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Fuels and fire at savanna-gallery forest boundaries in southeastern Venezuela

JASON BIDDULPH *and* MARTIN KELLMAN[1]

Department of Geography, York University, Toronto, Ontario, Canada M3J 1P3
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ABSTRACT. Factors contributing to the resistance of gallery forests in savannas to the entry of fire were investigated using field observations and manipulation experiments. Mass of savanna fuels did not decrease close to forest boundaries, and in some instances increased, while savanna fuels adjacent to forests were moister than in the savanna beyond for only 1 d after rainfall. A fuel drying experiment conducted in both forest and savanna microclimates indicated that both fuel type and microclimate contributed to the resistance of forests to fire entry, although the former played a larger role. While savanna fuels in a savanna microclimate became ignitable in *c.* 1 d after rain, forest fuels in a forest microclimate required 4 wk to achieve ignitability. A further experiment juxtaposing forest fuels to burning savanna indicated that fire entry into forests was faciliated by deep root mats and the presence of a superficial litter layer, both of which become attenuated at the forest/savanna contact. It is concluded that fuels in these forests can reach an ignitable state late in the dry season, but that frequent fire entry is probably precluded by the tendency of savanna fires to occur earlier in the dry season and by discontinuities in fuels at the savanna/forest contact.

RESUMEN. Se investigaron los factores que contribuyen a la resistencia de la entrada del fuego a los bosques en galería de las savanas mediante observaciones de campo y experimentos de manipulación. La masa de los combustibles de la savana no decrecieron cerca de los bordes del bosque; por el contrario, en algunos casos se incrementaron, mientras que los combustibles de la savana cercanos al bosque eran mas húmedos que en la savana restante, solamente por un día despues de un evento de lluvia. Un experimento de secado de combustible, que fue conducido en los microclimas de bosque y de savana, indica que tanto el tipo de combustible como el microclima contribuyen a la resistencia de los bosques a la entrada del fuego, aunque el primer factor tuvo un papel de mayor importancia. Mientras que los combustibles de la savana en el microclima de la savana se volvieron 'encendibles' cerca de un día despues de lluvia, los combustibles del bosque dentro del microlima del bosque tomaron cuatro semanas para llegar a dicho estado. Un experimento que sobrepuso combustibles del bosque a la savana ardiente indicó que la entrada del fuego a los bosques se facilitó por la presencia de mantillos

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[1] Corresponding author.

orgánicos profundos y de una capa superficial de hojarasca, presencia que se ve atenuada en la zona de contacto bosque/savana. Se concluye que los combustibles en estos bosques pueden alcanzar un estado de ignición tarde en la estación de sequía, pero que la entrada frecuente del fuego es probablemente evitada por la tendencia que tienen los fuegos de savana a presentarse temprano en la estación seca y por las discontinuidades de combustibles en la zona de contacto savana/bosque.

KEY WORDS: fire, fuel, gallery forest, Gran Sabana, root mat, savanna

INTRODUCTION

Patches of evergreen gallery forest exist in most savanna landscapes despite the high frequency of fires in these places. These gallery forests are normally comprised of species characteristic of continuous forests (Kellman *et al*. 1994, Meave & Kellman 1994), many of which tend to be fire-sensitive (Uhl & Kauffman 1990). While fire does occasionally enter gallery forests under extreme drought conditions, these intrusions are patchily distributed and most fires die out at gallery forest boundaries, even though these edges often experience higher fire frequencies than the savanna area generally (Kellman & Meave 1997). This fire regime serves to prevent expansion of tree populations into savanna, but also preserves a generally fire-free forest interior. The mechanisms that prevent most savanna fires from entering adjacent gallery forests, and therefore allow the coexistence of fire-tolerant and fire-sensitive floras in close proximity, are thus of considerable theoretical interest. These mechanisms are also of practical interest, as forest fragments created by human activities exist in tropical landscapes that are generally fire-prone (Goldammer 1990), and considerable concern exists about whether such fragments will be capable of persisting in the presence of these fire regimes (Uhl & Buschbacher 1985, Uhl & Kauffman 1990).

Fire propogation depends upon the availability of fuels and their arrangement (fineness, bulk density, continuity) as well as upon inherent flammability of the materials comprising the fuels. While a variety of properties, such as ash content and the presence of volatile substances, may affect fuel flammability, the dominant influence is moisture content (Whelan 1995), which varies continuously in response to temporal patterns of rainfall.

Tropical forests normally contain abundant and continuously distributed quantities of fuel in their litter layers, but these are poorly aerated and dry only slowly in the protected forest microclimate. Uhl *et al*. (1988) have concluded that sustained combustion of forest fuels in the San Carlos area of Venezuelan Amazonia requires a relative humidity ≤ 65%, and that these levels are achieved in mature closed-canopy forests less frequently than 1 d per year. On the rare occasions that fire does enter evergreen tropical forests, it is normally restricted to a surface fire (Bond & Van Wilgen 1996). While surface fires are of relatively low intensity, they may cause considerable damage to forests if trees are rooted primarily in a superficial root mat that ignites (see below).

