

Comparative fire ecology of tropical savanna and forest trees

WILLIAM A. HOFFMANN*‡, BIRGIT ORTHEN†§ and PAULA KIELSE VARGAS DO NASCIMENTO*

*Departamento de Engenharia Florestal, Universidade de Brasília, Caixa Postal 04357, Brasília, DF 70919–970;

†Departamento de Botânica, Universidade de Brasília, Caixa Postal 04457, Brasília DF 70919–970

Summary

1. Fire is important in the dynamics of savanna–forest boundaries, often maintaining a balance between forest advance and retreat.
2. We performed a comparative ecological study to understand how savanna and forest species differ in traits related to fire tolerance. We compared bark thickness, root and stem carbohydrates, and height of reproductive individuals within 10 congeneric pairs, each containing one savanna and one forest species.
3. Bark thickness of savanna species averaged nearly three times that of forest species, thereby reducing the risk of stem death during fire. The allometric relationship between bark thickness and stem diameter differed between these two tree types, with forest species tending to have a larger allometric coefficient.
4. The height of reproductive individuals of forest species averaged twice that of congeneric savanna species. This should increase the time necessary for forest species to reach reproductive size, thereby reducing their capacity to reach maturity in the time between consecutive fires.
5. There was no difference in total non-structural carbohydrate content of stems or roots between savanna and forest species, though greater allocation to total root biomass by savanna species probably confers greater capacity to resprout following fire.
6. These differences in fire-related traits may largely explain the greater capacity of savanna species to persist in the savanna environment.

Key-words: Bark, carbohydrates, TNC, gallery forest, cerrado

Functional Ecology (2003) **17**, 720–726

Introduction

Predicting the global distribution of biomes under changing climate and disturbance regimes requires an understanding of the factors and processes determining the current locations of the ecotones between biomes. In the tropics, the savanna–forest boundary has eluded a clear and widely accepted explanation. The savanna–forest boundary is commonly abrupt, with savanna grading into forest over distances of a few meters. Climate, fire, hydrology, herbivory, as well as soil nutrients, texture and depth are all important in determining the location of savanna and forest (Furley 1992; Hopkins 1992; Tinley 1982), but it appears

that multiple factors interact to determine the location of the boundary in many cases (Frost *et al.* 1986; Kellman 1984). Of these factors, only fire is primarily under human control, and is the most likely to cause observable changes within the time-frame of human observation.

Fire helps maintain a dynamic balance between savanna and forest (Hopkins 1992). Savanna vegetation is very flammable, and may burn at intervals of 1–3 years, whereas evergreen forest is typically less flammable due to the dense canopy that excludes grasses and maintains a more humid understorey. Most savanna fires do not penetrate far into undisturbed evergreen forest (Biddulph & Kellman 1998; Kellman & Meave 1997), thereby sharpening the savanna–forest boundary. However, under fire exclusion, forest commonly expands into savanna (Bowman & Fensham 1991; Hopkins 1992; King *et al.* 1997; Swaine *et al.* 1992).

The savanna–forest boundary is a discontinuity not only in tree density, but also in species composition, with few species common to savanna and forest (Adejuwon & Adesina 1992; Felfili & Silva Junior 1992).

‡Author to whom correspondence should be addressed: W.A. Hoffman, Department of Botany, Campus Box 7612, North Carolina State University, Raleigh, NC 27695-7612, USA. E-mail: hoffmann@unb.br

§Present address: Institut für Ökologie der Pflanzen, Westfälische Wilhelms-Universität, Hindenburgplatz 55, 48143 Münster, Germany.

Savanna species are much more fire-tolerant than forest species; in the Brazilian savannas (Cerrado), fire causes community-wide tree and shrub mortality rates of 5–19% (mean = 11%, $n = 10$ sites; Sato 1996; Sato & Miranda 1996; Silva 1999; Silva *et al.* 1996), while in Amazonian forests, fire causes mortality of 36–96% (mean = 62%, $n = 9$ sites; Cochrane & Schulze 1999; Holdsworth & Uhl 1997; Kauffman 1991; Peres 1999; Uhl & Buschbacher 1985), though mortality rate in a burned Bolivian dry forest was only 21% (Pinard *et al.* 1999). Due to a lack of comparative studies (Longman & Jenik 1992), we know little about the physiological, morphological, and ecological differences between savanna and forest species that explain this difference in fire tolerance.

