

Luquillo Forest Dynamics Plot, Puerto Rico, United States

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Site Location, Administration, and Scientific Infrastructure

The 16-ha Luquillo Forest Dynamics Plot (LFDP) is located near El Verde Field Station in the Luquillo Mountains of northeastern Puerto Rico, approximately 35 km southeast of San Juan (fig. 32.1). The field station and LFDP are within the Luquillo Experimental Forest (established in 1956), which is coterminous with the Caribbean National Forest (CNF). The CNF covers 11,330 ha, of which 4630 ha are designated for noncommercial uses including research (Brown et al. 1983). The CNF was proclaimed a forest reserve in 1903 and has been administered by the U.S. Department of Agriculture Forest Service since 1917 (Brown et al. 1983). El Verde Field Station is administered by the Institute for Tropical Ecosystem Studies, University of Puerto Rico, and has laboratories and housing for visiting researchers.

A large number of smaller tree demographic plots located in and around the Luquillo Mountains are regularly censused by the International Institute of Tropical Forestry (USDA Forest Service). These include eight 0.4-ha plots set up in 1945–46 that are remeasured every 10 years. There are also 83 circular (10-m diameter) plots that were set up in 1987 and are censused every 5 years (a subset of plots are assessed every year for seedlings). In forested areas in other locations in Puerto Rico, there are 50 circular plots of various diameters that are remeasured every 10 years. The Smithsonian Institution's Monitoring and Assessment of Biodiversity Program set up a 1-ha plot in Puerto Rico in 1988.

Climate

The climate is classified as tropical montane in Walsh's (1996) tropical climate system, and as subtropical wet in the Holdridge life zone system (Ewel and Whitmore 1973). Annual rainfall at El Verde averages just over 3500 mm/year (1975–99). On average, no month has less than 200 mm of rain, although a drier season occurs from January through April. Unusually heavy rainfall events occur about

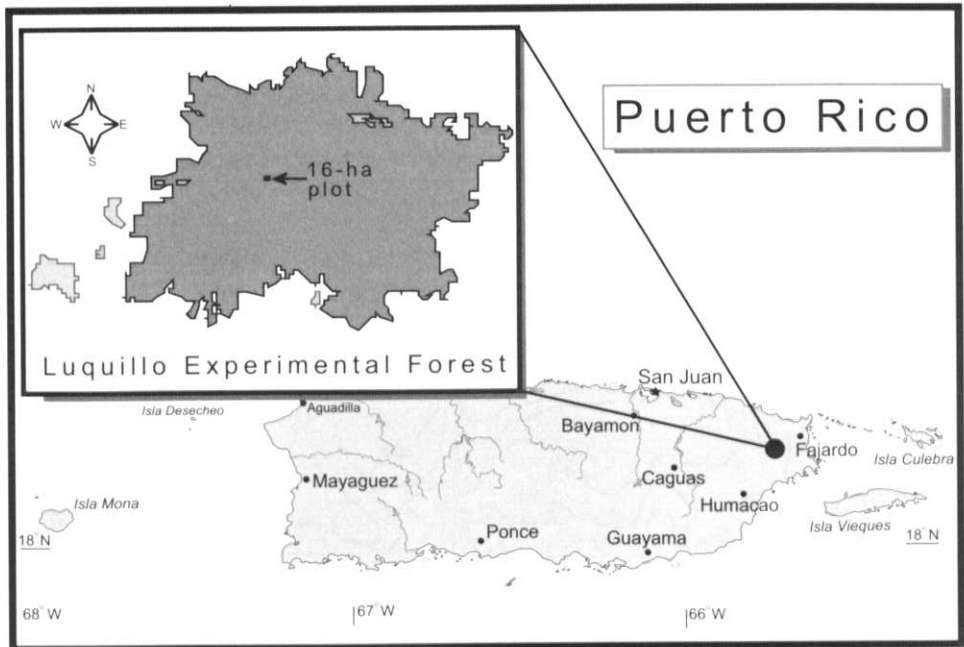


Fig. 32.1. Location of the 16-ha Luquillo Forest Dynamics Plot.

once every 6 years (Fred Scatena personal communication). The highest rainfall recorded at El Verde between 1975 and 2001 (370 mm in less than 12 hours) fell on 17 April 1997. There are also severe droughts, such as in 1994, when less than 70% of the average annual rain fell, and many small streams in the forest stopped flowing entirely for 2 months. Rainfall extremes are not closely linked to the El Niño cycle. Daily average maximum air temperature is 25.2°C, minimum is 20.5°C, and average is 22.8°C (Brown et al. 1983; and Luquillo LTER Internet Site <http://luq.lternet.edu>). See also table 32.1.

