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DIAMETER GROWTH AND DECLINE IN A TROPICAL MONTANE CLOUD FOREST OF THE SIERRA DE LAS MINAS, GUATEMALA

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HOLDER, C. D. 2008. Diameter growth and decline in a tropical montane cloud forest of the Sierra de las Minas, Guatemala. This study examined annualized diameter growth rates of 100 cloud forest trees over 5½ years in an experimental plot within an upper montane cloud forest near the summit of Montaña de Miranda (2550 m above sea level) in the Sierra de las Minas Biosphere Reserve, Guatemala. An experimental plot with an area of 0.24 ha was established in December 1996 and 433 trees with a diameter at breast height (dbh) ≥ 5 cm were marked with an aluminum tag for identification within the experimental plot. The marked vegetation was relocated and the dbh of 100 trees was remeasured 5½ years later in August 2002. The mean dbh of the 100 trees increased by 9.2% from 11.4 to 12.5 cm representing a mean annualized diameter growth rate of 2 mm $year^{-1}$. Twenty-five trees had a greater dbh in 1996 than 2002, of which 19 decreased in dbh by < 0.5 cm. The dbh of four trees remained unchanged between 1996 and 2002. Comparisons with other neotropical upper montane forests indicate that the cloud forest of the Sierra de las Minas has a larger annualized diameter growth rate.

Key words: Annual diameter growth, cloud forest, dbh measurement, growth rate, Guatemala

HOLDER, C. D. 2008. Pertumbuhan dan kemerosotan diameter di hutan awan gunung tropika di Sierra de las Minas, Guatemala. Kami mengkaji kadar pertumbuhan diameter tahunan 100 pokok hutan awan berusia lebih 5½ tahun di plot eksperimen yang terletak di hutan awan gunung atas berhampiran puncak Montaña de Miranda (2550 m atas aras laut) di Sierra de las Minas Biosphere Reserve, Guatemala. Plot eksperimen dengan keluasan 0.24 ha ditubuhkan pada bulan Disember 1996 dan 433 pokok di dalamnya yang berdiameter aras dada (dbh) ≥ 5 cm ditanda dengan tag aluminium. Setelah 5½ tahun iaitu pada bulan Ogos 2002, pokok yang ditanda itu dikesan semula dan dbh 100 pokok diukur. Min dbh 100 batang pokok itu meningkat sebanyak 9.2% iaitu dari 11.4 cm ke 12.5 cm. Peningkatan ini adalah bersamaan dengan peningkatan kadar dbh sebanyak 2 mm setahun. Sebanyak 25 batang pokok mempunyai dbh yang lebih tinggi pada tahun 1996 berbanding 2002 dengan 19 daripadanya mengalami pengurangan dbh < 0.5 cm. Dbh empat pokok pula tidak berubah sepanjang tempoh kajian. Perbandingan keputusan kajian ini dengan hutan gunung atas neotropika yang lain menunjukkan hutan awan di Sierra de las Minas mempunyai kadar pertumbuhan diameter tahunan yang lebih besar.

INTRODUCTION

Annual diameter growth of individual trees is commonly measured in permanent plots in various forest types (Phillips & Gentry 1994, Clark & Clark 1996, Phillips 1996, Laurance *et al.* 2004). The measurement of tree diameter as an indicator of growth may have limitations because of tree shrinkage during periods of moisture stress (Sheil 2003, Intrigliolo & Castel 2006, Martínez Pastur *et al.* 2007). Tree shrinkage can occur on a daily basis in orchards, and the measurement of tree diameter shrinkage is a good indicator for determining moisture stress and the best times to irrigate (Intrigliolo & Castel 2006, Moreno *et al.* 2006, Conejero *et al.* 2007, Intrigliolo & Castel 2007, Velez *et al.* 2007). In environments with seasonal changes in water availability to plants, such as seasonal wetlands, tropical savannas and tropical dry forests, individual trees may have significant diameter decreases from one year to the next because of moisture stress (Sheil 1995, Baker *et al.* 2002, Connor & Inabinette 2003, Sheil 2003, Martínez Pastur *et al.* 2007).

