A relict population of *Fagus grandifolia* var. *mexicana* at the Acatlan Volcano, Mexico: structure, litterfall, phenology and dendroecology

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Abstract

Aim *Fagus grandifolia* var. *mexicana* (Martinez) Little has an extraordinarily restricted distribution in the Mexican montane cloud forests. Isolated *Fagus* (beech) populations have been recorded in less than 10 small areas (2–40 ha) in the eastern Sierra Madre at altitudes from 1400 to 2000 m. The objectives were to determine tree and seedling age, forest structure, phenology, litterfall patterns and the relationship between mast and climatic variables.

Location We report on three *Fagus* stands at the Acatlan Volcano, Veracruz, Mexico.

Methods Changes in forest cover were determined using aerial photographs. Within each stand, basal area, density and tree species composition were determined in a 0.1-ha band transect. Additionally, litterfall production was quantified and phenophases were recorded monthly over a 3-year period, and 60 tree cores were collected to determine age distribution and tree-ring growth.

Results The forest was atypical in several respects. Fagus was the only dominant tree species in the crater stand, although in the rim and at the top of the volcano it was codominant with other tree species. Juveniles occurred only on the rim, but there was a seedling bank in the crater. Although forest cover in the area increased between 1968 and 1993, the *Fagus* stands did not change in size. Leaf production peaked in March and April, and leaf fall occurred from October through February. Litterfall production was the highest in November. During mast years, flowering started in February and between mast events there were no flowers or fruits. Minimum temperatures were highly correlated with *Fagus* litterfall and leaf fall. Seedlings ranged in age from 2 to 18 years and were 13–60 cm tall. Tree cores ranged from 76 to 120 years, but trees were older than the core samples.

Main conclusions Although beech is considered a gap regeneration species that reaches the canopy after alternating periods of release and suppression, the trees in the crater were released when less than 1.5 m tall and have suffered few periods of suppression since. The results indicate that the crater stand was established after a severe disturbance destroyed the existing forest. We conclude that the relict beech population should be able to maintain itself, if not severely disturbed by humans or by climatic changes related to global warming.

Keywords
Beech, cloud forest, dendroecology, *Fagus grandifolia*, litterfall, Mexico, phenology, rare species.

Resumen

Objetivo *Fagus grandifolia* var. *mexicana* (Martinez) Little tiene una distribución extraordinariamente restringida en los bosques de niebla de México. Se han registrado poblaciones

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de *Fagus* en áreas pequeñas (2–40 ha) en la Sierra Madre Oriental entre 1400 y 2000 m de altitud. Los objetivos fueron determinar la edad de árboles y plántulas, la estructura, fenología, producción de hojarasca en relación a años semilleros y variables climáticas.

Localidad Este estudio se realizó en tres rodales de *Fagus* en el volcán de Acatlán, Veracruz, México.

Métodos Los cambios en cobertura forestal se determinaron a partir de fotografías aéreas. En cada rodal, área basal, densidad y composición específica arbórea se determinaron en transectos de banda de 0.1 ha, la hojarasca se cuantificó y las fenofases se registraron mensualmente durante tres años. Sesenta virutas de árboles se colectaron para determinar la distribución de edades y el crecimiento radial.

Resultados Este bosque es atípico en varios aspectos. *Fagus* fue la única especie dominante en el rodal del cráter, aunque en el borde y en la cima del volcán fue codominante con otras especies arbóreas. Los juveniles ocurrieron sólo en el borde pero se detectó un banco de plántulas dentro del cráter. La cobertura forestal total en el área aumentó de 1968 a 1993, pero los rodales de *Fagus* mantuvieron la misma superficie. La producción foliar tuvo un pico en Marzo y Abril, la caída de hojas ocurrió de Octubre a Febrero, y la producción de hojarasca fue mayor en Noviembre. Durante los años semilleros, la floración se inició en Febrero y entre años semilleros no hubo flores o frutos. Las temperaturas mínimas estuvieron altamente correlacionadas con producción de hojarasca y caída de hojas de *Fagus*. Las plántulas tuvieron entre 2 y 18 años de edad y alcanzaron alturas entre 13 y 60 cm. Las virutas de los árboles tuvieron de 76 a 120 años pero los árboles fueron más viejos que las virutas.

Conclusiones Aunque *Fagus* se regenera en aberturas y alcanza el dosel después de periodos de liberación y supresión, los árboles en el cráter fueron liberados con menos de 1.5 m de altura y sufrieron pocos periodos de supresión. Los resultados indican que el rodal del cráter se estableció después de una perturbación severa que destruyó el bosque. Concluimos que esta población relicto puede mantenerse si no es fuertemente perturbada por humanos o por cambios climáticos producto del calentamiento global.

INTRODUCTION

Fagus grandifolia var. *mexicana* (Martinez) Little (Little, 1965) has an extraordinarily restricted distribution in the Mexican montane cloud forests. Although *Fagus* is locally superabundant, it is rare because it occurs in very specialized habitats that are geographically restricted. This situation makes it extremely vulnerable to local stochastic events or intentional habitat destruction (Meffe & Carroll, 1994). It has been recorded in less than 10 small areas (2–40 ha) on the eastern Sierra Madre at altitudes from 1400 to 2000 m in the Mexican states of Tamaulipas, San Luis Potosi, Hidalgo, Puebla and Veracruz (Miranda & Sharp, 1950; Little, 1965; Puig & Bracho, 1987; Hernández *et al.*, 1951; Fox & Sharp, 1954; Williams-Linera, Pérez & Tolome, 1996). A reported location in the state of Puebla (Fox & Sharp, 1954) has already been deforested and *Fagus* is apparently locally extinct.

The isolated populations of *Fagus* in Mexico are restricted to north or north-eastern facing slopes that always experience lesser total insolation and are much more humid than the south-facing slopes of the same region. Mexican *Fagus* populations are relicts of a more extended distribution during the late Miocene (Graham, 1973). At present, the species probably

grows at its ecological limits of maximum warmth and requires microhabitats with very high humidity. Because of shade tolerance, beech trees may be the best competitors in this microenvironment; they are the dominant canopy species in these southernmost beech stands. Outside of these microhabitats, in the warmer Mexican montane forests, competition with other temperate and tropical elements could be the limiting factor.

