UNIVERSIDADE ESTADUAL DE CAMPINAS

VALÉRIA FORNI MARTINS

DISPERSÃO DIRECIONAL POR FORMIGAS E FASE REGENERATIVA PÓS-DISPERSÃO DA ESPÉCIE RUDERAL

Ricinus communis L. (EUPHORBIACEAE)

Tese apresentada ao Instituto de Biologia para obtenção do Título de Mestre em Ecologia.

Orientador: Prof. Dr. João Semir

Co-Orientadora: Prof^a. Dr^a. Claudia Regina Baptista Haddad

Campinas, 2006



BIB 1D1 385911

FICHA CATALOGRÁFICA ELABORADA PELA BIBLIOTECA DO INSTITUTO DE BIOLOGIA – UNICAMP

Título em inglês: Directed dispersal by ants and post-dispersal regenerative phase of the ruderal species *Ricinus communis* L. (Euphorbiaceae).

Palavras-chave em inglês: Seed bank; Plant competition; Elaiosome; Ant nests; Germination.

Área de concentração: Ecologia.

Titulação: Mestre em Ecologia.

Banca examinadora: João Semir, Ivany Ferraz Marques Válio, Caio Graco Machado Santos.

Data da defesa: 01/06/2006.

Campinas, 01 de junho de 2006

BANCA EXAMINADORA

João Semir Prof. Dr. João Semir (Orientador) Prof. Dr. Ivany Ferraz Marques Válio Prof. Dr. Caio Graco Machado Santos

Prof. Dr. Flavio Antonio Maës dos Santos

Prof. Dr. Marco Antonio Assis

CONTEÚDO

Agradecimentos Página 05
Resumo Página 07
Abstract Página 09
Introdução Página 1
Objetivos Página 18
Descrição da espécie Página 19
Literatura citada Página 22
Do ants act as directed dispersers of a typically myrmecochorous species? An analysis
of myrmecochory effects on the multi-step process from post-dispersed seeds to
established juveniles of <i>Ricinus communis</i> (Euphorbiaceae) Página 29
Post-dispersal regenerative phase of Ricinus communis L. (Euphorbiaceae): do ruderal
features assure the species ability to successfully occupy new habitats? Página 49
Considerações finais Página 78
Literatura citada Página 80

AGRADECIMENTOS

Agradeço a:

Paulo Roberto Guimarães Jr., que muito me ajudou desde minha Iniciação Científica e que colaborou imensamente para a realização deste trabalho;

Profs. Drs. Paulo Sérgio de Oliveira, André Vítor L. Freitas e Ivany F.M. Válio, por suas valiosas sugestões ao longo do desenvolvimento deste trabalho;

Prof^a. Dr^a. Sandra Maria C. Guerreiro, pela ajuda na aplicação e na interpretação do teste de tetrazólio;

Dr. Roberto Usberti, pela orientação no procedimento de germinação de Brachiaria decumbens;

Fabiano Scarpa, pelas leituras indicadas;

Todos os funcionários dos Departamentos de Botânica e de Fisiologia Vegetal, Instituto de Biologia, UNICAMP, pela colaboração, pela dedicação e pela atenção ao trabalho desenvolvido;

Membros da pré-banca, Profs. Drs. Flavio Antonio M. dos Santos, Ivany F.M. Válio e Marco Aurélio Pizo, por suas importantes críticas e sugestões a este trabalho;

Funcionárias da Secretaria de Pós-Graduação do Instituto de Biologia da UNICAMP, pela enorme ajuda com as questões burocráticas;

Todos os professores, funcionários e amigos que, de alguma maneira, contribuíram para que este trabalho fosse desenvolvido;

Rogério R. da Silva, do Museu de Zoologia da Universidade de São Paulo, pela identificação das formigas;

Instituto Campineiro de Análise de Solo e Adubo S/C Ltda, pelas análises de solo;

Minha família, principalmente meus pais, Fernando Roberto Martins e Eliana Regina Forni-Martins, por sempre me apoiarem e me ajudarem incondicionalmente;

Guilherme B. Sanvido, meu namorado, por sua inestimável e infinita ajuda na montagem dos experimentos, na tomada de dados e na confecção de figuras, e também por sua imensa paciência e seu carinho em todos os momentos;

Meu orientador, João Semir, pela paciência e pelo carinho ao longo dos anos que estive sob sua orientação;

Minha co-orientadora, Claudia Regina B. Haddad, por sua carinhosa acolhida no Departamento de Fisiologia Vegetal e por sua enorme dedicação;

UNICAMP, por oferecer excelentes ensino e infra-estrutura;

Fundação de Amparo à Pesquisa do Estado de São Paulo, pelo auxílio concedido.

RESUMO

A reprodução vegetal por meio de sementes compreende duas fases: a de regeneração dos indivíduos de uma população e a de estabelecimento dos adultos. A fase regenerativa consiste de uma série de estádios, como liberação, dispersão, dormência/quiescência e germinação de sementes, e estabelecimento de plântulas, cada um com variações na duração e no mecanismo de acordo com a espécie ou a população. Desta forma, a dispersão de sementes é a etapa do ciclo reprodutivo das plantas que inicia a renovação das populações vegetais. Vantagens da dispersão incluem a deposição desproporcionalmente maior de sementes em sítios que são melhores para a sobrevivência de sementes e o estabelecimento de plântulas, sendo estes os componentes da hipótese de dispersão direcional. Apesar da dispersão direcional ser considerada de comum ocorrência e de grande importância ecológica, há poucos exemplos descritos na literatura. No entanto, um dos casos mais reconhecidos é a mirmecocoria, ou dispersão de sementes por formigas. Ricinus communis, popularmente conhecida como mamona, tem sementes tipicamente mirmecocóricas que são dispersas secundariamente por formigas. Estes insetos carregam as sementes com elaiossomo até seus ninhos, onde retiram e retêm este apêndice, e descartam as sementes sem elaiossomo no exterior dos formigueiros. Assim, formigas podem atuar como dispersores direcionais de R. communis, além de provavelmente desempenharem um importante papel na germinação de suas sementes, uma vez que é atribuída a existência de substâncias inibidoras de germinação ao elaiossomo. É popularmente conhecido que R. communis forma bancos de sementes persistentes, apesar de não existirem registros científicos dos mesmos. Devido à capacidade de ocupar os mais diversos habitats após perturbação, o que pode ser atribuído à regeneração a partir de bancos de sementes, esta espécie é considerada ruderal. Os objetivos deste estudo foram determinar se R. communis apresenta dispersão direcional por formigas e se a ocupação de novos habitats pode ser atribuída às possíveis características ruderais

da fase regenerativa pós-dispersão desta espécie. Foi encontrado um maior número de sementes sem elaiossomo, plântulas e jovens de R. communis nos locais de descarte de formigueiros, e sementes com elaiossomo foram igualmente encontradas nestes locais e em suas redondezas. A remoção de sementes pós-dispersas de R. communis não diferiu entre locais de descarte de formigueiros e suas redondezas. A remoção apresentou um pequeno aumento ao longo do tempo e foi inversamente dependente de densidade. No entanto, a redução da remoção não foi proporcional ao aumento da densidade de sementes originalmente depositadas nos locais de descarte de formigueiros e em suas redondezas. Solos de formigueiros não apresentaram maior concentração de nutrientes, e não houve diferença no número de sementes germinadas e no vigor de jovens entre locais de descarte de formigueiros e suas redondezas. Além disto, formigas não conferiram proteção diferencial contra herbivoria às plântulas crescendo nos locais de descarte de seus ninhos. Sementes de R. communis de diferentes idades apresentaram respostas de germinação distintas, porém, foi observada germinação em todas as condições às quais foram expostas. Além disto, sementes com um ano não apresentaram resposta de germinação esperada para sementes que são incorporadas em bancos de sementes. Foram encontradas poucas sementes viáveis de R. communis no solo, apesar de ser observada emergência maciça de plântulas após perturbação do solo em diversas áreas. A espécie é heliófila, porém capaz de ocupar habitats consideravelmente sombreados. Além disto, R. communis é uma fraca competidora, mas é capaz de se estabelecer em áreas que têm alta densidade de indivíduos. O presente estudo demonstrou que a deposição de sementes pós-dispersas em locais de descarte de formigueiros não confere vantagens adicionais a R. communis e que formigas não atuam como dispersores direcionais desta espécie. Além disto, R. communis não apresenta todas as características típicas de plantas ruderais, e seu sucesso em colonizar os mais variados habitats pode ser atribuído à sua plasticidade de respostas às diversas condições ambientais.

ABSTRACT

Plant reproduction through seeds has two phases: the regeneration of the individuals of a population and the establishment of the adult plants. The regenerative phase consists of many stages, such as seed release, dispersal, dormancy/quiescency and germination, and seedling establishment, each with differences in duration and in mechanisms according to the species or to the population. In this way, seed dispersal is the event of plant reproduction cycle that initiates plant population regeneration. Advantages of seed dispersal include the disproportional higher seed deposition in micro-habitats that are more suitable for seed survival and seedling establishment, which are the components of the directed dispersal hypothesis. Although directed dispersal is considered common and ecologically important, few examples are described in literature. However, one of the best-known cases is myrmecochory, or seed dispersal by ants. Ricinus communis, the commonly known castor, has typical myrmecochorous seeds that are secondarily dispersed by ants, which remove seeds with elaiosome into their nests and discard them out in the pile mound without the appendage. Therefore, ants may act as directed dispersers of this species, and may also play a major role in seed germination, once the elaiosome of R. communis seeds is regarded as having germination inhibitory substances. It is commonplace that this species forms persistent soil seed banks, though no study has demonstrated the existence of such seed banks. Due to its ability to occupy the most different habitats after local disturbance, which may be attributed to the regeneration through seed banks, R. communis is considered a ruderal species. This study aimed to determine whether seeds of R. communis present directed dispersal by ants and whether the ruderal features of the post-dispersal regenerative phase assure the species ability to successfully occupy new habitats. There was a greater number of R. communis seeds without elaiosome, seedlings and juveniles in ant nest pile mounds, and seeds with elaiosome were equally distributed between the pile mounds and their vicinities. The

removal of post-dispersed seeds of R. communis from the pile mounds did not differ from the removal in their vicinities. Also, the removal presented a small increase along time and was inversely density-dependent. However, the reduction in the removal was not proportional to the rise in the density of seeds originally placed in the pile mounds and in their vicinities. Ant nest pile mound soils were not nutrient-enriched, and we found no differences in the number of germinated seeds and in the juvenile vigor measurements between the pile mounds and their vicinities. Also, ants did not provide differential protection for seedlings in the piles mounds against herbivores. Fresh and one year old seeds presented distinguished germination response, although they germinated in all conditions they were submitted to. Also, one year old seeds did not present typical germination response of seeds that may constitute seed banks. We found few viable seeds of *R. communis* in the soil, though massive seedling emergence after soil disturbance was observed in many sites. *Ricinus communis* is light-demanding, but may occupy pretty shady sites. Also, the species is a poor competitor, especially with individuals of other species, but is capable of establishing in areas with high density of individuals. This study demonstrated that the deposition of post-dispersed seeds in the pile mounds does not provide additional advantages for R. communis and that ants do not act as directed dispersers of this species. Also, R. communis does not present all typical features of ruderal plants, and its success in colonizing the most different habitats may be attributed to the species' plasticity facing environmental conditions.

INTRODUÇÃO

A reprodução vegetal por meio de sementes compreende duas fases: a de regeneração dos indivíduos de uma população e a de estabelecimento dos adultos. A fase regenerativa consiste de uma série de estádios, como liberação, dispersão, dormência/quiescência e germinação de sementes, e estabelecimento de plântulas, cada um com variações na duração e no mecanismo de acordo com a espécie ou a população. A fase de estabelecimento é caracterizada por uma variedade de funções inter-relacionadas que incluem captura de recursos, manutenção, substituição e crescimento dos sistemas radicular e aéreo, sobrevivência a estresses e danos, e produção de sementes (Grime 1979, 2001).

Desta forma, a dispersão de sementes é a etapa do ciclo reprodutivo das plantas que inicia a renovação das populações vegetais (Willson 1993, Herrera *et al.* 1994, Wenny 2000, Jordano & Godoy 2002, Wang & Smith 2002). A dispersão influencia o fluxo gênico e a estruturação genética temporal e espacial dentro e entre populações (Willson 1993, Hamrick *et al.* 1993, Ouborg *et al.* 1999, Jordano & Godoy 2002), além de propiciar a manutenção da diversidade, com implicações para sucessão, regeneração e conservação da comunidade vegetal (Willson 1993, Wenny 2000, Wang & Smith 2002).

A dispersão de sementes pode aumentar o sucesso reprodutivo de um indivíduo de três maneiras: (1) por diminuir a mortalidade por competição, predação e infestação por patógenos, comuns em locais com grande densidade de sementes, como perto da planta parental (Janzen 1969, 1970, 1971, Stebbins 1974, Beattie & Lyons 1975, Handel 1976, Harper 1977, O'Dowd & Hay 1980, Bond & Slingsby 1984, Hölldobler & Wilson 1990, Willson 1993, Herrera *et al.* 1994, Cain *et al.* 2000); (2) pela colonização de novos habitats, que são geralmente raros, imprevisíveis, aleatórios ou efêmeros (Willson 1993, Wenny 2000, 2001, Wang & Smith 2002), e (3) pela alta deposição de sementes em micro-habitats que são melhores para a sobrevivência de sementes e o

estabelecimento de plântulas (Howe & Smallwood 1982, Willson 1993). Estas três vantagens da dispersão são, respectivamente, as bases das hipóteses de fuga, colonização e dispersão direcional (Howe & Smallwood 1982, Wenny 2001).

A hipótese da dispersão direcional tem dois componentes: (1) deposição não aleatória de sementes por um dispersor previsível, que remove grandes quantidades de sementes para sítios específicos (Willson 1993), e (2) maiores sobrevivência de sementes e estabelecimento de plântulas nestes sítios específicos (Howe & Smallwood 1982, Wenny 2001). Apesar da dispersão direcional ser considerada de comum ocorrência e de grande importância ecológica, há poucos exemplos descritos na literatura (Wenny & Levey 1998, Wenny 2001). No entanto, um dos casos mais reconhecidos é a mirmecocoria, ou dispersão de sementes por formigas (Hanzawa *et al.* 1988, Vander Wall & Longland 2004, Manzaneda *et al.* 2005).

Mais de 60 famílias de plantas ocorrentes no mundo todo possuem espécies com sementes mirmecocóricas, caracterizadas pela presença de um apêndice rico em lipídeos atrativos às formigas, conhecido por elaiossomo (van der Pijl 1972, Beattie 1985, Hölldobler & Wilson 1990). As formigas levam sementes com elaiossomo para seus ninhos, onde retiram-no e utilizam-no como fonte de alimento, e descartam as sementes sem seu apêndice e geralmente sem danificá-las fora dos formigueiros (Berg 1975, Davidson & Morton 1981, Beattie 1985).

Comumente é encontrado na literatura que o descarte de sementes no exterior de formigueiros confere melhores condições para a germinação e o estabelecimento de plântulas, devido à alta concentração de matéria orgânica e nutrientes no solo, sendo quantidades elevadas de nitrogênio especialmente importantes para desencadear o processo de germinação (Culver & Beattie 1978, Handel 1978, O'Dowd & Hay 1980, Davidson & Morton 1981, Horvitz 1981, Fenner 1985, Horvitz & Schemske 1986, Higashi *et al.* 1989, Salisbury & Ross 1992, Stiles 1993, Passos & Oliveira 2002, 2004, Teasdale & Pillai 2005). Porém, alguns trabalhos têm demonstrado que nem todos os solos de formigueiros são nutricionalmente mais ricos (Rice & Westoby 1986),

e que nem sempre a alta concentração de nutrientes apresenta correlação com as maiores taxas de germinação e crescimento de plântulas nestes locais (Horvitz & Schemske 1986).

