

Chapter 2

Forest Structure

Abstract This chapter reviews the literature on forest structure. There is no overall measure to quantify or express forest structure, and foresters measure a variety of attributes—aboveground biomass, abundance, basal area, canopy height, plant density—each of which contribute to the overall structure, but do not, individually, describe it completely. Studies reported great variations in the time needed for the various attributes to reach old-growth forest levels, which implies that the conditions or characteristics of the forest play a part in altering the regeneration of forest structure during succession. Authors also highlighted the importance of local species composition on influencing the changes in vegetation, which is seldom mentioned or examined in studies of forest succession.

Keywords Forest structure • Biomass • Trees abundance • Herbs abundance • Basal area • Canopy height • Plant density

2.1 Introduction

There is no overall measure to quantify or express forest structure, and foresters measure a variety of attributes—aboveground biomass, abundance, basal area, canopy height, plant density—each of which contribute to the overall structure, but do not, individually, describe it completely. This is well reflected in the dictionary definition of structure: “a complex system considered from the point of view of the whole rather than of any single part”. It is meaningless to simply add together the various measures, and produce some average quantification of forest structure. Hence, in this chapter we review the literature on changes in total aboveground biomass, total basal area, tree and herb abundance, canopy height and plant density in separate sections.

2.2 Total Aboveground Biomass

To estimate the changes in abundance of vegetation along ecological succession processes, total aboveground biomass and total basal area are commonly measured. Both measurements are calculated from stem diameters, thus are not independent of each other (Chazdon et al. 2007; Clark and Clark 2000). However, many think that aboveground biomass more accurately reflects the conditions of the study site (Chazdon et al. 2007; Brown 1997). Studies on the aboveground biomass have reached different conclusions. Some studies have shown that aboveground biomass increases with fallow age, while others have found that total aboveground biomass increases at first, but then remain constant. The two cases are now reviewed in turn.

2.2.1 Aboveground Biomass Increases with Fallow Age

In the mixed deciduous forest of central Burma, Fukushima et al. (2007) found a constant increase in total aboveground biomass (including herbs and grass) in relation to fallow length. The authors adopted the allometric equations of Ogawa et al. (1965) for the calculation of tree biomass:

$$\begin{aligned} W_s &= 0.0396(\text{DBH}^2H)^{0.9326}, \text{ (kg, cm}^2\text{m)} \\ W_b &= 0.00602(\text{DBH}^2H)^{1.027}, \text{ (kg, cm}^2\text{m)} \\ 1/W_l &= 26/(W_s + W_b), \text{ (kg, kg)} \end{aligned}$$

where W_s is the dry weight of the stem, W_b is the dry weight of branches and W_l is the dry weight of the leaves of a tree. For herbs and grasses, samples were collected and weighed after drying in an oven. Fukushima et al. (2007) reported that the total aboveground biomass contained 6.6 t/ha in the first year of fallow, then increased to 55.0 t/ha in the fifth year, and eventually reached 150.0 t/ha in year 40. 43.3–52.9 % of the total aboveground biomass of the old-growth forest was attained between 10 and 18 years after abandonment, and increased to 93.6 % approximately 40 years after abandonment.

Studies carried out in the upper Rio Negro (Uhl 1987), northern Thailand (Fukushima et al. 2008) and the southern Yucatan Peninsular region of Mexico (Read and Lawrence 2003) also found a general trend towards increases in aboveground biomass. In the permanent plots study carried out in the upper Rio Negro region, total aboveground biomass increased from the first year to the fifth year of fallow from 708 to 3,386 g/m² (Uhl 1987). In northern Thailand, Fukushima et al. (2008) carried out a chronosequence study of fallows with stand ages from 20 to 49 years of age. Allometric relations were used to calculate the aboveground biomass. For fallow stands between 20 and 29 years of age, the values of aboveground biomass ranged from 94 to 146 t/ha, with a median of 130 t/ha. For fallows that were 30–49 years old, the aboveground biomass values were

127–305 t/ha, with a median of 236 t/ha, higher than in fallows between 20 and 29 years old.

Read and Lawrence (2003) conducted a chronosequence study conducted in the dry tropical forest of Yucatan, Mexico, sampling a total of 36 fallow stands ranging from 2 to 25 years in age in three different regions (El Refugio, Nicolas Bravo and Arroyo Negro). They reported a significant increase in total aboveground biomass with regards to fallow age: total aboveground biomass increased threefold from about 20 Mg/ha (in the first 2 years of fallow) to around 70 Mg/ha (between 12 and 25 years of fallow). Using a regression analysis, the authors suggested that the biomass of fallow stands is correlated with fallow age based on the following relationship:

$$\text{TAG biomass (Mg/ha)} = 11.431 + 2.6615 \cdot \text{age} (R^2 = 0.57, n = 28, P < 0.0001)$$

The authors assumed in this calculation that the rate of increase of biomass would lessen when the succession processes continued, although they were unsure when the decline in growth rate would commence.

2.2.2 Total Aboveground Biomass Increases at First, but then Remains Constant

Uhl (1987) pointed out that biomass accumulation should not be linear with respect to time. The equation used to explain biomass accumulation:

$$\text{biomass (g/m}^2\text{)} = 842 \cdot \text{age of stand in years} - 89 (n = 27, r^2 = 0.68)$$

which he generated from studies of the Rio Negro region in Venezuela and other tropical areas, predicted that the total aboveground biomass of fallows should reach similar levels as those found in old-growth forests in about 40 years. However, he pointed out that different results in the same region were found in a study by Saldarriaga et al. (1988). Saldarriaga et al. found that when fallows reached 40 years, the aboveground biomass could only attain about half of the levels found in old-growth forests. Uhl concluded that after 10 years of fallow, the biomass accumulation rate would decline and the linear relationship would disappear (Uhl 1987).

Other studies came to similar conclusions. A study in a forest of Sarawak, Malaysia, examined 171 fallow plots selected in 44 areas following shifting cultivation. In this study, biomass was found to increase rapidly before 10 years of fallow, although no net growth of biomass at the beginning of succession could be found (Fig. 2.1a; Jepsen 2006). Despite this, the annual accumulation rate increased from 6.6 Mg/ha in the first 2 years, to 19.5 Mg/ha by the fourth year (Fig. 2.1a). After this rapid increase, the annual accumulation rate decreased to zero when fallows aged past 10 years. Tran et al. (2010a, b) also reported a similar trend of biomass accumulation in the forest of north-western Vietnam. Referring to

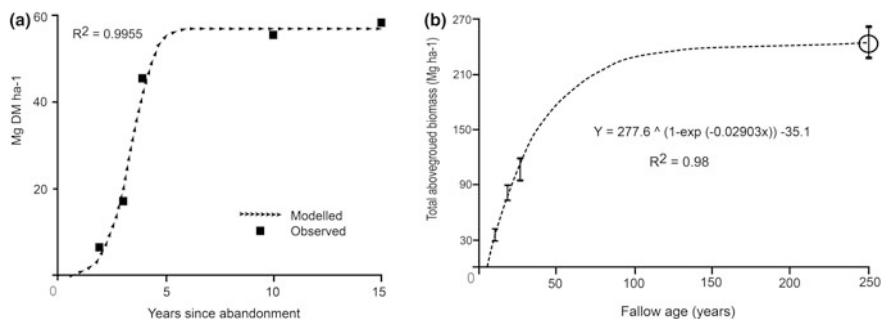


Fig. 2.1 Biomass accumulation dynamics. *Sources* **a** Jepsen (2006), **b** Tran et al. (2010b)

Fig. 2.1b, total aboveground biomass increased from 4.1 Mg/ha in 5-year-old fallows to 108.8 Mg/ha in the oldest age class (26 years). However, a slow increase was seen in the first 7 years; when fallows reached 10 years of age, the annual biomass increment rate increased rapidly to 7.77 Mg/ha. When succession proceeded, a slower growth rate was observed at first as it decreased to 5.75 Mg/ha when the fallows reached 18 years of age. The annual biomass increment rate declined further to 3.39 Mg/ha in the oldest fallow stand measured (26 years old). Tran et al. (2010b) pointed out that after 60 years of fallow, 60 % of the total aboveground biomass found in the old-growth forest was recovered. Saldarriaga et al. (1988) reported a linear increase in aboveground biomass for the first 40 years of fallow in the forest of the upper Rio Negro, but found that levels remained more or less the same for the next 40 years, ranging from 43.9 to 159 t/ha. Subsequently, levels continued to increase and ranged from 116 to 178 t/ha in 60–80-year-old fallows (Table 2.2). The stagnation of biomass accumulation might be because the growth of aboveground biomass is offset by the mortality of long-lived pioneer species (Saldarriaga et al. 1988). Uhl (1987) reached a similar conclusion: the biomass growth rate decreases at later stages due to replacement by slow-growing primary forest species. However, Uhl (1987) concluded that biomass growth rates would decrease after 10 years, earlier than that found by Saldarriaga et al. (1988).