In the northernmost part of its distribution, *Fagus grandifolia* is still spreading (e.g. Davis, 1981; Bennett, 1985; Davis *et al.*, 1986). The distribution range of *Fagus* is controlled by the rate at which seeds can be dispersed to new habitats, and the ability of invading seedlings to survive harsh climatic conditions (e.g. Davis, 1981; Davis *et al.*, 1986; but see Webb, 1987). However, *Fagus* populations at the southernmost limit of the distribution are probably no longer able to spread further. Chance and shade tolerance, rather than seed availability and seedling competition, may be the factors that permit the persistence of relict *Fagus* populations until now. Although global warming will eventually have a negative effect on the population persistence, habitat destruction is the major threat to the very few remaining *Fagus* populations in Mexico.

Beech forest dynamics have been widely studied at a global scale (see Peters, 1997). In the eastern United States, *Fagus grandifolia* Ehrh. has been studied in east Texas (Glitzenstein, Harcombe & Streng, 1986), North Florida (Batista, Platt & Macchiavelli, 1998), Louisiana (White, 1987), Hubbard Brook, New Hampshire (Poage & Peart, 1993), the Adirondack Mountains of New York (Canham, 1988, 1990), up to the Upper Great Lakes region (Brewer & Merrit, 1978; Poulson & Platt, 1996). Related species on other continents have been studied, e.g. *Fagus sylvatica* L. in Europe (Nilsson, 1985; Peltier *et al.*, 1997), *F. lucida* Rehd. et E. H. Wilson and *F. hayatae* Palib. in China (Cao, 1995), and *F. japonica* Maxim.–*F. crenata* Blume in Japan (Peters & Ohkubo, 1990). In Mexico, only a few descriptive studies have focused on beech forest floristic composition, but none have examined population ecology and dynamics (but see Peters, 1995; Alvarez-Aquino & Williams-Linera, 2001).

In this paper we report on a *Fagus* monodominant population growing inside the crater of the Acatlan Volcano, and *Fagus* codominant stands at the rim and top of the same volcano. Litterfall production and phenology were studied to learn how beech responded to local climate, and as an indicator of how the population is performing in relation to other montane forests in Mexico and beech forests in the eastern United States and other countries. Under warmer environmental conditions we expected phenological changes, such as leaf emergence and flowering, to occur earlier than in temperate regions, leading to enhanced relative growth rates. We also used dendroecological techniques to provide information that is otherwise unavailable when a forest has not been studied in the past. A ring-width chronology was established to provide data about the history of the plant community.

This study was designed to answer ecological questions about the establishment, permanence and spread of *Fagus* at the Acatlan Volcano. The specific objectives were to determine the age of trees and seedlings, forest structure, phenology, litterfall patterns and the relationship between mast and climatic variables.

METHODS

Study site

The study sites are in the Acatlan Volcano (19°41' N, 96°51' W) in the eastern Sierra Madre, Veracruz (Fig. 1). The volcano has a conical shape with very steep slopes and it is isolated in an almost completely deforested valley. *Fagus* trees grow inside the crater, along the rim and at the top of the volcano. The altitude inside the crater is 1840 m and 1900 m at the top of the volcano. The soil has been classified as Andept. The texture is sandy clay loam, with high cation exchange capacity and high organic matter content. Soil characteristics inside the crater and at the top are similar. The nearest meteorological station is representative of the climate at the volcano since it is located in the town of Acatlan, at 1700 m of elevation and 1 km away from the volcano. There are three seasons: a relatively dry cool season from October to March, a dry warm season (April and May) and a wet warm season (June to

September). The mean temperature is 15.2 °C, and total mean annual precipitation is 1532 mm. Monthly precipitation during the relatively dry season is 50–100 mm, and during the wet season it is > 200 mm. Humidity is high and fogs are frequent during most days of the year. Mean minimum temperature is 9.4 °C and mean maximum temperature is 20 °C.

Land use

Aerial photographs of the Acatlan Volcano from 1968, 1982 and 1993 were available from INEGI (Instituto Nacional de Estadística, Geografía e Informática, Mexico). Thus, changes in forest cover were determined between 1968 and 1993 and related to information on land use changes. The images were digitized and analysed using ILWIS1.4 ITC (Integrated Land Watershed Management Information System, Enschede, The Netherlands), and four broad cover types were identified: crops, pasture, secondary vegetation and primary forest. With this information, the temporal changes in forest cover were estimated for the study area.

Vegetation structure, litterfall and phenology

Three disconnected stands were located in the volcano area: crater, rim and top (Fig. 1). Within each stand, vegetation structure in terms of basal area (m² ha⁻¹), density (trees ha⁻¹) and tree species composition were determined using 0.1-ha band transects divided into 10 plots of 10 m². In each plot, all individuals ≥ 5 cm in diameter at breast height (d.b.h.) were tagged, measured and identified. Basal area and density were calculated for each stand. Importance value index was calculated per species within each stand. A line was painted on each tree with waterproof paint at 1.3 m above ground level, and d.b.h. was measured. Diameter at breast height was measured monthly for 3 years in the crater and for 2 years at the top and rim stands.

Litterfall was measured inside the crater and at the top. Twenty traps were placed at each site; two in each plot at stratified random points. Traps were made from wooden boxes 35 cm × 45 cm standing 30 cm above ground. The trap bottoms were 1-mm mesh plastic screen. Litterfall was collected monthly between March 1995 and February 1998. All samples were sorted into species and components (leaves, reproductive parts and unclassified material). Dry weights were obtained after oven-drying for 48 h at 70 °C. The litterfall data were log transformed to fit normality. Shapiro–Wilk's W-test was applied to test for normality. Litterfall was analysed using a repeated-measures ANOVA and significant differences were identified through a Tukey–Kramer HSD (honestly significant difference) multiple comparison procedure using the JMP statistical software package (SAS, 1997).

Phenophases were recorded monthly for the tagged trees. Inside the crater, trees were observed from February 1995 to February 1998, whereas at the top, observations were conducted from October 1996 to February 1998. Other observations were recorded during periodic visits in 1998 and 1999, but they were not included in any statistical analysis. All observations were made with binoculars from the forest floor. Phenological states were scaled from 0 to 4 (0, 1–25%, 26–50%, 51–75%

Figure 1 Aerial photograph 1 : 50,000 of the Acatlan Volcano, Veracruz, Mexico. The numbers indicate the area where *Fagus grandifolia* var. *mexicana* (Martinez) Little grows: 1 is crater, 2 is rim, and 3 is top.

and 76–100%, respectively), representing the proportion of each tree dropping or producing leaves, flowering or fruiting. These values were averaged monthly and used as a phenological index (see Williams-Linera, 1997). Pearson correlation coefficients were estimated between litterfall production and phenological variables, as were climatic data from the current and preceding months using JMP statistical package (SAS, 1997).