Sementes e plantas estabelecidas nos formigueiros também podem se beneficiar da associação com formigas devido ao comportamento destes insetos. Formigas costumam forragear nas redondezas de seus ninhos, de onde geralmente removem intrusos. Portanto, este comportamento pode resultar em menor predação ou remoção de sementes por outros agentes dispersores para locais menos favoráveis à germinação e ao estabelecimento de plântulas, além de acarretar em proteção diferencial contra herbivoria das plantas que crescem perto dos formigueiros (Beattie 1985, Davidson & Epstein 1989, Passos & Oliveira 2004). A proteção contra herbívoros proporcionada pelas formigas provavelmente é muito importante para o estabelecimento de plântulas, já que a herbivoria é considerada um dos principais fatores de mortalidade de indivíduos jovens de espécies tropicais (Steven 1994, Lieberman 1996, Basset 1999, Passos & Oliveira 2004).

Se formigas realmente atuam como dispersores direcionais, beneficiando a germinação de sementes e o estabelecimento de plântulas como citado por muitos autores (*e.g.* Horvitz 1981, Passos & Oliveira 2002, 2003, 2004, Martins *et al.* 2006), propõem-se as seguintes hipóteses: (1) sementes pós-dispersas e seus estádios subseqüentes devem ocorrer em maiores densidades nos locais de descarte dos formigueiros, que são os sítios específicos de deposição não aleatória de sementes pelas formigas, os dispersores previsíveis; (2) sementes nos locais de descarte devem ser protegidas pelas formigas contra predação ou remoção para sítios menos propícios; (3) assim, sementes nos locais de descarte dos formigueiros devem apresentar maior sucesso de germinação do que sementes em outros locais, principalmente se os solos dos descartes dos formigueiros tiverem quantidades elevadas de nitrogênio; (4) plântulas que crescem nos locais de descarte devem setabelecidos e vigorosos, já que solos de

formigueiros são supostamente mais ricos em nutrientes e formigas podem conferir proteção diferencial contra herbivoria.

No entanto, sementes não necessariamente germinam imediatamente após serem dispersas. Isto pode ser devido à falta de condições propícias à germinação, para sementes quiescentes, ou à existência de bloqueios inerentes à semente que devem ser removidos antes que o processo de germinação possa iniciar, no caso de sementes dormentes (Bewley & Black 1994). Enquanto a germinação não ocorre, seja devido à quiescência ou à dormência, a viabilidade das sementes precisa ser mantida. Isto só é possível para sementes ortodoxas, que podem sofrer dessecação sem que isto acarrete em danos decorrentes da baixa umidade, e cuja longevidade aumenta com o decréscimo de umidade e temperatura. Por outro lado, sementes que perdem viabilidade rapidamente são denominadas recalcitrantes (Murdoch & Ellis 1993, Probert 1993, Bewley & Black 1994).

Muitas espécies que produzem sementes ortodoxas dormentes ocupam habitats nos quais a regeneração é associada a grandes perturbações locais (Fenner 1985). Esta regeneração se dá a partir de bancos de sementes persistentes de tais espécies (Grime 1979, 2001, Thompson 1993). Bancos de sementes podem acarretar em estruturação genética temporal, em que os indivíduos resultantes são a progênie de plantas parentais de muitas gerações (Harper 1977). Tais bancos também permitem que a predação de sementes pré-dispersas tenham pouco ou nenhum impacto na dinâmica populacional (Crawley 1970). Além disto, em florestas tropicais os bancos de sementes possibilitam a regeneração vegetal em áreas que sofreram algum tipo de devastação (Harper 1977, Putz 1983, Fenner 1985).

Sementes que formam bancos geralmente respondem a alternância de temperatura e presença de luz para germinarem (Fenner 1985, Pons 1993, Probert 1993). A necessidade de luz para a germinação é uma importante resposta à presença de clareiras, que resultam da desestruturação da vegetação local acompanhada de provável perturbação do solo. Assim, esta

resposta germinativa acarreta em uma previsão razoável da redução na competição com os indivíduos adultos presentes na área (Pons 1993).

Após as sementes encontrarem condições propícias e germinarem, as plântulas podem enfrentar competição por recursos limitados, como espaço, luz e nutrientes. A competição é considerada um dos principais fatores que controlam os processos de crescimento e é crucial para o estabelecimento dos indivíduos (Fenner 1985, Lee et al. 1996, Whitmore 1996). Este tipo de interação ecológica pode ocorrer entre indivíduos da mesma espécie, no caso da competição intraespecífica, ou entre indivíduos de espécies diferentes, na competição inter-específica. Em ambos os casos, os indivíduos podem sofrer redução na fecundidade, sobrevivência e/ou crescimento devido à exploração compartilhada de recursos, com resultados mais acentuados quanto maior o número de competidores envolvidos na interação. O efeito da competição difere entre os indivíduos que estão interagindo, e muitas vezes um único lado da interação é favorecido. Competidores fortes não têm a sua contribuição para a próxima geração afetada e, inclusive, esta pode até aumentar em relação ao que se esperaria se não houvesse competição, principalmente no caso de espécies que alocam grande parte de seus recursos para reprodução sexuada em situações de alta densidade de indivíduos. Por outro lado, competidores fracos possuem pequena contribuição para as gerações seguintes (Grime 1979, 2001, Begon et al. 1996a, b, Watkinson 1997).

Plantas que produzem sementes ortodoxas dormentes que formam bancos persistentes e que são competidoras fracas enquadram-se no perfil de ruderais. Uma espécie ruderal é aquela que ocupa habitats pouco estressantes mas com muitas perturbações, ou seja, habitats que não restringem a taxa de produção de massa seca, porém limitam a biomassa devido a sua destruição total ou parcial (veja Grime 1979 e 2001 para uma extensa revisão).

Ricinus communis, popularmente conhecida como mamona, é uma espécie de ampla distribuição mundial (Singh 1976). Suas sementes possuem um elaiossomo e são dispersas

primariamente por autocoria e secundariamente por formigas, que carregam as sementes com elaiossomo até seus ninhos, onde retiram e retêm este apêndice, e descartam as sementes sem elaiossomo no exterior dos formigueiros (Martins *et al.* 2006). Provavelmente, ao retirarem o elaiossomo, as formigas desempenham um importante papel na germinação de sementes desta espécie, uma vez que é atribuída a existência de substâncias inibidoras de germinação a este apêndice (Lagôa & Pereira 1987). É popularmente conhecido que *R. communis* forma bancos de sementes persistentes, apesar de não existirem registros científicos dos mesmos. Devido à capacidade de ocupar os mais diversos habitats após perturbação, o que pode ser atribuído à possível existência de bancos de sementes, esta espécie é considerada ruderal.

Assumindo-se que R. communis é uma espécie ruderal e considerando sua dispersão secundária, propõem-se as seguintes hipóteses: (1) sementes recém-dispersas por formigas, portanto sem elaiossomo, devem germinar em quaisquer combinações de luz e temperatura, já que podem ser descartadas dentro ou fora de formigueiros em micro-sítios favoráveis para o futuro estabelecimento das plântulas; (2) sementes recém liberadas da planta parental, portanto com elaiossomo, não devem germinar em nenhuma combinação de luz e temperatura se este apêndice impuser dormência inata na semente, mas devem germinar em alguma combinação de luz e temperatura se a presença do apêndice acarretar em dormência induzida da semente; (3) sementes velhas sem elaiossomo devem ser viáveis e germinar em temperaturas alternadas e presença de luz, que são as condições às quais são expostas as sementes em bancos após a perturbação do solo; (4) sementes velhas com elaiossomo devem ser viáveis mas não devem germinar em nenhuma combinação de luz e temperatura se este apêndice impuser dormência inata ou induzida na semente; (5) se o elaiossomo impuser algum tipo de dormência na semente, sua remoção deve cessar o bloqueio da germinação mesmo em sementes velhas; (6) devem existir bancos de sementes persistentes; (7) plântulas/jovens devem ser heliófilos, uma vez que a resposta de germinação das sementes em bancos indica ausência de outros indivíduos na área, e,

devido à fraca habilidade como competidoras, ruderais devem ocorrer em áreas abertas, e (8) plântulas/jovens devem ser competidores fracos, principalmente com indivíduos de outras espécies, já que ocorrem em áreas abertas.

OBJETIVOS

Os objetivos deste estudo foram determinar se *R. communis* apresenta dispersão direcional por formigas e se a ocupação de novos habitats pode ser atribuída às possíveis características ruderais da fase regenerativa pós-dispersão desta espécie.

Para o estudo da dispersão direcional por formigas de *R. communis*, foram feitas as seguintes questões: (1) Há diferença nas densidades de sementes, plântulas e jovens entre o local de descarte dos formigueiros e suas redondezas? (2) O destino de sementes difere entre sementes no local de descarte dos formigueiros e nas suas redondezas, e este destino é dependente de densidade? (3) Locais de descarte têm solos nutricionalmente mais ricos? (4) O número de sementes germinadas e as medidas de vigor dos jovens diferem entre o local de descarte e suas redondezas? (5) Formigas conferem proteção diferencial contra herbívoros às plântulas crescendo nos locais de descarte?

Para o estudo da fase regenerativa pós-dispersão de *R. communis*, foram feitas as seguintes questões: (1) como é a resposta germinativa de sementes recém colhidas e com um ano de idade submetidas a combinações de luz, temperatura e elaiossomo? (2) Existem bancos de sementes persistentes? (3) Há alterações nas medidas de vigor de jovens expostos a diferentes quantidades e qualidades luminosas? (4) Há alterações nas medidas de vigor de vigor de jovens em situação de competição intra- e inter-específica?

DESCRIÇÃO DA ESPÉCIE

O gênero *Ricinus*, da família Euphorbiaceae, é monotípico e tem origem africana, apesar de alguns autores defenderem sua possível origem asiática. *Ricinus communis* L. apresenta como sinônimos *Ricinus hibridus* Bess, *Ricinus leucocarpus* Bert, e *Ricinus digitatus* Nor., sendo a espécie popularmente conhecida como mamona, rícino, carrapateiro e castor (Singh 1976, Mabberley 1998, Kissmann & Groth 1999, Lorenzi 2000, http://www.canalvip.com.br).

Ricinus communis é uma planta monóica, protogínica, com inflorescência do tipo racemo em cachos, sendo as flores femininas localizadas no ápice e as masculinas, na base. A espécie apresenta hábito variando de arbustivo até arbóreo, com caule geralmente fistuloso. A folha, peltada, com ampla lâmina palmada e margem lobada, é avermelhada quando jovem, tem filotaxia alterna e um pecíolo longo, carnoso e grosso. O fruto é uma cápsula esquizocárpica com protrusões espinescentes na superfície, e as sementes têm testa crustácea, quebradiça e com manchas irregulares. As sementes são ricas em substâncias oleaginosas e possuem um elaiossomo, chamado de carúncula (van der Pijl 1972, Singh 1976, Mabberley 1998, Kissmann & Groth 1999, Lorenzi 2000, Savy Filho 2000, http://www.canalvip.com.br). A espécie floresce o ano todo e uma planta de grande porte pode produzir 150.000 sementes por período de frutificação, enquanto que uma mais jovem produz em média 1.500 sementes (Hogan 1992).

As variedades selvagens de *R. communis* são muito variáveis em hábito, cor, quantidade de flores, dinâmica de floração, tipo de inflorescência, características dos frutos e sementes (Hilterbrandt 1935 *apud* Singh 1976, Kissmann & Groth 1999). Na espécie, também ocorrem cultivares desenvolvidos e selecionados por melhoramento genético, de acordo com os interesses econômico, médico e ornamental (Kissmann & Groth 1999, Savy Filho 2000, http://www.canalvip.com.br). *Ricinus communis* foi introduzida em praticamente todos os continentes e é largamente cultivada nos países tropicais, subtropicais e temperados, sendo o

Brasil um dos mais importantes produtores de óleo desta espécie, ao lado da Índia e da China (Singh 1976, http://www.canalvip.com.br). O óleo extraído por prensagem das sementes (Savy Filho 2000), chamado de óleo de rícino, é conhecido desde a antiguidade, sendo utilizado pelos egípcios para tratamento de pele, feridas e cabelo, entre outros (http://www.canalvip.com.br). Atualmente, o óleo é largamente utilizado em diversos setores. Na indústria, é usado principalmente como lubrificante de motores e na fabricação de tintas, isolantes, cosméticos, corantes e produtos farmacêuticos. Na medicina, é usado como um laxante suave, vermífugo (Singh 1976; http://www.canalvip.com.br), e mais recentemente, na constituição de próteses cirúrgicas (Ereno 2003). No entanto, nos últimos anos, o maior destaque do óleo das sementes de *R. communis* talvez tenha sido a sua utilização no setor energético, com a produção do biodiesel, um importante combustível biodegradável derivado de fontes renováveis que tem atraído grandes investimentos do governo brasileiro (www.biodiesel.gov.br). Após a extração do óleo das sementes, sobra um resíduo sólido, conhecido como torta de mamona, que é utilizado na agricultura como adubo orgânico de efeito nematicida (Singh 1976; http://www.canalvip.com.br).

As sementes de *R. communis* apresentam dispersão diplocórica, ou seja, são dispersas por dois tipos de agentes. A dispersão primária é abiótica e ocorre por autocoria, enquanto a dispersão secundária se dá por mirmecocoria (Martins *et al.* 2006). A resposta de germinação não é bem elucidada, especialmente no que diz respeito a presença ou ausência da carúncula. Lagôa & Pereira (1987) e Martins *et al.* (2006) obtiveram maior sucesso de germinação na ausência da carúncula, que aparentemente desencadeia dormência na semente (Lagôa & Pereira 1987). Porém, Lisci *et al.* (1996) e Bianchini & Pacini (1996) demonstraram que o sucesso de germinação é maior para sementes com carúncula, provavelmente porque este apêndice desempenha um papel importante na absorção de água do solo e na sua transferência para a sementes durante a germinação. No que diz respeito à luz, há um consenso de que sua ausência aumenta a germinação (Lagôa & Pereira 1987, Bianchini & Pacini 1996, Martins *et al.* 2006). Martins *et al.*

(2006) também demonstraram que o sucesso de germinação é maior em temperaturas alternadas. As diferenças na germinação de sementes de *R. communis* encontradas pelos diferentes autores sugerem que mais estudos devem ser realizados para o entendimento da resposta germinativa desta espécie.

Há um consenso entre o público leigo de que sementes de *R. communis* permanecem viáveis no solo por longos períodos de tempo, ou seja, formam bancos de sementes persistentes, sendo capazes de regenerar a população quando o solo é revolvido. Apesar de não existirem trabalhos que analisem tal estratégia de regeneração, a resposta à alternância de temperatura sugere que sementes de *R. communis* possam formar bancos (Martins *et al.* 2006). Além disto, estas sementes apresentam alta longevidade (Atsmon 1966), característica imprescindível em bancos de sementes persistentes.