2.3 Trees and Herbs Abundance

Delang (2007) examined the number of useful taxa found in forest fallows (1, 3, 5, 7, 9, 11 and 20 years old) of northern Laos. Delang found that the number of useable plants increased as fallows aged from 3 to 11 years, but then decreased when fallows reached 20 years of age (Fig. 2.2). El-Sheikh (2005), in a field site in Egypt, reported a rapid increase in the woody layers when fallows reach 5–6 years of age, but a slower increase in later stages of fallow (25 years of age). In eastern Madagascar, Klanderud et al. (2010) found that a positive relationship existed between the number of adult trees and tree saplings and the number of years the

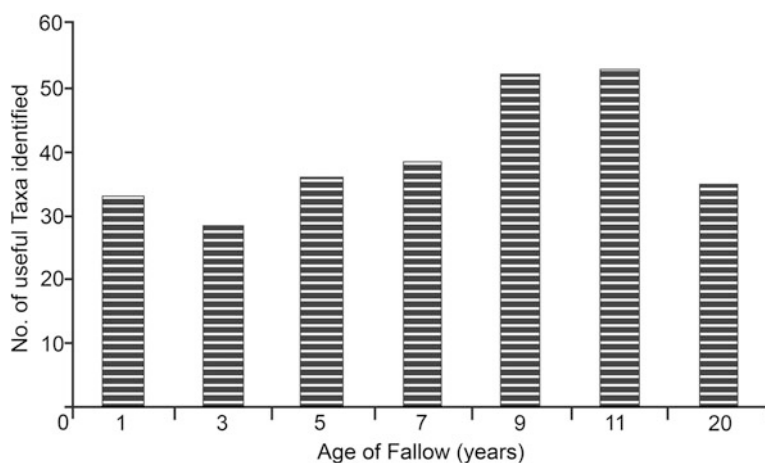


Fig. 2.2 Estimated number of usable taxa in fields with an 11-year swidden cycle. *Source* Delang (2007)

fields had been abandoned using Generalized Linear Model multiple regressions, but did not find great differences between fallows when using the Tukey's HSD post hoc test (Fig. 2.3). On the other hand, in the tropical moist forest of the upper Rio Negro Region, Saldarriaga et al. (1988) found a decreasing trend in the total number of trees with respect to fallow age, which ranged from 543 to 978 stems in 9- to 20-year-old fallows, and from 253 to 550 stems in 30- to 80-year-old fallows.

Significant differences between fallow ages can also be observed in the abundance of tree seedlings, calculated by the percentage cover of the forest floor, which show a decline with fallow duration (Fig. 2.4; Klanderud et al. 2010). The number of shrubs is also negatively correlated with years since abandonment, as estimated using Generalized Linear Model multiple regressions (Fig. 2.5; Klanderud et al. 2010).

Concerning the abundance of herbs, despite one study by Klanderud et al. (2010) in Eastern Madagascar demonstrating no great difference between fallows of different age classes, El-Sheikh (2005) found an increase in the amount of herbs in early fallow stages (1–3 years old) in the dry forests of Egypt. This trend was followed by a slight decrease from year 5 to 6, and a continued drop through later stages. Another chronosequence study conducted in the eastern lowlands of Bolivia also showed a decrease in understory vegetation when fallows aged, wherein understory cover was 100 % in the first year of fallow, but decreased to 50 % by the eighth year (Kennard 2002).

Although El-Sheikh (2005) and Klanderud et al. (2010) found an increase in the number of trees when fallows aged, a study by Saldarriaga et al. (1988) reported the opposite. However, their decreasing trend might be due to the abundance of small trees in the upper Rio Negro region (Saldarriaga et al. 1988). The authors pointed out that even though there is a gradual increase in bigger trees when fallows age, the number is not able to offset the decreasing trend of the smaller

Fig. 2.3 Species abundance of adults in fallows of different age classes, secondary, and primary forest in the Vohimana forest of Madagascar (measured in number of stems). Error bars are standard error. Bars not sharing a letter differ significantly (Tukey’s hsd, $P < 0.05$). *Source* Klanderud et al. (2010)

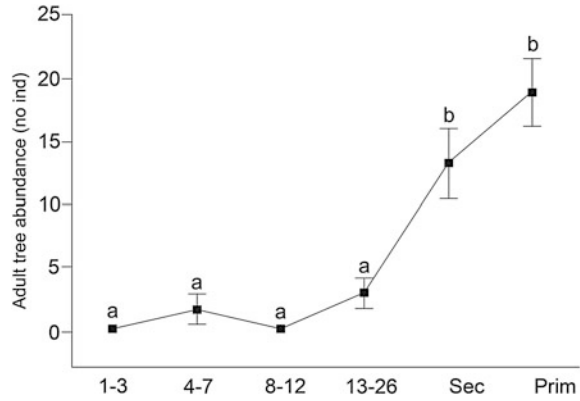


Fig. 2.4 Species abundance of tree seedlings in fallows of different age classes, secondary, and primary forest in the Vohimana forest, Madagascar (measured in % cover). Error bars are standard error. Bars not sharing a letter differ significantly (Tukey’s hsd, $P < 0.05$). *Source* Klanderud et al. (2010)

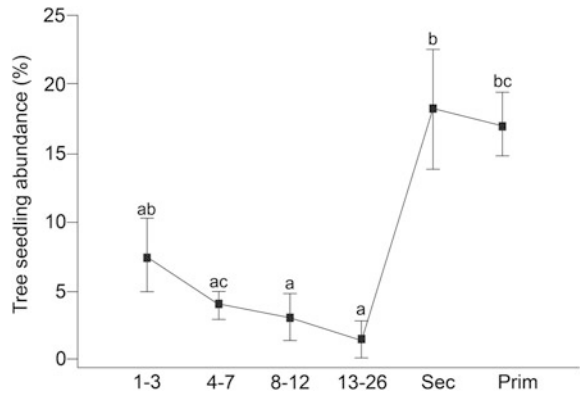
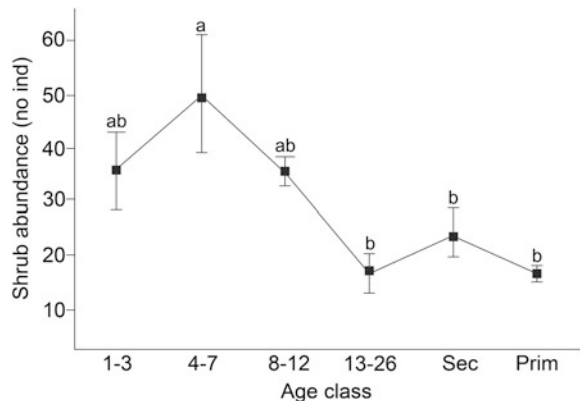


Fig. 2.5 Species abundance of shrubs in fallows of different age classes, secondary, and primary forest in the Vohimana forest of Madagascar (measured in number of stems). Error bars are standard error. Bars not sharing a letter differ significantly (Tukey’s hsd, $P < 0.05$). *Source* Klanderud et al. (2010)



trees, as they still had high representation, even in the older fallow stages. As a result, it is possible that the unique characteristics of forests in different geographic regions could result in different growth patterns during succession.

2.4 Total Basal Area

Different researchers have reported a general trend of an increase in total basal area as fallows age. For instance, 28 fallow sites with ages ranging from one to 36 years were sampled in a semi deciduous forest of Bolivia (Toledo and Salick 2006). In the overstory, total basal area increased from 2.9 m²/ha in 1- to 5-year-old fallows to 12.2 m²/ha in the oldest fallows (22–36 years of age), which contained more than 50 % of the biomass measured in old-growth mature forests (21.6 m²/ha; Table 2.2). Another chronosequence study of 36 fallow sites carried out in the tropical dry forest of the southern Yucatan Peninsular region in Mexico concluded that total basal area increased from about 10 m²/ha in 2- to 5-year-old fallows to about 30 m²/ha in 12- to 25-year-old fallows (Read and Lawrence 2003; Table 2.2). However, this increase was mainly driven by two dry study sites sampled—El Refugio and Nicolas Bravo. Regression analyses on the wettest site of Arroyo Negro showed no significant difference between basal area and age class of fallows (Read and Lawrence 2003).