In contrast, savanna fuel masses are often less than those of forests, but they are normally well-aerated and occur in a microclimate that promotes rapid drying. Consequently, fire probabilities are high in savanna communities, with return times of 1–2 y being common in moist savannas (>600 mm rainfall y^{-1}) where fuel regrowth is rapid (Trollope 1984a). Savanna fire intensities vary widely depending on fuel loads and time of burning. Maximum temperatures in savanna fires are normally achieved at the height of the grass canopy, rather than at ground level (Trollope 1984b).

A variety of phenomena and processes may contribute to the failure of most savanna fires to enter adjacent gallery forests. Savanna fuels may become less abundant close to forest edges as a result of root competition with forest trees, while fuels close to forest boundaries may dry more slowly due to a more protected microclimate. In either case, savanna fires would tend to die out as this near-forest zone was approached. Many gallery forest boundaries are composed of trees with deep lateral canopies that preserve a highly protected interior forest microclimate (Kellman *et al*. 1994, MacDougall & Kellman 1992). This protection may be sufficient to slow the drying of forest fuels and preserve them in a non-flammable state during most savanna fire encroachments. In contrast, ignition may be inhibited simply by the very different morphology of forest fuels relative to those of savannas, and their potentially much slower drying rates, even under identical microclimate conditions. Finally, the configuration of forest fuels at their contact with savanna may influence the ease with which fire penetrates forest. At gallery forest-savanna contacts, forest surface fuel layers (root mats and/or recently fallen litter) become attenuated and are therefore separated vertically from the stratum of most savanna fuel and highest savanna fire temperatures. Consequently, the probability of forest fuel ignition at these natural boundaries may be low relative to that which would be expected if thick forest fuel layers were to be juxtaposed to burning savanna fuels. The latter condition is only likely to occur at recent artificially-created forest boundaries, such as those forming the edge of a shifting cultivator's field.

In this paper we evaluate each of these effects using a combination of field observations and manipulation experiments conducted in the Gran Sabana area of southeastern Venezuela. Specifically, we test the following hypotheses: (a) The mass of savanna fuels decreases as forest edges are approached. (b) Savanna fuels dry more slowly with increased proximity to forest edges. As a subsidiary hypothesis, we also evaluate whether the savanna fuels on east-facing forest edges, that are exposed to prevailing winds, dry more rapidly than those on west-facing aspects. (c) Both forest and savanna fuels dry more slowly and reach an ignitable state with greater time delay in a forest microclimate than in a savanna microclimate. (d) Forest fuels dry more slowly and reach an ignitable state with greater time delay than savanna fuels when placed in the same microclimate. (e) Fire intrudes from savanna into thick forest fuel layers more readily than into thin forest fuel layers. (f) The absence of an undecomposed layer of forest litter inhibits the entry of savanna fires into forests.

STUDY SITE

The study was conducted in the northern part of the Gran Sabana, Venezuela, near the settlement of Kavanayen (5° 31′ N 61° 44′ W). The area lies at an elevation of *c*. 1200 m asl and receives 2576 mm of rainfall per year (1985–95) with a dry season (<100 mm mo^{-1}) from December to March. The area forms part of the Guiana Shield, comprised primarily of Pre-Cambrian sandstones that have weathered to exceptionally infertile entisols and ulitsols that are of low pH, low in CEC and available cations, and high in soluble Al (Dezzeo 1994). Diabase intrusions that are covered by more fertile oxisols are scattered throughout the area as sills and dikes.

Vegetation of the area consists primarily of a mosaic of forest and savanna, with forest within savanna zones restricted to riparian habitats and headwater basins. Paleoecological evidence indicates that forest has decreased relative to savanna throughout at least the last 5,000 y (Rull 1992), and the presence of extensive areas covered by *Pteridium aquilinum* (L.) Kuhn (bracken) and containing charred stumps of trees indicates that forest retreat has been widespread in the recent past. Older members of the indigenous Pemon population attribute these stump-fields to a series of ‘great fires’, some reputedly burning for more than a year, which affected this area during especially dry periods this century. Extensive forest fires occurred during a severe drought in 1925–26 (Tate 1930) and it is probable that many of the existing stump-fields originated at this time. Forest recovery in these areas seems to be exceptionally slow, and repeated fires in the bracken-covered areas appears to lead to their gradual transformation into graminoid-dominated savanna.

Savannas in the area are largely treeless. The savanna flora is impoverished relative to other savannas and contains no endemic species (Dezzeo 1994). Forest patches in the savanna vary in diversity but most contain *Dimorphandra macrostachya* Benth. as a prominent component, especially near forest edges. Most forests contain a prominent root mat up to 15 cm thick which comprises the principal fuel type. The root mat consists of a layer of dead organic matter thoroughly impregnated with live roots, above which exists a superficial layer of recently-fallen litter. Fires entering root mats burn slowly but result in death of all trees (M. Kellman, *pers. obs*.); this makes these communities especially vulnerable to fires and presumably accounts for the extensive stump fields created by ‘great fires’. Root mat thickness has been shown to be positively correlated with the levels of soluble Al in surface soils (Kingsbury & Kellman 1997).

Field observations and experiments took place in, and adjacent to, a strip of gallery forest along a N-S flowing stream located *c.* 10 km northeast of the settlement of Kavanayen. The forest varied in width from *c.* 100 m to several hundred metres, and was surrounded by treeless savanna. The forest/savanna boundaries were well-defined with graminoid species dominating to the forest edge in most areas, where some bracken was also present. The west-facing edge of the forest showed signs of recent expansion in the form of high densities of small trees. In contrast, the eastern side of the forest showed signs of recent retreat: the edge was more open, contained few small stems, and in many places was located at or near to the stream bank. According to local informants, the most recent savanna fires at the two forest edges had been 2 and 5 y previously for the eastern and western edges, respectively.

