Seedling bank dynamics of *Fagus grandifolia* var. *mexicana* before and after a mast year in a Mexican cloud forest

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Abstract. *Fagus grandifolia* var. *mexicana* seedling dynamics were studied in a relict forest inside the crater of a volcano where it is the only canopy tree species. The objectives of the study were (1) to determine changes in seedling density before and after a mast year, as well as to monitor seedling recruitment, mortality and growth rate in relation to the microenvironment, and (2) to discuss the impact of masting on seedling dynamics of the population. Before masting, seedling density was 8.8 seedlings m^{-2}, afterwards seedling density peaked at 51.5 seedlings m^{-2}, then decreased by 50% in 3 months and by 85% after 8 months, down to levels of before the mast year (9.9 seedlings m^{-2}) after 16 months. Seedlings in the forest floor before the mast-seeding event showed a low relative growth rate – 0.14 mm mm^{-1} mo^{-1} against 1.27 mm mm^{-1} mo^{-1} for seedlings that emerged immediately after masting. Seed germination was high (83%) and rapid ($L_{50} = 7$ days) following masting. Seedling growth was positively correlated with soil water content but not with temperatures and relative humidity. Data suggested that seed production in mast years is important in maintaining the seedling bank, and thus the viability of relict *Fagus* populations.

Keywords: Beech; Masting; Montane; Relict species; Tropics.

Abbreviations: PAR = Photosynthetically active radiation; RGR = Relative growth rate.

Introduction

Masting is the synchronous production of a large seed crop within a population of trees at intervals of 2 or more years. Several hypotheses have been proposed to explain the evolution of this phenomenon. These hypotheses include increased pollination efficiency, seed predator satiation and the potential impact of selection on seed size (Silvertown 1980; Nilsson & Wastljung 1987; Sork 1993). Successful seedling recruitment following a mast year is critical for some species (Ribbens et al. 1994; Shibata & Nakashizuka 1995; Negi et al. 1996; Akashi 1997; Forget 1997). While some masting species are shade intolerant as seedlings, others characteristically form persistent populations of tree seedlings, called a 'seedling bank', that survive for long periods under the forest canopy (Augspurger 1984; Hara 1987; Canham 1988; Latham 1992; Still 1996). The capacity of these seedlings to survive for long periods may maintain the regeneration potential of forest trees that do not produce seeds every year (Grime 1979; Taylor & Aarssen 1989).

Masting, and the presence of seedling banks, is common in *F. grandifolia* in North America (Gysel 1971; Harcombe et al. 1982; Canham 1990; Walters & Reich 1996), *F. sylvatica* in Europe (Nilsson 1985; Nilsson & Wastljung 1987; Peltier et al. 1997) and *F. crenata* in Japan (Hara 1987; Peters et al. 1992; Igarashi & Kamata 1997). Reproduction of *F. grandifolia* in the eastern deciduous forest of the USA also includes root sprouts (Fowells 1965; Held 1983; Jones & Raynal 1986). Root sprouting is considered important under unfavourable environmental conditions, but does also occur under normal conditions (Held 1983; Ward 1961). It also occurs when dense forest floor vegetation prevents the establishment of seedlings (Sain & Blum 1981; Nakashizuka 1984; Peters & Ohkubo 1990; Peters et al. 1992).

F. grandifolia seedlings and saplings represent an extreme of shade tolerance in northern hardwood forests (Canham 1990; Poage & Peart 1993; Batista et al. 1998). Such tolerance results in high *Fagus* seedling abundance beneath closed canopy forest (Fowells 1965; Glitzenstein et al. 1986; Canham 1990; Walters & Reich 1996) and produces a persistent seedling bank on the forest floor which is an important source of recruitment into the adult population. Factors of obvious importance to the number of seedlings in a stand are production of viable seeds (Ward 1961; Sain & Blum 1981) and environmental conditions that permit germination, establishment and survival (Harcombe et al. 1982; Held 1983; Glitzenstein et al. 1986).

We studied the influence of masting on the seedling populations of *Fagus grandifolia* var. *mexicana* in an isolated relict population in Mexico, near the extreme southern limit of *Fagus* species in North America. We hypothesized that masting increases seedling density in the year after mast events and results in distinct cohorts of seedlings that last across mast events. The objectives of this study were (1) to determine changes in seedling

density before and after a mast year, (2) to assess germination time and percentage, seedling recruitment, mortality and growth rate in relation to the micro-environmental conditions in the forest understorey and (3) to discuss the impact of mast year on seedling dynamics of the *Fagus* population.