In Colombia, another study on a tropical dry forest region also found a positive relationship between the total basal area and the fallow age (Ruiz et al. 2005). Total basal area was found to increase from 17.72 m²/ha in the youngest fallows (less than 6 years old) to 42.05 m²/ha in the older fallows (from 32 to 56 years of age) (Table 2.2; Ruiz et al. 2005). The fallows of that age bracket still had only less than 50 % of the basal area of oldest age class (forests older than 56 years). A chronosequence study by Kammesheidt (1998) examined 2- to 15-year-old fallows following swidden agriculture in the tropical moist forest of eastern Paraguay, and found that a positive relationship exists between basal area and fallow age. The basal area was found to increase from 3.2 m²/ha in 2- to 5-year-old stands to 9.1 m²/ha in 10 and 15-year-old ones (Table 2.2). The 15-year-old fallows had a basal area which was less than 50 % of that of old-growth forests (found to be 24.7 m²/ha; Kammesheidt 1998).

Peña-Claros (2003) found in his study of tropical moist forest fallows in Bolivia that the total basal area increased from 12.3 m²/ha in the 2-year-old fallow to 36.3 m²/ha in the 40-year-old fallow. When fallows further regenerated to 25 years of age, 70 % of the basal area found in the old-growth forest was reached (Fig. 2.6; Peña-Claros 2003). A similar pattern was reported in a study of the tropical dry forest of the eastern lowlands of Bolivia (Kennard 2002). Kennard reported that total basal area increased with fallow duration and reached 75 % of that of the old-growth forest levels by the 23rd year of fallow (Fig. 2.6). Lebrija-Trejos et al. (2008) surveyed the tropical dry forest of southern Mexico, and showed a continuous increase in basal area throughout the succession process (ranging from 0 to 25 m²/ha; Fig. 2.6). In this study, the increase in basal area was slower than that reported by Kennard (2002), and fallows required a longer time frame within which to reach the basal area of the mature forest. After 40 years, from 60 to 89 % of the basal area of mature forest was attained in southern Mexico (Lebrija-Trejos et al. (2008)). A longer chronosequence study of 20–100 years was

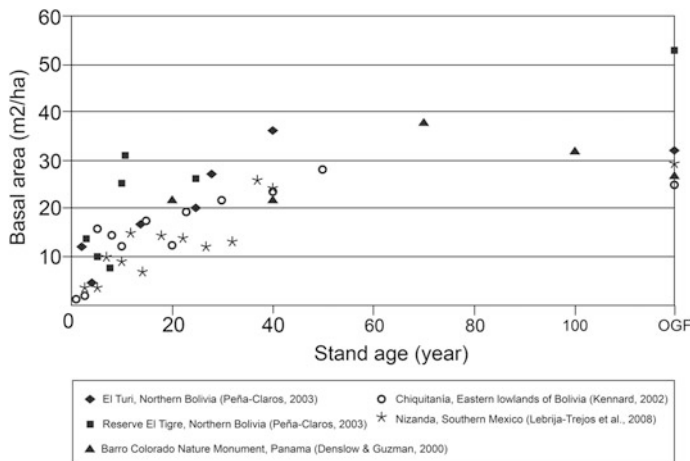


Fig. 2.6 Changes in basal area during succession in El Tigre and El Turi, northern Bolivia, Barro Colorado Nature Monument, Panama, Nizanda, southern Mexico and Chiquitanía, and the eastern lowlands of Bolivia. All individuals with ≥ 1 cm DBH were surveyed in northern Bolivia; all individuals with ≥ 5 cm DBH were surveyed in Panama; all individuals with ≥ 1 cm DBH, < 1 cm DBH, and height ≥ 30 cm were surveyed in southern Mexico; all individuals with height > 2 m were surveyed in the eastern lowlands of Bolivia. *Source* Figure derived from Peña-Claros (2003), Denslow and Guzman (2000), Lebrija-Trejos et al. (2008) and Kennard (2002). OGF refers to old-growth forest

conducted in the tropical moist forest of Panama. Denslow and Guzman (2000) selected sites that had been abandoned for 20, 40, 70 and 100 years, each with different land use history ranging from shifting cultivation to pastures. These authors reported that total basal area was the lowest in the youngest fallows, and continued to increase starting from year 40 until it peaked at year 70 (Fig. 2.6). At its peak, year 70 fallows had basal area values greater than those measured in the old-growth forest. Basal areas were found to subsequently drop (Fig. 2.6; (Denslow and Guzman 2000).

In a study on the upper Rio Negro, Saldarriaga et al. (1988) reported that 60- to 80-year-old fallows only had 60 % of the basal area of old-growth mature forest, a smaller number than that found by Peña-Claros (2003), Kennard (2002) or Ruiz et al. (2005). Saldarriaga et al. (1988) predicted that the time for basal areas of fallows to reach levels comparable to those of old-growth forest would be 199 years, based on the logarithmic regression:

$$\ln Y = 1.75 + 0.34 \ln X \quad (n = 19, r^2 = 0.65, P < 0.0001, CV = 6.46\%),$$

where Y is the mean basal area (m^2/ha), and X is the age (years). The study of permanent plots conducted in the rain forest of the upper Rio Negro region also indicated an increase of the basal area from $0.5 \text{ m}^2/\text{ha}$ in the first year to $7.0 \text{ m}^2/\text{ha}$ in the fifth year of fallow (Table 2.2; Uhl 1987).

2.5 Canopy Height

Canopy or tree height are often measured by researchers when examining the succession process in fallow fields. Different trends of change from various studies are presented below.

2.5.1 Canopy Height Increases with Fallow Age

Canopy height was measured in both dry and moist forests of Bolivia. In the dry forests of Bolivia, Kennard (2002) found that the maximum canopy height increased from about 6 m in 3-year-old fallows to about 25 m in the oldest fallows (50 years old; Fig. 2.7), and the canopy height in 23- to 40-year-old fallows attained approximately 75 % of that of the old-growth forest. On the other hand, in a Bolivian moist forest, the maximum canopy height increased from about 10 m in 10-year-old fallows to around 30 m in the oldest, 40-year-old fallows (Fig. 2.7; Peña-Claros 2003).

In Colombia and Mexico, a positive relationship also existed between mean tree height and fallow length. In Colombia, mean tree height increased from 5.8 m in fallows younger than 6 years old, to 7.7 m on 35- to 56-year-old fallows (the mean tree height of the old-growth forest was recorded to be 7.1 m) (Table 2.2; Ruiz et al. 2005). In southern Mexico's tropical dry forest, Lebrija-Trejos et al. (2008) concluded that the canopy height increased rapidly in the first 15 years, but remained stable afterwards, as shown in Fig. 2.8. After 13 years, canopy height

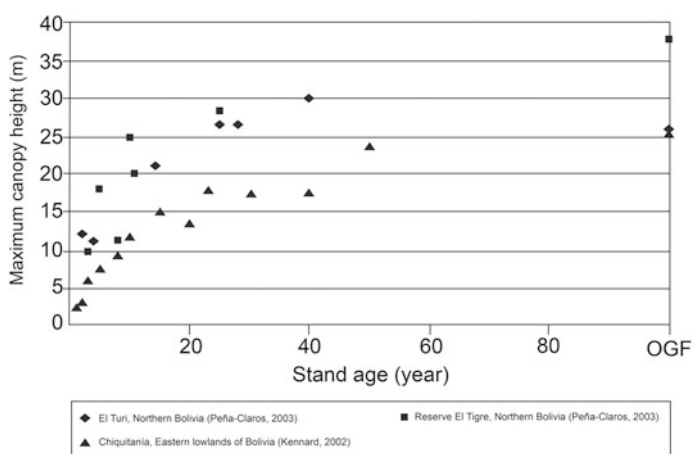
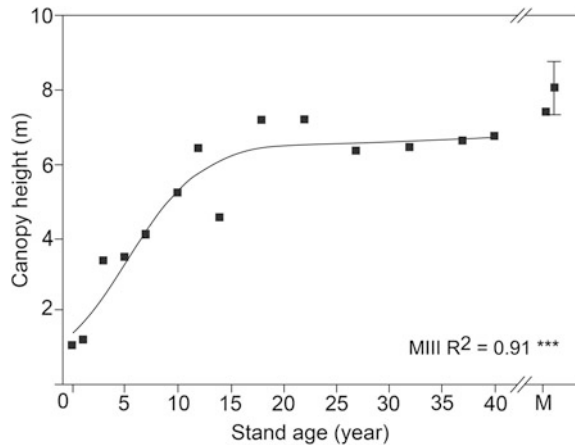


Fig. 2.7 Changes in maximum canopy height during succession in El Turi and Reserve El Tigre, northern Bolivia and Chiquitanía, and in the eastern lowlands of Bolivia. *Source* Figure derived from Peña-Claros (2003) and Kennard (2002). OGF refers to old-growth forest

Fig. 2.8 Canopy height for fallows ranging from a recently-abandoned field to a 40-yr-old field. Symbols represent actual stand values. Lines are time trends described by the best-fit HOF model (M I–V; *** $P < 0.001$). Mature forest values (M; chronosequence stand and mean with 95 % CI) are depicted for reference, but were not included in the regressions. *Source* Lebrija-Trejos et al. (2008)



reached approximately 75 % of that found in the mature forest, and also displayed a faster growth rate than that recorded in the dry forest of Bolivia (Kennard 2002).