METHODS

Savanna fuels at forest edges

Savanna fuel masses and moisture contents were measured in treeless savanna on eastern and western sides of the gallery forest at the end of the 1994–95 dry season following 18 rainless days, and twice later at 1 d and 2 d after rain events. On each occasion, samples of savanna fuels were taken along three transects orientated perpendicular to the forest edge, and randomly-located along a straight 40-m segment of the gallery forest boundary. Fuel samples were taken at distances of 0, 1, 2, 3, 4, 5, 10, 15, 20 and 25 m from the edge, with the edge defined as the point at which a continuous cover of graminoids or bracken began. Samples were taken using 50-cm × 50-cm or 30-cm × 30-cm quadrats, depending upon fuel quantities. All live and dead grasses, sedges, ferns and forbs were clipped at ground level and these, together with dead leaves, seeds, seed pods and dead wood <1 cm diameter were treated as fuels. Fresh mass of the fuel was measured in the field immediately after collection, and the samples were later oven-dried at 70 °C and re-weighed. Fuel sampling took place in the morning and required *c.* 3 h to complete. Consequently, sampling of eastern and western aspects 1 and 2 d after rain was conducted on different days to preclude the introduction of errors due to fuel drying over extended measurement periods.

The tendency for fuel mass and moisture content of fuels to change consistently away from eastern and western forest edges was assessed by Spearman's rank correlation, using the means of these two variables as dependent variables and samples' distance from the forest edge as the independent variable. Fuel mass data in these analyses comprised the pooled masses for all eastern and western samples taken ($n = 9$), while moisture content data comprised mean values for eastern and western transects ($n = 3$) after each drying interval. The significance of differences in fuel moisture contents at eastern and western aspects after each drying interval was assessed by Wilcoxon's paired-sample tests with data paired by distance from the forest edge.

Fuel drying and ignitability

The rate of drying of forest and savanna fuels in both forest and savanna microclimates was measured using open-ended clear plastic tents to simulate extended rainless periods. The forest tent measured 3 m × 3 m and was 1.5 m high at the ridge-pole. The savanna tent was also 1.5 m high and 3 m wide, but was 4 m long and had rain-flaps attached at both ends to prevent blowing rain from entering. The forest tent was located *c.* 40 m inside the forest, and the savanna tent *c.* 115 m into the savanna on the western side of the forest, and oriented so as to allow free movement of the prevailing NE airflow. Forty samples of each of two savanna grass species and 40 samples of forest rootmat and litter were placed in each rain exclusion tent, weighed regularly to record moisture loss, and a subsample of each tested for ignitability at each time of weighing.

Forest fuel samples consisted of 20-cm × 20-cm blocks of root mat and overlying undecomposed litter that were cut from the forest interior 1 d after a rain event and placed in pre-numbered and pre-weighed trays of 1 mm aluminum fly-screen mesh. Moisture content of these samples averaged 317% at the start of the experiment. Savanna fuel samples consisted of separate sets of *Trachypogon plumosus* (Humb. & Bonpl. ex. Willd.) and a *Paspalum* species, two grasses that were especially abundant at the study site. Grass samples were cut at ground level immediately after a rain event and placed in pre-numbered and pre-weighed cylinders of fly-screen mesh *c.* 10 cm in diameter and 30–40 cm tall. Average moisture content of *Trachypogon* and *Paspalum* fuel samples were 138 and 259%, respectively, immediately after being cut.

Forty samples of each of the three fuel types were randomly assigned to the two tents. All samples were weighed immediately before being placed in their respective tents. The savanna fuels were placed in a continuous block in the centre of each tent where there was sufficient headroom to accomodate these, while forest fuels were placed on either side of this block. Position of samples in these areas was randomly assigned and all samples were placed directly upon bare mineral soil. Strips of rootmat 10 cm wide, were placed on outer edges of the rootmat samples to limit exposure, and positions of samples in each tent were rotated after each weighing.

Ten of the 40 samples of each fuel type in each tent were randomly designated for moisture loss determination, and these weighed at each daily observation. The sample of the same fuel type from the remaining subset whose mass most closely matched the average of the 'weighing only' subset was used for an ignitability trial. This trial consisted of exposing the sample to 15 s of constant flame from a butane cigarette lighter at its highest setting, and a successful ignition was considered one in which the whole sample was consumed. Savanna fuel samples were discarded after an ignition attempt, even if this proved unsuccessful. An unsuccesful ignition attempt of forest fuel samples usually resulted in negligible weight loss (<0.1 g), and the samples were re-used. However, a different sample face was tested for ignition on each occasion, and the

Table 1. Summary of relative humidities (mean % ± SD and range) measured daily at 11h00–12h00 inside and outside of the experimental rain exclusion tents in forest and savanna during a 17-d period prior to the start of the fuel drying experiment. Results of paired t-tests applied to the data for each tent are provided.