LITERATURA CITADA

- Atsmon, D. 1966. Analysis of germination inhibition in the castor bean plant. Botanical Gazette 127: 140-146.
- Basset, Y. 1999. Diversity and abundance of insect herbivores foraging on seedlings in a Rainforest in Guyana. Ecological Entomology 24: 245-259.
- Beattie, A.J. 1985. The evolutionary ecology of ant-plant mutualisms. Cambridge University Press, New York.
- Beattie, A.J. & N. Lyons. 1975. Seed dispersal in *Viola* (Violaceaea): adaptations and strategies. American Journal of Botany 62: 714-722.
- Begon, M.; J. Harper & C. R. Townsend. 1996a. Intraespecific competition. Pp. 214-264. In: Ecology – Individuals, populations and communities. 4th Edition. Blackwell Science, Oxford.
- Begon, M.; J. Harper & C. R. Townsend. 1996b. Interespecific competition. Pp. 265-312. In: Ecology – Individuals, populations and communities. 4th Edition. Blackwell Science, Oxford.
- Berg, R.Y. 1975. Myrmecochorous plants in Australia and their dispersal by ants. Australian Journal of Botany 23: 475-508.
- Bewley, J.D. & M. Black. 1994. Seeds: Physiology of development and germination. 2nd Edition. Plenum Press, New York.
- Bianchini, M. & E. Pacini. 1996. The caruncle of *Ricinus communis* L. (castor bean): its development and role in seed dehydration, rehydration, and germination. International Journal of Plant Sciences 157: 40-48.
- Bond, W. & P.Slingsby. 1984. Collapse of an ant-plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. Ecology 65: 1031-1037.
- Cain, M.L.; B.G. Milligan & A.E. Strand. 2000. Long-distance seed dispersal in plant populations. American Journal of Botany 87: 1217-1227.

- Crawley, M.J. 1970. The population dynamics of plants. Philosophical Transactions of the Royal Society: Biological Sciences Series B 330: 125-140.
- Culver, D.C. & A.J. Beattie. 1978. Myrmecochory in *Viola*: dynamics of seed-ant interactions in some West Virginia species. Journal of Ecology 66: 53-72.
- Davidson, D.W. & W.W. Epstein. 1989. Epiphytic associations with ants. Pp. 200-233. In: Lüttge, U. (ed.). Phylogeny and Ecophisiology of epiphytes. Springer, Berlin Heidelberg New York.
- Davidson, D.W. & S.R. Morton. 1981. Myrmecochory in some plants (*F. chenopodiaceae*) of the Australian Arid Zone. Oecologia 50:357-366.
- Ereno, D. 2003. Próteses de mamona. Pesquisa FAPESP 91: 66-71.
- Fenner, M. 1985. Seed ecology. Chapman and Hall, London.
- Grime, J.P. 1979. Plant strategies and vegetation processes. John Wiley & Sons, Chichester.
- Grime, J.P. 2001. Plant strategies, vegetation processes and ecosystem properties. John Wiley & Sons, Chichester.
- Hamrick, J.L.; D.A. MurawskI & J.D. Nason. 1993. The influence of seed dispersal mechanisms on the genetic structure of tropical tree populations. Pp. 281-297. *In:* Fleming, T.H. & A. Estrada. (eds.). Frugivory and seed dispersal: ecological and evolutionary aspects. Kluwer Academic Publishers, Dordrecht.
- Handel, S.N. 1976. Dispersal ecology of *Carex pedunculata* (Cyperaceae): a new North American myrmecochore. American Journal of Botany 63: 1071-1079.
- Handel, S.N. 1978. The competitive relationship of three woodland sedges and its bearing on the evolution of ant-dispersal of *Carex pedunculata*. Evolution 32: 151-163.
- Hanzawa, F.M.; A.J. Beattie & D.C. Culver. 1988. Directed dispersal: demographic analysis of an ant-seed mutualism. The American Naturalist 131: 1-13.
- Harper, J.L. 1977. Population biology of plants. Academic Press, New York.

- Herrera, C.M.; P. Jordano; L. López-Soria & J.A. Amat. 1994. Recruitment of a mast-fruiting, bird dispersed tree: bridging frugivore activity and seedling establishment. Ecological Monographs 64: 315-344.
- Higashi, S.; S. Tsuyuzaki; M. Ohara & F. Ito. 1989. Adaptative advantages of ant-dispersed seeds in the myrmecochorous plant *Trillium tschonoskii* (Liliaceae). Oikos 54:389-394.
- Hilterbrandt, V.M. 1935. The plant resources of the world as initial material in plant breeding: the castor plant. Lenin Acad. Agri. Sci. Inst. Plant Industry, Moscow & Leningrad 6: 55-70. *In:* Singh, D. 1976. Castor *Ricinus communis* (Euphorbiaceae). Pp. 84-86. *In:* Simmonds, N.W. (ed.). Evolution of crop plants. Longman Group, New York.
- Hogan, E.L. (ed.). 1992. Sunset Western garden book. Sunset Publishing, Menlo Park.
- Hölldobler, B. & E.O. Wilson. 1990. The Ants. The Belknap Press, Cambridge.
- Horvitz, C.C 1981. Analysis of how ant behaviors affect germination in a Tropical Myrmecochore *Calathea microcehala* (P. & E.) Koernicke (Marantaceae): microsite selection and aril removal by Neotropical ants, *Odontomachus, Pachycondyla*, and *Solenopsis* (Formicidae). Oecologia 51:47-52.
- Horvitz, C.C. & D.W. Schemske. 1986. Ant-nest soil and seedling growth in a neotropical antdispersed herb. Oecologia 70: 318-320.
- Howe, H.F. & J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13:201-228.
- Janzen, D.H. 1969. Seed-eaters versus size, number, toxity and dispersal. Evolution 23: 1-27.
- Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. The American Naturalist 104: 501-528.
- Janzen, D.H. 1971. Seed predation by animals. Annual Review of Ecology and Systematics 2:465-492.

- Jordano, P. & J.A. Godoy. 2002. Frugivore-generated seed shadows: a landscape view of demographic and genetic effects. Pp. 305-322. *In:* Levey, D.J.; W.R. Silva & M. Galetti (eds.). Seed dispersal and frugivory: ecology, evolution and conservation. CABI Publishing, Wallingford.
- Kissmann, K.G. & D. Groth. 1999. *Ricinus communis* L. Pp. 814-818. *In:* Plantas infestantes e nocivas. Vol. 2. 2^a edição, BASF Brasileira S.A., São Paulo.
- Lagôa, A.M.M.A. & M.F. Pereira. 1987. The role of the caruncle in the germination of seeds of *Ricinus communis*. Plant Physiology and Biochemistry 25: 125-128.
- Lee, D.W.; B. Krishnapilay; M. Mansor; H. Mahamad & S.K. Yap. 1996. Irradiance and spectral quality affect Asian Tropical Rain Forest tree seedling development. Ecology 77: 568-580.
- Lieberman, D. 1996. Demography of Tropical tree seedlings: a review. Pp. 131-138. *In:* Swaine,M.D. (ed.). Ecology of Tropical Forest tree seedlings. UNESCO/Parthenon, Carnforth.
- Lisci, M., M. Bianchini & E. Pacine. 1996. Structure and function of the elaiosome in some Angiosperm species. Flora 191: 131-141.
- Lorenzi, H. 2000. *Ricinus communis. In:* Plantas daninhas do Brasil Terrestres, aquáticas, parasitas e tóxicas. Pp. 279. 3^a Edição. Instituto Plantarum de Estudos da Flora Ltda., Nova Odessa.
- Mabberley, D.J. 1998. *Ricinus*. Pp. 618. *In:* The plant-book: a portable dictionary of the Vascular Plant. 2nd Edition. Cambridge University Press, Cambridge.
- Manzaneda, A.J.; J.M. Fedriani & P.J. Rey. 2005. Adaptative advantages of myrmecochory: the predator-avoidance hypothesis tested over a wide geographic range. Ecography 28: 583-592.
- Martins, V.F.; P.R. Guimarães; R.R. Silva & J. Semir. 2006. Secondary seed dispersal by ants of *Ricinus communis* (Euphorbiaceae) in the Atlantic Forest in Southeastern Brazil: influence on seed germination. Sociobiology 47: 265-274.

- Murdoch, A.J. & R.H. Ellis. 1993. Longevity, viability and dormancy. Pp. 193-229. *In:* Fenner,M. (ed.). Seeds: the ecology of regeneration in plant communities. CAB International,Wallingford.
- O'Dowd, D.J. & M.E. Hay. 1980. Mutualism between harvester ants and a desert ephemeral: seed escape from rodents. Ecology 61: 531-540.
- Ouborg, N.J.; Y. Piquot & J.M. van Groenendael. 1999. Population genetics, molecular markers and the study of dispersal in plants. Journal of Ecology 87: 551-568.
- Passos, L. & P.S. Oliveira. 2002. Ants affect the distribution and performance of seedling of *Clusia criuva*, a primarily bird-dispersed rain forest tree. Journal of Ecology 90: 517-528.
- Passos, L. & P.S. Oliveira. 2003. Interactions between ants, fruits and seeds in a Restinga Forest in South-Eastern Brazil. Journal of Tropical Ecology 19: 261-270.
- Passos, L. & P.S. Oliveira. 2004. Interactions between ants and fruits of *Guapira opposita* (Nyctaginaceae) in a Brazilian Sandy Plain Rainforest: ant effects on seeds and seedlings. Oecologia 139: 376-382.
- Pons, T.L. 1993. Seed responses to light. Pp. 259-284. *In:* Fenner, M. (ed.). Seeds: the ecology of regeneration in plant communities. CAB International, Wallingford.
- Probert, R.J. 1993. The role of temperature in germination ecophysiology. Pp. 285-325. In: Fenner, M. (ed.). Seeds: the ecology of regeneration in plant communities. CAB International, Wallingford.
- Putz, F.E. 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. Ecology 64: 1069-1074.
- Rice, B. & M. Westoby. 1986. Evidence against the hypothesis that ant-dispersed seeds reach nutrient-enriched microsites. Ecology 67: 1270-1274.
- Salisbury, F.B. & C.W. Ross. 1992. Growth responses to temperature. Pp. 485-503. *In:* Plant physiology, 4th edition. Wadsworth, Inc., California.

- Singh, D. 1976. Castor *Ricinus communis* (Euphorbiaceae). Pp. 84-86. *In:* Simmonds, N.W.
 (ed.). Evolution of crop plants. Longman Group, New York.
- Stebbins, G.L. 1974. Adaptations for seed development and dispersal and for seedling establishment. *In:* Flowering plants – evolution above the species level. Pp. 68-101. The Belknap Press, Cambridge.
- Steven, D. 1994. Tropical tree seedlings dynamics: recruitment patterns and their population consequences for three canopy species in Panama. Journal of Tropical Ecology 10: 369-383.
- Stiles, E.W. 1993. Animal as seed dispersers. Pp. 87-104. *In:* Fenner, M. (ed.). Seeds: The ecology of regeneration in plant communities. CAB International, Wallingford.
- Teasdale, J.R. & P.Pillai. 2005. Contribution of ammonium to stimulation of smooth pigweed (*Amaranthus hybridus* L.) germination by extracts of hairy vetch (*Vicia villosa* Roth) residue. Weed Biology and Management 5: 19-25.
- Thompson, K. 1993. The functional ecology of seed banks. Pp. 231-258. *In:* Fenner, M. (ed.). Seeds: the ecology of regeneration in plant communities. CAB International, Wallingford.
- van der Pijl, L. 1972. Principles of dispersal in higher plants. 2nd Edition. Springer-Verlag, Würzburg.
- Vander Wall, S.B. & W.S. Longland. 2004. Diplochory: are two seed dispersers better than one? Trends in Ecology and Evolution 19: 155-161.
- Wang, B.C. & T.B. Smith. 2002. Closing the seed dispersal loop. Trends in Ecology and Evolution 17: 379-385.
- Watkinson, A.R. 1997. Plant population dynamics. Pp. 137-184. *In:* Crawley, M.J.(ed.). Plant ecology. 2nd Edition. Blackwell Science, London.
- Wenny, D.C. 2000. Seed dispersal, seed predation and seedling recruitment of a Neotropical Montane tree. Ecological Monographs 70: 331-351.

- Wenny, D. 2001. Advantages of seed dispersal: a re-evaluation of direct dispersal. Evolutionary Ecology Research 3: 51-74.
- Wenny, D.G. & D.J. Levey. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. Proceedings of the National Academy of Sciences of the United States of America 95: 6204-6207.
- Whitmore, T.C. 1996. A review of some aspects of tropical rain forest seedling ecology with suggestions for further enquiry. Pp. 3-39. *In:* Swaine, M.D. Ecology of tropical tree seedlings. Unesco/Parthenon, Carnforth.
- Willson, M.F. 1993. The ecology of seed dispersal. Pp. 51-85. *In:* Fenner, M. (ed.). Seeds: the ecology of regeneration in plant communities. CAB International, Wallingford.

http://www.biodiesel.gov.br

http://www.canalvip.com.br

Do ants act as directed dispersers of a typically myrmecochorous species? An analysis of myrmecochory effects on the multi-step process from post-dispersed seeds to established

juveniles of *Ricinus communis* (Euphorbiaceae)^{*}

Valéria Forni Martins¹, Paulo R. Guimarães Jr.², Claudia Regina Baptista Haddad³ &

João Semir⁴

¹Programa de Pós-Graduação em Ecologia, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, SP, Brazil.

²¹Programa de Pós-Graduação em Ecologia, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, SP, Brazil. Integrative Ecology Group, Estación Biológica de Doñana, CSIC, Sevilla, Spain.

³Departamento de Fisiologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas, C.P. 6109, 13083-970, Campinas, SP, Brazil.

⁴Departamento de Botânica, Instituto de Biologia, Universidade Estadual de Campinas, C.P. 6109, 13083-970, Campinas, SP, Brazil.

Correspondence author: Valéria F. Martins. Depto. PPG-Ecologia/IB/UNICAMP. Cx. Postal 6109. CEP 13083-970. vmartins@unicamp.br.

Directed dispersal of Ricinus communis

^{*}Format and style: Functional Ecology

SUMMARY

1. There was a greater number of *R*. *communis* seeds without elaiosome, seedlings and juveniles in ant nest pile mounds, and seeds with elaiosome were equally distributed between the pile mounds and their vicinities.

1. The removal of post-dispersed seeds of *R. communis* from the pile mounds did not differ from the removal in their vicinities. Also, the removal presented a small increase along time and was inversely density-dependent. However, the reduction in the removal was not proportional to the rise in the density of seeds originally placed in the pile mounds and in their vicinities.

2. Ant nest pile mound soils were not nutrient-enriched, and we found no differences in the number of germinated seeds and in the juvenile vigor measurements between the pile mounds and their vicinities.

3. Also, ants did not provide differential protection for seedlings in the piles mounds against herbivores.

4. There were no additional advantages for the *R*. *communis* seeds, seedlings and juveniles in the pile mounds. Therefore, this species is not benefited by myrmecochory and does not present directed dispersal by ants.

Key words: Ant nest pile mounds, differential protection against herbivory, elaiosome, nutrientenriched soil, vigor.

INTRODUCTION

Seed dispersal is the event of plant reproduction cycle that initiates plant population regeneration (Willson 1993, Herrera *et al.* 1994, Wenny 2000, Jordano & Godoy 2002, Wang &

Smith 2002). The reproductive success of an individual plant may be enhanced by seed dispersal in three different ways: (1) by decrease in mortality due to competition, predation and pathogen infestation, which usually occur in sites with great seed density, such as near parental plants (Janzen 1969, 1970, 1971, O'Dowd & Hay 1980, Hölldobler & Wilson 1990, Willson 1993, Herrera *et al.* 1994); (2) by colonization of new habitats, which are usually rare, unpredictable or ephemerous (Willson 1993, Wenny 2000, 2001, Wang & Smith 2002), and (3) by high seed deposition in micro-habitats that are better for seed survival and seedling establishment (Howe & Smallwood 1982, Willson 1993). The latter advantage is the basis of the directed dispersal hypothesis (Howe & Smallwood 1982, Wenny 2001). Although directed dispersal is considered common and ecologically important, few examples are described in literature (Wenny 2001, Wenny & Levey 1998). A remarkably exception are ants, since several studies show evidences that ants act as directed seed dispersers (Hanzawa, Beattie & Culver 1988, Vander Wall & Longland 2004, Manzaneda, Fedriani & Rey 2005).