The present study compares fire-related traits of savanna and gallery forest trees of the Cerrado, a region of predominantly savanna vegetation occupying approximately 2×10^6 km² in south-central Brazil. Evergreen gallery forests occur as narrow corridors along streams, giving them a large perimeter of contact between savanna and forest. This narrow, dissected shape makes them particularly susceptible to the high rates of anthropogenic burning in the adjacent savannas and grasslands (Kellman & Meave 1997), and appears to have created ample opportunities for reproductive isolation and speciation, as evidenced by the high degree of adaptive radiation among woody plants. In the cerrado, the radiation of woody plants into savanna and forest species has occurred independently in a large number of genera. For example, at one site where the flora has been particularly well described, 45 of the 82 genera of savanna trees and shrubs also contain forest species occurring in gallery forests in the same ecological reserve (Pereira, Silva & Mendonça 1992), and many of the remaining genera contain forest species native to other regions. For most genera containing both savanna and forest species, we have no information on whether the forest or savanna form is ancestral, though good information does exist for the Chrysobalanaceae (Prance 1992). In this family, savanna species are most commonly derived from forest species and the divergence of savanna and forest species occurred independently in at least 14 lineages within this family (Prance 1992). We used this large number of independent radiations to test the following hypotheses.

Savanna trees exhibit greater concentrations of total non-structural carbohydrates (TNC). Carbohydrate reserves are essential for resprouting following stem death (top-kill) or leaf scorch (Bowen & Pate 1993; Canadell & López-Soria 1998; Miyanishi & Kellman 1986). TNC concentration largely determines the capacity to survive fire (Bowen & Pate 1993), as well as the rate of regrowth (Kays & Canham 1991), so higher TNC content should be advantageous in savannas.

Savanna trees have thicker bark than forest trees. Bark insulates the cambium from high temperatures so

stem survival is strongly dependent on bark thickness (Hoffmann & Solbrig 2003; Gignoux *et al.* 1997), providing a clear advantage where fire is frequent.

The allometric coefficient for the relationship between bark thickness and stem diameter is greater for forest species. Frequent fire and high carbon gain in the high-light savanna environment should favour greater investment in bark early in tree development, while forest species should defer this investment until later (Jackson *et al.* 1999). This can be tested by comparing the coefficient (A) of the allometric relationship $T = BD^A$, where T is bark thickness and D is stem diameter. The allometric relationship relating bark thickness to stem diameter should be < 1 for savanna species and > 1 for forest species (Jackson *et al.* 1999).

Reproductive individuals of forest trees are taller than those of savanna trees. Among savanna species, fire response at the population level is strongly related to size at maturity, with taller species tending to be less abundant under frequent burning (Hoffmann & Moreira 2002). If sexual maturity is attained at a small individual size, then juveniles and top-killed individuals are more likely to reach reproductive size during the time between successive burns (Hoffmann & Solbrig 2003). In contrast, if reproduction requires large individual size, repeated top-kill under frequent burning will retain small individuals in an unreproductive state, thereby preventing them from contributing to future population growth.

We tested these predictions in the savannas and gallery forests of the Cerrado using congeneric species pairs. In the absence of detailed phylogenetic information, the use of congeneric species pairs is useful for ensuring phylogenetic independence, an important condition for inference in comparative studies (Felsenstein 1985), and to improve the statistical power of comparisons between the two groups (Ackerly 1999).

Methods

Ten savanna–forest species pairs (Table 1) were chosen based on availability at the study site. Each pair consists of one savanna tree species and one gallery forest tree species of the same genus. No two genera were chosen from the same family, and all species are evergreen, except for the *Aspidosperma* spp. All comparisons were based on these pairs to ensure phylogenetic independence.

For each species, at least 10 individuals in naturally occurring populations were located within the experimental farm *Fazenda Água Limpa*, of the University of Brasília, located within the Federal District, Brazil. Mean annual rainfall at the site is approximately 1500 mm, with a pronounced dry season from May to September. Fire is actively suppressed at the site, but occasional fires do enter the reserve from neighbouring areas. A detailed fire history is unavailable for all

Table 1. Congeneric species pairs studied

Savanna species	Forest species	Family
<i>Aspidosperma tomentosum</i> Mart.	<i>A. subicanum</i>	Apocynaceae
<i>Byrsonima crassa</i> Nied.	<i>B. laxiflora</i> Griseb	Malpighiaceae
<i>Didymopanax macrocarpum</i> (Cham. & Schl.) Seem	<i>D. morototoni</i> Aubl. Planch	Araliaceae
<i>Guapira noxia</i> (Netto) Lundell	<i>Guapira areolata</i>	Nyctaginaceae
<i>Hymenaea stigonocarpa</i> Mart. Ex Hayne	<i>H. courbaril</i> L.	Leguminosae (Caesalpinoideae)
<i>Miconia pohliana</i> Cogn.	<i>M. chartacea</i> Triana	Melastomataceae
<i>Myrsine guianensis</i> (Aubl.) O. Kuntz	<i>M. umbelata</i> Mez.	Myrsinaceae
<i>Ouratea hexasperma</i> (St. Hil.) Bail	<i>O. castaneaefolia</i> (St. Hil.) Engl.	Ochnaceae
<i>Salacia crassifolia</i> (Mart.) G. Don.	<i>S. elliptica</i> (Mart.) G. Don.	Hippocrateaceae
<i>Vochysia thyrsoides</i> Pohl.	<i>V. tucanorum</i> (Spreng.) Mart	Vochysiaceae

locations; populations with signs of recent burning (i.e. < 5 years) were avoided.