Dendrochronology

To determine age distributions and tree-ring growth, 30 tagged trees in the three stands were randomly sampled. We collected two cores per tree from opposite sides of the tree at 1.3 m. The

cores were air dried, mounted on wooden blocks and hand sanded with three increasingly fine grades of sandpaper. Cores were examined for defects; cores with indistinct rings or rotten spots were eliminated. Next we cross-dated the cores. In cross-dating, each ring in a tree-ring series is identified to its exact year of formation. Reliance on marker rings, interactive graphics and correlations of ring patterns helped to establish correct ring sequences, and dating was assisted and checked by the program XCHECK (Van Deusen, 1993).

The ring width indices of trees from a site may be averaged to form a mean ring-width chronology (Fritts, 1976). After cross-dating, we developed mean chronologies for crater, top and rim trees. Tree rings are made up of several elements, a

climate component, a biological growth trend, a disturbance signal unique to the individual tree, a disturbance signal common to most trees and a random disturbance (Graybill, 1982). In order to optimize the climate component of the ring widths and the disturbance signal common to most of the trees, we standardized the cores to eliminate the age-related biological growth signal which is unique to each tree. The ALLREGS program of the Dynaclim system of programs (Van Deusen, 1993) was used to screen all possible climate models to determine which factors had the most effect on growth. We analysed the 12 monthly precipitation and temperature variables and 1 and 2 year lags of these variables, meaning that the rain or temperature of the previous year or the year before that influenced the current year's growth. Climate data were also examined to find extreme values. We used the program DYNAOLS to study the climate models that we found by doing all possible regressions with ALLREGS. Climate models were fitted to the *Fagus* chronology. Peters (1995) defined periods of suppression for *Fagus* in Hidalgo, Mexico, as intervals in which there were 4 or more years of growth below 0.8 mm year^{-1} without 3 or more years of consecutive growth greater than 0.8 mm year^{-1}. We used his method to determine periods of suppression and free growth in the individual *Fagus* trees at Acatlan.

Seedlings were tagged 30 months before they were randomly collected and were measured bimonthly as part of a study on seedling bank dynamics (Alvarez-Aquino & Williams-Linera, 2001). Thirty-one seedlings were randomly collected in September 1997 and 30 seedlings were collected in July 1998. Several disks from the base of each seedling were cut and sanded with 600-grade sandpaper. The rings were counted for each seedling collected in September 1997 and rings, as well as bud scars, were counted for each seedling collected in July 1998. The current year's growth ring was not counted.

Meteorological data

Data on mean, minimum and maximum temperatures, and total annual precipitation are available since 1920 at the Xalapa, Veracruz, meteorological station, while at the nearest meteorological station located in the town of Acatlan, Veracruz, data are available only since 1980. Data were tested for normality using the Shapiro–Wilk's W-test with the JMP statistical software package (SAS, 1997), then Pearson correlation coefficients were estimated. Only mean maximum temperature ($r^2 = 0.48$, $n = 15$, $P = 0.004$) and total annual precipitation ($r^2 = 0.55$, $n = 14$, $P = 0.002$) were significantly correlated between Acatlan and Xalapa data. For the dendroecological analysis we used weather data from the Xalapa Station (20 km away, 1300 m of elevation) because it covered a longer period of time.

RESULTS

Land use

Acatlan Volcano has an area of 762.2 ha (Fig. 1). Forest cover increased from 60.7% in 1968 to 75.9% in 1993. The area covered with crops and pastures decreased from 39.3% in 1968
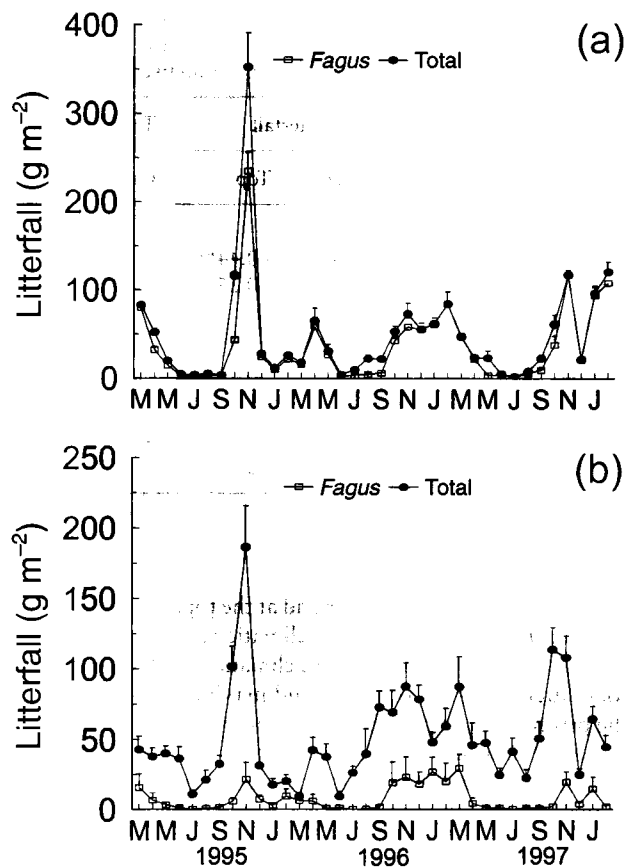

Figure 2 Litterfall production from March 1995 to February 1997. (a) In the *Fagus* stand located inside the crater, and (b) at the stand located at the top of the Acatlan Volcano, Veracruz, Mexico.

to 24.1% in 1993. The forest increased 8.8% in size compared with the area occupied by crops and pastures during the 1968–82 period, and 6.4% between 1982 and 1993. In total, there was a 15% increase in forest cover in the volcano in 25 years. However, the areas with stands of *Fagus* remained the same size.