Other researchers in Mexico reported an increase in tree height with respect to fallow age for larger trees (dbh 5–9.9 cm and dbh larger than 10 cm) from the youngest fallows (from 2 to 5 years old) to the oldest fallows sampled (from 12 to 25 years old; Read and Lawrence 2003). However, a Tukey post hoc test showed no significant difference between stand ages and the height of smaller trees (Fig. 2.9; Read and Lawrence 2003). In the moist evergreen forest of southwestern Nigeria, tree height increased from 1.3 m in the first-year-old fallow to 5.8 m in 10-year-old fallows. These latter fallows had recovered about half of the tree height measured in old-growth forest samples (10.4 m) (Table 2.2; Aweto 1981). Nyerges (1989) conducted a chronosequence study and sampled age classes of 1, 3, 7, 8 15 17 20 25 27, 30 and over 30 years old in the tropical deciduous forest of Sierra Leone, where sites were farmed for 1 year. Canopy height was found to have a positive relationship with fallow age: it increased from 6 m in the third year to from 15 to 20 m in the 30th year of fallow (Table 2.2; Nyerges 1989).

2.5.2 No Significant Difference with Fallow Age

A chronosequence study examining the tropical dry forest of Mexico found no significant relationship between fallow age and fallow duration, basal area, or tree height (Williams-Linera et al. 2011). These authors examined five fallow sites with ages of 7 months, 8 months, 3 years, 4 years and 6 years with different land use history ranging from agriculture to pasture. Referring to Figs. 11A and C, the results of this study reported no significant difference in basal area or tree height within fallows of different age classes (from 7 months to 6 years) during early succession periods. However, the authors did report a significant difference between the overstory of old-growth forest and fallow age based on the Tukey's

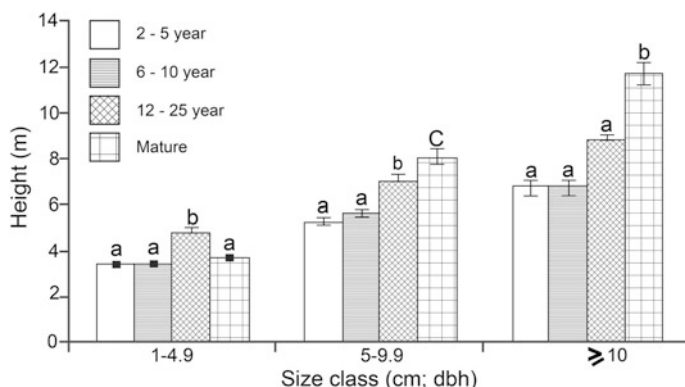


Fig. 2.9 Mean height of measured trees ($n = 1395$) by dbh size class. Bars are means ± 1 SE. Results are of ANOVAs (all $P < 0.0001$) within each size class, comparing tree heights as a function of forest age. Within each size class, bars with different letters are significantly different at a level of $\alpha = 0.05$ (Tukey post hoc test). Source Read and Lawrence 2003

honestly significant difference (hsd; Williams-Linear et al. 2011). Differences in basal area between fallows and old-growth forest in the understory, however, showed no significant difference and almost reached the same level of the old-growth forest (Fig. 2.10a; Williams-Linear et al. 2011).

2.6 Plant Density

Studies show great variation in the changes of plant density along the succession trajectory. Some research found that plant density increases as the fallows ages, or increases and then stabilizes. Other studies have found that stem density increases initially, but then declines in early or intermediate stages, that it varies among age classes, or that it decreases with fallow age. We now review studies that found each of these contrasting results in turn.

2.6.1 Stem Density Increases, or Increases and then Stabilizes

A chronosequence study carried out in north-western Vietnam reported an increase in the stem density of tree stratum from 60 to 960 stems/ha from year 7 to the oldest (26 years old) fallows (Table 2.4; Tran et al. 2010b). Kammesheidt (1998) found a positive relationship between the mean stem density in the tree stratum ($\text{dbh} \geq 5$ cm) and fallow age. The density was measured as 29.8/500 m^2 between 2 and 5 years, and then increased to 34.4/500 m^2 in 10- and 15-year-old fallows. This latter measurement corresponds to the stem density recorded in mature forests (33.9/500 m^2). However, the opposite was found to occur in the sapling stratum,

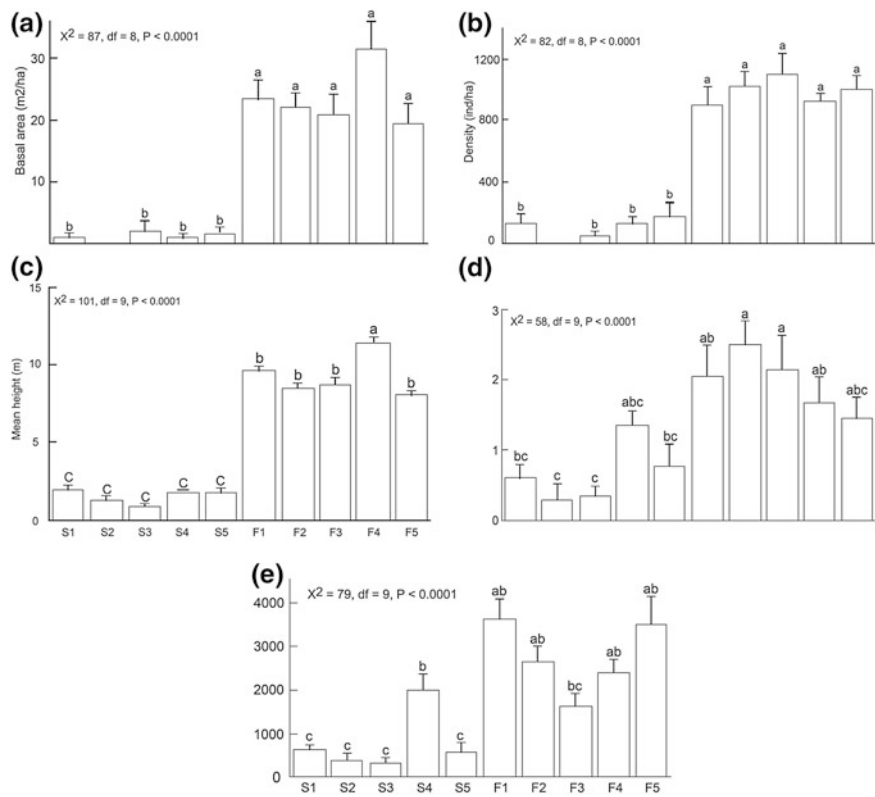


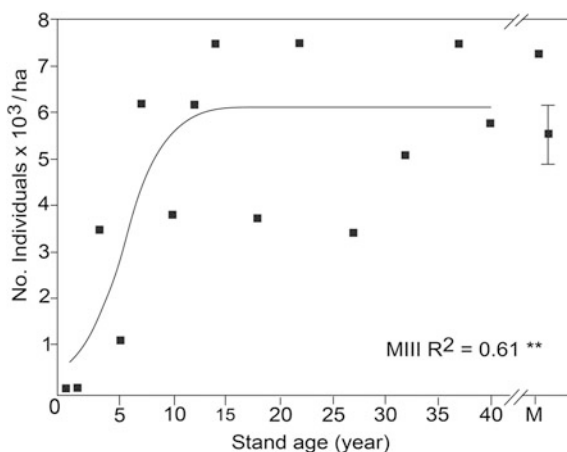
Fig. 2.10 Vegetation structure of early successional (S1-5) and forest sites (F1-5) in the tropical dry forest region of central Veracruz, Mexico. **a** Basal area, **b** density and **c** mean height of the overstory (trees ≥ 5 cm dbh). **d** Basal area and **e** density of the understory (woody plants < 5 cm dbh). Scale of the vertical axes differs between **a** and **d**, and between **b** and **e**. Different letters above the bars indicate significant differences between sites ($P < 0.05$) Source Williams-Linear et al. 2011

where mean stem density decreased from 68.0/100 m² in the young fallows to 40.3/100 m² in the oldest ones (Table 2.4; Kammesheidt 1998).