Stem diameter and bark thickness were measured at 30 cm height. Bark thickness was measured with a bark gauge (JIM-GEM) at two points along the circumference of the main stem. For species with fissured bark, measurements were made at the ridges rather than in the troughs between the ridges.

Four individuals of each species were sampled for stem and root carbohydrate in the peak of the rainy season (December 2002 and January 2003). In selecting these individuals, only apparently healthy individuals with a full crown of leaves were chosen. To the extent possible, shaded individuals were avoided. For forest species this meant selecting individuals at the forest edge or with the crown reaching the forest canopy. This was not possible only for *M. chartacea* and *S. elliptica*, two understorey trees occurring predominantly in moist sites along the stream in the interior of the forest.

Sapwood was sampled from the root and stem using an increment borer (4.5 mm diam.). The stem was sampled at 30 cm height and the root was sampled 15 cm below the soil surface. The samples were transported on ice from the field, and heated in a microwave oven to cease enzyme activity. Then the samples were dried to constant mass at 70 °C and finely ground. The ground material was extracted with water (20 mg dry mass mL⁻¹ distilled water) for 1 h at 100 °C. After centrifugation the supernatants were used for the determination of total non-structural soluble carbohydrates by the Anthrone assay (Scott & Melvin 1953). The insoluble residue was submitted to starch determination. After threefold extraction with 80% ethanol the starch was degraded by a heat-stable α -amylase (EC 3.2.1.1, Sigma) and amyloglucosidase (EC 3.2.1.2, Merck) into its monomer glucose which was determined enzymatically by the hexokinase-glucose-6-phosphate-dehydrogenase assay (Bergmeyer 1970). TNC content was expressed on structural dry mass (dry mass – TNC) basis.

To estimate the mean size of reproductive individuals, we relied on specimens from the herbarium of the Uni-

versity of Brasília. All specimens of the study species that presented fruit or flowers and were collected in the Federal District were included in the sample. If there were few such individuals for a species, then the sample was enlarged to include individuals collected in other parts of Brazil. The tree height estimated by the collector was recorded, with the assumption that collector bias was similar for savanna and tree species. The mean of 20 specimens per species were used, with the lowest number being eight (*G. areolata*).

ANALYSIS

The paired *t*-test was used to compare savanna and forest species for differences in bark thickness, carbohydrate content, and height of reproductive individuals. Prior to analysis, bark thickness was divided by stem radius to transform to a relative thickness.

We used least-squares regression to fit curves to the relationship between stem diameter and bark thickness. We used the program CurveExpert 1.2 to determine appropriate functions to be fit. For all species, the relationship was well described by either a linear equation or the modified exponential: $T = A \cdot \exp(B/D)$, where *T* is bark thickness and *D* is stem diameter. These are both two-parameter equations, hence precluding a statistical comparison of fit of these alternative functions, so the curve with the greater *r*² was chosen to represent a species.

To estimate stem diameters necessary to avoid top-kill, we relied on results of Hoffmann & Solbrig (2003) that bark thickness of 6.5 mm was sufficient to guarantee 50% stem survival of trees in low-intensity savanna fires (i.e. flame length < 2 m), while 11.4 mm was necessary in high-intensity savanna fires (flame length > 2 m). We used the equations relating stem diameter to bark thickness to estimate the stem diameters corresponding to these bark thicknesses.

To calculate the allometric coefficient for the relationship between stem diameter and bark thickness, log-transformed bark thickness was regressed on log-transformed inside-bark bole diameter using reduced major axis regression (Jackson *et al.* 1999).