Litterfall and phenology

Litterfall production was smaller in the crater stand (583.6 ± 62.4 g m^{-2} year^{-1}) than at the top of the volcano (612.5 ± 32.1 g m^{-2} year^{-1}; $F = 10.06$, $P = 0.003$; Fig. 2a). The *Fagus* litterfall was 452.8 ± 17.5 g m^{-2} year^{-1} in the crater, but only 92.6 ± 15.3 g m^{-2} year^{-1} at the top of the volcano ($F = 108.01$, $P < 0.0001$). In the crater, the litterfall was composed mostly of *Fagus* leaves (77.6%), while at the top, *Fagus* made up only 15.6% of the litterfall (Fig. 2b). Total litterfall and litterfall produced by *Fagus* were different among months ($F = 5.37$, $P = 0.004$; $F = 13.32$, $P < 0.0001$, respectively), but not among years. *Fagus* litterfall production in both stands and total litterfall inside the crater were significantly higher only in November (Fig. 2a, b). Total litterfall production at the top of the volcano was significantly higher during October and November (Fig. 2b).

Table 1 Pearson correlation coefficients between climatic variables (precipitation, minimum and maximum temperatures), and litterfall and phenophases recorded inside the crater and at the top of the Acatlan Volcano, Veracruz, Mexico. 'Same' and 'previous' refer to the climatic variables recorded in the same and previous months, respectively.

	Fagus litterfall		Total litterfall		Leaf fall		Leafing		Flowering	Fruiting
	Crater	Top	Crater	Top	Crater	Top	Crater	Top	Crater	Crater
Precipitation										
Same	−0.34*	−0.44**	−0.21	−0.15	−0.35*	−0.62*	−0.34*	−0.43	−0.06	0.22
Previous	−0.05	−0.25	0.05	0.21	−0.17	−0.45	−0.38*	−0.46	−0.18	0.02
Minimum temperature										
Same	−0.4*	−0.40*	−0.33	−0.14	−0.78***	−0.79***	0.10	−0.02	−0.12	0.28
Previous	−0.37*	−0.43**	−0.26	0.04	0.45***	−0.72**	−0.27	−0.44	−0.37*	0.18
Maximum temperature										
Same	−0.3	−0.50**	−0.23	−0.29	−0.47**	−0.53*	0.15	0.08	0.13	0.34*
Previous	−0.48**	−0.47**	−0.37*	−0.30	−0.29	−0.45	−0.26	−0.50*	0.13	0.44**

$*P < 0.05, **P < 0.01, ***P < 0.001.$

Fagus litterfall, in the crater and at the top, was significantly and negatively correlated with climatic variables, while total litterfall was not correlated with climatic variables, except for total litterfall inside the crater and maximum temperature of the preceding month (Table 1). The increase in *Fagus* litterfall is related to a decrease in precipitation and mean minimum temperatures, and also to a decrease in maximum temperatures of the previous month, which is the beginning of the dry cool season (Table 1).

Phenological observation indicated that leaf fall occurred from October through to February. Leaf production starts in February, however, peaks of new leaf emergence were observed between March and April. Flowering (peaking in February and March) and fruiting (May to August) were observed exclusively in trees inside the crater in 1996, but not at all in 1995, 1997 and 1998 (Fig. 3a–d). Trees in both stands flowered and fruited heavily in 1999, which was a mast year. Leaf fall was strongly correlated with minimum temperatures. Also, higher leaf fall was correlated with lower precipitation and lower maximum temperatures of the same month. Leaf flushing increased when precipitation was low during the same and the previous month, but the correlation was significant only for inside the crater. Flowering was negatively correlated with minimum temperature of the preceding month, while fruiting was positively correlated with maximum temperatures (Table 1).

Forest structure

The three stands differed in terms of density, basal area, species richness and dominance of trees ≥ 5 cm d.b.h. (Tables 2 & 3). Density in the crater and rim stands was lower than in the top stand, whereas basal area at the rim and top of the volcano was higher than in the crater (Table 2). Additionally, relative dominance of *Fagus* in both basal area and density was different in the three stands. Inside the crater, *Fagus* represented 99.6% of the total basal area while along the rim and at the top it constituted 85.6% and 67.8% of basal area,

respectively. In terms of density, *Fagus* made up 83.3% of the individuals in the crater, 44.1% at the rim and only 26.4% at the top (Table 2). The only dominant tree species inside the crater was *Fagus*, while on the crater rim and at the top of the volcano, *Fagus* became codominant with other tree species (Table 3). Juveniles of *Fagus* were found at the rim and at the top, but inside the crater there were only mature trees and a seedling bank (Alvarez-Aquino & Williams-Linera, 2001). Also, sprouts from roots were not observed inside the crater, and they were very scarce at the rim and top stands.

Fagus individuals with the greatest diameters were found at the rim ($F = 5.54, P < 0.01$, Fig. 4a). Diametric annual growth was 0.9 mm year^{-1} inside the crater, 5.4 mm year^{-1} at the rim and 1.5 mm year^{-1} at the top. The correlation between diameter and growth rate was significant ($r^2 = 0.34, P < 0.01$, Fig. 4b).

Dendrochronology

The cross-dated cores of trees growing inside the crater ranged from 76 to 120 years. The oldest core dated back to 1877, but climate data were available only since 1920. Twenty-two cores from 15 trees were used for the analysis. Current February mean temperature and February and July precipitation of the previous year were the best predictors of growth of the *Fagus* population in the crater. The variation explained in the transformed chronology was 16% ($r^2 = 0.16, P = 0.006$). The correlation between the transformed chronology and February temperature was −0.25 ($P = 0.007$), for February precipitation of the previous year it was −0.24 ($P = 0.05$), and for July precipitation of the previous year it was 0.13 ($P = 0.08$). Observed and expected values of the crater ring widths over time were similar. The predicted growth model was obtained from the DYNAOLS program using the climate variables of current February mean temperature, and February and July precipitation of the previous year.