On the other hand, Aweto (1981) found in the moist evergreen forest fallows of Nigeria that tree density increased rapidly in the first 7 years, but then stabilized afterwards. According to Aweto’s results, tree density increased from 56 stems/ha in the first year of fallow to 2,270 stems/ha in year seven, already reaching levels equivalent to those of the old-growth mature forest (2,260 stems/ha). However, these values then stabilized by 10 years to 2,670 stems/ha (Table 2.4; Aweto 1981). A similar pattern was found in the tropical dry forest of southern Mexico. Lebrija-Trejos et al. (2008) reported that stem density increased rapidly in the first 15 years of succession, but subsequently stabilized (Fig. 2.11). These authors concluded that between eight and 13 years, stem density was able to reach the

Fig. 2.11 Density of individuals for fallows ranging from a recently abandoned field to 40-year-old plots. Symbols represent actual stand values. Lines are time trends described by the best-fit HOF model (M I–V; ** $P \leq 0.01$). Mature forest values (M; chronosequence stand and mean with 95 % CI) are depicted for reference but were not included in the regression calculations.

Source Lebrija-Trejos et al. (2008)



same value of the mature forest (approximately 5,511 individuals/ha). In contrast, a longer time to reach old-growth forest levels was required in forests of Nigeria (Aweto 1981).

2.6.2 Stem Density Increases, but Shows a Decline in Early or Intermediate Stages

Other studies also report an increase in stem density, but these studies observe a decline after reaching a peak in early to intermediate successional stages (Toledo and Salick 2006; Ruiz et al. 2005; Uhl 1987). In Bolivia, for example, plant density in the overstory increased from 55.4/0.1 ha in the early fallows (from 1 to 5 years old), peaked at 105.4/0.1 ha in the intermediate stage of 6- to 10-year-old plots, and then declined after 10 years (Table 2.4; Toledo and Salick 2006). Tree density in the overstory also demonstrated a similar picture as it increased from 52.4 stems/30 m² in the youngest age class (from 1 to 5 years old) to a peak of 97 stems/30 m² in the intermediate stage of six to 10 years (Toledo and Salick 2006). From 10 years onwards, tree density in this site declined to 69 stems/30 m² in the oldest age class (22–26 years old) (Toledo and Salick 2006). Similar trends were observed in the tropical dry forest of Colombia and the tropical rain forest of the upper Rio Negro. In Colombia, mean tree density of the youngest age class (under 6 years old) was about 30 stems/0.01 ha (Ruiz et al. 2005). Density increased and peaked at between 11 and 16 years of age, when mean tree density reached approximately 40 stems/0.01 ha, but then decreased after 16 years (Ruiz et al. 2005). However, in this study, there was a slight increase in the oldest age class (32–56 years old) (Fig. 2 in Ruiz et al. 2005). In the upper Rio Negro region, mean tree density (number of stems/m²) steadily increased from the first 4 years of fallow, but then decreased after reaching the fifth year (Fig. 2.12; Uhl 1987).

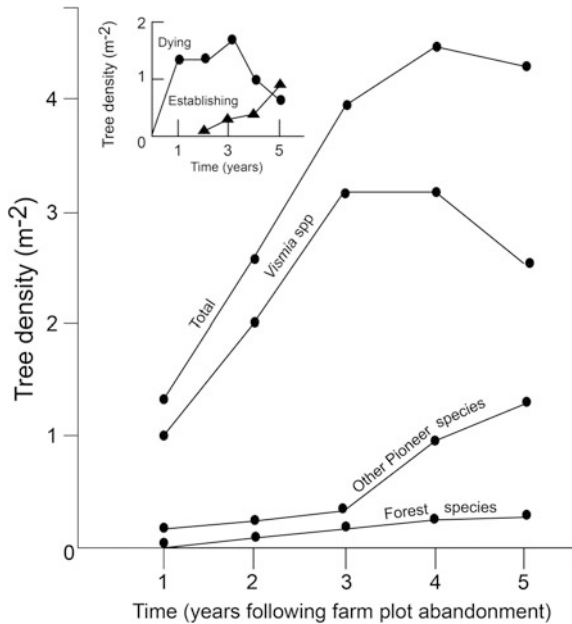


Fig. 2.12 Changes in density establishment and mortality for trees (≥ 2 m tall) Tree density in the 0.15 ha main study plot during the first 5 years of succession following slash-and-burn agriculture near San Carlos de Rio Negro, Venezuela. *Source* Uhl (1987)

2.6.3 Stem Density Varies Among Age Classes

Great variation in stem density among age classes was reported in a number of studies. For instance, in the tropical dry and moist forests of Bolivia, both forest types demonstrate fluctuations in the total stem density among stand ages (Kennard 2002; Peña-Claros 2003). In the eastern lowlands of Bolivia, Kennard (2002) found that total stem density (number of stems/ha) varies greatly up until year 30 of fallow. In 23-year-old stands, stem density was surprisingly high. The author suggested that the high values in year 23 might have been due to variations in field conditions, such as differences in soil types, location, fire occurrence and land history. From year 30 total stem density gradually dropped (Fig. 2.14). Similar to results reported by Kennard (2002), Peña-Claros (2003) reported great variation among age classes, with no clear correlation found between stem density (number of stems/ha *1000) and fallow age in either Reserve El Tigre or in El Turi of Bolivia (Fig. 2.13). On the other hand, a chronosequence study conducted in the dry tropical forest in Mexico using Tukey's honestly significant difference test showed that woody plant density had similar values among age classes from 7 months to 6 years old in both overstory and understory, although a great difference could be seen between fallows and old-growth forests in the overstory (Fig. 2.10b, e; Williams-Linera et al. 2011). However, differences between fallows

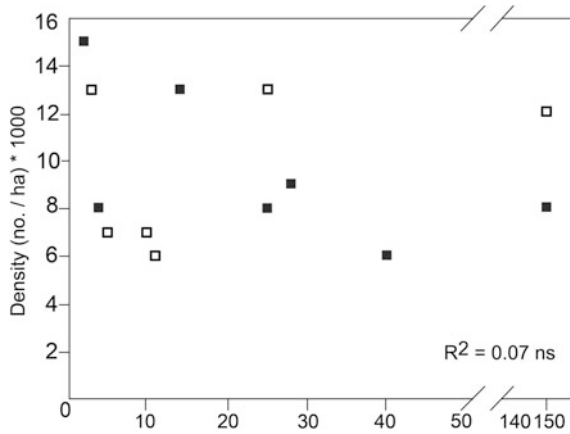


Fig. 2.13 Density of all individuals ≥ 1 m height. *Open circles* are data from the Reserve El Tigre and *filled circles* are data from El Turi. *Source* Peña-Claros (2003)

and old-growth forest were found to be smaller in the understory, where some plots had already reached values comparable with those of old-growth forests (Williams-Linera et al. 2011).

2.6.4 Stem Density Decreases with Fallow Age

Stem density was found to decline in the study conducted in the southern Yucatan Peninsular region of Mexico, despite the positive relationship between total aboveground biomass and fallow age (Read and Lawrence 2003). For 2- to 5-year-old plots, stem density ranged from 13,000 to 33,000 stems/ha, whereas in the old-growth forest, average stem density was found to be 12,900 stems/ha. Read and Lawrence (2003) reported a greater decline in density with fallow age in Nicolas Bravo and Arroyo Negro, while the driest region of El Refugio had a smaller drop compared to the other two sites (Fig. 2.14).