Although several studies have examined annual diameter growth of lowland tropical forest trees (Clark & Clark 1992, Milton *et al.* 1994, Clark & Clark 1999), fewer studies have examined the annual diameter growth of upper montane cloud forest trees (Tanner 1980, Tanner *et al.* 1992). Slow growth of upper montane cloud forests may be influenced by cool temperatures, low light levels with persistent cloud cover and fog, nutrient-poor soils and exposure to wind (Tanner 1977, Bruijnzeel & Veneklaas 1998, Bellingham & Tanner 2000, Nadkarni *et al.* 2000). These adverse environmental conditions are commonly cited as explanations for the smaller stature and stunted structure of upper montane cloud forests (Grubb & Whitmore 1966, Lawton 1982, Bruijnzeel *et al.* 1993, Matelson *et al.* 1995). Tropical montane cloud forests are one of the most endangered ecosystems and better understanding of growth rates of cloud forest trees is needed to design restoration strategies (Williams-Linera 1996, Williams-Linera 2002).

Studies of upper montane cloud forest sites have found annual diameter growth rates of < 1 mm year^{-1} (Weaver *et al.* 1986, Tanner *et al.* 1992, Walker *et al.* 1996). Saenz and Guariguata (2001) investigated growth rates of five species of seedlings and saplings in a Costa Rican montane forest following logging, and reported annual diameter growth rates of 1.8–3.0 mm year^{-1} for saplings with reduced competition from overstorey competition. Although these growth rates are for saplings rather than large trees in tropical montane forests, the data suggest that microsite conditions may influence growth rates as equally as macroclimatic influences such as cool temperatures, wind and low light levels with persistent cloud cover and fog.

The objectives of this study are to examine annualized diameter growth rate of cloud forest trees in an experimental plot in the Sierra de las Minas Biosphere Reserve, Guatemala over 5½ years and to compare the annualized diameter growth rate in Guatemala with those reported in other tropical forests. This paper provides the first account of the growth rates of cloud forest trees in the Sierra de las Minas, Guatemala.

MATERIALS AND METHODS

Site description

An examination of cloud forest tree growth was conducted within an upper montane cloud forest near the summit of Montaña de Miranda (15° 05' N, 90° 00' W) in the Sierra de las Minas Biosphere Reserve, Guatemala. The elevation of the study site is approximately 2550 m above sea level (asl) and is located approximately 10 km east of the village of Chilascó. The Sierra de las Minas is an east-west oriented mountain range in eastern Guatemala. North-east trade winds create extremely moist conditions along the northern slope of the Sierra de las Minas. Annual precipitation in the Sierra de las Minas exceeds 3000 mm, 80% of which occurs during the rainy season from May to October. Annual mist and fog precipitation is > 200 mm (Holder 2004, Holder 2006).

The Sierra de las Minas creates a rain shadow along the southern slope and the Río Motagua. Cloud forests occur above 2200 m asl on the leeward slope. Pine forests extend from approximately 800–2200 m along the leeward slope. Xerophytic vegetation occurs in the leeward Río Motagua valley below 800 m. The northern slope of the Sierra de las Minas is humid with dense stands of uninterrupted cloud forest from approximately 2000 m to the mountain summits. Below 2000 m are pine forests. Temperature is determined largely by elevation. Nightly low temperatures range from 5–15 °C. Slightly lower temperatures occur during the winter months. Elevations as low as 1300–1500 m in the Sierra de las Minas may experience occasional frost.

The Sierra de las Minas Biosphere Reserve was established in 1990 to protect the high diversity of plant and animal life in the evergreen cloud forest (Catling & Lefkovitch 1989, Ack & Lehnhoff 1992). Above 2000 m cloud forest species including a rich diversity of epiphytes and tree ferns are dominant (Hartshorn 2000). This vegetation type is classified as a lower montane cloud forest as the percentage cover of bryophytes is conspicuous from the lower elevations (Frahm & Gradstein 1991). The vegetation type along summits > 2400 m is classified as upper montane cloud forest based on the stunted trees and presence of mossy epiphytes, and may have formed at this elevation because of the *Massenerhebung* effect (Frahm & Gradstein 1991, Bruijnzeel *et al.* 1993). Tree ferns form a subcanopy in the cloud forest and the species dominant at 2550 m is *Cyathea divergens* var. *tuerkheimii.*

