (f1; f2) were characterized by *S. serrata*, *Allophylus edulis*, *G. opposita*, *M. cuspidata* and *Zanthoxylum rhoifolium*, followed by *M. cassineformis*, *M. palustris*, *Styrax leprosum* and *L. brasiliensis*. The innermost plots (f5; f6), characterized by *Gymnanthes concolor* and *S. bonplandii*, which are both medium trees typical of tree understory strata in forest interior (Brack *et al*. 1998), in general were at the left part of the ordination diagram. Intermediate plots between both extremes of the gradient were in general characterized by understory shrubs (*e.g. P. leiocarpa, P. brachyceras* and *M. elegans*).

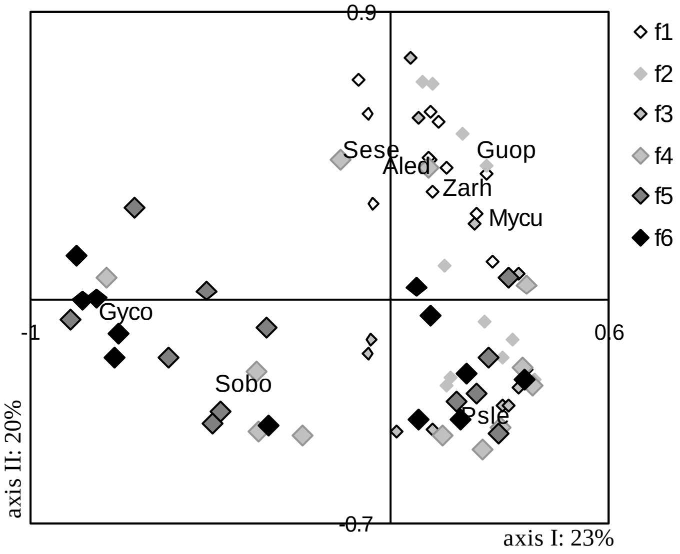

Figure 2. Ordination diagram (PCoA) of forest LPs based on individual densities of each species after chord distance between sampling units. The legend corresponds to plot position inside the forest, being f1 closest and f6 farthest from the border. Taxa correlated more than 0.5 with the ordination axes are shown in the diagram (see the codes in Appendix 1).

Along the gradient, the main differences were between plots close to the border and furthest inside the forest. This can be seen as well in the diameter class distribution of trees species in the forest, considering all transects together (Fig. 3). The first plot (closest to the border) differed significantly from all the others but the second, and the second, from all except the third plot. Most of the differences were due to the higher number of individuals less than 15 cm of basal diameter in plots closed to the border. From circa 10 m inwards into the forest, forest structure became similar along the transect. Plants with basal diameter larger than 50 cm only occurred after 13 m and tended to be evenly scattered. Plots along the gradient in the forest also differed in diversity and structure. Closer to the border, there were more individuals and species, and likewise diversity and evenness were greater (Table 1).

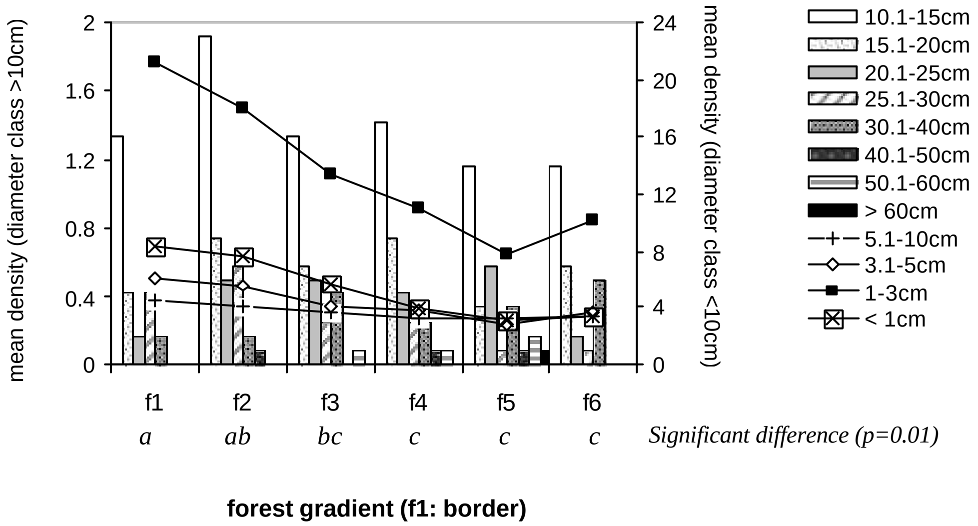

Figure 3. Mean densities of tree species with different basal diameter classes, considering all transects (12) of six 4.5 x 4.5 m plots in the forest gradient (f1: closest border plot and f6: innermost forest plot). Lines and columns correspond respectively to the right and left scale. Plots with different letters under the x-axis have different size class composition (*P*≤ 0.01).

TABLE 1. Richness, Shannon diversity index and evenness of tree species in all forest large plots (f1: the closest border plot and f6: innermost forest plot), and the mean value of richness, density and diversity with n= 12 (243 m^2). Different letters indicate significant differences (*P*= 0.01) between plot positions, given by randomization test.

Diversity indexes	**f1**	**f2**	**f3**	**f4**	**f5**	**f6**
Richness (S) - trees	55	52	44	37	40	41
Shannon index (nats)	3.50	3.16	3.10	2.91	2.98	2.74
Evenness (J)	0.87	0.80	0.82	0.81	0.81	0.74
Mean of richness (n= 12)	16.58^{a}	14.58^{ab}	12.42^{bc}	9.42^{c}	8.67^{c}	8.75^{c}
Mean of tree density (n= 12)	42.75^{a}	39.25^{ab}	30.00^{bc}	25.17^{c}	19.75^{c}	22.92^{c}
Mean of Shannon index (n= 12)	2.50^{a}	2.30^{ab}	2.09^{bc}	1.91^{cd}	1.90^{cd}	1.66^{d}

At the small plots scale of observation, the forest-grassland gradient depicted a clear spatial trend (Fig. 4A). The grassland plots displayed variation in composition along the second ordination axis, while most of the differences between grassland and forest were reflected along the first axis. As expected, border plots (three SPs in forest and three in grassland) showed wider species composition variation. Despite the presence of pioneer or edge species (*e.g. D. viscosa*, *Agarista eucalyptoides*, *M. palustris*, *Eugenia hyemalis*, *Symplocos uniflora*, *S. tetrandra*, *Styrax leprosum* and *Calliandra tweediei*) on these transitional areas, some border plots presented only grassland shrubs. Three trajectory types of similar transects were found (Fig. 4B).

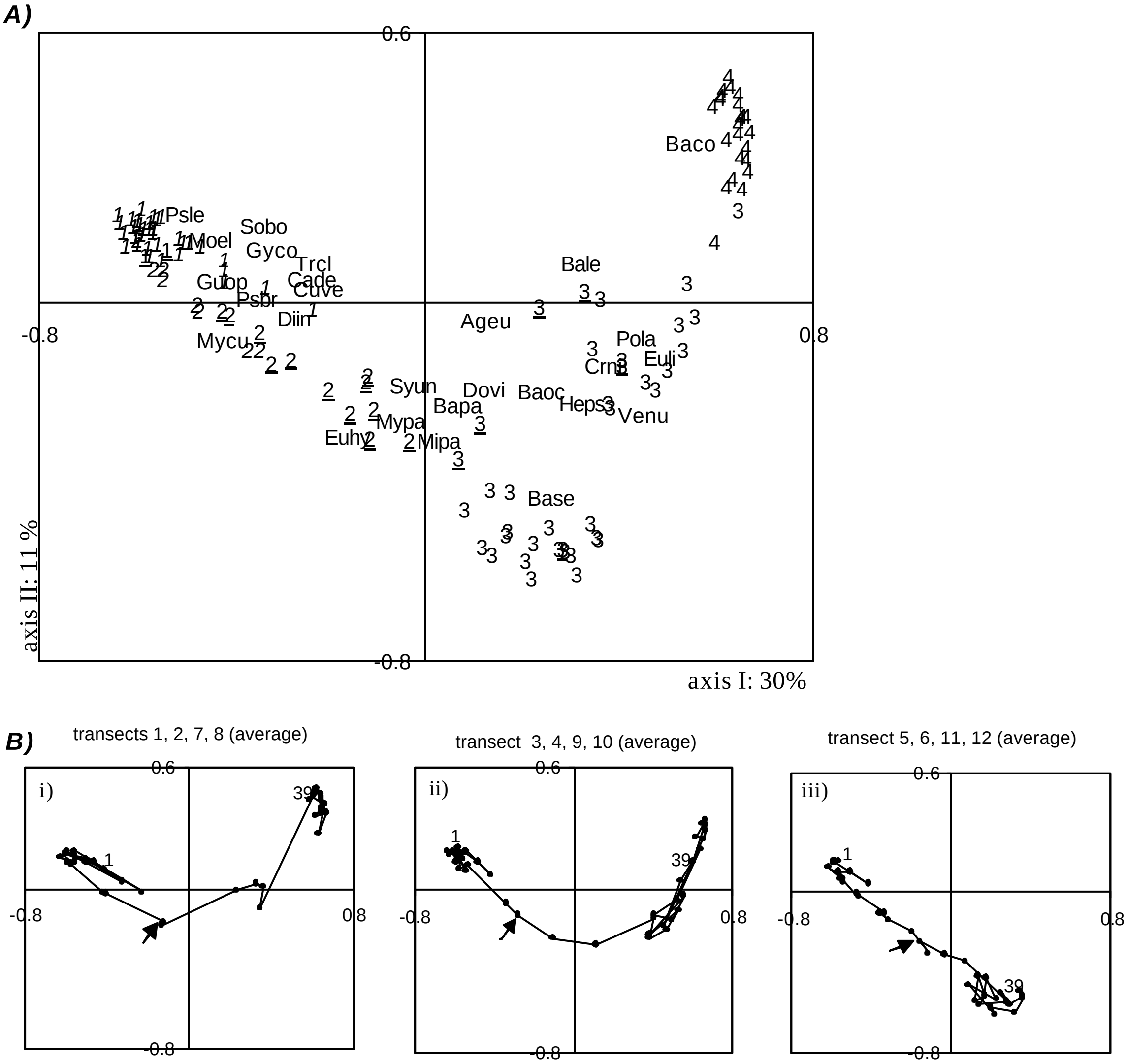

Figure 4. Ordination diagram (PCoA) based on chord distances between sampling units. The variables are species described by an average cover value in plots of transects with similar trajectories. In (A) labels identify the 3 x 39 small plots in the pooled transects according to groups (1-4) found by cluster analysis. Labels in italics refer to forest plots, underlined ones to border plots and the other ones to grassland plots. In (B i-iii) the same plots are depicted separated by trajectory type and the labels refer to plot 1 (forest) to 39 (the last grassland plot). i) top/south, ii) top/southwest, and iii) north. The arrow indicates the forest limit. Ordination axes were stable by bootstrap resampling. Taxa correlated more than 0.35 with ordination axes are shown on diagram (codes are in Appendix 1).

Four groups of such average-sampling units were identified by cluster analysis (labels on Fig. 4A) and each one was characterized by different species composition (Fig. 5). Groups 3 and 4 were dominated by grassland shrubs. Group 4 was characterized especially by Asteraceae species that are short individuals and sprouters (*e.g. B. cognata*, *E.*

ligulaefolium, *V. nudiflora*). Group 3 also presented Asteraceae species, but predominantly non-sprouters and potentially taller species (*e.g. H. psiadioides* and *B. dracunculifolia*). Additionally, species such as *D. viscosa*, *A. eucalyptoides*, *Croton* cf. *nitrariaefolius*, *S. uniflora* and *M. palustris* characterized this group. In spite of these differences, both groups presented similar species in a continuum of dominance change. Group 1 mainly comprised species from inner forest (*P. leiocarpa*, *M. elegans*, *S. bonplandii*, *G. concolor*), whereas group 2 presented forest species with broader ecological amplitude, which were able to establish in the grassland plots, as well as edge species (*P. carthagenensis*, *L. brasiliensis*, *S. serrata*, *G. opposita*, *M. cuspidata*, *S. uniflora* and *M. palustris*).

The trajectory patterns show some structural features that should be considered (Fig. 4B). Average transects with south aspect presented a very sharp border, indicated by a large compositional distance connecting adjacent plots at the forest edge. In north-exposed transects, the gradient between grassland and forest was more gradual, as showed by shorter distances between adjacent plots, and the shrub species typical of south-exposed grassland plots were absent (compare the plot position and correlated species in Fig. 4A). Therefore, the general pattern on the northern side indicated a wider border, further characterized by trees of group 2 and grassland shrubs of group 3 (Fig. 5) in the *Campos* portion. Southwest transects were composed of grassland shrubs (similar to south) and of pioneer woody species, especially near the border.

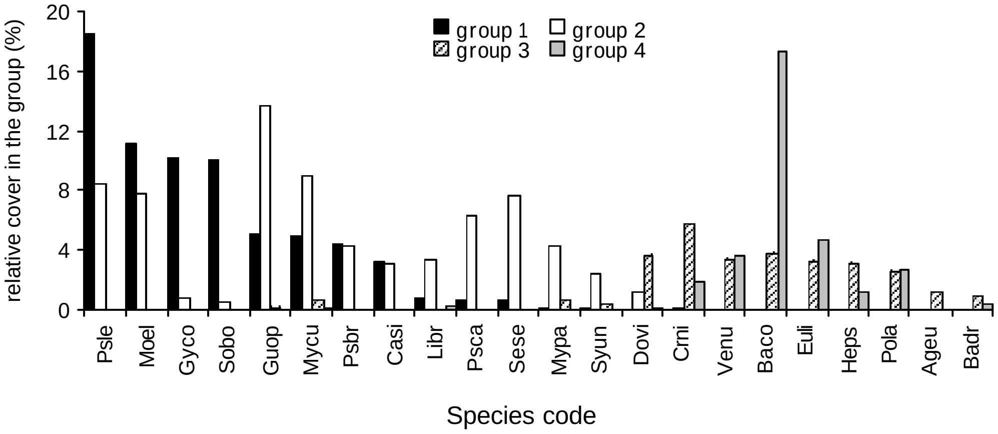

Figure 5. Species relative cover in four sharp groups (labels in Fig. 4A) identified by cluster analysis based on the same data of Fig. 4A. The species codes are in the Appendix 1.

Examining the composition structure of the three main trajectories identified in the studied gradients (south, southwest and north – Fig. 4B), differences regarding diversity may be perceived as well (Fig. 6). Considering that only woody species were sampled, forest and grassland ecosystems greatly differed in diversity. Forest communities on the north side were significantly more diverse than the communities on south and southwest (*P*=0.001, based on data of Fig. 6). The lowering of diversity towards the inner forest was especially clear in southern and southwestern transects, compared to northern transects. Grassland plots on the south side had lower values of diversity compared to north and southwest plots (*P*=0.001, based on data of Fig. 6), the latter two not differing significantly.

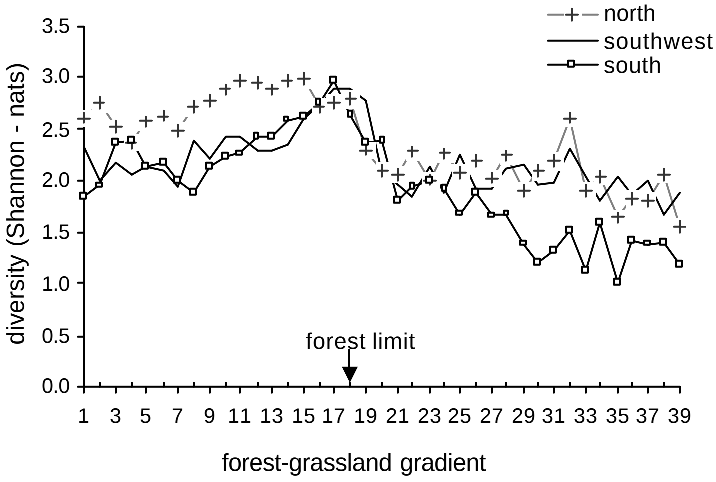

Figure 6. Shannon diversity values (nats) for each small plot along the forest-grassland gradient following the pooled transects of south, southwest and north trajectories indicated in Fig. 4B.

TREE SPECIES DENSITY ALONG THE FOREST-GRASSLAND GRADIENT

Colonization of forest species over grassland occurred gradually starting from the border, and also near small isolated tree individuals forming nucleus of forest vegetation patches inside the *Campos* matrix (Fig. 7). The transition between forest and grassland was more abrupt in recently burned areas than in unburned areas for at least three years. Another interesting aspect is the clumped pattern of seedlings and saplings (size classes 1 and 2) along the grassland portion. For instance, the peak of seedlings and saplings between 19 and 21 m in Fig. 7B coincided with a tall individual of *Myrcia palustris* in one of the transects, a tree growing protected between boulders of a rock outcrop and serving as nucleus for the colonization of other tree species. Similar situations occur on many other sites of the study area and with other species.

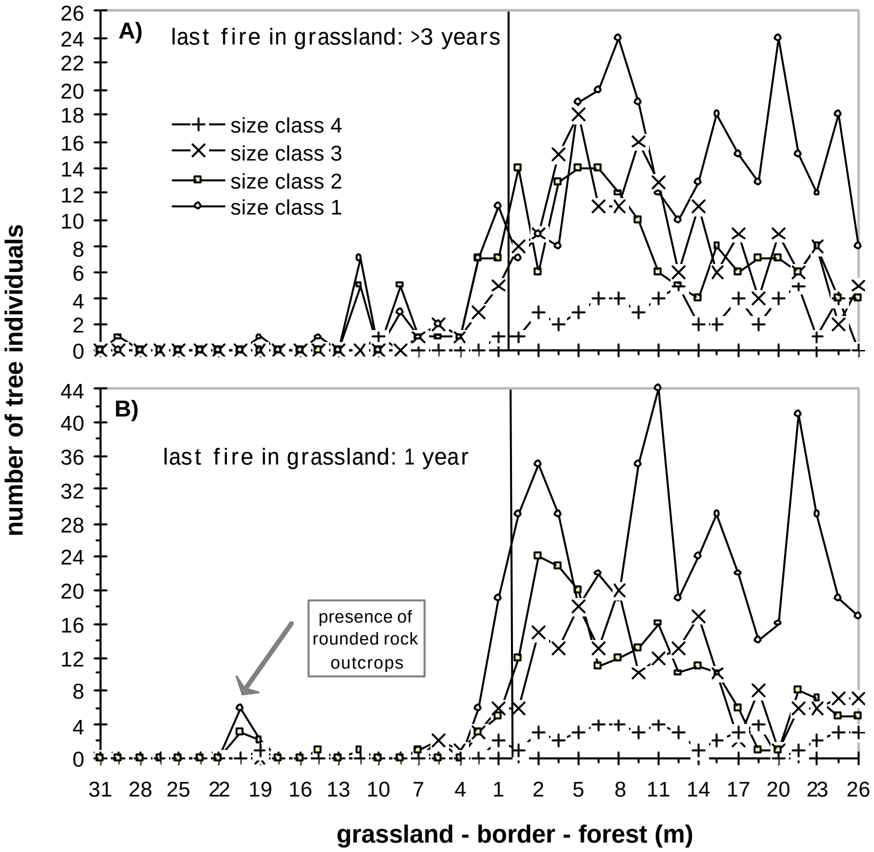

Figure 7. Number of tree individuals along the forest-grassland gradient according to size classes (height). In ***A*** are presented the unburned transects and in ***B*** the experimentally burned transects. Plant size classes correspond to: 1= below 30 cm of height; 2= between 30 and 79 cm; 3= higher than 80 cm but less than 5 cm of basal diameter; 4= all others.

Regarding the forest portion in Fig. 7, a similar pattern of juveniles and adults distribution was observed along the gradient at both unburned and recently burned sites. The newly established trees (size class 1) were almost always clumped (small peaks along the gradient), and are mostly zoochorous species. The greater density of tree individuals of size classes 2 and 3 to *ca.* 13 m near the forest limit is corroborating the data of Fig. 3.

ENVIRONMENTAL VARIABLES

Distance from the forest limit, soil depth and a number of soil properties (chemical and textural, see methods) were considered as possible explanatory variables for the observed vegetation patterns. The differences between transects on the south and north side were significant (*P*=0.05); thus we analyzed both sides separately (Appendix 2). In Table 2 each variable is analyzed separately. Soil textural properties differed mainly according to aspect, as can be seen for clay, sand and gravel fractions. Soil chemical properties as phosphorus

(P), potassium (K), calcium (Ca) and magnesium (Mg) differed along forest-grassland gradients, independent of aspect. K, Ca and Mg showed a peak right at the border, probably because of higher concentration of dead biomass, considering the presence of a dense liana component and sharp changes in litter accumulation at the abrupt boundary caused by frequent grassland fire. Depth, pH and gravel presented significant differences for both factors. At the south side, the soil was deeper and more acidic than at the north and with higher cation exchange capacity (CEC) than at the other aspects. Aluminum content was lower at northern transects, allowing for a higher base saturation.

Table 2. Mean values of soil variables that differed significantly between sites with different aspect and/or spatial position on the forest-grassland gradient. Values followed by same letters are not different for the respective factor, as indicated by randomization testing (*P*=0.05). For complete data, see Appendix 2.

variable	Average transects according to *aspect*			variable	Average transects according to the *forest-grassland gradient*					
	south	southwest	north		**f6+5**	**f4+3**	**f3+2**	**c1+2**	**c3+4**	**c5+6+7**
depth (cm)	96.6^{a}	93.3^{b}	63.4^{cb}	depth (cm)	99.9^{ab}	99.0^{ab}	90.8^{b}	79.0^{b}	77.7^{bc}	68.1^{bc}
pH	4.7^{a}	4.9^{b}	5.0^{cb}	pH	4.6^{a}	4.7^{a}	4.9^{ab}	4.9^{ab}	5.0^{b}	5.0^{b}
Al	2.7^{a}	1.4^{b}	1.4^{cb}	P	3.4^{a}	3.1^{a}	3.8^{a}	2.1^{b}	2.0^{b}	1.9^{b}
Al+H	9.9^{a}	7.4^{b}	6.5^{cb}	K	154.7^{ac}	151.2^{abc}	235.8^{b}	148.4^{c}	155.3^{c}	175.2^{c}
CEC	14.5^{a}	12.9^{b}	11.8^{cb}	Ca	3.4^{ac}	3.7^{ab}	4.8^{b}	2.5^{c}	2.5^{c}	2.4^{c}
bases$_{sat}$	30.7^{a}	41.5^{b}	46.1^{cb}	Mg	1.5^{ac}	1.5^{ac}	2.1^{b}	1.2^{c}	1.2^{c}	1.2^{c}
Al$_{sat}$	19.0^{a}	11.0^{b}	10.6^{cb}	O.M.	5.9^{a}	5.6^{a}	6.7^{a}	4.6^{b}	4.5^{b}	4.6^{b}
clay	40.5^{a}	33.7^{b}	27.6^{c}	silt	29.0^{a}	28.1^{a}	26.2^{a}	21.9^{b}	22.4^{b}	21.3^{b}
thick sand	26.5^{a}	28.4^{a}	35.0^{b}	gravel	22.2^{a}	13.9^{a}	24.0^{a}	38.6^{a}	52.2^{b}	46.2^{b}
fine sand	9.0^{a}	10.4^{a}	12.0^{b}							
gravel	35.9^{ab}	24.8^{a}	40.8^{b}							

Congruence analysis revealed that the spatial distance from the forest limit responded alone for the best correlation with the observed vegetation pattern, so much with the large plots (0.52) as with the small plots (0.61, following the ordination pattern at Fig. 4A). By ranking of all environmental variables to find the highest correlation value, only for the pattern using pooled transect plots (Fig. 4A) the congruence value increased, reaching 0.71 considering distance from the forest limit, phosphorous, depth and bases saturation together. Addition of the variables clay, pH, organic matter and gravel left the correlation value practically unchanged (0.69).

DISCUSSION

Species richness, considering only the forest portion, is relatively high if compared to other studies on Morro Santana of both tree and shrub strata, with *ca.* 40 percent more species (Mohr 1995, Forneck 2001). Comparing the present study to other southern Brazil areas, we found on average 12 more species when taking individuals with diameter larger than 5 cm, but on average eight less species when taking only those larger than 10 cm (Jarenkow & Waechter 2001, Jurinitz & Jarenkow 2003). Most of species that occurred in our study are widespread species in South Brazilian forest regions (Rambo 1954a, Jarenkow & Waechter 2001, Waechter 2002). While species like *Mollinedia elegans, Psychotria brachyceras, Pachystroma longifolia, Coussapoa microcarpa, Ficus organensis, Ocotea silvestris* and *O. indecora* suggest the influence of the Atlantic rain forest, some of the dominants (such as *Guapira opposita, Cabralea canjerana, Casearia decandra, C. sylvestris, Sorocea bonplandii, Matayba elaeagnoides*) are considered "supertramp" species of both rain forest and semi-deciduous forests (Oliveira-Filho & Fontes 2000). Like species richness, diversity and evenness can be considered to be relatively high, with a tendency of decreasing from forest border to the 'interior' (the portion between 20 and 30m from the forest limit). Close to the forest limit no strong dominance was observed. Furthermore, some species sampled in the forest portion were already cited as occurring in grassland areas, such as *Myrciaria cuspidata, M. elaeagnoides, Myrcia palustris, Eugenia* spp., *Maytenus cassineformis, Lithrea brasiliensis, Myrsine umbellata*, and *Symplocos* spp., as tree clusters or as isolated individuals (Leite & Klein 1990, Brack *et al.* 1998, Müller & Forneck 2004). Their presence, as well the richness and diversity patterns, are probably related to border conditions, where the total species pool is increased due to presence of colonizer (pioneer) species (Hopkins 1992), as observed by the high number of species (44) that were common to forest and grassland plots.

Grassland communities in South Brazil are in general very rich in species (Boldrini 2002). The grasslands of Morro Santana may be composed of 450 to 500 species in total (Overbeck *et al.* in press). The present study only considered woody plants, of which a considerable number of species (71) could be found in grassland plots. The exclusive grassland shrub species (27 species) are efficient colonizers, considering that they had much more individuals than woody forest species, reflecting population traits related to dispersal mode, colonization and recruitment success in the grassland matrix. Grassland shrubs form a distinct layer over the graminoid component, which may favour subsequent establishment of trees, since they can improve local site conditions, by increasing shading, and reducing competition from grasses (Hoffmann 1996, Holl 2002). In our study, that was the case only at border plots, suggesting that such facilitation by shrubs would occur under longer fire return intervals than the prevailing conditions.