Location	Inside tent	Outside tent	t-value
Forest	87.7 ± 9.9 (68–98)	89.1 ± 10.5 (65–100)	1.66^{NS}
Savanna	53.0 ± 10.9 (40–82)	55.9 ± 10.3 (42–80)	2.01^{NS}

NS, $P > 0.05$

sample discarded after four attempts. Weighing of most samples continued until no further weight loss was recorded, at which time they were removed for oven-drying. However, forest fuel samples in the forest tent were wetted during a severe rain event and measurement could not be continued to the moisture equilibrium point. Because the samples had already become ignitable prior to this wetting, the experiment was discontinued.

The mean percent moisture content of the three fuel types in each tent were plotted against exposure time to establish drying curves for each fuel type. As these curves were generally exponential in form, moisture content was log-transformed and regressed upon exposure time, using the 10 individual data points generated at each time of measurement. Slopes of these regressions were compared by pair-wise t-tests.

To evaluate whether tents were affecting the relative humidity of the atmosphere within them, and hence the drying rates of fuels, relative humidity inside and outside of each tent was measured daily over a 17-d period from 3–19 June 1995 during an experimental 'dry run', with fuel samples present in tents. Measurements began at 1100 h at the savanna tent. The results (Table 1) showed that humidities inside and outside of tents were very similar, and paired t-tests performed on these data indicated that differences were not significant at either location. The fuel drying experiment proper began on 19 June 1995, and was ended on July 18, a period representing early wet-season conditions.

Fuel configurations at forest/savanna boundaries

The effects of root mat thickness and the presence of superficial undecomposed litter at forest edges on the ease with which savanna fire entered forests was evaluated in a manipulation experiment that juxtaposed forest fuel samples to burning savanna. The experiment was performed using forest fuel samples that had been protected from rain for 7 and 15 d in the savanna rain-exclusion tents described previously.

Four 7-m × 5-m plots were established in homogeneous savanna on the western side of the gallery forest. These were surrounded by a fire-break that was 1 m wide on three sides and 2 m wide on the down-wind side. Two plots were randomly assigned to the first trial that involved fuel samples that had been dried for 7 d; the remaining two plots were used in trials involving fuels that had been dried for 15 d. In both sets of plots, a 2-m wide strip of savanna on

Table 2. Mass of oven-dry savanna fuels at differing distances from the forest edge on eastern and western sides of the study site gallery forest (mean ± SD, n = 9).

	Mean fuel mass (g m^{-2})	
Distance from forest edge (m)	West-facing aspect	East-facing aspect
0	1157 ± 418	1263 ± 523
1	1006 ± 274	966 ± 470
2	755 ± 166	800 ± 231
3	954 ± 283	836 ± 305
4	950 ± 261	836 ± 305
5	844 ± 251	755 ± 209
10	848 ± 150	456 ± 166
15	720 ± 171	384 ± 198
20	910 ± 265	375 ± 154
25	814 ± 235	290 ± 116

the down-wind edge of the plot was covered with a clear plastic tent for 7 d before the burn to assure dry savanna fuels. Forest fuel samples in each burning trial consisted of five samples each of thick root mats with a normal superficial litter layer, thin root mats with a superficial litter layer, and each root mat type with the superficial litter layer removed.

Each sample consisted of a 25-cm × 25-cm block of rootmat and overlying litter collected beneath canopies of *Dimorphandra macrostachya* close to the gallery forest edge. Thick root mats were 13–15 cm thick, and thin root mats 2–3 cm thick. Litter layer samples collected at the same sites averaged 1738 g m^{-2}. Prior to burning, five replicates of each sample type were randomly assigned to locations on the downwind side of the plots and positioned against the savanna fuels. Samples were placed contiguous with each other, but separated by a piece of thick aluminum foil as a fire barrier. Fires were started at 12h45 on each day of burning at the upwind edge of the plot, using a drip-torch, and allowed to burn to the down-wind edge where the forest fuel samples were positioned. Fire was judged to have successfully entered a forest fuel sample only when this was completely consumed; this provided ranked scores of 0–5 for each treatment and drying time. The frequency of fire entry into forest fuel samples of different type were compared by χ^2 analysis of 2 × 2 contingency tables.

RESULTS

Savanna fuels at forest edges

Savanna fuel masses at varying distances from the eastern and western edges of the gallery forest are provided in Table 2. Contrary to the pattern hypothesized, savanna fuel masses tended to increase with proximity to the forest edge, a trend that was significant on the eastern edge, but not on the western edge (eastern $r_s = 0.976$, df = 8, $P < 0.001$; western $r_s = 0.612$, df = 8, $P > 0.05$).

Moisture content of savanna fuels near forest edges at 1 and 2 d after rain, and at the end of the dry season, are presented in Figure 1 together with the

