ELSEVIER

Forest Ecology and Management 109 (1998) 33–49

Forest Ecology and Management

Impacts of disturbance initiated by road construction in a subtropical cloud forest in the Luquillo Experimental Forest, Puerto Rico

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Received 10 September 1997

Abstract

The impacts of road construction and the spread of exotic vegetation, which are common threats to upper elevation tropical forests, were evaluated in the subtropical cloud forests of Puerto Rico. The vegetation, soil and microclimate of 6-month-old roadfills, 35-year-old roadfills and mature forest with and without grass understories were compared. Recent roadfills had higher light levels, soil temperatures, bulk densities, larger pools of exchangeable soil nutrients and higher soil oxygen concentrations; but lower soil moisture, soil organic matter and total soil N than the mature forest. On the 35-year-old roadfills, bulk density, soil pH and P pools were statistically similar to the mature forest while soil moisture, total N and base cations were different. The total aboveground biomass of 6-month-old roadfills was about 2 Mg/ha and dominated by a variety of monocot and herbaceous species. The 35-year-old roadfill areas had a biomass of 10.5 Mg/ha, 77% of which was non-woody. Seedling density, tree density and total woody biomass were 12, 28 and 2% of mature forest sites, respectively. In these areas, where soils were disturbed during construction, accumulation of biomass is the slowest known for the LEF. It may take 200–300 years for biomass to attain mature forest levels. In areas that were not directly disturbed during construction, the road has had little effect on the vegetative composition beyond a 5–10 m zone immediately adjacent to the pavement. Although non-native monocots, one of which had been planted along the road 35 years earlier, were copious along the disturbed roadside, they were generally absent from the mature forest and only abundant in habitats of anthropogenic origin. © 1998 Elsevier Science B.V.

Keywords: Non-native species; Aboveground biomass; Ecosystem recovery; Soil nutrients; Succession

1. Introduction

Tropical and subtropical montane cloud forests, one of the world's most threatened ecosystems, are being deforested at a rate greater than all other tropical forests (Doumenge et al., 1995 and Hamilton et al., 1995). These forests typically have high levels of endemism, low rates of net primary production and play an essential role in the hydrologic cycles of tropical mountains (Stadtmuller, 1987; Tanner et al., 1990; Bruijnzeel and Proctor, 1995 and Grubb, 1995 and others). Due to the slow growth rates of these forests, disturbed areas can take centuries to recover. Managing

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PII S0378-1127(98)00261-8

these ecosystems is a complex and very long-term endeavour (Byer and Weaver, 1977 and Scatena, 1995a).

A survey of participants at a recent international symposium on tropical montane cloud forests indicated that road building and the spread of non-native species are common threats to these ecosystems (Hamilton et al., 1995). In other ecosystems it has been shown that roads can have both direct and indirect impacts on surrounding vegetation (Auerbach et al., 1997 and Guariguata and Dupuy, 1997). They can be major sources of landslides and sediments (Larsen and Parks, 1997; Larsen and Torres Sanchez, 1992, 1996 and Megahan and Ketcheson, 1996) and can increase forest fragmentation by creating barriers to migration and gene flow (Andrews, 1990 and Mader, 1984). In addition, the presence of roads can increase the extent of anthropogenic activities in remote areas and provide a conduit for the introduction of exotic flora and fauna (Hamilton et al., 1995; Raynor, 1995; Whistler, 1995; Wein et al., 1992; Andrews, 1990 and Mader, 1984). The spread of non-native grasses and other exotics can become a serious threat to a native forest ecosystem (Hughes et al., 1991 and Hughes and Vitousek, 1993).

Although the importance of managing tropical cloud forests is widely recognized, their small size and their susceptibility to physical disturbance has limited the use of multiple experimental trials to evaluate different management and restoration techniques. In this study we examined the effects of road construction and subsequent management on the subtropical cloud forest of the Luquillo Experimental Forest (LEF) of Puerto Rico (Fig. 1). The principal questions addressed were: (1) How has road construction and subsequent management altered the natural vegetation? (2) What are the relevant time periods needed for edaphic conditions and mature forest vegetation to become established on highly disturbed roadfills? (3) What influence has the road and its management had on the presence of non-native species in this forest?

2. Methods

2.1. Study area

The focus of this study is a 6 km, two lane, paved road that was built by the U.S. Navy in 1960 to provide access to the East Peak communication facilities (Sowers, 1971 and Scatena, 1995b). The road ranges in elevation from 760 to 1050 m.a.s.l. and passes through all the forest associations of the upper elevations of the LEF, i.e. colorado forest, palm forest and cloud forest (Weaver, 1995). Average annual rainfall along the road ranges from 4270 to 4530 mm/yr (Garcia-Martino et al., 1996). Air temperature ranges between 18°C and 20°C, humidity is high, saturation deficits are low and the area is normally enshrouded in clouds.

While the East Peak road was being constructed serious engineering problems were encountered. These included numerous and large landslides, unexpected rock falls and the sinking of earth moving equipment into 5 m of 'jelly-like' saturated silt (Sowers, 1971). The road required 3 years instead of the estimated 8 months to complete and cost more than twice the original estimate. After 34 years of continual use and maintenance, road related slope failures were still a chronic and expensive problem. In response, sections of the road were reconstructed or realigned during the first half of 1995. During both the original construction and the reconstruction, areas along the roadside were filled with compact, rocky, saprolitic material that had been excavated during the reconstruction. These roadfill areas were initially devoid of vegetation and ranged in size from 15 to 200 m in length and 5 to 30 m in width.

2.2. Vegetation sampling and analysis

Vegetation was sampled in plots and transects that were located along the entire length and elevation gradient of the East Peak road (Fig. 1, Table 1). Rectangular plots, 120 m^2 in area, were established in each of the site types considered: 6-month-old roadfills (new road, NR); 35-year-old roadfills (old road, OR); mature forest (MF); and mature forest with a grass understory (GMF). Because the East Peak Road traverses four mature forest associations, MF plots were established in all; 3 in short stature cloud forest (SCF), 3 in tall stature cloud forest (TCF), 3 in palm forest (PAL) and 3 along the lower elevation sections of the road in Colorado forest (COL). NR and OR plots span all 4 forest associations. Additional information on the ecology and vegetation of these mature forest types can be found elsewhere (Weaver, 1995).