Along the forest gradient, seedlings and saplings were significantly more abundant and species diversity, evenness and richness were higher close to the forest edge than at the center. Local site conditions and the heterogeneity of environmental factors seem to favour more species at edges (Gehlhausen *et al.* 2000, Oosterhoorn & Kappelle 2000). Microclimatic variables, as light intensity and duration, relative humidity, air temperature, wind, and soil conditions normally differ strongly over grassland-forest boundaries, in general within less than 50 m (Hopkins 1992). Under edge conditions, many shade intolerant tree species are able to germinate, enhancing diversity and often advancing gradually on adjacent grassland communities. Concordantly, in the present study a change in floristic composition and structure along the forest gradient has been detected, especially at south and southwest aspects, where the boundary was sharper than at the north side. At the latter, microclimatic conditions of the edge seem to work further into the forest, thus allowing for a wider edge, compared to south and southwest aspects. Transects on the north side of the hill did not show a clear difference in diversity between edge and the forest interior, and the community composition trajectory from forest to grassland was the most gradual. We may assume that forest expansion process is more recent at the north side and, therefore, in order to see a better gradient or a more pronounced forest structure, we would have to consider more than 27 m into the forest. In contrast, despite the transect size, the south side clearly demonstrated this gradient in diversity values and community trajectories, allowing us to see a more stationary and sharp boundary along the present spatial pattern. Because of deeper soil and consequently higher density of the grass layer, fire disturbance in grassland should be more severe at the south expositions, killing almost all seedlings and/or little saplings in the grassland matrix. On the north side, where the presence of rounded rock outcrops is common and the soil was relatively shallow, the grass layer was lower and less dense, leading to lower fire intensity and offering more safe sites. On the other hand, more frequent fires may occur at the north slope, which is drier (aspect, shallower soils), leading to more frequent pushing back of forest elements. Thus, both fire frequency and intensity may have been critical for the success of tree species recruitment within grassland plots, and these factors together influence forest expansion processes and spatial patterns of woody species distribution.

At other hills around Porto Alegre we can observe, such as in the present study, a very heterogeneous pattern of shrub densities within grassland ecosystems and different structural arrangements at the grassland-forest border. The tree-grass balance in savannas (Scholes & Archer 1997), just as the characteristics of forest expansion processes (Pillar 2003), depend on several factors and their interactive effects over local vegetation patterns. It has been demonstrated that bush encroachment can be a consequence of an increased level of grazing, as a decrease in grass biomass leads to fewer and lower intensity fires, and consequently less damage to trees (Langevelde *et al.* 2003). However, interactions with local differences in topography, drainage and soil conditions may promote discontinuous spatial changes (Furley 1999). Higgins *et al.* (2000), using a spatially explicit individual-based model, concluded that trees can coexist with grasses under conditions between 500 and 1600 mm mean annual rainfall; at lower rainfall their establishment is limited by moisture conditions. In contrast, with high annual rainfall, grass productivity is higher and consequently high-intensity fires should be more frequent, leading to a decrease in tree recruitment, since most of them do not survive under severe burn events. In a similar way, sites with shallower soil, many rock outcrops or yet high proportions of gravel and sand present lower grass densities, leaving open sites for the establishment of new pioneer trees as well as of grassland shrubs.

In concordance with other research on savanna-forest mosaics (Archer 1990, Guillet *et al.* 2001, Puyravaud *et al.* 2003), we identify two main mechanisms that may promote forest expansion. First, a slow gradual encroachment of the edge by the establishment of trees under the liana component or under the canopy shadow at the border zone can be observed. This occurs principally in the absence of constant disturbance or disturbances at high frequency, like under grazing and fire, respectively, but is slow (Hopkins 1992). On Morro Santana, we could observe increased density in tree seedlings and saplings close to forest boundaries in transects without fire since at least three years, in contrast to recently burnt areas. In the plateau region of Rio Grande do Sul, the colonization process of trees over grassland communities also seems to be correlated with an earlier bush encroachment near forest edges, which may lead to less competition with grasses and better microclimatic conditions for tree establishment (Oliveira & Pillar 2004).

A second mechanism is linked to the recruitment of isolated pioneer tree species within the grassland matrix and not necessarily close to the border, which may lead to development of island patches of forest species. This process is linked to safe sites in the grassland matrix, and has been described for various regions with forest-grassland or forest-savanna mosaics. For instance, for Cameroon it has been suggested that termite mounds with or without plants protect tree seedlings from yearly fires, because of less grass biomass (fuel material) near them, guaranteeing their survival (Guillet *et al.* 2001). In Argentinean savanna-type vegetation, the encroachment of woody species occurs at some sites with certain edaphic characteristics, such as saline soils and microrelief created by ant hills, also leading to their development into circular patches, although adjacent areas still remain with a domain of grasses (Cabral *et al.* 2003). In a similar way, in Porto Alegre's hills region, rock outcrops played the role giving initial conditions (attractive to birds as perches, Holl (1998)) and protecting seedlings from fire, due to lack of fuel between or close to the rocks. Such mechanism of forest expansion normally is discontinuous in time and space, but much more effective than the very slow advance of the forest border, which may be pushed back by irregular and rather infrequent more intense fires (Guillet *et al.* 2001, Puyravaud *et al.* 2003). Puyravaud *et al.* (2003) emphasized a progression process in the thickets from early to late successional species. A similar situation is noticed on Morro Santana, structuring and expansion process of thicket formations leads to an increase in diversity and are strongly related to patch size, with the most structured patches being more similar to the near forest edge (Müller & Forneck 2004). Some larger forest patches inside the grassland matrix, regionally known as *capões* in the complex vegetation mosaic in southern Brazilian highlands, have been described as analogous to forest edge structure, considering the high number of seedlings and saplings inside the thicket and of the tendency in expanding over adjacent *Campos* vegetation (Machado 2004). In all those places, dispersers are a key factor in the initial phase of trees nucleation, since zoochorous species (especially bird-dispersal) are the most important group of colonizer plants (Holl 1999, Forneck *et al.* 2003, Duarte *et al.* submitted).

We conclude that vegetation patterns at grassland-forest boundaries on Morro Santana differ according to main aspect and to time since the last fire, although it is difficult to affirm which factors have stronger influence on the spatial pattern, since they are interacting with each other through population and community mechanisms. South and southwest exposed forest edges are more abrupt and show a sharper floristic composition gradient from inner forest plots to the border than on the north exposed sites. In the forest portion of transects with north aspect, the edge seems to be wider and the transition to grassland communities more gradual, considering the arrangement of woody species and individuals density in the grassland. Consequently, this vegetation pattern gives the impression of being under more recent or stronger colonization than in south or southwest exposed sites. In addition, the presence of rock outcrops seems to provide increased possibilities of tree nucleation on the northern slope. Environmental variables, measured by soil conditions and depth, do not appear to limit forest expansion, since sites with shallower soil, more gravel and sand proportion (favourable to dissecation) presented high levels of shrub encroachment and tree establishment. These conditions seem to be more favourable for woody plant recruitment than on sites where soil has better moisture conditions (increased clay fraction and deeper horizons), as increased grass productivity on these sites may lead to higher fire intensity, thus limiting young trees recruitment. The most important factor in explaining the observed vegetation pattern was the spatial distance from the forest limit, not just by itself, but with all correlated parameters that are changing according to the grassland-forest gradient, mostly as a consequence of local boundaries dynamic (Furley 1992). This strong correlation with the floristic composition pattern was expected, since all analyzed transects consistently showed directness in the trajectories from forest interior to grassland.

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Appendix 1. List of woody species and their families* surveyed in the forest-grassland gradient. Values of the parameters density (DA, number of individuals), frequency (FA, %), basal cover (CbA, cm²) and the importance value index (IVI, %) are indicated. All parameters were estimated for each sample scale (LP= large plots and SP= small plots), separately for the forest and grassland portions. The sampling included only individuals taller than 80 cm in LPs and taller than 10 cm in SPs.

				Forest								**Grassland**							
				(LP= 72 plots; 1458m²)				(SP= 216 plots, 486m²)				LP= 84 plots; 1701m²				SP= 252 plots; 567m²			
Family	**Species**	**Habit**	**Code**	**DA**	**FA**	**CbA**	**IVI**	**DA**	**FA**	**CbA**	**IVI**	**DA**	**FA**	**CbA**	**IVI**	**DA**	**FA**	**CbA**	**IVI**
ACANTHACEAE	*Justicia brasiliana* Roth	shrub	jubr	12	9.72	17.6	0.35	18	8.45	11.4	0.39	-	-	-	-	-	-	-	-
ANACARDIACEAE	*Lithrea brasiliensis* March.	tree	libr	27	20.8	11380.1	4.38	8	3.76	4411.7	4.81	11	9.52	46.6	2.14	5	1.59	15.0	0.44
	Schinus molle L.	tree	scmo	1	1.39	9.6	0.04	1	0.47	9.6	0.04	-	-	-	-	-	-	-	-
	Schinus weinmanniaefolius Engl.	shrub	scwe	-	-	-	-	1	0.47	0.0	0.03	11	4.76	5.4	1.17	92	12.7	14.8	1.73
ANNONACEAE	*Rollinia sylvatica* (A.St.Hil.) Mart.	tree	rosy	15	12.5	503.0	0.6	11	5.16	180.5	0.43	-	-	-	-	-	-	-	-
AQUIFOLIACEAE	*Ilex dumosa* Reiss.	tree	ildu	1	1.39	639.6	0.25	1	0.47	639.6	0.7	1	1.19	3.5	0.22	-	-	-	-
ARECACEAE	*Butia capitata* (Mart.) Becc.	tree	buca	-	-	-	-	-	-	-	-	1	1.19	86.6	1.22	3	1.19	182.0	3.73
	Syagrus romanzoffiana (Cham.) Glassm.	tree	syro	2	2.78	8.8	0.09	10	4.69	3.2	0.2	-	-	-	-	-	-	-	-
ASTERACEAE	*Baccharidastrum triplinervium* (Less.) Cabrera	shrub	btri	-	-	-	-	-	-	-	-	3	2.38	11.6	0.55	3	0.79	11.4	0.3
	Baccharis articulata (Cham.) Pers.	shrub	baar	-	-	-	-	-	-	-	-	13	8.33	32.3	1.97	52	9.52	33.9	1.64
	Baccharis cf. *pseudotenuifolia* Teodoro Luis	shrub	baps	-	-	-	-	-	-	-	-	-	-	-	-	2	0.79	0.1	0.07
	Baccharis cognata DC.	shrub	baco	-	-	-	-	-	-	-	-	31	25	42.4	4.78	760	51.6	159.5	11.6
	Baccharis dracunculifolia DC.	shrub	badr	-	-	-	-	-	-	-	-	22	8.33	41.6	2.59	39	10.3	16.9	1.3
	Baccharis leucopappa DC.	shrub	bale	-	-	-	-	-	-	-	-	3	2.38	1.1	0.42	293	24.2	15.1	3.82
	Baccharis ochracea Spreng.	shrub	baoc	-	-	-	-	-	-	-	-	4	4.76	2.6	0.74	59	14.3	6.9	1.46
	Baccharis patens Baker	shrub	bapa	-	-	-	-	-	-	-	-	52	11.9	118.2	5.57	29	3.17	59.1	1.58
	Baccharis sessilifolia DC.	shrub	base	-	-	-	-	-	-	-	-	2	2.38	0.6	0.36	181	26.2	31.1	3.53
	Baccharis trimera (Less.) DC.	shrub	batr	-	-	-	-	-	-	-	-	1	1.19	2.1	0.2	31	8.73	5.7	0.89
	Eupatorium intermedium DC.	shrub	eupi	1	1.39	1.1	0.04	1	0.47	1.1	0.03	14	7.14	116.3	2.92	7	2.78	31.1	0.85
	Eupatorium ligulaefolium Hook. et Arn.	shrub	euli	-	-	-	-	-	-	-	-	58	36.9	78.3	7.95	377	53.6	61.3	7.22
	Heterothalamus psiadioides Less.	shrub	heps	-	-	-	-	-	-	-	-	29	11.9	130.0	4.41	830	16.3	132.1	9.19
	Porophyllum lanceolatum DC.	shrub	pola	-	-	-	-	-	-	-	-	76	33.3	28.8	8.01	321	43.7	32.6	5.63
	Trixis stricta Spreng.	shrub	trst	-	-	-	-	-	-	-	-	2	2.38	6.8	0.43	2	0.79	1.3	0.09
	Verbesina subcordata DC.	shrub	vesu	-	-	-	-	-	-	-	-	-	-	-	-	661	80.6	33.3	10.3
	Vernonia nudiflora Less.	shrub	venu	-	-	-	-	-	-	-	-	4	4.76	1.4	0.72	16	3.57	4.9	0.44
BORAGINACEAE	*Cordia ecalyculata* Vell.	tree	coec	1	1.39	7.1	0.04	-	-	-	-	-	-	-	-	-	-	-	-

CACTACEAE	*Cereus hildmannianus* K. Schum.	cactus	cehi	5	5.56	264.3	0.26	7	3.29	268.5	0.43	-	-	-	-	-	-	-	-
	Opuntia monacantha Haw.	cactus	opmo	1	1.39	33.2	0.05	1	0.47	33.2	0.06	2	1.19	74.4	1.13	1	0.4	10.8	0.25
CELASTRACEAE	*Maytenus cassineformis* Reiss.	tree	maca	16	12.5	118.2	0.49	15	7.04	10.5	0.32	5	3.57	4.4	0.7	4	0.79	0.3	0.08
CLUSIACEAE	*Garcinia gardneriana* (Pl. et Tr.) Zappi	tree	gaga	28	20.8	2035.5	1.41	37	17.4	506.0	1.2	-	-	-	-	-	-	-	-
EBENACEAE	*Diospyros inconstans* Jacq.	tree	diin	56	31.9	3404.9	2.39	224	105	553.7	4.17	-	-	-	-	13	1.98	0.1	0.22
ERICACEAE	*Agarista eucalyptoides* (Cham. et Schl.) G. Don	tree	ageu	1	1.39	748.7	0.28	-	-	-	-	14	5.95	68.3	2.22	19	3.97	45.8	1.3
ERYTHROXYLACEAE	*Erythroxylum argentinum* O.E. Schulz.	tree	erar	12	8.33	63.6	0.33	64	30.1	9.1	1.35	1	1.19	2.5	0.21	13	1.59	0.3	0.19
	Erythroxylum microphyllum A.St.Hil.	shrub	ermi	-	-	-	-	-	-	-	-	1	1.19	1.2	0.19	2	0.79	0.6	0.08
EUPHORBIACEAE	*Alchornea triplinervia* (Spreng.) M.Arg.	tree	altr	4	4.17	773.7	0.38	-	-	-	-	-	-	-	-	1	0.4	0.0	0.03
	Croton cf. *nitrariaefolius* Baill.	shrub	crni	-	-	-	-	-	-	-	-	11	7.14	2.9	1.38	809	50.8	43.1	9.53
	Croton cf. *thermarum* Müll.Arg.	shrub	crth	-	-	-	-	-	-	-	-	4	2.38	1.1	0.48	57	7.94	6.3	1.02
	Gymnanthes concolor Spreng.	tree	gyco	168	38.9	2439.0	3.41	225	106	954.0	4.24	-	-	-	-	-	-	-	-
	Pachystroma longifolium (Nees) Johnst.	tree	palo	4	4.17	23.0	0.14	6	2.82	23.6	0.17	-	-	-	-	-	-	-	-
	Sebastiania brasiliensis Spreng.	tree	sebr	35	18.1	191.9	0.83	23	10.8	52.4	0.51	7	1.19	5.7	0.59	6	1.19	3.5	0.19
	Sebastiania serrata (M.Arg.) M.Arg.	tree	sese	107	15.3	3790.5	2.67	61	28.6	2214.0	3.32	5	2.38	9.9	0.64	2	0.79	4.9	0.16
FABACEAE	*Calliandra tweediei* Benth.	shrub	catw	36	11.1	146.4	0.67	28	13.2	73.7	0.61	5	2.38	6.5	0.6	3	0.79	1.9	0.11
	Collaea stenophylla Benth.	shrub	cost	-	-	-	-	-	-	-	-	5	2.38	1.4	0.54	8	1.59	0.5	0.17
	Mimosa parvipinna Benth.	shrub	mipa	-	-	-	-	-	-	-	-	12	8.33	15.1	1.7	21	5.16	14.6	0.77
ICACINACEAE	*Citronella paniculata* (Mart.) R.A.Howard	tree	cipa	-	-	-	-	1	0.47	0.8	0.03	-	-	-	-	-	-	-	-
LAURACEAE	*Aiouea saligna* Meis.	tree	aisa	2	2.78	4.6	0.08	4	1.88	3.3	0.11	-	-	-	-	-	-	-	-
	Endlicheria paniculata (Spreng.) Macbr.	tree	enpa	1	1.39	0.8	0.04	1	0.47	0.1	0.03	-	-	-	-	-	-	-	-
	Nectandra megapotamica (Spreng.) Mez	tree	neme	1	1.39	0.3	0.04	7	3.29	0.3	0.19	-	-	-	-	-	-	-	-
	Ocotea indecora Schott ex Meissn.	tree	ocin	9	11.1	36.2	0.36	9	4.23	2.2	0.23	-	-	-	-	-	-	-	-
	Ocotea puberula Nees	tree	ocpu	14	15.3	581.7	0.68	46	21.6	514.5	1.5	-	-	-	-	1	0.4	0.0	0.03
	Ocotea pulchella Mart.	tree	ocop	68	40.3	1159.3	1.99	36	16.9	250.2	1.12	-	-	-	-	-	-	-	-
	Ocotea silvestris Vattimo-Gil	tree	ocsi	2	2.78	2.6	0.08	2	0.94	2.6	0.06	-	-	-	-	-	-	-	-
LOGANIACEAE	*Strychnos brasiliensis* (Spreng.) Mart.	shrub	stbr	3	4.17	7.2	0.13	5	2.35	1.2	0.14	-	-	-	-	-	-	-	-
MALVACEAE	*Pavonia hastata* Cav.	shrub	paha	-	-	-	-	-	-	-	-	27	15.5	7.5	3.18	107	16.7	9.3	1.98
	Sida rhombifolia L.	shrub	sirh	-	-	-	-	-	-	-	-	-	-	-	-	15	2.38	0.2	0.26
	Triumfetta semitriloba Jack.	shrub	trse	-	-	-	-	3	1.41	0.5	0.06	-	-	-	-	-	-	-	-
MELASTOMATACEAE	*Miconia hyemalis* A.St.Hil. et Naud.	tree	mihy	7	5.56	3.6	0.2	7	3.29	2.2	0.14	1	1.19	1.1	0.19	1	0.4	1.1	0.06
MELIACEAE	*Cabralea canjerana* (Vell.) Mart.	tree	caca	15	12.5	1415.9	0.89	16	7.51	29.4	0.44	-	-	-	-	2	0.79	0.2	0.07
	Guarea macrophylla Vahl	tree	guma	1	1.39	1.0	0.04	-	-	-	-	-	-	-	-	-	-	-	-
	Trichilia claussenii C.DC.	tree	trcl	39	31.9	369.3	1.24	48	22.5	119.6	1.27	1	1.19	4.5	0.23	-	-	-	-
	Trichilia elegans A.Juss.	tree	trel	27	23.6	121.5	0.85	21	9.86	35.8	0.53	-	-	-	-	-	-	-	-

MONNIMIACEAE	*Mollinedia elegans* Tul.	shrub	moel	333	80.6	969.8	5.6	295	139	398.3	5.12	-	-	-	-	2	0.4	0.1	0.04
MORACEAE	*Ficus organensis* (Miq.) Miq.	tree	fior	2	2.78	8121.7	2.67	-	-	-	-	-	-	-	-	1	0.4	0.1	0.04
	Sorocea bonplandii (Bail.) Burg. Lanj. et Boer	tree	sobo	178	68.1	3318.7	4.45	379	178	1014.7	6.13	-	-	-	-	-	-	-	-
MYRSINACEAE	*Myrsine coriacea* (Sw.) R. Br.	tree	myco	11	6.94	112.6	0.31	6	2.82	18.5	0.16	8	3.57	20.6	1.06	13	2.78	228.3	4.82
	Myrsine guianensis (Aubl.) Kuntze	tree	mygu	17	19.4	10496.7	3.96	6	2.82	3628.2	3.96	3	3.57	62.8	1.29	-	-	-	-
	Myrsine umbellata Mart.	tree	myum	24	20.8	666.9	0.93	30	14.1	296.8	0.99	7	4.76	7.8	0.97	7	2.78	5.6	0.34
MYRTACEAE	*Blepharocalyx salicifolius* (Kunth) O.Berg	tree	blsa	5	2.78	35.1	0.13	1	0.47	1.3	0.03	-	-	-	-	-	-	-	-
	Calyptranthes concinna DC.	tree	caco	3	4.17	59.1	0.14	-	-	-	-	-	-	-	-	-	-	-	-
	Campomanesia aurea O.Berg	shrub	caau	-	-	-	-	-	-	-	-	4	1.19	2.0	0.37	29	4.37	2.7	0.53
	Campomanesia xanthocarpa O.Berg	tree	caxa	-	-	-	-	2	0.94	0.0	0.04								
	Eugenia dimorpha O.Berg	tree	eudi	-	-	-	-	-	-	-	-	2	1.19	5.9	0.3	-	-	-	-
	Eugenia hyemalis Camb.	tree	euhy	18	8.33	11.0	0.38	43	20.2	10.5	0.71	1	1.19	0.2	0.18	16	1.98	10.4	0.44
	Eugenia involucrata DC.	tree	euin	1	1.39	42.1	0.06	1	0.47	0.2	0.03	-	-	-	-	-	-	-	-
	Eugenia rostrifolia D.Legrand	tree	euro	10	12.5	66.5	0.41	124	58.2	60.5	2.32	-	-	-	-	-	-	-	-
	Eugenia schuechiana O.Berg	tree	eusc	25	22.2	310.8	0.86	22	10.3	120.6	0.64	-	-	-	-	-	-	-	-
	Eugenia uniflora L.	tree	euun	10	9.72	141.5	0.37	3	1.41	42.5	0.12	1	1.19	0.4	0.18	-	-	-	-
	Eugenia uruguayensis Cambess.	tree	euur	43	33.3	852.1	1.47	50	23.5	151.9	1.17	-	-	-	-	1	0.4	0.2	0.04
	Myrcia glabra (Berg) Legr.	tree	mygl	9	9.72	441.7	0.45	9	4.23	296.6	0.53	8	5.95	513.4	7.25	11	3.17	33.6	0.95
	Myrcia multiflora (Lam.) DC.	tree	mymu	1	1.39	66.5	0.06	-	-	-	-	-	-	-	-	-	-	-	-
	Myrcia palustris (DC.) Kausel	tree	mypa	28	25	1141.2	1.22	42	19.7	792.7	1.68	-	-	-	-	-	-	-	-
	Myrcianthes gigantea (Legr.) Legr.	tree	mygi	11	9.72	636.8	0.54	21	9.86	519.7	1	-	-	-	-	-	-	-	-
	Myrciaria cuspidata O.Berg	tree	mycu	232	68.1	3029.4	4.92	224	105	1179.0	5.06	25	14.3	109.1	4.17	20	5.16	29.1	1.05
	Psidium cattleyanum Sab.	tree	psic	3	2.78	11.5	0.1	-	-	-	-	-	-	-	-	-	-	-	-
	Psidium sp.	shrub	pssp	1	1.39	0.8	0.04	1	0.47	0.8	0.03	-	-	-	-	-	-	-	-
NYCTAGINACEAE	*Guapira opposita* (Vell.) Reitz	tree	guop	290	77.8	20473.3	11.3	293	138	5868.9	10.6	3	2.38	28.0	0.75	6	1.59	2.0	0.18
OPILIACEAE	*Agonandra brasiliensis* Benth. & Hook.f.	tree	agbr	-	-	-	-	2	0.94	0.9	0.04	-	-	-	-	-	-	-	-
PIPERACEAE	*Piper gaudichaudianum* Kunth	shrub	piga	6	5.56	11.6	0.19	5	2.35	5.0	0.14	-	-	-	-	-	-	-	-
PROTEACEAE	*Roupala brasiliensis* Klotz.	tree	robr	34	23.6	3924.1	2.14	37	17.4	46.2	0.91	-	-	-	-	-	-	-	-
QUILLAJACEAE	*Quillaia brasiliensis* (St.Hil. et Tul.) Mart.	tree	qubr	5	2.78	35.1	0.13	2	0.94	8.1	0.04	1	1.19	0.5	0.18	1	0.4	0.5	0.04
ROSACEAE	*Prunus myrtifolia* Koehne	tree	prse	23	23.6	177.1	0.83	37	17.4	68.1	0.9	-	-	-	-	-	-	-	-
RUBIACEAE	*Faramea montevidensis* Cham.	tree	fama	56	34.7	524.3	1.53	53	24.9	277.3	1.42	-	-	-	-	-	-	-	-
	Guettarda uruguensis Cham. et Schtdl.	tree	guur	8	9.72	128.7	0.34	3	1.41	68.0	0.15	3	2.38	10.9	0.54	2	0.79	10.2	0.27
	Psychotria brachyceras M.Arg.	shrub	psbr	131	62.5	177.7	2.83	112	52.6	73.7	2.38	-	-	-	-	-	-	-	-
	Psychotria carthagenensis Jacq.	shrub	psca	106	40.3	194.1	2.08	100	47	71.3	1.89	4	2.38	4.2	0.52	8	1.59	3.5	0.23
	Psychotria leiocarpa Cham. et Schtdl.	shrub	psle	410	77.8	1090.5	6.38	451	212	477.1	7.25	-	-	-	-	4	0.4	0.2	0.06

	Randia armata (Sw.) DC.	tree	raar	1	1.39	4.9	0.04	-	-	-	-	-	-	-	-	-	-	-	-
	Rudgea parquioides (Cham.) M.Arg.	tree	rupa	15	11.1	41.2	0.42	9	4.23	10.8	0.25	-	-	-	-	-	-	-	-
RUTACEAE	*Zanthoxylum rhoifolium* Lam.	tree	zarh	56	40.3	2176.1	2.19	35	16.4	731.8	1.58	4	3.57	5.6	0.65	5	1.59	0.6	0.15
SALICACEAE	*Banara parviflora* (Gray) Benth.	tree	bpar	4	4.17	29.9	0.15	5	2.35	13.7	0.15	-	-	-	-	-	-	-	-
	Casearia decandra Jacq.	tree	cade	92	54.2	2717.3	3.05	103	48.4	923.7	2.95	4	2.38	14.9	0.65	1	0.4	0.0	0.03
	Casearia sylvestris Sw.	tree	casy	73	55.6	3813.8	3.23	36	16.9	1645.0	2.61	-	-	-	-	-	-	-	-
	Xylosma pseudosalzmannii Sleumer	tree	xyps	6	5.56	11.1	0.19	8	3.76	1.6	0.18	-	-	-	-	-	-	-	-
SAPINDACEAE	*Allophylus edulis* (A.St.Hil.) Radlk.	tree	aled	52	31.9	2197.3	1.96	64	30.1	59.1	1.33	2	2.38	0.7	0.36	4	1.59	0.5	0.14
	Cupania vernalis Cambess	tree	cuve	32	25	234.9	0.97	84	39.4	34.9	1.96	1	1.19	1.8	0.2	2	0.79	1.8	0.1
	Dodonaea viscosa (L.) Jacq.	shrub	dovi	7	4.17	126.3	0.21	3	1.41	58.2	0.14	39	16.7	330.5	7.88	29	5.95	220.3	4.97
	Matayba elaeagnoides Radlk.	tree	mael	27	26.4	1344.9	1.31	57	26.8	14.0	0.93	4	4.76	44.6	1.24	2	0.79	0.0	0.07
SAPOTACEAE	*Chrysophyllum marginatum* (Hook. et Arn.) Radlk.	tree	chma	11	13.9	686.1	0.65	13	6.1	618.7	0.98	-	-	-	-	-	-	-	-
SOLANACEAE	*Cestrum strigillatum* Ruiz et Pav.	shrub	cest	7	5.56	7.9	0.2	7	3.29	5.0	0.19	2	2.38	7.9	0.45	1	0.4	3.3	0.1
	Solanum americanum Mill.	shrub	soam	-	-	-	-	-	-	-	-	-	-	-	-	2	0.4	0.1	0.04
	Solanum pseudoquina St. Hil.	tree	sops	3	2.78	7.9	0.1	-	-	-	-	-	-	-	-	3	0.79	0.2	0.08
	Solanum sanctaecatharinae Dunal	tree	sosa	-	-	-	-	1	0.47	0.4	0.03	-	-	-	-	-	-	-	-
STYRACACEAE	*Styrax leprosum* Hook. et Arn.	tree	styl	21	16.7	632.6	0.8	17	7.98	168.8	0.54	3	3.57	6.6	0.61	2	0.79	0.4	0.07
SYMPLOCACEAE	*Symplocos tetrandra* Mart. ex Miq.	tree	syte	11	12.5	554.0	0.57	12	5.63	281.2	0.62	1	1.19	2.0	0.2	8	0.79	3.6	0.18
	Symplocos uniflora (Pohl) Benth.	tree	syun	6	6.94	448.8	0.36	7	3.29	173.2	0.37	17	8.33	607.9	9.14	12	2.78	123.7	2.73
THYMELAEACEAE	*Daphnopsis racemosa* Griseb.	shrub	dara	5	4.17	7.5	0.15	3	1.41	1.9	0.08	-	-	-	-	-	-	-	-
URTICACEAE	*Cecropia catarinensis* Cuatr.	tree	ceca	1	1.39	1108.0	0.4	-	-	-	-	-	-	-	-	-	-	-	-
	Coussapoa microcarpa (Schott) Rizzini	tree	comi	5	5.56	749.8	0.42	3	1.41	690.6	0.8	-	-	-	-	-	-	-	-
VERBENACEAE	*Lantana camara* L.	shrub	laca	-	-	-	-	-	-	-	-	3	2.38	8.8	0.52	1	0.4	0.2	0.04
42 families	**119 species**	**Number of individuals**:		forest LP= 3191				forest SP= 3769				Campos LP= 589				Campos SP= 5041			

Appendix 2. Values of soil variables, averaged according to the position in relation to the forest edge (**1** is the closest edge plot, being **f** in the forest and **c** in the grassland) and to the main aspect on Santana hill (south, southwest and north).