The directed dispersal hypothesis has two components: (1) non-random seed deposition by a predicted vector, which removes higher amount of seeds to specific sites (Willson 1993), and (2) higher seed survival and seedling establishment in such specific sites (Howe & Smallwood 1982, Wenny 2001). Several studies suggest that ants perform both tasks (*e.g.* Passos & Oliveira 2002, 2003, 2004). Ants usually carry seeds into their nest, eat their pulp or elaiosome, and discard the seeds out often in viable condition (Berg 1975, Davidson & Morton 1981, Beattie 1985). Moreover, seeds deposited near to ant nests usually show higher germination success and seedling growth for two different reasons: (1) higher concentration of organic matter and nutrients in the soil, being elevated quantities of nitrogen especially important to trigger seed germination (Culver & Beattie 1978, O'Dowd & Hay 1980, Davidson & Morton 1981, Horvitz 1981, Salisbury & Ross 1982, Passos & Oliveira 2002, 2004, Teasdale & Pillai 2005, but see Horvitz & Schemske 1986, Rice & Westoby 1986 and Passos & Oliveira 2002), and (2) ants foraging

behavior that may render protection for both seeds against predation or further removal to less suitable sites by other disperser vectors, and established plants against herbivory (Davidson & Epstein 1989, Passos & Oliveira 2004), which seems to be an important source of seedling mortality of tropical tree species (Lieberman 1996, Basset 1999, Passos & Oliveira 2004).

If ants do act as directed dispersers, we propose the following hypothesis: (1) postdispersed seeds and subsequent developmental stages are expected to occur in higher densities in ant nest pile mounds, which are the specific sites for non-random seed deposition by ants – the predicted seed dispersal vectors; (2) seeds in pile mounds are likely to be protected by ants against predation or further removal to less suitable sites; (3) therefore, seeds in these sites are supposed to present higher germination success than seeds elsewhere, especially if pile mound soils have elevated quantities of nitrogen; (4) seedlings growing in pile mounds are more likely to progress to established and vigorous juveniles, because ant nest soils are supposed to be nutrientenriched and ants may render differential protection against herbivory.

This study was designed to cover the multi-step process from post-dispersed seeds to established juvenile plants of a typical myrmecochorous species. Our main objective was to determine whether seeds of *Ricinus communis* L. present directed dispersal by ants. The following questions were addressed: (1) Are there differences in seed, seedling and juvenile densities between the pile mound and its vicinities? (2) Does seed fate differ between seeds in the pile mound and seeds in its vicinities, and is it density-dependent? (3) Are ant nest soils nutrientenriched? (4) Do the number of germinated seeds and the juvenile vigor measurements differ between the pile mound and its vicinities? (5) Do seedlings growing in pile mounds gain differential protection from ants against herbivores?

MATERIALS AND METHODS

Study site and species studied

Fieldwork was undertaken between April 2005 and January 2006 in Campinas municipality, Southeast Brazil (22°54' S, 47°03' W). According to Koeppen's climate classification, the climate of Campinas region is Cwa, macrothermal temperate with mild dry winter (Camargo 1966). The experiments were performed in fallow grounds, which we considered as an open area with no considerable shady sites located in urban scenarios. The study sites were dominated by few plant species and the most abundant were *Brachiaria decumbens* (Poaceae) and *R. communis*, which occurred in clumped pattern.

Ricinus communis, the commonly known castor, is a shrub or treelet originated in Africa (Singh 1976, Mabberley 1998). This species was introduced in all continents and nowadays occurs worldwide as a ruderal species. Its seeds are primarily dispersed by autochory and present secondary dispersal by ants, which are attracted by the lipid-rich elaiosome of the seeds. Ants remove intact seeds into their nest and discard them out in the pile mound without the appendage (Martins *et al.* 2006).

Seed, seedling and juvenile densities

In order to find ant nests, we placed tuna and honey baits (attractive to virtually all ant species; W. Benson, pers. comm.) at a 5 m distance from each other around the *R. communis* clumps in three study sites. We followed ants visiting baits to their nest entrance and checked for pile mounds in its vicinities. A pile mound is here characterized as an opening in the ground surrounded by rejected material, such as insect corpses, seeds, plant remains and soil particles. We established 30 paired experimental plots of 0.5 m x 0.5 m (Passos & Oliveira 2002, 2003,

2004). In each pair, one of the plots was placed in the pile mound and the other was a control plot, located 5 m away from any ant nest and at the same distance from the *R. communis* clump.

We counted the number of seeds with and without elaiosome, seedlings and juveniles of *R*. *communis* in the plots, which in the analysis were considered as categories. We considered as seedling the individual that still retained its cotyledons and as juvenile the one without cotyledons (maximum height found of 47.8 cm).

Fate of post-dispersed seeds

We investigated whether the fate of seeds discarded from ant nests (therefore without elaiosome) was different between seeds in the pile mound and in its vicinities and whether it was density-dependent. We removed each seed, seedling and juvenile of *R. communis* from the previously established plots, and placed *R. communis* seeds without elaiosome (manually removed) at different densities in each plot. The densities were 1, 3, 9, 27 e 81 seeds/plot. The number of seeds placed in each pair of plots was determined by sorting two series of random numbers, one related to plot number and the other related to the number of seeds placed. The seeds were equidistantly placed in the plots. We recorded twice a week the number of removed seeds and emerged seedlings in each plot during six weeks. A seed was considered removed when it was no longer in the plot. We took off the plots every seed or seedling not provided by us.

Ant collection, soil analysis, seed germination, and juvenile vigor

We established ten additional paired experimental plots as previously described in only one study site. For each nest, we collected ants interacting with tuna and honey baits using a soft brush and preserved the specimens in alcohol 70%. The collection was performed during the morning and voucher specimens were deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP). We collected soil from each plot in order to fill a plastic box (11 cm each side and 3.3 cm depth), totalizing 20 boxes (ten with pile mounds soil and ten with control plots soil). We also collected approximately 200 g of soil from each pile mound for macro- and micro-nutrients analysis. For chemical analysis of control soil, we collected approximately 20 g of soil from each control plot and mixed the samples for only one analysis.

We equidistantly placed ten *R. communis* seeds without elaiosome (manually removed) in each box. The boxes were placed inside a germination cabinet with white light and alternated temperatures of 20 °C and 30 °C. We adjusted the cabinet for uninterrupted 12 h light and 12 h darkness, and the dark period was coincident with the 20 °C period. We humidified the boxes with distilled water whenever necessary. After three weeks, we counted the number of seeds germinated in each box. We considered a seed germinated when there was protrusion of the hypocotile-radicle axis.

Only three individuals were kept in each box, whereas the others were discarded. We placed the boxes under natural conditions and exposed to sunlight. The boxes were watered four times a day. After one week most of the seedlings had progressed to juveniles, we performed vigor measurements. We gently removed all the content of the plastic boxes and washed away the soil from the roots. We measured the length of the roots and the aerial system of each plant with a milimetric ruler. For the whole plant set of each box, we obtained the fresh mass (FM) of roots, stems plus leaf petioles (hereafter called just stems), and leaf blades (hereafter called just leaves) with an analytical scale. We also counted the number of leaves and obtained leaf area with a leaf area meter (LI-COR, Inc., model LI-3100, Lincoln, Nebraska, USA). Roots, stems, and leaves were dehydrated in an 80 °C cabinet for more than two days, and then weighted in an analytical scale to determine their dry mass (DM). We calculated total dry mass (DM_{total}), root mass ratio (RMR), roots/aerial system ratio (R/AS), stem mass ratio (SMR), stem robustness (ROB), specific

leaf mass (SLM), leaf mass ratio (LMR), and leaf area ratio (LAR) as the following (Hunt 1982, Lee *et al.* 1996):

 $DM_{total} = DM_{root}+DM_{stem}+DM_{leaf}$ $RMR = DM_{root}/DM_{total}$ $R/AS = DM_{root}/DM_{stem+leaf}$ $SMR = DM_{stem}/DM_{total}$ $ROB = DM_{stem}/Length_{stem}$ $SLM = DM_{leaf}/Area_{leaf}$ $LMR = DM_{leaf}/DM_{total}$ $LAR = Area_{leaf}/DM_{total}$

Seedling protection from ants against herbivores

In order to evaluate whether *R. communis* seedlings growing near ant nests can gain protection from ants against herbivory, we performed an experiment using termites, which are often used to investigate deterrence of herbivores by ants (Freitas & Oliveira 1996). Live termite workers (*Neocapritermes opacus* Hagen; Termitidae) were glued by the dorsum on leaves using white glue (Tenaz[®]), in one seedling growing in both ant nest pile mound plots and in control plots, established as early described (n = 30 plot pairs) in one study site. To allow free access by ants and exclude vertebrates, the seedlings were protected with wire cages (20 x 20 x 30 cm, 1 cm mesh) closed at the top and staked to the ground. We recorded whether termites were attacked by ants at 30-min intervals from 0800 to 1000 h (Passos & Oliveira 2004).
RESULTS

Seed, seedling and juvenile densities

There was a greater number of seeds without elaiosome (Wilcoxon paired-sample sign rank test Z = -2.968, P = 0.003), seedlings (Z = -2.216, P = 0.034) and juveniles (Z = -3.852, P = <0.001) of *R. communis* in the pile mounds than in the control plots. Seeds with elaiosome were equally distributed between the plots (Z = -0.941, P = 0.347) (Figure 1).



Figure 1: Differences in the number of *Ricinus communis* seeds with elaiosome (a), seeds without elaiosome (b), seedlings (c) and juveniles (d) in ant nest pile mound plots (PM) and in control plots (CP). Two marks connected by a line represent one experimental pair.* P < 0.05.

Fate of post-dispersed seeds

We found no difference between seed removal in the pile mounds (simple linear regression coefficient b = -0.066; t = 8.241; P < 0.001) and in the control plots (b = -0.067; t = -9.739; P < 0.001) (F-ratio = 0.015, Sum of squares < 0.000, P = 0.902) for all seed densities in the

12 observations. Also, there was a small increase in seed removal along time. The removal of seeds of *R. communis* without elaiosome was inversely density-dependent. However, the reduction in the removal was not proportional to the rise in the density of seeds originally placed in the plots (Figures 2 and 3).



Figure 2: Regression coefficients (b) for *Ricinus communis* seeds without elaiosome in ant nest pile mound plots (full marks) (y = -0.066x + 5.310, $r^2 = 0.872$, P < 0.001) and in control plots (empty marks) (y = -0.067x + 5.249, $r^2 = 0.905$, P < 0.001) for 12 observations along time. Each b was obtained from a simple linear regression between the total number of non-removed seeds in the pile mounds and in the control plots and the five seed densities originally placed in the plots.



Figure 3: Percentages of non-removed *Ricinus communis* seeds without elaiosome in five densities in ant nest pile mound plots (full bars) and in control plots (empty bars) after six weeks.

We did not find any predation signs or fungal proliferation on the seeds. During the realization of this experiment there were two heavy rain episodes, which did not result in seed rearrange.

Ant collection, soil analysis, seed germination, and juvenile vigor

We found five ant species in our collection, all from the Myrmicinae subfamily (Tables 1, 2). Soil analysis showed great heterogeneity in the nutrient content among the soils of ant nest pile mounds, even when considering the same ant species. Moreover, there was apparently no difference in the macro- and micro-nutrient content between the pile mound soils altogether and the control soils (Tables 1, 2). Also, there was no difference in the number of seeds germinated in the pile mound soils and in the control soils (paired t test t = 1.103, df = 9, P = 0.299). Juveniles growing in the pile mound soils presented lower R/AS (median = 0.293, 95% upper limit = 0.500, 95% lower limit = 0.108) than those growing in the control soils (median = 0.416, 95% upper limit = 0.560, 95% lower limit = 0.291) (Z = 2.240, P = 0.025). The other vigor measurements did not differ (P > 0.05).

	Macronutrients													
Soil from	pН	g/dm ³	mg/dm ³	mmolc/dm ³						%				
	CaCl ₂	Organic Matter	Р	K	Ca	Mg	H+Al	Н	SB	CEC	v	Ν	Ca/Mg	Mg/K
Control	6.4	46	54	6.5	100	19	18	16	125.5	143.5	87.4	0.36	5.26	2.92
Dorymyrmex brunneus	6.4	29	22	6.3	80	19	16	16	105.3	121.3	86.8	0.19	4.21	3.01
Pheidole gertrudae	6.0	44	130	5.2	72	15	22	22	92.3	114.3	80.7	0.25	4.80	2.88
Pheidole gertrudae	6.4	36	140	9.8	100	24	16	16	134.2	150.2	89.3	0.26	4.16	2.44
Pheidole sp. 1	6.4	29	60	7.6	62	17	15	15	86.7	101.7	85.2	0.20	3.64	2.23
Pheidole sp. 2	6.3	84	130	9.1	100	19	20	20	128.2	148.2	86.5	0.47	5.26	2.08
Pheidole sp. 2	5.8	96	90	10.8	100	22	34	34	132.8	166.8	79.6	0.65	4.54	2.03
Pheidole sp. 2	6.1	44	38	5.2	76	16	20	20	97.2	117.2	82.9	0.28	4.75	3.07
Solenopsis sp. 1	6.1	30	61	10.3	60	22	20	19	92.4	112.4	82.2	0.22	2.72	2.13
Solenopsis sp. 1	5.9	27	63	11.8	45	15	20	19	72.0	92.0	78.2	0.25	3.00	1.27
Solenopsis sp. 1	7.5	30	50	3.9	95	8	8	8	107.7	115.8	93.0	0.20	11.87	2.05

Table 1: Macronutrients quantities in soils of ant nest pile mound plots and control plots.

SB is sum of basis, CEC is cation exchange capacity, and BS is basis saturation

Table 2: Micronutrients quantities in soils of ant nest pile mound plots and control plots.

	Micronutrients								
Soil from	mg/dm ³		mg/dm ³						
	S	Na	Fe	Mn	Cu	Zn	В		
Control	36	1	29	9.5	3.6	5.3	0.54		
Dorymyrmex brunneus	16	1	20	11.3	3.8	3.4	0.01		
Pheidole gertrudae	14	3	112	5.9	5.7	12.1	0.21		
Pheidole gertrudae	18	10	48	14.5	5.8	10.5	0.46		
Pheidole sp. 1	14	3	41	9.1	3.2	4.9	0.27		
Pheidole sp. 2	22	4	26	11.5	3.6	8.9	0.41		
Pheidole sp. 2	22	1	69	10.6	2.9	13.3	0.39		
Pheidole sp. 2	14	1	44	11.1	4.1	6.8	0.16		
Solenopsis sp. 1	20	3	109	8.2	5.7	4.4	0.04		
Solenopsis sp. 1	18	5	29	17.0	3.6	3.5	0.02		
Solenopsis sp. 1	22	19	11	5.8	4.8	16.9	0.71		

Seedlings protection from ants against herbivores

There was no difference in the number of termites attacked by ants in the pile mound plots and in the control plots (qui square test $\chi^2 = 0.100$, df = 1, P > 0.999).

DISCUSSION

After autochorous dispersal, seeds of *R. communis* are carried by ants into their nests, where the elaiosome is removed and retained. The seed without the appendage is then discarded out in pile mounds (Martins *et al.* 2006). So, we expected the post-dispersed seeds to occur in higher density in the pile mounds, as shown by our results. Providing this, we also expected the seedlings and, therefore, the juveniles, to occur in higher densities in such sites. This is accordingly to the results of Passos & Oliveira (2002, 2003, 2004) for *Clusia criuva* (Clusiaceae) seedlings in *Odontomachus chelifer* and *Pachycondyla striata* (Ponerinae) nests, and for

Anthurium sp. (Araceae), *Myrcia rostrata*, *Psidium cattleyanum* (Myrtaceae) and *Guapira opposita* (Nyctaginaceae) in *O. chelifer* nests. Once we found no difference in the distribution of seeds with elaiosome between the pile mounds and their vicinities, we may conclude that this is an outcome of the primary seed dispersal mechanism of *R. communis*.

