

Long-distance Dispersal of Invasive Grasses by Logging Vehicles in a Tropical Dry Forest

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ABSTRACT

Predicting responses of vegetation to environmental factors in human-altered tropical ecosystems requires an understanding of the controls on plant population expansion across landscapes (*i.e.*, long-distance dispersal) as well as of factors affecting recruitment at local scales (*i.e.*, microsite conditions). We studied the roles of light availability, habitat type, soil disturbance, and seed dispersal in a selectively logged forest in lowland Bolivia where the exotic forage grass *Urochloa* (*Panicum*) *maxima* is abundant on roads and log landings but does not invade felling gaps or unlogged forest. Shade-house trials and seed addition experiments with *U. maxima* revealed that this C₄ grass thrives in high light but also grows in partial shade (10% full sun, but not 1% full sun), and that felling gaps, but not undisturbed forest, are suitable for grass establishment. To determine if seed dispersal by logging vehicles explains the discrepancy between actual and potential grass recruitment sites, we collected grass seeds that fell from trucks onto log landings located long distances (> 500 m) from established grass populations. Trucks dispersed an estimated 1800 alien grass seeds per log landing during the early dry season; automobiles also transported seeds of grass (135 seeds/vehicle). The seeds collected (and relative abundances) were the exotics *U. (Panicum) maxima* (97%) and *Urochloa (Brachiaria) brizantha* (2%), and the pan-tropical weeds *Sorghum halapense* (1%) and *Rottboellia cochinchinensis* (0.2%). Grasses invade this forest where disturbance coincides with seed dispersal by motor vehicles, while dispersal limitation apparently prevents invasion of many sites otherwise suitable for grass recruitment (*i.e.*, felling and natural gaps).

Key words: Bolivia; Chiquitania; *Megathyrsus maximus*; *Panicum maximum*; roads; savanna; selective logging; vehicle-dispersed flora.

THERE IS LAGGING (BUT GROWING) AWARENESS of novel tropical ecosystems (Lugo 2009) and complex vegetation transitions (Putz & Redford 2010), as well as increasing recognition that ecosystems resulting from human activities have not been adequately studied (Hobbs *et al.* 2006). Although novel disturbances can simply result in altered abundances of native species, plant invasions can cause drastic changes in community compositions, ecosystem functions, or both (*e.g.*, Mack & D'Antonio 1998). As scientists consider the effects of environmental change on tropical vegetation (*e.g.*, Barlow & Peres 2008), it will be important to understand the biology of not only the pool of species present in native plant communities, but also the species (native or exotic) that are likely to expand their current ranges (Higgins & Richardson 1999).

Range shifts, migrations, and biological invasions cannot occur if propagules do not reach suitable establishment sites or if suitable sites are lacking. To conceptualize the suite of factors that limit recruitment, many studies are conducted within a framework of barriers or filters, physical or biological in nature, that a species must pass through in order to invade (*e.g.*, Parendes & Jones 2000). Numerous human activities break down these barriers by creating conditions suitable for invasive plant establishment (*e.g.*, increased resource availability via disturbance) or by enhancing propagule dispersal (*e.g.*, Hodkinson & Thompson 1997). Ecosystem-altering human activities that both create appropriate establishment sites and enhance propagule dispersal of invasive species demand particular attention.

Roadways represent a familiar example of the coupling of human-mediated dispersal and the creation of novel environments. Roads are essentially corridors of repeatedly disturbed habitat (Gel-

bard & Belnap 2003) along which plant propagules are transported by motor vehicles (Clifford 1959; but see Christen & Matlack 2006). Roadside floras are often dominated by nonnative species, and studies from high-traffic urban areas demonstrate that motor vehicles disperse a disproportionately large number of seeds of invasive species (Von der Lippe & Kowarik 2007).