Plot position	***f6***			***f5***			***f4***			***f3***			***f2***			***f1***		
Exposition	S	SW	N	S	SW	N	S	SW	N	S	SW	N	S	SW	N	S	SW	N
depth (cm)	100.0	100.0	100.0	100.0	100.0	99.4	100.0	100.0	100.0	100.0	100.0	94.0	100.0	100.0	81.8	100.0	100.0	63.0
pH	4.5	4.7	4.5	4.3	4.9	4.9	4.4	4.7	4.7	4.4	4.9	4.9	4.4	5.0	4.8	5.1	5.1	5.0
P	4.4	3.4	3.3	3.4	3.1	2.9	3.9	2.8	2.7	3.7	2.7	3.1	4.0	3.1	3.1	4.8	3.7	4.0
K	157.9	188.8	115.8	121.1	220.1	124.6	168.0	154.6	116.3	152.3	148.8	167.4	221.4	195.1	200.0	292.6	242.9	262.5
O.M.	7.2	5.9	5.0	6.4	6.4	4.8	7.5	5.1	4.5	6.2	5.0	5.6	7.3	5.7	6.0	7.4	7.8	6.2
Al	2.2	1.3	2.6	3.5	1.2	2.2	2.6	1.3	1.8	3.4	0.7	1.7	2.6	0.5	1.6	1.5	0.4	1.2
Ca	4.0	3.7	2.5	2.3	4.2	3.4	4.3	3.2	3.2	2.9	4.4	4.3	3.0	4.8	3.9	6.7	6.0	4.3
Mg	1.5	1.9	1.0	1.2	2.0	1.3	1.7	1.5	1.2	1.6	1.8	1.6	2.0	2.1	1.6	2.6	2.2	2.3
Al+H	9.3	7.7	9.2	11.5	8.2	7.3	11.1	7.1	7.7	11.0	5.9	6.8	10.8	5.7	7.8	8.0	6.2	6.5
CEC	15.3	13.8	13.0	15.3	14.9	12.3	17.5	12.2	12.4	15.8	15.2	13.1	16.3	13.1	13.8	18.0	15.0	13.7
bases saturation	37.2	44.0	32.0	24.8	45.0	45.8	35.5	42.0	42.0	30.3	53.3	51.3	34.0	56.5	42.8	54.8	59.0	53.5
Al saturation	15.1	9.6	18.6	22.7	7.7	14.8	15.0	10.5	12.4	21.3	5.7	11.5	15.8	4.1	8.1	8.5	2.1	8.4
clay	34.0	30.8	22.0	33.8	28.5	21.5	35.8	28.8	23.3	38.0	30.5	26.3	37.0	32.8	29.8	38.3	31.8	30.8
thick sand	30.0	21.5	38.0	27.0	27.5	36.0	22.0	27.0	37.5	23.0	26.5	38.0	26.0	29.5	29.0	20.0	28.0	33.5
fine sand	10.0	10.5	14.5	10.0	10.0	14.5	9.0	10.0	16.0	10.0	11.5	14.5	9.0	11.0	11.5	8.0	11.0	13.0
silt	27.0	37.0	26.0	23.0	31.5	29.5	29.0	33.0	25.0	25.0	31.5	25.0	26.0	28.5	29.5	24.0	26.0	23.0
gravel	30.0	31.0	11.5	39.0	20.5	1.0	24.0	17.5	1.0	27.0	5.0	9.0	9.0	5.5	25.0	28.0	24.0	52.5

continue...

Plot position	***c1***			***c2***			***c3***			***c4***			***c5***			***c6***			***c7***		
Exposition	S	SW	N	S	SW	N	S	SW	N	S	SW	N	S	SW	N	S	SW	N	S	SW	N
Depth (cm)	100.0	100.0	43.3	94.3	100.0	36.3	88.3	99.4	38.3	95.0	90.4	55.1	98.6	86.0	31.6	93.9	69.0	35.0	85.5	67.5	46.1
pH	4.6	4.9	5.0	4.7	4.9	5.1	4.8	5.1	5.3	4.8	5.0	5.2	4.9	4.9	5.2	4.9	4.9	5.2	4.9	4.9	5.2
P	2.4	2.0	2.1	2.1	2.0	2.0	1.8	2.2	2.0	1.5	2.0	2.4	1.8	2.1	1.8	1.8	2.1	1.7	1.6	2.3	1.9
K	143.1	112.1	182.1	132.0	121.5	199.4	126.9	145.9	215.6	128.9	139.0	175.5	175.8	169.3	178.0	152.9	190.8	170.1	154.0	219.9	166.3
O.M.	4.8	4.3	4.8	5.0	4.1	4.8	5.0	4.0	4.7	4.5	4.3	4.7	4.7	4.5	4.4	4.6	4.6	4.4	4.8	5.2	4.7
Al	3.4	2.0	1.8	2.8	1.9	1.2	2.6	1.3	0.7	2.6	1.7	1.3	2.5	1.8	0.9	2.8	2.2	0.7	2.6	2.1	1.0
Ca	1.7	2.7	2.8	2.1	2.4	3.5	1.7	2.3	4.1	1.7	2.4	2.8	2.0	2.2	2.8	1.9	2.2	2.7	2.2	2.7	3.2
Mg	1.0	1.2	1.4	1.1	1.0	1.6	1.1	1.2	1.6	1.0	1.1	1.2	1.0	1.3	1.3	1.2	1.1	1.2	1.3	1.3	1.3
Al+H	10.6	8.5	7.3	10.0	7.8	6.5	9.6	7.0	4.6	9.2	7.5	6.0	8.6	7.6	5.2	9.4	8.4	4.9	9.0	9.1	5.5
CEC	13.7	12.7	12.0	13.3	11.6	12.1	13.0	10.9	10.8	12.3	11.3	10.5	12.2	11.5	9.7	12.9	12.2	9.2	12.9	13.6	10.5
bases saturation	22.3	34.0	41.8	24.5	32.5	47.0	25.5	37.3	58.0	25.0	35.5	44.8	29.0	34.5	46.3	27.0	31.3	47.5	30.0	34.8	47.3
Al saturation	24.3	14.9	12.8	21.1	15.9	9.2	21.2	10.9	6.6	20.1	13.9	10.9	20.3	15.5	8.9	21.8	17.5	6.4	20.5	15.3	9.4
clay	42.0	32.5	32.3	43.8	33.0	30.5	45.0	35.5	28.3	45.8	34.0	29.8	43.3	38.5	26.0	45.8	40.0	27.8	44.0	41.8	30.8
thick sand	33.0	30.0	39.0	29.0	31.5	30.5	28.0	30.5	32.5	25.0	30.0	35.0	28.0	28.5	33.5	26.0	29.0	42.0	27.0	29.5	31.0
fine sand	9.0	11.5	10.0	8.0	11.0	10.5	9.0	11.5	12.0	8.0	11.0	10.5	9.0	9.5	11.0	9.0	9.0	9.5	9.0	7.5	9.0
silt	18.0	23.5	20.0	21.0	25.5	23.5	21.0	24.0	23.5	20.0	24.0	22.0	19.0	20.5	24.5	23.0	19.5	19.0	25.0	19.5	22.0
gravel	36.0	13.5	54.5	45.0	22.5	60.0	58.0	29.5	65.0	65.0	30.0	65.5	55.0	25.0	58.0	31.0	47.5	66.0	20.0	51.0	62.0

SEGUNDO CAPÍTULO

WOODY VEGETATION DYNAMICS IN BURNED SUBTROPICAL GRASSLAND IN A FOREST-GRASSLAND MOSAIC[2]

Trabalho realizado em conjunto com:

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[2] O trabalho será submetido à revista JOURNAL OF VEGETATION SCIENCE. A formatação está conforme as orientações da revista, exceto pelo espaçamento entre linhas e o alinhamento do texto.

Abstract

Question: How woody species react to fire in frequently burned grassland in grassland-forest ecotones?

Location: A natural mosaic of grassland and forest in South Brazil (30°03’ S, 51°07’ W, 311m a.s.l.).

Methods: Woody plants (minimum 10 cm height) were sampled in two consecutive years in plots on 12 grassland transects subject to frequent fire, located at forest borders. Species composition, diversity and category (resprouter, non-sprouter) were analyzed according to time elapsed since last fire. Life-history features of some species were examined.

Results: A total of 76 species (31 grassland shrubs; 45 forest species) were sampled; 65.8% were resprouters. Species composition differed with elapsed time since fire. Density, richness and diversity were lower in recently burned plots, especially on south exposed sites. For grassland shrubs, species richness and density was higher in plots unburned for one and two years than in unburned for three years. Resprouter shrubs were always denser than non-sprouter. Resprouter trees predominated in north exposed sites, having similar density with elapsed time since fire, but non-sprouters were denser in longer unburned plots. Differences in recruitment dynamics of single- and multi-stemmed shrubs or trees were also detected.

Conclusions: The high proportion of resprouter species in burned grassland and the recruitment rate of seeders characterize communities under frequent disturbance with well-adapted species. Fire intervals of two to three years cannot avoid shrub encroachment but retard the advance of forest species over grassland, except on sites very close to the forest border or on island patches protected from intense fire.

Keywords: shrub encroachment, fire, disturbance, resprouting ability, forest expansion, South Brazil

Nomenclature: Family identities follow APG II (2003) and species names IPNI electronic data base.

Introduction

Savanna and grassland ecosystems cover about 20% of the land surface of the Earth, occupying extensive areas of tropical and subtropical regions in Africa, Asia and South America (Bond & Midgley 2000). In such ecosystems, disturbance plays an important role in community dynamics. Periodic fire, for instance, is essential for the maintenance of open vegetation types and their diversity, as a consequence of burning that promote spatio-temporal mosaics of areas in varying stages of recovery from disturbance (Pickett & White 1985, Bond & van Wilgen 1996, Braithwaite 1996). Approaches for ecological generality about grassland and savanna dynamics consider the role of fire, grazing, nutrient and moisture availability, and principally concerns communities responses to those factors (‘disturbances’), often focusing on relative dominance or biomass productivity of grasses (mostly C_4 species), forbs and woody plants (mostly C_3 species) (Knapp et al. 2004, Bond et al. 2003, Langevelde et al. 2003). Similarities in community structure responses, related to the influence of fire and grazing on the balance of C_4/C_3 plants (grasses/forbs), have been found between North American grasslands and South African savannas (Knapp et al. 2004), but there are no comparable long term ecological studies in South America grasslands to attest the applicability of such a general ecological rule.

Scholes & Archer (1997) stressed out that the balance of woody and grass growth forms in all savannas and related grassland ecosystems is determined by a number of interacting factors. Nevertheless, fire disturbance has been hypothesized as the maintenance factor of savannas where climatic conditions are favourable for the development of forest (Bond et al. 2003). Fire directly affects plant growth, survival and reproduction, whereas it can indirectly improve conditions for seed germination and/or seedling establishment, removing inhibitory effects, such as accumulated litter or shading by a closed canopy, thus lowering competition or increasing resource availability (Bond & van Wilgen 1996). In the Brazilian Cerrado (neotropical savanna), however, higher temperature and solar insulation in recently burned areas may lead to desiccation and thus impede seedling survival (Hoffmann 1996, 1998). In such situations, facilitation by cover of higher individuals seems to improve seedling establishment by diminishing local water deficits (Hoffmann 1996, Li & Wilson 1998, Holl 2002). In ecosystems submitted to frequent burning, species depending of sexual reproduction must reproduce, disperse seeds, establish seedlings, and achieve a fire-tolerant size despite the burns or within the period between burns. An alternative strategy for these species is to establish on “safe sites”, i.e. sites protected from fire, at least from high intensity fires. Termite mounds (Furley 1999, Guillet et al. 2001), thickets or adult trees (Hochberg et al. 1994), and rock outcrops (Clarke 2002a, b, Müller & Forneck 2004) have been cited as safe sites for woody plants in a matrix of frequently burned vegetation, since they locally allow for depression of growth of grasses and hence reduce flammability.

Other successful plant strategies to survive fire are vegetative reproduction by root suckerings or rhizomes and the capacity to resprout from the old stem base or the root crown, following above-ground biomass removal by fire (Bond & van Wilgen 1996, Hoffmann 1998, Bellingham & Sparrow 2000, Drewa et al. 2002). Fire resistance at the individual level depends on a combination of traits, as height of the plant, its bark and stem characteristic, and fire intensity, and, consequently, response at the population level differs between fire events (Bond & Midgley 2000). Most shrubs and trees of savannas, chaparral and fire-prone Mediterranean vegetation are able to resprout and a continuum of responses following less intense disturbance can be observed across broad species sets and vegetation types (Lloret et al. 1999, Guo 2001, Vesk & Westoby 2004).

Considering the variability of plant strategies and adaptations to resist or tolerate fire, many savanna landscapes and their species diversity appear to be maintained by fire regime (Braithwaite 1996, Furley 1999, Sternberg 2001, Bond et al. 2003). In climate suitable for forest development, grassland areas protected from fire show a steady increase in forest species, but the rate of increase also depends on site conditions, like soil and water regime. In southern Brazil, both soil and water regime do not seem to impede establishment of woody plants on grassland vegetation, as evidences (Behling 1998, 2001, Behling et al. 2004, Oliveira & Pillar 2004, Müller et al. Chapter 1) had confirmed conjectures (Lindman 1906, Rambo 1956, Klein 1975, Pillar & Quadros 1997) that forest expansion occur in absence of disturbance by fire and grazing. Nonetheless site variation, like soil patchiness, relief declivity and exposure, bracket together with unpredictable seasonal drought, can promote spatial or temporal stress to the establishment and recruitment of new individuals, especially for rain forest species (Knoop & Walker 1985, Kauffman et al. 1994). Such situations can be responsible for more or less fluxes of forest species colonization in adjacent grassland areas in a temporal scale.

In South Brazilian grassland, absence of fire over three to five years lead to a reduction in diversity of grasses and herbs, mainly as a consequence of tussock grasses dominance on decreasing herb species, but no group of fire-following species has been observed, indicating a community adapted to the current fire regime (Overbeck & Pillar 2004, Overbeck et al. in press). No studies have focused on woody species dynamics in burned grassland vegetation under short fire intervals. Are woody species killed by fire or is recruitment facilitated or stimulated by fire? How high and how common is the capacity to resprout in woody species present in these grasslands? To assess these questions, the present study describes short-term dynamics of woody plants in frequent burned grassland in ecotone with rainforest areas. Specific objectives were to analyse (1) changes of woody species composition over two consecutive years in areas with different time elapsed since fire and (2) dynamics of diversity and richness along a spatial gradient from the forest border into burned and unburned grassland areas, related to (3) tree or shrub species recruitment and/or (4) recover capacity of shrubs and trees by resprouting after fire events.

Methods

Study site

The study was carried out on Morro Santana (30°03’ S, 51°07’ W, 311m a.s.l.), Porto Alegre, Rio Grande do Sul (RS), Brazil. Vegetation cover in the area is a mosaic of grassland and forests, with almost 70% being covered by forest and grassland found especially on the top and on northern slopes of the hill (Aguiar et al. 1986, Porto et al. 1998). Situated at the 30° S parallel, a distribution limit of most tropical elements, forest formations of Morro Santana are a mix of elements of Atlantic rain forest, from the northeast, and of Deciduous Forest, from the northwest (Rambo 1961, Teixeira et al. 1986). The grasslands are very species rich, with a total of 430 species cited for an area of approx. 220 ha and characterized by a matrix of caespitose grasses with a large number of sparsely distributed herbs and grassland shrubs. Without frequent fire disturbances, an expansion process of forest species and a shrub encroachment on grassland areas has been observed in the study area, similarly to other regions in south Brazil (Oliveira & Pillar 2004).

Climate in the study region is subtropical humid without dry season (Köppen’s Cfa). Maximal and minimal annual mean temperature are, respectively, 24.8 and 15.6°C and annual average rainfall ranges from 1300 to 1500 mm (Nimer 1990). The predominant soil types are Acrisols and Umbrisols (FAO classification; Garcia Martinez (2005)), with good drainage conditions, developed from a granite matrix. Rounded rock outcrops are abundant, especially on the northern side of the hill.

Field survey

Woody species individuals were sampled in two consecutive years in grassland areas adjacent to the forest border (first survey in January/February 2003, second survey in November/December 2003). Sampling was conducted in six pairs of transects perpendicular to the grassland-forest limits, from the border to the grassland interior. Each transect consisted of seven consecutive plots of 4.5 by 4.5 m (large plots, LPs), where species identity, height, basal stem diameter, and two diameters of crown size were recorded for all woody plants with or higher than 80 cm. Within each LP, three consecutive small plots (SPs= 1.5 by 1.5 m) were set, i.e. forming a 21-plot transect, in order to measure all woody plants with a minimal height of 10 cm. The same parameters (except crown size) were recorded, with cover of each species in the plot estimated by a decimal cover scale (Londo 1976). Additionally, cover data of structural variables of the lower strata (herbs, graminoid component, and lianas) and of cover by litter, rocks or open soil were recorded one month before both field surveys.

In October 2002 a controlled burn was carried out in one transect each in four transect pairs, unburned for three years or more. The other two transect pairs had burned earlier in January 2002, and thus the transects designated for a burn did not have sufficient biomass to support spreading of a fire. Thus, four transects each comprised a group of plots with different elapsed time since the last fire (GROUP 1: three months, GROUP 2: one year, GROUP 3: at least three years; considering time interval after the controlled burn in October 2002). The same three groups were considered for the second survey, but with additional ten months of time elapsed since fire. For analysis that considered both surveys together, the groups correspond to a range of time interval between the first and the second survey (i.e. GROUP 1: 3mo-1y, GROUP 2: 1y-2y, GROUP 3: at least 3y-4y). GROUPS 1 and 3 had transects at (top-)southern and northern aspect (landscape position) and GROUP 2 only at (top-)south-western aspect. Four LPs (12 SPs) of one protected transect at southern aspect, i.e. from GROUP 3, suffered an accidental anthropogenic burn right after we had conducted our first survey. Thus, GROUP 3 had less plots for data analysis in the second survey, with plots having passed to GROUP 1.

Data analysis

General approach – Each plot was described by species richness, Shannon's diversity (based on the natural logarithm), density (number of woody plants per plot) and total basal stem cover. Values were compared between the two surveys, between plots with different exposition/aspect, and between plots with different elapsed time since fire, each factor being analysed independently. Then, species composition in plots was compared between groups of elapsed time since fire and the two field surveys by randomization testing with 1000 iterations (Pillar 1996), based on relative Euclidian distances between sampling units (Podani 2000). For data from the second survey, we pooled the three SPs situated in one LP (1.5 by 4.5 m, denominated MPs) for ordination analysis, using principal coordinates analysis, and testing stability of the axes by bootstrap resampling (Pillar, 1999). In addition to species data, the variables of lower strata and soil surface cover were used to generate a general pattern of community structure in a second ordination analysis, differentiating plots according to elapsed time since fire. All analyses of randomization testing and ordination were carried out using the application program *MULTIV* (Pillar 2004), with a = 0.05 used in randomization testing, unless otherwise specified.

Species category groups – Species were grouped into resprouters and non-sprouters. For this study, only species that are able to resprout stems from the base of the old individual were considered resprouter species. Further, within these two strategies of post-fire recovery, species were grouped according to their main habitat, considering them as grassland, border or forest species. Grassland species are those shrubs that normally grow in grassland vegetation but not in forest, characterizing grassland communities with a higher stratum dominated by shrubs like *Baccharis* spp., *Vernonia nudiflora*, and *Eupatorium* spp. Border species are trees and/or shrubs uncommon either in grassland or in forest vegetation, e.g. *Dodonaea viscosa*, *Agarista eucalyptoides*, *Symplocos uniflora*. Forest species are all trees and/or shrubs common to surrounding forest vegetation, e.g. *Myrciaria cuspidata*, *Myrsine* spp., *Myrcia palustris*, *Lithrea brasiliensis*, *Maytenus cassineformis*, *Matayba elaeagnoides*, *Psychotria* spp.

Groups of elapsed time since fire were tested by randomization analysis according to the dynamic of each species category. LPs directly at the forest-border, which did not burn completely in any group, were separated from grassland plots, named as border plots, and compared with the three groups of grassland plots. For characterization of density changes per square meter of plants sampled only in LPs (i.e. = 80 cm high) we considered border and forest species together, because of the low number of border species. Further, to verify the recruitment dynamics between the two surveys, only tree or shrub species below 30 cm were taken, comparing differences between border and the three groups of grassland plots, considering single-stemmed and multi-stemmed plants. This information was taken during the field data collection in both surveys.

Life-history features – Six species were chosen for a closer analysis of life history features of the main strategy groups (resprouter grassland shrubs: *Baccharis cognata*, *Eupatorium ligulaefolium*; non-sprouter grassland shrubs: *Baccharis dracunculifolia*, *Heterothalamus psiadioides*; resprouter forest tree: *Myrciaria cuspidata* and non-sprouter forest tree: *Myrsine umbellata*). Since we had many multi-stemmed plants, a plant was considered to be an individual when no visible connection at the soil surface (aboveground) among neighbour plants of the same species was observed. Density per square meter in height classes were compared between the groups of grassland plots in both years of field surveys. The classes of height comprised individuals below 30 cm (class 1), 30 to 79 cm (class 2), 80 to 119 cm (class 3) and = 120 cm (class 4). For the forest tree species, additional information from plots inside the forest was taken to compare distribution patterns in the grassland and at the border with patterns in the forest. For this, border plots were again separated from the grassland plots. The information on forest plots came from the data of Müller et al. (Chapter 1) and these plots consisted of a continuation of the present grassland transects into the adjacent forest areas, with six LPs (18 SPs) in each transect.

Results

Species composition dynamic

A total of 76 species (53 genera, 30 families) was sampled considering both years of survey[3]; 31 species were grassland shrubs, 36 forest species and 9 border species; 65.8% were resprouter species. Considering number of individuals, grassland species were the most important of the woody community composition, achieving more than 90% of all individuals. 3,295 individuals were sampled in the first survey, and species number rose markedly in the second survey. Considering number of individuals, grassland species

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[3] The complete list of families and species is accessible on Anexo 4

increased by 66%, forest species by 47% and border species by 28%. Woody density per hectare was 370 for forest/border species and 2,620 for all sampled woody individuals with at least 80 cm height in grassland LPs. This estimation did not include border plots, where density of forest species was higher.

Species composition in grassland plots differed between south/south-western and northern aspect (see below). Nonetheless, border plots were similar in composition and Shannon diversity, but their species richness and density also differed between north and south (Table 1). All measured parameters tended to increase after one year at border plots (only species richness significantly), even though only woody plants higher than 80 cm (LPs criterion) were considered. Considering transects of southern and northern aspect (GROUP 1, burned and 3, unburned), a clear difference ($p \leq 0.001$) among species richness (mean value in burned and unburned plots, 0.81 and 3.68) and density (1.5 and 9.5, respectively) within large plots was observed. Northern sites had higher densities and species richness, but the pattern of fire disturbance influence was the same for both aspects.

Table 1. Diversity (H'), richness, density and total basal stem cover of large border plots (LPs), comparing two consecutive years of field survey (n= 12) and the main aspect of transects (n = 8, both surveys together). ns= non-significant, * $p \leq 0.05$, *** $p \leq 0.001$.