The removal of post-dispersed seeds of *R. communis* is similar for seeds deposited in the pile mounds and in their surroundings, and therefore, seeds gain no protection from ants against predators nor become unavailable for further removal by other dispersal vectors. Though, once the seed removal presented only a small increase over time, seeds probably remain in the spot where they were first deposited and may either germinate if conditions are satisfactory or be incorporated into soil seed bank. It is possible that we observed only a small number of emerged seedlings during the realization of this experiment because the weather was very dry, in spite of the occurrence of two heavy rain episodes. Stochastic events, such as rain, did not result in seed rearrangement, contrary to examples described in literature (*e.g.* Hampe 2004).

The inversely density-dependent removal of seeds of *R. communis* without elaiosome is contrary to the predictions of many authors for seed predation, which ultimately results in seed removal from the spot it was deposited. For many neotropical species, high seed densities result in higher seed mortality due to predation and pathogens attack (Janzen 1969, 1970, 1971, Augspurger 1990). Although we did not find any predation signs or fungal proliferation on the seeds, we do not discard the possibility of seed predation by rodents or mortality caused by pathogens. The disproportional higher removal of seeds in low densities may result in predation or reallocation of the seeds without elaiosome discarded in the pile mounds, since they occur in small numbers, though in higher density than in their vicinities. Reallocated seeds may suffer mortality, but may also either germinate or be incorporated into soil seed bank.

Myrmicinae ants often feed on seeds and/or their appendages (Hölldobler & Wilson 1990). Viable seeds discarded in the pile mounds could, therefore, germinate and benefit from higher

nutrient availability in such microsites (Culver & Beattie 1978, O'Dowd & Hay 1980, Davidson & Morton 1981, Horvitz 1981, Passos & Oliveira 2002, 2004). However, we did not find any evidence to support this hypothesis, and so, our results are in agreement with Rice & Westoby (1986) and Passos & Oliveira (2002). Therefore, there is no additional advantage to the seeds discarded in the pile mounds: not only do they not gain protection by ants, but also they are not provided with a nutrient-enriched environment. Besides, the higher abundance of seeds in the pile mound than in its vicinities may result in further higher seedling competition.

Seed dispersal and germination, and early seedling growth/survival are the most critical stages in determining where plants recruit within a landscape (Herrera *et al.* 1994, Schupp 1995). Though we found no specific nutrient characteristics for the soils of the pile mounds, ant nests are known to have specific temperature, moisture and texture. Since ant nests present higher moisture and penetrability (Hölldobler & Wilson 1990, Farji-Brener & Medina 2000), such characteristics may be accounted for the lower R/AS of plants growing in the pile mound soils than in the surrounding soils. However, we do not believe that there is such greater advantage for plants growing in the pile mound soils than in the ant nests' vicinities, once we did not observe differences in the number of germinated seeds in the pile mound soils and in the control soils, and only one out of 18 juvenile vigor measurements difference in the total dry mass of plants growing in the pile mound soils and in the control soils, indicating that biomass gain, which is the ultimate importance of a nutrient-enriched soil, is similar anywhere the plant is established.

Besides not providing any additional advantage for the seeds of *R. communis*, ants also do not render differential protection against herbivory for the seedlings growing in the pile mounds. This result is contrary to many findings in literature, such as those of Davidson & Epstein (1989) and Passos & Oliveira (2004) for other species studied. The non-differential patrol of ants regarding the location of the seedlings may be due to the presence of extrafloral nectaries on leaf

petioles and nerves of *R. communis*, even in the early developmental stages of the plant (pers. observ.). Therefore, ants may patrol the plants in order to collect nectar and eventually attack herbivores as a defense of their resource (as explained by *e.g.* Beattie 1985 and Beattie & Hughes 2002) anywhere the plant is established. *Ricinus communis* also presents high quantities of toxic compounds (Windor 2004), and the interaction between this plant and the foraging ants deserves further investigation.

This study shows that seed dispersal of *R. communis* by ants had a markedly effect on the distribution pattern of the seeds, seedlings and juveniles of this species. Moreover, there were no additional advantages for the seeds, seedlings and juveniles in the pile mounds. In spite of the suggestion that seed dispersal by ants affects recruitment in many species, we found no evidence to support this hypothesis for *R. communis*. Therefore, there is no reason at all for us to believe that ants act as directed dispersal vectors of the seeds of this species, although myrmecochory is widely recognized as a directed dispersal mechanism. The consequences of seed dispersal by ants to plants deserve further and careful investigations, so that the term "directed dispersal" may be used in a more accurate way.

ACKNOWLEDGEMENTS

The authors wish to thank Dr. Paulo S. Oliveira and André V. Freitas for valuable suggestions, Guilherme B. Sanvido for help during field work, Rogério R. da Silva for ant identification, and Flavio A. M. dos Santos for statistical advice. Soil analysis were performed at Instituto Campineiro de Análise de Solo e Adubo S/C Ltda. V. F. Martins was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo grant (# 03/11123-4).

REFERENCES

Augspurger, C.K. (1990) The potential impact of fungal pathogens on tropical plant reproductive biology. *Reproductive ecology of tropical forest plants* (eds K. S. Bawa & M. Hadley.), pp. 237-

245. The Parthenon Publishing Group, Carnforth.

Basset, Y. (1999) Diversity and abundance of insect herbivores foraging on seedlings in a Rainforest in Guyana. *Ecological Entomology* **24**, 245-259.

Beattie, A.J. (1985) *The evolutionary ecology of ant-plant mutualisms*. Cambridge University Press, New York.

Beattie, A.J. & Hughes L. (2002) Ant-plant interactions. *Plant-animal interactions: an evolutionary approach* (eds C. Herrera & O. Pellmyr), pp. 211-236. Blackwell, Oxford.

Berg, R.Y. (1975) Myrmecochorous plants in Australia and their dispersal by ants. *Australian Journal of Botany* **23**, 475-508.

Camargo, A.P.; Pinto, H.S.; Brunini, O.; Pedro Jr., M.J.; Ortolani, A.A. & Alfonsi, R.R. (1996) Clima do Estado de São Paulo. *Atlas climático e ecológico do Estado de São Paulo* (ed. J.

Setzer), pp. 51-87 Comissão Interestadual da Bacia Paraná-Uruguai, São Paulo.

Culver, D.C. & Beattie A.J. (1978) Myrmecochory in *Viola*: dynamics of seed-ant interactions in some West Virginia species. *Journal of Ecology* **66**, 53-72.

Davidson, D.W. & Epstein, W.W. (1989) Epiphytic associations with ants. *Phylogeny and Ecophisiology of epiphytes* (ed U. Lüttge), pp. 200-233. Springer, Berlin Heidelberg New York. Davidson, D.W. & Morton, S.R. (1981) Myrmecochory in some plants (*F. chenopodiaceae*) of the Australian Arid Zone. *Oecologia* **50**, 357-366.

Farji-Brener, A.G. & Medina, C.A. (2000) The importance of where to dump the refuse: seed bank and fine roots in nests of the leaf-cutting ants *Atta cephalotes* and *Atta colombica*.

Biotropica **32**, 120-126.

Freitas, A.V.L. & Oliveira, P.S. (1996) Ants as selective agents on herbivore biology: effects on the behaviour of a non-myrmecophilous butterfly. *Journal of Animal Ecology* 65, 205-210.
Hampe, A. (2004) Extensive hydrochory uncouples spatialtemporal patterns of seedfall and seedling recruitment in a "bird-dispersed" riparian tree. *Journal of Ecology* 92, 797-807.
Hanzawa, F.M.; Beattie, A.J. & Culver, D.C. (1988) Directed dispersal: demographic analysis of an ant-seed mutualism. *The American Naturalist* 131, 1-13.

Herrera, C.M.; Jordano, P.; López-Soria, L.& Amat, J.A. (1994) Recruitment of a mast-fruiting, bird dispersed tree: bridging frugivore activity and seedling establishment. *Ecological Monographs* **64**, 315-344.

Hölldobler, B. & Wilson, E.O. (1990). The Ants. The Belknap Press, Cambridge.

Horvitz, C.C 1981. Analysis of how ant behaviors affect germination in a Tropical

Myrmecochore *Calathea microcehala* (P. & E.) Koernicke (Marantaceae): microsite selection and aril removal by Neotropical ants, *Odontomachus*, *Pachycondyla*, and *Solenopsis* (Formicidae). *Oecologia* **51**, 47-52.

Horvitz, C.C. & Schemske, D.W. (1986) Ant-nest soil and seedling growth in a neotropical antdispersed herb. *Oecologia* **70**, 318-320.

Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics* **13**, 201-228.

Hunt, R. (1982) The functional approach to growth analysis. Edward Arnold, London.

Janzen, D.H. (1969) Seed-eaters versus size, number, toxicity and dispersal. Evolution 23, 1-27.

Janzen, D.H. (1970) Herbivores and the number of tree species in Tropical Forests. *The American Naturalist* **104**, 501-528.

Janzen, D.H. (1971) Seed predation by animals. *Annual Review of Ecology and Systematics* **2**, 465-492.

Jordano, P. & Godoy, J.A. (2002) Frugivore-generated seed shadows: a landscape view of demographic and genetic effects. *Seed dispersal and frugivory: Ecology, evolution and conservation* (eds D. J. Levey; W. R. Silva & M. Galetti), pp. 305-322. CABI Publishing, Wallingford.

Lee, D.W.; Krishnapilay, B.; Mansor, M.; Mahamad, H. & Yap, S.K. (1996) Irradiance and spectral quality affect Asian Tropical Rain Forest tree seedling development. *Ecology* **77**, 568-580.

Lieberman, D. (1996) Demography of Tropical tree seedlings: a review. *Ecology of Tropical Forest tree seedlings* (ed M. D. Swaine), pp. 131-138. UNESCO/Parthenon, Carnforth.

Mabberley, D. J. (1998) *Ricinus. The plant book: A portable dictionary of the vascular plant*, 2nd edition, pp. 618. Cambridge University Press, Cambridge.

Manzaneda, A.J.; Fedriani, J.M. & Rey, P.J. (2005) Adaptative advantages of myrmecochory: the predator-avoidance hypothesis tested over a wide geographic range. *Ecography* **28**, 583-592.

Martins, V.F.; Guimarães, P.R.; Silva, R.R. & Semir, J. (2006) Secondary seed dispersal by ants of *Ricinus communis* (Euphorbiaceae) in the Atlantic Forest in Southeastern Brazil: influence on seed germination. *Sociobiology* **47**, 265-274.

O'Dowd, D.J. & Hay, M.E. (1980) Mutualism between harvester ants and a desert ephemeral: seed escape from rodents. *Ecology* **61**, 531-540.

Passos, L. & Oliveira, P.S. (2002) Ants affect the distribution and performance of seedling of *Clusia criuva*, a primarily bird-dispersed rain forest tree. *Journal of Ecology* **90**, 517-528.

Passos, L. & Oliveira, P.S. (2003) Interactions between ants, fruits and seeds in a Restinga Forest in South-Eastern Brazil. *Journal of Tropical Ecology* **19**, 261-270.

Passos, L. & Oliveira, P.S. (2004) Interactions between ants and fruits of *Guapira opposita* (Nyctaginaceae) in a Brazilian Sandy Plain Rainforest: ant effects on seeds and seedlings.

Oecologia **139**, 376-382.

Rice, B. & Westoby, M. (1986) Evidence against the hypothesis that ant-dispersed seeds reach nutrient-enriched microsites. *Ecology* **67**, 1270-1274.

Salisbury, F.B. & Ross, C.W. (1992) Growth responses to temperature. *Plant physiology*, 4th edition, pp. 485-503. Wadsworth, Inc., California.

Schupp, E.W. (1995) Seed-seedling conflicts, habitat choices, and patterns of plant recruitment. *American Journal of Botany* **82**, 399-409.

Singh, D. (1976) Castor – *Ricinus communis* (Euphorbiaceae). *Evolution of crop plants* (ed N. W. Simmonds), pp. 84-86. Longman Group, New York.

Teasdale, J.R. & Pillai, P. (2005) Contribution of ammonium to stimulation of smooth pigweed (*Amaranthus hybridus* L.) germination by extracts of hairy vetch (*Vicia villosa* Roth) residue. *Weed Biology and Management* **5**, 19-25.

Vander Wall, S.B. & Longland, W.S. (2004) Diplochory: are two seed dispersers better than one? *Trends in Ecology and Evolution* **19**, 155-161.

Wang, B.C. & Smith, T.B. (2002) Closing the seed dispersal loop. *Trends in Ecology and Evolution* **17**, 379-385.

Wenny, D.C. (2000) Seed dispersal, seed predation and seedling recruitment of a Neotropical Montane tree. *Ecological Monographs* **70**, 331-351.

Wenny, D. (2001) Advantages of seed dispersal: a re-evaluation of direct dispersal. *Evolutionary Ecology Research* **3**, 51-74.

Wenny, D.G. & Levey, D.J. (1998) Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences of the United States of America* **95**, 6204-6207.

Willson, M.F. (1993) The Ecology of seed dispersal. *Seeds: The ecology of regeneration in plant communities.* (ed M. Fenner), pp. 61-85. CAB International, Wallingford.

Windor, C. (2004) Toxicity of Ricin. Journal of Toxicology – Toxin Reviews 23, 97-103.

Post-dispersal regenerative phase of *Ricinus communis* L. (Euphorbiaceae): do ruderal features assure the species ability to successfully occupy new habitats?^{*}

Valéria Forni Martins¹, Claudia Regina Baptista Haddad² & João Semir^{3*}

¹Programa de Pós-Graduação em Ecologia, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, SP, Brazil.
²Departamento de Fisiologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas, C.P. 6109, 13083-970, Campinas, SP, Brazil.
³Departamento de Botânica, Instituto de Biologia, Universidade Estadual de Campinas, C.P. 6109, 13083-970, Campinas, SP, Brazil.

Correspondence author: Valéria Forni Martins. PPG-Ecologia/IB/UNICAMP. Cx. Postal 6109. CEP 13083-970. Telephone 55 19 37886167, Facsimile 55 19 37886168. E-mail: vmartins@unicamp.br.

Post-dispersal regenerative phase of castor

The authors confirm that there is no commercial interest in the findings presented.

^{*}Format and style: Weed Biology and Management

ABSTRACT

Ricinus communis, the commonly known castor, is considered to be a ruderal species. Its seeds have a lipid-rich elaiosome that attracts ants for secondary seed dispersal but also is regarded as having germination inhibitory substances. Hence, ants may play an important role in seed germination by removing the elaiosome. Seeds with the elaiosome and non-germinated seeds without the elaiosome may be incorporated into persistent seed banks, and so, old seeds are likely to present specific germination responses in order to occupy a habitat after its disturbance. The seedlings emerged should be light-demanding and poor competitors, especially with individuals of other species. This study was designed to assess the post-dispersal regenerative phase of castor. Our main objective was to determine whether ruderal features assure the species ability to successfully occupy new habitats. The following questions were addressed: (1) how is germination response of freshly harvested and one year old seeds to combinations of light, temperature and elaiosome conditions? (2) Are there persistent seed banks? (3) How is juvenile response to light quantity and quality? (4) How is juvenile response to intra- and inter-specific competition? Fresh and one year old seeds presented distinguished germination response, although they germinated in all conditions they were submitted to. Also, one year old seeds did not present typical germination response of seeds that may constitute seed banks. We found few viable seeds of *R. communis* in the soil, though massive seedling emergence after soil disturbance was observed in many sites. *Ricinus communis* is light-demanding, but may occupy pretty shady sites. Also, the species is a poor competitor, especially with individuals of other species, but is capable of establishing in areas with high density of individuals. This study demonstrated R. *communis* does not present all typical features of ruderal plants, and its success in colonizing the most different habitats may be attributed to the species' plasticity facing environmental conditions.

