

Dynamic equilibrium and decelerating growth of a seasonal Neotropical gallery forest in the Brazilian savanna

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Abstract: Describing and understanding growth patterns in tropical forests is crucial to assessing their role in carbon balance. Growth and vital rates of protected gallery forest in central Brazil were estimated, based on six measurement intervals between 1985 and 2009. The sample consisted of all stems ≥ 10 cm diameter at breast height measured in 151 permanent plots (10 × 20 m), distributed in 10 transects perpendicular to the watercourse and 100 m apart from each other. Statistical significance of changes in density, basal area, growth and vital rates were tested using Wilcoxon signed-rank test. Vital rates oscillated during the study period. Growth, recruitment and turnover rates fluctuated, but had a net decrease over the whole study period, whereas mortality seemed to be affected by a high disturbance event during the 1994–1999 period. The oscillatory behaviour of growth suggests that the forest is pulsating around a stable state (dynamic equilibrium). Nonetheless, persistence of decelerating growth trends may force the site's carrying capacity to a lower density or biomass state.

Key Words: dynamic equilibrium, forest dynamics, forest growth, gallery forest, riparian forest, savanna, tropical forest

INTRODUCTION

Detecting growth patterns in tropical forests can help recognize their role either as carbon sinks or as sources in response to climatic changes. Long-term studies based on permanent plots in tropical forests worldwide have shown contradictory trends. Several studies demonstrated that Amazon rain forests have been functioning as carbon sinks since the 1980s (Baker *et al.* 2004, Laurance *et al.* 2009, Lewis *et al.* 2004a, b; Phillips & Gentry 1994, Phillips *et al.* 2004). However, the vulnerability of rain forests to increasing moisture stress can turn them into sources and cause great impact on carbon balance (Phillips *et al.* 2009). These authors reported decelerating growth in Amazon forests in response to a drought event in 2005. Others have found decelerating growth rates in La Selva, Costa Rica (1984–2000) (Clark 2003), Barro Colorado Island, Panama (1985–2005) and Pasoh, Malaysia (1986–2000) (Feeley *et al.* 2007).

Tropical forests vary in how they respond to increasing global temperatures and CO₂ levels because of regional and historical differences. Regional climatic differences between Amazon rain forests and seasonal Neotropical forests (subject to seasonal drought) may lead to different trends between them. Detecting responses of seasonal tropical forests to high temperature and low precipitation may offer important insights on their role in terrestrial carbon balance and the forces driving tropical forest dynamics. However, most long-term dynamics studies rely on few measurement intervals. Changes between two successive periods (single changes) may express transient dynamics of the forest rather than a dominant trend in growth and vital rates, especially for shorter census intervals. On the other hand, single long-term intervals can overlook important changes within the period, which may be revealing of forest dynamics. Understanding short-term and successive behaviour of forests can help determine their response to environmental changes and help management and conservation strategies.

The present work examines stand growth, mortality and recruitment rates of a tropical gallery forest in the Brazilian savanna for six successive periods, spanning

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² *In Memoriam.*

Table 1. Annual precipitation (mm) and mean annual temperature (°C) between 1984 and 2009, recorded close to the study area, at the Brazilian Institute of Geography and Statistics' Ecological Reserve (RECOR-IBGE). * = forest inventory census years in the present study.

Year	Mean annual temperature (°C)	Annual precipitation (mm)	Year	Mean annual temperature (°C)	Annual precipitation (mm)
1984	22.2	1141	1997	22.4	1479
1985*	21.1	1416	1998	23.1	1334
1986	21.5	881	1999*	23.3	1207
1987	22.1	1676	2000	22.2	1706
1988*	21.6	1257	2001	22.1	972
1989	22.1	1598	2002	22.2	1000
1990	22.5	1172	2003	22.3	1188
1991*	21.0	1624	2004*	22.0	1253
1992	21.4	1559	2005	22.4	1652
1993	22.4	1543	2006	22.0	1667
1994*	22.6	1604	2007	22.8	1184
1995	22.6	1684	2008	22.3	1607
1996	22.5	1384	2009*	22.1	1419

61 a 24-y period (1985–2009). We described size-class
62 dynamics of the forest in another paper (Roitman &
63 Vanclay 2015). Here we hypothesize that, although the
64 forest is protected from direct human disturbances, it is
65 not undergoing accelerated growth.