Although it is plausible that long-distance seed dispersal by motor vehicles occurs in remote regions of the tropics, the effects of roads on plant migrations have received little attention in the tropical conservation literature (but see Corlett 2009). Perhaps this disregard is based on the perception that tropical forests resist plant invasions (Fine 2002), or that in comparison with promoting wildfires, logging, hunting and, ultimately, agricultural conversion (Angelsen & Kaimowitz 1999, Nepstad *et al.* 2001), any roles roads play in plant invasions seem secondary.

Roads that extend into forests in advance of agricultural frontiers are usually constructed for selective logging (Uhl *et al.* 1991). In addition to increasing forest access to people, logging opens forest canopies, disturbs surface soils, and renders forests more fire prone (Uhl & Buschbacher 1985, Laurance 2003; but see Blate 2005). Of these disturbances, exposed mineral soil and increased light availability are thought to be important for the establishment of invasive grasses from seed (Setterfield *et al.* 2005), and fires can further exacerbate grass invasions (D'Antonio & Vitousek 1992). Indeed, both native and alien grasses were reported to colonize a Bolivian tropical dry forest in areas most severely disturbed by selective logging and fire (Veldman *et al.* 2009), but how grass propagules arrived at the invaded sites remains unclear.

We investigated factors expected to influence patterns of alien grass invasion following selective logging in a tropical dry forest in eastern lowland Bolivia where alien grasses regularly colonize roads and log landings but not other anthropogenic microhabitats created

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by selective logging (*i.e.*, not felling gaps and skid trails) or unlogged forest (Veldman *et al.* 2009). The aggregation of alien grasses on sites most severely disturbed by logging might reflect habitat specialization due to microsite conditions, but could also be due to high propagule pressure from seeds dispersed by logging vehicles. We conducted a seed addition experiment, along with a shade house study to determine the microsite requirements for grass establishment and to determine if microsite availability limits grass establishment in felling gaps and unlogged forest. To determine whether long-distance dispersal by logging vehicles contributes to grass invasion in this forest, we collected debris falling from logging trucks and inspected automobiles to look for invasive grass seeds. The results of these studies should yield a more complete picture of how grasses invade selectively logged tropical forest, inform strategies to mitigate invasive seed dispersal, and, draw attention to motor vehicles as dispersers of plant propagules in remote tropical regions.

METHODS

STUDY SITE.—This research was carried out in a seasonally dry tropical forest owned by a vertically integrated logging and parquet flooring manufacturer (INPA Parket Ltd., hereafter INPA) located in a region of eastern lowland Bolivia known as Chiquitania. The study site (16°15' S, 61°40' W; 440 m asl; mean annual precipitation: 1200 mm) covers 30,000 ha of Forest Stewardship Council certified forest of which 900 ha/yr has been harvested since 2002 at an intensity of *ca* 4 trees/ha. The majority of timber is extracted during the dry season (May–October), during which trees are felled, skidded to log landings, loaded onto flatbed trucks (18 m long with 14–18 wheels), and transported 40 km to a sawmill in the town of Concepción (population 6000).

An indirect consequence of logging in INPA is forest invasion by grasses, the most abundant of which is the African forage grass *Urochloa maxima*. Alien grass distributions are generally limited to roads and log landings (*i.e.*, the most severely disturbed microhabitats); in a survey of selectively logged areas within INPA, alien grasses were not encountered in unlogged forest, felling gaps, or skid trails (Veldman *et al.* 2009). A single road provides access to INPA from Concepción and traverses a landscape mosaic of fragmented forests, swidden agriculture plots, cattle ranches, and native savannas. These anthropogenic and semi-natural areas, and the roadside itself, are presumably sources of grass propagules that invade INPA. Alien grasses occur in even the most remote portions of the property that were logged extending some 30 km from the forest entrance.