Mean annual wind speed above the canopy is 4.1 km/hr (Waide and Reagan 1996). Monthly averages at Catalina, the most comparable site in Puerto Rico (5.6 km from El Verde, same exposure) with appropriate data, are 2–6 km/hr (Brown et al. 1983).

Average total daily radiation at Bisley (latitude 18.5°18', longitude 65.5°44') was 155 \pm 59 W/m² (mean for 1993 - 02). These data were collected by the USDA Forest Service (Luquillo LTER Internet Site <http://luq.lternet.edu>). The site is also subject to tropical storms and hurricanes (see below).

Table 32.1. Luquillo Climate Data

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total/ Averages
Rain (mm)	233	227	203	232	351	242	307	361	350	288	401	353	3548
ADTMx (°C)	23.0	23.2	24.2	25.3	26.0	27.1	26.7	26.8	26.5	25.8	24.4	23.4	25.2
ADTMn (°C)	18.8	18.7	19.0	19.7	20.7	21.7	21.9	22.0	21.7	21.2	20.6	19.6	20.5

Notes: Raw data are on the Luquillo website for 1975–1999 (<http://luq.lternet.edu>).

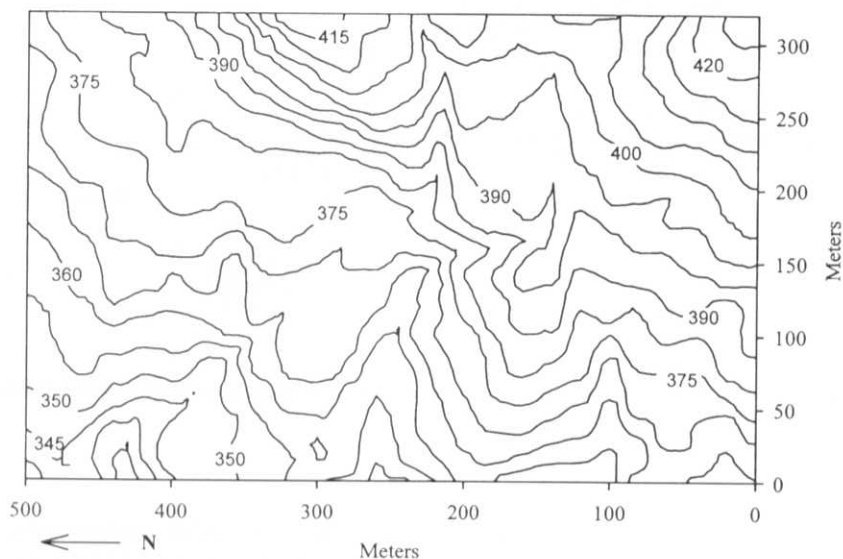


Fig. 32.2. Topographic map of the 16-ha Luquillo Forest Dynamics Plot with 5-m contour intervals.

Topography and Soil

Topography on the LFDPlot has northwest-running drainages producing steep northeast and southwest-facing slopes, with an elevation across the plot of 333–428 m above sea level (figs. 32.2 and 32.3). The mean slope of the plot is 17% but ranges from 3 to 60%. Soils were formed in residual volcanic ash that fell in the ocean to form volcanoclastic sandstones and siltstones, which were subsequently uplifted (E. Scatena personal communication). Soils are dominated by old, deeply weathered kaolinitic Oxisols (zarzal) and Ultisols (cristal), and young, less-developed Entisols (coloso and fluvaquents) and Inceptisols (prieto) in stream channels. Zarzal, cristal, and prieto are deep clay soils, while coloso and fluvaquents are formed from alluvium in the stream channels (Soil Survey Staff 1995).