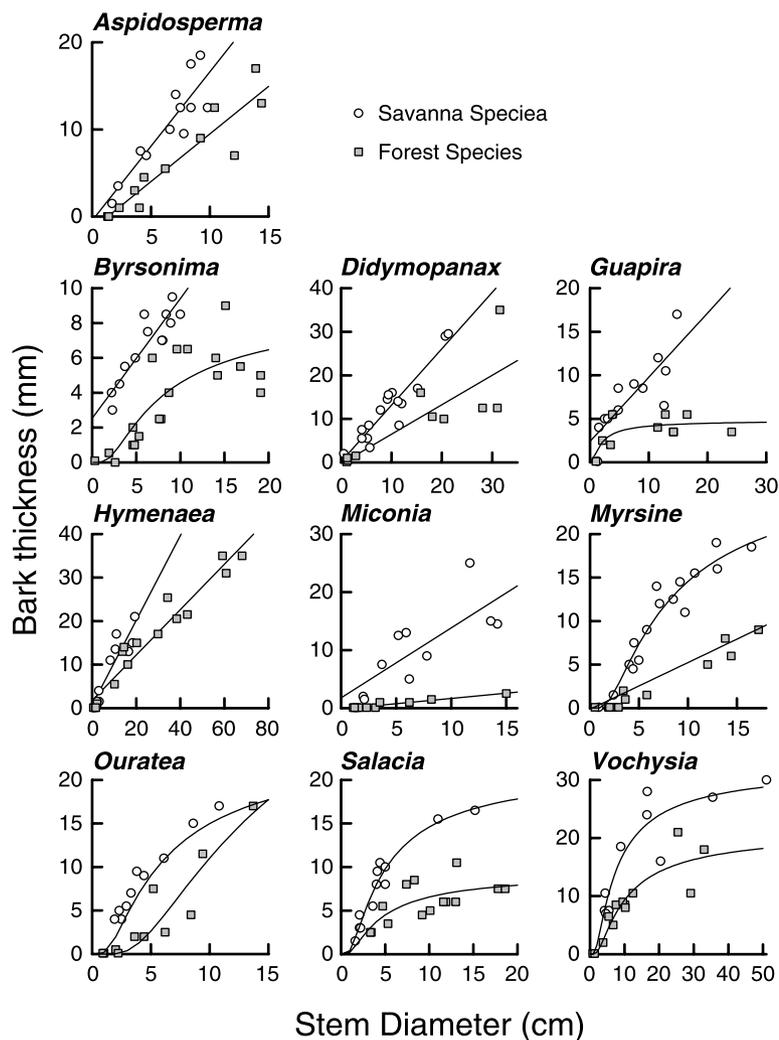


Fig. 1. Relationship between stem diameter and bark thickness of congeneric savanna and forest trees. See Table 1 for species names.

Results

For every one of the species pairs, the savanna species had significantly thicker bark than the forest species ($t > 2.6$, $P < 0.02$, Fig. 1). Similarly, when compared

over all species, savanna species had thicker bark (Paired $t_{9d.f.} = 10.2$, $P < 0.001$). On average, bark accounted for 28.5% of the stem radius of the savanna species but only 10.1% of the stem radius of the forest species, so forest species require considerably greater stem diameters to ensure stem survival during burns (Table 2). For four forest species, the fitted relationships between stem diameter and bark thickness indicate that even the largest individuals do not produce sufficiently thick bark to ensure 50% stem survival during high-intensity savanna fires. and for two of these species, *G. areolata* and *M. chartacea*, even low-intensity fires should top-kill more than 50% of the individuals in the largest size classes.

The allometric coefficient for the relationship between stem diameter and bark thickness was greater for forest species (mean = 1.27) than for savanna species (mean = 0.86; paired $t_{9d.f.} = 2.08$, $P = 0.03$; Table 2).

Overall, there was no difference between savanna and forest species in TNC content of roots (paired $t_{9d.f.} = 0.62$, $P = 0.55$) or stems (paired $t_{9d.f.} = 1.24$, $P = 0.25$). When examined individually, four genera exhibited differences between the savanna and forest species. For *Miconia*, the savanna species had greater TNC in both roots and shoots, while the savanna *Guapira* had greater stem TNC. In contrast, for *Salacia* and *Ouratea*, the forest species had greater root TNC than the congeneric savanna species (Fig. 2).

Over all species, TNC content was greater in roots than in stems (paired $t_{19} = 3.41$, $P = 0.003$). Among savanna species, there was no difference between root TNC (14.1%) and stem TNC (12.7%; paired $t_{9d.f.} = 1.42$, $P = 0.19$), though for forest species, TNC was greater in root (12.7%) than in stems (10.1%) paired $t_{9d.f.} = 3.95$, $P = 0.003$).

Reproductive individuals of forest species were significantly taller than those of savanna species in eight of the 10 genera ($t > 2.14$, $P < 0.05$), and when tested over all genera (paired $t_{9d.f.} = 3.58$, $P = 0.006$). For forest species, the height of reproductive individuals averaged 8.0 m, compared to 3.6 m for savanna species (Fig. 3).