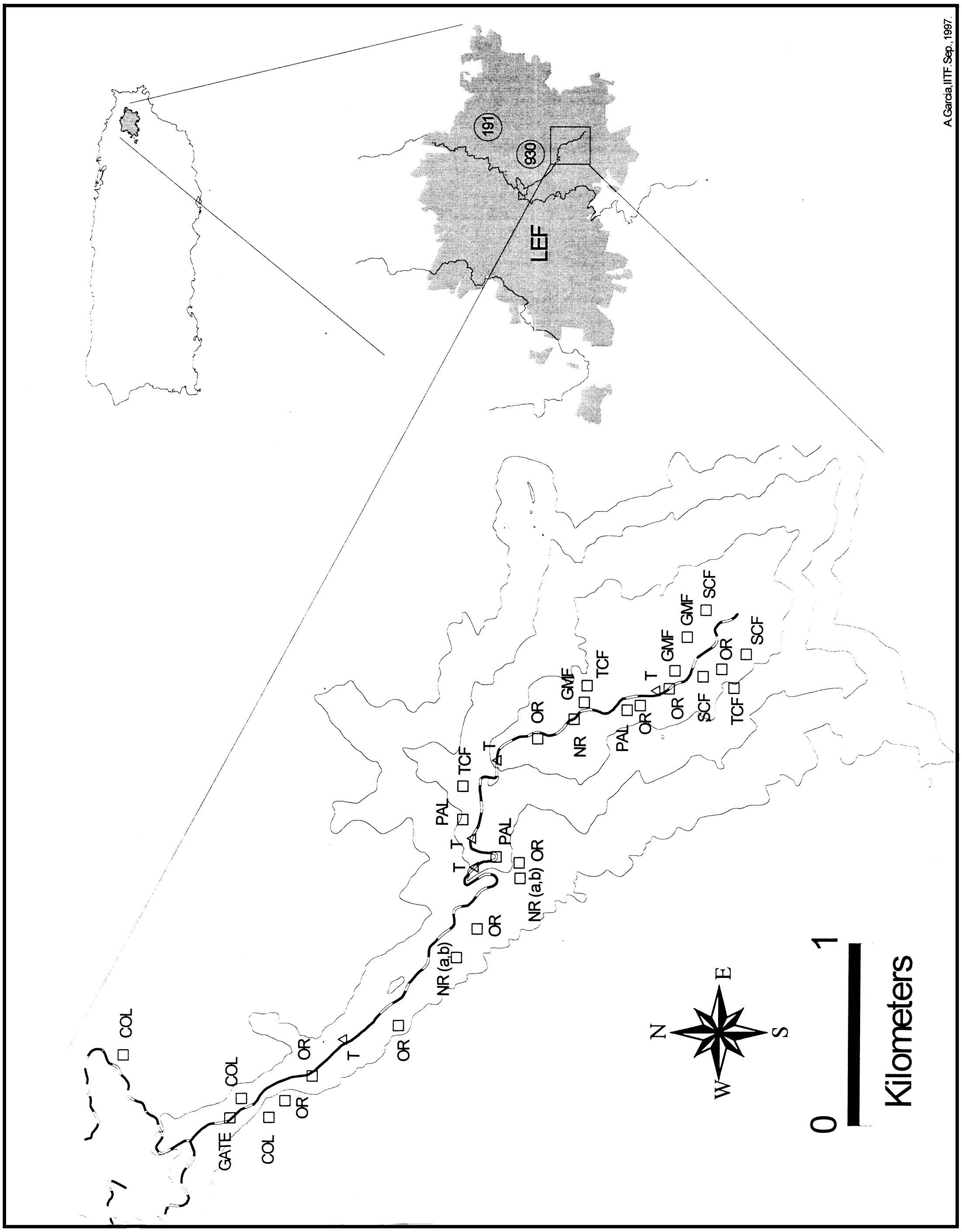

Fig. 1. Location of plots and transects for study of the impacts of road construction and management along East Peak Road, Luquillo Experimental Forest, Puerto Rico. Mature forest plots consist of SCF=short stature cloud forest, TCF=tall stature cloud forest, GMF=cloud forest with grass understory, Pal=palm forest and Col=Colorado forest. Roadfill plots are indicated by NR=new road and OR=old road. T indicates the location of transects.

Table 1
Plot designation for study of road construction and management impacts in Luquillo Experimental Forest, Puerto Rico. Forest types: SCF=short stature cloud forest, TCF=tall stature cloud forest, Pal=palm forest, Col=Colorado forest. The number of plots or transects is designated by *n*. Plots are 120 m^2, subplots are 1 m^2 and transects are 100 m long

Plot designation	Forest type	Elevation range (m)	Sampling design	*n*	Subplots per plot/transect
New roadfill (NR)	Spans SCF to COL	800–1000	Plot	5	12
Old roadfill (OR)	Spans SCF to COL	750–1000	Plot	9	12
Mature forest (MF)	Spans SCF to COL	720–1050	Plot	12	12
	SCF	950–1050		3	
	TCF	850–1000		3	
	PAL	850–950		3	
	COL	720–800		3	
Mature forest with grass understory (GMF)	SCF and TCF	900–1050	Plot	3	12
Transect (T)	Spans SCF to COL	800–1000	Transect	6	28

The GMF plots were all located in areas of mature cloud forest and had a pronounced and dominant understory of grasses. These plots were established to assess which factors influence the establishment of grasses within mature forests. The GMF areas were located within 100 m of the road and had windward aspects. Two of the sites were adjacent to research trails and two of the sites suffered partial crown damage during the passage of Hurricane Hugo in 1989. Since all of the GMF plots were located in the cloud forest zone, they were only compared to the 6 mature cloud forest sites without grass understories.

The OR sites were established on roadfilled areas that were created when the road was initially constructed in 1960. To minimize erosion and sediment production after the road was completed, these barren areas were seeded once with a mixture of fertilizer and seed of the exotic grass *Melinis minutiflora* (F.H. Wadsworth, personal communication). Aerial photos and interviews with Forest Service Personnel indicate that these areas had not been modified since they were established and planted with grasses in 1963.

The NR plots were established on roadfills that had been created during the 1995 reconstruction. On the newly created roadfills, resource managers from the Caribbean National Forest used a variety of experimental treatments that included combinations of fertilizer, mulch and plantings of native seedlings (Olander et al., 1996). Because these treatments were done in an experimental mode several techniques were used and several areas were left as untreated controls. Unfortunately, road related landslides associated with high rainfall events in September 1995 and 1996 damaged many of these treatments and made their remeasurement impossible.

In all of the plots, percent cover by life form, tree species composition, monocot species composition and species richness (#species/m^2) were assessed in twelve, 1×1 m subplots that were randomly located within the 120 m^2 plot. Percent canopy cover was measured at 1.3 m height in each subplot using a spherical densiometer. The diameter of all stems greater than 1.5 m in height were recorded by species and used in calculations of stem density, basal area and woody biomass. Biomass for these individuals was estimated using allometric equations that were developed specifically for the upper elevation Luquillo forests (Frangi and Lugo, 1985 and Weaver, 1990). All individuals less than 1.5 m in height were counted and recorded by species for calculations of seedling density. The biomass of all vegetation <1.5 m in height was determined by the destructive sampling of 2 or 3 m^2 subplots in each of the plots, except the MF plots.

To assess the influence of the road on the adjacent forest, vegetation was sampled along six transects that were situated perpendicular to the road (Fig. 1). Each transect extended 50 m on either side of the road and had two 1×1 m subplots at 2, 5, 10, 20, 30, 40 and 50 m. Percent cover by life form, monocot species composition and tree species composition were recorded in each of the subplots. Species richness and a spherical densiometer index of canopy cover were also recorded for each subplot.