SHADE HOUSE AND SEED ADDITION EXPERIMENTS.—We conducted two experiments to assess the establishment requirements of *U. maxima*, and thereby to determine if there are suitable establishment sites in the forest where *U. maxima* does not typically invade (*i.e.*, the degree to which *U. maxima* is microsite as opposed to dispersal limited). To assess the viability of seeds used in the experiments (seeds were purchased 2 wk before the experiments from the *Union Centro Veterinario* in Santa Cruz), we scattered 50 seeds into

each of twelve 10 × 14.5 cm plastic trays lined with paper towels, maintained water in the trays at the saturation point for the paper, and counted/removed germinated seeds daily for 2 wk. An average of 48 percent of the seeds germinated, of which 97 percent germinated within the first 7 d.

To estimate the light requirements of *U. maxima*, we assessed seed germination and 1 mo seedling survival (*i.e.*, emergence *sensu* Setterfield *et al.* 2005) under a range of light conditions in shade houses during the early rainy season (October–November 2005); shade houses were located in Santa Cruz at the Bolivian Institute for Forestry Research (IBIF; Poorter & Markesteijn 2008). We filled 48 plastic trays (10 × 14.5 cm) 2-cm deep with forest soil and placed them in one of four light treatments: 0, 1, 10, or 70 percent full sun ($N = 12$ per light treatment); light intensities were measured using an LI-COR model LI-250 light meter (LI-COR, Lincoln, Nebraska, U.S.A.). We saturated each tray with water and after the water drained (*i.e.*, the soil reached field capacity), we scattered 50 seeds on the soil surface; the soil was then maintained at about field capacity during the entire experiment. We counted the number of plants in each tray after 7 d to assess initial germination, and then counted and harvested entire plants after 1 mo; seedlings were washed and oven-dried to constant weight at 60°C before weighing. We compared seedling survival and plant biomass between light treatments using analysis of variance (ANOVA) and Tukey *post-hoc* tests. All analyses were performed using SPSS 12.0 statistics software (SPSS Inc., Chicago, Illinois, U.S.A.).

To investigate how soil disturbance and microhabitat conditions influence *U. maxima* establishment, we sowed seeds in experimental plots in an area of selectively logged forest. In the early rainy season (October 2005), we randomly selected 20 felling gaps and adjacent areas of closed canopy forest within a 100-ha area that was harvested during the preceding dry season. In each felling gap and forest, we established plots of either mechanically scarified or untreated soil in a 2 × 2 factorial complete block design with soil treatment and microhabitat as factors and gap-forest pairs as blocks ($N = 20$ blocks). In each felling gap and forest, we scattered 100 seeds on each of two scarified and two untreated sub-plots of 0.1-m² such that 200 seeds were sown per 0.2 m² per treatment per block. For the scarified (*i.e.*, disturbed surface soil) treatment, we used a machete to remove all litter and plants and to expose a 1.5-m² area of mineral soil before scattering 100 seeds in the center 0.1 m² of each scarified area. We measured canopy cover over each sub-plot using a spherical canopy densiometer held 1.3 m above the ground (Lemmon 1956). After 1 mo, we counted the grass seedlings, collected the above- and belowground grass biomass, and weighed the plants after oven drying at 60°C.

We used a two-way ANOVA to test for main effects of soil treatment, microhabitat, and their interaction, on the number of seedlings, total grass biomass, and biomass per individual; blocks were treated as a random effect and Tukey *post-hoc* tests were used to compare means among treatments. To reveal which sites in the seed addition experiment were suitable for grass establishment, as opposed to those with plants so small they were unlikely to survive, we counted the plots that had a mean per plant biomass > 3 mg. This biomass cutoff was based on the results of the shade house

experiments in which the minimum biomass measured for plants exposed to 10 percent full sun was 3 mg/individual; 10 percent full sun was the minimum sunlight exposure required for high grass survival and growth. We compared the frequency of 'suitable establishment sites' among treatments with χ^2 .