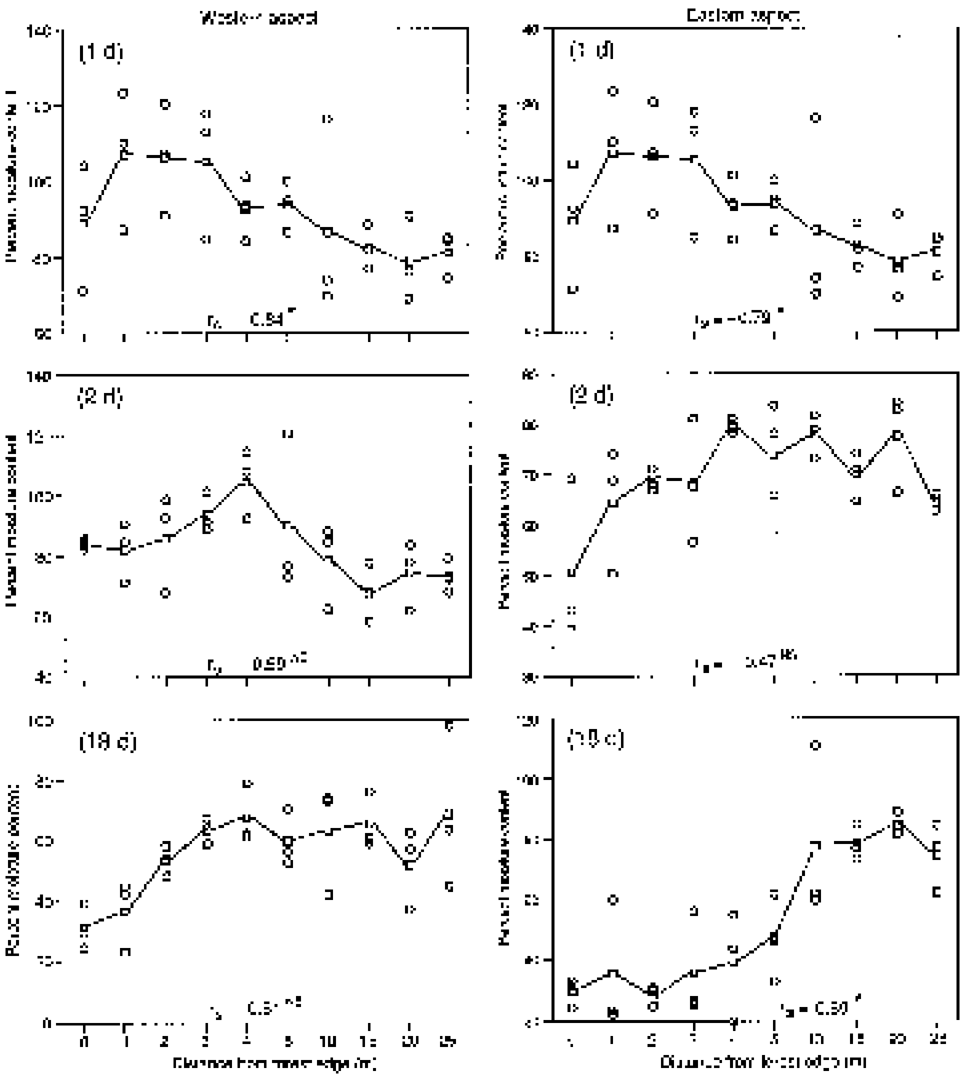

Figure 1. Changes in moisture content of savanna fuels with distance from eastern and western aspects of a gallery forest at 1, 2 and 18 d after rainfall. Mean of three samples designated as boxes and connected by line. Spearman's rank correlation coefficients (r_s) between mean moisture content and distance from forest shown for each analysis.

results of rank correlation analysis of these data. On both the eastern and western aspects of the gallery forest, there was a significant trend toward increased moisture content near to forest edges 1 d after rain. However, this trend had disappeared by 2 d after rain, and after prolonged drying the trend had become reversed, with moisture contents decreasing as the forest edge was approached. This reversed trend was significant on the eastern aspect but not on the western.

On both the first and second days after a rain, fuels on the eastern aspect had significantly lower moisture contents than those on the western aspect (Wilcoxon's paired-sample test, $P < 0.05$). However, after the prolonged drying period there was no significant difference between aspects.

Fuel drying and ignitability

The drying curves and ignition points for the two savanna fuel types and the forest root mat-plus-litter samples are provided in Figure 2 and moisture content at ignition and the drying time to achieve this are summarized in Tables 3 and 4. Both savanna fuel types became ignitable in *c.* 1 d when exposed to savanna conditions, and required only a further 1–2 d to become ignitable when exposed to a forest microclimate. In contrast, forest root mats required 7 d to become ignitable in the savanna microclimate and 27 d to reach the same condition in the forest microclimate. However, the percent moisture content at the time of ignition in all fuel types was comparable (Figure 3, Table 3).

Regression lines fitted to log-transformed fuel moisture content data are provided in Figure 3. Comparison of regression slopes for the same fuel type in forest and savanna microclimates showed that all fuel types dried significantly more rapidly in the latter. A comparison of regression slopes for different fuel types in the same microclimate (Table 5) showed that savanna fuels consistently dried more rapidly than the forest root mat. *Paspalum* fuels dried more rapidly than *Trachypogon* fuels in the savanna, but drying rates were not significantly different in the forest microclimate.

Fuel configuration and ignitability at forest/savanna edges

The frequencies of fire entry into the four forest fuel types after 7 and 15 d drying (Table 6) were not significantly different ($P > 0.05$) and the two data sets were pooled. Comparison among the pooled data showed that the presence of a litter layer increased the frequency of fire entry significantly for both thick and thin root mats, and that fire entered litter-covered root mats significantly more frequently when these were thick than when they were thin (for both analyses, $\chi^2 = 6.67$, df = 1, $P < 0.01$).