Table 2
Percent cover of monocot species by historic distribution and perpendicular distance from East Peak Road, Luquillo Experimental Forest, Puerto Rico. Native monocots are those which are native to the upper elevation forests of Puerto Rico or the Caribbean. Introduced monocots are those known to be from places outside the Caribbean. Regional monocots are found throughout the neotropics. Percent monocot cover by species is calculated as the percent of the total live monocot cover at each distance, based on the average of 12 plots at each distance

Distance	2	5	10	20	30	40	50	Total
Introduced	**47.8**	**21.5**	**14.2**	**8.6**	**0.0**	**0.0**	**0.0**	**21.7**
Melinis minutiflora Beauv.[a]	8.6	1.6	14.2	8.6	0.0	0.0	0.0	6.2
Pennisetum purpureum Schumach.	39.2	19.9	0.0	0.0	0.0	0.0	0.0	15.5
Regional	**16.4**	**21.9**	**22.6**	**16.8**	**1.7**	**0.0**	**3.6**	**15.1**
Andropogon bicornis L.	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.1
Paspalum conjugatum Berg.	2.2	4.2	0.8	0.4	0.0	0.0	0.0	1.6
Eriochrysis cayennensis Beauv.	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6
Fuirena umbellata Rottb.	0.0	0.0	6.1	0.0	0.0	0.0	0.0	0.9
Kyllinga pumila Michx.	0.2	0.3	0.0	0.0	0.0	0.0	0.0	0.1
Panicum laxum (Sw)	12.0	17.4	10.9	16.4	1.7	0.0	3.6	11.2
Typha domingensis Pers.	0.0	0.0	4.0	0.0	0.0	0.0	0.0	0.6
Ichnanthus pallens (Sw) Munro[b]	**8.2**	**13.2**	**18.2**	**12.7**	**36.8**	**23.3**	**32.8**	**16.3**
Native	**14.3**	**43.4**	**45.0**	**61.9**	**61.5**	**75.0**	**63.6**	**42.8**
Isachne angustifolia Nash	13.3	41.8	42.1	44.3	24.6	74.2	62.0	36.5
Scleria canescens Boeck	1.0	1.6	2.8	17.6	36.8	0.8	1.6	6.3
Unknown	**13.3**	**0.0**	**0.0**	**0.0**	**0.0**	**1.7**	**0.0**	**4.1**
Total live	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**100**

[a] Melinis minutiflora was planted for roadside restoration in 1960.
[b] Ichnanthus pallens is highlighted because it has a distribution which suggests it may be native.

Monocot species in both the transects and the 120 m^2 plots were identified to species and separated into three groups on the basis of their origin as defined in local floras (Davidse et al., 1994; Liogier and Martorell, 1982 and Howard, 1979). These groups were: (1) 'native' to the high elevation forests of the LEF; (2) 'regional' and (3) 'introduced' (Table 2). Out of 12 identified monocot species, only two, *Isachne angustifolia* and *Scleria canescens* are considered 'native' in the local floras. The 'introduced' group included Melinis minutiflora. and Pennisetum purpureum, both of which are African forage grasses. The remaining eight 'regional' species are widespread throughout Puerto Rico, the Caribbean and the neotropics.

2.3. Microclimate

Over a three month period photosynthetic active radiation (PAR) and soil temperature were measured in 3 NR plots, 4 OR plots and 3 GMF plots and in adjacent mature forest. Each of the plots and their paired mature forest sites were sampled simultaneously and continuously for at least 1 week. At each site, light sensors were placed at two different heights; 0.05 m (i.e. seedling height) and 1 m (i.e. sapling height). Soil temperature was measured at a depth of 5 cm at 1 location per site.

2.4. Soils

All soil samples were collected to 10 cm in depth and were analyzed with methods previously used in the LEF (Silver et al., 1994). Gravimetric soil moisture was determined on five cores per plot (n=30) that were collected on the same rainless day and dried at 105°C for 2 days. Soil samples for chemical analysis were taken from composites of approximately five, 2.5 cm diameter cores at each site. Bulk density was measured by excavating 15×15×10 cm soil pits at each location (Silver et al., 1994)

Soil pH was determined on fresh soils placed in a KCl solution (McLean, 1982). Soils for other analyses were air-dried, ground and passed through a 2 mm sieve prior to analysis. Subsamples were extracted with 1 M KCl for exchangeable Ca, Mg and Al and with a modified Olsen solution ($NaHCO_3$ with EDTA) for exchangeable P (Wilde et al., 1979 and Hunter, 1982). Extraction solutions were analyzed on a DCP Spectraspan V spectrophotometer at the International Institute for Tropical Forestry (IITF) in Puerto Rico. Soil organic matter content was determined using Walkley Black technique (Nelson and Sommers, 1982) and total N using a modified Kjeldahl method (Bremner and Mulvaney, 1982).

Percent soil oxygen was monitored at 9 plots; the 3 tall stature mature cloud forest, 3 OR and 3 GMF plots using techniques that have been used throughout the LEF (Silver et al., submitted). At each plot, 5 buried equilibration chambers (Faulkner et al., 1989) were placed at 10 cm depth. Measurements were made on chambers weekly in the OR and GMF plots and every 2 weeks in the cloud forest using a YSI O_2 electrode and meter. Oxygen was not measured in the NR plots because the chambers could not be placed in the rocky substrate. However, the reddish colors and hues of NR soils indicated that these areas were probably oxidized to a depth greater than 10 cm.

2.5. Statistical analysis

Statistical analyses were conducted using Systat (Wilkinson, 1990). Vegetative structure and composition by plot type were compared using a two-way ANOVA on log transformed data and with a Tukey's range test. Importance values for tree species were calculated as the sum of percent density and percent basal area. For plots and transects, percent cover of each plant type was calculated as the percent of total cover. Percent cover of individual monocot species was calculated as the percent of total monocot cover.

Mean and standard deviation of daytime (6 a.m.–6 p.m.) PAR and soil temperature for each treatment were compared using a *T*-test at the 99% significance level. All soil data was log transformed prior to conducting analysis of variance with Fisher's least significance test.

3. Results

3.1. Microclimate

The average daily PAR at seedling and sapling heights in the NR sites was 27 and 11 times greater, respectively than that observed in adjacent forest (Table 3). In the OR plots, average daily PAR at the seedling level was not significantly different from the adjacent forest. However, PAR at the sapling level was 5 times greater. In the GMF plots, the average PAR was twice that of the adjacent forest at both the seedling and sapling levels. Light levels in the OR and GMF plots were not significantly different. Soil temperatures in the OR and GMF plots were similar and slightly cooler than in the adjacent forest, while in

Table 3
Impacts of road construction and management on average photosynthetically active radiation (PAR) (mml/m^2/hr) from 6 a.m. to 6 p.m. in roadside and adjacent forest plots, East Peak Road, Luquillo Experimental Forest, Puerto Rico. Mean and standard deviation of daily averages of 1–2 sensors placed at 0.1 m (low) and 1 m (high) above the ground surface in 3 different plots of each site type; n=number of sample days, L_t/L_f and H_t/H_f are ratios of mean values in treatment and adjacent forest for the low and high sensors respectively. Mean light levels for a given height in treatment and adjacent forest followed by different letter are significantly different at the 0.01% level, based on *T*-test. See text for details

Site		Low (seedling)			High (sapling)			Ratio of mean PAR	
		Mean	Std	n	Mean	Std	n	L_t/L_f	H_t/H_f
New road	Roadfill	34.8 a	13.4	19	33.0 c	13.1	19	27	11
	Forest	1.3 b	1.0	19	2.9 d	3.0	19		
Old road	Roadfill	5.3 e	4.2	22	19.8 f	10.4	22	2	5
	Forest	3.4 e	3.0	17	4.3 g	4.8	22		
Mature forest	Forest w/grass understory	9.2 h	6.6	19	18.3 j	11.0	19	2	2
	Forest	4.7 i	1.2	17	9.3 k	3.8	17		