SEED RAIN FROM LOGGING VEHICLES.—During the early dry season (May 2008), we sampled alien grass seed rain falling from logging trucks ($N=8$), and collected seeds from automobiles ($N=3$) on three different log landings in the forest. Log landings are large (*ca* 700 m²) clearings where logs are organized and loaded onto trucks; abandoned log landings are often colonized by grasses. New log landings are appropriate sites for studying long-distance seed dispersal by motor vehicles because they are the primary destination of trucks and automobiles entering the forest. We verified that each log landing used in this study was accessed by a newly created road and was at least 500 m from previously logged forest, pre-existing roads, or existing alien grass populations with a geographic positioning system and a map of the property. In addition, we searched for grasses within 3 m of the road (200 × 6 m sampled) leading away from each log landing to confirm that alien grasses were not present.

To estimate the number of seeds dispersed by trucks to log landings, we randomly positioned 12 plastic tarps (115 × 74 cm each) totaling 10.2 m² beneath each truck immediately after it arrived at the landing. As timber was loaded onto the trucks, dirt and seeds were dislodged and fell onto the tarps. After each truck was loaded, we removed the 12 tarps and combined the material collected into a single sample. In addition to the seed rain from log loading, we collected debris that workers swept off truck beds. Flat-bed trailers can accumulate bark and soil that is removed before log loading; we collected this debris onto a 5 × 5-m tarp as it was swept off the trailer. We did not ask forest managers to clean the truck beds for the sake of this study and did not anticipate this source of seed rain.

We estimated the number of seeds carried by automobiles by collecting all soil and other debris that we were able to dislodge by hand using brushes and wooden spatulas from one randomly selected front and one rear wheel well from each car sampled. We also collected seeds present on the removable interior floor mats from the passenger compartments. In comparison with the truck data, which represent a true estimate of seed rain (Von der Lippe & Kowarik 2007), we do not know what proportion of the automobile seed is deposited on log landings—a limitation of all studies that collect seeds attached to motor vehicles (*e.g.*, Clifford 1959, Zwaenepoel *et al.* 2006).

To determine the number of alien grass seeds in the truck and automobile debris, we manually sorted through the samples to separate seeds from other material. For samples too large to process in their entirety, we analyzed a series of sub-samples. For samples up to 2.5 kg, the sub-samples comprised at least 10 percent of the total sample fresh weight; for larger samples a minimum of 0.25 kg was sub-sampled. We identified the seeds to species and determined the number of full seeds (as opposed to empty caryopses) in the samples by cutting each seed with a razor blade and inspecting it under a

dissecting microscope. We report only the number of full seeds collected. We chose visual inspection of the samples rather than germination trials to assess the numbers and identities of grass seeds carried to log landings by vehicles because the seeds of the most common alien grasses in this forest are relatively large (3–6 mm) and are easily separated from soil and other debris. Furthermore, grass seedlings are extremely difficult to identify to species, whereas seed characteristics are often diagnostic. Finally, required seed dormancy periods can be long and vary even within species (Usberti & Martins 2007) making reliable germination trials lengthy.

Based on the number of seeds that fell onto tarps (10.2 m²) during log loading, we calculated total seed rain per truck by extrapolating to the area of each truck (*ca* 48 m²). To calculate total seed rain densities in seeds/m² for log landings, we assumed ten truck visits per landing and 700 m² as the area of each landing. To calculate the number of seeds per vehicle for passenger cars, we extrapolated from the two tires/wheel wells sampled to four and used the total number of seeds from the interior floor mats. By sampling only tires and wheel wells, we underestimate the total number of seeds carried on the exterior of vehicles. Likewise, more exhaustive cleaning of vehicle interiors would certainly yield higher seed numbers than the floor mats alone. On the other hand, because we do not know what proportion of the seeds attached to automobiles is deposited in log landings, our estimates of alien grass seed rain on log landings are conservative insofar as they only include seeds that fell from logging trucks.