Study site

Fagus grandifolia var. *mexicana* is restricted to the Sierra Madre Oriental in Mexico where a few populations occur in small stands (2-40 ha) (Miranda & Sharp 1950; Hernandez X. et al. 1951; Fox & Sharp 1954; Little 1965; Puig & Bracho 1987; Williams-Linera et al. 1996), 2 of which have recently been destroyed by deforestation (Williams-Linera et al. in press). The relict *Fagus* population that we studied is located in a recently discovered site in the crater of the relict Acatlan Volcano (19° 41' N, 96° 51' W). The steep slopes of this conically shaped volcano rise from an almost completely deforested valley in which land has been converted into fields and pastures. Isolated, and thus protected, forests inside the crater and at the top of the volcano appear to be thriving with numerous *Fagus* trees, several exceeding 50 cm DBH. In a stand on the northern slope of the crater, *Fagus grandifolia* var. *mexicana* is the only canopy tree species present (Williams-Linera et al. 2000). Tree species growing in the understorey are *Podocarpus matudai* and *Magnolia schiedeana*. The altitude is 1840 m a.s.l. at the base of the crater and 1900 m a.s.l. at the top of the volcano. Mean annual temperature is 15.2 °C and mean annual precipitation is 1532 mm. Minimum and maximum mean temperatures are 9.4 °C and 20 °C, respectively. Climatic data were obtained from the meteorological station located in the nearby town of Acatlan, Veracruz. The soil has been classified as Andept, with a pH of 4.7, sandy clay loam texture with high cation exchange capacity (13.3) and organic matter content (11.2%).

Methods

A 10 m × 100 m area of the stand was identified inside the crater. This was divided into 10 equal sized units (10 m × 10 m). Within each of these units a 2 m × 2 m plot was established. In January 1995, all seedlings less than 50 cm height in these plots were tagged. A seed mast event occurred in August 1996 and in the following 2 weeks 10 additional 1 m × 1 m plots were randomly established in each 10 m × 10 m unit. Within these plots all newly germinated seedlings were counted. To estimate survival,

seedlings were recensused 2, 8 and 16 months later. Total surviving seedlings from old and new cohorts were counted in December 1997.

Seedling height was measured at 2 month intervals during the subsequent year using a ruler running from ground level to the tip of the apical shoot. Relative growth rate (RGR) for old and new seedling cohorts were calculated as:

$$\text{RGR} = \log_e H_2 - \log_e H_1 / t_2 - t_1 \qquad (1)$$

where, H_2 and H_1 are mean heights and times t_1 and t_2 (Hunt 1978). Recently dispersed (1-3 days) seeds were collected from the forest floor to carry out seed germination and seedling growth experiments in the 'Clavijero' Botanical Garden, Xalapa, Veracruz. Experiments were conducted in the Botanical Garden due to logistic constraints and because environmental conditions are similar to those of a montane cloud forest (1300 m a.s.l., mean temperature 18°C, total annual precipitation 1517 mm). In the understorey of a forest fragment (2 ha) in the Botanical Garden, seeds were germinated in Petri dishes to determine germination time and percentage, they were then transplanted into plastic bags. Seedlings were tagged and height was measured at 2 month intervals. A mixture of soil from the local and the *Fagus* forest was used.

Micro-environmental variables at the study site were recorded monthly during the forest experiment. We measured relative humidity with a sling psychrometer, gravimetric soil water, soil and air temperature with a digital thermometer and photosynthetically active radiation (PAR) with light sensors (LICOR LI-190SA) connected to a data logger (LICOR 1000) placed in the open and in the forest interior. During the Botanical Garden experiment, soil and air temperature and PAR were also recorded with light sensors and a data logger. All statistical analyses were performed using the JMP package (Anon. 1997).
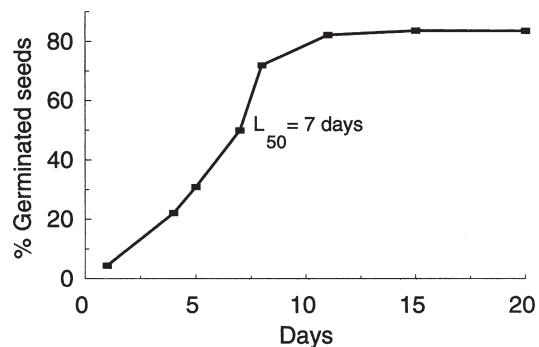
Fig. 1. Percentage of germinated seeds of *Fagus grandifolia* var. *mexicana* collected inside the Acatlan Volcano crater, Veracruz, Mexico.