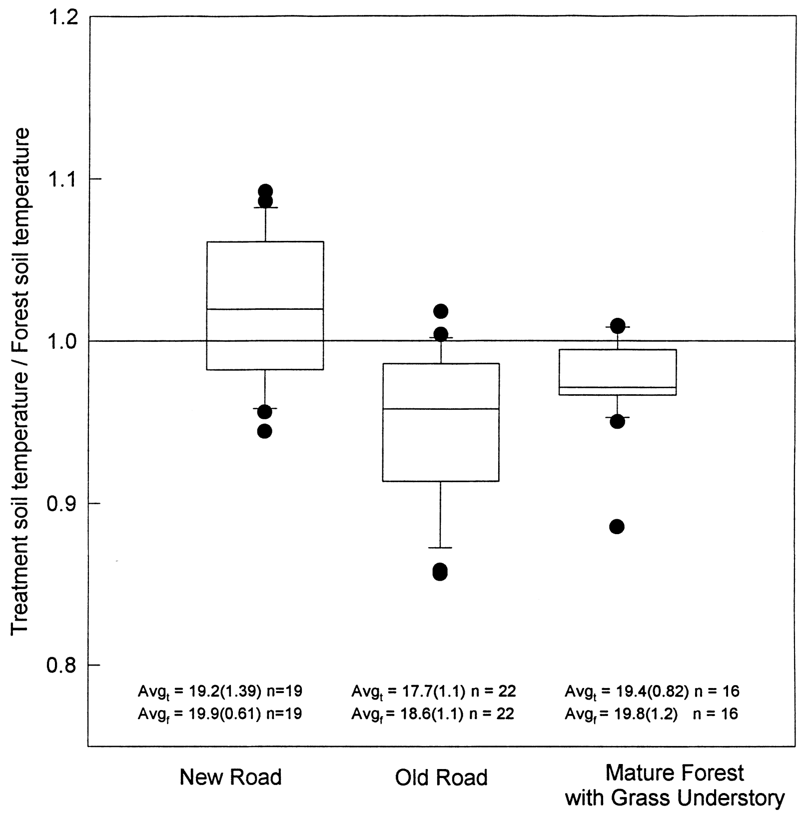

Fig. 2. Impacts of road construction and management on soils temperature along East Peak Road, Luquillo Experimental Forest, Puerto Rico. Ratio of average daily soil temperature in treatment plots to adjacent mature forest. Treatments are new roadfills, old roadfills and mature forest with a grass understory. For box plots, the outer edges of the box define the interquartile range, the center line is the median and the bars indicate 1.5 times the interquartile range. Dots lie outside 3 times the interquartile range.

the NR plots soil temperature was slightly warmer than in the adjacent forest (Fig. 2).

3.2. Structure and composition of vegetation on roadfills

Average species richness was similar between the different plot types and ranged from 9 to 14 species per m^2 (Table 4). However, the dominant life form differed between plot types. In both the new and old roadfill sites, monocots comprised about a third of the total richness. In both the MF and GMF plots, trees comprised over a third of the total richness. In the NR sites, herbs and monocots were dominant, but 26% of their area was still devoid of vegetation after 6 months (Table 5). The 35-year OR plots had similar composition to the NR sites but were almost completely covered with vegetation. A descriptive survey of these roadside areas in 1977 described a similar vegetation and suggests that the composition of these roads has not changed significantly in the past 19 years (Byer and Weaver, 1977, P.L. Weaver, personal communication 1996).

Large differences in woody species dominance were observed between OR and MF sites, but not between the GMF and cloud forest sites (Table 6). The OR sites were dominated by six early successional species: *Piper aduncum*, *Alsophila bryophila* and four Melastomataceae; *Mecranium amygdalinum*, *Miconia miribilis*, *M. faveolata* and *M. racemosa*. In contrast, MF plots were dominated by species that were generally absent from the OR: *Tabebuia rigida*, *A. bryophila*, *Ocotea spathulata*, *Clusia clusioides*, *Eugenia borinquensis* and *Prestoea montana*. Both the GMF

Table 4
Impacts of road construction and management on species richness (number of species per m^2) for plots along East Peak Road, Luquillo Experimental Forest, Puerto Rico. Monocot species richness includes grasses, sedges and rushes. The number of 1×1 m subplots is designated by *n*. Means with the same letter are not significantly different at the 0.01 level according to Tukey's range test on log transformed data. Cloud forest consists of both short cloud forest (SCF) and tall cloud forest (TCF) plots

Species richness		New road	Old road	Mature forest	Cloud forest	w/Grass understory
Total species[a]	Mean	11.20 a	9.03 b	12.03 a	14.39 A	9.61 B
	SE	0.47	0.24	0.87	1.68	0.39
Tree species	Mean	0.17 a	0.77 b	4.86 c	5.28 A	4.28 B
	SE	0.07	0.09	0.15	1.66	0.20
Monocot species	Mean	4.10 a	3.07 a	0.76 b	0.96 A	1.75 B
	SE	0.28	0.11	0.06	0.81	0.18
Count	*n*	60	108	144	72	36

[a] Bryophytes were all considered one species.

Table 5
Impacts of road construction and management on percent cover and biomass by life form of plots along East Peak Road, Luquillo Experimental Forest, Puerto Rico. Percent cover is calculated as the percent of average total cover on all plots for each plot type. The number of biomass removal plots per forest type is specified by *n*. Means with the same letter are not significantly different at the 0.01 level according to Tukey's range test on log transformed data

	New road		Old road		Mature forest		Forest with grass understory		Cloud forest
Life form	% Cover	Biomass (Mg/ha)	% Cover	Biomass (Mg/ha)	% Cover	Biomass (Mg/ha)	% Cover	Biomass (Mg/ha)	%Cover
Bare	26.09 a	NA	1.80 b	NA	16.22 a		0.60_A	NA	7.38_B
Tot. Monocot	35.06 a	1.56_A	33.59 a	3.14_A	3.90 b		38.26_A	3.45	6.32_B
Native	0.34 a	0.00_A	8.40 b	0.50_A	2.49 ab		37.16_A	3.45	5.82_B
Introduced	3.95 a	NA	15.48 b	NA	1.41 c		0.00_A	NA	0.00_A
Regional	30.76 a	NA	9.71 b	NA	0.00 c		1.10_A	NA	6.62_A
Intro and region	NA	1.56_A	NA	2.65_A	NA		NA	0.00	NA
Vine	9.37 a	0.13_A	19.04 b	0.74_A	3.33 a		4.95_A	0.49	4.89_A
Herb	20.43 a	0.40_A	17.78 a	0.86_A	2.99 b		0.10_A	0.00	0.88_A
Bryophyte	2.95 a	NA	1.21 a	NA	20.38 b		23.64_A	NA	29.12_B
Fern	1.61 a	0.00_A	11.82 b	0.57_B	6.10 b		3.41_A	0.42	5.78_A
Lycopodium	0.13 a	0.00_A	5.56 b	0.26_A	0.00 a		0.00_A	0.00	0.65_A
Bromo	0.00 a	0.00_A	0.14 a	0.00_A	2.52 b		2.57_A	0.07	3.20_A
Orchid	0.00 a	NA	0.14 a	NA	0.14 a		0.29_A	NA	0.14_A
Seedling	NA	0.03_A	NA	0.21_A	NA		NA	1.06	NA
Tree[a]	0.00 a	0.00_A	8.93 b	2.17_A	44.41 c	91.67_B	26.15_A	33.13	42.30_B
Misc[b]	NA	0.00_A	NA	2.54_B	NA		NA	1.53	NA
Total non-woody		2.09_A		8.10_B				5.95	
Total	100	2.12_A	100	10.48_A	100	91.67_B	100	40.14	100
n	60	9	108	18	144	NA	36	9	72

[a] For MF plots, tree biomass is calculated from allometric equations since these plots could not be destructively sampled.
[b] Miscellaneous (Misc.) is a combination of all the remaining vegetative material including bryophytes, live and dead monocots and above ground roots.