In a chronosequence study conducted in north-western Vietnam, Tran et al. (2011) examined the density of seedlings, saplings and trees of four species of trees (*Wendlandia paniculata*, *Schima wallichii*, *Camellia tsaii* and *Lithocarpus ducampii*) on fallows of different age. The researchers found that the seedling density of the first three species first increased slightly, and then decreased sharply, while the seedlings of *L. ducampii* remained more or less constant (Fig. 2.15). A similar pattern was observed with the saplings for the first three species, with the sapling density increasing from 5-year old fallows to 10-year old fallows, and then decreasing (no saplings of *L. ducampii* were found). On the other hand, tree density decreased from 10-year old fallows onward (again, no *L. ducampii* were found). According to the authors, the decrease in seedling and sapling density

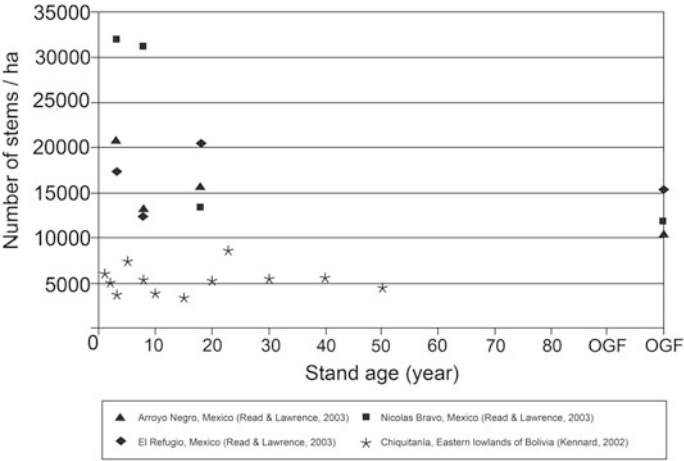


Fig. 2.14 Changes in stem density during succession in El Refugio, Arroyo Negro and Nicolas Bravo, Mexico and Chiquitania, and the eastern lowlands of Bolivia. Trees, palms, and lianas >1 cm DBH were surveyed in Mexico; individuals with height>2 m were surveyed in Eastern lowlands of Bolivia. Figure derived from Read and Lawrence (2003) and Kennard (2002). OGF refers to old-growth forest

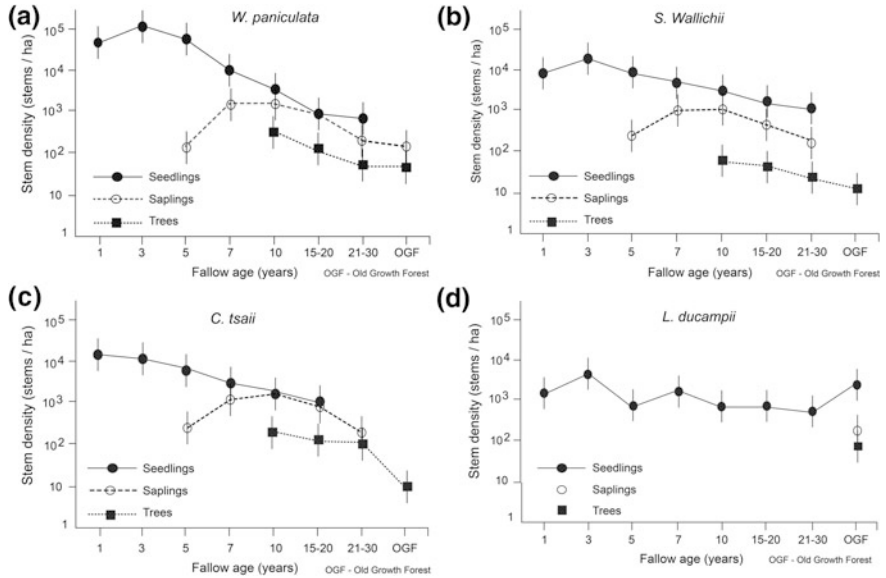


Fig. 2.15 Change in seedling, sapling and tree density ($\pm$ SD) **a** *Wendlandia paniculata*, **b** *Schima wallichii*, **c** *Camellia tsaii*, and **d** *Lithocarpus ducampii* in different ages of secondary forest regrowth and in the old-growth forest in north-western Vietnam. Vertical bars indicate $\pm$ standard deviation. Source Tran et al. (2011)

might have been due to the increase in total crown area, as not sufficient sunlight penetrated through the canopy, which decreased the amount of forest-floor light, and may have inhibited the growth of seedlings. Tran et al. (2011) suggested that their results agreed with the findings of Whitmore (1983), who concluded that the decrease in the amount of light was responsible for tree mortality.

2.7 Discussion and Conclusions

Table 2.1 summarises the various patterns of change in total aboveground biomass, total basal area and canopy height in different places, and Table 2.2 presents the various results reported by the case studies we examined. Referring to Table 2.2, a general trend in the increase in total aboveground biomass as fallows age is observed, in spite of some researchers suggesting that this increase will eventually reach a threshold. The time needed to reach this threshold also varies from study to study (Table 2.1). For example, in Malaysia, total aboveground biomass on fallows became constant after 10 years, whereas in the upper Rio Negro region of Colombia and Venezuela, total aboveground biomass only became constant after 40 years.

Different studies also reported variations in the time needed for aboveground biomass on fallows to reach levels comparable to those of old-growth forests. For instance, in forests of Puerto Rico, the fallows failed to reach levels comparable to those of old growth forests, even after 80 years (Brown and Lugo 1990b). Likewise, in the upper Rio Negro region, 80-year-old fallows only had about two thirds the amount of total aboveground biomass of the old-growth forest, with a mean of only 179 t/ha for 80-year-old stands, while total aboveground biomass of old-growth forest reached 255 t/ha. Thus, the authors inferred that it would take a projected 189 years in order for total aboveground biomass in fallows to attain values equivalent to those of old-growth forests (Saldarriaga et al. 1988). Similarly, studies of forests of Mexico and northern Thailand concluded that the aboveground biomass of fallows could not reach equivalent values to those of old-growth forests even within 50 years (Hughes et al. 1999; Fukushima et al. 2008). Read and Lawrence (2003) studied the dry tropical forests of Yucatan in Mexico, and concluded that, assuming biomass and fallow age have a linear relationship, total aboveground biomass would recover to the same level of old-growth forest in 65–120 years.

In other cases, researchers found that total aboveground biomass does recover almost to the same levels as old-growth forests within 30–40 years. For example in northern Thailand, old-growth forest above-ground biomass measured 185–260 t/ha, with a median value of 254 t/ha, while 30- to 49-year-old fallows only measured 127–305 t/ha, with a median of 236 t/ha, only slightly less than that of the old-growth forest (Table 2.2; Fukushima et al. 2008). Fallows in the forest of Central Burma were found to be the fastest to reach the equivalent amount of

Table 2.1 Summary of changes in total aboveground biomass, total basal area, tree/canopy height when fallows age and the number of years needed to attain old-growth forest levels

Place	Forest Type	Changes in total aboveground biomass along succession	Changes in total basal area along succession	Changes in tree/canopy height along succession	Years to reach comparable amount of aboveground biomass with OGF	Years to reach comparable amount of total basal area with OGF	Years to reach comparable amount of tree/canopy height with OGF	Source
Central Burma	Mixed deciduous forest	Increase	/	/	About 40 years	/	/	Fukushima et al. (2007)
Upper Rio Negro region of Venezuela	Tropical moist forest	Increase	Increase	/	/	/	/	Uhl (1987)
Northern Thailand	Lower montane forest / Primary evergreen forest	Increase	/	/	More than 49 years	/	/	Fukushima et al. (2008)
Mexico	Tropical dry forest	Increase	Increase	/	65–120 years	/	/	Read and Lawrence (2003)
Malaysia	/	Increase but remained constant after 10 years	/	/	/	/	/	Jepsen (2006)
Upper Rio Negro region of Colombia and Venezuela	Tropical moist forest	Linear increase but remained constant after 40 years	Increase	/	189 years	199 years; Reaching 60% after 60–80 years	/	Saldarriaga et al. (1988)
North-western Vietnam	Evergreen broad-leaved forest	Slow increase in first 7 years; rapid increase from 10 year and growth rate reduce from 18 years onwards	/	/	More than 60 years	/	/	Tran et al. (2010a, b)

(continued)

aboveground biomass as the old-growth forest (Table 2.1). For example, Fukushima et al. (2007) reported that the total aboveground biomass on fallows already contained 34.8 % of that of the old-growth forest in the fifth year, and reached 93.6 % in year 40. The authors suggested that this rapid increase in the early stages might be due to the presence of bamboo, which can survive fire exposure. Similar results were reported in other studies carried out in tropical forests, where authors concluded that 30- to 40-year-old fallows could reach aboveground biomass levels comparable to those of old-growth forests (Snedaker 1970; Lugo et al. 1974; Scott 1977). As shown in Table 2.1, fallows in the tropical dry forests of Mexico (Read and Lawrence 2003) had a faster growth rate than those in the tropical moist forest of the upper Rio Negro region (Saldarriag et al. 1988). However, due to a lack of information, it is not clear if tropical dry forests have a faster aboveground biomass growth rate than humid forests. In short, the examples we highlight demonstrate a gradual increase in total aboveground biomass with fallow length, but different rates of biomass accumulation have been reported by different studies. Other factors such as climate and land use patterns in the past (Brown and Lugo 1990a; Silver et al. 2000; Guariguata and Ostertag 2001), soil fertility and soil condition (Johnson et al. 2000; Moran et al. 2000; Zarin et al. 2001; Chazdon 2003) likely have an impact on the biomass accumulation rate. We will address this in later sections of the book.