Results

Seedling density from February 1995 to August 1996 was 8.8 individuals m^{-2}. There was no natural recruitment during 1995 because the population did not produce flowers or seeds. Annual seedling survival during the 18 months prior to the mast-seeding event was 92%.

In August 1996 there was a seed mast event. During this period, there was massive and simultaneous generation of *Fagus* seeds. Recently dispersed seeds collected from the forest floor had a high germination percentage (83%) and rapid germination (L_{50} = 7 days, Fig. 1). However, seedling mortality was high at 25% during the first 37 days after germination.

Immediately after mast-seeding, new seedling density peaked at 51.5 individuals m^{-2}. Seedling density decreased by 50% in 3 months (25.5 individuals m^{-2}) and by a further 35% in 8 months (18.0 individuals m^{-2}).

During the 8 months following the new seedling cohort recruitment, density of the old cohort decreased by 80% (1.8 individuals m^{-2}, Fig. 2). Within the new cohort of seedlings, mortality was also high. After 8 months only 38% of these seedlings survived, and this number declined to 17% after 16 months (Fig. 2b). Thus, despite the high seed input and germination caused by masting, total seedling density 16 mo after the mast-seedling event was only 12% higher than density before the event (9.9 individuals m^{-2}, $P > 0.05$, Fig. 2a).
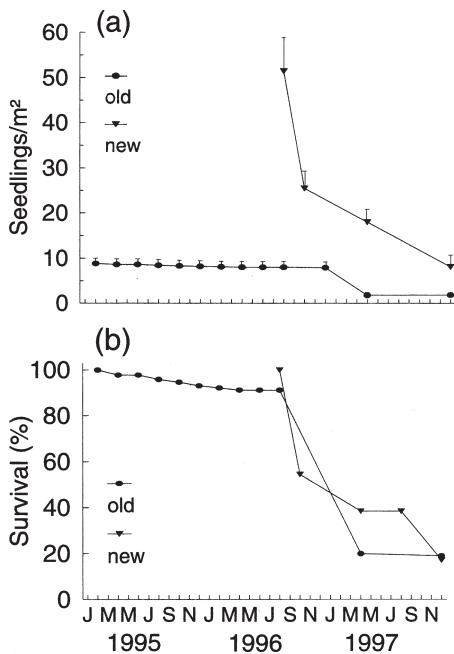

Fig. 2. Density and survival of *Fagus grandifolia* var. *mexicana* seedlings in Acatlan, Veracruz, Mexico. **a.** Seedling density before and after masting; **b.** Seedling survival before and after masting. Error bars represent 1 SE.
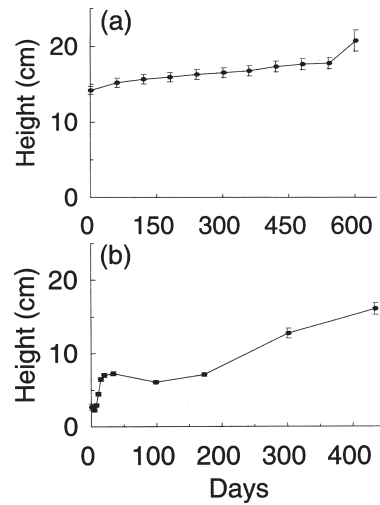
Fig. 3. Mean height of *Fagus grandifolia* var. *mexicana* seedlings growing (**a**) in the understorey of the Acatlan Volcano forest and (**b**) in the understory of the Botanical Garden forest, Xalapa, Veracruz, Mexico. Monitoring in the volcano forest understorey began at no particular seedling age, while in the Botanical Garden the cohort of new germinants was followed from emergence. Error bars represent 2 SE.

Old cohort seedlings growing for 26 mo in the forest understorey had a RGR of 0.14 mm mm^{-1} mo^{-1} (Fig. 3a). Seedlings germinating and growing in the Botanical Garden understorey for 14 months had a RGR of 1.27 mm mm^{-1} mo^{-1} (Fig. 3b). Although seedlings in the Botanical Garden might have experienced reduced root and resources competition, differences between growth rates suggest that seedling growth is rapid immediately after germination, levelling off after the first year or when seed resources have been depleted.