Table 6
Impacts of road construction and management on species composition along East Peak Road, Luquillo Experimental Forest, Puerto Rico. Importance values (%density+%basal area) for woody species (>1.5 m height) that had at least 1.0% in at least one plot. No tree species (>1.5 m height) were found in the NR plots. Mature forest is subdivided into SCF=short stature cloud forest, TCF=tall stature cloud forest, Pal=palm forest, Col=Colorado forest

Family	Species	Old road	Grass forest	Mature forest	SCF	TCF	Pal	Col
Bignoniaceae	*Tabebuia rigida* Urban	0.0	37.1	31.2	80.6	44.4	0.0	7.5
Boraginaceae	*Cordia borinquesis* Urban	0.0	0.0	1.9	0.0	0.0	0.0	8.6
Celastraceae	*Torralbasia cuneifolia* (C.Wright) Krug and Urban	0.0	2.0	0.2	0.0	0.8	0.0	0.0
Chloranthaceae	*Hedyosmum arborescens* Sw.	0.0	0.0	2.4	0.0	0.8	9.1	1.9
Compositae	*Clibadium erosum* (Sw.) DC.	9.6	0.0	0.9	0.0	0.0	4.0	0.0
Cyatheaceae	*Alsophila bryophilta* Tyron	25.3	7.4	16.2	11.7	23.2	26.8	0.0
Cyrillaceae	*Cyrilla racemiflora* L.	0.0	0.0	2.9	0.0	0.0	0.0	12.0
Euphorbiaceae	*Croton poecilanthus* Urban	0.0	0.0	1.1	0.0	0.0	0.0	5.1
Gesneriaceae	*Gesneria veridiflora*	0.0	0.0	0.9	0.0	0.0	4.4	0.0
Guttiferae	*Clusia clusiodies* (Griseb.) D'Arcy	4.9	0.0	17.9	0.0	2.0	0.0	69.2
Lauraceae	*Ocotea spathulata* Mez	0.4	75.5	21.7	35.3	36.7	1.6	8.1
Lauraceae	*Ocotea leucoxylon* (Sw.) Mez	0.0	0.0	0.9	0.0	0.0	1.3	3.3
Melestomataceae	*Calycogonium squamulosum* Cogn.	0.0	13.1	11.2	1.1	19.1	9.7	14.2
Melestomataceae	*Mercranium amygdalinum* (Dest.) C.Wright	10.2	0.5	3.6	0.0	4.1	10.6	1.3
Melestomataceae	*Miconia miribilis* (Aubl.) L.O.Wms.	89.2	0.5	2.7	0.7	5.9	2.7	0.7
Melestomataceae	*Miconia foveolata* Cogn.	23.1	1.0	1.1	0.0	2.1	2.1	0.0
Melestomataceae	*Miconia racemosa* (Aubl.) DC.	18.7	0.0	0.1	0.0	0.0	0.0	0.3
Melestomataceae	*Miconia tetrandra* (Sw.) D.Don	0.0	4.8	0.1	0.0	0.0	0.0	0.6
Meliaceae	*Guarea glabra* Vahl	0.0	0.0	0.8	0.0	0.0	0.0	3.8
Myrsinaceae	*Ardisia. Luquillensis* (Britton) Alain	0.0	1.3	1.5	2.3	1.6	0.0	2.4
Myrtaceae	*Eugenia borinquensis* Britton	2.5	15.2	14.8	35.0	18.1	3.6	2.6
Myrtaceae	*Calyptranthes krugii* Kiaersk	0.0	24.0	8.1	21.0	7.2	0.0	0.0
Myrtaceae	*Myrcia leptoclada* DC.	0.0	0.0	0.5	0.0	0.0	0.0	2.3
Palmae	*Prestoea montana* (R.Grah.) Nichols	3.2	0.0	30.3	0.0	5.9	98.8	7.6
Piperaceae	*Piper aduncum* L.	10.1	0.0	0.0	0.0	0.0	0.0	0.0
Rubiaceae	*Psychotria berteriana* DC.	0.0	2.5	5.2	0.0	2.4	20.2	1.3
Rubiaceae	*Psychotria maleorens* Urban	0.0	0.0	1.6	0.0	0.0	0.0	8.0
Sapotaceae	*Micropholis garcinifolia* Pierre	0.0	13.4	14.2	11.2	23.7	0.0	20.5
Thymelaeaceae	*Daphnopsis philippiana* Krug and Urban	0.0	0.0	4.1	0.0	1.7	0.0	17.0
Verbenaceae	*Citharexylum caudatum* L.	0.3	0.0	0.5	0.0	0.0	2.4	0.0
Other		2.5	2.0	1.4	1.3	0.5	2.5	1.6
Total (out of 200)		200	200	200	200	200	200	200

and cloud forest sites were dominated by *T. rigida*, *O. spathualata*, *E. borinquensis* and *Calypthranthes krugii*.

The only significant difference between the vegetative cover of the GMF and cloud forest areas was the abundance of monocots in the GMF plots. No non-native monocots were found in either the GMF or MF plots (Tables 6 and 7). In contrast, new roadfills were dominated (88%) by regional species and had less than 1% native grass cover. In the 35-year-old roadfills, all three groups of monocots were important with introduced species comprising 46% of the monocot cover. Of the non-native monocots, *P. purpureum* dominated cover in both the OR and NR sites, even though *M. minutiflora* had been planted on the OR roads 35 years earlier.