DISCUSSION

Savanna fuels at forest edges

The results provide no evidence for savanna fuel masses decreasing close to forest edges, and indeed suggest that in some instances fuel masses increase close to edges (Table 2). Forest edges promote moister savanna fuels for only 1 d after rain and thereafter the effect disappears. This suggests that the additional moisture measured during the first day after a rainfall was primarily external moisture that was evaporated from plant and litter surfaces over the course of a day, rather than moisture contained within live graminoid biomass. While there was some evidence for savanna fuels on the more wind-exposed

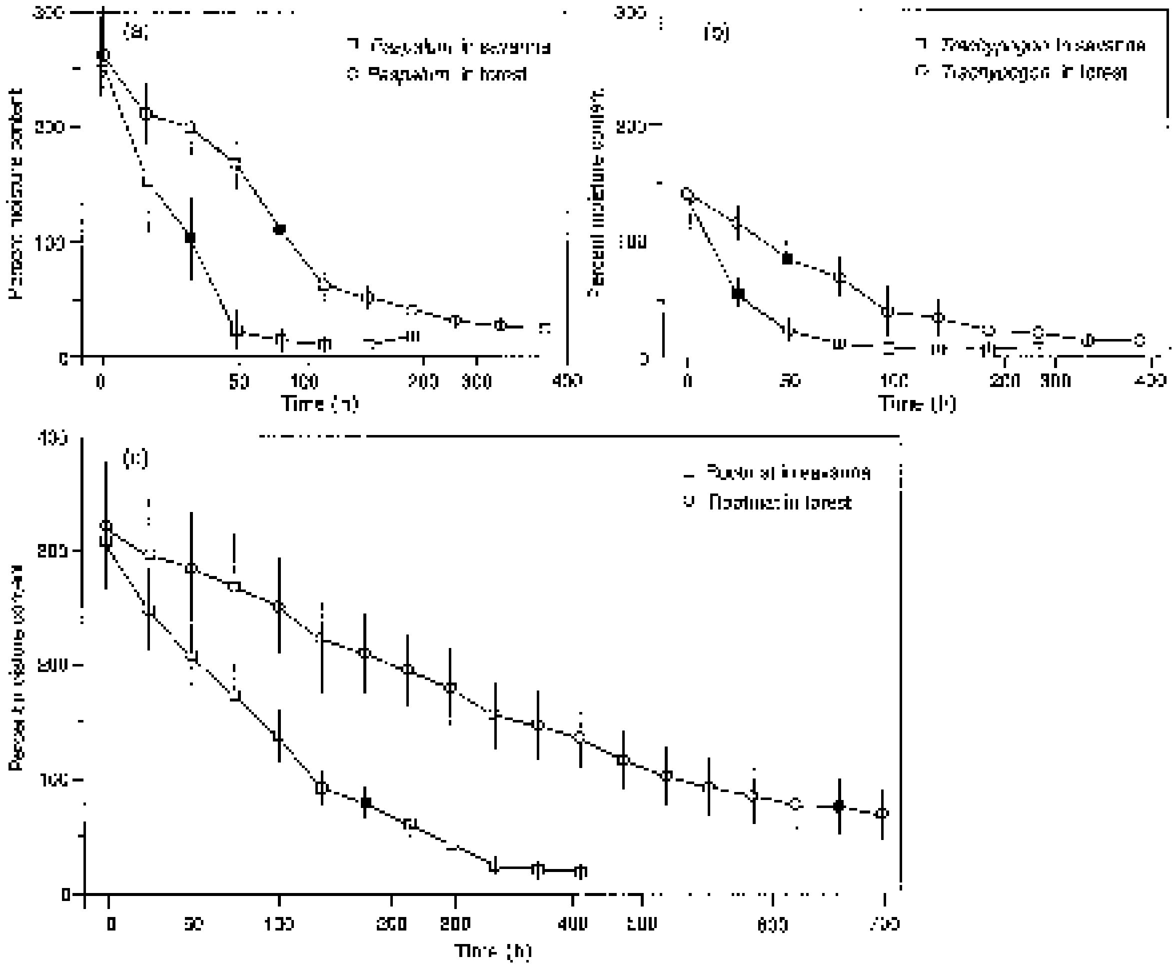

Figure 2. Change through time in moisture content of three fuel types placed in rain-exclusion tents located in forest and savanna: (a) *Paspalum*, (b) *Trachypogon*, (c) forest root mat. Data shown are mean % moisture content (± SD, n = 10) for each sample point. Solid symbols indicate the point at which samples became ignitable.

Table 3. Mean moisture content of three fuel types at the time when fuel ignition was first achieved during drying in rain-exclusion tents located in forest and savanna (% ± SD, n = 10).

Fuel type	Forest	Savanna
Trachypogon	86.1 ± 15.4	55.4 ± 11.2
Paspalum	110.6 ± 19.7	102.1 ± 37.4
Forest root mat	75.2 ± 23.6	78.8 ± 16.1

Table 4. Drying time necessary for different fuel types to become ignitable after drying in rain-exclusion tents located in forest and savanna.