According to Table 2.2, in general, total basal area was found to increase during succession. However, Fig. 2.6 showed that in Panama, total basal area dropped when fallows reached 100 years of age. Additionally, some studies demonstrated that the old-growth forests do not necessarily have a greater basal area than fallows (Fig. 2.6). As a result, some variations in the successional pathway could be observed among studies. On the other hand, the time needed to attain levels similar to the old-growth forest differed among studies. For instance, in the tropical dry forests of Colombia, eastern lowlands of Bolivia and southern Mexico, growth rates of total basal area varied greatly. Of the three sites, the eastern lowlands of Bolivia required the shortest time to reach old-growth forest levels (23 years; Table 2.1). Differences could not only be observed among dry forests, but also among moist forests. The tropical moist forest of Bolivia had the fastest growth rate of total basal area among moist forests, with 25 years to reach 70 % of the old-growth forest value (Table 2.1). In contrast, in the moist forest of the upper Rio Negro region of Colombia and Venezuela, 60–80 years was required.

As mentioned earlier, the trends of changes in total basal area and changes in total aboveground biomass are thought to be related (Chazdon et al. 2007; Clark and Clarl 2000). Uhl (1987), Read and Lawrence (2003) and Saldarriaga et al. (1988) measured both aboveground biomass and basal area in their studies (Table 2.1). Results of Uhl (1987) and Read and Lawrence (2003) seem to agree in the sense that they both report aboveground biomass and basal area as increasing along the succession. On the other hand, Saldarriaga et al. (1988) found a trend in total basal area, but did not find a constant increase in total aboveground biomass (levels remained constant after 40 years). Saldarriaga et al. (1988) examined the longest chronosequence of 80 years; in contrast, Uhl (1987) and Read and Lawrence (2003) did not consider fallows beyond 25 years of age (Table 2.2). As

Table 2.2 Values of total aboveground biomass, total aboveground biomass accumulation rate, total basal area and canopy/tree height from different studies

Forest type	Soil	Age (yr)	Total aboveground biomass (t/ha)	Total aboveground biomass accumulation rate (t/ha/yr)	Total basal area (m ² /ha)	Canopy/tree height (m)	Source
Mixed deciduous forest	Ultisols	1	0.3	/	/	/	Fukushima et al. (2007) ^a
		2	0.6	/	/	/	
		5	53.9	/	/	/	
		10	67.8	/	/	/	
		15	79.0	/	/	/	
		18	82.9	/	/	/	
		>40	147.6	/	/	/	
Tropical rain forest	Oxisols/ Ultisols	OGF	156.6	/	/	/	Uhl (1987)
		1	708 ^b	5–9	0.5	/	
		2	1282 ^b		1.8	/	
		3	1995 ^b		4.0	/	
		4	2861 ^b		5.7	/	
Lower montane forest / Primary evergreen forest	Coarse sandy loamy soil	5	3386 ^b		7.0	/	Fukushima et al. (2008)
		20–29	94–146	/	/	/	
		20–29	(median	/	/	/	
		20–29	130)	/	/	/	
		20–29		/	/	/	
		20–29		/	/	/	
		30–39	127–305	/	/	/	
		30–39	(median	/	/	/	
		30–39	236)	/	/	/	
		40–49		/	/	/	
		40–49		/	/	/	
		40–49		/	/	/	
		OGF	185–260	/	/	/	
		OGF	(median	/	/	/	
		OGF	254)	/	/	/	
		OGF		/	/	/	
		OGF		/	/	/	
Moist evergreen forest	Ferrallitic tropical soils	OGF		/	/	/	Aweto (1981)
		1	/	/	/	1.3	
		3	/	/	/	2.5	
		7	/	/	/	4.7	
		10	/	/	/	5.8	
Tropical deciduous forest	/	OGF	/	/	/	10.4	Nyerges (1989)
		1	/	/	/	/	
		3	/	/	/	6	
		7	/	/	/	8	
		8	/	/	/	/	
		15	/	/	/	10	
		17	/	/	/	/	
		20	/	/	/	13	
		25	/	/	/	/	
		27	/	/	/	/	
		30	/	/	/	15–20	
		>30	/	/	/	/	

(continued)

Table 2.2 (continued)

Forest type	Soil	Age (yr)	Total aboveground biomass (t/ ha)	Total aboveground biomass accumulation rate (t/ha/yr)	Total basal area (m ² /ha)	Canopy/ tree height (m)	Source
Tropical dry forest	/	2 ^c	22.36 ^c	/	9.3	/	Read and Lawrence (2003)
		3	10.60 ^c	/	4.4	/	
		4	16.30 ^c	/	7.7	/	
		5	17.48 ^c	/	7.2	/	
		8	29.07 ^c	/	10.5	/	
		8	20.53 ^c	/	9.1	/	
		10	39.67 ^c	/	15.9	/	
		12	45.56 ^c	/	20.7	/	
		12	54.70 ^c	/	18.3	/	
		12	60.98 ^c	/	24.6	/	
		OGF	120.34 ^c	/	36.5	/	
		OGF	138.54 ^c	/	37.7	/	
		OGF	123.68 ^c	/	37.7	/	
		3 ^f	18.17 ^c	/	17.5	/	
		5	34.44 ^c	/	14.6	/	
		5	64.06 ^c	/	28.0	/	
		6	20.74 ^c	/	9.2	/	
		8	24.87 ^c	/	10.8	/	
		16	50.02 ^c	/	19.2	/	
		18	20.41 ^c	/	20.6	/	
		24	97.57 ^c	/	34.3	/	
		25	94.20 ^c	/	26.5	/	
		25	60.46 ^c	/	29.2	/	
		OGF	163.30 ^c	/	43.8	/	
		OGF	133.11 ^c	/	39.1	/	
		OGF	157.88 ^c	/	45.0	/	
		4 ^g	12.34 ^c	/	5.9	/	
		5	31.60 ^c	/	13.8	/	
		5	25.17 ^c	/	12.8	/	
		7	11.89 ^c	/	5.1	/	
		8	62.55 ^c	/	18.8	/	
		9	20.42 ^c	/	10.2	/	
		15	36.19 ^c	/	24.4	/	
		18	27.59 ^c	/	64.2	/	
		OGF	136.31 ^c	/	38.0	/	
		OGF	118.16 ^c	/	30.9	/	

(continued)

Table 2.2 (continued)

Forest type	Soil	Age (yr)	Total aboveground biomass (t/ ha)	Total aboveground biomass accumulation rate (t/ha/yr)	Total basal area (m ² /ha)	Canopy/ tree height (m)	Source
Between northern Amazonian forests and southern dry forests	/	2	/	6.6 ^d	/	/	Jepsen (2006)
		4	/	19.5 ^d	/	/	
		10	/	0.0 ^d	/	/	
Tropical moist forest	Oxisols, Ultisols Poor in nutrient	9	43.9	/	11.17	/	Saldarriaga et al. (1988)
		11	52.9	/	11.52	/	
		12	81.8	/	17.31	/	
		14	53.4	/	11.12	/	
		20	83.3	/	17.50	/	
		20	61.5	/	14.45	/	
		20	63.8	/	17.06	/	
		20	97.6	/	18.70	/	
		30	53.8	/	11.70	/	
		35	109	/	19.61	/	
		35	108	/	20.07	/	
		40	159	/	22.98	/	
		60	116	/	17.68	/	
		60	197	/	31.04	/	
		60	138	/	24.74	/	
		80	134	/	22.31	/	
		80	178	/	26.44	/	
		80	144	/	23.92	/	
		80	142	/	23.20	/	
		OGF	223	/	30.45	/	
		OGF	262	/	35.62	/	
		OGF	264	/	36.21	/	
		OGF	271	/	36.95	/	
	Oxisols	2	/	/	3.2	/	Kammesheidt (1998)
		3	/	/		/	
		4	/	/		/	
		5	/	/		/	
		10	/	/	9.1	/	
		15	/	/		/	
		OGF	/	/	24.7	/	
Evergreen broad- leaved forest	Ferralic Acrisols Acidic, poor in nutrient	1	/	/	/	/	Tran et al. (2010b)
		3	/	/	/	/	
		5	4.1 ^c	0.82 ^d	/	/	
		7	12.4 ^c	4.15 ^d	/	/	
		10	35.7 ^c	7.77 ^d	/	/	
		18	81.7 ^c	5.75 ^d	/	/	
		26	108.8 ^c	3.39 ^d	/	/	
		OGF	240.5 ^c	/	/	/	