Table 2. Allometric coefficient for the diameter–bark relationship and estimates of minimum stem diameters (cm) that ensure 50% stem survival for low-intensity (flame length < 2 m) and high-intensity (flame length > 2 m) savanna fires. Missing values indicate cases in which no stem diameter would guarantee 50% stem survival

Genus	Bark allometric coefficient		Min. diam., low-intensity fires		Min. diam., high-intensity fires	
	Savanna species	Forest species	Savanna species	Forest species	Savanna species	Forest species
<i>Aspidosperma</i>	0.82	1.28	4.1	7.3	6.4	11.8
<i>Byrsonima</i>	0.52	1.10	5.8	20.3	12.9	–
<i>Didymopanax</i>	0.43	1.36	4.9	10.0	8.7	17.3
<i>Guapira</i>	0.74	0.65	5.6	–	12.2	–
<i>Hymenaea</i>	1.38	1.30	6.0	9.1	11.0	18.5
<i>Miconia</i>	0.49	1.09	3.9	–	8.0	–
<i>Myrsine</i>	0.69	1.97	4.5	12.3	7.4	21.5
<i>Ouratea</i>	1.66	1.62	3.1	7.2	5.5	10.2
<i>Salacia</i>	0.77	0.47	3.3	9.4	6.2	–
<i>Vochysia</i>	1.09	1.92	3.8	7.0	5.9	13.2

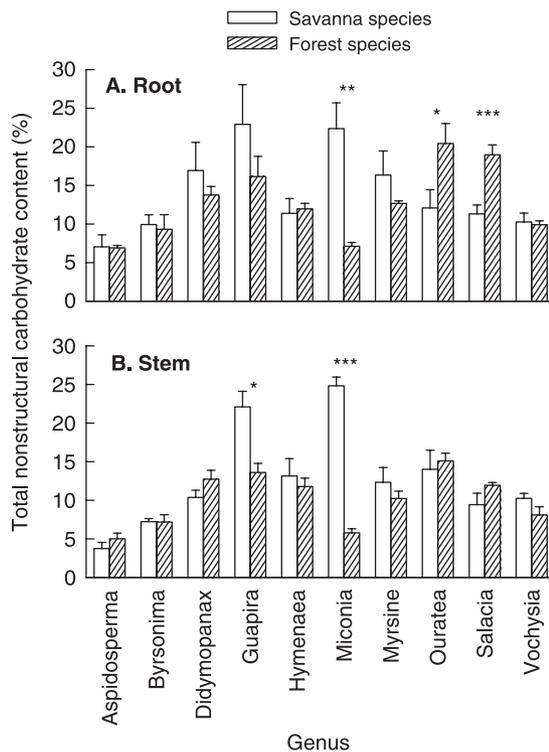


Fig. 2. Mean TNC content (\pm SE) of (a) roots and (b) stems of congeneric savanna and forest trees. TNC is presented as percentage of structural dry mass. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$ for differences within genera.

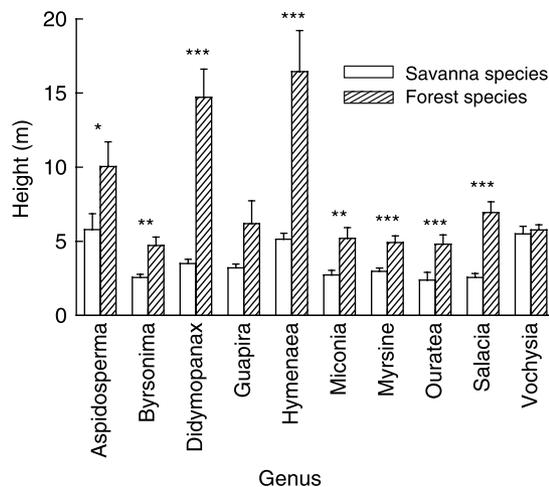


Fig. 3. Mean height (\pm SE) of reproductive individuals of congeneric savanna and forest trees as determined from herbarium specimens. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$ for differences within genera.

Discussion

There are large and consistent differences in tree height and bark thickness between savanna and forest species. The thicker bark of savanna species relative to forest species undoubtedly confers a greater ability to avoid top-kill during fire, but requires considerable investment of carbon. Investment in bark should be particularly costly for saplings in the forest environment

where light is considered a limiting resource. As predicted by Jackson *et al.* (1999), savanna species were found here to make greater investments in bark early in development, while forest species defer this investment until later. More precisely, the allometric coefficient of the bark-diameter relationship averaged < 1 for savanna trees and > 1 for forest trees.