The cross-dated cores of trees at the top of the volcano ranged from 88 to 115 years (1909 and 1882, respectively),
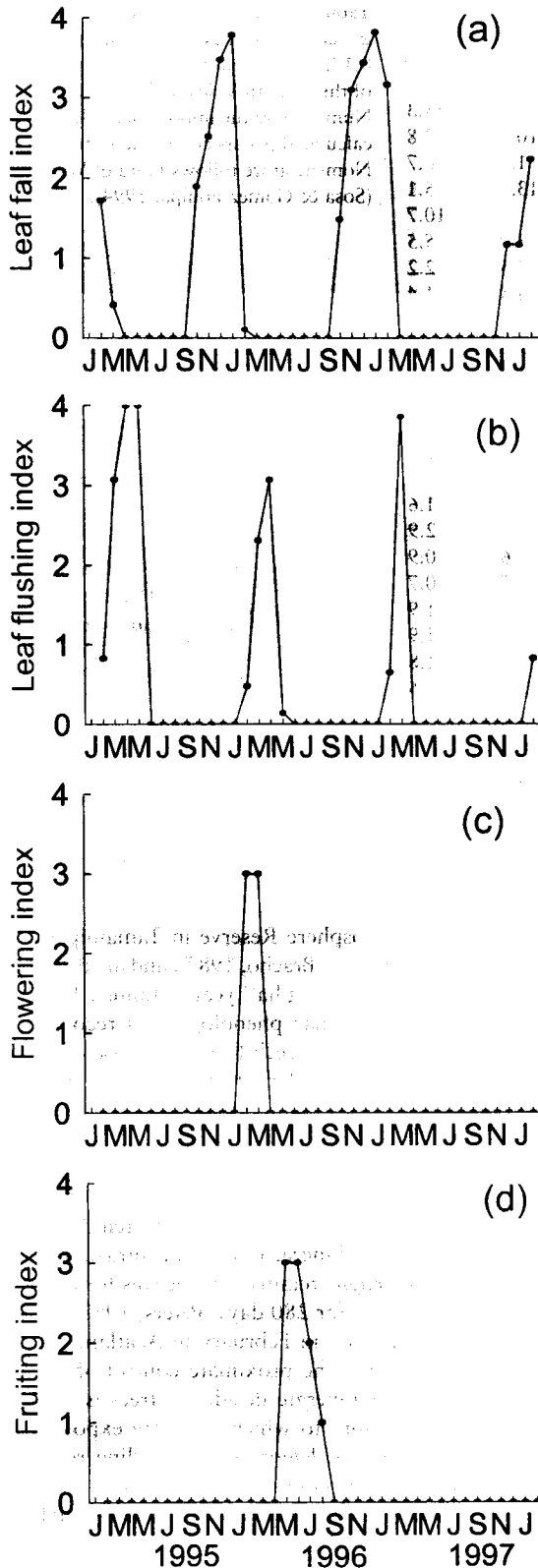
Figure 3 Phenological patterns of the *Fagus* populations located inside the crater of the Acatlan Volcano, Mexico. (a) Leaf fall, (b) leaf production, (c) flowering and (d) fruiting.

Table 2 Number of trees ≥ 5 cm diameter at breast height, density and basal area of *Fagus grandifolia* var. *mexicana* (Martinez) Little and of all tree species within the crater, at the rim and top of the Acatlan Volcano, Veracruz, Mexico. Standard errors are in parentheses.

Stand	Density (no. 0.1 ha^{-1})	Density (no. ha^{-1})	Basal area (m^2 ha^{-1})
Crater			
Fagus grandifolia	30	300 (42)	37.51 (4.76)
Other species	6	60 (14)	0.15 (0.04)
Total	36	360 (40)	37.66 (4.76)
Rim			
Fagus grandifolia	26	260 (50)	69.51 (11.60)
Other species	33	330 (76)	11.72 (5.26)
Total	59	590 (57)	81.23 (11.14)
Top			
Fagus grandifolia	34	340 (52)	48.11 (13.12)
Other species	95	950 (168)	22.86 (7.68)
Total	129	1290 (126)	70.93 (10.53)

and trees on the rim ranged from 88 to 98 years (1909 and 1899). Cores from the top and rim were not analysed in the same way as those from the crater because the sample size was smaller. We collected 12 cores from six trees at the top, and only six cores from three trees at the rim of the volcano. The number of trees, however, is proportional to the actual number of *Fagus* individuals in each stand and the stand size.

The trees growing on the rim showed no suppressed growth (Fig. 5a). Trees growing at the top of the volcano had a mean of 1.3 periods of suppression with 88% less than 20 years and 2.0 periods of free growth with only 17% less than 20 years (Fig. 5b). Half of the suppression periods of trees at the top of the volcano began in the 1950s. Inside the crater, only one of the trees we cored showed evidence of suppression in the earliest years: tree number 2 (20.1 cm d.b.h.) has three small rings near the pith, then 4 years of release, then a 25-year period of suppression. The trees in the crater had a mean of 1.1 periods of suppression with 72% less than 20 years and 1.4 periods of free growth with only 18% less than 20 years in length (Fig. 5c). Eleven of 16 trees in the crater are experiencing periods of slow growth at present, but they are canopy trees not classified as suppressed trees. In general, periods of suppression were short and periods of free growth were long. Small rings occurred in 1950–51, 1971 and 1996 in many of the trees. The average radial growth rate was 2.53 mm year^{-1} in the crater, 2.79 mm year^{-1} in the rim and 1.53 mm year^{-1} at the top stand.

The seedlings collected in September 1997 had between two and nine rings besides the current year's growth; the mean was 5.1 rings. Their heights ranged from 18 to 44.5 cm. Two seedlings did not have clear rings and could not be analysed. The seedlings collected in July 1998 had between two and 18 complete rings, with a mean of 6.6 rings. They were between 13.1 and 59.8 cm in height. The number of bud scars was identical to the number of rings in 28 out of 30 cases.

Species	Family	Crater	Rim (S)	Top
Fagus grandifolia var. mexicana (Martinez) Little	Fagaceae	81.8	52.2	35.3
Podocarpus matudai Lundell	Podocarpaceae	12.2	10.3	3.8
Magnolia schiedeana Schldl.	Magnoliaceae	6.1	1.5	0.7
Quercus laurina Humb. & Bonpl.	Fagaceae		13.5	5.1
Carpinus caroliniana Walter	Betulaceae			10.7
Symplocos limoncillo Humb. & Bonpl.	Symplocaceae		3.0	5.5
Ilex discolor Hemsley	Aquifoliaceae		4.5	2.2
Cleyera theoides Choisy, L. C.	Theaceae		4.5	1.4
Ternstroemia sylvatica Cham. & Schldl.	Theaceae		1.5	4.2
Clethra mexicana DC.	Clethraceae		1.6	3.1
Oreopanax xalapensis (Kunth) Decne. & Planchon	Araliaceae		1.5	3.1
Chiococca pachyphylla Wernham	Rubiaceae			3.9
Cytharexylum ligustrinum (Thuret ex Decne.) Van Houtte	Verbenaceae		1.5	2.1
Cornus excelsa Kunth	Cornaceae		1.5	1.6
Gymnanthes longipes Muell. Arg.	Euphorbiaceae			2.9
Quercus sp.	Fagaceae		1.6	0.9
Ilex tolucana Hemsley	Aquifoliaceae		1.5	0.7
Weinmania intermedia Schldl. & Cham	Cunoniaceae			1.9
Vaccinium leucanthum Schldl.	Ericaceae			1.9
Rhamnus capreaeifolia Schldl.	Rhamnaceae			1.8
Styrax glabrescens Benth	Styracaceae			1.6
Persea aff. americana Miller	Lauraceae			1.4
Arachnotrix capitellata (Hemsl.) Borhidi	Rubiaceae			1.0
Prunus capuli Cav.	Rosaceae			0.8
Saurauria belizensis Lundell	Actinidaceae			0.8
Prunus brachybotrya Zucc.	Rosaceae		(S)	0.7