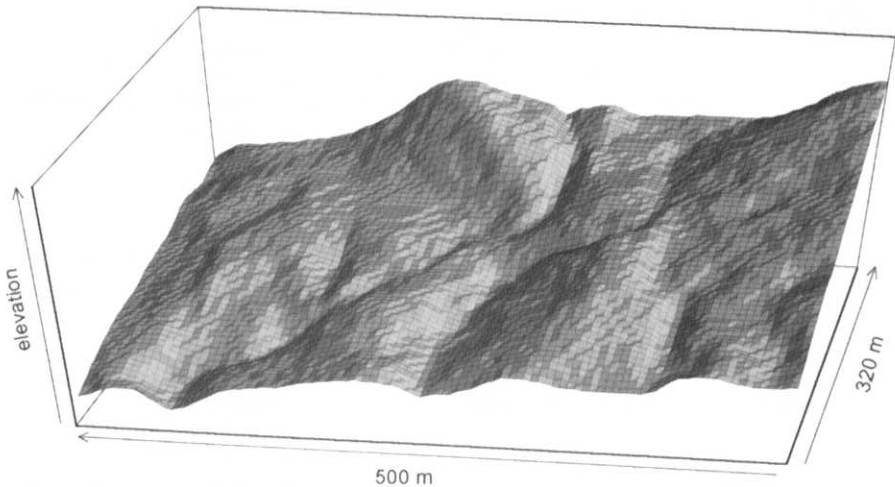


Fig. 32.3. Perspective map of the 16-ha Luquillo Forest Dynamics Plot. Modified from Willig et al. (1996), © 1996 by the Association for Tropical Biology. Reprinted with permission.

The plot lies mainly within the 265-ha Quebrada Sonadora Catchment, which exports 410 kg/ha/year of dissolved solids (the sum of inorganic ions excluding silica and bicarbonate, for which data are not available), calculated from data of Schaefer et al. (2000). The closest catchment (within 5 km) for which data on suspended solids are available is the 1782-ha Quebrada Mameyes, which exports 1000 kg/ha/year on average (USGS 1993–98). The flux of suspended solids is sensitive to short-term variations in stream flow. During 1998, the flux was eight times greater than the usual annual rate, mainly as a result of the greater stream flows during Hurricane Georges. Based on a surface soil bulk density of 0.8 g/cm^3 (Soil Survey Staff 1995) and excluding dissolved solid exports of atmospheric origin, the sum of the average exports is equivalent to a soil erosion rate of approximately 0.14 mm/year (the inclusion of silica and bicarbonate fluxes would increase that estimate).

Forest Type and Characteristics

Within the Luquillo Experimental Forest, there are four forest types: tabonuco, colorado, palm-brake, and dwarf forest. These forest types are associated with different soil types and roughly stratified by elevation (Brown et al. 1983). Dwarf (cloud) forest grows on peaks and ridges above 750 m above sea level. Colorado forest grows above the average cloud condensation level (600 m asl), while tabonuco

Table 32.2. Luquillo Plot Census History

Census	Dates	Number of Trees (≥ 1 cm dbh)	Number of Species (≥ 1 cm dbh)	Number of Trees (≥ 10 cm dbh)	Number of Species (≥ 10 cm dbh)
First	August 1990–September 1993	85,607	145	12,917	89
Second	November 1994–October 1996	67,170	138	13,988	86

Notes: Third census was completed in April 2002 (data available for two censuses); the next census is expected to begin in 2005.

We first tagged all trees ≥ 10 cm dbh in the whole plot and then tagged all trees ≥ 1 cm dbh. These data have been combined to comprise the first census. For the second census all stems ≥ 1 cm dbh were measured in the same census.

We measure *Prestoea acuminata* (Palmae) as soon as its youngest leaf arises from the plant at a height of 130 cm from the ground. For the data in this table, however, only those *P. acuminata* that had a “woody bole” at 130 cm from the ground at the time of the census are included.

forest is found below 600 m asl and is best developed on low, protected, well-drained ridges. Palm-brake forest is interspersed within the tabonuco, colorado, and dwarf forests and is limited to areas of steep slopes, poor drainage, and saturated soils (Brown et al. 1983). The 16-ha Luquillo Forest Dynamics Plot lies within the tabonuco forest, a forest named after the dominant tree, *Dacryodes excelsa* Vahl (Burseraceae). Mean canopy height is about 20 m, with the tallest trees nearing 35 m. Canopy height is lower, and forest structure broken, in the years after hurricanes (chap. 13). Few trees in the LFDP exceed 1 m dbh. *Buchenavia tetraphylla* (formerly *B. capitata*) (Aubl.) R. A. Howard (Combretaceae) is one of the few deciduous species in the forest; it drops its leaves all at once and flowers soon afterward (Sastre-de-Jesús 1979). See tables 32.2–32.7 for census data and rankings.