66 METHODS

67 Gallery forests

68 In Central Brazil's savanna biome, called cerrado,
69 the climate is marked by alternating wet and dry
70 seasons. Cerrado gallery forests are riparian forests
71 bordering narrow rivers. They play a strategic role
72 in biodiversity conservation and act as natural forest
73 corridors connecting the Amazon and Atlantic rain forests
74 (Oliveira-Filho & Ratter 1995). These riparian forests are
75 adapted to seasonal climate and are naturally exposed
76 to higher levels of disturbance, due to border effects
77 and, sometimes, flooding regime (Appolinário *et al.* 2005,
78 Fontes & Walter 2011). The watercourse provides a soil
79 humidity gradient, which determines a compositional
80 shift from fire- and drought-resistant outer edge species to
81 inner forest species that are shade-tolerant and sensitive
82 to fire and drought (Silva Júnior 2001).

83 Study site

84 The Gama gallery forest covers 64 ha in the East-Central
85 region of Brazil, near the city of Brasília (~ 16°S, 48°W)
86 at an altitude of approximately 1100 m asl. It is located
87 in the University of Brasília's experimental field station.
88 Permanent plots were established in 1985 (Felfili 1993),
89 and are one of the oldest sets of permanent plots in gallery
90 forests.

The southern side of the forest is bordered by natural
dry grassland vegetation, called campo limpo, with an
abrupt transition between the two vegetation types, and
the northern side is bordered by a road and suburban
housing, both outside the limits of the field station. The
soil is well-drained, dystrophic, with high aluminium
saturation and low nutrient concentration (Felfili 1993).

The regional climate is Aw, according to Köppen's
(1900) classification, with marked rainy and dry seasons.
Long-term temperature and rainfall data were obtained
from the meteorological station at the Brazilian Institute
of Geography and Statistics' Ecological Reserve (RECOR-
IBGE) approximately 10 km east of the study area
([http://www.recor.org.br/cid360/download/17-dados-
meteorológicos.html](http://www.recor.org.br/cid360/download/17-dados-meteorológicos.html)).

Mean annual rainfall between 1985 and 2009
was 1403 mm, with a mean annual temperature of
22.2°C. These values are within the range observed
for historical series since 1965 ([http://www.inmet.
gov.br/projetos/rede/pesquisa/](http://www.inmet.gov.br/projetos/rede/pesquisa/)). General trends show
temperature increases after 1991, and that low-rainfall
years became more frequent after 1994 (Table 1). The
1991–1994 period was marked by an increase in mean
annual temperature (from 21°C to 22.6°C) and relatively
high precipitation in all years (between 1543 to 1684
mm). In the following five years (1994–1999), mean
annual temperature remained high (and reached its peak
in 1999) but rainfall was low, especially in the years 1998
and 1999.

Floristic structure

In 1985, the Gama gallery forest contained 106 tree
species distributed in 52 families. Species richness
gradually increased to 112 in 2009. The richest families
were Myrtaceae, Rubiaceae, Lauraceae, Fabaceae,

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125 Apocynaceae and Vochysiaceae. Lists of species recorded
 126 since 1985 are given in Felfili (1993), Oliveira &
 127 Felfili (2008) and Roitman (2011). Species abundance
 128 distribution was typical of tropical forests, with more than
 129 half of the species represented by 10 stems or fewer, and
 130 the 10 most abundant species comprised almost half of
 131 the total number of stems. The strong presence of shade-
 132 tolerant species and the small number of pioneer species
 133 and trees suggests that this gallery forest is in a late-
 134 successional stage. In 1985, there was a large proportion
 135 of shade-tolerant (49.1%) and light-demanding species
 136 (41.5%), with relatively few pioneers (9.43%). Shade-
 137 tolerant trees also comprised 55.1% of tree numbers
 138 and 40.1% of basal area, while pioneers comprised
 139 only 2.29% of trees and 1.87% of basal area (Felfili
 140 1993). These proportions remained relatively constant
 141 throughout the study period. The five most dominant
 142 species in 1985, in terms of relative abundance and basal
 143 area, were *Lamanonia ternata* Vell., *Copaifera langsdorffii*
 144 Desf., *Aspidosperma olivaceum* Müll. Arg., *Licania apetala* (E.
 145 Mey.) Fritsch and *Metrodorea stipularis* Mart. Most of the
 146 dominant species have maintained their relative density
 147 and basal area since 1985 (Roitman 2011).