Border plots	Jan/Feb 2003	end of 2003		south	north	southwest	
H'	1.07	1.31	ns	1.71	1.89	1.66	ns
Richness	6.50	8.41	*	6.25^{a}	9.25^{b}	6.87^{ab}	*
Density	13.17	17.41	ns	9.75^{a}	23.50^{b}	12.62^{a}	***
Stem cover (cm^2)	101.03	109.11	ns	107.86	121.73	86.00	ns

No differences existed in the species composition of all sampled grassland plots comparing the two consecutive years of survey. But, species composition differed significantly according to elapsed time since fire ($p \leq 0.01$), for both surveys, even considering differences among main aspect. The second survey is represented in Figure 1A. The first axis of the ordination still separated southern from northern plots (southern plots are principally at the left and northern plots at the right of the diagram A). Nonetheless the main direction from unburned to burned plots was similar in both aspects. Sampling units of GROUP 2 (i.e. two years since the last fire; at south-western aspect) tended to keep on within both extreme groups, having non-significant differences. With structural variables of the lower strata and features of soil surface cover, difference between treatment groups of elapsed time since fire were stronger, especially in respect to open soil and graminoid cover (grasses) (Fig. 1B). Increased presence of rock outcrops characterized northern site sampling units. Resprouter species, e.g. *Baccharis cognata*, *Vernonia nudiflora* and *Eupatorium ligulaefolium* predominated in recently burned plots and non-sprouter species, e. g. *Heterothalamus psiadioides* and *Dodonaea viscosa* in unburned plots, although sprouting species occurred as well (*Mimosa parvipinna, Baccharis patens and B. leucopappa*), here often with one stem only. Species richness in grassland plots rose in all groups from the first to the second survey, but differences between treatment groups were not significant (mean of 1.35 ± 0.47 species more per plot). Considering the second survey, all treatments differed from each other also for species richness ($p \leq 0.001$); GROUP 1 (1y burned) had a mean of 4.14 species per plot, GROUP 2 (2y burned) had 6.04 and at unburned plots (GROUP 3) the mean richness was 5.20.

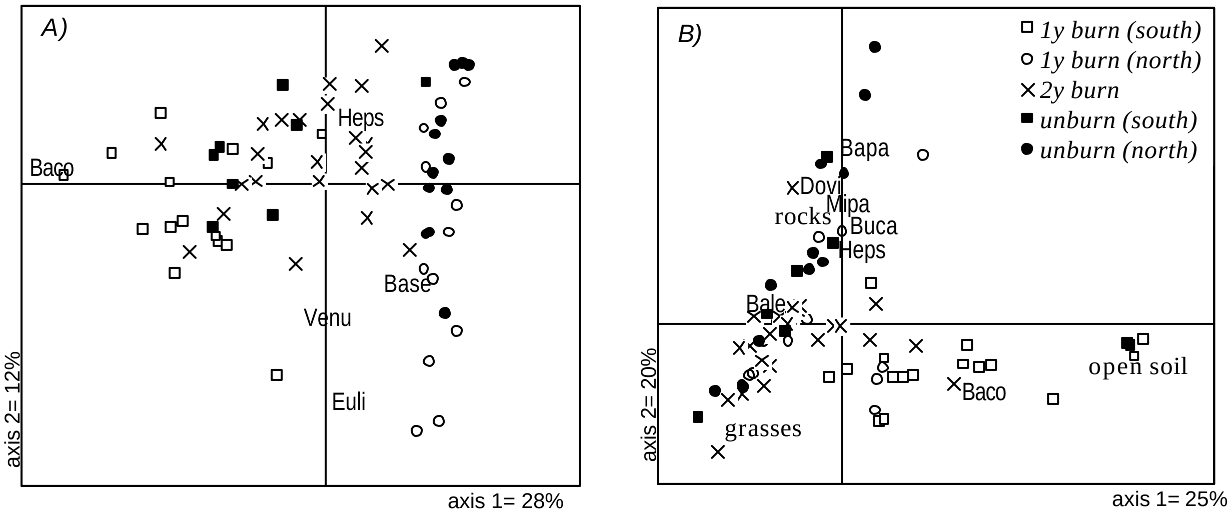

Figure 1. Ordination diagram of grassland plots (*MPs*; 1.5 by 4.5 m) based on (A) species cover and (B) species and structural variables cover in the second year of field survey. The method was principal coordination analysis with relative Euclidian distance between sampling units. Both diagrams were considered stable by bootstrap testing. Species or structural variables that correlated more than 0.5 with ordination axis were Baco= *Baccharis cognata*, Base= *B. sessilifolia*, Bale= *B. leucopappa*, Bapa= *B. patens*, Euli= *Eupatorium ligulaefolium*, Venu= *Vernonia nudiflora*, Heps= *Heterothalamus psiadioides*, Dovi= *Dodonaea viscosa*, Mipa= *Mimosa parvipinna*, Buca= *Butia capitata*.

Species category - resprouters versus non-sprouters

The next step in this study was to identify patterns with the categories of all sampled species. Based on the complete community data of individuals =10 cm high (84 MPs of 6.75 m^2 in each survey) of all species groups, only density of grassland shrubs changed significantly between the two surveys, both for resprouter (1º survey= 25.7; 2º survey= 36.5) and non-sprouter species (1º survey= 8.0; 2º survey= 20.7). Mean density of forest and border species was very low (1.4 and 0.6 in the 1º survey, respectively) and did not change much after one year. Considering border plots (12 MPs) separately from grassland plots (72 MPs), and those in each group of elapsed time since fire, we analysed the differences between all groups and the dynamic changing in one year after the first field observation (Table 2).

Table 2. Mean density of species groups in different groups of elapsed time since fire (following the 1º survey: GROUP 1= 3 months; GROUP 2 = 1 year; GROUP 3= at least 3 years) and relating border plots to grassland plots. All individuals larger than or with 10cm were considered. One MP (n) = $6.75m^2$; different letters show significant differences between groups of elapsed time since fire or between border and grassland plots (capital letters $p \leq 0.001$; lower cases $p \leq 0.05$).

First survey (Jan/Feb 2003)	GROUP **1** (n=24)	GROUP **2** (n=24)	GROUP **3** (n=24)	Border (n=12)	Grassland (n=72)
border resprouter spp.	0.29	0	0.21	0.83^{a}	0.17^{b}
border non-sprouter spp.	0.08	0	0.42	1.08^{a}	0.17^{b}
grassland resprouter spp.	28.25^{A}	36.96^{B}	19.58^{C}	10.33^{A}	28.26^{B}
grassland non-sprouter spp.	3.71^{a}	14.42^{b}	6.29^{a}	7.17	8.14
forest resprouter spp.	0.50	0.13	0.96	3.42^{A}	0.53^{B}
forest non-sprouter spp.	0	0.08	0.04	3.33^{A}	0.04^{B}
Second survey (end of 2003)					
border resprouter spp.	0.32	0	0.35	1.25^{a}	0.22^{b}
border non-sprouter spp.	0.11^{ab}	0^{b}	0.55^{a}	1.33^{a}	0.19^{b}
grassland resprouter spp.	38.75^{a}	53.75^{C}	26.15^{b}	13.83^{A}	40.25^{B}
grassland non-sprouter spp.	11.36^{A}	51.13^{B}	5.45^{A}	7.25	22.97
forest resprouter spp.	0.54	0.17	0.65	4.75^{A}	0.44^{B}
forest non-sprouter spp.	0.00^{a}	0.13^{ba}	0.6^{b}	5.92^{A}	0.21^{B}

Density of grassland shrubs was higher in plots burned one and two years ago, being more pronounced in the GROUP 2. At the one hand, resprouter shrubs were dominant in all groups of grassland plots, including recently burned plots (1º survey, GROUP 1), comparing to density of non-sprouter shrubs. On the other hand, non-sprouter shrubs became denser on the second year in both burned groups (GROUP 1 and 2), while a small decrease in the unburned group was observed. This category of plants did not differ between border and grassland plots. In border plots, only forest species - clearly more abundant here than in grassland plots - changed from the first to the second year. Considering forest resprouter species, no differences were observed between the groups. Non-sprouter forest species increased in density in unburned plots between the two survey periods, differently to plots from GROUP 1. In the same way, density of forest non-sprouter species tended to increase in border plots after one year.

Species from forest or border habitats (forest resprouter and non-sprouter) above 80 cm were clearly more frequent at border plots when compared to grassland plots even those left unburned (Fig. 2). Practically only individuals of forest species with capacity to resprout after fire occurred on grassland plots, non-sprouter species were restricted to unburned areas. Unburned grassland also presented more grassland shrubs in comparison to the other groups. Considering the second year of the survey, non-sprouter species tended to decrease in unburned plots (GROUP 3), while resprouting shrubs became denser especially in the plots burned 2 years before, since they now entered into the height limit of 80 cm.

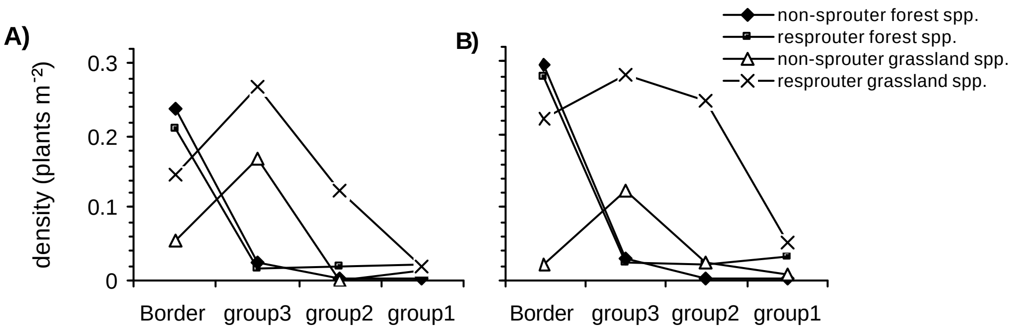

Figure 2. Density per square meter (only plants = 80cm high) of species categories at border plots and grassland plots (GROUP 1= burned in Oct/02, GROUP 2= burned in Jan/02, GROUP 3= unburned) in the two consecutive surveys (A – Jan/Feb 2002; B – end of 2003).

Recruitment dynamics, considering only plants lower than 30cm, showed differences between groups of elapsed time since fire both in grassland and border plots (Table 3). Single-stemmed shrubs increased in density in all groups of grassland plots, but remained stable at the border. Multi-stemmed shrubs only increased in unburned grassland plots (GROUP 3) and single-stemmed trees only in border plots, while multi-stemmed trees did not change at all. Considering both field surveys together, all categories of plants responded differently according to the treatment of plots. Single-stemmed shrubs were more abundant at GROUP 2 and then GROUP 1, whereas multi-stemmed shrubs were denser in GROUP 1. Density of single-stemmed trees was higher at border and then at unburned plots (GROUP 3), while the multi-stemmed trees were more abundant in GROUP 1 and then at the border.

Table 3. Density of single- and multi-stemmed shrubs and trees, lower than 30cm, sampled in both field surveys, separated for border plots and the 3 groups of grassland plots. The first part of the table shows differences between both surveys, and the second part between the treatments of plots according to range of elapsed time since fire. *ns*= non-significant, * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

first survey: Jan/Feb 2003 *second survey: end of 2003*	n	single-stemmed shrubs	multi-stemmed shrubs	single-stemmed trees	multi-stemmed trees
GROUP 1 - *first survey*	24	6.21**	18.79 ^{ns}	0.08 ^{ns}	0.46 ^{ns}
second survey	28	16.18	16.86	0.07	0.32
GROUP 2 - *first survey*	24	14.42***	12.79 ^{ns}	0	0
second survey	24	49.92	11.71	0	0
GROUP 3 - *first survey*	24	4.96*	1.46***	0.42 ^{ns}	0 ^{ns}
second survey	20	8.30	6.05	0.65	0.1
border plots - *first survey*	12	6.83 ^{ns}	0.83 ^{ns}	1.67*	0.33 ^{ns}
second survey	12	5.08	1.67	4.42	0.08
both surveys together		*	*	*	*
GROUP 1	52	11.58 ^{a}	17.75 ^{a}	0.08 ^{a}	0.38 ^{a}
GROUP 2	48	32.17 ^{b}	12.25 ^{b}	0.00 ^{a}	0.00 ^{b}
GROUP 3	44	6.48 ^{c}	3.55 ^{c}	0.52 ^{b}	0.05 ^{ab}
border plots	24	5.96 ^{dc}	1.25 ^{d}	3.04 ^{c}	0.21 ^{a}

Life-history features - approach of some species

B. cognata and *E. ligulaefolium* produce a large number of seeds dispersed by wind, but they are able to resprout basal stems after fire events very quickly (about 2 to 3 weeks) and vigorously. In the first survey, 81% of sampled individuals of *B. cognata* had multiple stems at the base, and only 8% could be considered young plants (single-stemmed individuals less than 30 cm). For the second survey, the number of young plants diminished (3%) and the multi-stemmed plants summed 91%. The percentage of young plants for *E. ligulaefolium* was much higher in the second (37%) than in the first survey (9%) and, additionally, the total contribution of multi-stemmed plants was lower than for *B. cognata* (55% in the first and 35% in the second year). Considering all plants (single- or multi-stemmed), both species had a similar pattern of frequency in the study area according to time since fire. They changed in relative frequency in plots of GROUP 1 and 2 from about 30% in the first year to almost 50% at the end of 2003, while they decreased slightly in unburned plots (from ≅ 25 to 18%). The density per square meter (Fig. 3) reveals that *B. cognata* was very abundant especially in the recent burned areas, and most individuals were of small size (less than 80 cm), but multi-stemmed (see above). For *E. ligulaefolium* it was notable that, despite its ability to resprout, there was recruitment (class 1 became more abundant/frequent in the second survey at GROUP 1 and 2) and some individuals were higher than 120 cm, mostly single-stemmed at the base. Furthermore, a common pattern for both species was the proportionally smaller density in unburned plots (GROUP 3), when compared to the two other groups.

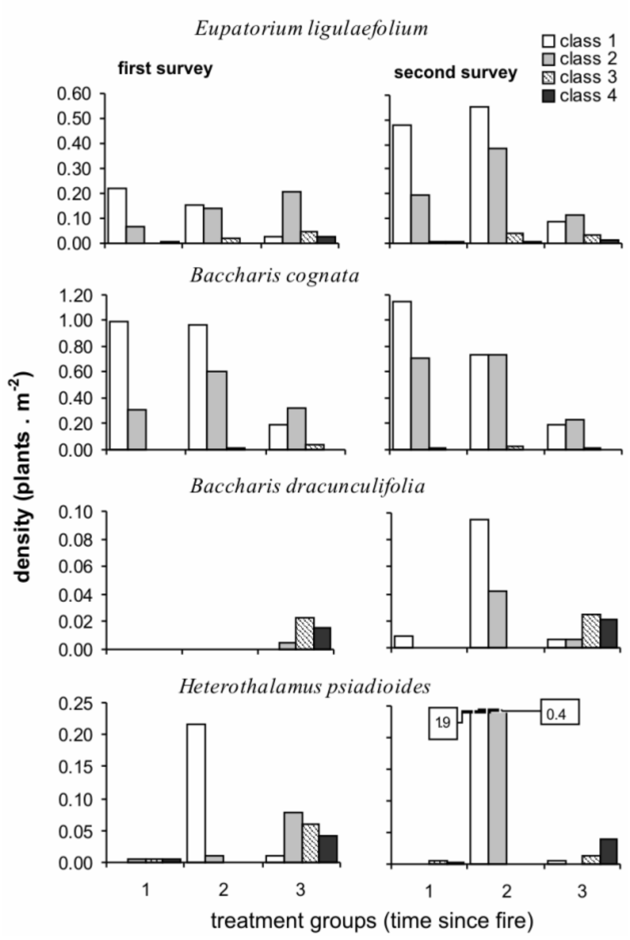

Figure 3. Plant density per square meter of resprouter shrubs (*E. ligulaefolium*, *B. cognata*) and non-sprouter shrubs (*B. dracunculifolia*, *H. psiadioides*) divided in size classes of height (1= 10-29cm, 2= 30-79cm, 3= 80-119cm, 4= =120 cm) according to time since fire (GROUPS 1 to 3) in two surveys.

H. psiadioides and *B. dracunculifolia* are anemochoric grassland shrubs with no ability to resprout. Frequency and density changes between the two surveys varied for the two species. *H. psiadioides* decreased from 14 to 6% of frequency in unburned areas and increased from 7 to 26% in areas of GROUP 2. On recently burned areas (GROUP 1) it stayed stable with less than 2%. A great change in number of young individuals (class 1) occurred among the two years of observation, from 42 (50%) to 668 (80%) plants, most of them in plots of GROUP 2 (Fig. 3). On the other hand, there was a clear mortality of older plants in unburned plots, without new recruitments. In the first survey, *B. dracunculifolia* was present only in unburned plots and just with individuals higher than 120 cm (class 4). In the second year, density of classes 3 and 4 stayed practically stable, while young plants started to colonize both burned areas. The number of young plants accounted for 51% of all sampled individuals.

M. cuspidata and *M. umbellata* are examples of forest species that can be found in grassland areas. In general, this group of species was less represented in the study area. *M. cuspidata* was one of the most frequent species occurring in grassland areas, with a frequency of about 6% in unburned plots and 3% in plots of GROUP 1 e 2. Data of plots inside the adjacent forest were used to compare densities of height classes with the border plots and the grassland according the three groups of elapsed time since fire (Fig. 4).

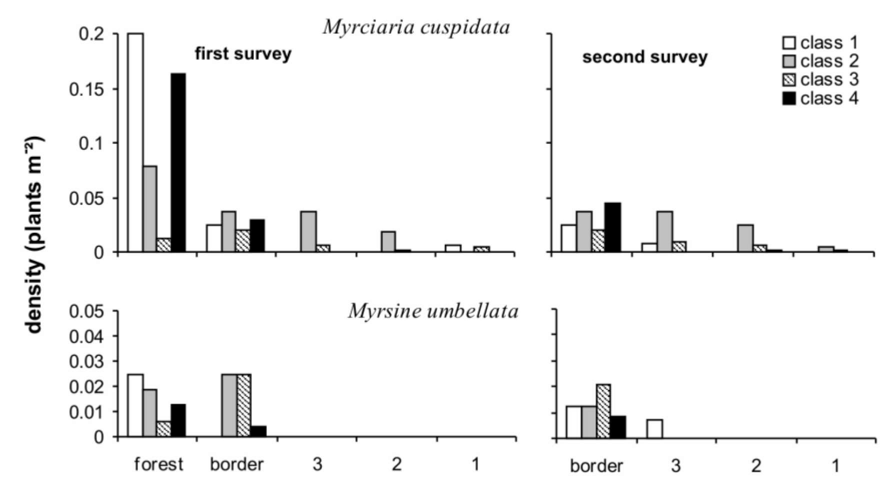

Figure 4. Plant density per square meters of forest tree species (*M. cuspidata* – resprouter and *M. umbellata* - non-sprouter) divided in size classes of height (1= 10-29cm, 2= 30-79cm, 3= 80-119cm, 4= =120 cm) comparing forest plots with border and grassland plots (GROUPS 1 to 3) in two surveys.

M. cuspidata is a common low Myrtaceae tree in the forest area, presenting plants in all classes, especially of class 1. In border plots the density was lower and almost constant concerning both survey data, and in grassland plots only some individuals were found, mainly in GROUP 3 and 2. A great difference existed among plants of *M. cuspidata* considering plant architecture in forest and grassland areas. In the forest, practically all individuals were single-stemmed (92%), while in grassland areas most were multi-stemmed (76%), indicating resprouting after fire events. *M. umbellata*, like the majority of forest tree species (Appendix 1), presented a very low density even in border plots. *M. umbellata* is a mid-size to high tree in the forest area, presenting few individuals per square meter in general. No individuals were sampled in grassland areas in the first survey (although some were observed in surrounded areas) and, in the second, a few (class 1) colonized sites at the border and plots of GROUP 3, i.e. in unburned areas. Both species are dispersed by birds.

Discussion

The lack of importance of the family Leguminosae in the present study constitutes a notable difference from the savanna regions of South Africa (Bond et al. 2003) and Brazilian Cerrado (Furley 1999). Puyravaud et al. (2003) in a site with rain forest expansion over savanna/grassland areas in south-western India noticed a large pool of families of evergreen species forming clumps of thicket in the grassland matrix beyond the limit of rain forest. Similarly, the study site presents many species common in local forests playing the role of pioneer woody trees, expanding forest vegetation over the grassland matrix under appropriate conditions (absence of fire or safe sites).

The predominant vegetation type seems to be a shrubby grassland (*Campo sujo*), a two layer vegetation where shrub species, mostly from the Asteraceae family, are forming a more or less open canopy over the ground layer of grasses, mainly tussocks, and herbs. The Brazilian Cerrado vegetation composes a gradient from open grassland (*Campo limpo*) to savanna woodland (*Cerradão*) along a continuum of decreasing incidence of fire and some coincidence with increasing soil fertility (Coutinho 1990, Furley 1999, Moreira 2000). South Brazilian grasslands have been described according to physiognomic aspects (presence or absence of shrubs; dominance of tussocks or reptant species) and dominant species (Boldrini 1997) and similarly as in the Cerrado vegetation, when fire or grazers are excluded or the pressure is diminished, the woody plant component becomes more dominant (Boldrini & Eggers 1996, Boldrini & Eggers 1997). Afterwards, there is a tendency of adjacent forest to expand over the grassland, since climate and most of soil types are not a drawback for forest formation (Rambo 1956, Pillar & Quadros 1997, Müller et al. Chapter 1). In the present study the estimated density of woody plants per hectare in the grassland (2,620 for plants above 0.8 m), even considering the three different elapsed times since fire together, is close to the density in the *Campo cerrado* vegetation (open woody savanna, Furley 1999), but the mean height and the species category group are completely different. While in the woody savanna of Cerrado the general height is between 3-7 m and most of species are trees, in the present study site the great majority are grassland shrubs with a general height between 0.8-2 m, being rare trees higher than 3 m and still frequent shrubs below 0.8 m.

Influences of the elapsed time since fire could be observed for species composition and richness, considering the main differences between recently burned (until 1y) and protected (3-5y) grassland areas. Bond and van Wilgen (1996) considered fire as "a large herbivore", since aerial biomass is removed and, considering that frequently patches in the vegetation cover remain untouched, the responses of individual species or of total community may be similar to different levels of real cattle grazing. The present study demonstrates lower density, richness and diversity of woody species in recently burned plots, especially where burning was more homogeneous (at south sites), which can be comparable with the effect of a high grazing pressure on composition and density of tree species (McIntyre et al. 2003). At border areas protected from fire, species richness and density of non-sprouter trees increased in a one-year period (establishment of single-stemmed young plants in the second survey). For grassland shrubs density changes were at their maximum two years after the burns, both for resprouters and obligate seeders, with both groups tending to decrease in density in longer unburned areas. As a consequence of this density changes, the mean species richness was higher for GROUP 2 than at unburned grassland plots. With longer fire-free periods, establishment of non-sprouter trees would continue, as was observed in the second survey on unburned plots and on border plots.

The architecture of woody plants and resprouting ability can be viewed as a response to disturbance in a hierarchical framework along a continuum of disturbance severity or site productivity (e.g. moisture and/or fertility) (Bellingham & Sparrow 2000). This is especially true for species that are growing as a monopodial tree on moister/fertile habitat which under adverse site conditions or frequent disturbance events produce a multi-stemmed resprouting architecture, as for instance in the present study the species *Myrciaria cuspidata*, *Eugenia* spp., *Matayba elaeagnoides*, *Lithrea brasiliensis* and *Myrcia palustris*. Species or single plants perceive and respond to disturbance severity differently, according to its disturbance resistance adaptations or yet to its age, and thus a variety of types of resprouting may occur in a site (Bellingham & Sparrow 2000). While resprouter species at the present study were considered only those that had showed a basal multi-stemmed architecture, adult individuals of, for instance, *M. umbellata* had induced aerial resprouting related to its stem damage gravity, which correspond to another level of resprouting.

For successful establishment of forest species, plants must achieve a fire-tolerant size during the disturbance interval, growing higher than the grass layer, where injury of fire temperature is higher, unless on safe sites protected from fire. Clarke (2002a, b) showed that rock outcrops can act as safe sites for species that would be killed by fire in sclerophyll forest that are prone to fires. Likewise, our results indicate that forest tree species, which are more susceptive to fire than most grassland shrubs, show higher densities at the northern sites, where soils are shallower and presence of rounded granite rock outcrops is higher. Places near rock outcrops have longer fire-free intervals or at least less intense fire regime, since grasses (the main fuel) produce less biomass on shallower soils. Furley (1999) showed that grassland vegetation in Brazilian Cerrado (*Campo limpo*) predominates over down-slopes, where the increasing water accumulation can lead to seasonally wet conditions at the surface, favouring grasses, while woody patches are found on well drained sites, such as outcrops or mounds formed from termite activity. In such local mosaics of vegetation structure, ground layer vegetation receives less homogeneous treatment by fire, increasing patchiness, which is consistent with the intermediate disturbance hypothesis promoting species diversity (Pickett & White 1985, Braithwaite 1996, McIntyre et al. 2003). This point is corroborated by our results of higher diversity and species richness on northern sites in both senses, by the opportunity of safe sites and the most frequent patchiness of the ground layer.

As the disturbance frequency increases, the proportion of resprouting species in the community is expected to increase too, and the few seeders must have higher relative growth rates and set seeds earlier than the resprouters (Bellingham & Sparrow 2000). At neotropical savannas, species that reproduce vegetatively had been 15 times more productive in burned plots than in unburned controls (Hoffmann 1998). The great proportion of resprouter species at our study site and their increasing density in burned grassland plots (GROUP 1 and 2), as well as the high recruitment rate of non-sprouter anemochoric shrubs species after two years of fire, are features from communities under high disturbance frequency with well-adapted species.

Non-sprouter grassland shrubs increased establishment on grassland more expressively after two years of the fire disturbance, like in neotropical savannas, where despite the overall negative effect of fire on seedling establishment in the first year following burning, normal levels of recruitment had returned by the second year (Hoffmann 1996, 1998). In chaparral and savanna-type vegetation, shrub seedling density is related to post-fire conditions, with some species being dependent on fire to persist in the community (Smith & Taiton 1985, Tyler 1995, DeSimone & Zedler 2001). In South Brazil no study has focused on such dependences, but the life-history features of species like *H. psiadioides* and *B. dracunculifolia* are indicating some advantages of post-fire event to seedling establishment. On unburned plots, the height size proportion of these shrubs stayed almost stable along two consecutive years, with a slight decrease of adult individuals, indicating a possible senescence at the population level, and a lack of new seedlings, which are probably dependent on bare soil sites to establishment. Number of shrub seedlings increased much more in burned plots than in protected areas in one-year period.

The above dynamic pattern was valid to most grassland shrubs; while for the forest tree species no clear pattern was observed (Appendix 1). Density of forest tree species increased only in border plots; on unburned grassland, some species increased and others decreased in density, and on recent burned areas most established species were resprouters and had being already present before those fire events, especially in between rock outcrops. Only at the forest border significant seedling recruitment took place, and no changes occurred on unburned plots, even though they initially presented more individuals than both burned groups. It has been demonstrated that shrubs can have favourable effects on tree seedling establishment, such as increasing seed dispersal and seedling survival by facilitation (Holl 2002). The present study did not show any significant relationship between woody crown cover and tree seedling establishment in grassland, which may be a consequence of the short time of fire absence, since a slight increase in tree seedling establishment in the second survey was already observed in places with larger shrubs (*e.g. B. dracunculifolia* in unburned plots). *M. cuspidata* was one of the most frequent forest species on grassland and can survive recurrent fires, as it was present on all three grassland groups of elapsed time since fire. The individuals of this species in grassland areas had a basal stem structure like a woody swelling at the stem base, from which many new stems were sprouting right after fire (sometimes more than hundred). Studies are needed addressing morphology of below-ground structure of *M. cuspidata* and other species occurring in the grassland matrix, to understand how investment in low stature and multi-stemmed architecture can be beneficial for survival in fire-prone communities (Bellingham & Sparrow 2000) and how the structural patterns of woody species is being defined by the fire regime.