To estimate the production of seeds readily available to passing vehicles, we counted the seeds of *U. maxima*, the most invasive grass in INPA, along 200 m of road abandoned 1 yr before our study. The compact soil of the road, lack of traffic, and scarce rain during the period of seed production (early dry season) made it possible to collect fallen seeds from the surface of the roadbed as an estimate of total availability. We collected seeds from twelve 50 × 50 cm plots in June 2008 (soon after seed shattering) and counted the number of full seeds, as described above. We used these data as an estimate of potential *U. maxima* seed rain onto grass-invaded roads.

RESULTS

CONDITIONS REQUIRED FOR GRASS ESTABLISHMENT.—In shade houses, mean initial (7 d) germination rates were equal among treatments, but were lower than in seed viability trials (33–38% and 48%, respectively). *Urochloa maxima* emergence (*i.e.*, germination and survival to 1 mo) was equal under high light (70% full sun; 38% survival) and moderate shade (10% full sun; 38% survival); few seedlings survived for 1 mo under deep shade (1% full sun; 3% survival) and none survived without light (Fig. 1A). Although, emergence did not differ between 70 and 10 percent full sun, the seedlings in high light were nearly four times larger than those grown in moderate shade (19 and 5 mg/plant, respectively); the few seedlings that survived 1 mo in 1 percent full sun appeared moribund and weighed only 0.5 mg/plant (Fig. 1B). Although not as large as those grown in 70 percent full sun, plants in 10 percent light were clearly maintaining positive carbon balances as evidenced by their growth and apparent vigor. The minimum biomass

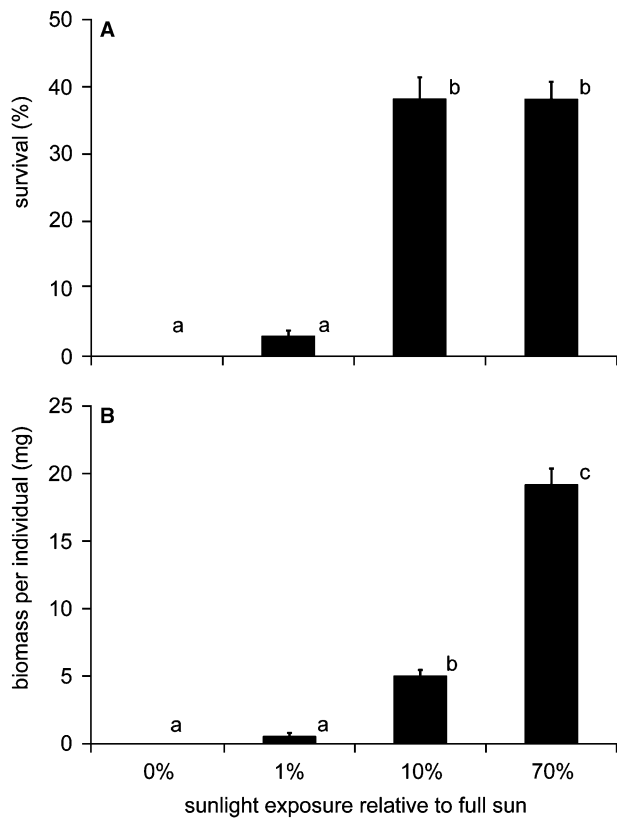


FIGURE 1. Survival and total biomass at 1 mo of *Urochloa maxima* seedlings emerging from 50 seeds sown and grown under 0, 1, 10, or 70 percent sunlight for 1 mo (mean \pm SE; letters indicate differences between light treatments at $P < 0.05$, analysis of variance [ANOVA], *post-hoc* Tukey, $N = 12$). (A) Number of seedlings surviving 1 mo as a proportion of the number of seeds planted. (B) Average biomass per seedling for live plants at the end of 1 mo.

measured for any of the 12 flats under moderate shade was 3 mg/individual. In the *in situ* studies that follow, we used this value (3 mg/plant) as a cutoff to separate suitable establishment sites from plots with plants that are so small that they are unlikely to survive.