	Time to achieve ignitability (h)	
Fuel type	Forest	Savanna
Trachypogon	48	24
Paspalum	72	27
Forest root mat	648	168

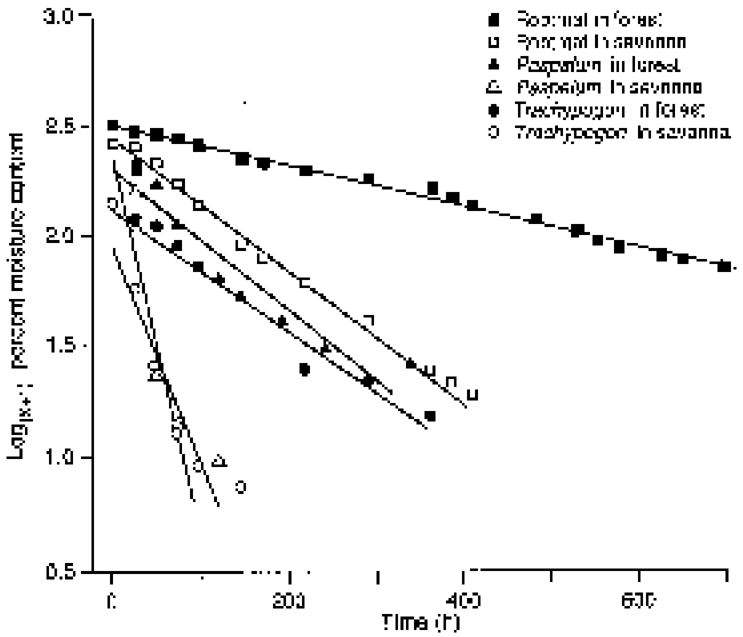

Figure 3. Log-transformed drying curves from Figure 2 with fitted regression lines. For clarity, only means are shown at each sample point, but the full data set (n = 10 per point) was used in calculating the regressions.

eastern aspects of the gallery forest drying more rapidly than those on the western aspect, this was a transient phenomenon.

These data do not suggest that the fuel characteristics in savannas immediately adjacent to gallery forests play a large role in preventing fire entry into these forests. While increased moisture contents occurred close to forest edges for 1 d after a rain, the effect disappeared during the dry season which is the

Table 5. Comparison of regression slopes of drying curves (Figure 3) for different fuel types in the same microclimate.

Comparison	t-value
In forest:	
Paspalum vs. root mat	19.56*
Trachypogon vs. root mat	17.42*
Paspalum vs. *Trachypogon*	0.84^{NS}
In savanna:	
Paspalum vs. root mat	14.84*
Trachypogon vs. root mat	15.76*
Paspalum vs. *Trachypogon*	3.65*

*, $P < 0.001$; ^{NS}, $P > 0.05$.

Table 6. Frequency of fire entry from savanna into forest fuel samples of different type during a fire-spread simulation experiment (n = 5 per treatment).

	Frequency of fire entry	
Fuel type	7-d drying	15-d drying
Thick root mat with litter	5	5
without litter	2	3
Thin root mat with litter	3	2
without litter	0	0

only time at which most forest fuels are likely to be ignitable. The drier savanna fuels that exist for a few days on eastern forest aspects also seems unlikely to explain the tendency for many eastern forest edges to show signs of recent retreat. A more plausible explanation is an increased frequency of fires due to recent human activities. Because fires approaching eastern aspects of gallery forests are characteristically intense headfires, the effects of increased fire frequencies are likely to become apparent sooner at these edges, rather than at other more protected aspects.

The variability that exists in savanna properties close to forest edges elsewhere in the tropics means that these conclusions can be generalized only cautiously. Observations made at other forest/savanna boundaries suggest that increased fuel quantities near to forest edges is a common phenomenon. For example, elsewhere in the Gran Sabana, where forest edges have retreated recently, a zone of dense bracken frequently exists between the forest and the graminoid-dominated savanna (Dezzeo 1994), while in the savannas of Belize, a zone of the large (*c.* 2 m) grass *Tripsacum latifolium* Hitchcock or thickets of the fern *Dicranopteris pectinata* (Willd.) Underw. are almost universal at forest edges (Kellman & Tackaberry 1993). While the drying characteristics of these fuel types are unknown, they normally possess much higher biomass than the savanna proper, and burn intensely during dry-season fires (M. Kellman, *pers obs*.; L. Hernandez, *pers comm*.). In so far as the greatest probability of fire entering forests occurs under dry-season conditions, these high-biomass edge communities would appear to increase, rather than decrease, the vulnerability of forest edges to fire. Consequently, it would appear that the reasons for the resistance of gallery forests to fire intrusion must be sought in conditions within the forest, or at the forest/savanna contact, rather than in the savanna beyond the forest edge.

Fuel drying and ignitability

The tendency for all fuel types to reach ignitability at approximately the same moisture content, despite being of very different morphology and chemistry (Figure 2, Table 3) confirms the over-riding role that moisture plays in controlling fuel flammability. These data would probably have possessed even less variability had ignition tests been performed at more frequent intervals than once daily. For example, the *Trachypogon* sample in the savanna tent ignited at a lower moisture content than other samples, but probably reached ignitability several hours, and at a higher % moisture content, before being evaluated.