Field measurements

An experimental plot with an area of 0.24 ha subdivided into eight rectangular units of

10 × 30 m was established in December 1996 approximately 20 m from the ridge crest. A total of 433 trees, 60 tree ferns and 10 lianas with a diameter at breast height (dbh) ≥ 5 cm were marked with a nail and an aluminum tag for identification within the experimental plot. Each nail was positioned on the tree trunk at 1 m above the ground surface and dbh was measured 0.3 m above the nail with a diameter tape. Identification of species within the plot is incomplete. A plot map was drafted to illustrate the spatial organization of forest and location of potential gaps in the canopy. The terrain of the plot has considerable relief with a south-west aspect and a slope > 30° in most sections of the plot.

The marked vegetation was relocated and the dbh of each tree was remeasured at the same location on the tree trunk approximately 5½ years later in August 2002. Of the original vegetation marked, aluminum tags of only 100 trees, 9 tree ferns and 1 liana were relocated. To avoid errors in identifying trees with small diameters in the experimental plot, only the relocated trees with the original aluminum tags were evaluated in this study rather than attempting to relocate the original trees using the plot map drawn in December 1996. Growth rates over the 5½-year period were assessed on the basis of dbh growth increments.

RESULTS

Twenty-three percent of the trees, 15% of the tree ferns and 10% of the lianas marked with aluminum tags in December 1996 were relocated and remeasured in August 2002. These percentages of the found trees are approximately equal across the dbh classes from 5–30 cm and 60–65 cm (Figure 1). The percentage of the found trees to the original number varied from 0 to 14.3% for dbh classes 30–60 cm and > 65 cm. The mean dbh between the two years was significantly different (paired sample *t*-test, $p < 0.001$). The mean dbh of the 100 trees remeasured increased by 9.2%, i. e. from 11.4 cm in 1996 to 12.5 cm in 2002. This represents a mean annualized diameter growth rate of 2 mm year^{-1}. The range of dbh values varied from 5.0–70.9 cm in 1996 to 5.0–72.3 cm in 2002. The largest dbh class was 5.0–9.9 cm for both years (Figure 1). Sixty-two percent of the trees measured in 1996 were in the lowest dbh class compared with 58% of the trees in 2002.

Twenty-five trees had a greater dbh in 1996 than 2002, of which 19 decreased in dbh by < 0.5 cm (Figure 2). The dbh of four trees remained unchanged between 1996 and 2002. One tree that shrank in dbh died between 1996 and 2002, and was not reported in the data analysis. Trees

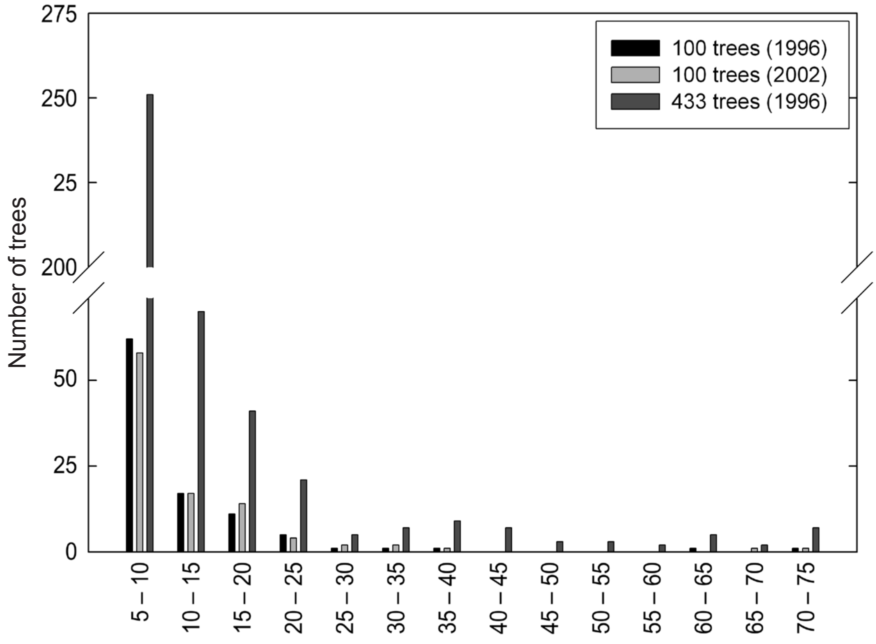

Figure 1 Dbh classes for 100 trees ≥ 5 cm measured in 1996 and remeasured in 2002 along with the original 433 trees ≥ 5 cm measured in 1996