Despite the investment in thick bark, savanna species are unable to avoid top-kill altogether, especially for small individuals and in intense fires. Although resprouting is an essential strategy for surviving frequent savanna fire following top-kill, savanna species did not have higher TNC concentrations, contrary to predictions. Savanna species may nevertheless have a greater capacity to resprout, despite similar carbohydrate concentrations, because of greater investment in total below-ground biomass. As seedlings, the root : shoot ratio of savanna species averages 82% greater than forest species (Hoffmann & Franco 2003), probably explaining the greater fire tolerance of savanna species (Hoffmann & Moreira 2002). Field estimates of root : shoot ratios of tree-dominated cerrado have ranged from 1.03 to 2.9 (Abdala *et al.* 1998; Castro & Kauffman 1998), compared with 0.1–0.17 for Neotropical rainforests (Castro & Kauffman 1998; Jipp *et al.* 1998) and 0.42–0.84 for Neotropical dry forests (Castro & Kauffman 1998). We know of no similar data for gallery forest, but due to the relatively high incidence of fire (Kellman & Meave 1997), root : shoot ratios may be higher than for other evergreen forest types, but are not likely to be as high as in savanna. Therefore, despite similar root TNC concentrations, forest trees will have less total below-ground carbohydrate reserves available per unit of above-ground biomass, reducing resprout capacity.

The range of root TNC content (7–23%; Fig. 2) was similar to woody species with resprouting ability in other savannas (Miyaniishi & Kellman 1986; Wan & Sosebee 1990) and fire-prone ecosystems (Bell *et al.* 1996; Bowen & Pate 1993; Canadell & López-Soria 1998), although herbaceous and subshrub species can have considerably higher concentrations (Medina & Bilbao 1991). The lowest TNC values were measured for the two *Aspidosperma*, the only deciduous species in the study. These low values may reflect the sampling several months after leaf flush, since deciduous species frequently exhibit considerable seasonality in TNC content (Loescher *et al.* 1990; Wan & Sosebee 1990).

Since bark thickness largely determines top-kill during a fire, forest tree species must be larger than savanna species to ensure stem survival. For adult individuals, this is partially compensated by the fact that reproductive individuals of forest species tend to be larger than reproductive individuals of savanna species. But when burning is frequent, the large size at reproduction presents a different problem. Given similar growth rates, species that reach maturity at small size are more likely to reach reproductive size in the period between burns (Hoffmann & Solbrig 2003), so

frequent fire favours smaller growth forms (Hoffmann 1999; Hoffmann & Moreira 2002). For forest species, which have thin bark and large reproductive sizes, frequent fire may preclude the possibility of individuals reaching adulthood within the savanna environment. However, the time to reach a fire-tolerant size also depends on growth rate (Gignoux *et al.* 1997), so if forest species have higher above-ground growth rates, this would partially compensate for the larger size necessary to ensure fire resistance and maturity. Species with low root : shoot ratios tend to exhibit greater growth rates (Kitajima 1994), so forest species may indeed grow faster than savanna species, though this was not observed for seedlings (Hoffmann & Franco 2003).

We cannot overlook alternative explanations for the difference in tree height between savanna and forest species. Specifically, the greater competition for light in the forest environment should select for greater investment in height growth than in the savanna environment. The shorter stature of savanna species, combined with their shade-intolerant nature (Hoffmann & Franco 2003), probably explains their absence in forest.

Conclusion

Differences in species traits have important implications for the response of savanna and forest species to fire at the savanna–forest boundary. Occasional forest individuals establishing within the savanna environment are more likely to be top-killed, may exhibit lower resprout rates, and provided they survive fire, should be less likely to reach reproductive size within the time between burns. All of these differences should place forest species at a strong disadvantage in comparison to savanna species under frequent burning, effectively restricting forest advance.

Fire can occasionally extend more than 1 km into evergreen forest (Cochrane & Laurance 2002), causing widespread mortality, and potentially shift forest retreat. With intensification of land use and increasing rural populations, this problem is likely to increase in the future.

Acknowledgements

This research was funded by an NSF Postdoctoral Fellowship (INT-9803013) to William Hoffmann and PRONEX.

References

- Abdala, G.C., Caldas, L.S., Haridasan, M. & Eiten, G. (1998) Below-ground organic matter and root-shoot ratio in a cerrado in central Brazil. *Brazilian Journal of Ecology* **2**, 11–23.
- Ackerly, D.D. (1999) Comparative plant ecology and the role of phylogenetic information. *Physiological Plant Ecology* (eds M.C. Press, J.D. Scholes & M.G. Barker), pp. 391–412. Blackwell Science, Oxford.
- Adejuwon, J.O. & Adesina, F.A. (1992) The nature and dynamics of the forest–savanna boundary in south-western