Species composition varies markedly across the plot, depending on land use history (Thompson et al. 2002). *Dacryodes excelsa* characterizes less disturbed areas, while *Casearia arborea* (Rich.) Urb. (Flacourtiaceae) dominates more disturbed areas. The midstory palm, *Prestoea acuminata* (Willd.) H.E. Moore (Palmae), is common in poorly drained areas, including stream channels, and on slopes.

Canopy heights recorded at 6565 grid points (every 5 m) between April 1999 and March 2000 showed 19.1% of points with a canopy height of ≤ 2 m, 33.8% ≤ 10 m, and 47.1% > 10 m. The relatively high percentage of low canopy is a result of the damage caused by Hurricane Georges in September 1998.

Total annual litter fall near the LFDP was 568.25 g/m² (mean for 1990–2001), comprised of leaves 419.7 g/m², wood 55.3 g/m², and miscellaneous 93.19 g/m² (Mathew Warren unpublished data).

Table 32.3. Luquillo Summary Tally

Size Class (cm dbh)	Mean per Hectare							16-ha Plot				
	BA	<i>N</i>	<i>S</i>	<i>G</i>	<i>F</i>	<i>H'</i>	α	<i>S</i>	<i>G</i>	<i>F</i>	<i>H'</i>	α
≥1	38.3	4171.7	73.3	58	33.6	1.45	13.54	138	102	47	1.41	16.60
≥10	34.4	875.7	42.1	37	24.0	1.01	9.27	86	71	39	1.13	12.20
≥30	18.3	109.7	22.2	21	15.5	1.08	8.78	57	49	29	1.29	11.30
≥60	5.3	11.4	5.6	5.5	5.5	0.64	5.76*	23	22	19	1.01	7.05

* Does not include three 1-ha plots with fewer than nine species, each species with only one individual.

Notes: BA represents basal area in m², *N* is the number of individual trees, *S* is number of species, *G* is number of genera, *F* is number of families, *H'* is Shannon–Wiener diversity index using log₁₀, and α is Fisher's α . Basal area includes all multiple stems for each individual. Individuals are counted using their largest stem. Mean values are based on 15 nonoverlapping, 1-ha plots. Data are from the second census. 8 individuals were not identified to species or morphospecies.

Table 32.4. Luquillo Rankings by Family

Rank	Family	Basal Area		Family	Trees	%	Family	Species
		(m ²)	%					
1	Palmae	106.0	17.3	Rubiaceae	22,874	34.1	Rubiaceae	16
2	Burseraceae	83.6	13.7	Palmae	5,896	8.8	Melastomataceae	8
3	Flacourtiaceae	50.5	8.3	Flacourtiaceae	5,889	8.8	Lauraceae	8
4	Combretaceae	44.8	7.3	Cecropiaceae	4,845	7.2	Flacourtiaceae	7
5	Sapotaceae	40.3	6.6	Elaeocarpaceae	3,215	4.8	Piperaceae	7
6	Leguminosae	39.8	6.5	Araliaceae	2,884	4.3	Euphorbiaceae	7
7	Meliaceae	36.2	5.9	Piperaceae	2,255	3.4	Myrtaceae	7
8	Cecropiaceae	31.6	5.2	Burseraceae	2,208	3.3	Leguminosae	6
9	Euphorbiaceae	30.3	5.0	Leguminosae	1,800	2.7	Moraceae	4
10	Elaeocarpaceae	21.9	3.6	Euphorbiaceae	1,755	2.6	Meliaceae	4
							Sapotaceae	4
							Solanaceae	4

Notes: The top 10 families for trees ≥ 1 cm dbh are ranked in terms of basal area, number of individual trees, and number of species, with the percentage of trees in the plot. Data are from the second census.