After 6 months there was virtually no natural tree regeneration in the NR plots. After 35 years, the total biomass in the OR sites was 11% and woody biomass was 2.6% of that found in the MF plots (Table 5, Table 8). The density of seedling and trees in the OR sites were 12% and 28% of that found in the MF sites,

Table 7
Impacts of road construction and management on average percent monocot cover per plot type along East Peak Road, Luquillo Experimental Forest, Puerto Rico. The number of 1 m^2 subplots per site is designated by *n*. Mature forest is subdivided into SCF=short stature cloud forest, TCF=tall stature cloud forest, PAL=palm forest, Col=Colorado forest

Species	New road	Old road	Mature forest	Grass forest	SCF	TCF	Pal	Col
n	**60**	**108**	**144**	**36**	**36**	**36**	**36**	**36**
Native	**0.4**	**10.2**	**4.8**	**57.7**	**18.3**	**0.0**	**0.0**	**0.7**
Isachne angustifolia Nash	0.4	10.2	4.3	46.7	17.0	0.0	0.0	0.0
Scleria canescens Boeck	0.0	0.0	0.4	11.0	1.0	0.0	0.0	0.7
Arthrostylidium sarmentosum Pilger	0.0	0.0	0.1	0.0	0.3	0.0	0.0	0.0
Regional	**35.8**	**11.8**	**2.7**	**1.7**	**4.6**	**3.0**	**3.3**	**0.3**
Ichnantus pallens (Sw) Munro	1.8	0.3	2.1	0.0	4.3	1.3	2.3	0.3
Andropogon bicornis L.	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0
Paspalum conjugatum Berg.	2.8	2.0	0.1	0.0	0.0	0.0	1.0	0.0
Kyllinga peruviana Lam.	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eleocharis elegans (H.B.K.)	3.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fuirena umbellata Rottb.	5.2	1.8	0.0	0.0	0.0	0.0	0.0	0.0
Eleocharis geniculata (L.)	9.4	0.0	0.1	1.0	0.3	0.0	0.0	0.0
Panicum laxum (Sw)	3.6	4.4	0.4	0.0	0.0	1.7	0.0	0.0
Typha domingensis (Pers.)	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Fimbristylis dichotoma (L.) Vahl.	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paspalum virginatum L.	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Eriochloa polystachya H.B.K.	3.6	0.8	0.0	0.0	0.0	0.0	0.0	0.0
Paspalum pleostachyum Doell	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cyperus surinamensis Rottb. and *Pycreus polystachyus* Rottb. P. Beauv.	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhynchospora holoschoenoides (L.C. Richard)	0.4	0.0	0.0	1.7	0.0	0.0	0.0	0.0
Exotic	**4.6**	**18.8**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**
Melinis minutiflora Beauv.[a]	0.0	6.2	0.0	0.0	0.0	0.0	0.0	0.0
Pennisetum purpureum Schumach.	4.6	12.6	0.0	0.0	0.0	0.0	0.0	0.0
Unknown	**0.8**	**0.7**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**
Dead	0.0	0.2	0.0	2.3	0.0	0.0	0.0	0.0
Total	**41.6**	**42.6**	**7.4**	**62.7**	**23.0**	**3.0**	**2.7**	**1.0**

[*] Melinis minutiflora was planted for roadside restoration in 1960.

respectively. Woody biomass in these OR areas increased with elevation, the reverse of what is observed in the MF (Weaver, 1995). Although stem densities and total biomass of the GMF plots were lower than that observed in the cloud forest plots, these differences were not statistically significant.

3.3. Spatial extent of road disturbance.

The percent cover of trees, bryophytes and ferns increased with distance from the road while the percent cover of vines and bromeliads and total species richness exhibited no apparent trend. In contrast, the percent cover of monocots decreased with distance from the road (Table 2, Fig. 3). The two introduced species dominated the first 2 m but decline to zero by 30 m. All of the regional species, expect *I. Pallens*, also decreased substantially with distance from the road. However, the occurrence of the two native monocot species increased greatly with distance from the road (Table 2, Fig. 3). *Ichnanthus pallens* increased with distance from the road in the same

Table 8
Impacts of road construction and management on vegetative structure by plot type along the East Peak Road, Luquillo Experimental Forest, Puerto Rico. Totals of individuals <1.5 m height for each plot type with standard error of the mean in parentheses. The number of 120 m^2 plots measured is specified by *n*. Means with the same letter are not significantly different at the 0.01 level according to Tukey's range test on log transformed data. Means for grass dominated plots were compared to the means for the 6 MF plots located in the cloud forest

Site type	*n*	Seedling density (ha^{-1})	Tree density (ha^{-1})	Basal area (m^2ha^{-1})	Woody biomass ($Mg\ ha^{-1}$)[a]
New road (6 months)	5	0 a	0 a	0.00a	0.00 a
Old road (35 years)	9	4185 b	3148 a	2.07a	2.17 a
		(1167)	(747)	(0.46)	(0.52)
Mature forest	12	34014 c	11257_A	37.56b	91.67 b
		(4202)	(1079)	(3.85)	(11.65)
Mature cloud	3	37236_A	13722_A	32.70A	73.05_A
Forest		(6098)	(821)	(3.02)	(13.36)
Forest with	3	28222_A	12028 b	15.79A	33.13_A
grass undestory		(3192)	(2816)	(6.67)	(15.80)

[*] Woody biomass was calculated using an equations for dicots (Weaver, 1990) and palms (Frangi and Lugo, 1985).

manner as that of the native species. This species is common throughout the LEF and was the only regionally distributed monocot growing successfully in the mature upper elevation forest. In addition, it appears to be specialized by elevation, splitting the range with the native species, *I. angustifolia*, which was found mainly above 900 m, while *I. pallens* was more common below 900 m. These observations suggests that *I. pallens* is well adapted to the LEF and may be native.

3.4. Soil Characteristics

Assuming initial, pre-disturbance conditions at all sites were similar to the MF plots measured here, soil moisture, bulk density and soil organic matter changed systematically with time since disturbance (Table 9). The GMF areas had the highest soil moisture, highest concentration of soil organic matter and the lowest bulk densities of all the plot types. The NR plots had

Table 9
Impacts of road construction and management on soil nutrient properties for the 0–10 cm horizon by plot type along the East Peak Road, Luquillo Experimental Forest, Puerto Rico. Standard error in parentheses. Different lower case letters identify statistically significant differences among sites.

	Mature tall stature (Cloud forest)	Mature tall stature (Grass understory)	Old road	New road	
				Fertilized	Unfertilized
Bulk density $g\ cm^{-2}$	0.39 a	0.24 (0.01) a	0.6 (0.04) ab	1.03	1.04 bc
% Soil moisture	0.59 (0.02) a	0.67 (0.05) b	0.45 (0.01) c	na	0.32 (0.02) d
% Soil O_2	8 (0.8) a	11 (0.65) b	15 (0.4) c	na	na
pH (KCl)	3.8 (0.04) a	3.7 (0.07) a	4.1 (0.07) a	5.3 (0.3) b	5.4 (0.4) b
C : N	22.1 (0.35) a	24 (0.4) a	19 (0.5) b	31 (3) c	34 (5.8) c
C $Mg\ ha^{-1}$	55.7 (2.4) a	57 (4.6) a	19 (1.2) b	1.2 (2.5) c	13 (1.9) c
N $Mg\ ha^{-1}$	2.5 (0.1) a	24 (0.2) a	1 (0.06) b	0.4 (0.1) c	0.5 (0.1) c
P $kg\ ha^{-1}$	1.18 (0.26) ab	0.85 (0.2) a	0.75 (0.06) b	1.3 (0.1) b	1.7 (0.14) b
Ca $kg\ ha^{-1}$	138 (22) a	114 (−11) a	529 (100) b	2152 434 c	2784 (615) c
Mg $kg\ ha^{-1}$	34 (6.6) a	20 (5.8) a	74 (14) b	84 (12) b	49 (6) b
K $kg\ ha^{-1}$	35 (2.6) a	14 (2.1) b	65 (2.3) c	1.8 (9) d	88 (11) d
Mn $kg\ ha^{-1}$	6.1 (1.5) a	3.9 (0.6) a	84 (113) b	81 (11) b	1.9 (16) b
Al $kg\ ha^{-1}$	753 (47) a	430 (24) ab	510 (58) b	524 (194) c	310 (66) c