Key words: Elaiosome, *Brachiaria decumbens*, germination, inter-specific competition, intraspecific competition, light, photon flux density, persistent soil seed bank, ratio red:far red, seed age, temperature, vigor.

INTRODUCTION

The successful occupation of a wide array of habitats by plants relies on the species' ability to overcome external factors which limit the plant growth. Therefore, plant survival strategies are a result of combinations of different intensities of habitat stress and disturbance. Grime (1979) suggested three primary plant functional types, namely, competitives, stress-tolerants, and ruderals. Ruderal plants occupy low stressful but highly disturbed habitats, that is, habitats that do not constrain the rate of dry matter production but limit the plant biomass by causing its partial or total destruction. In order to succeed in these habitats, ruderals shall present common morphological, physiological and life-history characteristics (see Grime 1979 and 2001 for an extensive review).

Ricinus communis, the commonly known castor, is a shrub or treelet that occurs worldwide and is considered to be a ruderal species. Its seeds are primarily dispersed by autochory and present secondary dispersal by ants, which are attracted by the lipid-rich elaiosome of the seeds. Ants remove intact seeds into their nest and usually discard them out in the pile mound without the appendage. So, there can be three different scenarios for castor seed germination, considering that the removal of the elaiosome can only be performed by the ants: (1) seeds with elaiosome exposed to light and alternated temperatures, as a result of no interaction between castor seeds and ants; (2) seeds without elaiosome kept in both constant darkness and temperature, for those removed into the ant nest but not discarded outside it in a pile mound; (3)

seeds without elaiosome exposed to light and alternated temperatures, as a result of being discarded outside the ant nest after elaiosome removal (Martins *et al.* 2006).

The elaiosome of castor seeds is regarded as having germination inhibitory substances, and, therefore, may impose innate dormancy on the seed (Lagôa & Pereira 1987). Hence, seeds with elaiosome may be incorporated into soil seed banks, as well as post-dispersed nongerminated seeds which elaiosome had been removed by the ants. It is commonplace that castor forms persistent soil seed banks, though, to the extent of our knowledge, no study has demonstrated the existence of such seed banks.

In order to form persistent seed banks, castor seeds must have high longevity. This is only possible only for orthodox seeds, which can be dried out without damage due to low moisture content, and keep longevity with decrease in both seed storage moisture content and temperature (Murdoch & Ellis 1993, Probert 1993, Bewley & Black 1994).

Seeds that constitute soil seed banks usually respond to alternated temperatures and presence of light as indicators of when and where to germinate (Fenner 1985, Pons 1993, Probert 1993). Light-requirement is also an important germination response for gap-detection: seeds excluded from light in the soil can be brought up to the surface where they are exposed to light during disturbance of the soil. This kind of disturbance generally coincides with complete destruction of the established vegetation, and hence, is a good predictor of reduced competition with adult plants (Pons 1993).

Persistent soil seed banks are constituted by seeds of different ages (Garwood 1989), being well documented that, for many species, after-ripening changes in seeds are accompanied by an usual reduction in the specificity of germination requirements (Probert 1993). Therefore, it is expected to be differences in the required germination response of the seeds into persistent seed banks in comparison to that of newly post-dispersed seeds. If this statement is true, then probably there are changes in castor germination response along time.

Not only are seed dispersal and germination important to plant population regeneration, but also early seedling growth/survival is one of the most critical stages in determining where plants recruit within a landscape (Herrera *et al.* 1994, Schupp 1995). Seedlings are known to present high mortality due to factors such as herbivory, pathogen infestation, and competition (Janzen 1970, Lieberman 1996, Basset 1999). The latter is considered to be one of the main factors controlling growth processes and is crucial for seedling establishment (Fenner 1985, Lee *et al.* 1996, Whitmore 1996). According to Fenner (1985), ruderal species seem to be unable to withstand competition in the earliest stages of growth, which may imply the light-requirement for the germination of seeds in the seed banks and may lead to the exclusion of ruderals from closed vegetation types. However, seed banks are usually constituted by seeds of more than one species (Garwood 1989), and environmental conditions that lead one species to germinate probably result in the germination of other species as well. This situation clearly results in co occurrence of species, and the outcome of this interaction remains unknown for castor.

Assuming that castor is a ruderal species and considering its seed secondary dispersal by ants, we propose the following hypothesis: (1) recently post-dispersed seeds, therefore without elaiosome, are expected to germinate in any combination of light and temperature, since the removal of the appendage should indicate a satisfactory microsite for seedling establishment, either inside or outside the ant nest; (2) recently released seeds from parental plants, therefore with elaiosome, are expected not to germinate in any combination of light and temperature if the appendage does impose innate dormancy on the seed, but are expected to germinate in some combination of light and temperature if the presence of the appendage leads to an induced dormancy of the non-germinated seed; (3) old seeds without elaiosome are expected to be viable and to germinate under alternated temperatures and presence of light, which are the conditions met by the seeds in seed banks after soil disturbance; (4) old seeds with elaiosome are expected to be viable and not to germinate in any combination of light and temperature if the appendage

imposes innate or induced dormancy on the seed; (5) if the elaiosome does impose some kind of dormancy on the seed, its removal should cease the germination blockage even in old seeds; (6) it is likely to occur persistent soil seed banks; (7) seedlings/juveniles should be light-demanding, due to both the germination response of the seeds in seed banks and the supposed poor competition ability of ruderals, which then occur in open vegetation types, and (8) seedlings/juveniles should be poor competitors, especially with individuals of other species, since ruderals occur in open-vegetation types and may germinate synchronously with other species.

This study was designed to assess the post-dispersal regenerative phase of the ruderal castor. Our main objective was to determine whether ruderal features assure the species ability to successfully occupy new habitats. The following questions were addressed: (1) How is germination response of freshly harvested and one year old seeds to combinations of light, temperature and elaiosome conditions? (2) Are there persistent soil seed banks? (3) Are there alterations in vigor measurements of juveniles growing under different light quantity and quality? (4) Are there alterations in vigor measurements of juveniles growing in intra- and inter-specific competition?

MATERIALS AND METHODS

Seed collection sites

Castor seeds were collected from parental plants by involving infrutescences with tule bags until fruits were ripen. The collection was performed in Campinas municipality, Southeast Brazil (22°54' S, 47°03' W). According to Koeppen's climate classification, the climate of Campinas region is Cwa, macrothermal temperate with mild dry winter (Camargo *et al.* 1966). Castor occurred basically in fallow grounds, which we considered as an open area with no considerable shady sites located in urban scenarios. It is usually dominated by few plant species and, at the collection sites, the most abundant were *Brachiaria decumbens* (Poaceae) and castor, which occurred in clumped pattern.

Seed germination

We performed two germination experiments in order to analyze possible modifications of the germination response as seeds got older. We used part of freshly harvested seeds in the first experiment, and kept the rest of the seeds in tule bags on a laboratory table for a year. Half of these seeds had the elaiosome manually removed as soon as they were collected. The other half had the elaiosome removed by the time we performed the second experiment. This procedure was necessary in order to check for possible innate or induced dormancy of castor seeds with elaiosome.

There were ten Petri dishes with filter-paper for each treatment of both experiments, each dish with ten castor seeds, totalizing 100 seeds per treatment. We humidified the Petri dishes with distilled water whenever necessary. We considered a seed germinated when there was protrusion of the hypocotile-radicle axis. Seeds kept in constant darkness were observed inside dark room with green light. We recorded the number of germinated seeds for 90 d. The effects of light, temperature and elaiosome on germination were investigated using a nominal logistic regression. To adjust the final model, we removed the non-significant interactions one by one (Dobson 2001).

In order to evaluate the viability of fresh and one year old castor seeds, we applied the tetrazolium test to 30 seeds of each age. We manually removed the elaiosome and cut the seeds longitudinally and parallel to the cotyledons in two equal halves. The parts containing the embryo were placed in glass recipients, which were wrapped in aluminum paper. The recipients contained 0.5% tetrazolium solution and were kept under constant 30° C for 48 h. Then we rinsed the seed parts in running water for one minute. We interpreted the colored parts of the seeds after Grabe (1976).

Experiment 1

This experiment was designed to investigate germination responses to combinations of light (present or absent), temperature (alternated or constant), and elaiosome (present or absent). We used two germination cabinets with white light, one with constant temperature of 30 °C and other with alternated temperatures of 20 °C and 30 °C. We adjusted both cabinets for uninterrupted 12 h light and 12 h darkness. In the alternated temperature cabinet, the dark period was coincident with the 20 °C period. Seeds kept in constant darkness were placed in Petri dishes inside black plastic bags, and seeds exposed to light were placed in Petri dishes inside transparent plastic bags, only for humidity retention.

Experiment 2

The germination treatments were the same as described above but the fact that we used three types of seeds: (1) seeds with elaiosome; (2) seeds which elaiosome had been removed as soon as they were collected, and (3) seeds which elaiosome was removed by the time we performed this experiment.

Soil seed banks

To check for castor seed banks, in August 2005 we collected soil from six sites located in fallow grounds, in Campinas municipality. These sites used to be occupied by castor populations and were monitored for about three and half years. So, it was possible to determine the approximate time at which there were no longer castor populations in the sites. We used a metal square of 25 cm side and 5 cm depth (Garwood 1989 and authors therein) to collect soil and a metal sieve with a 0.5 mm mesh to separate the castor seeds from the soil. In each area, we collected five soil samples, which were at least 5 m apart from each other. In order to test seed viability, we applied the tetrazolium test as early described.

Juvenile vigor in different light quantity and quality

We sowed four freshly harvested seeds without elaiosome (manually removed) in pots filled with soil. The pots were submitted to conditions of different photon flux densities (PFD) and spectral qualities (variation in the ratio of red:far red, hereafter R:FR). In order to decrease PFD, we used one to three layers of fine plastic mesh, and to alter R:FR, we used a special filter which pigmentation absorbs red light (purple cloth). Seeds in control pots were not submitted to any alteration of light quantity or quality (Sanches 2004). We performed a measurement of PFD and R:FR for all treatments on a spring bright sunny day, about noon time, using a radiation linear sensor (Line Quantum Sensor, model LI 191 AS) coupled to a datalogger (model LI 1000) and a R:FR radiation sensor (650/730 nm, Skye Instruments). We estimated the percentage of PFD and R:FR for each treatment in relation to the total PFD and R:FR at exposed sunlight, which were 1730.33 μ mol m⁻² s⁻¹ and 1.19, respectively, during the experiment in October and November 2005 (Table 1). Ambient temperature variation during this period was 13.8 °C to over 36.9 °C on exposed sunlight.

There were ten pots for each treatment and all pots were laid on tables under natural conditions and exposed to sunlight. The pots were watered four times a day. All seeds were equidistantly placed at 1 cm depth in the pots, which were of same volume and filled with similar quantity of soil. After 51 d, we counted the number of established plants. We used Kruskal-Wallis test to check for differences in the number of established plants per pot growing under different PFD, and we used Mann-Whitney test to check for differences in the number of established plants per pot growing under different R:FR (Zar 1999).

Then, we performed vigor measurements for all individuals that had lost both cotyledons (so, considered as juveniles) at least one week before the measurements. We measured the length of the roots and the aerial system of each plant with a milimetric ruler. For the whole plant set of each pot, we obtained the fresh mass (FM) of roots, stems plus leaf petioles (hereafter called just

stems), and leaf blades (hereafter called just leaves) with an analytical scale. We also counted the number of leaves and obtained leaf area with a leaf area meter (LI-COR, Inc., model LI-3100). Roots, stems, and leaves were dehydrated in an 80 °C cabinet for more than two days, and then weighted in an analytical scale to determine their dry mass (DM). We calculated total dry mass (DM_{total}), root mass ratio (RMR), roots/aerial system ratio (R/AS), stem mass ratio (SMR), stem robustness (ROB), specific leaf mass (SLM), leaf mass ratio (LMR), and leaf area ratio (LAR) as the following (Hunt 1982, Lee *et al.* 1996):

 $DM_{total} = DM_{root} + DM_{stem} + DM_{leaf}$

 $RMR = DM_{root}/DM_{total}$

 $R/AS = DM_{root}/DM_{stem+leaf}$

 $SMR = DM_{stem}/DM_{total}$

 $ROB = DM_{stem}/Length_{stem}$

 $SLM = DM_{leaf} / Area_{leaf}$

 $LMR = DM_{leaf}/DM_{total}$

 $LAR = Area_{leaf}/DM_{total}$

To check for differences in vigor measurements per pot for plants growing under different PFD we used analysis of variance (Bonferroni for *ad hoc* tests) and Kruskal-Wallis (Mann-Whitney for *a posteriori* tests) when data had no normality. For plants growing under different R:FR, we used t test and Mann-Whitney test when data had no normality (Zar 1999).

Juvenile vigor in intra- and inter-specific competition

To analyze castor intra-specific competition response, we sowed freshly harvested castor seeds without elaiosome (manually removed) in pots at four different densities: 1, 4, 16 and 64 seeds/pot. In order to analyze castor inter-specific competition response, we sowed freshly harvested castor seeds without elaiosome and *B. decumbens* young plants (previously germinated

inside germination cabinet) in proportion of 1:1 in pots at three different densities: 4, 16 and 64 individuals/pot. *Brachiaria decumbens* was used as a model for inter-specific competition because it is commonly observed co-occurring with castor plants in fallow grounds (pers. obervs.). The castor seeds were sowed only after *B. decumbens* plants were established, simulating conditions observed in fallow grounds (pers. obervs.). Ambient temperature variation was 15.3 °C to 36.9 °C between December 2005 and March 2006, when the experiment was carried out.

This experiment and measurements were performed as described in the previous topic. Vigor measurements were performed after 5 mo. We used Kruskal-Wallis test to check for differences in the arcsine of the square root of proportions of established plants per pot in the intra- and inter-specific competition experiments. We used Mann-Whitney test to check for differences in the arcsine of the square root of proportions of established plants per pot of same plant density in the intra and inter-specific competition experiments (Zar 1999).

For analysis of vigor measurements, we unconsidered the original treatments and used the number of established castor juveniles per pot for the intra-specific competition experiment, and the number of established castor juveniles plus the number of established *B. decumbens* plants per pot for the inter-specific experiment. To check for differences in vigor measurements within the intra- and inter specific competition experiments, we made a correlation analysis for all measurements between the mean vigor per pot of established castor juveniles for each density and the number of established plants in each pot. In order to compare the vigor measurements of castor juveniles growing in pots only with co-specifics or in pots with co-specifics and *B. decumbens*, we made two categories: (1) four or less established plants per pot, and (2) five or more established plants per pot. Then we compared both categories between the intra- and inter-specific experiments with t-test or Mann-Whitney test when data had no normality (Zar 1999).

RESULTS

Seed germination

The germination of fresh castor seeds was influenced by light, temperature and elaiosome $(\chi^2 = 448.16, df = 4, P < 0.001)$. Seed germination was higher under presence of light ($\chi^2 = 74.15$, P < 0.001, odds ratio = 0.128), constant temperature ($\chi^2 = 196.54$, P < 0.001, odds ratio = 0.021), and absence of the elaiosome ($\chi^2 = 23.21$, P < 0.001, odds ratio = 2.770). There was interaction between light and elaiosome, with a rise in the germination of seeds kept under constant darkness and without the elaiosome ($\chi^2 = 5.84$, P < 0.016, odds ratio = 1.652). Total germination of fresh seeds was 40.63%, although tetrazolium test indicated 100% of seed viability.