Like *M. cuspidata*, *B. cognata* and *E. ligulaefolium*, most of the shrub and tree species present were resprouting and shorter than obligate seeders, but more efficient in post-fire colonization. Data about how long such resprouting species populations are able to survive without recruitment of new generations, as well about the seeders recruitment rates in present fire regime, would be fundamental keys for managing grassland vegetation in southern Brazil, so much for the maintenance of pure grasslands (avoiding shrub/tree encroachment) as to allow natural forest expansion process. From the present study, analysing short-term dynamics of woody vegetation in a burned grassland without grazing, we can conclude that fire intervals of two to three years do not avoid shrub encroachment but retard the advance of forest species over the grassland matrix, except on sites very close to the border (maximal 5 m) or yet on island patches protected from intense fire, as rock outcrops. The process of forest expansion is, consequently, retarded by fire. In the absence of fire, micro-site conditions as well as life-history features of pioneer species combined with annual variation in water stress are key factors for forest expansion, which are not yet well understood in subtropical Brazil. In a general way, absence of fire can alter the mosaic of habitat types by increasing the proportion of forest, thus diminishing habitat diversity, which has been recognized as an important component of biodiversity (Braithwaite 1996).

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Appendix 1. List of species[*] with density (plant.m^{-2}), mean basal diameter of individuals (cm²) in the first survey (Jan/Feb 2003), and density change in % from first to second survey (end of 2003), separated for the three grassland groups (elapsed time since fire) and border plots (close to the forest). For species, main habitat (b= border, g= grassland, f= forest) and information on resprouting capacity is given.

			burn (Oct./02)			burn (Jan./02)			unburned			border		
Species	Habitat	Sprout capacity	Plants/m²	% change	Mean cover of stem (cm²)	Plants/m²	% change	Mean cover of stem (cm²)	Plants/m²	% change	Mean cover of stem (cm²)	Plants/m²	% change	Mean cover of stem (cm²)
Agarista eucalyptoides	b	x	0.04	-22.4	0.36	-	-	-	0.027	38.5	3.06	0.062	-33.3	3.81
Baccharis articulata	g	x	0.15	-10.7	0.07	0.049	41.7	0.30	0.097	30.2	0.13	-	-	-
Baccharis cognata	g	x	1.46	40.8	0.02	1.837	-4.8	1.42	0.646	-19.4	0.38	0.148	36.1	0.35
Baccharis dracunculifolia	g		-	1.1	-	-	15.4	-	0.049	35	1.75	0.004	300	0.64
Baccharis leucopappa	g	x	-	4.8	-	0.012	13500	0.14	0.002	2420	1.13	-	4.9	-
Baccharis ochracea	g	x	0.04	185.7	0.14	0.049	58.3	2.95	0.084	113.7	0.21	-	2.9	-
Baccharis patens	g	x	0.03	-8.2	14.60	0.012	-100	0.08	0.142	-13	1.20	-	2.1	-
Baccharis sessilifolia	g	x	0.17	16.3	0.23	0.080	23.1	0.26	0.494	77.5	0.85	0.136	-24.2	0.13
Baccharis trimera	g	x	0.06	-33.3	0.10	0.037	-44.4	0.15	0.086	80	0.08	-	-	-
Butia capitata	g		-	-	-	0.004	-	2.95	0.006	20	3.14	0.004	-	17.51
Campomanesia aurea	g	x	0.17	-38.8	0.03	0.037	-50	0.07	0.047	-68.7	0.17	0.136	-51.5	0.05
Collaea stenophylla	g	x	-	-	-	0.078	-23.7	0.21	-	-	-	-	-	-
Croton nitriariaefolium	g		0.25	487.1	0.14	1.870	26.1	0.19	0.570	-2.5	0.14	0.914	5.0	0.05
Croton thermarum	g		0.28	-25.5	0.02	-	-	-	0.076	10.3	0.23	0.086	-42.9	0.02
Diospyros inconstans	f		-	-	-	-	-	-	-	-	-	0.016	875	0.26
Dodonaea viscosa	b		0.02	-14.3	0.64	-	-	-	0.043	14.3	11.07	0.123	16.7	8.74
Erytroxylum argentinum	f		-	-	-	-	-	-	-	5.2	-	0.008	850	1.78
Eugenia hyemalis	f	x	0.03	37.1	0.55	-	-	-	0.006	380	0.58	0.012	333.3	0.28
Eupatorium ligulaefolium	g	x	0.34	122.6	0.29	0.366	209.6	0.27	0.354	-16.3	0.47	0.016	625	0.19
Eupatorium intermedium	g	x	0.10	-94.6	21.58	0.006	-	0.27	0.043	-65.7	3.30	0.008	450	1.36
Guapira opposita	f		-	-	-	-	-	-	-	-	-	0.066	31.3	2.95
Guettarda uruguensis	f		-	-	-	0.002	-	2.11	-	-	-	0.008	-	1.78
Heterothalamus psiadioides	g		0.02	-61.9	1.76	0.265	1802.3	0.01	0.222	-63.3	1.71	-	0.4	-
Lithrea brasiliensis	f	x	0.01	-14.3	2.00	0.006	166.7	3.74	-	-	-	0.016	100	4.90
Maytenus cassineformis	f	x	0.01	59.2	0.46	-	-	-	0.025	-70	0.14	-	0.4	-
Matayba elaeagnoides	f	x	-	-	-	0.004	-	9.09	0.002	-100	27.90	0.029	14.3	0.76
Mimosa parvipinna	g	x	0.02	32.5	0.63	-	-	-	0.076	49.2	0.82	-	-	-
Myrsine coriaceae	f		-	-	-	-	-	-	0.006	140	0.31	0.053	100	4.91
Myrciaria cuspidata	f	x	0.01	-42.9	2.37	0.021	60	0.45	0.051	5.6	4.78	0.091	40.9	2.04
Myrsine guianensis	f	x	-	-	-	-	-	-	0.002	20.0	23.76	0.008	-	10.77
Myrcia palustris	f	x	0.01	-28.6	213.48	0.004	-100	3.73	0.062	-100	2.26	0.070	41.2	4.48
Myrsine umbellata	f		-	-	-	0.004	-100	0.20	0.002	260	0.64	0.041	30	0.91
Pavonia hastata	g	x	-	5.5	-	0.228	67.6	0.11	0.025	100	0.15	0.091	268.2	0.05
Porophyllum lanceolatum	g	x	0.26	224.5	0.04	0.512	-2.0	1.18	0.115	127.1	0.16	0.280	92.6	0.05
Psychotria carthagenensis	f		-	-	-	0.006	-100	0.44	-	-	-	0.029	214.3	1.81
Schinus weinmanniaefolius	g	x	0.07	-42.9	0.06	0.605	-34	13.50	0.021	-16	0.15	0.115	57.1	0.58
Sebastiania brasiliensis	f		-	-	-	0.006	-100	0.99	-	-	-	0.049	33.3	0.03
Styrax leprosus	f	x	-	-	-	-	-	-	0.002	260	3.81	0.029	-57.1	0.43
Symplocos tetrandra	f	x	-	-	-	0.002	-100	1.54	-	-	-	0.078	15.8	0.27
Symplocos uniflora	f	x	0.03	-67	16.88	0.004	-	11.00	0.006	-60	58.63	0.016	725	116.32
Vernonia nudiflora	g	x	1.19	2.3	0.08	1.551	11.8	0.07	0.638	49.4	0.45	0.284	-7.2	0.07
Verbesina subcordata	g	x	0.03	71.4	0.28	-	3.1	-	-	0.7	-	0.012	-100	0.19
Zanthoxylum rhoifolium	f	x	-	-	-	0.002	-100.0	3.81	-	1.0	-	0.037	66.7	0.13

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[*] Only species with at least 5% of frequency considering both surveys.

TERCEIRO CAPÍTULO

PLANT FUNCTIONAL TYPES OF WOODY SPECIES RELATED TO FIRE DISTURBANCE IN FOREST-GRASSLAND ECOTONES [*]

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[*] O trabalho será submetido à revista OIKOS. A formatação está conforme as orientações da revista, exceto pela posição das figuras no texto, pelo espaçamento entre linhas e pelo alinhamento do texto.

ABSTRACT

Assessing plant functional types (PFTs) has been widely emphasized for search landscape or community changes relating climate and disturbances. In this study we search for PFTs of woody species in forest-grassland boundaries in South Brazil, where a current tendency of forest expansion exist, but fire in grassland is frequent. Two questions were thus addressed to know i) which plant functional types of forest woody species can establish in adjacent grassland subject to fire disturbance and ii) which plant functional types of forest and grassland woody species are related to short-term dynamics in frequently burned grassland. Traits were assessed in woody plants in 156 plots (6.75 m²) arranged in 12 transects across forest-grassland boundaries with different fire treatments in grassland. The analysis used a recursive algorithm to search for traits and PFTs maximally associated to spatial distance from forest limit in one analysis and elapsed time since last fire in other. As a result, nine PFTs of forest woody species were identified maximally associated to distance from forest. Resprouting ability characterized forest plants able to colonize grasslands. PFT diversity was higher in border plots than inside forest. Four PFTs of forest and grassland woody species were identified maximally associated to elapsed time since fire. Taller individuals of single-stemmed shrubs predominated in late post-fire recovery (3-4 years), while shorter multi-stemmed shrubs in recently burned areas (3 months to 1 year). PFTs of forest trees occurred in border plots or as established adults in grassland, remaining unaffected by fire. We concluded that identification of PFTs of woody plants in grassland associated to elapsed time since last fire suggests that easy-measurable traits are sufficient to evaluate post-fire community dynamics. Forest PFTs in burned grassland are restricted to those with resprouting ability to survive recurrent fire events, and establishing on protected sites with less-intensity fire.

Keywords: forest expansion, resprouter, shrubs, tree establishment, South Brazil, vegetation dynamics

Introduction

Assessing plant functional types has been widely emphasized as an alternative to determining species composition in order to evaluate the influence of climatic change, atmospheric composition (*e.g.* rising CO2 concentration) and land-use changes over present-day vegetation communities in a global sense (Box 1996, Woodward and Cramer 1996, Díaz and Cabido 1997, Pausas 1999). These are major factors that may act simultaneously on scales from local patches to global landscape structure, promoting changes in ecosystem functions and responses (McIntyre et al. 1999a, Rusch et al. 2003).

In spite of some conceptual differences, definitions agree that plant functional types (PFTs) are groups of functionally similar plant types for responses to certain conditions and/or for effects on ecosystems processes (Pillar and Orlóci 1993a, Box 1996, Noble and Gitay 1996, Woodward and Cramer 1996), although function is not easily defined or classified. Based on the assumption of relationships between form and function (Barkman 1988), the structural-functional approach permits the use of visible structural attributes as surrogates for functional patterns, these thus being widely applied as basic features for PFTs classifications and, when possible, further complemented by physiological traits (Box 1996, Weiher et al. 1999). Methods by which to elaborate PFT classifications may follow two main approaches; one where groups of plants derive from numerical analysis, with a more inductive selection of traits related to environmental (or disturbance) variables, and other where groups are deduced *a priori* based on assumed features that operate certain functionality in the system (Bugmann 1996, Noble and Gitay 1996, Woodward and Cramer 1996). A combination of both approaches had been used as well, considering that the process of trait selection has a previous deductive base (McIntyre et al. 1999b).

Although an universal plant functional classification has been recognized to be unlikely to accomplish, a classification becomes more useful when plant types are determined for a particular purpose, such as phenological/life-form approaches commonly applied to landscape change relating disturbance (Noble and Gitay 1996, Campbell et al. 1999) or broadly applied to contrasting floras of regions differing greatly in climate, biogeography and land use (Pillar and Orlóci 1993b, Díaz et al. 2004). The functional classification adopted by Noble and Gitay (1996), based on features derived from the vital attributes model by Noble and Slatyer (1980), define plant groups to reveal changes in vegetation patterns under fire disturbance. Other studies, however, access plant function based on physiological processes (“hard” traits like photosynthesis, respiration, competitive ability) (Grime et al. 1997), but for highly diverse communities this may be impractical (McIntyre et al. 1999b), and where no sufficient information about species composition exists, the applicability of some traits is unfeasible as well. Thus, if the aim is to evaluate not only some well-known species in relation to a certain environmental function, but a whole community or at least a large group of species, structural traits may be more useful.

Another fundamental topic to be considered is the target variables of trait analysis, since the functionality of subsequently defined groups of plants will be directly linked to the trait set selection. Obtaining interspecific traits measurement in the field, in contrast to traits resulted from laboratorial testing of greenhouse plants, has the advantage of not needing extrapolation of natural conditions (environmental influence). But, if only adult plants are measured, many important continuous traits that show ample variability within species can affect species ranking for such traits (Cornelissen et al. 2003). Such variability may result from genetic variation within or between populations, environmental conditions, and/or disturbance restrictions. Thereby, trait sampling that considers plants apart from species identity and measures variability between traits within species directly in the field avoids the above cited problem and individuals of a single species may belong to different PFTs, taking into account genotypic or phenotypic plasticity (Pillar and Sosinski Jr. 2003, Sosinski Jr. and Pillar 2004, Overbeck et al. submitted). So, we adopt the definition that a “PFT is a group of plants that, irrespective of phylogeny, are similar in a given set of traits and similar in their association to certain variables”, which may be factors of environmental conditions (*e.g.* soil, temperature, moisture), disturbance regimes (*e.g.* fire, grazing) or ecosystem effects (*e.g.* biomass production, litter, diversity) (Pillar and Sosinski Jr. 2003).

In ecotones of grassland-forest formations in southern Brazil, studies have focused on the causes of their maintenance, since present climate conditions are suitable for forest formations (Rambo 1956, Pillar and Quadros 1997) and no restrictions by soil properties for forest expansion have been observed (*e.g.* Garcia Martinez 2005). A process of forest expansion starting after mid Holocene is well documented by palynological studies in peat profiles in southern Brazilian regions (Behling 2001, Behling et al. 2004); where abundant charcoal particles since much earlier in the Holocene have also been recorded. Thus fire has from the start been present in grassland-forest mosaics, probably a factor preventing successful forest tree species establishment within grassland, with or without grazing (Hoffmann et al. 2003, Pillar 2003).

In this paper we define PFTs in forest-grassland ecotones in subtropical Brazil based on traits described in woody plants. In one case, with forest woody plants only and presuming a forest expansion process into grassland we search for PFTs related to spatial distance from the forest limit. In other case, with all woody plants present in grassland, we search for PFTs related to short-term response to fire disturbance.

Methods

Study area – The study was carried out on Morro Santana (Santana hill; 30°03' S, 51°07' W) situated on a chain of granitic hills, in Porto Alegre, Rio Grande do Sul, Brazil. Natural vegetation cover of this region is a mosaic of grassland (*Campos*) and forest, the latter preferentially on sites with south and southeast aspects, with many patches of woody plants in the grassland matrix and riparian forest along creeks or rivers (Rambo 1954, Rambo 1956, Teixeira et al. 1986). On Morro Santana, almost 50% of the area (approx. 400 ha) are covered by forest, a mixture of floristic elements of Atlantic rain forest (northeastern influence) and of deciduous seasonal forest (western influence); however, most of the dominant species came from the Atlantic forest (Rambo 1954, Rambo 1961, Brack et al. 1998). *Campos* vegetation predominates on the top of the hill (altitude max. 311 m a.s.l.) and on the north side, comprising approx. 220 ha. On grassland fire is a frequent disturbance, usually caused by local residents, with return intervals of three to five years. The present mosaic of vegetation is supposedly maintained by anthropogenic fire, since the area is not grazed and climate conditions are suitable to forest formation (Overbeck et al. in press). Forest is too moist to burn and thus grassland fire spread stops at the border, causing more or less abrupt transitions, according to local topography and fire regime (Müller et al. Chapter 1).

The climate is subtropical humid without drought season. It corresponds to the Cfa's type according to Köppen's classification, with mean annual precipitation of 1348 mm and an average annual temperature of 19.5°C (Nimer 1990). The soil types are typical dystrophic red-yellow argisols, developed from granite (Streck et al. 2002), corresponding to acrisols, alisols and umbrisols in the FAO-classification (Garcia Martinez 2005). Rounded rock outcrops are abundant on the hill.

Experimental setting and data collection – Data of woody plants were collected in 1.5 by 1.5 m plots arranged in 12 transects located on transitional zones of forest-grassland vegetation. Transect location was defined based on differences in the woody vegetation physiognomy in the grassland matrix. Transects were arranged in pairs and transects in each pair, as much as possible similar to each other, were separated by five meters. Two of these pairs were on north, two on top/south and two on top/southwest aspect. Each transect consisted of 39 contiguous plots, with 21 being in grassland and 18 in forest. The limit between grassland and forest was defined by the last adult forest tree. In October 2002, before sampling, we subject the grassland portion of one randomly selected transect in each pair to a controlled burn. The transects located on top/southwest aspect had last burned in January 2002 and by the time of the experimental burn had not accumulated sufficient flammable biomass to support spreading of a fire. Therefore, the experimental burn succeed only on four transects located on grassland that was unburned for three years or more (two on north and two on top/south aspect). The survey of the grassland plots was conducted in January/February 2003 (first survey). Such a design of burned and unburned transects thus allowed us to define three groups of plots, based on time elapsed since last fire event in the grassland plots: group 1= 3 months (plots of the transects experimentally burned in October 2002), group 2: 1 year (plots of the transect pairs last burned in January 2002), group 3: 3-4 years (unburned plots in the transect pairs subject to experimental burns). Further, the first three grassland plots (closest to the forest) in each transect were considered border plots (group 4) for the analysis involving the influence of fire, since they did not burned well in any transect due to lack of flammable biomass. It was assumed that transects in a pair had similar plant composition before the experimental burn; differences found between groups 1 and 3 were thus due to influence of a single recent fire. Space for time substitution was adopted in defining groups 2 and 4. The survey of the forest plots was carried out from July to September 2003. Later, in November/December 2003, a second survey was carried out in the grassland plots of groups 1 and 3, allowing in these the analysis of short-term post-fire vegetation dynamics.

In each survey, all woody plants above 10 cm high were considered in grassland and forest plots, recording species identity, plant height, stem shaft height (height to the first branch) and basal stem diameter. Other attributes were recorded at individual, population or species level (Table 1). Habit, dispersal syndrome, resprouting ability and leaf texture were recorded at the species level, based on field observations and literature. Resprouting ability was considered only as basal sprouting response related to fire reaction (Bellingham and Sparrow 2000, Bond and Midgley 2001), thus not including species with sprouting capacity that occurred exclusively inside forest areas, where fire does not spread in the study site. All other traits were measured in individuals directly in the field and extrapolated for a population taken as homogenous. In this study, we define "population" as a group of plants of the same species occurring in the same plot and being acceptably homogenous for the traits being considered. Later, in data handling, individuals belonging to the same species and sharing the same states for *plant phase* and *stem base* in a plot were grouped as a different population. The other traits were then averaged in each of these populations and categorized into classes of states. For example, a population state for *plant height* or *leaf area* was obtained by the mean value of individuals in the same *plant phase* and *stem base* state belonging to the same species in a plot. The aim of this choice was to avoid excess of continuous trait variability, *e.g.* among seedlings and adult trees (Cornelissen et al. 2003).

Table 1. Traits used for description of woody plants in grassland, border and forest in the present study. Alternative states for habit (*) were used for trees and understory shrubs in forest-grassland transition analysis (see below).

Nr	Attribute	Code	States
1	habit	*ha*	*1*: shrub, *2*: tree
1*	habit[1]	*ha*	*1*: shrub, *2*: treelets, *3*: low-size tree, *4*: mid-size trees, *5*: large trees
2	dispersal syndrome	*ds*	*1*: autochory, *2*: anemochory, *3*: zoochory
3	resprouting ability	*ra*	*1*: non-sprouter, *2*: resprouter
4	plant *phase*	*pp*	*1*: below 30cm high, *2*: 30-79, *3*: >80cm high, but less than 5cm of basal diameter, *4*: above state 3
5	plant height	*ph*	*1*: <0.2 m; *2*: 0.2-0.5; *3*: 0.5-1.5; *4*: 1.5-3; *5*: 3-6; *6*: 6-9; *7*: >9 m
6	shaft height	*sh*	*0*: unbranched; *1*: <0.2m; *2*: 0.2-0.5; *3*: 0.5-1.5; *4*: 1.5-3; *5*: 3-6; *6*: 6-9; *7*: >9m
7	stem base	*sb*	*1*: single-stemmed, *2*: multi-stemmed
8	stem consistency	*sc*	*1*: semi-woody, *2*: woody
9	stem structure	*se*	*1*: unbranched stem, *2*: branched stem
10	leaf shape	*ls*	class of width leaf:length leaf ratio – *0*: no leaf; *1*: <0.1; *2*: 0.1-0.3; *3*: 0.3-0.6; *4*: 0.6-0.8; *5*: 0.8-1; *6*: >1
11	leaf area	*la*	*0*: no leaf; *1*: <1cm²; *2*: 1-5; *3*: 5-15; *4*: 15-25; *5*: 25-35; *6*: 35-50; *7*: 50-80; *8*: >80cm²
12	leaf texture	*lt*	*0*: no leaf, *1*: coriaceous, *2*: intermediate between 1 and 3, *3*: membranous

[1]- Groups according to Brack et al. 1998 referring to a species' maximum height (shrubs: less than 2.5 m; treelets: 2.5-5 m, low-size trees: 5-9 m, mid-size trees: 9-15 m, large trees: above 15 m).

Data analysis – For the analysis we used data defined for larger (4.5 x 1.5 m) plots generated by pooling sets of three adjacent 1.5 x 1.5 m plots, resulting in 13 plots per transect. To define PFTs, we followed the methodology developed by V. Pillar (Pillar and Orlóci 1993a, Pillar 1999, Pillar and Sosinski Jr. 2003) for the identification of PFTs maximally associated to the forest-grassland transition (position of plots on the gradient) and fire disturbance. The analysis used the algorithm for trait subset optimization involving polythetic clustering (Pillar and Sosinski Jr. 2003) implemented in SYNCSA software (Pillar 2004). In short, the algorithm involves three data matrices: one matrix (**B**) of plant populations described by the states of traits, a second matrix (**W**) of populations describing by their performance in the communities (our pooled plots) and a third matrix (**E**) of community sites described by environmental variable(s) (fire, distance from forest limit). The recursive algorithm searches for a subset of traits in matrix **B** and groups of populations based on cluster analysis with these traits (PFTs) in such a way to maximize the congruence between vegetation described by the PFTs and the chosen environmental variable. Congruence is measured by the matrix correlation $\rho(\mathbf{D},\mathbf{\Delta})$, where **D** contains community dissimilarities (chord distances) based on the PFT performances (population performances in matrix **W** rearranged and pooled in each plot according to the defined PFTs), and $\mathbf{\Delta}$ the community sites' dissimilarities (Euclidean distances) based on the chosen environmental variables (**E**) standardized if needed. For the analysis all traits were taken as quantitative or semi-quantitative according to states logically ordered as in Table 1 (e.g., for habit, trees are taller than shrubs; for dispersal syndrome zoochory is more complex than autochory).

For the analysis we categorized the woody species (shrubs and trees) into typical grassland species (never present in forest) and forest species (typical of forest, but sometimes present in grassland as pioneer species). The following analyses were conducted:

1) With the objective of identifying PFTs associated to a presumed forest expansion process into grassland (forest-grassland transition analysis), we considered only forest species, excluding plots where no forest species were found, and used in matrix **E** the distance to the forest limit. In this analysis, matrix **W** was defined by population density per plot.

2) With the objective of identifying PFTs associated to fire disturbance in grassland, we considered all woody species present in grassland plots only and used, as a proxy for post-fire recovery stage, time elapsed since the last fire event as the variable in matrix **E**

(groups ordered 1 to 4). Matrix **W** was defined by population’s basal area per plot in the first survey.

3) With the objective of further exploring PFTs related to short-term response to fire, we considered the plots of groups 1 and 3 in the two consecutive years of survey. For this, two variables were used in matrix **E**: fire (burned *versus* unburned plots) and time (1st *versus* 2nd survey). Matrix **W** was defined by population’s basal area per plot.

In each analysis, as a consequence of redundancy among traits, the algorithm found several solutions differing regarding trait subset and defined PFTs but that were very close in terms of $\rho(\mathbf{D},\Delta)$ congruence values. Among these, we chose a solution which was a compromise between congruence level and interpretability of the results. For a synthesis of the results, we used ordination by Principal Coordinates Analysis (PCoA) with the matrix of plots described by the defined PFTs, based on chord distances (Podani 2000). In order to complement the interpretation of defined PFTs according to the traits, a PCoA ordination analysis of PFTs based on the mean value of states in the optimal trait subset was performed using Gower’s index as resemblance measure, and for aiding interpretation all traits (optimal and suboptimal) were depicted on the diagram accordingly to their correlation value with the two first ordination scores. This step was conducted only for forest-grassland transition analysis. Groups of plots based on time elapsed since last fire were compared for PFT composition and PFT diversity, by analysis of variance with randomization testing, using 1000 random permutations (Pillar and Orlóci 1996). Diversity was measured by the Shannon index based on the natural logarithm (nats).

Results

Forest plants in forest-grassland transition

This trait-based analysis involved 1344 populations, belonging to 80 species of 40 families. Myrtaceae (14 spp), Lauraceae (7 spp) and Rubiaceae (6 spp) were the most species rich families, followed by Sapindaceae, Euphorbiaceae and Salicaceae, each one with four species. Some species, like *Dodonaea viscosa* (L.) Jacq., *Agarista eucalyptoides* (Cham. et Schl.) G. Don, *Campomanesia aurea* O. Berg, *Opuntia monacantha* Haw. and *Cereus hildmannianus* K. Schum., which are uncommon inside forest formations, were considered in this analysis as well, considering their commonness at border sites. The complete list of species according to their presence in one of the PFT-based analyses is in Appendix 1.

The optimization algorithm found six optimal traits, defining nine PFTs (Table 2). The traits were habit (*ha*), resprouting ability (*ra*), shaft height (*sh*), stem consistence (*sc*), leaf area (*la*) and leaf texture (*lt*), maximizing congruency with distance to the forest limit at a level of 0.60 (the analysis found 14 close solutions of PFTs number and trait subset with congruency value ranging from 0.61 to 0.60, results not shown). The ordination of plots by these PFTs clearly separated grassland plots from forest plots (Fig. 1A). Correlation of ordination axis 1 to distance from forest limit was 0.82 (-0.09 for axis 2). Grassland plots farther from forest were characterized by PFT2 and grouped closely in ordination space, while forest plots were more dispersed at one end of the gradient and characterized by several PFTs. Plots near the forest limit (f5, f6) were spread over the diagram, indicating higher diversity of PFT composition and transition to grassland. The ordination of PFTs by the optimal traits (Fig. 1B) helps characterizing each PFT and their similarities. The first ordination axis denotes variation in resprouting ability (from resprouter to non-sprouter; left: state 2, right: state 1), stem consistence (semi-woody to woody stems), leaf area and shape (larger and broader leaves to the right), leaf texture (from coriaceous to membranous) and habit (shrubs/treelets to mid-size trees). The second axis indicated variation principally of resprouting ability, stem consistence, and plant height. Redundancy among suboptimal and optimal traits was evident in this ordination analysis, as indicated also by the several very close solutions pointed by the recursive algorithm.