Table 3 Species and families of woody plants ≥ 5 cm diameter at breast height recorded in 0.1 ha plots inside the crater, at the rim and top of the Acatlan Volcano, Veracruz, Mexico. Numbers are the importance value indexes calculated per species in each site. Nomenclature follows Flora of Veracruz (Sosa & Gómez-Pompa, 1994).

DISCUSSION

Land use

The forested area in the volcano grew 15% between 1968 and 1993. This increment coincided with a milk price decrease in the early 1970s. Many people abandoned their cattle pastures and migrated to the United States due to the decrease in dairy and cattle prices (Martinez, 1993). The abandoned pastures are now converting to forest. However, the beech forest area did not change. The area occupied by beech stands inside the crater, at the rim and at top of the volcano have remained the same for at least the last 30 years.

Litterfall and phenology

Litterfall production in the Acatlan Volcano was well within the range of litterfall production reported for several temperate beech forests in America (e.g. Hubbard Brook, New Hampshire, 5.7 Mg ha^{-1} year^{-1}; Gosz, Likens & Bormann, 1972) and Europe (Sierra de la Demanda, Burgos, Spain, 5.39 Mg ha^{-1} year^{-1}; Santa Regina & Tarazona, 1995). However, litterfall production in the Acatlan Volcano (5.84, 6.12 Mg ha^{-1} year^{-1}) was less than litterfall recorded in other tropical montane forests in Mexico, such as the Ecological Park, Xalapa, Veracruz (19° N, 8.45 Mg ha^{-1} year^{-1}; Williams-Linera & Tolome,

1996) or El Cielo Biosphere Reserve in Tamaulipas (23° N; 7.3 Mg ha^{-1} year^{-1}; Puig & Bracho, 1987), and in other montane forests (e.g. Jamaica, 6.6 Mg ha^{-1} year^{-1}; Tanner, 1980).

At Acatlan, longer foliar phenology was recorded when compared with temperate beech forests because of an earlier start of leaf production and later leaf drop. In Acatlan, leaves are retained for around 305 days. In Zacualtipan, Hidalgo (20° N), beech trees retain leaves for c. 340 days (Peters, 1995). Similarly, in nearby montane forests, leaf drop for temperate deciduous tree species occurs during the dry cool season that also corresponds to minimum temperature and shorter days (Williams-Linera, 1997). In contrast, in southern Michigan (42° N), Fagus retains green leaves for c. 180 days and in Florida (30° N) for 280 days (Peters, 1997).

Leaf production starts in February in Acatlan. Lechowicz (1984) established that the proximate control of initial leaf emergence in most temperate deciduous trees is usually the cumulative thermal sum to which buds are exposed after a prerequisite cold period. Fagus lacks a chilling requirement and bud break is under photoperiodic control.

Flowering during mast years starts in February, but between seed mast events there is no production of flowers and fruits. In temperate forests, Fagus has at least a little fruit production every year with peaks every number of years. The behaviour observed in Acatlan (and also in Mesa de La Yerba, Veracruz, the closest beech stand c. 25 km away) could be a result of
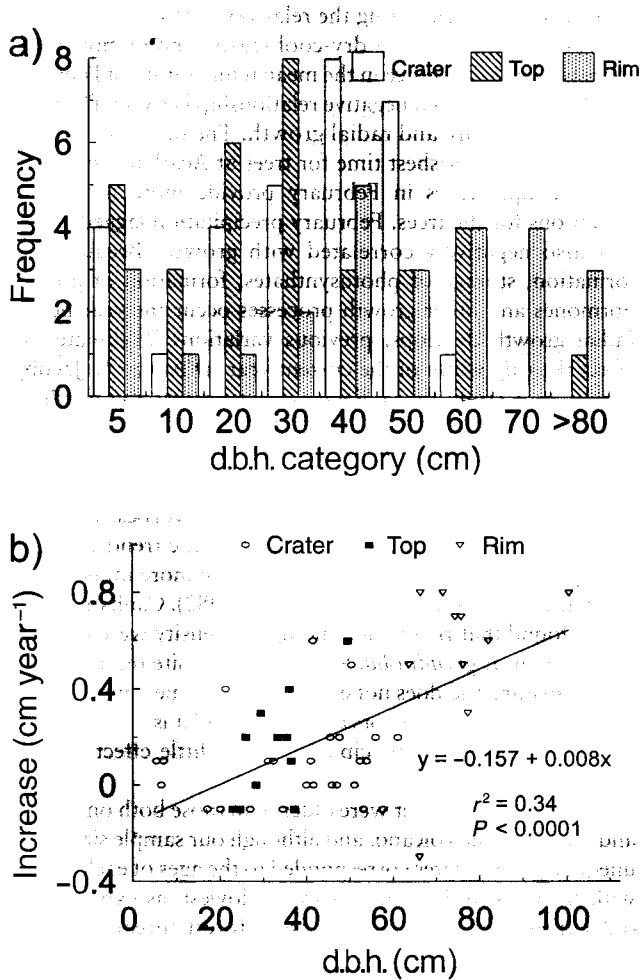
Figure 4 (a) Frequency of *Fagus* trees in the diameter classes 5–9.9 cm, 10–19.9, 20–29.9, 30–39.9, 40–49.9, 50–59.9, 60–69.9, 70–79.9 and > 80.0 cm. (b) Diameter at breast height of *Fagus* trees and annual diameter increment in the forest stand located inside the crater, at the rim and at the top of the Acatlan Volcano, Veracruz, Mexico.