148 Sample

149 Sampling followed a systematic strip sampling design
 150 (Felfili 1995), with 151 contiguous permanent plots
 151 (10 × 20 m), divided in 10 transects perpendicular to
 152 the main watercourse, 100 m apart, sampling a total
 153 area of 3.02 ha. A topographic survey was made prior to
 154 plot establishment for topographical corrections. Transect
 155 length varied with forest width. Transect 5 was the
 156 shortest, with seven plots, whilst transect 9 contained 32
 157 plots. The initial measurements were made in 1985 with
 158 subsequent censuses in 1988, 1991, 1994, 1999, 2004
 159 and 2009. All stems with girth at breast height ≥ 31 cm
 160 (~10 cm diameter at breast height (dbh)) were mapped,
 161 marked with permanent tags, and measured with a girth
 162 tape. In cases of trunk anomalies, such as buttress roots or
 163 termite colonies, measurements were taken 2 cm above
 164 imperfections. Tags missing in subsequent measurements
 165 were replaced.

166 Analysis

167 Mortality and recruitment rates were based on
 168 the Lieberman *et al.* (1985) model for instant
 169 mortality: $m = 100 \cdot \frac{[\ln(N_0) - \ln(N_0 - N_m)]}{t}$ and $r =$
 170 $100 \cdot \frac{[\ln(N_0) - \ln(N_0 + N_r)]}{t}$, where m = mortality rate, r = re-
 171 cruitment rate, N_0 = number of trees at time t_0 , N_m =
 172 number of trees that died during the period, N_r = number
 173 of trees recruited during the period and t = time.

Forest growth was described in terms of the rate
 of basal area increase, as follows: $BA_I = 100 \cdot$
 $\frac{[\ln(BA_0) - \ln(BA_0 + BA_r - BA_g)]}{t}$, where: BA_I = basal area
 increase rate, BA_0 = basal area at time t_0 (m^2), BA_r =
 basal area gain due to recruitment (m^2), BA_g = basal area
 gain due to growth of surviving trees. We tested statistical
 significance of changes in structure and dynamics with
 Wilcoxon signed-rank test ($P < 0.05$), using each transect
 as a point sample.

The rate of basal area decrease included loss
 by mortality and stem loss of living trees: $BA_D =$
 $100 \frac{[\ln(BA_0) - \ln(BA_0 - BA_M - BA_d)]}{t}$, where BA_D = basal area
 decrease rate, BA_0 = basal area at time t_0 , BA_M = basal
 area loss due to mortality, BA_d = basal area loss due to
 decrement of surviving trees.

RESULTS

Density and basal area

In 1985, tree density was 650 ind. ha^{-1} and basal area
 was 30.6 $m^2 ha^{-1}$ (Table 2). In 2009, density and basal
 area decreased by 4.89% and 6.52%, respectively (not
 significant, $P > 0.05$) (Table 3). Basal area loss due
 to shrinkage or bark loss was less than 1.03% in all
 measurement intervals and most basal area increase was
 due to growth of surviving trees rather than recruitment.
 Density and basal area had no significant change between
 successive years (Table 3), except for year 1999, when
 both reduced significantly.

Growth and survival rates

Growth, recruitment and turnover rates oscillated, but
 had a net decrease for the whole study period (Table 2).
 Growth decreased significantly in the 1994–1999 period,
 and all subsequent growth rates were significantly smaller
 than in the first census interval (Table 4). Greatest
 growth was observed in the first (1985–1988) and
 third measurement periods (1991–1994). Growth had
 an oscillatory behaviour: an increase in BA_I immediately
 followed a decrease, and vice-versa. All other rates had at
 least one consecutive reduction or increase (Figure 1).
 After 1994, successive changes in BA_I became more
 pronounced (significant at $P < 0.05$) (Table 4).

Mortality varied little in the first three census intervals
 (Table 4). In the following period (1994–1999), mortality
 increased significantly and presented the highest observed
 mortality (4.10% y^{-1}). This elevated mortality may have
 contributed to the substantial reduction ($P < 0.05$) in
 mortality for the following period (1.62% y^{-1}). Mortality
 directly affects BA_D and, therefore, both had similar
 behaviour (Figure 1), except for period 1991–1994, in
 which mortality increased but BA_D decreased in relation

Table 2. Structure and dynamics of the Gama gallery forest for six successive periods between 1985 and 2009. Where d = density, m = mortality rate, r = recruitment rate, BA = basal area, Ste (transects) = standard error among transects, SE (plots) = standard error among plots, BA_I = rate of basal area increase (growth), BA_D = rate of basal area decrease, MA_I = mean annual increment in diameter, t_{1/2} = half-life, t₂ = duplication time.