The speed with which fuel ignition points were achieved varied both with microclimate and fuel type. Both savanna fuels reached ignitability within 1 d in the savanna microclimate, emphasizing the persistent vulnerability of this community to fire, even under wet season conditions. In contrast, forest fuels in the savanna microclimate required 1 wk to become ignitable. In the field, forest fuels are likely to be exposed to savanna-like microclimates only where human activities have destroyed the forest canopy during logging or agricultural clearing. The present data indicate that such exposed fuels would become vulnerable to ignition well before a vegetation canopy is likely to be re-established at the site. In the Gran Sabana, such conditions occur primarily in shifting cultivators' fields and in the forest immediately adjacent to these, into which root mat fires often intrude (M. Kellman, *pers. obs.*). More generally, such conditions are likely to be characteristic of selectively-logged forest (Uhl & Buschbacher 1985), and the extreme vulnerability of logged tropical forests to fire was illustrated in the Borneo fires of 1982–83 during a severe El Niño drought (Leighton & Wirawam 1986, Goldammer & Siebert 1990).

Even in the forest microclimate, savanna fuels dried to ignitability in only 2–3 d, emphasizing the vulnerability of disturbed forest to burning once these become invaded by graminoids. The fire protection provided by a closed forest canopy can therefore be attributed not only to the slowing of fuel drying that it provides, but also to its ability to prevent establishment of grasses and sedges. In contrast, forest fuels in the forest microclimate required 4 wk to reach an ignitable state. This slow rate of drying would preclude ignition during much of the year, but allow occasional drying to ignitability during the dry season. For example, daily rainfall records for Kavanayen during 1995 indicate that forest root mats in this area would have been vulnerable to ignition for a 29-d period in the dry season, due to prolonged drought.

Although the experimental treatments provided protection from rain during the fuel drying process, they did not control for atmospheric humidity. Because the experiments were performed during the wet season when atmospheric humidity was high, rates of drying may have been underestimated relative to those to be expected in the dry season when most fires occur. Consequently, the 29-d period of forest fuel vulnerability in 1995 represents a minimal estimate. In contrast, the fact that grass fuels were cut rather than having remained rooted probably accelerated their rate of drying and led to an underestimate of the time needed for them to become ignitable. This underestimate is likely to be greatest for wet-season conditions, when much of the grass biomass is alive and actively transpiring, but probably is much less for dry-season conditions when much of the grass fuels are dead, and when most fires are likely to occur.

Some idea of the relative roles of fuel type and microclimatic conditions in influencing fuel flammability can be gained by comparing the time necessary to achieve ignitability of different fuel types in the same microclimate and the same fuel types in different microclimates (Table 4). Savanna fuels dried 7–14 times more rapidly than forest fuels when exposed to the same microclimate, while the two fuel types dried 2–4 times more rapidly in the savanna than in the forest. From this we infer that fuel type plays a larger role than microclimate in influencing ignitability, although both factors clearly contribute to the phenomenon.

Fuel configurations and ignitability at forest/savanna edges

Forest fuels at forest/savanna boundaries that have dried for a week are vulnerable to incursions of savanna fire, and these incursions are facilitated by both a superficial layer of litter and a thick root mat (Table 6). The fuels most vulnerable to fire incursions are therefore thick root mats covered by litter. These are properties that are most characteristic of fuels in forest interiors, rather than at forest edges, which again emphasizes the vulnerability of these fuels to fire during protracted droughts or after canopy opening. In contrast, both quantities of litter and root mat depths tend to be more variable at the contact lines between savanna and forest, making these places less vulnerable to fire than forest interiors.

However, the simplified experimental configurations of fuel juxtaposition used in this experiment limit the generality of the results achieved with it. In particular, the placement of forest fuels next to a well-developed mass of burning savanna fuel is likely to have led to over-estimates of the probability of fire spread into the former. In the field, and at the micro-spatial scale of fire propagation processes, savanna fuels are likely to decrease in mass at the immediate forest edge and be replaced with increasing quantities of forest fuel. This discontinuity, especially if accompanied by a slope convexity, is likely to lower the probability of fire spread from one fuel type to the other. Further, more realistic burning experiments in this critical transition zone are necessary to fully evaluate the importance of fuel configurations and discontinuities there in preventing most savanna fires from entering adjacent forests.

Concluding comments

The characteristics of fuels in savannas adjacent to gallery forests play no role in preventing savanna fires from entering these forests and may even increase the probability of this happening. Rather, it is the properties of the forest fuels, and the forest microclimate within which these exist, that provide the primary protection against fire entry. These forest fuels are of inherently low ignitability and dry much more slowly than savanna fuels, resulting in their being in a non-ignitable state throughout most of the year. However, after *c*. 4 wk of drying, forest fuels become ignitable, and they are thus vulnerable during prolonged rainless periods in the dry season. The failure of most gallery forests to be burned at these times can probably be attributed to two processes: (i) the tendency for savannas to burn earlier in the dry season before forest fuels become ignitable, and (ii) discontinuities in fuel properties at at the savanna/forest contact. Neither process provides absolute protection to gallery forests from fire entry, and increased instances of this happening would be expected to accompany increased savanna fire frequencies. Increased population densities and levels of human activities in the Gran Sabana over the past half-century have almost certainly increased the frequency of savanna fires dramatically, and it is therefore not surprising that there are increased signs of forest destruction due to fires. Considerable effort is expended by the local hydro-electric authority on containing dry season savanna fires when these encroach on forests. A more viable management strategy may be prescription burning of savannas adjacent to forests early in the dry season when the fuels in forests are non-ignitable. While this would preclude forest re-expansion into adjacent savanna, it would prevent further deterioration of the threatened forest resource.

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