Micro-environmental variables were measured monthly from April 1995 to April 1996, then from October 1996 to December 1997 in the understorey of the crater forest. Monthly mean soil temperatures were always lower than air temperatures (Fig. 4a). Relative humidity was high most of the year (above 80%), except in February (Fig. 4b). Soil water content was also relatively high, always above 30% (Fig. 4c). PAR was low when the forest canopy was closed (4.17 mmol m^{-2} s^{-1}), increasing by a factor of 10 when trees were leafless from October to February (45.82 mmol m^{-2} s^{-1}) (Fig. 4d). In the Xalapa forest, PAR was 4.08 mmol m^{-2} s^{-1}, mean soil and air temperatures were 18.9 °C and 18.8 °C, respectively. Seedling growth under field conditions was significantly correlated with gravimetric soil water in the same month (r^2 = 0.585, $P < 0.05$) but not with the other micro-environmental variables.
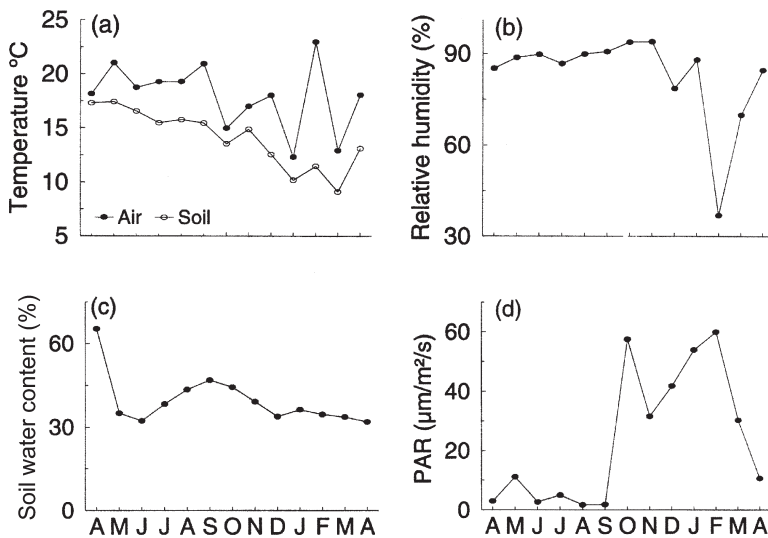
Fig. 4. Micro-environmental variables recorded in the forest understorey on the Acatlan Volcano, Veracruz, Mexico from April 1995 to April 1996. **a.** Air and soil temperatures; **b.** Percent relative humidity; **c.** Percent soil water content; **d.** PAR.

Discussion

A persistent *F. grandifolia* seedling bank of constant size was found inside the Acatlan Volcano crater, although plants originated from different cohorts (old seedlings ranged in age from 2 to 18 yr; Williams-Linera et al. 2000). Seedling density is relatively high when compared with *F. grandifolia* density in temperate forests of the USA (2.4 seedlings m^{-2} in Wisconsin, 4.7 in Tennessee, 4 in Indiana, 3.2 in Ohio and 0.6 in Michigan; Ward 1961) and with *F. sylvatica* in Sweden (0.2 seedlings m^{-2}; Nilsson 1985) or *F. crenata* in Japan (1.0 individuals m^{-2}; Hara 1987 and 2.9; Akashi 1997).

The seedling bank size fluctuated considerably after the mast event of 1996. Seedling density increased 5-fold after germination of seeds that fell during August and September but decreased again to that before the mast event. Increases in seedling density following mast years were reported for *Quercus floribunda* in the Himalayas (Negi et al. 1996) and *Betula alleghaniensis* in Quebec, Canada, where seedling abundance varied among years (from 5.5 to 1423 seedlings m^{-2}; Houle 1998). In *Vouacapoua americana* in French Guiana, seedlings from mast years have different recruitment success (Forget 1997). The age structure of *F. crenata* seedlings in Japan suggests the presence of several cohorts recruited in springs following a mast year (occurring at 6-8 yr intervals) and, thus, these seedlings were concentrated in years following the good seed year (Hara 1987).

Seedling establishment immediately after the mast year was high, while 16 months after the mast, survival percentage was slightly higher for old seedlings (20%) than for seedlings belonging to the new cohort (16%). Density dependent mortality has been suggested as a component affecting the size of the seedling population in temperate and tropical forests. A mast year therefore does not always result in successful seedling establishment. In Sweden, after a mast year, the density of *Fagus* seedlings was 0.2 individuals m^{-2} indicating that only 0.04% of the estimated seed production resulted in established seedlings (Nilsson 1985). High seedling mortality has been reported for a *F. grandifolia* cohort in Texas (92.7%; Glitzenstein et al. 1986) and *F. crenata* in Japan (79.2%; Akashi 1997). In general, mortality rate is high during the first year for temperate (Mulcahy 1975; Taylor & Aarssen 1989; Berkowitz et al. 1995; Shibata & Nakashizuka 1995; Negi et al. 1996) and tropical seedlings (Augspurger 1984; Still 1996; Forget 1997). In woody seedlings, annual mortality rates decline after the first year (Berkowitz et al. 1995).