In the seed addition experiment, canopy openness values for plots located in closed canopy forest ($N = 20$) and felling gaps ($N = 20$) were 8 ± 2 and 61 ± 13 percent (mean \pm SD), respectively. Overall, *U. maxima* emergence was low; only 1.8 percent of all seeds sown survived for 1 mo. The individuals that did survive were overwhelmingly those sown in closed canopy forest plots on scarified soil (10.5 seedlings/0.2 m² of 200 sown; Fig. 2A), but despite the between treatment differences in numbers of seedlings, total grass biomass did not differ (Fig. 2B). This result was partly because of high variability in total grass biomass values for felling gaps (*i.e.*, many plots with no emergence), but was primarily due to the huge discrepancy in plant sizes between gaps and forests; seedlings in gaps were eight times larger than plants growing in the shaded understory (Fig. 2C). In felling gaps, 35 percent of untreated soil plots and 20 percent of scarified plots had plants > 3 mg/individual; in contrast only 5 percent of scarified plots and

none of untreated soil in the forest had a per plant biomass that indicated the site was suitable for grass establishment (Fig. 2D).

SEED DISPERSAL BY LOGGING VEHICLES.—Log trucks were estimated to have dispersed 1800 alien grass seeds per log landing in the early dry season (Table 1). The majority of seeds came from flatbed cleaning (1750 seeds/log landing). The seed rain during log loading was more modest: five seeds/truck visit or 50 seeds/landing. Automobiles carried alien grass seeds attached to tires and wheel wells (50 seeds/vehicle) and on interior floor mats (90 seeds/vehicle; Table 1).

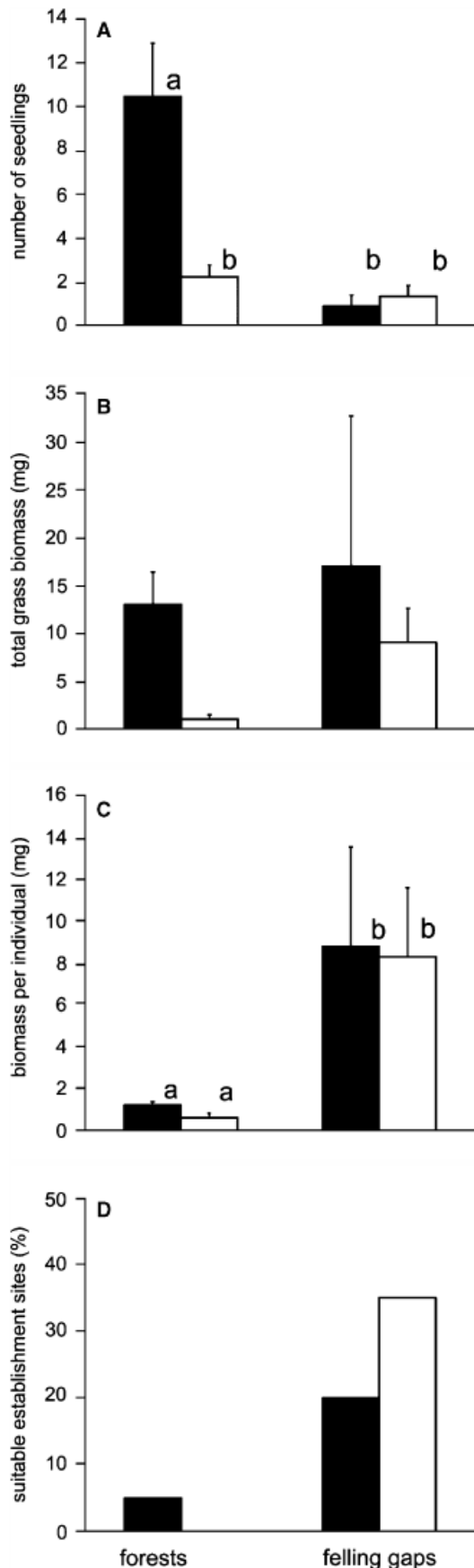
Alien grass seeds collected from vehicles on log landings included three species known to colonize selectively logged forest (*U. maxima*, *Urochloa brizantha*, and *Sorghum halepense*; Veldman *et al.* 2009), and another exotic grass, *Rottboellia cochinchinensis*, not previously documented in INPA. The majority of seeds were *U. maxima* (97%) followed by *U. brizantha* (2%), *S. halepense* (1%), and *R. cochinchinensis* (0.2%). Both *U. maxima* and *U. brizantha* are highly productive African grasses planted as forage throughout the Neotropics (Parsons 1972). *Sorghum halepense* and *R. cochinchinensis* are large (2–3 m tall) pantropical weeds that are common along roadsides in Chiquitania, particularly on wet sites. The number of *U. maxima* seeds collected from the surface of a grass-invaded road was estimated as 1270 seeds/m², equivalent to *ca* 8000 seeds/m of road.