Measurement year Period	1985	1988 1 st	1991 2 nd	1994 3 rd	1999 4 th	2004 5 th	2009 6 th	2009 1985—2009
d (trees ha ⁻¹)	650	645	652	637	593	617	618	
Dead trees	198	170	194	357	139	215	951	951
Recruits		185	189	151	224	211	217	855
m (% y ⁻¹)		3.55	3.04	3.46	4.1	1.62	2.45	2.76
r (% y ⁻¹)		3.00	3.09	2.46	2.2	2.23	2.2	1.51
Tree turnover (% y ⁻¹)		3.28	3.06	2.96	3.15	1.92	2.33	2.14
t _{1/2} (y)		19.2	22.4	19.7	16.5	42.6	27.9	24.7
t ₂ (y)		23.4	22.8	28.5	31.8	31.5	31.8	46.3
BA (m ² ha ⁻¹)	30.59	30.3	30.1	30.3	29.1	30.0	28.6	28.6
BA SE (transects)	0.697	0.752	0.618	0.617	0.743	0.812	0.758	0.697
BA SE (plots)	0.001	0.001	0.001	0.001	0.002	0.002	0.002	0.001
BA loss (mortality) (m ² ha ⁻¹)		2.68	2.15	2.07	4.15	2.34	3.52	13.58
BA loss (decrement) (m ² ha ⁻¹)		0.00	0.00	0.00	0.00	0.02	0.31	0.01
BA gain (growth) (m ² ha ⁻¹)		1.80	1.34	1.77	2.15	2.54	1.71	7.20
BA gain (recruitment) (%)		1.80	1.34	1.77	2.15	2.54	1.71	7.20
MA _I (cm y ⁻¹)		0.58	0.61	0.50	0.83	0.71	0.71	4.39
BA _D (% y ⁻¹)		0.26	0.21	0.26	0.21	0.24	0.14	0.2
BA _I (% y ⁻¹)		3.05	2.46	2.37	2.95	1.69	2.73	2.45
BA turnover (% y ⁻¹)		2.78	2.27	2.40	2.41	1.90	2.14	1.89

Table 3. Results of Wilcoxon's paired test to detect changes in tree density and basal area in the Gama gallery forest between 1985 and 2009.

Year	1988	1991	1994	1999	2004	2009
Density						
1985	0.60	0.95	0.26	0.01	0.24	0.45
1988		0.31	0.50	0.04	0.04	0.65
1991			0.08	0.03	0.21	0.51
1994				0.04	0.51	0.72
1999					0.06	0.06
2004						0.72
Basal area						
1985	0.58	0.51	0.80	0.08	0.51	0.11
1988		0.20	0.21	0.08	0.65	0.10
1991			0.24	0.14	0.96	0.29
1994				0.02*	0.51	0.08
1999					0.24	0.51
2004						0.09

223 to the previous census interval. In this interval, fewer
 224 larger trees suffered mortality. Recruitment decreased
 225 after 1991 (Figure 1). Changes in recruitment had no
 226 statistical significance ($P > 0.05$) but caused significant
 227 reduction ($P < 0.05$) in tree turnover rates (Tables 2
 228 and 3).

229 DISCUSSION

230 Census interval effect

231 Considering the effect of census interval size on growth
 232 and vital rates, mortality rate for the total period

(24 y) was mostly smaller than mortality for shorter
 233 census intervals (3- and 5-y intervals) (Table 1), whereas
 234 recruitment for the total period was significantly smaller
 235 than for all other census intervals (Table 3). Thus, the
 236 present study empirically confirmed the notion that
 237 mortality and recruitment rate should decrease with
 238 census intervals (Korning & Balslev 1994, Lewis *et al.*
 239 2004b, Lieberman *et al.* 1985, Sheil & May 1996,
 240 Sheil *et al.* 1995). On the other hand, short intervals
 241 are more sensitive to environmental stochasticity and,
 242 therefore, mortality rates are not always smaller in
 243 shorter intervals. Mortality rate for the last two census
 244 intervals was smaller than mortality for the total
 245 period. Mortality rate decreases with census interval
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Table 4. Results of Wilcoxon's paired test to detect changes in basal area increase, mortality, recruitment and turnover rates between 1985 and 2009.