- Nigeria. *Nature and Dynamics of the Forest–Savanna Boundaries* (eds P.A. Furley, J. Proctor & J.A. Ratter), pp. 331–352. Chapman & Hall, London.
- Bell, T.L., Pate, J.S. & Dixon, K.W. (1996) Relationships between fire response, morphology, root anatomy, and starch distribution in South-west Australian Epacridaceae. *Annals of Botany* **77**, 357–364.
- Bergmeyer, H.U. (1970) *Methoden der Enzymatischen Analyse*. Verlag Chemie, Weinheim.
- Biddulph, J. & Kellman, M. (1998) Fuels and fire at savanna gallery forest boundaries in southeastern Venezuela. *Journal of Tropical Ecology* **14**, 445–461.
- Bowen, B.J. & Pate, J.S. (1993) The significance of root starch in post-fire shoot recovery of the resprouter *Stirlingia latifolia* R. Br. (Proteaceae). *Annals of Botany* **72**, 7–16.
- Bowman, D.M.J.S. & Fensham, R.J. (1991) Response of a monsoon forest–savanna boundary to fire protection, Weipa, northern Australia. *Australian Journal of Ecology* **16**, 111–118.
- Canadell, J. & López-Soria, L. (1998) Lignotuber reserves support regrowth following clipping of two Mediterranean shrubs. *Functional Ecology* **12**, 31–38.
- Castro, E.A. & Kauffman, J.B. (1998) Ecosystem structure in the Brazilian cerrado: a vegetation gradient of aboveground biomass, root mass and consumption by fire. *Journal of Tropical Ecology* **14**, 263–283.
- Cochrane, M.A. & Laurance, W.F. (2002) Fire as a large-scale edge effect in Amazonian Forests. *Journal of Tropical Ecology* **18**, 311–325.
- Cochrane, M.A. & Schulze, M.D. (1999) Fire as a recurrent event in tropical forests of the eastern Amazon: effects on forest structure, biomass, and species composition. *Biotropica* **31**, 2–16.
- Felfili, J.M. & Silva Junior, M.C.D. (1992) Floristic composition, phytosociology and comparison of cerrado and gallery forests at Fazenda Agua Limpa, Federal District, Brazil. *Nature and Dynamics of the Forest–Savanna Boundaries* (eds P.A. Furley, J. Proctor & J.A. Ratter), pp. 393–429. Chapman & Hall, London.
- Felsenstein, J. (1985) Phylogenies and the comparative method. *American Naturalist* **125**, 1–15.
- Frost, P., Medina, E., Menaut, J.-C., Solbrig, O., Swift, M. & Walker, B. (1986) Responses of savannas to stress and disturbance. *Biology International, Special Issue* **10**, 1–82.
- Furley, P.A. (1992) Edaphic changes at the forest–savanna boundary with particular reference to the neotropics. *Nature and Dynamics of Forest–Savanna Boundaries* (ed. P.A. Furley), pp. 91–117. Chapman & Hall, London.
- Gignoux, J., Clobert, J. & Menaut, J.-C. (1997) Alternative fire resistance strategies in savanna trees. *Oecologia* **110**, 576–583.
- Hoffmann, W.A. (1999) Fire frequency and population dynamics of woody plants in a neotropical savanna. *Ecology* **80**, 1354–1369.
- Hoffmann, W.A. & Franco, A.C. (2003) Comparative growth analysis of tropical forest and savanna woody plants using phylogenetically-independent contrasts. *Journal of Ecology* **91**, 475–484.
- Hoffmann, W.A. & Moreira, A.G. (2002) The role of fire in population dynamics of woody plants. *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna* (eds P.S. Oliveira & R.J. Marquis), pp. 159–177. Columbia University Press, New York.
- Hoffmann, W.A. & Solbrig, O.T. (2003) The role of topkill in the differential response of savanna woody plants to fire. *Forest Ecology and Management* **180**, 273–286.
- Holdsworth, A.R. & Uhl, C. (1997) Fire in Amazonian selectively logged rain forest and the potential for fire reduction. *Ecological Applications* **7**, 713–725.
- Hopkins, B. (1992) Ecological processes at the forest–savanna boundary. *Nature and Dynamics of the Forest–Savanna*