DISCUSSION

Although logging opens forest canopies and disturbs soil—factors generally thought to influence the success of grass invasions (*e.g.*, Setterfield *et al.* 2005)—it appears that canopy openness is more important to establishment of *U. maxima* in this forest. Soil disturbance increased grass emergence in closed canopy forest, but in felling gaps (*i.e.*, open canopy, high light conditions), there was no effect of soil scarification on survival of sown grass seeds. *Urochloa maxima* seeds probably contain sufficient energy reserves to grow through leaf litter but can only then survive where there is sufficient light. The growth and survival of plants grown in shade houses under 10 percent full sun nonetheless demonstrates that this C₄ pasture grass is more shade tolerant than might be expected, and suggests that areas of logged forest with even intermediate levels of

TABLE 1. Alien grass seeds collected from motor vehicles arriving at log landings during selective logging of a seasonally dry Bolivian forest (mean \pm SD).

Vehicle class	Source	N	Seeds/sample	Alien grass seed rain	
				Seeds/log deck	Seeds/m ²
Log trucks	Log loading	8	5 \pm 6	50	0.1
	Flatbed cleaning	5	350 \pm 140	1750	2.4
Automobiles	Tires/wheel wells	3	50 \pm 80	—	—
	Interior floor mats	3	90 \pm 50	—	—
Total				1800	2.5



canopy and soil disturbance (*i.e.*, skid trails) are suitable recruitment sites.

In the months following disturbance by selective logging, the forest contains more potential than realized recruitment sites for alien grasses. The seed addition experiment showed that felling gaps are suitable sites for *U. maxima* establishment. Given that alien grasses were not found in felling gaps (*ca* 10% of the area of selectively logged forest) but were common in the 1 percent of logged forest occupied by roads and log landings (Veldman *et al.* 2009), we conclude that few seeds ever arrive in felling gaps. It is also unlikely that seeds are regularly dispersed into unlogged stands, but even if they were, low light availability and lack of disturbed soil would preclude their establishment. This contention is consistent with the assertion by Fine (2002) that undisturbed tropical forests are perceived as resistant to invasion because many introduced species, like the grass in this study, are light demanding.

Seed transport by trucks appears to be the primary method of grass seed dispersal into this selectively logged forest. In the early dry season, during the peak of grass seed production and the commencement of timber extraction activities, log trucks dispersed large quantities of alien grass seeds long distances into what was old growth tropical forest. Sixty-nine percent of log landings in this forest contain alien grasses (Veldman *et al.* 2009); we provide at least circumstantial evidence that these populations were largely established from seeds dispersed by trucks. We also found grass seeds on the tires and in the wheel wells of passenger vehicles, a well documented phenomenon (Clifford 1959), but did not estimate the number of seeds they actually deposited on log landings. The seeds collected from logging vehicles almost certainly originated from roadsides between the sawmill and the log landings; given *ca* 8000 seeds/m produced along an estimated 4 km of exotic grass-invaded roadside, some 30 million alien grass seeds were available to vehicles traveling into the forest. In general, motor-vehicle dispersal helps explain why alien grasses are limited to roads and log landings when many other appropriate establishment sites are opened by selective logging.