Period	Basal area increase rate					
	1988–1991	1991–1994	1994–1999	1999–2004	2004–2009	1985–2009
1985–1988	0.22	0.22	0.04	0.05	0.04	0.00
1988–1991		0.40	0.22	0.22	0.12	0.07
1991–1994			0.03	0.12	0.05	0.01
1994–1999				0.04	0.17	0.22
1999–2004					0.04	0.00
2004–2009						0.36
Mortality rate						
1985–1988	0.09	0.51	0.33	0.02	0.04	0.07
1988–1991		0.58	0.09	0.06	0.28	0.96
1991–1994			0.04	0.03	0.04	0.06
1994–1999				0.01	0.01	0.01
1999–2004					0.06	0.01
2004–2009						0.06
Recruitment rate						
1985–1988	0.68	0.33	0.33	0.33	0.17	0.01
1988–1991		0.07	0.14	0.14	0.11	0.01
1991–1994			0.96	0.65	0.58	0.01
1994–1999				0.88	0.88	0.01
1999–2004					0.58	0.01
2004–2009						0.02
Turnover rate						
1985–1988	0.68	0.14	0.88	0.01	0.04	0.01
1988–1991		0.44	0.80	0.02	0.11	0.02
1991–1994			0.24	0.03	0.09	0.02
1994–1999				0.01	0.01	0.01
1999–2004					0.04	0.17
2004–2009						0.24

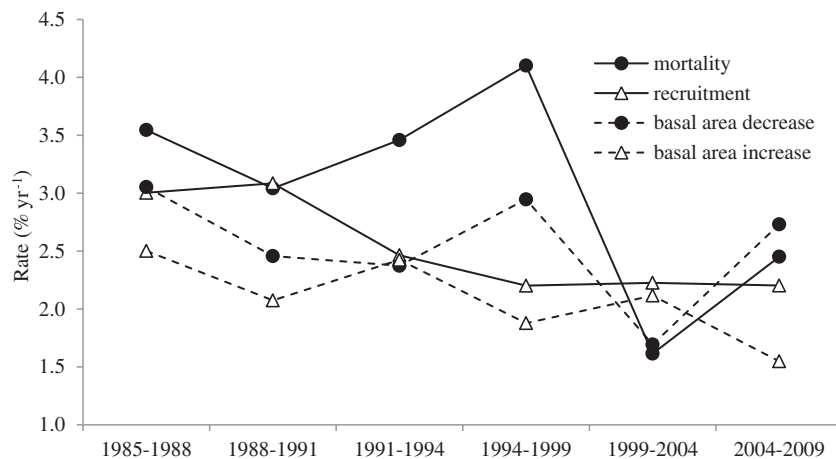


Figure 1. Forest dynamic rates (rates of mortality, recruitment, basal area increase, and basal area decrease) observed in the Gama gallery forest between 1985–2009.

247 length because longer intervals do not include trees
 248 that recruited and died within the census interval. For
 249 example, in the longest census interval (24 y), mortality
 250 rate ignored 322 trees that had recruited after 1985 but
 251 died by 2009. Since mortality is often higher among

smaller trees, such as new recruits, the census interval
 effect on mortality of recruits is higher than it is for
 overall mortality. Recruitment rates based on longer
 calibration periods tend to be smaller for the same
 reason.

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Table 5. Mortality, recruitment and mean annual increment found in gallery forests in the Brazilian savanna.