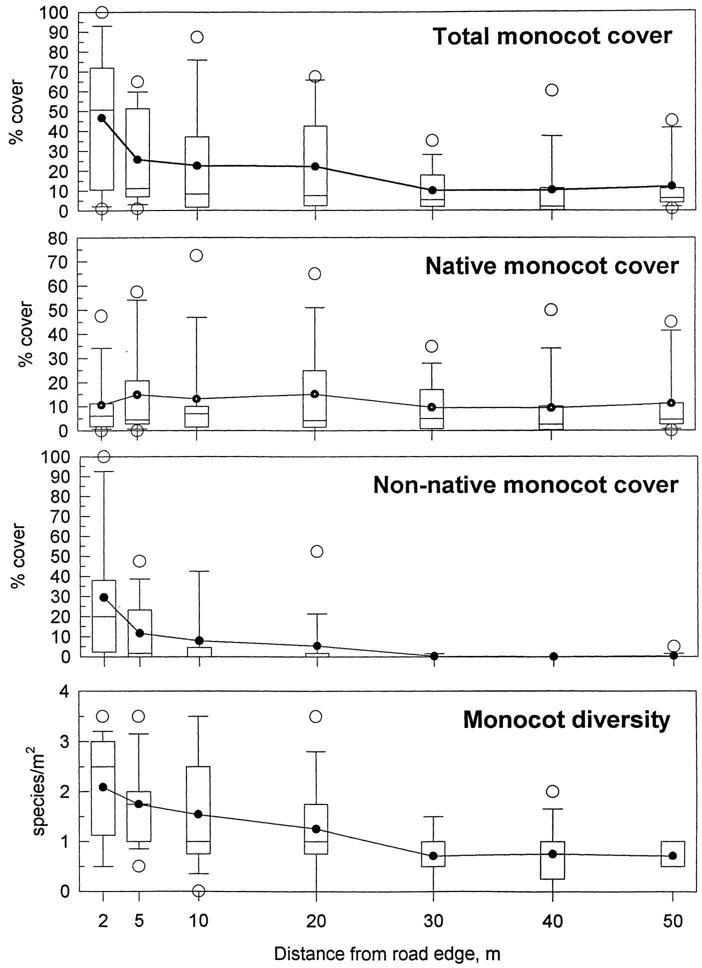

Fig. 3. Impacts of road construction and management on the average percent cover of (a) all monocots, (b) native monocots, (c) introduced monocots and (d) monocot diversity (# species/m^2) along transects by distance from the road edge, East Peak Road, Luquillo Experimental Forest, Puerto Rico. For box plots, the outer edges of the box define the interquartile range, the center line is the median and the bars indicate 1.5 times the interquartile range. Dots lie outside 3 times the interquartile range.

the lowest soil moisture, soil organic matter and total soil N, but the highest bulk densities, exchangeable Ca pool and pH. Across all plot types, total soil N was positively correlated with the soil organic matter (r^2=0.96, p<0.001, n=66) and exchangeable Ca (cmol+kg^{-1}) was positively correlated with pH (r^2=0.67, p<0.001, n=50).

Sizes of all soil nutrient pools, except K, did not vary significantly between the MF and the GMF plots. Potassium was significantly lower in the GMF plots. The cloud forest had a larger pool of exchangeable Al (Table 9) and higher concentrations of Al than all the other plot types. Exchangeable Ca, Mg, K and Mn (kg ha^{-1}) content was significantly greater in the NR and OR plots than in the cloud forest and GMF plots. There were no significant differences between unfertilized NR areas and NR areas that had been fertilized 9 months earlier. The NR had the highest C : N ratio while OR had the lowest. Total soil N (μg/g) decreased significantly from mature cloud forest to OR to NR plots but there was no difference between the cloud forest and GMF areas.

Significant declines in plant growth have been observed at O_2 concentrations $\leq$10% and $\leq$3% soil O_2 is often thought to be a critical threshold for plant survival (Stolzy, 1974 and Crawford, 1989). In all the plot types considered here average soil O_2 concentrations were always below ambient conditions (21%) (Table 9) and decreased significantly from the OR>GMF>cloud forest plots (P<0.01, F_3=80.5, n=468). The frequency of low soil oxygen concentrations also differed among sites. In the MCF plots, 62% of the measurements had O_2 concentrations $\leq$10% compared to 35% of the measurements in the GMF plots and 12% of the OR measurements. Periods of $\leq$3% soil O_2 occurred during 8% of the measurements in the MCF, 5% in the GMF plots and only 2% in the OR plots.

4. Discussion

After 35 years of continual use, the impacts of the East Peak road on forest composition and structure were generally limited to an area 5–10 m from the pavement and to those areas directly disturbed during construction (Fig. 3). However, mass wasting can be increased 5 to 8 times along sections of these roads (Larsen and Parks, 1997). In the roadfills that were created during construction large differences in soil properties and in the structure and composition of vegetation have persisted. Many factors have been considered important in contributing to the slow growth and recovery of the mature cloud forest of the LEF. These include saturated anoxic soils, impeded root respiration, reduced transpiration, low nutrient availability, graminoids that inhibit the penetration of seeds and seedlings in disturbed areas, the insufficient production and dispersal of seeds and the relatively harsh climate (Ewel, 1980 and Weaver, 1995). In addition to these factors, growth in roadfill habitats maybe further suppressed by, compacted soils, decreased soil organic matter, decreased N availability and increased monocot abundance. Comparisons between the various plot types sampled here provide additional insights into the relative importance of these factors and the strategies needed to mitigate road related impacts.

4.1. Biomass recovery

The rate of aboveground biomass accumulation observed in the OR sites, 0.3 Mg/ha/yr, is the lowest rate ever measured in the LEF and much lower than that observed following other types of disturbances in other forest types of the LEF. For comparison, the average rate of aboveground biomass accumulation during the first 5 years after a hurricane was 16.3 Mg/ha/yr in a highly damaged Tabonuco forest that is located a few kilometers from East Peak (Scatena et al., 1996). Abandoned pastures at the edge of the LEF between 100 and 150 m in elevation had accumulated 50% of the aboveground woody biomass of adjacent forests after 35 years (Aide et al., 1995). Over the same length of time, the cloud forest roadfills accumulated only 3% of the woody biomass of the MF sites. After 50 years, landslides in the Colorado forest have basal areas and biomass similar to the adjacent forest (Guariguata, 1990 and Zarin and Johnson, 1995a). After 35 years, the OR sites studied here had basal areas and biomass that were less than 6% and 3% of the MF, respectively.

The only known area in the LEF with rates of aboveground biomass accumulation that are similar to the roadfills studied here is a nearby mature cloud forest site that suffered extensive damage during the crash landing of an airplane (Weaver, 1990). During the first 18.5 years of recovery this site accumulated biomass at an average rate of 0.42 Mg/ha/yr. At the rates observed in the OR sites and at the airplane crash it could take between 200 and 300 years to accumulate a biomass comparable to the mature forest. In both of these areas monocots and herbs dominated vegetative cover and regeneration of native mature forest species was extremely slow.