Resprouting ability was the most defining trait for PFTs on grassland plots (compare both ordination diagrams of Fig. 1 and the densities of PFT2 in grassland plots in Table 2). PFT2, characterizing grassland plots, was formed mainly by treelets and low-size trees with resprouting ability and leaves with less than 15 cm² of area and intermediate texture (most species had coriaceous leaves, but also intermediate and membranous leaves). PFT1 was formed most by low-size trees able to resprout, with larger leaves than PFT2 (as all other PFTs too), while PFT4 did not have resprouting ability and leaves were membranous; both PFTs were significantly denser at border plots. PFT7 comprised most of understory shrubs and young treelets/low-size trees (Appendix 2) with mid-size membranous leaves, being more abundant inside the forest, while PFT8 were saplings of mid-size trees, with unbranched (*sh*) and semi-woody (*sc*) stems, with large leaves of intermediary texture. PFT8 had similar densities in all forest plots and was completely absent in grassland plots. PFT5 comprised only cactus species at the border plots. PFT diversity was significantly higher at the border than inside forest or in the grassland (Table 2).

TABLE 2. PFTs of forest species in forest-grassland transitions according to an optimal trait subset (*ha*, *ra*, *sh*, *sc*, *la*, *lt*) for congruency (0.60) with distance from forest limit. PFTs are described by mean states in the selected trait subset (see Table 1 for traits' description), the total frequency in plots, and the average density per groups of plots, following Fig. 1A (1= f1, f2; 2= f3, f4; 3= f5, f6; 4= g7, g8; 5= g9, g10; 6= g11, g12, g13). The mean PFT diversity is given for each group. Values followed by different letters differed significantly among groups ($p \leq 0.005$).

PFT code	Mean trait state						Freq. (%)	Density (average/groups* of plots)						axis1; axis2
	ha	*ra*	*sh*	*sc*	*la*	*lt*		1	2	3	4	5	6	(correlation)
PFT2	*2*	*2*	*1*	*2*	*3*	*2*	79.25	0.75^{a}	1.54^{ac}	3.04^{b}	1.98^{bc}	1.40^{a}	4.31^{b}	-0.96; -0.12
PFT3	*3*	*1*	*1*	*2*	*5*	*2*	76.42	4.31^{a}	4.83^{a}	3.58^{a}	0.45^{b}	0.17^{bc}	0^{c}	0.68; 0.45
PFT4	*3*	*1*	*2*	*2*	*4*	*3*	72.64	1.55^{a}	2.75^{b}	3.96^{c}	0.62^{d}	0.25^{d}	0^{d}	0.21; 0.65
PFT7	*2*	*1*	*1*	*1*	*4*	*3*	67.92	6.98^{a}	6.64^{a}	4.61^{b}	0.06^{c}	0^{c}	0^{c}	0.87; -0.43
PFT1	*3*	*2*	*2*	*2*	*4*	*2*	53.77	0.75^{ab}	0.64^{a}	1.46^{b}	0.28^{a}	0^{a}	0.13^{a}	-0.09; 0.42
PFT8	*4*	*1*	*0*	*1*	*4*	*2*	49.06	0.80^{a}	0.63^{a}	0.85^{a}	0^{b}	0^{b}	0^{b}	0.42; -0.03
PFT6	*2*	*2*	*1*	*1*	*4*	*2*	45.28	0.53^{ab}	0.74^{bc}	1.32^{c}	0.13^{a}	0^{a}	0.38^{ab}	0.01; 0.11
PFT9	*3*	*1*	*5*	*2*	*4*	*1*	7.55	0.06	0.04	0.04	0	0	0	0.15; -0.09
PFT5	*2*	*2*	*1*	*1*	*0*	*0*	4.72	0	0	0.11	0.02	0	0	-0.05; 0.20
PFT diversity (H') – average – * n° of plots (n) in each group:								1.24^{a} (24)	1.35^{a} (24)	1.63^{b} (24)	0.69^{c} (18)	0.11^{d} (8)	0.08^{d} (8)	

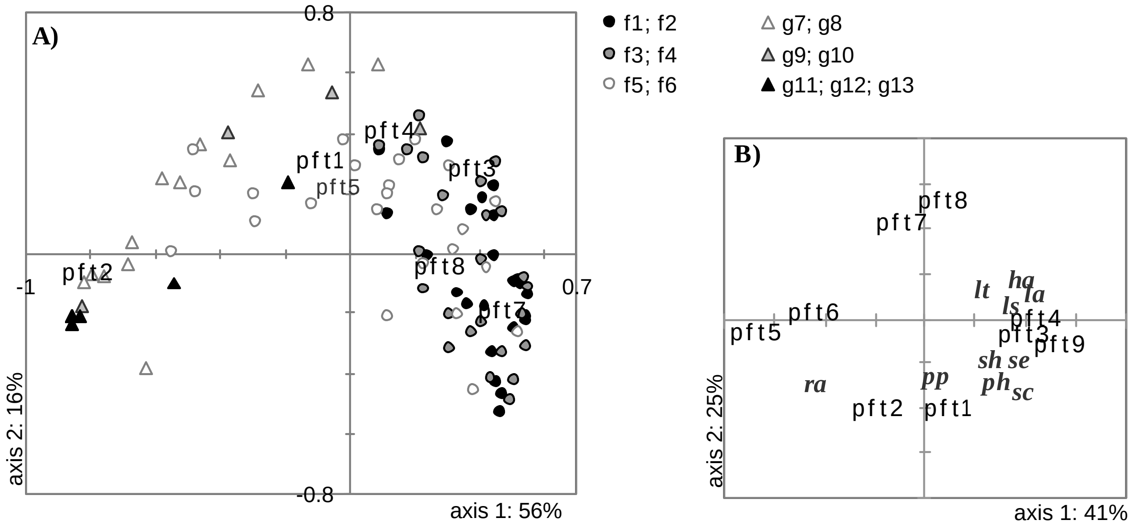

Figure 1. Ordination by PCoA of 106 plots described by PFTs of forest species in the forest-grassland transition (**A**) and of the same PFTs described by the optimal traits (**B**). The traits and PFTs are in Table 2 In **A** each point is a plot on the gradient (1 to 13), being f: forest and g: grassland. PFTs depicted on biplot had correlation higher than 0.4 to al least one of the axes,

except PFT5 with only 0.2. In **B** traits (optimal and suboptimal) were placed in the biplot according to their rescaled correlation with the ordination axes (codes in Table 1).

Woody plants and time elapsed since last fire in grassland

This analysis involved 605 populations belonging to 58 species of 25 families. Asteraceae was the richest one, with 17 species, followed by Myrtaceae (5), Euphorbiaceae (4), Sapindaceae (3), Fabaceae (3) and Rubiaceae (3). From these, 24 species occurred only at border plots. Border plots differed from other grassland plots due to proximity of forest and, consequently, absence of direct fire influence on plant composition, but had no adult forest tree species.

The optimization algorithm found six optimal traits, defining four PFTs (Table 3).

TABLE 3. PFTs of woody plants in grassland defined by the trait subset (*ph*, *sh*, *sb*, *sc*, *ha*, *ra*) that maximized the congruency (0.52) with elapsed time since fire (1: 3 months; 2: 1 year; 3: 3 years; 4: border plots). PFTs' frequency (%) and mean basal stem cover, as well as the diversity of PFTs in groups are indicated. Values followed by different letters differ significantly among groups by randomization testing ($p \leq 0.001$). See Table 1 for trait description.

PFTs code	Mean trait state						Frequency in each group (%)				Mean basal stem cover in group (cm^2)			
	ph	*sh*	*sb*	*sc*	*ha*	*ra*	1	2	3	4	1 (n= 24)	2 (n= 24)	3 (n= 24)	4 (n= 12)
PFT4	*2*	*1*	*1*	*1*	*1*	*2*	92	100	96	100	0.17^{a}	0.35^{a}	2.42^{b}	2.94^{b}
PFT2	*2*	*0*	*2*	*1*	*1*	*2*	100	100	87	67	0.95^{a}	0.69^{a}	0.14^{b}	0.16^{b}
PFT3	*3*	*0*	*2*	*2*	*1*	*2*	54	87	75	83	1.75^{ns}	0.59^{ns}	1.30^{ns}	3.93^{ns}
PFT1	*3*	*1*	*1*	*2*	*2*	*2*	4	0	17	92	0.001^{a}	0	0.38^{b}	8.36^{c}
PFT diversity (H') – average per group											0.41^{a}	0.83^{b}	0.64^{c}	0.72^{cb}

The optimal traits were plant height (*ph*), shaft height (*sh*), stem base (*sb*) and consistence (*sc*), habit (*ha*), and resprouting ability (*ra*), maximizing congruence with elapsed time after last fire at a congruence level of 0.52. PFTs 2 and 4 are shrubs with semi-woody stems, that can resprout and most plants were less than 0.8 m height and dispersed by wind, but these PFTs differed at the stem base. Multi-stemmed shrubs were in PFT2, characterizing recently burned plots (Table 3), while PFT4, single-stemmed shrubs with a mean basal cover higher than PFT2, was typical for longer unburned areas (groups 3 and 4). Group 2 was intermediate, but considering performance of PFTs 2 and 4, it was closer to group 1. PFT3, with woody multi-stemmed plants (shrubs and trees; see Appendix 3) between 0.5 and 1.5m high, did not present any difference at basal cover between groups.

PFT1 characterized border plots (group 4) and was mainly single-stemmed tree individuals, no resprouting ability, with large leaves and zoochorous dispersal syndrome (the last two traits were not selected, though); it did not occur well in burned areas. For PFT diversity (Table 3), differences were significant ($p < 0.001$) between recently burned plots and the other groups.

Short-term dynamics in burned and unburned grassland plots

This trait-based analysis, for prescribed burned (group 1) and unburned (group 3) plots in two consecutive years of survey, involved 583 populations belonging to 41 species of 17 families. The optimization algorithm found an optimal trait subset with stem base (*sb*), plant *phase* (*pp*), and habit (*ha*), reaching the maximal congruence of 0.35 with the variables fire and year of survey. This congruence value was achieved by the combination of both variables, but, if considering only fire (burned *versus* unburned) in relation to PFTs community resemblance, the congruence rose to 0.47. Thirteen PFTs were formed by this trait subset, but only those more correlated to community variation (Fig. 2) are described (Table 4).

PFTs 7, 5 and 9 were very similar; all were multi-stemmed shrubs differing in plant *phase* (actually, height classes). PFT7 was the shortest, followed by PFT5 and then PFT9, which characterized shrubs higher than 0.8 m. The first two types were particularly represented in burned plots of both survey years, while PFT9 was characteristic for unburned grassland (Fig. 2). Despite this pattern, differences of basal stem cover between burned and unburned plots were significant only for PFT7 and PFT5 (Table 4). For PFT5, a short-dynamic change could be observed in burned plots between years, considering the significant increase of basal cover. This change can also be interpreted as a replacement of PFT7 by PFT5 as a result of the plants' growing process. Further, for these two types, changes in basal cover occurred in unburned plots as well, with values becoming significantly higher in the second survey. PFT2, single-stemmed shrubs with ca. 0.8 m height characterized unburned plots, where basal cover was significantly higher than in burned plots, staying stable over two years. PFTs 1 and 11 were representing multi-stemmed tree plants at different height classes present in the grassland matrix independent of elapsed time since fire, with no significant differences of basal cover between groups (Table 4). Fire had a correlation of -0.75 with the first community ordination axis described by PFTs (Fig.

2), while survey year had only 0.14. Both variables were not correlated to the second axis. Considering whole PFT composition, burn plots differed significantly between the 1st and 2nd survey and, as expected, from unburned areas. However, unburned plots did not differ between both surveys. In spite of PFTs composition distinction, no significant differences occurred for PFT-diversity, which ranged from 0.78 to 0.93 in burned and unburned areas in both surveys.

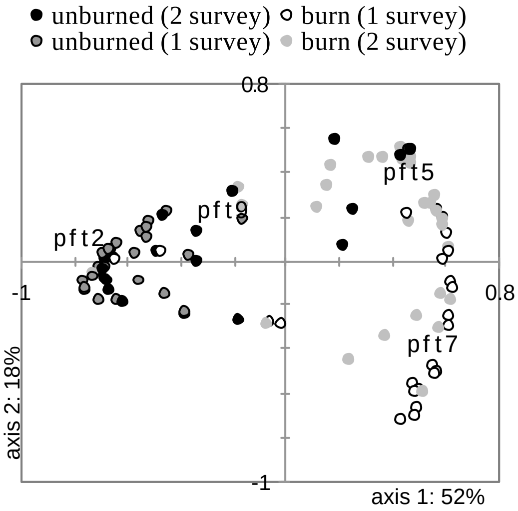

Figure 2. Ordination by PCoA of 96 plots described by 13 PFTs of woody plants in grassland plots of groups 1 (burn) and 3 (unburned) in two consecutive years of survey. PFTs depicted on diagram have correlation higher than 0.4 to one of the axes. PFTs described in Table 4.

TABLE 4. PFTs description of woody plants in grassland according to a trait subset (*sb*, *pp*, *ha*) maximizing congruence (0.35) with fire (burned *versus* unburned) and time (1st *versus* 2nd survey). PFTs are described by frequency, mean basal cover in each group of grassland plots in both survey years, correlation with axes and mean value of states in the selected traits subset (see Table 1 for traits description). Only PFTs with correlation higher than 0.4 to at least one of the ordination axes (Fig. 2), plus PFT1 and PFT11 are included. Differences between basal cover values in each group were tested separately for each PFT by randomization testing (*: p≤ 0.001; *ns*: not significant).

	Mean state				Basal cover (cm²)					Correlation	
					BURN		UNBURN				
PFT	*sb*	*pp*	*ha*	Freq. (%)	1st.	2nd.	1st.	2nd.		Axis1	Axis2
PFT5	*2*	*2*	*1*	100	0.51^{a}	1.09^{b}	0.26^{c}	0.67^{ab}	*	0.73	0.65
PFT7	*2*	*1*	*1*	91.67	0.51^{a}	0.41^{a}	0.03^{b}	0.13^{c}	*	0.75	-0.58
PFT2	*1*	*2*	*1*	81.25	0.13^{a}	0.41^{a}	2.36^{b}	2.97^{b}	*	-0.94	0.04
PFT9	*2*	*3*	*1*	29.17	0.15	0.15	0.53	0.75	*ns*	-0.36	0.18
PFT1	*2*	*2*	*2*	14.58	0.12	0.12	0.62	0.58	*ns*	-0.19	-0.16
PFT11	*2*	*4*	*2*	3.125	1.38	1.13	1.12	1.65	*ns*	-0.04	-0.16

Discussion

The selected traits

The present study focused mainly on structural traits measurable and perceptible in the field, later complemented with additional traits assigned per species, such as habit, dispersal syndrome and resprouting ability. Despite the nature of the traits (*easy* traits, Weiher et al. 1999) and the great range of plant populations and species number, the selected trait subsets are surrogates for functions similarly to other studies that used more physiological trait sets. Functional robustness of traits frequently relate leaf (*e.g.* specific leaf area, leaf weight ratio, photosynthetic ratio) and stem features (*e.g.* wood density, ramification), biomass, maximal plant height and seed mass (Díaz et al. 1999, Weiher et al. 1999, Cornelissen et al. 2003). Here, maximal species height was taken in *habit* (for the grassland-forest transition analysis) as potential height, an architectural feature according to Brack et al. (1998). Biomass was in part accessed by *plant height* and *stem base* (*sb*). These traits plus *resprouting ability*, *leaf area* and *leaf texture* of woody plants in grassland-forest ecotones were relevant for defining PFTs, presumably functional in relation to selected environmental variables (forest limit distance and elapsed time since fire). The decision to delimit as basic units more homogeneous populations according to *plant phase* and *stem base* within the same species was helpful to reveal consistent vegetation patterns and short-term dynamics in forest-grassland ecotones and burned grassland, since trait-stage shifts within a species from seedlings to adults are considered a norm rather than an exception, principally for trees (Cornelissen et al. 2003), and it is well know that plants of the same species may have different responses to environmental factors when growing in different habitats (Bellingham and Sparrow 2000, Vesk and Westoby 2004).

Studies approaching functional types for forests frequently access growth form and phenology, usually distinguishing canopy *versus* understory trees and deciduous *versus* evergreen species as important attributes relating to ecological function (Condit et al. 1996). In our case, this was of less importance, since we aimed to understand spatial patterns of forest species in forest-grassland ecotones, and understory treelets (*e.g. Myrciaria cuspidata* O. Berg, *Eugenia hyemalis* Camb.) as well as canopy species (*e.g. Myrsine umbellata* Mart., *Matayba elaeagnoides* Radlk.) were found colonizing grassland areas, and practically all sampled plants were evergreen species. This underlines the importance to make local observation of traits and to define PFTs in relation to local disturbance pressure or environmental conditions, as context-dependent classifications (Lavorel et al. 1997). Regarding the dichotomy between pioneer/shade-tolerant species (Swaine and Whitmore 1988), the present study was carried out in a narrow part of forest, where most species were "early secondary species" (long-lived pioneers, Whitmore (1989)), a few were shade-tolerant species with broad distribution pattern (*e.g. Sorocea bonplandii* (Bail.) Burg. Lanj. et Boer, *Gymnanthes concolor* Spreng., and understory shrubs) and typical forest pioneers were absent (Jarenkow 1994). Although we did not use successional classification as a trait, because of divergences in some species, it should be considered in further broad forest dynamic studies for traits accessing functional types on tree species (Box 1996, Condit et al. 1996). The trait *dispersal syndrome* did not contribute to congruence between vegetation data and spatial position in the forest-grassland transition because of the low variability among species, while for the analysis of the burned grassland it was indirectly indicated by *habit*, since practically all trees were zoochorous against most anemochorous grassland shrubs. Additional fruit/seeds attributes (*e.g.* shape, type, weight) would have probably more significance than dispersal mode in general in determining more detailed patterns of woody-PFTs on a small scale.

PFTs in forest-grassland transitions

Among the PFTs defined in the analysis of forest-grassland transition, the traits characterizing types occurring in grassland provided advantages for persistence under the current fire regime, such as resprouting ability. Resprouting trees invest in storage organs, with generally slow growth and high persistence in time (Díaz and Cabido 1997), in contrast to pioneer trees. However, in our case, trees playing the role of pioneer clearly were from species that could resprout. Despite the apparent incoherence, we should take into account that for an individual tree that is colonizing a grassland submitted to frequent burns, not just the dispersal, establishment and recruitment phases are restricting its success, but also (if not principally) the capacity to survive recurrent fire events. Therefore, the generally known "typical" pioneer trees with fast (above-ground) growth but low investment in storage organs were absent in these areas subject to frequent burns. There is also a stochastic component for successful persistence in grassland, which can be related to patchiness in fire events, giving more opportunities to trees surviving on sites where fire is less intense (Bond and Midgley 2001), as on northern aspects (Müller et al. Chapter 1). Furthermore, other related attributes of PFT2 (one important type in grassland plots; Fig. 1), mid-size leaves with no membranous texture, low-high branched woody stems and shorter plants are reflecting water conservation strategies in sunny habitats (diminishing leaf area and increasing cuticle), with no advantage in investment in height but in underground storage organs (Bellingham & Sparrow 2000). The fact that forest plots closest to the forest limit presented higher PFT-diversity, may suggest that in absence of fire other PFTs would tend to advance further in adjacent grassland plots, even slowly. Probably only PFT7 and 8 (most understory shrubs and shade-tolerant treelets) should be always restricted under dense canopy forest.

PFTs in burned grassland

Considering forest and non-forest woody plants established in grassland, but predominantly grassland shrubs, our results revealed PFTs associated to vegetation dynamics since the last fire event. We have confidence in the assumption that groups 1-4 in our experimental setup correspond to correctly ordered post-fire recovery stages. In this short period comparing recently burned (3 months) with longer time without fire (3-4 years), some differences in PFTs indicate important features of woody plants in frequently burned grassland and of adjacent forest border sites, where fire is less frequent. The analysis distinguished two types representing trees with established individuals on grassland. One type (with resprouting ability and multi-stemmed base) is occupying grassland plots independently of post-fire recovery stage, and border plots; its persistence in grassland plots seems to be linked to stochastic events of establishment or recruitment in sites with less fire severity, considering the constancy in basal cover across post-fire recovery stages. Another type (with resprouting ability, single-stemmed base and potentially taller than the first one) was more abundant in plots close to the forest border and in grassland plots at late post-fire recovery stage, being practically absent in recent burned plots (3mo-1y), except for few individuals that were established under adult tree plants (field observation). Some species are able to assume different structural growth forms in contrasting environmental conditions (e.g. forest and grassland) or under distinct disturbance pressures (e.g. fire and herbivory) (Archibald and Bond 2003). In the present study, *M. cuspidata* and *Myrcia palustris* (DC.) Kausel are examples of such species displaying a range of growth forms corresponding to different PFTs.

The presence of forest species establishing on grassland suggests that if fire could be suppressed in the area for a longer period they would more successfully colonize grassland, first at sites with higher density of taller shrubs, such as in current group 3 plots. Taller shrubs (PFT4: single-stemmed shrubs with or without resprouting ability, Table 3) were occurring in all post-fire recovery stages, but covering less in recently burned areas. Some species of this type were *D. viscosa*, *Heterothalamus psiadioides* Less. and *Baccharis dracunculifolia* DC., which can be considered as fast growing pioneer species with a large amount of seeds dispersed by wind, but unable to resprout after fire events. In contrast, multi-stemmed grassland shrubs (PFT2) were less frequent in border plots and denser in recently burned plots. Although most species of this type could also be considered as fast growth species, they invest in storage underground organs too, which result in shorter individuals if compared to single-stemmed shrubs (Bellingham and Sparrow 2000). Some important species of this type were *Baccharis cognata* DC., *B. trimera* (Less.) DC., *B. ochracea* Spreng., *B. sessilifolia* DC., *Vernonia nudiflora* Less., *Schinus weinmanniaefolius* Engl. and *Eupatorium ligulaefolium* Hook. et Arn.. The presence of only four PFTs of woody plants in grassland at different post-fire recovery stages suggests that a very simple classification is sufficient to evaluate the dynamic of communities under fire disturbance, as supported by Noble and Gitay (1996) and Pausas (1999). Therefore, a detailed list of hard plant traits (like physiologic hard traits) may be unnecessary to describe community changes.

As shown in the short-term dynamics analysis of burned and unburned areas, species present before the disturbance led to vegetation recover closely related to their own properties of persistence ability (persistence niche) (Bond and Midgley 2001). For example, the two main PFTs with resprouting ability (PFT 5 and 7, Table 4), already present in the community, recovered very quickly after nearly one year of the prescribed fire. On the other hand, PFTs representing seeders obligate species (PFT9) could not achieve similar abundance as in adjacent unburned plots in the same period, i.e. time for germination and growth was too short, since adult plants did not resist the prescribed burn. In this analysis, tree types have shown again the similar above described pattern of traits and no significant change occurred between survey years. Here, considering that only transect pairs of northern and southern aspect were taken into account, it was clearly documented that tree individuals were already present before fire and did not suffer damage at the stem base (no differences for basal cover; Table 4). Considering fire severity as a measure of the plant's perception of a disturbance event (Bellingham and Sparrow 2000), severity may range among individuals of different development stages, allowing less damage to adult trees that had already achieved sufficient height to escape more dangerous flame from the grass stratum (Bond and Midgley 2000).

In general, short-term vegetation dynamics of adjacent transect plots showed that fire effect was significant in reducing cover of tall single-stemmed shrubs, but in increasing cover of multi-stemmed shrubs. Woody species abundance in grassland vegetation is frequently related to disturbances, including fire, grazing and CO_2 concentration changes, and may increase in a complex trade-off with grasses dominance (Bond and Midgley 2000, Roques et al. 2001, Langevelde et al. 2003), often for some specific types only, such as resprouter especies (Pendergrass et al. 1998). On the other hand, fire can decrease diversity of woody regenerative types, due to the elimination of those without effective mechanisms to post-fire regeneration (non-sprouting and non seed germination promotion), as observed by Lloret and Vilà (2003) who compared fire disturbance in a mosaic of uncultivated and old field stands in Mediterranean woodland vegetation. In the present study, PFT-diversity was low in the grassland only in very recently burned plots, when considering composition of all woody plants (grassland and forest species), suggesting stability of woody plants community under present fire regime. But, when considering PFT-diversity for forest species in forest-grassland transition, a drastic decrease occurred from the border to the grassland plots, indicating fire influence on this ecotone pattern.

By analyzing all plants of the woody component to define PFTs revealed that not only common species are important to characterize community changes, as had been supposed (Díaz et al. 2004), but all species, even or especially the less frequent ones, since these may compose specific PFTs in the system. PFTs formed by infrequent species of similar attributes, thus supposing similar function, could be related to plants that are more endangered in those communities under present environmental conditions or disturbance regimes. In contrast, frequent types in communities susceptible to disturbance, as the multi-stemmed grassland shrubs in present study, may be responsible for ecosystem resilience, since they remain practically unaffected under recurrent disturbance events (Eriksson 2000).

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Appendix 1. List of families and species, their code, habit and inclusion in the PFTs-based analyses (a: forest-grassland transition; b: border + grassland plots (groups 1 to 4); c: only plots of groups 1 and 3 in both survey years. See methods for more explanations). For trait *habit* = *1*: shrub, *2*: treelets, *3*: low-size tree, *4*: mid-size trees, *5*: large trees.