Figure 5 The untransformed chronologies of selected *Fagus* trees from the Acatlan Volcano, Veracruz, Mexico. (a) Tree number 38 growing on the top of the volcano, showed one period of suppressed growth from 1959 to 1964. (b) Tree number 44 growing on the rim, showed free growth with no periods of suppression. (c) Tree number 1 from the population growing inside the crater, showing suppressed growth only recently, from 1987 to 1996. Horizontal lines are periods of suppression.

different environmental conditions or a consequence of trees needing to accumulate reserves. Interestingly, the flower peak is correlated with low minimum temperature of the previous month, which was in fact the lowest mean minimum temperature during this study. Fruiting was positively correlated with maximum temperatures, which were higher than other years' temperature during the same month. In a Malaysian dipterocarp rain forest, Ashton, Givinish & Appanah (1988) observed that a drop of only 2 °C for several nights may be sufficient to promote flowering. Mast fruiting is related to heavy flowering apparently promoted by a drop in minimum temperature. In Mexican montane forests, flower production of other temperate tree species was also correlated with minimum temperatures. Beech fruiting was correlated with high maximum temperatures, as were other temperate tree species in a nearby montane forest (Williams-Linera, 1997).
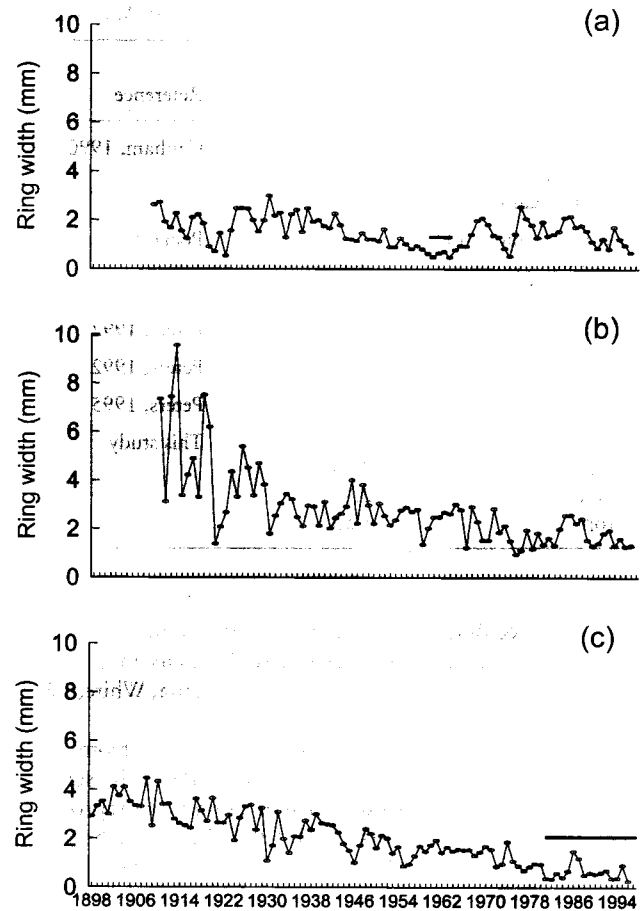
Forest structure

The vegetation structure and the tree species diversity of the stand inside the crater are not typical of the Mexican montane forests, since the only canopy tree species was *Fagus*. The stands at the rim and top of the volcano are more diverse, but also different from the cloud forest. The distance to the unconnected stand at the top is relatively short, and there *Fagus* is codominant with many other canopy species. Other Mexican *Fagus* stands in Mesa de la Yerba, Veracruz, Zacualtipan, Hidalgo and El Cielo Biosphere Reserve, Tamaulipas, are more diverse, probably because they have a different disturbance history (discussed later).

Common understorey trees in the Acatlan stands are *Podocarpus* and *Magnolia*. In all Mexican beech forests, *Magnolia schiedeana* Schldl. is always growing in the same stands as

Table 4 Radial growth rates in beech forests of North America.

Location	Latitude (N)	Radial growth rate (mm year^{-1})	Reference
New York	44°		Canham, 1990
Shade trees		0.29	
In small gaps		0.62	
New Hampshire	44°		Poage & Peart, 1993
Shade trees		0.40	
In small gaps		0.61	
Michigan	41°	1.71	Peters, 1992
Florida	30°	1.82	Peters, 1992
Hidalgo	20°	2.09	Peters, 1995
Acatlan Volcano	19°		This study
Crater		2.53	
Rim		2.79	
Top		1.53	

Fagus (Puig & Bracho, 1987; Peters, 1995). Similarly, a related species, *M. grandiflora* L. grows with *Fagus* in southern USA (Texas, Glitzenstein *et al.*, 1986; Louisiana, White, 1987; Florida, Peters & Platt, 1995).

A seedling bank and the scarcity of sprouts from roots suggest that reproduction of *Fagus* in Acatlan is by seed. In the northern part of its range, *Fagus grandifolia* reproduces vegetatively by root sprouts (Held, 1983). In the southern part of its range, in eastern deciduous forest, root sprouting does not occur (Peters, 1992). There is a partial shift from successful seedling establishment toward a dependence on vegetative reproduction at high elevations and northern latitudes where the physical environment is more severe (Held, 1983). Observations in Mexico support this pattern (see Alvarez-Aquino & Williams-Linera, 2001).

Mature *Fagus* trees grow slowly in the crater and at the top of the Acatlan Volcano. The d.b.h. tape technique probably did not detect the small changes. However, the dendroecological data confirmed slow current growth. In other montane forests in the region, the average diameter growth rate was 2.9 mm year^{-1} (Williams-Linera, 1996). However, diametric tree growth in Acatlan was in the range reported for trunk diameter growth rates in other montane forests in Venezuela (0.6 mm year^{-1}; Tanner, Kapos & Franco, 1992) and Jamaica (0.2 mm year^{-1}, Tanner *et al.*, 1990).

In Acatlan, average radial growth rate was 2.35 mm year^{-1}. The growth season for beech increases with the increase of temperatures to the south. One of the effects of a longer growing season is an increase in the yearly radial growth in canopy trees (Table 4). In Mexican beech sites, a humid summer is important. If climate change results in an increase in temperature and humidity, then beech will remain (co)dominant (Peters, 1992).