- Boundaries* (eds P.A. Furley, J. Proctor & J.A. Ratter), pp. 21–33. Chapman & Hall, London.
- Jackson, J.F., Adams, D.C. & Jackson, U.B. (1999) Allometry of constitutive defense: a model and a comparative test with tree bark and fire regime. *American Naturalist* **153**, 614–632.
- Jipp, P.H., Nepstad, D.C., Cassel, D.K. & Carvalho, C.R. (1998) Deep soil moisture storage and transpiration in forests and pastures of seasonally-dry Amazonia. *Climatic Change* **39**, 395–412.
- Kauffman, J.B. (1991) Survival by sprouting following fire in tropical forests of the Eastern Amazon. *Biotropica* **23**, 219–224.
- Kays, J.S. & Canham, C.D. (1991) Effects of time and frequency of cutting on hardwood root reserves and sprout growth. *Forest Science* **37**, 524–536.
- Kellman, M. (1984) Synergistic relationships between fire and low soil fertility in neotropical savannas: a hypothesis. *Biotropica* **16**, 158–160.
- Kellman, M. & Meave, J. (1997) Fire in the tropical gallery forests of Belize. *Journal of Biogeography* **24**, 23–34.
- King, J., Moutsinga, J.-B. & Doufoulon, G. (1997) Conversion of anthropogenic savanna to production forest through fire protection of the forest–savanna edge in Gabon, Central Africa. *Forest Ecology and Management* **94**, 233–247.
- Kitajima, K. (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* **98**, 419–428.
- Loescher, W.H., McCamant, T. & Keller, J.D. (1990) Carbohydrate reserves, translocation, and storage in woody plant roots. *Hortscience* **25**, 274–281.
- Longman, K.A. & Jenik, J. (1992) Forest–savanna boundaries: general considerations. *Nature and Dynamics of Forest–Savanna Boundaries* (eds P.A. Furley, J. Proctor & J.A. Ratter), pp. 3–20. Chapman and Hall, London.
- Medina, E. & Bilbao, B. (1991) Significance of nutrient relations and symbiosis for the competitive interactions between grasses and legumes in tropical savannas. *Modern Ecology: Basic and Applied Aspects* (eds G. Esser & D. Overdieck), pp. 295–319. Elsevier, Amsterdam.
- Miyaniishi, K. & Kellman, M. (1986) The role of root nutrient reserves in regrowth of two savanna shrubs. *Canadian Journal of Botany* **64**, 1244–1248.
- Pereira, B.A.S., Silva, M.A.d. & Mendonça, R.C.D. (1992) *Reserva Ecológica do IBGE, Brasília (DF): Lista das Plantas Vasculares*. IBGE, Rio de Janeiro.
- Peres, C.A. (1999) Ground fires as agents of mortality is a central Amazonian. *Journal of Tropical Ecology* **15**, 535–541.
- Pinard, M.A., Putz, F.E. & Licona, J.C. (1999) Tree mortality and vine proliferation following a wildfire in subhumid tropical forest in eastern Bolivia. *Forest Ecology and Management* **116**, 247–252.
- Prance, G.T. (1992) The phytogeography of savanna species of neotropical Chrysobalanaceae. *Nature and Dynamics of the Forest–Savanna Boundaries* (eds P.A. Furley, J. Proctor & J.A. Ratter), pp. 295–330. Chapman & Hall, London.
- Sato, M.N. (1996) *Mortalidade de Plantas Lenhosas Do Cerrado Sensu Stricto Submitidos a Diferentes Regimes de Queima*. Masters Thesis, University of Brasília, Brasília, Brazil.
- Sato, M.N. & Miranda, H.S. (1996) Mortalidade de plantas lenhosas do cerrado sensu stricto submetidos a diferentes regimes de queima. *Impactos de Queimadas Em Áreas de Cerrado E Restinga* (eds H.S. Miranda, C.H. Saito & B.F.D.S. Dias), pp. 102–111. Universidade de Brasília, Brasília.
- Scott, T.A. & Melvin, E.H. (1953) Determination of dextran with anthrone. *Analytical Chemistry* **25**, 1656–1661.
- Silva, E.P.D.R. (1999) *Efeito Do Regime de Queima Na Taxa de Mortalidade E Estrutura Da Vegetação*. Masters Thesis, Universidade de Brasília, Brasília.
- Silva, G.T., Sato, M.N. & Miranda, H.S. (1996) Mortalidade de plantas lenhosas em um campo sujo de cerrado submetidos a queimadas prescritas. *Impactos de Queimadas Em Áreas de Cerrado E Restinga* (eds H.S. Miranda, C.H. Saito & B.F.D.S. Dias), pp. 93–101. Universidade de Brasília, Brasília.
- Swaine, M.D., Hawthorne, W.D. & Orgle, T.K. (1992) The effects of fire exclusion on savanna vegetation at Kpong, Ghana. *Biotropica* **24**, 166–172.
- Tinley, K.L. (1982) The influence of soil moisture balance on ecosystem patterns in southern Africa. *Ecology of Tropical Savannas* (eds B.J. Huntley & B.H. Walker), pp. 175–192. Springer-Verlag, Berlin.
- Uhl, C. & Buschbacher, R. (1985) A disturbing synergism between cattle ranching burning practices and selective tree harvesting in the eastern Amazon. *Biotropica* **17**, 265–268.
- Wan, C. & Sosebee, R.E. (1990) Relationship of photosynthetic rate and edaphic factors to root carbohydrate trends in honey mesquite. *Journal of Range Management* **43**, 171–176.

Received 4 April 2003; revised 5 July 2003; accepted 16 July 2003