The germination of one year old castor seeds was influenced by light and elaiosome (χ^2 = 141.35, df = 5, P < 0.001), but no longer by temperature (P > 0.05). Seed germination was enhanced by absence of light (χ^2 = 60.59, P < 0.001, odds ratio = 5.547), and presence of the elaiosome in comparison to those seeds which appendage had been removed as soon as they were collected (χ^2 = 8.94, P = 0.003, odds ratio = 0.635). Germination was also higher for seeds which elaiosome was removed by the time we performed the experiment in comparison to those seeds which elaiosome had been removed when they were collected (χ^2 = 29.80, P < 0.001, odds ratio = 2.262). When comparing the germination odds ratios of seeds with elaiosome, seeds which elaiosome was removed as soon as seeds were collected, and seeds which elaiosome was removed by the time of the experiment, it is noticeable that the germination was higher for seeds which elaiosome was removed at the collection. Total germination of one year old seeds was 54.17%, although tetrazolium test indicated 100% of seed viability. Therefore, total germination of old seeds was higher than of fresh seeds (χ^2 = 35.23, df = 1, P < 0.001).

Soil seed banks

Only few of the castor seeds found, all without elaiosome, were in viable conditions (Table 2). We found seed coat fragments in every study site, and many of the seeds we found were only composed by their coats. In some cases, there were still some portions of endosperm collapsed inside the seed coat, and less frequently we found seeds with a black powdering endosperm, which may indicate decomposition.

Juvenile vigor in different light quantity and quality

There was no difference in the number of established plants growing under different PFD ($\chi^2 = 6.453$, df =3, P = 0.092) and R:FR (U = 55.000, df =1, P = 0.691). There was a tendency to increase the length of roots, FM_{roots}, FM_{stems}, DM_{roots}, DM_{stems}, RMR, R/AS, ROB and SLM (P \leq 0.05) with increasing light quantity. On the other hand, there was a tendency to decrease the length of aerial system, number of leaves, leaf area, DM_{total}, SMR, LMR and LAR (P \leq 0.05) with increasing light quantity (Figure 1). FM_{leaves} and DM_{leaves} did not differ among plants growing under different PFD (P > 0.05).

Plants in the control pots had higher length of roots (t = 6.761, df =18, P < 0.001), FM_{roots} (U = 100.000, df = 1, P < 0.001), DM_{roots} (t = 5.432, df =18, P < 0.001), RMR (t = 11.222, df = 18, P < 0.001), R/AS (t = 10.629, df =18, P < 0.001), ROB (U = 92.000, df =1, P = 0.001) and SLM (U = 100.000, df =1, P < 0.001) than plants in altered R:FR. Plants in the control pots had lower length of aerial system (U = 10.000, df =1, P = 0.002), leaf area (t = 3.558, df = 18, P = 0.002), SMR (t = 10.473, df =18, P < 0.001), LMR (t = -3.233, df = 18, P = 0.005) and LAR (t = -10.384, df = 18, P < 0.001) than plants in altered R:FR. Number of leaves, FM_{stems}, FM_{leaves}, DM_{stems}, DM_{leaves} and DM_{total} did not differ between plants growing under different R:FR (P > 0.05).

There was no difference in the proportion of established plants growing in the intra ($\chi^2 = 4.493$, df =3, P = 0.213) and inter-specific competition ($\chi^2 = 1.121$, df =2, P = 0.571) experiments. Also, there was no difference in the proportion of established plants in the pots of same plant density in the intra and inter-specific competition experiments (P > 0.05).

In the intra-specific experiment, SMR increased with increasing number of castor plants per pot (F-ratio = 3.226, Sum of squares = 0.100, P = 0.010), while number of leaves decreased with increasing number of castor plants per pot (F-ratio = 2.524, Sum of squares = 15.160, P = 0.031). The other vigor measurements did not differ within the intra-specific experiment (P > 0.05).

In the inter-specific experiment, there was an increase in DM_{root} (F-ratio = 14.882, Sum of squares = 0.035, P < 0.001), DM_{total} (F-ratio = 4.606, Sum of squares = 0.032, P = 0.014), RMR (F-ratio = 8.299, Sum of squares = 0.517, P = 0.002) and R/AS (F-ratio = 60.948, Sum of squares = 36.901, P < 0.001) with increasing number of plants per pot, while there was a decrease in DM_{stem} (F-ratio = 3.317, Sum of squares = 0.008, P = 0.040) and SMR (F-ratio = 4.656, Sum of squares = 0.418, P = 0.015) with increasing number of plants per pot. The other vigor measurements did not differ within the inter-specific experiment (P > 0.05).

Castor juveniles growing in the intra-specific experiment had higher length of aerial system and roots, FM_{roots}, FM_{stems}, FM_{leaves}, leaf area, DM_{roots}, DM_{stems}, DM_{leaves}, DM_{total}, ROB, LMR and LAR than those growing in the inter-specific experiment. Number of leaves was higher for castor juveniles growing in pots with four or less plants in the intra-specific competition experiment, and it was similar for castor juveniles growing in pots with five or more plants in both experiments. RMR, R/AS and SMR were higher for castor juveniles growing in pots with four or less plants for castor juveniles growing in pots with four or less plants for castor juveniles growing in pots with four or less plants for castor juveniles growing in pots with four or less plants in the inter-specific competition experiment, and they were similar for castor

juveniles growing in pots with five or more plants in both experiments. There was no difference in SLM for castor juveniles growing in the intra- and inter specific experiments (Table 3).

DISCUSSION

The recruitment of an individual plant within a landscape greatly relies on its seed dispersal and germination, and early seedling growth/survival (Herrera *et al.* 1994, Schupp 1995). After autochorous dispersal, castor seeds may be carried by ants into their nests, where the elaiosome is removed and retained by the ants. Then, the seed without the appendage is usually discarded out in pile mounds (Martins *et al.* 2006). The higher germination of fresh castor seeds in the presence of light and in constant temperature means that germination is assured wherever the seeds are deposited. If seeds are not secondarily dispersed by ants, they may benefit from the presence of light on the soil surface, whereas, if they interact with ants, seeds may present higher germination either inside the ant nest, where the temperature is nearly constant, or outside it, where there is presence of light (Martins *et al.* 2006). However, contrary results were found by other authors, with increased germination in the absence of light and in alternated temperatures (Lagôa & Pereira 1987, Bianchini & Pacini 1996, Martins *et al.* 2006).

The interaction between ants and castor seeds, which results in the removal of the elaiosome, seems to play an important role in castor seed germination, since we observed that fresh seeds without the appendage presented higher germination. This was also recorded by other authors (Lagôa & Pereira 1987, Martins *et al.* 2006), though Lisci *et al.* (1996), and Bianchini and Pacini (1996) showed that germination success was enhanced by the presence of the elaiosome, probably due to its important role in absorbing water from the soil and transferring it to the rest of the seed during germination. However, the increase in germination of fresh seeds due to the interaction between the absence of both light and elaiosome may highlight the importance of ants

in enhancing castor seed germination success, which was already demonstrated by Martins *et al.* (2006).

One year old castor seeds showed germination responses to light and temperature conditions that differed from that of fresh seeds. There was a shift from high germination in the presence of light for fresh seeds to high germination in the absence of light for old seeds. Also, temperature no longer influenced germination, which may be explained by the usual reduction in the specificity of germination requirements accompanying after-ripening changes in many species (Probert 1993). Therefore, changes in germination response along time do not conform to our expectations and are different from the described in literature for seeds that constitute seed banks.

We also observed higher germination of one year old castor seeds without the elaiosome, when this appendage was removed at the moment of the experiment. Nevertheless, seeds with elaiosome germinated in greater number than those seeds which appendage was removed as soon as they were collected, which is according to Bianchini and Pacini (1996), and Lisci *et al.* (1996). However, if the beneficial hygroscopic function of the elaiosome was more important than the germination inhibition due to the presence of such appendage, it would be expected that seeds with elaiosome showed higher germination, which we did not observe. Thus, there is no clear germination response to the presence or absence of the elaiosome in one year old seeds. Therefore, our results do not corroborate or refuse the hypothesis that the elaiosome of the castor seeds plays an important hygroscopic role (Lisci *et al.* 1996, Bianchini & Pacini 1996), but we do refuse the hypothesis that the elaiosome of the castor seeds imposes some kind of dormancy (Lagôa & Pereira 1987), once we recorded germination of both fresh and one year old seeds with this appendage.

Overall, castor seeds germinate in a wide range of conditions, and therefore successfully occupy available habitats. Though germination is enhanced by some factors, seeds are able to germinate under various circumstances, and the differences in germination response found by

authors may be explained by inter-population variability (Probert 1993) and/or influence of parental environment during seed maturation (Fenner 1985). Castor germination success in natural conditions may also be ensured by seed longevity, since both fresh and one year old seeds showed 100% viability. Actually, older seeds may experience higher germination than recently dispersed seeds, ensuring the regeneration even after some time the habitat has been disturbed. This feature, and the seed water content of about 13% (pers. obsev.), which lies within the expected range for orthodox seeds (10-15%, Bewley & Black 1994), assures castor seed orthodoxy.

However, castor seed longevity is harshly maintained in the soil superior layer (5 cm depth). This, together with the different germination response of such seeds in comparison to the response of seeds in seed banks, may lead to the rather mistaken conclusion that castor does not form persistent soil seed banks. Though, fallow grounds are often submitted to plough and other human activities, which allowed us to observe that after soil disturbances, there was massive emergence of seedlings. This was even noticeable in sites where castor populations no longer existed for periods such as two years. Hence, it is impossible to state that castor does not form seed banks, as well as to accurately determine its strategy (see Garwood 1989 for a review of tropical soil seed banks) or to infer it from the seed germination response.

Despite the decrease in seed density at increasing soil depths, it is still possible to find seeds in 50 cm depth, with distributions varying according to the species (Garwood 1989 and authors therein). Therefore, deeper soil sampling could assess more precisely the distribution of castor seeds in the seed banks. Such regeneration strategy seems to be of great importance to the occupation of disturbed habitats by castor population, and the relation between the distribution and age of seed banks, and the germination response of the seeds deserves further investigation.

Although many studies describe the effects of the reduced photosynthetically active radiation on the plant growth, only few attempt to explore the effects of the spectral quality

changes. While alterations in the light quantity usually affect the plant growth, changes in the spectral composition, especially in the red region, are known to induce morphological alterations (*e.g.* Dale & Causton 1992, Stuefer & Huber 1998). This was corroborated by our results, once castor plants growing under altered R:FR did not present alteration in the total biomass, as well as in the number of established plants. The most remarkable feature of the plants growing under such condition is etiolation (Aphalo & Ballaré 1995, Tinoco-Ojanguren & Pearcy 1995, Hinsberg & Tienderen 1997), which we observed in the higher stem length of the castor plants growing under altered R:FR. Such result indicates that castor plants present high plasticity and may develop morphological differences according to environmental conditions.

On the other hand, plants growing under different light quantity presented alteration in the total biomass, though the number of the established plants in each treatment was similar. This means that, although the patterns found for vigor descriptors suggest that castor is light-demanding, it is capable of utilizing the photosynthetically active radiation even in pretty shady sites, where the species presents morpho-physiological changes so that the leaves are capable of capturing and converting light into chemical energy in the most efficient way as possible (Fetcher *et al.* 1983, Kwesiga & Grace 1986, Walters *et al.* 1993, Lee *et al.* 1996). The light-demanding behavior of castor not only is in accordance with the expectations for ruderal plants that form seed banks, but also within the expectation for epigeal seedlings, in which the hypocotyl elongates and exposes the cotyledons to the light (Fenner 1985), such as castor seedlings.

Competition for space and/or nutrients in the soil is considered to be one of the main factors controlling growth processes and is crucial for seedling establishment (Fenner 1985, Whitmore 1996). However, our results show that intra- and inter-specific competition does not restrict the establishment of castor seedlings, since the same proportion of established plants was found in the different densities. Though, the co-occurrence of castor plants with co-specifics or with a potential competitor of another species (*B. decumbens*) markedly affected the vigor of

castor juveniles. Intra-specific competition does not seem to impose severe restrictions for castor, since only the number of leaves decreased, and the contribution of stem dry mass in the total biomass increased with increasing density of plants. Nevertheless, inter-specific competition resulted in the alteration of a greater number of vigor measurements. These alterations indicate that, when facing competition with another species, castor invests more in root growth (biomass, and length in relation to the aerial system), which may be a mechanism of escape from competition by reaching deeper soil layers.

The greater impact of inter-specific competition over castor vigor was also noticeable when comparing the vigor measurements of castor juveniles growing in the same category of density of plants of the same species, and of co-specifics and another species. In general, castor juveniles co-occurring exclusively with co-specifics were more vigorous than castor juveniles co-occurring also with *B. decumbens*, indicating that castor is a poor inter-specific competitor. Exceptions were the greater contribution of root and stem dry masses in the total biomass, and the greater root length in relation to the length of the aerial system of castor juveniles facing interspecific competition. These may also be attributed to a mechanism of escape from competition by concentrating resources in roots and stems for further growth in length. The results of competition for castor deserve further investigations in order to elucidate the growth processes of this species.

Overall, castor did not conform to all of our hypothesis, and though considered a ruderal species, there is still much to elucidate about its regenerative phase, especially regarding its seed banks and the germination of seeds in such banks. Possibly, castor plastic characteristics facing germination and seedling establishment ensure the species ability to successfully occupy habitats all around the globe. Further studies on intra-specific variation as a response to environmental conditions should be considered and used in broader models of plant survival strategies.

ACKNOWLEDGEMENTS

The authors wish to thank Dr. Ivany F. M. Valio for valuable suggestions, Guilherme B. Sanvido for help during the realization of the experiments, and Paulo R. Guimarães Jr. for statistical advice. V. F. Martins was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo grant (# 03/11123-4).

REFERENCES

Aphalo P.J. and Ballaré C.L. 1995. On the importance of information: acquiring systems in plantplant interactions. *Functional Ecology* **9**, 5-14.

Basset Y. 1999 Diversity and abundance of insect herbivores foraging on seedlings in a Rainforest in Guyana. *Ecological Entomology* **24**, 245-259.

Bewley J.D. and Black M. 1994. Seeds: Physiology of development and germination. 2nd edition. Plenum Press, New York.

Bianchini M. and Pacini E. 1996. The caruncle of *Ricinus communis* L. (castor bean): its development and role in seed dehydration, rehydration, and germination. *International Journal of Plant Sciences* **157**, 40-48.

Camargo A.P., Pinto H.S., Brunini O., Pedro Jr. M.J., Ortolani A.A. and Alfonsi R.R. 1996.

[Clima do Estado de São Paulo]. In: Atlas climático e ecológico do Estado de São Paulo (ed. by

Setzer J.). Comissão Interestadual da Bacia Paraná-Uruguai, São Paulo, 51-87 (in Portuguese).

Dale M.P. and Causton D.R. 1992. The ecophysiology of *Veronica chamaedrys*, *V. montana* and *V. officinalis*. I: light quality and light quantity. *Journal of Ecology* **80**, 483-492.

Dobson A.J. 2001. *An introduction to generalized linear models*. 2nd edition. Chapman & Hall, New York.

Fenner M. 1985. Seed ecology. Chapman and Hall, London.

Fetcher N., Strain B.R. and Oberbauer S.F. 1983. Effects of light regime on the growth, leaf morphology, and water relations of seedlings of two species of tropical trees. *Oecologia* **58**, 314-319.

Garwood N.C. 1989. Tropical soil seed banks: a review. In: Ecology of soil seed banks (ed. by

Leck M.A., Parker V. T. and Simpson R.L.). Academic Press, San Diego, 149-209.

Grabe D.F. 1976. [*Manual do teste de tetrazólio em sementes*]. AGIPLAN, Brasília (in Portuguese).