Fauna

At El Verde, the diversity of birds (31 resident species, density 33 individuals/ha, Waide 1996) and mammals (13 native species, all of which are bats) is low compared to mainland tropical forests (Reagan and Waide 1996). The Puerto Rican Tody (*Todus mexicanus*), for example, is the only understory insectivorous bird. This low diversity of homeothermic vertebrates is compensated by a high density of frogs (11 species of *Eleutherodactylus*), with the most common, *E. coqui*, at a density of 25,570 individuals/ha (Stewart and Woolbright 1996), and lizards

Table 32.5. Luquillo Rankings by Genus

Rank	Genus	Basal			Genus	Trees	% Trees	Genus	Species
		Area (m ²)	% BA	% Trees					
1	<i>Prestoea</i> (Palmae)	100.8	16.5	8.7	<i>Palicourea</i> (Rubiaceae)	13,190	19.6	<i>Piper</i> (Piperaceae)	7
2	<i>Dacryodes</i> (Burseraceae)	78.3	12.8	2.5	<i>Psychotria</i> (Rubiaceae)	8,684	12.9	<i>Ocotea</i> (Lauraceae)	6
3	<i>Buchenavia</i> (Combretaceae)	44.8	7.3	0.28	<i>Prestoea</i> (Palmae)	5,853	8.7	<i>Miconia</i> (Melastomataceae)	6
4	<i>Manilkara</i> (Sapotaceae)	39.8	6.5	2.46	<i>Casearia</i> (Flacourtiaceae)	5,295	7.9	<i>Psychotria</i> (Rubiaceae)	4
5	<i>Guarea</i> (Meliaceae)	34.2	5.6	1.38	<i>Cecropia</i> (Cecropiaceae)	4,848	7.2	<i>Myrcia</i> (Myrtaceae)	3
6	<i>Cecropia</i> (Cecropiaceae)	31.6	5.2	7.2	<i>Sloanea</i> (Elaeocarpaceae)	3,215	4.8	<i>Eugenia</i> (Myrtaceae)	3
7	<i>Inga</i> (Leguminosae)	30.9	5.1	2.19	<i>Schefflera</i> (Araliaceae)	2,665	4.0	<i>Coccoloba</i> (Malvaceae)	3
8	<i>Casearia</i> (Flacourtiaceae)	29.5	4.8	7.9	<i>Piper</i> (Piperaceae)	2,255	3.4	<i>Casearia</i> (Flacourtiaceae)	3
9	<i>Sloanea</i> (Elaeocarpaceae)	21.9	3.6	4.8	<i>Manilkara</i> (Sapotaceae)	1,650	2.5	<i>Solanum</i> (Solanaceae)	2
10	<i>Homalium</i> (Flacourtiaceae)	17.9	2.9	0.4	<i>Dacryodes</i> (Burseraceae)	1,649	2.5	<i>Palicourea</i> (Rubiaceae)	2
								<i>Micropholis</i> (Sapotaceae)	2
								<i>Inga</i> (Leguminosae)	2
								<i>Guarea</i> (Meliaceae)	2
								<i>Ficus</i> (Moraceae)	2
								<i>Cordia</i> (Boraginaceae)	2
								<i>Citharexylum</i> (Verbenaceae)	2
								<i>Byrsonima</i> (Malpighiaceae)	2

Notes: The top 10 tree genera for trees ≥ 1 cm dbh are ranked by basal area, number of individual trees, and number of species with the percentage of trees in the plot. Data are from the second census.

(five *Anolis* species), with the most common three species at a density of 25,000 individuals/ha (Reagan 1996). Of consequence for forest dynamics, mammalian herbivores (e.g., deer, tapir, agouti) are absent from the LFDP. The black rat (*Rattus rattus*) and the mongoose (*Herpestes auropunctatus*) are introduced species and the only mammals, other than the native bats, that inhabit the forest.