In Acatlan, survival of the old seedlings present on the forest floor before the mast event was high (92%), probably because *Fagus* is shade-tolerant and the population of small mammals is very low (we saw no signs of herbivory). In Los Tuxtlas, Mexico, seedlings fail to show evidence of damage by vertebrate herbivores as a consequence of a forest fragmentation and 'general defaunation' in the remaining forest fragments (Dirzo & Miranda 1990). In Japan seedlings survived 5 yr with only 2% daylight (Peters 1995), 10 yr in the presence of bamboo (*Sasa*) in dense canopies (Peters et al. 1992) and 15 yr without bamboo under closed canopies (Nakashizuka 1987). In some Japanese forests, 90% of seedlings died when bamboo was present (Nakashizuka 1987). Ground vegetation may have indirect negative effects on seedling survival by providing a habitat for small mammal herbivores (Ostfeld et al. 1997). In Sweden (Nilsson 1985) and Britain (Nielsen 1977) rodents and invertebrates are responsible for the death of most *Fagus* seedlings during their first year. Seed predation,

mammalian herbivory and seasonal drought were the main causes of lack of seedling regeneration in the Great Smoky Mountains National Park, USA (Sain & Blum 1981).

Seeds produced during the mast year germinated within a month after dispersal while in temperate forests propagules are usually dispersed in the fall and seedling emergence occurs the next spring (e.g. *F. grandifolia* in USA, Fowells 1965; *F. crenata*, Hara 1987, Akashi 1997; *Acer saccharum*, Taylor & Aarssen 1989; *Carpinus* spp. Shibata & Nakashizuka 1995). *Fagus* seed germination in Veracruz was high (83%) and fast ($L_{50} = 7$ d) compared to *F. grandifolia* in Tennessee with 38% germination and 180 d stratification (Sain & Blum 1981).

At Acatlan, germination occurred toward the end of the rainy season, but air relative humidity and gravimetric soil water content were high, even during the relatively dry season (October - March). A baseline level of moisture appears necessary for germination and seedling survival (Harcombe et al. 1982; Peters 1995). High seedling emergence observed during the germination peak (October) may be facilitated by the scarce vegetation at ground level and a thin litter layer on the ground (Williams-Linera et al. 2000). Also, forest floor vegetation affects seedling establishment by competition (Sain & Blum 1981; Nakashizuka 1984; Peltier et al. 1997).

High density of seedlings in the persistent seedling bank and low number of root sprouts (pers. obs.) suggested that most *Fagus* reproduction in the Acatlan forest is by seed, which may be related to the warmer and more humid climate here and the open understorey. In Japan, bamboo (*Sasa*) makes germination of *F. crenata* difficult (Nakashizuka 1987; Peters & Ohkubo 1990). In Europe, regeneration of *F. sylvatica* may be inhibited by the fern *Pteridium aquilinum* (Peters et al. 1992).

RGR was greater for seedlings of the new cohort than for old seedlings. High initial growth rates have been reported for *Castanea*, *Fagus* and *Quercus* in eastern deciduous forests, USA (Latham 1992). The growth rate of a new cohort of *Fagus* in Texas was twice that of seedlings from older cohorts (Glitzenstein et al. 1986).

The height growth of the seedlings germinated experimentally in the Botanical Garden was greater than seedlings from the same cohort remaining on the Acatlan forest floor. PAR was similar in both sites and mean air and soil temperatures were higher in Xalapa than at Acatlan. *F. grandifolia* seedlings respond with increased growth rates when light levels increase and have higher growth rates in small gaps than under canopy trees (Fowells 1965; Canham 1988). The greater height of seedlings at Xalapa may be due to higher temperatures since light levels were similar, but other factors such as root competition and presence of leaf litter (Molofsky & Augspurger 1992) may also affect growth rates.

In the Acatlan forest, the effect of the mast year disappears quickly and older seedlings from previous mast years had higher mortalities after a subsequent mast crop. Thus, seed production during mast years appears to be enough to maintain the seedling bank due to the high mortality of newly emerging seedlings.

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