Family	Species	Code	Habit	Analysis
ACANTHACEAE	*Justicia brasiliana* Roth	Jubr	1	a
ANACARDIACEAE	*Schinus molle* L.	Scmo	4	a
	Lithrea brasiliensis March.	Libr	4	a, b
	Schinus weinmanniaefolius Engl.	Scwe	1	b, c
ANNONACEAE	*Rollinia sylvatica* (A.St.Hil.) Mart.	Rosy	3	a
AQUIFOLIACEAE	*Ilex dumosa* Reiss.	Ildu	2	a
ARECACEAE	*Syagrus romanzoffiana* (Cham.) Glassm.	Syro	4	a
	Butia capitata (Mart.) Becc.	Buca	4	a, b, c
ASTERACEAE	*Baccharidastrum triplinervium* (Less.) Cabrera	BAtr	1	b, c
	Baccharis articulata (Cham.) Pers.	Baar	1	b, c
	Baccharis cf. *pseudotenuifolia* Teodoro Luis	Bacf	1	c
	Baccharis cognata DC.	Baco	1	b, c
	Baccharis dracunculifolia DC.	Badr	1	b, c
	Baccharis leucopappa DC.	Bale	1	b, c
	Baccharis ochracea Spreng.	Baoc	1	b, c
	Baccharis patens Baker	Bapa	1	b, c
	Baccharis sessilifolia DC.	Base	1	b, c
	Baccharis trimera (Less.) DC.	Batr	1	b, c
	Eupatorium intermedium DC.	Euin	1	b, c
	Eupatorium ligulaefolium Hook. et Arn.	Euli	1	b, c
	Eupatorium pedunculosum Hook. et Arn.	Eupe	1	b
	Eupatorium tweendianum Hook. et Arn.	Eutw	1	b, c
	Heterothalamus psiadioides Less.	Heps	1	b, c
	Porophyllum lanceolatum DC.	Pola	1	b, c
	Verbesina subcordata DC.	Vesu	1	b, c
	Vernonia nudiflora Less.	Venu	1	b, c
CACTACEAE	*Cereus hildmannianus* K. Schum.	Cehi	2	a
	Opuntia monacantha Haw.	Opmo	1	a,b
CELASTRACEAE	*Maytenus cassineformis* Reiss.	Maca	2	a, b, c
CLUSIACEAE	*Garcinia gardneriana* (Pl. et Tr.) Zappi	Gaga	2	a
EBENACEAE	*Diospyros inconstans* Jacq.	Diin	3	a, b
ERICACEAE	*Agarista eucalyptoides* (Cham. et Schl.) G. Don	Ageu	2	a, b, c
ERYTHROXYLACEAE	*Erythroxylum argentinum* O.E. Schulz	Erar	3	a, c
	Erythroxylum microphyllum A.St.Hil.	Ermi	1	b, c
EUPHORBIACEAE	*Gymnanthes concolor* Spreng.	Gyco	2	a
	Pachystroma longifolium (Nees) Johnst.	Palo	4	a
	Sebastiania brasiliensis Spreng.	Sebr	3	a, b
	Sebastiania serrata (M.Arg.) M.Arg.	Sese	3	a, b
	Croton cf. *nitrariaefolius* Baill.	Crni	1	b, c
	Croton cf. *thermarum* Müll.Arg.	Crth	1	b, c
FABACEAE	*Calliandra tweediei* Benth.	Catw	2	a, b
	Collaea stenophylla Benth.	Cost	1	b
	Mimosa parvipinna Benth.	Mipa	1	b, c
ICACINACEAE	*Citronella paniculata* (Mart.) R.A.Howard	Cipa	2	a

LAMIACEAE	*Hyptis mirabilis* Briq.	Hymi	1	b
LAURACEAE	*Aiouea saligna* Meis.	Aisa	4	a
	Endlicheria paniculata (Spreng.) Macbr.	Enpa	2	a
	Nectandra megapotamica (Spreng.) Mez	Neme	5	a
	Ocotea indecora Schott ex Meissn.	Ocin	4	a
	Ocotea pulchella Mart.	OCpu	4	a
	Ocotea silvestris Vattimo -Gil	Ocsi	4	a
	Ocotea puberula Nees	Ocpu	5	a, b
LOGANIACEAE	*Strychnos brasiliensis* (Spreng.) Mart.	Stbr	2	a
MALVACEAE	*Triumfetta semitriloba* Jack.	Trse	1	a
	Pavonia hastata Cav.	Paha	1	b, c
	Sida rhombifolia L.	Sirh	1	b, c
MELASTOMATACEAE	*Miconia hyemalis* A.St.Hil. et Naud.	Mihy	1	a
MELIACEAE	*Cabralea canjerana* (Vell.) Mart.	Caca	5	a
	Trichilia claussenii C.DC.	Trcl	4	a, b
	Trichilia elegans A.Juss.	Trel	2	a
MONNIMIACEAE	*Mollinedia elegans* Tul.	Moel	1	a,b
MORACEAE	*Sorocea bonplandii* (Bail.) Burg. Lanj. et Boer	Sobo	2	a
	Ficus organensis (Miq.) Miq.	Fior	5	c
MYRSINACEAE	*Myrsine guianensis* (Aubl.) Kuntze	Mygu	3	a
	Myrsine coriacea (Sw.) R. Br.	Myco	4	a, b, c
	Myrsine umbellata Mart.	Myum	4	a, b, c
MYRTACEAE	*Blepharocalyx salicifolius* (Kunth) O.Berg	Blsa	3	a
	Campomanesia xanthocarpa O.Berg	Caxa	4	a
	Eugenia involucrata DC.	EUin	3	a
	Eugenia rostrifolia D.Legrand	Euro	4	a
	Eugenia schuechiana O.Berg	Eusc	2	a
	Eugenia uniflora L.	Euun	2	a
	Eugenia uruguayensis Camb.	Euur	2	a
	Myrcia glabra (Berg) Legr.	Mygl	2	a
	Myrcianthes gigantea (Legr.) Legr.	Mygi	3	a
	Psidium sp.	Pssp	1	b
	Campomanesia aurea O.Berg	Caau	2	a, b, c
	Eugenia hyemalis Camb.	Euhy	2	a, b, c
	Myrcia palustris (DC.) Kausel	Mypa	2	a, b, c
	Myrciaria cuspidata O.Berg	Mycu	2	a, b, c
NYCTAGINACEAE	*Guapira opposita* (Vell.) Reitz	Guop	4	a, b
OPILIACEAE	*Agonandra brasiliensis* Benth. & Hook.f.	Agbr	3	a
PIPERACEAE	*Piper gaudichaudianum* Kunth	Piga	1	a
PROTEACEAE	*Roupala brasiliensis* Klotz.	Robr	4	a
QUILLAJACEAE	*Quillaia brasiliensis* (A.St.Hil. et Tul.) Mart.	Qubr	4	a, b
ROSACEAE	*Prunus myrtifolia* Koehne	Prse	4	a
RUBIACEAE	*Faramea montevidensis* Cham.	Fama	2	a
	Psychotria brachyceras M.Arg.	Psbr	1	a
	Rudgea parquioides (Cham.) M.Arg.	Rupa	1	a
	Psychotria carthagenensis Jacq.	Psca	1	a, b
	Psychotria leiocarpa Cham. et Schtdl.	Psle	1	a, b
	Guettarda uruguensis Cham. et Schtdl.	Guur	2	a, b
RUTACEAE	*Zanthoxylum rhoifolium* Lam.	Zarh	4	a, b, c
SALICACEAE	*Casearia decandra* Jacq.	Cade	2	a
	Casearia sylvestris Sw.	Casi	3	a

	Xylosma pseudosalzmannii Sleumer	Xyps	4	a
	Banara parviflora (Gray) Benth.	Bapa	4	a
SAPINDACEAE	*Allophylus edulis* (A.St.Hil.) Radlk.	Aled	3	a
	Cupania vernalis Cambess	Cuve	4	a, b
	Matayba elaeagnoides Radlk.	Mael	4	a, b
	Dodonaea viscosa (L.) Jacq.	Dovi	2	a, b, c
SAPOTACEAE	*Chrysophyllum marginatum* (Hook. et Arn.) Radlk.	Chma	2	a
SOLANACEAE	*Cestrum strigillatum* Ruiz et Pav.	Cest	1	a, b
	Solanum sanctaecatharinae Dunal	Sosa	2	a, c
STYRACACEAE	*Styrax leprosum* Hook. et Arn.	Stle	3	a, b, c
SYMPLOCACEAE	*Symplocos tetrandra* Mart. ex Miq.	Syte	2	a, b
	Symplocos uniflora (Pohl) Benth.	Syun	2	a, b, c
THYMELAEACEAE	*Daphnopsis racemosa* Griseb.	Dara	2	a
URTICACEAE	*Coussapoa microcarpa* (Schott) Rizzini	Comi	5	a

Appendix 2. Species belonging to the defined PFTs in the forest-grassland transition analysis (Table 2). Understory shrubs are underlined. See species code in Appendix 1.

PFT	nº sp	Species code
PFT 1	11	Mael, Zarh, Stle, Guur, Casi, Libr, Sese, Xips, Blsa, Mygu, Bapa
PFT 2	17	Syun, Ageu, Catw, Mycu, Syte, Caau, Guur, Euhy, Mypa, Psca, Euur, Cest, Maca, Mihi, Dara, Stbr, Ildu
PFT 3	29	Myco, Myum, Ocin, Guop, Rupa, Mygi, Ocpu, Euro, Trcl, Aisa, Sobo, Gaga, Mygl, OCpu, Buca, Fama, Syro, Caca, Gyco, Euun, Scmo, Qubr, Neme, Ocsi, Cipa, Robr, Euin, Palo, Comi
PFT 4	20	Dovi, Chma, Stle, Aled, Trel, Eusc, Moel, Diin, Cuve, Erar, Psle, Guur, Aisa, Sebr, Rosy, Prse, Caca, Cade, Jubr, Enpa
PFT 5	2	Opmo, Cehi
PFT 6	18	Mael, Syun, Zarh, Catw, Mycu, Syte, Casi, Euhy, Psca, Sosa, Xips, Euur, Cest, Maca, Mihi, Mygu, Trse, Bapa
PFT 7	25	Dovi, Chma, Stle, Aled, Trel, Eusc, Rupa, Moel, Diin, Cuve, Psbr, Erar, Psle, Sobo, Gaga, Sebr, Fama, Prse, Caca, Cade, Piga, Gyco, Jubr, Caxa, Agbr
PFT 8	14	Myco, Myum, Ocin, Guop, Mygi, Ocpu, Euro, Trcl, Aisa, OCpu, Syro, Neme, Ocsi, Robr
PFT 9	4	Guop, Mygi, Mygl, Euun

Appendix 3. Species belonging to the defined PFTs in border and grassland plots in relation to elapsed time since last fire (Table 3). Treelets or tree species have underline code (Appendix 1).

PFT	nº sp.	Species code
PFT 1	21	Mael, Syun, Zarh, Myco, Myum, Ageu, Mycu, Mypa, Maca, Syte, Guop, Cuve, Sebr, Ocpu, Trcl, Diin, Stle, Euhy, Sese, Qubr, Buca
PFT 2	21	Venu, Baco, Scwe, Mycu, Hymi, Baoc, Euli, Batr, Baar, Euin, Pola, Bapa, Base, Paha, Eupe, Maca, Eutw, Vesu, Bale, Euhy, Cost
PFT 3	27	Syun, Myco, Ageu, Baco, Scwe, Mycu, Libr, Baoc, Euli, Euin, Caau, Bapa, Base, Paha, Mypa, Crni, Cest, Guur, Syte, Mipa, Psca, Catw, Stle, Euhy, Sese, Cost, BAtr
PFT 4	30	Venu, Pssp, Dovi, Baco, Scwe, Hymi, Baoc, Euli, Batr, Baar, Euin, Pola, Caau, Badr, Bapa, Base, Heps, Crth, Paha, Eupe, Crni, Psle, Moel, Mipa, Psca, Eutw, Sirh, Opmo, Cost, Ermi

CONSIDERAÇÕES FINAIS

Os padrões de borda de floresta-campo das espécies lenhosas em relação às variáveis químicas e estruturais do solo demonstraram que estas não são um impedimento para o avanço de espécies florestais sobre o campo, uma vez que a distância espacial do limite florestal e as mudanças graduais destas variáveis no gradiente floresta-campo parecem sugerir que o solo é antes uma conseqüência da expansão florestal sobre as áreas de campo que um fator condicionante. Há, entretanto, diferenças significativas entre as exposições norte e sul, principalmente relacionadas à profundidade do solo, ao pH, às proporções de alumínio (Al, Al+H, Al_{sat}), à percentagem de saturação de bases e às proporções de argila, cascalho e areia nos primeiros 10 cm de profundidade do solo. Diferenças entre norte e sul também ocorrem no padrão de densidade de espécies lenhosas no campo, porém o maior número de espécies e indivíduos de arbustos e árvores nas áreas com exposição predominante norte demonstram que estas diferenças não são um fator limitante para os processos de expansão e adensamento de lenhosas no campo. Além disso, o maior conteúdo de argila nos locais de exposição sul, associada à menor riqueza, diversidade e densidade de arbustos e árvores parece sugerir que condições de déficit hídrico não seriam um fator limitador para a colonização de espécies arbóreas no campo, pelo menos em anos normais. Estudos específicos sobre processos de germinação, estabelecimento e recrutamento de arbustos e árvores na matriz campestre são necessários para conclusões mais apuradas.

As queimadas regulares, o histórico de fogo da região, parecem, todavia, ser o fator mais limitante do avanço florestal sobre o campo. As variáveis de solo supracitadas, assim como a maior ou menor presença de matacões no relevo, também condicionam diferenças no estrato de gramíneas, a principal fonte de combustão para o fogo. As áreas do topo-sul, com solos mais profundos, maior conteúdo de argila e menor quantidade de matacões, geralmente apresentam um estrato de gramíneas mais denso e contínuo que as áreas de exposição norte. A passagem do fogo é, portanto, mais heterogênea nesta última. A heterogeneidade das queimadas proporciona sítios de menor intensidade de fogo, que por sua vez podem permitir o recrutamento de espécies arbóreas, normalmente mais suscetíveis ao fogo.

Locais com indivíduos arbóreos isolados no campo freqüentemente coincidiram com a presença de rochas, matacões. Estes indivíduos, uma vez estabelecidos, conseguem resistir às injúrias freqüentes pelo fogo, pois a intensidade tende a ser menor nestes locais (menor produção de biomassa de gramíneas). Tais indivíduos, assim como os blocos de rochas no campo, conduzem a um tipo de mecanismo de expansão florestal que ocorre “aos saltos”. Ou seja, a fauna dispersora seria atraída até estes locais pela oferta de alimento, refúgio ou heterogeneidade vertical na paisagem, trazendo consigo novas sementes e a possibilidade de novos indivíduos arbóreos serem recrutados, formando pequenos núcleos de espécies arbóreas florestais no campo. A expansão destes núcleos estaria, porém, condicionada por períodos de menor freqüência/intensidade das queimadas, em anos de pluviosidade regular.

Ambientes menos suscetíveis à severidade do fogo, à falta de umidade e à competitividade das gramíneas também ocorrem próximo ao limite florestal. O avanço gradual de espécies florestais junto à borda constitui outro mecanismo de expansão florestal nas áreas de mosaicos de floresta-campo. Se considerássemos a ausência ou a menor freqüência do fogo, este mecanismo de expansão florestal seria, porém, relativamente mais lento que o avanço aos saltos, conforme sugerem os padrões de transição floresta-campo nas áreas de encosta norte.

A atuação continuada de eventos de fogo nas áreas de campo adjacentes às florestas tem resultado num padrão de bordas abruptas. A transição do limite da borda florestal para áreas mais internas da floresta ocorre muito bruscamente. Diferenças estruturais relacionadas principalmente ao componente arbóreo florestal, tais como riqueza, diversidade e densidade de espécies arbóreas, ocorrem mais marcadamente nos primeiros 15 metros do limite com o campo.

A presença de um grande número de espécies lenhosas, principalmente arbustos, com capacidade de rebrote após o fogo nas áreas de campo também corrobora o fato destas comunidades estarem condicionadas pela influência das queimadas. O recrutamento de indivíduos de espécies que não apresentam esta habilidade (emitir novos ramos da base do caule, junto à superfície do solo, após a passagem do fogo) limita-se às áreas próximas da borda florestal e ou áreas de campo com maior intervalo de tempo sem fogo.

O atual regime de fogo, com uma freqüência de queimadas entre (dois)três e cinco anos, não limita nem diminui a densidade das espécies arbustivas do campo, principalmente asteráceas, considerando que a maioria têm habilidade para rebrotar vigorosa e rapidamente já no primeiro ano após o evento de fogo e que arbustos que não rebrotam (*seeders obligate*) atingem taxas bastante elevadas de estabelecimento/recrutamento num período de dois anos. Por outro lado, o número de indivíduos arbóreos no campo é bastante restrito em decorrência do atual regime de fogo. A maior densidade de indivíduos jovens e a tímida taxa de recrutamento observada nas áreas não queimadas (por aproximadamente 4 anos), onde havia maior densidade de arbustos potencialmente maiores (*seeders obligate*), e na borda permitem sugerir a ocorrência de um processo de facilitação na colonização de árvores no campo pela presença de um estrato arbustivo mais alto, caso houvesse períodos mais longos de exclusão do fogo. Outros estudos especificamente focados neste aspecto são imprescindíveis para corroborar essa idéia.

A avaliação dos padrões na transição floresta-campo pelos tipos funcionais de plantas (*plant functional types,* PFTs) de espécies lenhosas florestais demonstra claramente que atributos relacionados com a sobrevivência ao fogo nas áreas de campo, principalmente a capacidade de rebrote, são fundamentais para o potencial avanço e expansão da floresta. Como conseqüência, poucas espécies tipicamente pioneiras são observadas na matriz campestre, uma vez que estas normalmente são de crescimento rápido, o que não condiz com tipos que investem em órgãos subterrâneos e que rebrotam após o fogo.

Ainda em relação ao mecanismo de nucleação florestal na matriz campestre, a restrição de PFTs florestais jovens a locais próximos da borda ou sob indivíduos florestais adultos na matriz campestre corrobora a potencial expansão florestal em sítios favoráveis. A diversidade de PFTs arbóreos, assim como foi verificado para a diversidade específica, é maior nas áreas de borda, principalmente até aproximadamente os primeiros 15 metros.

A dinâmica de PFTs arbustivos com e sem capacidade de rebrote nas áreas de campo conforme o período de tempo após a última queimada reforçam o fato de que tais comunidades são resilientes ao atual regime de fogo. Isto é, eventos de queimadas em intervalos de três a cinco anos não inibem a presença nem a densidade de indivíduos arbustivos típicos de vegetação campestre, porém favorecem aqueles que rebrotam, restringindo os demais aos locais com maior intervalo sem fogo. Esse padrão espacial é dinâmico no tempo, alternando diferentes fisionomias de campo conforme os intervalos de queima, de um a cinco anos. Processos de expansão florestal ficam, portanto, restritos a pequenas manchas, cuja intensidade do fogo tende a ser menor. O atual regime de fogo é o principal mantenedor da paisagem de mosaicos de floresta-campo na área de estudo.

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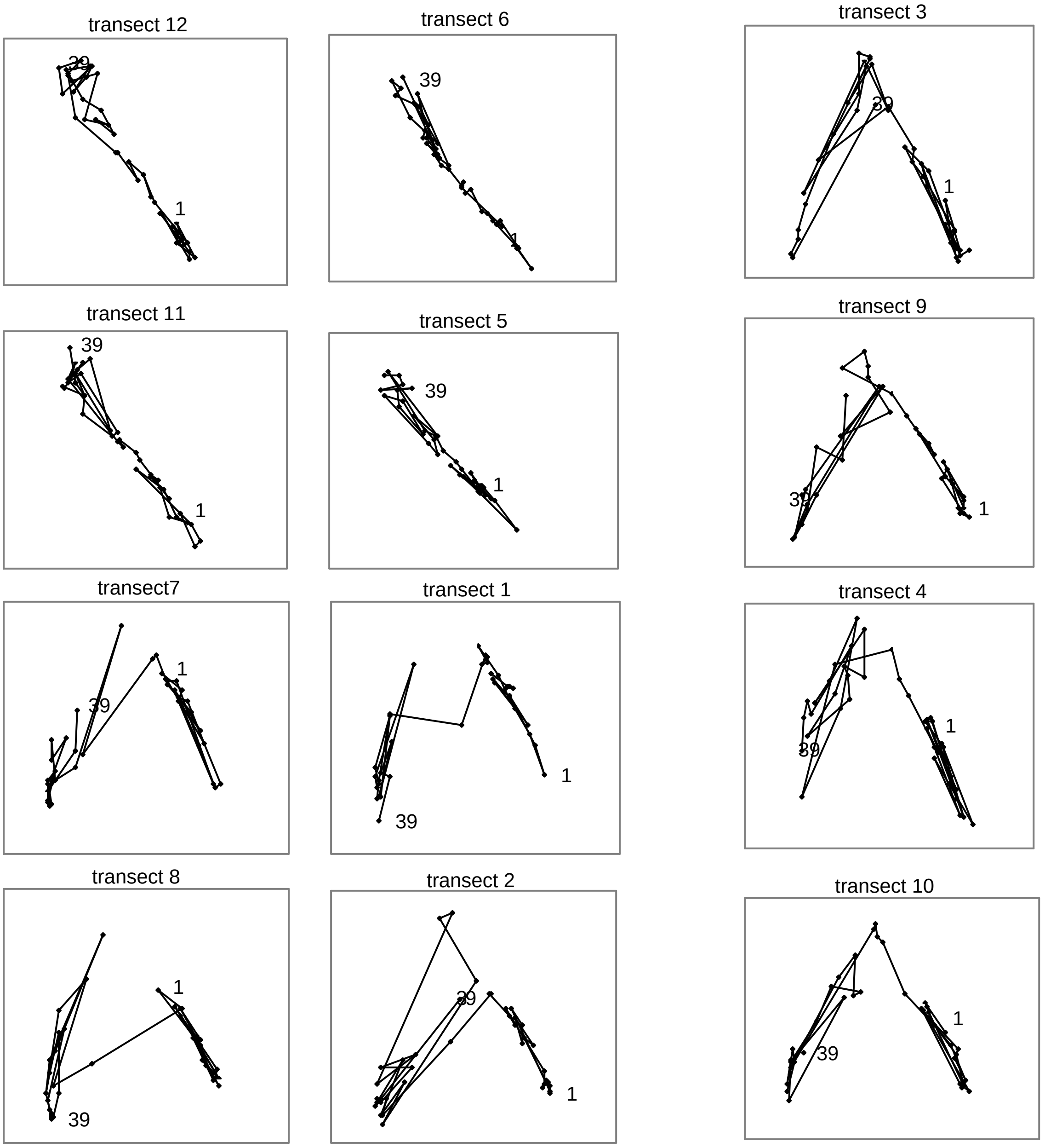
ANEXOS

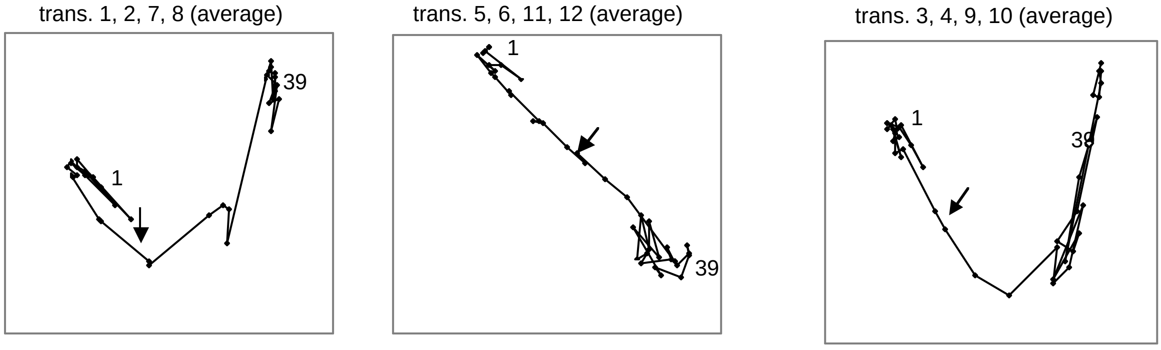
Anexo 1: Trajetórias individuais de cada transecção, com base nos quadros pequenos do PRIMEIRO CAPÍTULO, e trajetórias médias, conforme figura 4 do capítulo.

a) Pares onde foi realizada a queima experimental (outubro, 2002). Na esquerda, as transecções queimadas e na direita seu respectivo par não-queimado

Transecções onde não houve a queima experimental, pois a área tinha queimado Janeiro de 2002.

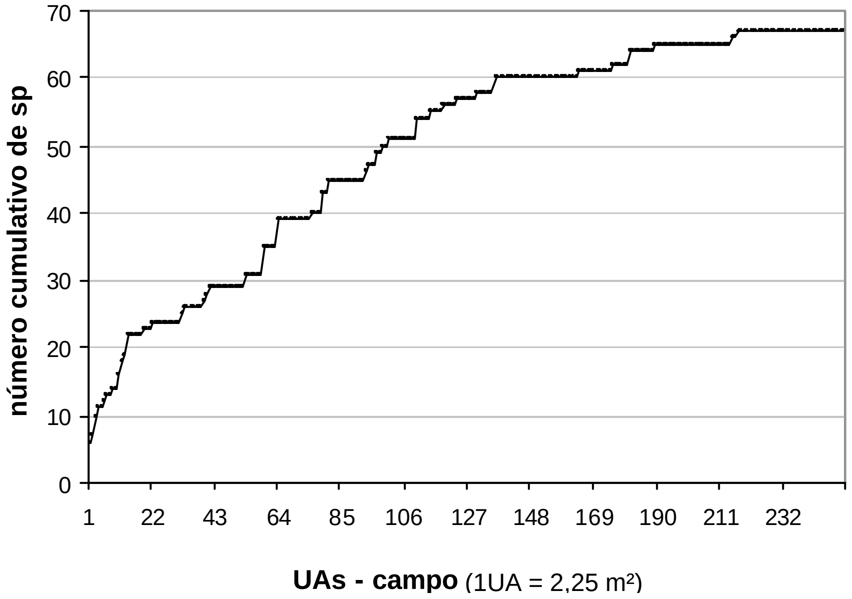


b) Três trajetórias médias. Resultado da junção de trajetórias similares (acima). Os três padrões coincidem com a exposição do relevo (da esquerda para a direita: sul, norte e sudoeste)

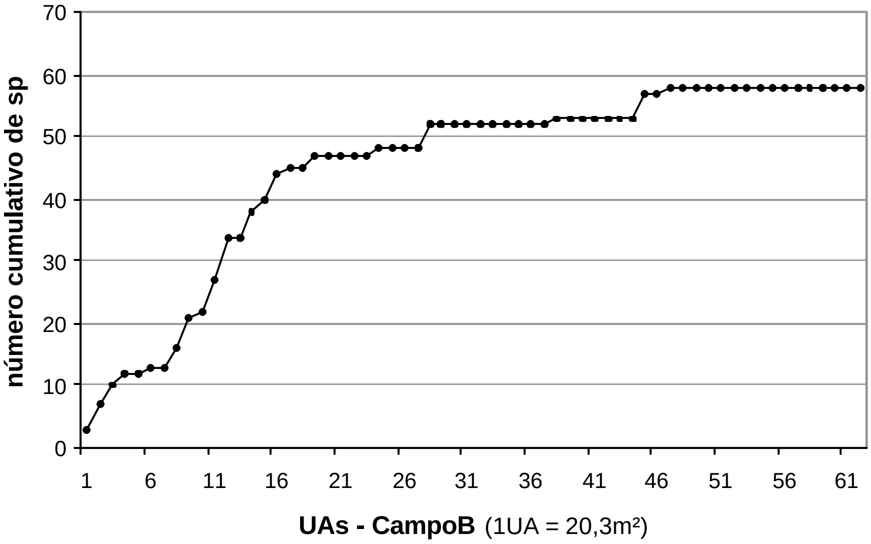


Anexo 2: Curvas de espécie área considerando todos os quadros de campo, conforme o levantamento realizado em novembro-dezembro/2003 (2º levantamento). Na fig. A foram considerados os quadros pequenos (small plots; critério de inclusão =10cm de altura) e na fig. B os quadros grandes (large plots, critério de inclusão =80cm de altura). O total de área amostrada foi 567 m² (252 unidades amostrais, UAs) e 1701 m² (84 UAs) nas Figs. A e B, respectivamente.