Dendrochronology

In the study area, there are three seasons: a relatively dry cool season, a dry warm season and a wet warm season, but humidity

is always high, even during the relatively dry seasons. February is near the end of the dry-cool season and in most years there is a large difference in the mean temperature of February and March. There is a negative relationship between February mean temperature and radial growth. The dry warm season is probably the harshest time for trees at Acatlan. Therefore, cooler temperatures in February provide more favourable conditions for the trees. February precipitation lagged 1 year was also negatively correlated with growth. Because bud formation, storage of photosynthates, formation of growth hormones and other growth processes occur the year before radial growth develops, previous variations in climate can affect the ring width of the current year (D'Arrigo & Jacoby, 1992). In a study of 11 *Fagus* forests across the northern hemisphere, Peters & Poulson (1994) found that radial growth in *Fagus* spp. reflected events that opened up the canopy, such as storms and hurricanes, and not cool or dry summers (but see Eckstein *et al.*, 1984; Makowa, Stickan & Worbes, 1991). In eastern North American forests, non-climatic trends, such as tree age, light level or growing space, have more influence on ring width than climatic factors (Phipps, 1982). Canham (1988, 1990) found that ring width and light intensity were strongly correlated in *F. grandifolia*. Since our study site receives sufficient moisture and does not experience extreme temperatures, these are not limiting factors at Acatlan, and it is not surprising that temperature and precipitation have little effect on ring width.

The trees in the crater were older than those both on the rim and the top of the volcano, and although our sample sizes were unequal, growth rates corresponded to the ages of each group, with the trees in the crater growing slowest, as expected for older trees. This indicates the *Fagus* forest spread from the crater to the rim and then to the top, where the d.b.h. is smallest and the trees are growing the fastest. Dispersion by mammals and birds would be a good explanation for the presence of *Fagus* at the unconnected stand at the top. Today, the large seeds of species, such as beech and oak, in both North America and Europe are dispersed by jays and pigeons that may well have been responsible in the past for creating small nascent foci well beyond the trees' main front of advance (Webb, 1987; Silvertown & Lovett Doust, 1993). In fact, the extinct passenger pigeon was reported from central Veracruz in 1897–1904.

Canham (1990) found that beech saplings in three old-growth hardwood forests in the north-eastern USA had 1.9–2.4 periods of suppression before recruitment at 66–80 years of age and *c*. 1 m of height. He defined suppression as intervals of 4 or more years of growth below 0.5 mm year^{-1} with no periods of 4 or more years of consecutive growth greater than 0.5 mm year^{-1}. Our cores were taken at d.b.h., and although growth varied, only one of our sample trees was still suppressed according to Canham's definition after it reached d.b.h., indicating that the Acatlan trees were released when less than 1.5 m tall. Released growing beech seedlings take *c*. 5 years to grow taller than 0.5 m (Peters, 1992), and *Fagus* spp. usually need extended periods of time to reach the canopy (100 years, Peters & Poulson, 1994; 148 years, Poulson & Platt, 1996). Considering that *Fagus grandifolia* trees grow faster in southerly

areas (Peters & Poulson, 1994) than in northern areas (Table 4), transition from suppression to recruitment was faster in Acatlan. The trees must be at least 12–15-year-older than our samples if they germinated after the catastrophic event that knocked down the mature trees, but they could be considerably older than that if they were suppressed seedlings that survived the disturbance.

The large number of seedlings growing at Acatlan since 1992 indicates that this may have been a mast year. The small ring in the mature trees in 1996 was probably the result of another mast year. Kozlowski (1971) and Kozlowski & Keller (1996) state that vegetative growth of many species is reduced during mast years. In Zacualtipan, Hidalgo, beech juveniles smaller than 1 m were in age classes from 1 to 14 years with a clear peak at 6 years likely resulting from yearly establishment with changing rates of success and one masting year (Peters, 1995). In our study, beech juveniles smaller than 60 cm in height were found in age classes from 2 to 18 years, suggesting annual establishment but with different rates of success.

The growth ring chronologies of the trees we cored indicate that the Acatlan crater trees did not grow up in a mosaic of ecounits in different phases of development, with gaps occurring regularly as in the forest at Zacualtipan and in many other beech forests (Glitzenstein et al., 1986; Canham, 1988; Peters, 1995; Poulson & Platt, 1996; Batista et al., 1998). At least from the time they reached d.b.h. height, the trees experienced long periods of free growth. It appears that an event such as a hurricane or fire opened up the canopy and allowed existing seedlings and/or germinating seedlings to grow freely until recently. Most of the trees reached d.b.h. height between 1891 and 1903, so the event must have occurred some years before that.

It appears that a number of trees in the crater are entering the senescent phase, since their growth has slowed in recent years. Turnover times for canopy trees in a wide range of temperate and tropical forests are often in the range of 100–200 years (Canham, 1990). Trees in the Acatlan crater are in this age range, and are probably starting to die. In October 1995, very strong winds ('nortes') threw a huge tree near our permanent sampling plots. Three years later, in October 1998, we recorded the fall of another huge tree, adjacent to the previous one, again coinciding with strong winds. In the southern Appalachians, beech showed relatively high levels of border-tree mortality: light gaps in those forests serve to boost species already present in the understorey, not to create opportunities for a new set of species (Runkle, 1998).

Monodominance of Fagus of the same age inside the crater suggests a major disturbance. Since human population density was low in the Acatlan region (from 468 to 2500 people from 1500s to 1990s), and other forests located in topographically easier situations were abundant, a massive deforestation inside the crater is very unlikely. A major hurricane with strong sustained winds could have felled most of the mature trees over 120 years ago, leaving sites with saplings or sites ready for regeneration. A masting event could have occurred a little before the catastrophe, and Fagus seedlings and saplings grew fast and created this stand.

In summary, the monodominant forest at Acatlan is an unusual Fagus forest in several respects and an atypical tropical montane forest. Unlike temperate Fagus forests, there is no production of flowers and fruit between mast years, and the trees are only deciduous for a brief period. Litterfall is within the range for beech forests, although it is less than the amount recorded for other Mexican tropical montane forests. As in many other beech forests, there was low correlation between ring widths and temperature or precipitation. The structure and composition of the Acatlan Fagus stand in the crater, as well as the history of periods of suppression, indicate that this monodominant stand was established after a severe disturbance, probably a hurricane, destroyed the existing forest over 120 years ago, with later dispersal to the top and rim of the volcano. Canopy trees in the crater are senescent and are beginning to fall. As this occurs, the forest will slowly become a gap regeneration forest as the seedlings present on the forest floor respond to the increased light in newly created gaps. The area of the Fagus forest has not changed in the last 30 years, and the forest should be able to maintain itself, if not severely disturbed by humans.

ACKNOWLEDGMENTS

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