Location: city, state abbreviation	Sample (ha)	m (% y ⁻¹)	r (% y ⁻¹)	MA _I (cm y ⁻¹)	Period	Reference
Brasília, DF	3.02	2.76	1.51	0.20	1985–2009	present study
Brasília, DF	0.66	5.55	1.42	0.20	1994–2005	Braga & Rezende 2007
Brasília, DF	0.8	4.25	3.67	0.22	2000–2008	Fontes & Walter 2011
Poços de Caldas, MG	1.01	1.88	1.28	–	1998–2005	Guimarães <i>et al.</i> 2008
Uberlândia, MG	0.3	2.85	1.88	–	1989–2002	Lopes & Schiavini 2007
Nova Xavantina, MT	0.5	1.5	2.3	–	1999–2006	Marimon <i>et al.</i> 2014
Nova Xavantina, MT	0.5	2.92	2.99	–	1999–2006	Marimon <i>et al.</i> 2014
Nova Xavantina, MT	0.5	5.79	7.12	–	1999–2006	Marimon <i>et al.</i> 2014
Chapada dos Guimarães, MT	1.08	2.68	3.25	0.21	1996–1999	Pinto 2002

257 Forest deceleration and driving forces

258 Mortality, recruitment and mean annual increment rates
 259 in the Gama forest are within the range found in
 260 other gallery forests in the Brazilian savanna (Table 5).
 261 Seasonal tropical gallery forests are highly dynamic
 262 and imbalances in favour of mortality are common
 263 and represent natural fluctuations of dynamic systems
 264 (Felfili 2000). Growth, recruitment and turnover rates
 265 fluctuated, but had a net decrease for the whole study
 266 period, whereas mortality seemed to be affected by a
 267 high disturbance event during the 1994–1999 period.
 268 The observed decelerating growth trend after 1994
 269 coincides with the rise in mean annual temperature.
 270 The 1994–1999 period had highest mortality and BA_D
 271 (influenced by high mortality of large trees), and low
 272 recruitment and growth rates. In this period, there was
 273 a combination of high temperature and low precipitation
 274 (especially in the years 1998 and 1999). In the following
 275 period (1999–2004), there were 4 y of low precipitation,
 276 which may have prevented a stronger growth response
 277 of the forest. Observed trends in temperature and
 278 precipitation suggest that higher temperatures and low
 279 rainfall may be contributing to decreases in growth and
 280 recruitment and abnormal mortality rates. However,
 281 statistical confirmation of such hypotheses was not
 282 possible because of the small number of measurement
 283 periods (six) and the nature of the data set: census intervals
 284 are of 3 and 5 y, whereas precipitation and temperature
 285 data are annual, and their anomalies and effects are
 286 dissipated over the census intervals.

287 In the Brazilian savanna, basal area or biomass increase
 288 has been reported for closed woodland forests, such
 289 as dry forests (Carvalho & Felfili 2011) and gallery
 290 forests (Guimarães *et al.* 2008, Lopes & Schiavini 2007),
 291 and for Amazon-savanna transition-zone gallery forests
 292 (Marimon *et al.* 2014, Pinto & Hay 2005). Our results
 293 show an opposite trend for the Gama gallery forest, and
 294 suggest that the combination of high temperature and
 295 low precipitation may be a limiting factor for carbon
 296 assimilation in gallery forests. In seasonal tropical regions,

reduced growth and high mortality are often associated
 with years of high temperature and low rainfall, as in El
 Niño episodes (Clark 2004). Laurance *et al.* (2009) found
 increasing mortality rates between 1981 and 2003 in
 Amazon, associated to ENSO. In the Amazon-savanna
 transition zone, Marimon *et al.* (2014), reported biomass
 reduction of monodominant (1996–2010) and semi-
 deciduous forests (2003–2008) after a drought event in
 2005. Braga & Rezende (2007) also observed reduction
 in density and basal area in a gallery forest close to the
 Gama gallery forest (1994–2005).

Dynamic equilibrium

Reduced growth and imbalance in favour of mortality
 caused non-significant reduction in density (4.89%) and
 basal area (6.52%). Forests are dynamic systems and their
 growth and vital rates should vary around an assumed
 stability point. If this assumption is true, then in mature
 and stable forests it should be possible (and perhaps
 expected) to detect such a pattern in turnover and growth
 rates, using long-term observation of permanent plots.
 The long-term (24 y) and fine-scale assessment (3- and
 5-y census intervals) of the study allowed us to detect an
 oscillatory pattern of growth. This balanced behaviour
 shows that growth responses to changes are fast, and
 suggests that the forest is pulsating around a stable
 state (dynamic equilibrium). Nonetheless, persistence
 of decelerating trends, due to high frequency of high
 temperature and low precipitation events, may force the
 site's carrying capacity to a lower density or biomass state.
 On-going monitoring is needed to show whether the forest
 will continue to oscillate around a stable state or trend
 toward a lower biomass one.

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