Grime J.P. 1979. Plant strategies and vegetation processes. John Wiley & Sons, Chichester.

Grime J.P. 2001. *Plant strategies, vegetation processes and ecosystem properties*. John Wiley & Sons, Chichester.

Herrera C.M., Jordano P., López-Soria L. and Amat J.A. 1994. Recruitment of a mast-fruiting, bird dispersed tree: bridging frugivore activity and seedling establishment. *Ecological Monographs* **64**, 315-344.

Hinsberg van A. and Tienderen van P. 1997. Variation in growth form in relation to spectral light quality (red/far-red ratio) in *Plantago lanceolata* L. in sun and shade populations. *Oecologia* **111**, 453-459.

Hunt R. 1982. The functional approach to growth analysis. Edward Arnold, London.

Janzen D.H. 1970. Herbivores and the number of tree species in Tropical Forests. *The American Naturalist* **104**, 501-528.

Kwesiga K. and Grace J. 1986. The role of the red/far-red ratio in the response of tropical tree seedlings to shade. *Annals of Botany* **57**, 283-290.

Lagôa A.M.M.A. and Pereira M.F. 1987. The role of the caruncle in the germination of seeds of *Ricinus communis. Plant Physiology and Biochemistry* **25**, 125-128.

Lee D.W., Krishnapilay B., Mansor M., Mahamad H. and Yap S.K. 1996. Irradiance and spectral quality affect Asian Tropical Rain Forest tree seedling development. *Ecology* **77**, 568-580.

Lieberman D. 1996. Demography of Tropical tree seedlings: a review. In: *Ecology of Tropical Forest tree seedlings* (ed by Swaine M. D.). UNESCO/Parthenon, Carnforth, 131-138.

Lisci M., Bianchini M. and Pacine E. 1996. Structure and function of the elaiosome in some Angiosperm species. *Flora* **191**, 131-141.

Martins V.F., Guimarães P.R., Silva R.R. and Semir J. 2006. Secondary seed dispersal by ants of *Ricinus communis* (Euphorbiaceae) in the Atlantic Forest in Southeastern Brazil: influence on seed germination. *Sociobiology* **47**, 265-274.

Murdoch A.J. and Ellis R.H. 1993. Longevity, viability and dormancy. In: *Seeds: the ecology of regeneration in plant communities* (ed. by Fenner M.). CAB International, Wallingford, 193-229

Pons T.L. 1993. Seed responses to light. In: *Seeds: the ecology of regeneration in plant communities* (ed. by Fenner M.). CAB International, Wallingford, 259-284.

Probert R.J. 1993. The role of temperature in germination ecophysiology. In: *Seeds: the ecology of regeneration in plant communities* (ed. by Fenner M.). CAB International, Wallingford, 285-325.

Sanches M.C. 2004. [*Crescimento e atividade fotossintética em duas espécies de lianas de uma floresta estacional semidecidual*]. Universidade Estadual de Campinas, Campinas (in Portuguese).

Schupp E.W. 1995. Seed-seedling conflicts, habitat choices, and patterns of plant recruitment. *American Journal of Botany* **82**, 399-409.

Stuefer J.F. and Huber H. 1988. Differential effects of light quantity and spectral light quality on growth, morphology and development of two stoloniferous *Potentilla* species. *Oecologia* **117**, 1-8.

Tinoco-Ojanguren C. and Pearcy R.W. 1995. A comparison of light quality and quantity effects and steady-state and dynamic photosynthetic characteristics of tropical tree species. *Functional Ecology* **9**, 222-230.

Walters M.B., Kruger E.L. and Reich P.B. 1993. Growth, biomass distribution and CO₂ exchange of northern hardwood seedlings in high and low light: relationships with successional status and shade tolerance. *Oecologia* **94**, 7-16.

Whitmore T.C. 1996. A review of some aspects of tropical rain forest seedling ecology with suggestions for further enquiry. In: *Ecology of Tropical Forest tree seedlings* (ed by Swaine M. D.). UNESCO/Parthenon, Carnforth, 3-39.

Zar J.H. 1999. *Biostatistical analysis*. 4th edition. Prentice-Hall, New Jersey.

Table 1: Percentages of densities of photons flux (PFD) and ratio of red:far red (R:FR) as a function of total PFD (1730.33 μ mol m⁻² s¹) and R:FR (1.19) at exposed sunlight at November 2005. Treatments were zero to three layers of fine plastic mesh and a special filter whose pigmentation absorbs red light (purple cloth) sustained above pots containing freshly harvested seeds of *Ricinus communis* without elaiosome (manually removed).

Treatment	PFD (%)	R:FR (%)			
0 layer	88.24	92.44			
1 layer	49.32	90.76			
2 layers	28.76	93.28			
3 layers	11.91	138.66			
Special filter	6.35	30.25			
Table 2: Totals and means (+/- standard deviation) per plot of *Ricinus communis* seeds found and of viable seeds in sites which used to be occupied by *R. communis* populations. 1 plot = 3125 ml of soil.

Time without <i>R</i> communis population	Se	eds found	Viable seeds		
	Total	Mean +/- SD	Total	Mean +/- SD	
2 months	6	1.20 +/- 1.79	0	0	
3 months	9	1.80 +/- 4.03	0	0	
10 months	26	5.20 +/- 6.94	1	0.20 +/- 0.48	
30 months	11	2.20 +/- 2.77	0	0	
36 months	5	1.00 +/- 1.73	1	0.20 +/- 0.48	
36 months	14	2.80 +/- 2.28	5	1.00 +/- 1.41	

Figure 1: Means (+/- standard deviation) or medians (+/- confidence interval of 95%) of vigor measurements of *Ricinus communis* juveniles growing under different photon flux densities (PFD). (a-) Length of roots, (b-) length of aerial system, (c-) number of leaves, (d-) leaf area, (e-) root fresh mass, (f-) stem fresh mass, (g-) root dry mass, (h-) stem dry mass, (i-) total dry mass, (j-) root mass ratio, (k-) roots/aerial system, (l-) stem mass ratio, (m-) stem robustness, (n-) specific leaf mass, (o-) leaf mass ratio, (p-) leaf area ratio. Same numbers represent statistically similar groups (P > 0.05) and different numbers represent statistically distinct groups (P \leq 0.05).





Table 3: Mann-Whitney or t-test statistical values and probabilities of comparisons between vigor measurements of *Ricinus communis* juveniles growing in pots with *Brachiaria decumbens* in two plant density categories: (1) four or less established plants per pot, and (2) five or more established plants per pot. FM_{root} is root fresh mass, FM_{stem} is stem fresh mass, FM_{leaves} is leaf fresh mass, No. leaves is number of leaves, DM_{roots} is root dry mass, DM_{stem} is stem dry mass, DM_{leaves} is leaf dry mass, DM_{total} is total dry mass, RMR is root mass ratio, R/AS is roots/aerial system ratio, SMR is stem mass ratio, ROB is stem robustness, SLM is specific leaf mass, LMR is leaf mass ratio and LAR is leaf area ratio.

Length of aerial system Lenth of roots		FN	FMroots		FMstems		FMleaves		No. leaves			
	1	2	1	2	1	2	1	2	1	2	1	2
_	U = 133.000	t = 8.928	U = 150	t = 3.787	t = 4.361	U = 165.000	U = 158.000	t = 7.023	t = 4.229	t = 6.83	U = 159.000	t = 0.572
	df = 1	df = 24	df = 1	df = 24	df = 28	df = 1	df = 1	df = 24	df = 27	df = 24	df = 1	df = 24
	P = 0.010	P < 0.001	P = 0.001	P = 0.001	P ≤ 0.001	P < 0.001	P < 0.001	P < 0.001	P ≤ 0.001	P < 0.001	P < 0.001	P = 0.573

Length of aerial system		Lenth of roots		FMroots		FMstems		FMleaves		No. leaves	
1	2	1	2	1	2	1	2	1	2	1	2
U = 133.000	t = 8.928	U = 150	t = 3.787	t = 4.361	U = 165.000	U = 158.000	t = 7.023	t = 4.229	t = 6.83	U = 159.000	t = 0.572
df = 1	df = 24	df = 1	df = 24	df = 28	df = 1	df = 1	df = 24	df = 27	df = 24	df = 1	df = 24
P = 0.010	P < 0.001	P = 0.001	P = 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P = 0.573

Table 3: cont.

R/AS		SMR		ROB		SLM		LMR		LAR	
1	2	1	2	1	2	1	2	1	2	1	2
t = 4.404	U = 48.000	t = 2.486	t = 0.694	U = 158.000	t = 4.615	U = 48.500	U = 81.5	t = 4.31	t = 2.799	t = 4.412	t = 2.321
df = 28	df = 1	sd = 28	df = 24	df = 1	df = 24	df = 1	df = 1	df = 27	df = 24	df = 27	df = 24
P < 0.001	P = 0.073	P = 0.019	P = 0.495	P < 0.001	P < 0.001	P = 0.242	P = 0.952	P < 0.001	P = 0.01	P < 0.001	P = 0.029

CONSIDERAÇÕES FINAIS

A dispersão de sementes não oportunística é resultado da interação mutualística entre dispersor e diásporo (*i.e.* unidade de dispersão): enquanto este se beneficia por ter sua mortalidade reduzida, colonizar novos habitats e/ou atingir sítios propícios para a sobrevivência de sementes e o estabelecimento de plântulas, aquele se beneficia pela utilização dos diásporos como fonte de alimento (van der Pijl 1972, Howe & Smallwood 1982, Beattie 1985, Stiles 1993, Willson 1993). Formigas dispersoras de sementes de *R. communis* utilizam sua carúncula como alimento (Martins *et al.* 2006), e indivíduos desta espécie supostamente encontrariam melhores condições nos locais de descarte dos formigueiros, como discutido por alguns autores para sementes mirmecocóricas (Hanzawa *et al.* 1988, Vander Wall & Longland 2004, Manzaneda *et al.* 2005).

No entanto, o presente estudo demonstrou que a deposição de sementes pós-dispersas em locais de descarte de formigueiros não confere vantagens adicionais a *R. communis*. Tal deposição pode acarretar, inclusive, em competição intra-específica devido à maior densidade de plântulas e jovens nos locais de descarte, situação potencialmente desvantajosa para a espécie estudada. Investigações futuras sobre este tema poderão determinar os exatos efeitos da interação entre formigas e sementes para os indivíduos de *R. communis*.

Além da espécie estudada não apresentar dispersão direcional, também não há evidências de que a mirmecocoria resulte em vantagens devido à fuga ou à colonização. Sementes de *R. communis* apresentam dispersão primária por autocoria (Martins *et al.* 2006), logo não são encontradas em alta densidade perto da planta parental. Além disto, a mirmecocoria não resulta em dispersão a longas distâncias, impossibilitando as sementes de colonizarem novos habitats (Davidson & Morton 1981, Willson 1993a, b).

Assim, a única vantagem aparente da interação entre sementes de *R. communis* e formigas seria a retirada da carúncula, o que aumenta o sucesso de germinação das sementes. No entanto, a

não ocorrência de benefícios diretos da dispersão desta espécie por formigas precisa ser investigada em um contexto mais amplo: uma vez que *R. communis* tem origem africana (apesar de ser sub-espontânea em praticamente todo o mundo; Singh 1976, Mabberley 1998, Kissmann & Groth 1992, Lorenzi 2000, http://www.canalvip.com.br), é possível que tenha ocorrido um colapso do sistema mutualístico devido à interação de espécies que não apresentam a mesma história evolutiva, como já demonstrado por outros autores (*e.g.* Bond & Slingsby 1984).

Como a interação de sementes de *R. communis* com formigas não acarreta em vantagens diretas para a dispersão da espécie no sistema estudado, sua grande habilidade colonizadora não pode ser atribuída à uma dispersão (pelo menos secundária) eficiente. Sendo assim, *R. communis* deve apresentar características que possibilitem seu sucesso como espécie ruderal. Tais características consistem, como demonstrado neste estudo, de germinação de sementes sob as mais variadas condições, ortodoxia das sementes, possível formação de bancos de sementes persistentes, estabelecimento e crescimento dos indivíduos em habitats sombreados, e ocupação do espaço mesmo em presença de indivíduos competidores.

Apesar das características de *R. communis* não se encaixarem perfeitamente no perfil de espécie ruderal (*e.g.* Grime 1979, 2001), certamente ela pode ser definida como tal, uma vez que é notória sua ocupação de habitats perturbados. Assim, a classificação desta espécie como ruderal está muito mais relacionada com os habitats que ela ocupa do que com suas estratégias para ocupá-los. Estudos mais aprofundados poderão contribuir para o entendimento da estratégia desta espécie tão importante economicamente.

- Beattie, A.J. 1985. The evolutionary ecology of ant-plant mutualisms. Cambridge University Press, New York.
- Bond, W. & P.Slingsby. 1984. Collapse of an ant-plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. Ecology 65: 1031-1037.
- Davidson, D.W. & S.R. Morton. 1981. Myrmecochory in some plants (F. chenopodiaceae) of the Australian Arid Zone. Oecologia 50:357-366.
- Grime, J.P. 1979. Plant strategies and vegetation processes. John Wiley & Sons, Chichester.
- Grime, J.P. 2001. Plant strategies, vegetation processes and ecosystem properties. John Wiley & Sons, Chichester.
- Hanzawa, F.M.; A.J. Beattie & D.C. Culver. 1988. Directed dispersal: demographic analysis of an ant-seed mutualism. The American Naturalist 131: 1-13.
- Howe, H.F. & J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13:201-228.
- Kissmann, K.G. & D. Groth. 1992. Plantas infestantes e nocivas. Vol. 2. BASF Brasileira S.A., São Paulo.
- Lorenzi, H. 2000. *Ricinus communis. In:* Plantas daninhas do Brasil Terrestres, aquáticas, parasitas e tóxicas. Pp. 279. 3^a Edição. Instituto Plantarum de Estudos da Flora Ltda., Nova Odessa.
- Mabberley, D.J. 1998. *Ricinus*. Pp. 618. *In:* The plant-book: a portable dictionary of the Vascular Plant. 2nd Edition. Cambridge University Press, Cambridge.
- Manzaneda, A.J.; J.M. Fedriani & P.J. Rey. 2005. Adaptative advantages of myrmecochory: the predator-avoidance hypothesis tested over a wide geographic range. Ecography 28: 583-592.

- Martins, V.F.; P.R. Guimarães; R.R. Silva & J. Semir. 2006. Secondary seed dispersal by ants of *Ricinus communis* (Euphorbiaceae) in the Atlantic Forest in Southeastern Brazil: influence on seed germination. Sociobiology 47: 265-274.
- Singh, D. 1976. Castor *Ricinus communis* (Euphorbiaceae). Pp. 84-86. *In:* Simmonds, N.W. (ed.). Evolution of crop plants. Longman Group, New York.
- Stiles, E.W. 1993. Animal as seed dispersers. Pp. 87-104. *In:* Fenner, M. (ed.). Seeds: the ecology of regeneration in plant communities. CAB International, Wallingford.
- van der Pijl, L. 1972. Principles of dispersal in Higher Plants. 2nd Edition. Springer-Verlag, Würzburg.
- Vander Wall, S.B. & W.S. Longland. 2004. Diplochory: are two seed dispersers better than one? Trends in Ecology and Evolution 19: 155-161.
- Willson, M.F. 1993a. The ecology of seed dispersal. Pp. 51-85. *In:* Fenner, M. (ed.). Seeds: the ecology of regeneration in plant communities. CAB International, Wallingford.
- Willson, M.F. 1993b. Dispersal mode, seed shadows, and colonizing patterns. Pp. 261-280. In Fleming, T.H. & Estrada, A. (eds.). Frugivory and seed dispersal: ecological and evolutionary aspects. Kluwer Academic Publishers, Dordrecht.

http://www.canalvip.com.br