with no growth or shrinkage were not clustered within the experimental plot. Dbh growth was not correlated with the original dbh of the tree ($r^2 = 0.05$, $p < 0.05$, Figure 3). A strong relationship existed between dbh in 1996 and dbh 2002. The model showed a significant relationship with an r^2 value of 0.97. The relationship between the percentage change in dbh and change in centimeters dbh between 1996 and 2002 was also significant, but with a weaker r^2 value of 0.67.

DISCUSSION

The mean annualized diameter growth rate of cloud forest trees in the Sierra de las Minas (2 mm year^{-1}) is comparable with other results from

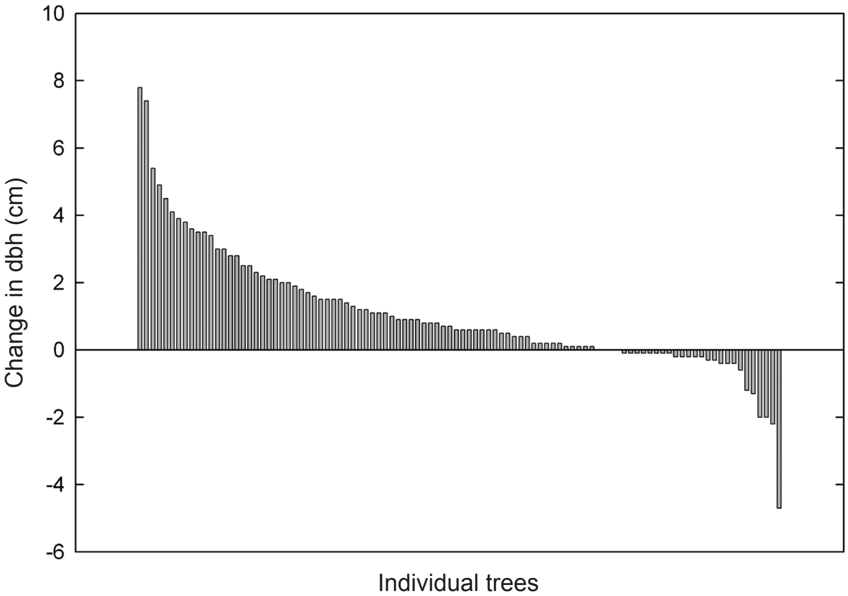

Figure 2 Change in dbh of 100 individual trees measured between 1996 and 2002. Note that 25% of the trees decreased in dbh over the 5½ year period.

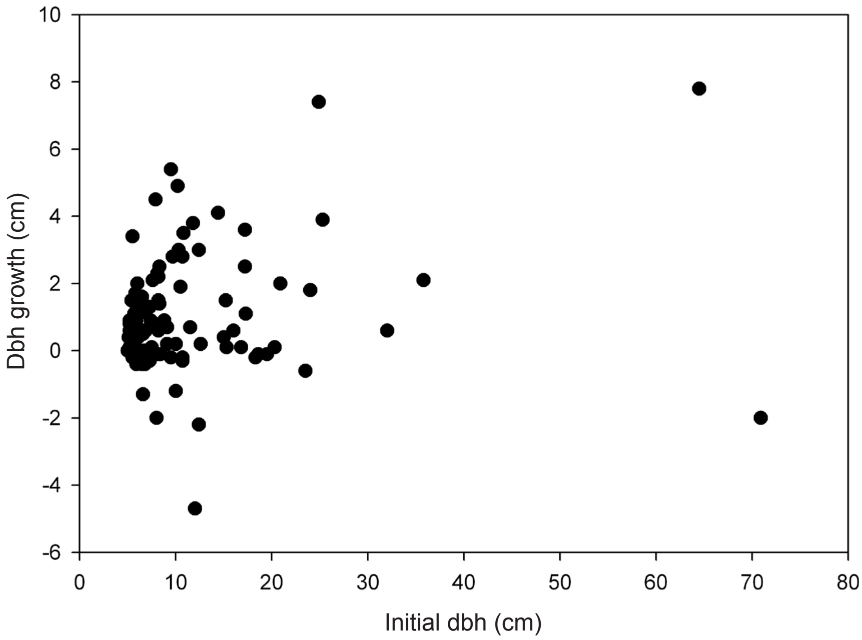

Figure 3 Relationship between growth in dbh (cm) over 5½ years and the original dbh of 100 trees ≥ 5 cm measured in 1996 and remeasured in 2002 ($r^2 = 0.05$, $p < 0.05$)