Table 32.6. Luquillo Rankings by Species

Rank	Species	No. Trees	% Trees	Species	Basal Area (m ²)	% BA	% Trees
1	<i>Palicourea riparia</i> (Rubiaceae)	13,186	19.63	<i>Prestoea acuminata</i> (Palmae)	100.8	16.49	8.71
2	<i>Psychotria berteriana</i> (Rubiaceae)	6,416	9.55	<i>Dacryodes excelsa</i> (Burseraceae)	78.3	12.81	2.45
3	<i>Prestoea acuminata</i> (Palmae)	5,853	8.71	<i>Buchenavia tetraphylla</i> (Combretaceae)	44.8	7.33	0.28
4	<i>Cecropia schreberiana</i> (Cecropiaceae)	4,848	7.22	<i>Manilkara bidentata</i> (Sapotaceae)	39.8	6.50	2.46
5	<i>Casearia arborea</i> (Flacourtiaceae)	3,477	5.18	<i>Guarea guidonia</i> (Meliaceae)	33.5	5.47	0.86
6	<i>Sloanea berteriana</i> (Elaeocarpaceae)	3,215	4.79	<i>Cecropia schreberiana</i> (Cecropiaceae)	31.6	5.16	7.22
7	<i>Schefflera morototoni</i> (Araliaceae)	2,665	3.97	<i>Inga laurina</i> (Leguminosae)	27.9	4.57	1.90
8	<i>Psychotria brachiata</i> (Rubiaceae)	2,236	3.33	<i>Casearia arborea</i> (Flacourtiaceae)	23.5	3.85	5.18
9	<i>Piper glabrescens</i> (Piperaceae)	2,028	3.02	<i>Sloanea berteriana</i> (Elaeocarpaceae)	21.9	3.58	4.79
10	<i>Casearia sylvestris</i> (Flacourtiaceae)	1,809	2.69	<i>Homalium racemosum</i> (Flacourtiaceae)	17.9	2.93	0.39

Notes: The top 10 tree species for trees ≥ 1 cm dbh are ranked by number and percentage of trees and basal area.

Table 32.7. Luquillo Tree Demographic Dynamics

Size Class (cm dbh)	Growth Rate (mm/yr)	Mortality Rate (%/yr)	Recruitment Rate (%/yr)	BA Losses (m ² /ha/yr)	BA Gains (m ² /ha/yr)
1–9.9*	1.6	14.05	5.25	0.43	0.031
10–29.9**	3.4	5.0	4.78	0.71	1.85
≥ 30 **	2.7	2.4	2.52	0.23	2.99
<i>P. acuminata</i> * 1–9.9		1.78	11.01	0.003	1.78
<i>P. acuminata</i> ** 10–29.9		1.1	6.14	.006	0.12

Notes: Table shows growth, mortality, and recruitment rates for three size classes of trees and mortality and recruitment rates for *Prestoea acuminata* between the first (1990) and second census (1996). The data include the effects of Hurricane Hugo (September 1989) on recruitment, mortality, and growth rates.

*Calculated between 1993 and 1996, mean time between censuses of each 20 × 20m quadrat was 2.91 years.

**Calculated between 1990 and 1996, mean time between censuses of each 20 × 20m quadrat was 4.46 years.

Growth rate includes all live stems on all plants, including those stems with negative growth.

Basal area losses and gains include all live stems on all plants, including those stems with less than 5% negative growth.

Natural Disturbances

The average return interval of severe hurricanes to the area is 50–60 years (Scatena and Larsen 1991), but the forest was damaged by severe hurricanes in both 1989 (Hugo) and 1998 (Georges). Local topography and local exposure to winds influence the extent of wind damage (Boose et al. 1994). Stands on exposed sites are continually trimmed by the trade winds and as a result they suffer proportionately less damage during major storms than do areas that are usually more sheltered. Individual tree damage varies according to species (Zimmerman et al. 1994). Treefall gaps that are not associated with major storms tend to be fewer and smaller than in some other tropical forests (chap. 13). Landslides also cause natural disturbance. Landslides affect on average 1% of the forest area at any time and are mainly related to heavy rainfall events and the reshaping of stream channels.

Human Disturbance

The LFDP has a varied land use history but has been covered by forest since the 1930s (cf. Foster et al. 1999). Before then, 1.16 ha of the 16-ha plot was farmed; 9.6 ha was variably clearcut, then allowed to regrow but planted in places with coffee or fruit trees; and 5.24 ha has always been in forest but was selectively logged (Thompson et al. 2002). A small area (320 m²) was clearcut in the 1960s as part of an experiment (Odum and Pigeon 1970). In addition, the introduction of the black rat and mongoose to the forest is an indirect form of human disturbance.

Plot Size and Location

LFDP is 16-ha, 500 × 320 m plot, the long axis lies north-south. The southwest corner is located at 18° 19' 26" N and 65° 49' 3" W.

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