In contrast to the slow recovery found on the roadfills and plane wreck, the rate of aboveground biomass recovery during the first 6 years in a nearby experimental MCF site that had been clear-cut without significant disturbance to the soil substrate was 1.79 Mg/ha/yr (Byer and Weaver, 1977). At this rate it would take approximately 50 years for the biomass to recovery to mature forest levels. This recovery period is similar to that observed in other forest types of the LEF (Guariguata, 1990; Zarin and Johnson, 1995b and Scatena, 1995a). While such linear projections should be viewed cautiously, the large difference in recovery times between MCF with and without soil disturbance indicate the important role soil resources have on the recovery of these forests.

4.2. Soils

After 35 years of soil development on the roadfills, bulk density, pH, the P pool and mineral N pools attained levels that were statistically similar to those of the mature forests. The OR areas were still drier, more oxygenated and had larger base cations pools than soils in the MF. The rate and characteristics of soil development on these roadfills was similar but slower than that observed on nearby landslide scarps in the Colorado forest (Zarin and Johnson, 1995a, b). On these landslides, base cation concentrations increased over time, exchangeable Al concentrations decreased and most soil nutrients attain concentrations that are comparable to adjacent mature forest soils within 30–55 years. In the OR site, concentrations and pools of base cations and total N were lower and exchangeable Al concentrations were higher than in the MF. The accumulation of total soil N on roadfills (16 kg/ha/yr, Table 9) was also much slower than on nearby landslides (50–100 kg/ha/yr, Zarin and Johnson, 1995a and Walker et al., 1996). Soil development in this ecosystem resembles the soil processes observed in wetland soils. Soil moisture content increases, soil oxygen availability decreases, organic matter increases and soil pH decreases over time.

While additional studies will be needed to determine process level soil nutrient dynamics in this ecosystem, the present data do indicate that after 35 years, soil nutrient dynamics and pools sizes differed significantly between the OR and the MF. The lack of significant differences in nutrient content between the fertilized and unfertilized new roads plots raises questions about the effectiveness of fertilization treatments on organic poor soils in an environment highly susceptible to leaching. The low recruitment and establishment of native species in the relatively cation rich roadfill sites suggests that cation pools alone are not limiting the establishment and growth of native vegetation in these sites. Instead, water stress may be a critical hindrance to their success. Mortality of planted seedlings appeared to increase greatly after dry periods.

4.3. Non-native monocots

After 35 years, introduced and regional monocots have successfully established along roadsides and in the airplane crash area. However, these same species have not been able to establish within the undisturbed forest, even in areas of mature forest where native grasses are abundant in the understory. A similar pattern was documented in a relatively remote boreal forest in Canada where non-native vascular plants were found along roadsides, in fire disturbed areas and on floodplains but not in the undisturbed forest (Wein et al., 1992). Nevertheless, two of the non-native species found on East Peak, *P. conjugatum* and *M. minutiflora*, have been found invading montane forests in Hawaii (Medeiros et al., 1995). Both of these species are found in the cloud forests of Maui County, but only *P. conjugatum* has been classified as a serious threat. *Melinis minutiflora*, the species planted along the East Peak road 35 years ago, is more of a problem in the seasonal submontane zone of the Hawaii Volcanoes National Park (Medeiros et al., 1995) where it and other non-native monocots have apparently increased fire frequency and consequently displaced the native ecosystem (Hughes et al., 1991 and Hughes and Vitousek, 1993).

The resistance of the upper elevation forests of the LEF to non-native monocots, that are highly successful invaders in other areas, is apparently due to edaphic and pedologic conditions. Light availability does not appear to be a limiting factor in the establishment of these monocots since average light levels were similar in the GMF plots where only native grasses were successful and OR areas where non-native monocots dominated (Table 3). Soil temperature does not appear to be a limiting factor since these non-native species have established in both new and old road sites that have temperatures that are warmer and colder respectively than the GMF sites (Fig. 2). Likewise, seed dispersal does not appear to inhibit their establishment since these same monocots have successfully established at the plane wreck site which is completely surrounded by forest and over 500 m from the nearest road. Instead, the spread of non-native monocots appears to be limited by their inability to establish or grow in the edaphic and pedologic conditions of the upper elevation forests of the LEF. In contrast, the native grasses are adapted to this soil environment and are efficient colonizers in naturally disturbed areas. However, their relatively low abundance in both the NR and OR sites suggests that the native species are less well adapted to anthropogenically disturbed areas than either the regional or non-native monocots.

4.4. Implications for management

The 35-year history of construction, maintenance and reconstruction of the East Peak Road indicates that in this environment road related disturbances are likely to be frequent. The road has required continual and expensive maintenance since it was built and construction has created disturbed areas that may take 200–300 years to attain a biomass comparable to the adjacent mature forest. While this forest is highly susceptible to soil substrate disturbance, undisturbed areas have been highly resistant to the spread of non-native species. This combination of being highly resistant to biotic invasions when intact, but having extremely long recovery periods following substrate disturbance, highlights the importance of minimizing physical disturbance in these unique ecosystems.

The planting of barren roadside areas with *M. minutiflora* in 1960 appears to have been successful in providing ground cover and in reducing soil erosion. Nevertheless, after 35 years these planted areas have had the lowest rate of biomass accumulation ever recorded in the LEF. It has been suggested that the formation of a dense cover of monocots and ferns can prevent seedling establishment in disturbed cloud forests (Scowcroft and Hobdy, 1987; Weaver, 1990 and Byer and Weaver, 1977). The low seedling density and absence of mature forest species in the 35-year-old roadside areas indicates this may be occurring along East Peak. However, the presence of seedlings in the grass dominated forest sites suggests that grass induced physical barriers may not be the only factor limiting seedling establishment in these areas. Establishment of the native vegetation appears to be most successful in soils with low bulk density, high soil moisture and high organic matter content. Moreover, because the native forest is adapted to acidic, water logged soils that have low levels of base cations and because non-native monocots are inhibited by these soil characteristics, fertilization treatments or plantings in dry, organic poor soils may not be an appropriate restoration technique for disturbed areas in this environment. Instead restoration efforts should focus on the development of edaphic and pedologic conditions that are similar to those found in the mature forest.

The development of soils and vegetation on the East Peak roadfills over the past 35 years indicates that in upper elevation wet environments (areas not prone to fires) the planting of monocots, or just allowing them to grow, is one method of hastening the development of edaphic and pedologic conditions characteristic of the mature forests. However, once the initial edaphic conditions are established, which may take between 19 and 35 years, removal of the dense monocot cover and the planting of mature forest species may be an effective way to promote the establishment of natural vegetation. Given the history of road construction and revegetation that has been described here, it is apparent that regardless of the restoration techniques used, recovery of these ecosystems will be extremely slow and costly. Therefore road building and disturbances to the soil resources of these unique ecosystems should be minimized.

Acknowledgements

This research was supported by the International Institute of Tropical Forestry (IITF), U.S.D.A. Forest Service and the Luquillo Long-Term Ecological Research Program. Additional support was provided by a grant from the A.W. Mellon Foundation to W. Silver and from BSR-8811902 from the NSF to TED and IITF as part of the Long Term Ecological Research Program. Special thanks to IITF lab for analyses, Carlos Estrada, Juan Ramirez and S. Moya for field identification, Frank Axelrod of UPR-Rio Piedras Herbarium for identification and confirmation and C. Torrens, S. Moya, A. Garcia and D. Bradbury for field assistance.

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