A) small plots – grassland portion

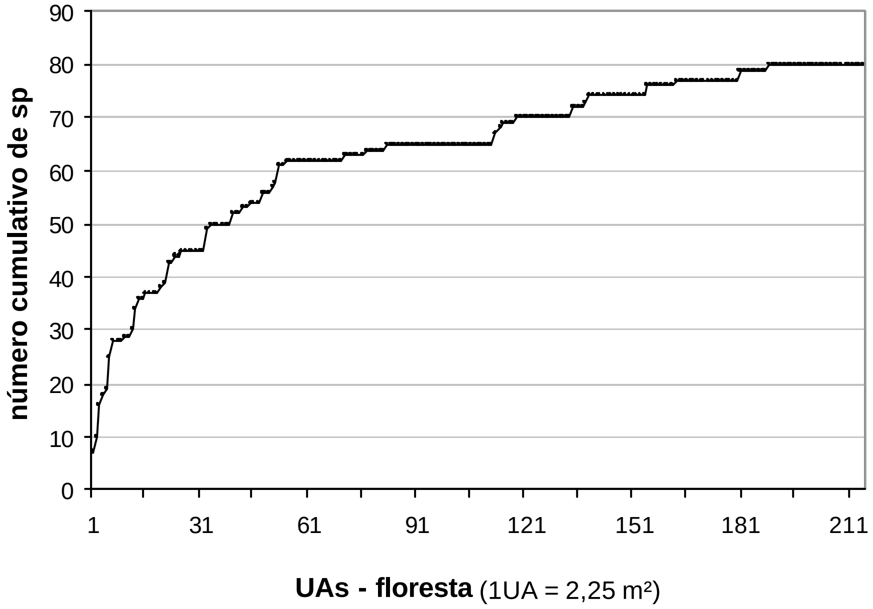


B) large plots – grassland portion

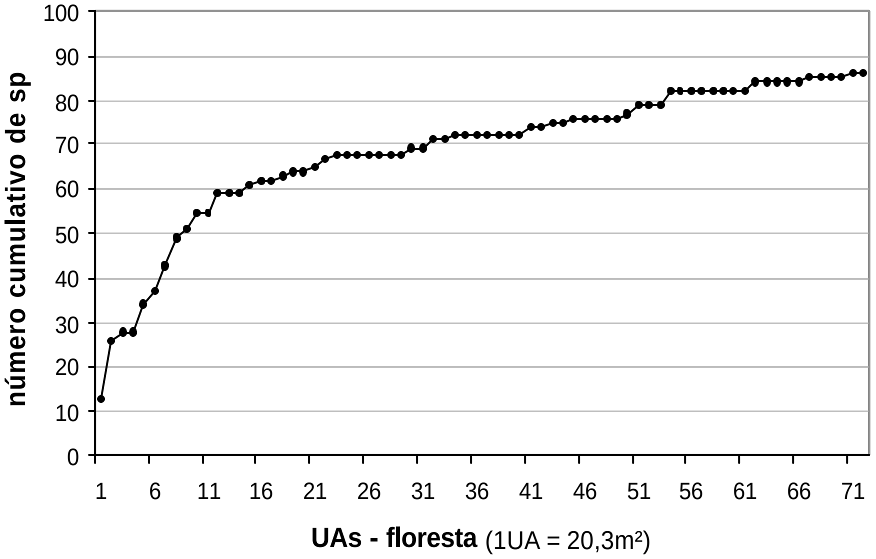


Anexo 3: Curvas de espécie área considerando todos os quadros da floresta. Na fig. A foram considerados os quadros pequenos (small plots; critério de inclusão =10cm de altura) e na fig. B os quadros grandes (large plots, critério de inclusão =80cm de altura). O total de área amostrada foi 486 m² (216 unidades amostrais, UAs) e 1458 m² (72 UAs) nas Figs. A e B, respectivamente.

A) small plots – forest portion



B) large plots – forest portion



Anexo 4: Lista espécies amostradas nos dois levantamentos dos quadros de campo, ordenadas por família, referentes aos dados do SEGUNDO CAPÍTULO. Os códigos (*code*) deste anexo servem como base para os anexos

Family	**Species**	**Code**
ANACARDIACEAE	*Lithrea brasiliensis* March.	Libr
	Schinus weinmanniaefolius Engl.	Scwe
AQUIFOLIACEAE	*Ilex dumosa* Reiss.	Ildu
ARECACEAE	*Butia capitata* (Mart.) Becc.	Buca
ASTERACEAE	*Baccharidastrum triplinervium* (Less.) Cabrera	Btri
	Baccharis articulata (Cham.) Pers.	Baar
	Baccharis cf. pseudotenuifolia Teodoro Luis	Baps
	Baccharis cognata DC.	Baco
	Baccharis dracunculifolia DC.	Badr
	Baccharis leucopappa DC.	Bale
	Baccharis ochracea Spreng.	Baoc
	Baccharis patens Baker	Bapa
	Baccharis sessilifolia DC.	Base
	Baccharis trimera (Less.) DC.	Batr
	Eupatorium intermedium DC.	Eupi
	Eupatorium ligulaefolium Hook. et Arn.	Euli
	Eupatorium pedunculosum Hook. et Arn.	Eupe
	Eupatorium tweendianum Hook. et Arn.	Eutw
	Heterothalamus psiadioides Less.	Heps
	Porophyllum lanceolatum DC.	Pola
	Trixis stricta Spreng.	Trst
	Verbesina subcordata DC.	Vesu
	Vernonia nudiflora Less.	Venu
CACTACEAE	*Opuntia monacantha* Haw.	Opmo
CELASTRACEAE	*Maytenus cassineformis* Reiss.	Maca
EBENACEAE	*Diospyros inconstans* Jacq.	Diin
ERICACEAE	*Agarista eucalyptoides* (Cham. et Schl.) G. Don	Ageu
ERYTHROXYLACEAE	*Erythroxylum argentinum* O. Schulz	Erar
	Erythroxylum microphyllum A.St.Hil.	Ermi
EUPHORBIACEAE	*Alchornea triplinervia* (Spreng.) M.Arg.	Altr
	Croton cf. *nitrariaefolius* Baill.	Crni
	Croton cf. *thermarum* Müll.Arg.	Crth
	Sebastiania brasiliensis Spreng.	Sebr
	Sebastiania serrata (M.Arg.) M.Arg.	Sese
FABACEAE	*Calliandra tweedii* Benth.	Catw
	Collaea stenophylla Benth.	Cost
	Mimosa parvipinna Benth.	Mipa
LAMIACEAE	*Hyptis mirabilis* Briq.	Hymi
LAURACEAE	*Ocotea pulchella* Mart.	OCpu
MALVACEAE	*Pavonia hastata* Cav.	Paha
	Sida rhombifolia L.	Sirh

MELASTOMATACEAE	*Miconia hyemalis* A.St.Hil. et Naud.	Mihi
MELIACEAE	*Cabralea canjerana* (Vell.) Mart.	Caca
	Trichilia claussenii C.DC.	Trcl
MONNIMIACEAE	*Mollinedia elegans* Tul.	Moel
MORACEAE	*Ficus organensis* (Miq.) Miq.	Fior
MYRSINACEAE	*Myrsine coriacea* (Sw.) R. Br.	Myco
	Myrsine guianensis (Aubl.) Kuntze	Mygu
	Myrsine umbellata Mart.	Myum
MYRTACEAE	*Campomanesia aurea* O.Berg	Caau
	Eugenia dimorpha O.Berg	Eudi
	Eugenia hyemalis Camb.	Euhy
	Eugenia uniflora L.	Euun
	Eugenia uruguayensis Camb.	Euur
	Myrcia palustris (DC.) Kausel	Mypa
	Myrciaria cuspidata O.Berg	Mycu
	Psidium sp.	Pssp
NYCTAGINACEAE	*Guapira opposita* (Vell.) Reitz	Guop
QUILLAJACEAE	*Quillaia brasiliensis* (A.St.Hil. et Tul.) Mart.	Qubr
RUBIACEAE	*Psychotria carthagenensis* Jacq.	Psca
	Psychotria leiocarpa Cham. et Schtdl.	Psle
	Zanthoxylum rhoifolium Lam.	Zarh
SALICACEAE	*Casearia decandra* Jacq.	Cade
	Casearia decandra Jacq.	Cade
SAPINDACEAE	*Allophylus edulis* (A.St.Hil.) Radlk.	Aled
	Cupania vernalis Cambess	Cuve
	Dodonaea viscosa (L.) Jacq.	Dovi
	Matayba elaeagnoides Radlk.	Mael
SOLANACEAE	*Cestrum strigillatum* Ruiz et Pav.	Cest
	Solanum americanum Mill.	Soam
	Solanum sanctaecatharinae Dunal	Sosa
STYRACACEAE	*Styrax leprosum* Hook. et Arn.	Stle
SYMPLOCACEAE	*Symplocos tetrandra* Mart. ex Miq.	Syte
	Symplocos uniflora (Pohl) Benth.	Syun
VERBENACEAE	*Lantana camara* L.	Laca
	Lantana montevidensis (Spreng.) Briq.	Lamo

Anexo 5: Diversidade de Shannon* (H'), riqueza (S), densidade (ni), cobertura de copa (m^2) e cobertura basal (cm^2) de espécies lenhosas (valores médios e respectivas significâncias após análise de variância pelo método de aleatorização), considerando os quadros grandes (large plots, LP= somente plantas =80 cm de altura) das áreas de campo do sul e do norte, os quais compunham transecções paralelas com e sem o tratamento de queima experimental em outubro de 2002. As transecções do sudoeste não foram incluídas nesta análise por não permitirem o contraste do tratamento de queima experimental. ns= non-significant, * $p \le 0.05$, ** $p \le 0.01$, *** $p \le 0.001$. (Referente ao SEGUNDO CAPÍTULO)

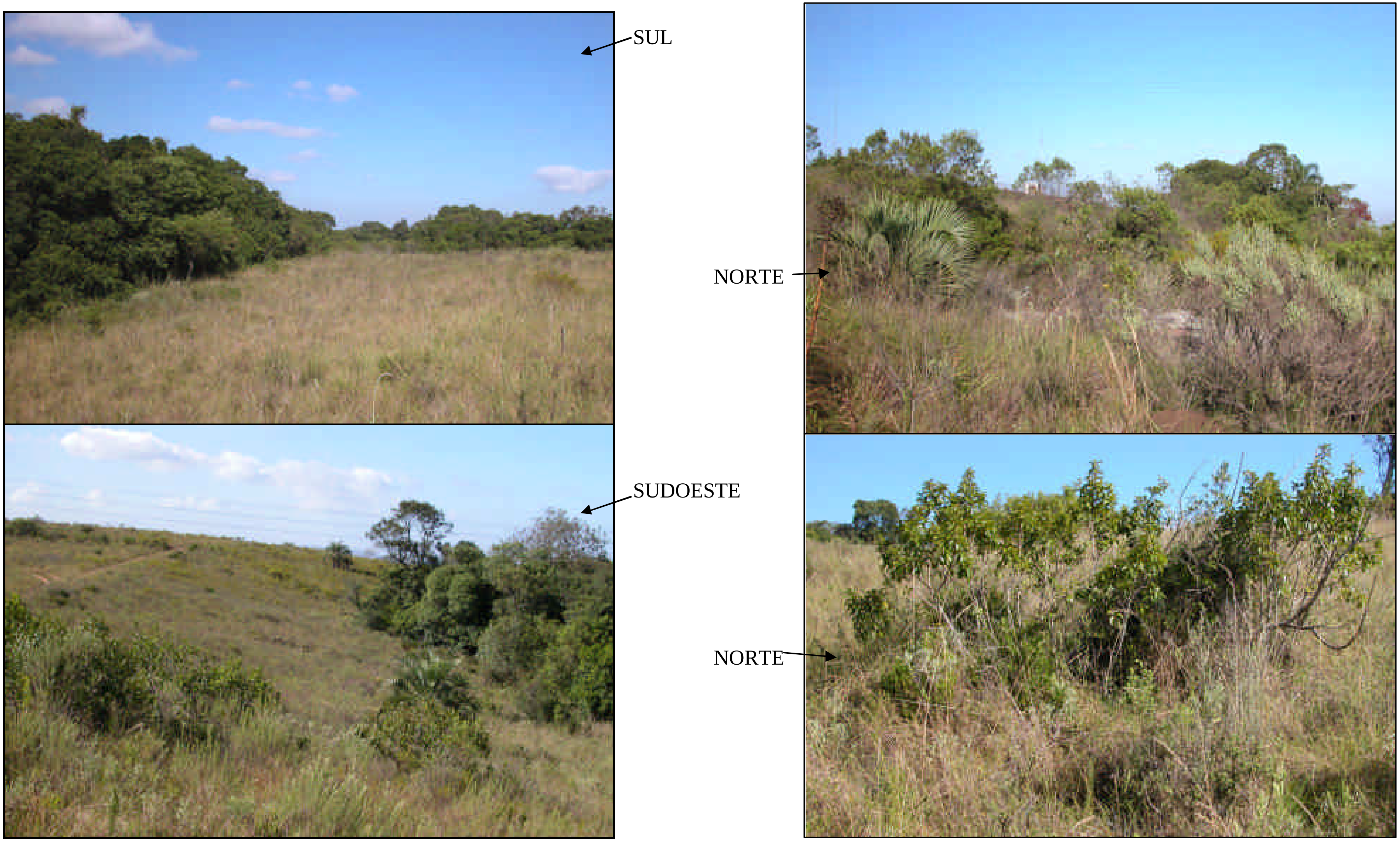
Parâmetro	*sul*	*norte*		*queima*	*não-queima*		*1º lev.*	*2º lev.*	
NORTE & SUL (2º lev.)	(n=52)	(n=44)		(n=52)	(n=44)				
H' (nats)				0,71	1,06	**			
Riqueza (S)	1,15	3,10	***	0,81	3,68	***			
Densidade (ni)	2,00	8,33	***	1,50	9,50	***			
Cobertura copa (m^2)	0,81	4,05	***	1,02	4,10	***			
Cobertura basal (cm^2)	5,60	53,24	***	30,08	28,64	ns			
SUL (1º & 2º lev.)				(n=28)	(n=20)		(n=24)	(n=24)	
Riqueza (S)				0,32	2,30	***	1,08	1,21	ns
Densidade (ni)				0,573	4,00	***	2,00	2,00	ns
Cobertura copa (m^2)				0,10	1,79	***	0,75	0,86	ns
Cobertura basal (cm^2)				0,71	12,45	***	4,93	6,27	ns
NORTE (1º & 2º lev.)				(n=24)	(n=24)		(n=24)	(n=24)	
Riqueza (S)				1,37	4,83	***	2,87	3,33	ns
Densidade (ni)				2,58	14,08	***	8,79	7,87	ns
Cobertura copa (m^2)				2,09	6,02	*	3,98	4,12	ns
Cobertura basal (cm^2)				64,35	42,13	ns	53,24	55,20	ns

* = somente os quadros com pelo menos 1 indivíduo foram considerados para o cálculo de H'.

Anexo 6: Lista de espécies amostradas nos quadros grandes (LP, large plots: =80 cm de altura) no 1º e no 2º levantamento de acordo com os valores totais de densidade (ni), cobertura basal (Cbasal) e cobertura de copa (Ccopa) em cada um dos grupos de tempo após o último fogo (groups of elapsed time since the last fire in grassland – groups 1 to 3) nos quadros de campo e na borda (border). (Referente ao SEGUNDO CAPÍTULO)

	1º LEVANTAMENTO												**2º LEVANTAMENTO**											
	Group1			**Group2**			**Group3**			**Border**			**Group1**			**Group2**			**Group3**			**Border**		
code	(ni)	Cbasal (cm^2)	Ccopa (m^2)	(ni)	Cbasal (cm^2)	Ccopa (m^2)	(ni)	Cbasal (cm^2)	Ccopa (m^2)	(ni)	Cbasal (cm^2)	Ccopa (m^2)	(ni)	Cbasal (cm^2)	Ccopa (m^2)	(ni)	Cbasal (cm^2)	Ccopa (m^2)	(ni)	Cbasal (cm^2)	Ccopa (m^2)	(ni)	Cbasal (cm^2)	Ccopa (m^2)
Ageu	-	-	-	-	-	-	1	14.3	0.9	3	20.6	1.8	4	11.8	0.7	-	-	-	3	18.3	2.1	7	38.1	2.9
Aled	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	0.7	0.2
Baar	-	-	-	-	-	-	11	16.6	1.9	-	-	-	-	-	-	1	3.9	0.6	12	28.4	3.9	-	-	-
Baco	-	-	-	8	9.5	2.4	20	27.7	3.7	-	-	-	4	5.4	1.5	16	21.3	5.5	7	12.5	1.6	4	3.3	0.7
Badr	-	-	-	-	-	-	21	38.2	7.0	1	0.6	0.2	-	-	-	-	-	-	21	40.8	7.4	1	0.8	0.1
Bale	-	-	-	-	-	-	1	1.1	0.4	-	-	-	-	-	-	3	1.1	0.2	-	-	-	-	-	-
Baoc	-	-	-	3	1.1	0.2	2	1.2	0.5	-	-	-	-	-	-	2	1.7	0.4	1	0.4	0.1	1	0.5	0.2
Bapa	8	13.3	1.0	-	-	-	33	50.8	19.6	-	-	-	6	10.3	1.5	-	-	-	44	104.0	15.5	2	3.9	0.5
Base	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0.3	0.1	1	0.3	0.0
Batr	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2.1	0.3	-	-	-	-	-	-
Btri	-	-	-	-	-	-	-	-	-	2	13.3	1.5	-	-	-	-	-	-	-	-	-	3	11.6	2.4
Buca	-	-	-	2	5.1	1.6	-	-	-	1	107.5	0.8	-	-	-	-	-	-	-	-	-	1	86.6	0.8
Caau	-	-	-	-	-	-	5	1.5	0.1	-	-	-	-	-	-	-	-	-	-	-	-	4	2.0	0.2
Cade	-	-	-	-	-	-	-	-	-	3	10.1	2.7	-	-	-	-	-	-	-	-	-	4	14.9	3.1
Catw	1	1.0	0.1	-	-	-	1	4.2	1.1	-	-	-	-	-	-	-	-	-	-	-	-	5	6.4	1.8
Cest	-	-	-	1	2.2	0.7	-	-	-	1	3.1	0.5	-	-	-	1	4.5	1.0	-	-	-	1	3.3	1.2
Cost	-	-	-	2	1.5	0.4	-	-	-	-	-	-	-	-	-	5	1.4	0.6	-	-	-	-	-	-
Crni	-	-	-	-	-	-	4	1.7	0.4	-	-	-	-	-	-	9	2.2	0.8	-	-	-	2	0.7	0.3
Crth	-	-	-	-	-	-	1	0.2	0.0	-	-	-	-	-	-	-	-	-	4	1.1	0.2	-	-	-
Cuve	-	-	-	-	-	-	1	1.1	0.2	-	-	-	-	-	-	-	-	-	-	-	-	1	1.8	0.3
Diin	-	-	-	-	-	-	-	-	-	1	0.5	0.0	-	-	-	-	-	-	-	-	-	-	-	-
Dovi	2	2.5	0.4	-	-	-	15	188.0	18.7	18	192.0	18.9	2	1.7	0.4	-	-	-	11	92.3	13.3	26	236.5	22.1
Erar	-	-	-	-	-	-	-	-	-	2	3.1	0.7	-	-	-	-	-	-	-	-	-	1	2.5	0.6
Ermi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1.2	0.2	-	-	-
Eudi	-	-	-	-	-	-	1	2.5	0.2	-	-	-	-	-	-	-	-	-	2	5.9	0.8	-	-	-
Euhi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0.2	0.2
Euli	5	5.5	0.9	13	13.3	3.3	40	34.4	6.3	1	0.2	0.0	6	12.0	1.6	23	33.7	6.6	21	21.7	3.0	8	11.0	1.9

Eupe	-	-	-	-	-	-	2	0.8	0.3	3	1.2	0.3	-	-	-	-	-	-	-	-	-	-	-	-
Eupi	6	42.2	4.2	-	-	-	9	42.4	3.9	2	2.7	0.1	-	-	-	-	-	-	6	38.6	3.8	8	77.7	8.8
Eutw	-	-	-	-	-	-	1	1.1	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Euun	-	-	-	-	-	-	-	-	-	1	0.1	0.0	-	-	-	-	-	-	-	-	-	1	0.4	0.2
Guop	-	-	-	-	-	-	-	-	-	1	17.3	0.8	-	-	-	-	-	-	-	-	-	3	28.0	1.5
Guur	-	-	-	1	2.1	0.4	-	-	-	2	3.1	0.6	-	-	-	1	6.9	0.6	-	-	-	2	4.0	0.9
Heps	6	12.2	1.4	-	-	-	57	122.3	20.8	-	-	-	4	12.1	1.5	-	-	-	24	112.6	13.6	1	5.3	0.5
Hymi	-	-	-	-	-	-	-	-	-	2	0.8	0.2	-	-	-	-	-	-	-	-	-	-	-	-
Ildu	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3.5	0.2
Laca	-	-	-	-	-	-	-	-	-	2	1.5	2.5	-	-	-	-	-	-	-	-	-	3	8.8	4.0
Libr	4	8.0	0.8	3	11.2	1.8	-	-	-	1	9.7	0.6	4	9.9	1.4	2	17.4	2.1	-	-	-	5	19.3	3.2
Maca	1	1.3	0.1	-	-	-	-	-	-	-	-	-	4	3.6	0.4	-	-	-	-	-	-	1	0.8	0.1
Mael	-	-	-	2	18.2	0.7	1	27.9	1.9	1	2.3	0.2	-	-	-	2	14.2	1.2	-	-	-	2	30.4	1.2
Mihi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1.1	0.1
Mipa	2	2.6	0.4	-	-	-	16	14.7	4.1	-	-	-	2	6.7	2.2	-	-	-	10	8.4	3.1	-	-	-
Myco	-	-	-	-	-	-	-	-	-	7	43.8	3.5	-	-	-	-	-	-	-	-	-	8	20.5	2.4
Mycu	3	9.5	0.7	1	1.1	0.3	7	36.3	2.6	7	23.5	1.1	1	3.9	0.2	4	6.4	1.0	4	38.0	2.0	16	60.8	5.6
Mygu	-	-	-	-	-	-	1	23.8	1.7	2	21.5	2.6	-	-	-	-	-	-	1	28.3	2.5	2	34.5	3.6
Mypa	3	853.9	7.6	2	7.5	0.6	3	25.6	6.2	2	24.1	1.5	2	469.9	6.0	-	-	-	-	-	-	6	43.6	3.2
Myum	-	-	-	2	0.4	0.1	1	0.6	0.1	4	4.4	0.4	-	-	-	-	-	-	-	-	-	7	7.8	1.3
Opmo	-	-	-	-	-	-	2	89.5	0.4	-	-	-	-	-	-	-	-	-	-	-	-	2	74.4	0.7
Paha	-	-	-	3	0.4	0.1	3	0.8	0.3	1	0.1	0.0	1	0.2	0.0	15	4.8	0.9	2	0.4	0.1	9	2.1	0.5
Pola	-	-	-	27	6.4	1.8	5	1.4	0.1	2	0.4	0.0	9	3.3	0.7	49	19.1	4.5	4	1.4	0.4	14	5.0	1.0
Psca	-	-	-	3	1.3	0.6	-	-	-	1	5.0	1.0	-	-	-	-	-	-	-	-	-	4	4.1	1.1
Qubr	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0.5	0.1
Scwe	-	-	-	3	0.9	0.1	1	0.3	0.0	1	0.1	0.0	-	-	-	8	3.2	0.4	1	1.6	0.2	2	0.6	0.2
Sebr	-	-	-	3	2.9	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	5.7	0.7
Sese	-	-	-	-	-	-	-	-	-	2	8.1	0.4	-	-	-	-	-	-	-	-	-	5	9.9	2.2
Styl	-	-	-	-	-	-	1	3.8	0.6	1	1.1	0.1	-	-	-	-	-	-	-	-	-	3	6.6	1.4
Syte	-	-	-	1	1.5	0.2	-	-	-	1	1.3	0.2	-	-	-	-	-	-	-	-	-	1	2.0	0.3
Syun	10	185.4	27.1	2	22.0	2.3	3	175.9	9.4	1	232.6	8.3	2	123.7	15.0	2	30.9	3.2	1	81.0	11.0	12	372.3	25.0
Trcl	-	-	-	2	4.0	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	4.5	0.6
Trst	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	5.7	0.7	1	1.1	0.0
Venu	-	-	-	1	0.8	0.0	1	0.3	0.2	-	-	-	1	0.4	0.1	-	-	-	2	0.8	0.6	1	0.2	0.1
Zarh	-	-	-	1	3.8	0.1	-	-	-	-	-	-	-	-	-	-	-	-	1	1.3	0.2	3	4.3	0.4



Anexo 7: Imagens comparativas de transição floresta-campo em áreas no sul, sudoeste e norte do Morro Santana, Porto Alegre, RS.

Área próxima as transecções T3 e T4, antes da queimada ocorrida em Janeiro de 2001

esmo local, cerca de 9 meses depois do fogo

Recrutamento de arbustos (*H. psiadioides*), cerca de 1 anos após

Mesmo local que das fotografias acima, em janeiro de 2004

⇐ vista do *Baccharis dracunculifolia* e *H. psiadioides* em áreas de campo sem fogo a pelo menos 3 anos. Espécies sem capacidade de rebrotar

Anexo 8: Seqüência temporal de uma área de campo onde predominam espécies “seeders obligate” no Morro Santana, Porto Alegre, RS.

Agarista eucalyptoides na borda da floresta

Indivíduo jovem de *A. eucalyptoides*

Detalhe da caule

Myrciaria cuspidata e *Maytenus casseniformis* nos matacões

Lithrea brasiliensis rebrotando após
o experimento de queima

Anexo 9: Alguns detalhes em espécies de arbóreas relacionados à capacidade de tolerar o fogo e continuar pemanecendo no campo.

Myrsine umbellata e *M. cuspidata*

Myrcia palustris

núcleos de expansão florestal em áreas de campo

Anexo 10: Seqüência de fotos que demonstram a preferência no estabelecimento de espécies arbóreas nas áreas de campo do Morro Santana e a tendência na formação de núcleos (manchas) florestais na matriz campestre.

Anexo 11: Demonstração do experimento de queimada e do rápido rebrote de espécies lenhosas. P.ex.: *Baccharis cognata*.