published studies in tropical ecosystems (Table 1). Comparisons with other neotropical upper montane forests such as in Puerto Rico (Weaver *et al.* 1986, Walker *et al.* 1996), Jamaica (Bellingham & Tanner 2000), and Venezuela (Tanner *et al.* 1992) indicate that the cloud forest of the Sierra de las Minas has a larger annualized diameter growth rate. Herwitz and Young (1994) reported a larger annualized diameter growth rate in a montane rain forest of Australia.

Although dbh was recorded at the same location on the trunk in 1996 and 2002, measurement errors may still be likely. Clark and Clark (1992) reported in their study of a lowland forest in Costa Rica that saplings < 4 cm in diameter measured with callipers may have a measurement error of ± 0.3 mm and trees > 4 cm in diameter measured with a diameter tape may also have a measurement error of ± 0.3 mm. Oberbauer *et al.* (1993) reported measurement errors of ± 0.4 mm in measuring small saplings with callipers. Provided the measurement errors using a diameter tape, 25% of the trees remeasured in the Sierra de las Minas had a larger dbh in 1996 than in 2002, and four trees showed no growth in dbh between 1996 and 2002.

A total of 23% of the initial trees measured in December 1996 were relocated and remeasured in August 2002. The tags of small or rapidly growing trees may have ingrown as reported in previous studies (Jönsson *et al.* 2007). Assuming a 2% annual mortality (Phillips & Gentry 1994), approximately 45 trees may have died. Although social paths are common in the forest, it is not likely that the tags were vandalized because the spatial distribution of the remaining trees with tags in the experimental plot was not clustered. The remaining tagged trees in the forest were representative of the total forest and similar to other tropical cloud forests. Of the individual trees measured in the Sierra de las Minas in August 2002, 42% had a dbh ≥ 10 cm. Kappelle *et al.* (1996) reported 66% of trees had dbh > 10 cm in a cloud forest in Costa Rica. Only 2% of trees we measured in 2002 were > 50 cm. In a permanent plot of Monteverde, Costa Rica > 20% of trees had dbh > 50 cm (Matelson *et al.* 1995). Trees with large dbh provide habitats for a different association of epiphytes from trees with small dbh in the Sierra de las Minas (Catling & Lefkovitch 1989).

Several long-term studies of annual diameter growth in tropical trees have established that no growth is common. Several understorey species of a lowland rainforest in Costa Rica showed no growth over a 13-year period (Lieberman & Lieberman 1987). In another study, it was reported that 20% of the trees measured with dendrometers over a four-year period in a tropical montane forest in Jamaica exhibited no growth in dbh (Tanner 1980). Drought may influence the dbh of trees sampled in long-term studies of annualized diameter growth rates as tree shrinkage may result from a decrease in soil moisture (Baker *et al.* 2002, Sheil 2003, Intrigliolo & Castel 2006, Martínez Pastur *et al.* 2007). For example, 2002 was a drier year in Guatemala than 1996. The decrease in precipitation may result in a decrease in dbh given that vascular tissues in the stem may contract with the loss of turgor.

This study found that the dbh of 29 trees in the Sierra de las Minas remained unchanged or decreased over a 5½-year period. Negative growth of trees in experimental plots has been reported in several published studies (Condit *et al.* 1993, Herwitz & Young 1994, Milton *et al.* 1994, Burslem *et al.* 1998, Clark & Clark 1999, Connor & Inabinette 2003). Individual trees with decreases in dbh are often considered outliers and are deleted from data analysis (Herwitz & Young 1994, Milton *et al.* 1994, Clark & Clark 1999, King *et al.* 2005, King *et al.* 2006).