The mechanism of seed attachment to motor vehicles for the grasses encountered in this study appears to be different than is commonly proposed for other vehicle-dispersed roadside floras.

FIGURE 2. Emergence of *Urochloa maxima* seedlings (mean \pm SE) 1 mo after planting 200 seeds in 0.2 m² plots in a 2 \times 2 factorial design combining two habitat treatments (unlogged forests and felling gaps) and two soil treatments (scarified soil and untreated soil; bar colors: black, mechanically scarified soil; white, untreated soil). (A) Number of seedlings per 0.2 m² plot; there were significant effects of soil treatment, habitat type, and an interaction between factors; letters indicate differences between treatments at $P < 0.05$ (two-way analysis of variance [ANOVA], *post-hoc* Tukey, $N = 20$ treatment blocks). (B) Total grass biomass per 0.2 m² plot; no differences. (C) Biomass per individual for plots with live plants; effect of habitat type only ($N = 17, 15, 6, 9$; plots with no plants were excluded). (D) Proportion of plots suitable for *U. maxima* establishment defined as plots with a biomass per individual ≥ 3 mg ($\chi^2 = 10.0$, $df = 3$, $P < 0.02$).

Other studies have emphasized the importance of precipitation and mud for attaching seeds to passing motor vehicles (Zwaenepoel *et al.* 2006), but in this forest seeds were transported and dispersed in the absence of precipitation and were primarily carried on or in vehicles as opposed to being stuck in attached mud. Fertile culms of *U. maxima*, *U. brizantha*, *S. halepense*, and *R. cochinchinensis* grow 1–3 m tall with inflorescences that hang over roadways. When vehicles pass with the windows open, seeds fall into the passenger compartments; when people exit automobiles they presumably carry some of these seeds with them (Wichmann *et al.* 2009). The flatbed trailers of trucks are *ca* 1.5 m tall, an ideal height to collect grass seeds that get lodged amongst bark fragments from logs from previous trips. Indeed, the vast majority of seeds delivered to log landings in this study were swept from the beds of log trucks.

Alien grass invasions in forests are worrisome for various reasons including their effects on forest flammability (D'Antonio & Vitousek 1992) and because their vigorous growth during the rainy season (when logging operations cease) makes transit of primary logging roads difficult. Clearing the roads using bulldozers has become both a nuisance and cost for forest managers (D. Velasquez, pers. comm.). Fortunately, simple measures could be taken during periods of grass seed production (late rainy and early dry season) to substantially reduce seed dispersal by logging activities in this forest. Truck beds should be swept off at the sawmill after delivery of timber from the forest and once again before entering the property to remove accumulated seeds. Seed transport by automobiles could be minimized if both the interior and exterior of vehicles were regularly cleaned to remove accumulated seeds. Although not included in this study, we expect that heavy equipment (*i.e.*, bulldozers and graders) also move invasive plant propagules. Forest managers should time road maintenance activities so that grass-invaded areas are avoided during periods of seed production. When this is not feasible, clearing of roadways using machetes or mowers such that grass seeds fall to the ground at the site of seed production would limit the number of seeds that could fall onto truck beds or accumulate in the passenger compartments of automobiles.

This study links vehicle dispersal of invasive species to an active invasion process in a remote area of tropical forest. The sampling design used guaranteed that collected seeds traveled at least 500 m, but given that new roads that extend up to 5 km into previously unlogged forest support populations of alien grasses and that alien grasses occur at the farthest points of the property (30 km from the entrance), it is clear that grass seeds are commonly transported much farther from parent populations. In light of our results, and the previously demonstrated potential of motor vehicles to drive biological invasions (Von der Lippe & Kowarik 2007), biologists and ecosystem managers should be aware that human movements can unintentionally disperse seeds even in areas intended for native ecosystem conservation through natural forest management.

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