Although a large percentage of trees in the Sierra de las Minas experienced no growth or a decrease in dbh, the overall mean dbh of the 100 cloud forest trees sampled increased from 11.4 cm in 1996 to 12.5 cm in 2002 representing an annualized diameter growth rate of approximately 2 mm $year^{-1}$. This growth rate is larger than those reported in upper montane forests of Venezuela (Tanner *et al.* 1992) and Puerto Rico (Weaver *et al.* 1986, Walker *et al.* 1996), and Jamaica (Bellingham & Tanner 2000). The rate of growth would be larger if trees that experienced unchanged or decreased dbh were not included in the data analysis as previous studies have done.

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Table 1 Comparisons of the mean annual diameter growth between this study and other studies from tropical ecosystems

Location	Elevation (m)	Growth rate (mm year^{-1})	Methods	Vegetation type	Reference
Australia	1582	2.7	Measuring tape	Montane rain forest	Herwitz & Young (1994)
Australia	700	1.6	Measuring tape	Submontane rain forest	Herwitz *et al.* (1998)
Brazil	50–100	0.25–7.01	Measuring tape	Moist lowland forest	Laurance *et al.* (2004)
Costa Rica	35–137	1.9–5.2	Measuring tape	5 species; lowland rainforest	Clark & Clark (1996)
Costa Rica	37–150	0.9–14.1		6 species; lowland rainforest	Clark *et al.* (2003)
Costa Rica	35–137	0.2–0.6	Callipers	3 species; saplings; lowland forest	Oberbauer *et al.* (1993)
Costa Rica	2600–2800	1.8–3.0	Measuring tape	5 species; saplings; montane forest	Saenz & Guariguata (2001)
Guatemala	2550	2.0	Measuring tape	Upper montane cloud forest	This study
Jamaica	1580–1740	0.4–0.9	Measuring tape	Montane rain forest	Bellingham & Tanner (2000)
Malaysia		2.4–4.6	Measuring tape	11 species; dipterocarp forest	Davies (2001)
Malaysia	100–240	0.63–6.08	Measuring tape	Dipterocarp forest	King *et al.* (2005)
Malaysia	30	0.8–4.9	Measuring tape	Lowland dipterocarp forest	Manokaran & Kochummen (1987)
Malaysia		0.4–3.0	Measuring tape	Moraceae trees; dipterocarp forest	Primack *et al.* (1985)
Malaysia	0	0.9–3.5	Measuring tape	2 species; mangrove forest	Putz & Chan (1986)
Mexico	10	0.6–1.2	Measuring tape	Secondary tropical dry forest	Campo & Vázquez-Yanes (2004)
Nicaragua	< 300	0.4–2.6	Measuring tape	Tropical dry forest	Marín *et al.* (2005)
Nicaragua	< 300	1.6–2.8	Measuring tape	Gallery forest	Marín *et al.* (2005)
Panama	< 200	0.49–0.96	Measuring tape	Moist lowland forest	Condit *et al.* (2004)
Panama	30–200	0–11.5	Measuring tape	Moist lowland forest	Lang & Knight (1983)
Peru		4.0–6.8	Measuring tape	Floodplain forest	Nebel *et al.* (2001)
Puerto Rico	180–600	2.5–8.1	Measuring tape	Lower montane rain forest	Crow & Weaver (1977)
Puerto Rico	350–500	3.0	Dendrometers	Moist lowland forest	Walker *et al.* (1996)
Puerto Rico	1050	0.25	Dendrometers	Montane elfin forest	Walker *et al.* (1996)
Puerto Rico		0.2–1.1	Measuring tape	Subtropical dry forest	Weaver (1979)
Puerto Rico		0.1–3.9	Measuring tape	Subtropical moist forest	Weaver (1979)
Puerto Rico		4.6	Measuring tape	Mangrove forest	Weaver (1979)
Puerto Rico		0.0–5.8	Measuring tape	Lower montane forest	Weaver (1979)
Puerto Rico	450–1000	0.3	Measuring tape	Elfin cloud forest	Weaver *et al.* (1986)
Venezuela	2450–2650	0.5–0.6	Dendrometers	Montane rain forest	Tanner *et al.* (1992)
Zambia	1260	0.8–2.6	Measuring tape	7 species; wooded savanna	Chidumayo (2005)

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