(continued)

Table 2.2 (continued)

Forest type	Soil	Age (yr)	Total aboveground biomass (t/ ha)	Total aboveground biomass accumulation rate (t/ha/yr)	Total basal area (m ² /ha)	Canopy/ tree height (m)	Source
Semideciduous forest	/	1–5	/	/	2.9	/	Ruiz et al. (2005)
		6–10	/	/	8.9	/	
		12–20	/	/	12.7	/	
		22–36	/	/	12.2	/	
		OGF	/	/	21.6	/	
Tropical dry forest	/	<6	/	/	17.72	5.8	
		6–10	/	/	24.88	6.3	
		11–16	/	/	20.46	6.5	
		17–31	/	/	26.37	6.6	
		32–56	/	/	42.05	7.7	
		>56	/	/	111.09	9.0	

OGF refers to old-growth forest

^a excluding herbs and grass

^b g/m²

^c Mg/ha

^d Mg/ha/yr

^e Region: El Refugio

^f Region: Nicolas Bravo

^g Region: Arroyo Negro

^h Overstory total basal area

suggested by Uhl (1987), biomass growth rate should not be linear in the long run; thus, the different trends of biomass and basal area observed in the upper Rio Negro region (Saldarriaga et al. 1988) could be due to the longer chronosequence. Because of these uncertainties, it would be useful to carry out additional research on longer periods of succession.

Table 2.1 and Fig. 2.7 showed the changes in tree and canopy heights during succession that are reported in different studies. A positive relationship between tree and canopy height and age along succession was observed in most studies, except that of Williams-Linear et al. (2011) in the tropical dry forests of Mexico. The Mexico study showed no great difference among fallows. This might have been due to the short period of fallows observed by the authors (only 1- to 5-year-old fallows), as tree heights might not have increased significantly during early stages of fallow, as shown in Table 2.2. Aweto (1981), Nyerges (1989) and Ruiz et al. (2005) examined longer periods of succession in their studies, and reported greater differences in tree height between early and late fallows. More and longer studies in the dry forests of Mexico will improve our understanding of the forest regeneration pattern along the successional process in this region, and help us determine if it is congruent with patterns found in other forests.

The time needed to reach a height similar to that found in old-growth forests varies among studies (Table 2.1). In southern Mexico and the eastern lowlands of Bolivia (both sites are in tropical dry forest) different times were needed to reach

Table 2.3 Summary of changes in plant density when fallows aged, and the number of years needed to reach the level of old-growth forest from different studies

Place	Forest type	Changes in stem density along succession	Years to reach comparable amount with old-growth forest	Source
North-western Vietnam	Evergreen broad-leaved forest	Increase in overstory stem density	Reaching more than 90 % after 26 years	Tran et al. (2010a, b)
Paraguay	Tropical moist forest	Increase in tree stratum; Decrease in sapling stratum	10–15 years in tree stratum	Kammesheidt (1998)
Bolivia	Semi-deciduous forest	Increase but decline after 10 years in overstory	About 5 years	Toledo and Salick (2006)
Colombia	Tropical dry forest	Increase before 11–16 years	Less than 6 years	Ruiz et al. (2005)
Upper Rio Negro region of Venezuela	Tropical moist forest	Increase but decline after 4 years	/	Uhl (1987)
Nigeria	Moist evergreen forest	Increase in first 7 years then remains stable	7 years	Aweto (1981)
Eastern lowland Bolivia	Tropical dry forest	Great variation	/	Kennard (2002)
Bolivia	Tropical moist forest	Great variation, no correlation found	/	Peña-Claros (2003)
Mexico	Tropical dry forest	No significant difference in overstory and understory	/	Williams-Linera et al. (2011)
Mexico	Tropical dry forest	Decrease	/	Read and Lawrence (2003)
Southern Mexico	Tropical dry forest	Increase in first 15 years then remains stable	8–13 years	Lebrija-Trejos et al. (2008)
North-western Vietnam	Evergreen broad-leaved forest	Decrease	/	Tran et al. (2011) ^a

^a Four species were examined: *W. paniculata*, *S. wallichii*, *C. tsaii* and *L. ducampii*

75 % of the height of old-growth forest (13 years in southern Mexico and from 23 to 40 years in the eastern lowlands of Bolivia). There are only a few studies that provided data on these regions (see Table 2.1), thus, it is difficult to draw conclusions about the forest regeneration rates.

Table 2.4 Values of stem densities of overstory and understory, and total stem density from different studies

Forest type	Soil	Age (yr)	Stem density/ha (overstory)	Stem density/ha (understory)	Total stem density/ha	Source
Tropical moist forest	Oxisols	2	68.0 ^c	29.8 ^d	/	Kammesheidt (1998)
		3			/	
		4			/	
		5			/	
		10	40.3 ^c	34.4 ^d	/	
		15			/	
Evergreen broad-leaved forest	Ferralic Acrisols Acidic and poor in nutrient	OGF	30.8 ^c	33.9 ^d	/	Tran et al. (2010b)
		1	/	/	/	
		3	/	/	/	
		5	/	/	/	
		7	60	/	/	
		10	730	/	/	
		18	830	/	/	
		26	960	/	/	
		OGF	1020	/	/	
		OGF	1020	/	/	
Between northern Amazonian forests and southern dry forests	/	1–5	55.4 ^a	239.4 ^b	/	Toledo and Salick (2006)
		6–10	105.4 ^a	292.0 ^b	/	
		12–20	82.7 ^a	314.7 ^b	/	
		22–36	75.9 ^a	232.4 ^b	/	
		OGF	69.5 ^a	222.4 ^b	/	
Moist evergreen forest	Ferrallitic tropical	1	/	/	56	Aweto (1981)
		3	/	/	512	
		7	/	/	2270	
		10	/	/	2670	
		OGF	/	/	2260	

^a ind./0.1 ha^b ind./30 m²^c Sapling stratum 1–4.9 cm dbh/100 m²^d Tree stratum, dbh ≥ 5 cm/500 m²

The different changes reported in levels of plant density are summarized in Table 2.3. Many researchers observed that younger fallows have higher tree density, lower canopy height and lower basal area (Saldarriaga et al. 1988; Denslow and Guzman 2000; Guariguata and Ostertag 2001). Chazdon et al. (2007) also pointed out that the stem density of fallows is often higher than that of old-growth mature forests. Studies of the eastern lowlands of Bolivia (Kennard 2002), lowland Costa Rica (Guariguata et al. 1997) and Nigeria (Aweto 1981) agreed with this observation. However, others observed variation along the chronosequence, and it is clear that change in stem density along succession varies greatly among the studies reviewed here. Ruiz et al. (2005) suggested that stem density is

likely to peak at the intermediate age class, which is demonstrated in their study in the dry forests of Colombia, and a study by Kennard (2002) in the eastern lowlands of Bolivia. Table 2.4 reports the values of plant densities from various studies, and also shows patterns of variations along the chronosequence, and peaks at the intermediate age classes, for both overstory and understory composition. As suggested by Chazdon et al. (2007), stem density does not show a predictable pattern. Thus, we can conclude that in the successional process, fluctuation in tree density level is greater than both basal area and aboveground biomass. The great variation of stem density shows that a wide range of factors influence its change. These factors are likely to be soil, land use intensity and other locational or temporal factors not addressed in the papers reviewed (Chazdon et al. 2007; Kennard 2002).

A few studies estimated similar lengths in the number of years needed for fallows to reach comparable plant densities as old-growth forests. Fallows in the tropical dry forest of Colombia, semi-deciduous forests of Bolivia and moist evergreen forests of Nigeria had similar plant density growth rates, requiring from 5 to 7 years to reach levels of the old growth forest (Table 2.3). In the tropical dry forests of southern Mexico, however, between 8 and 13 years were required. As shown in Table 2.3, the longest period of time to attain old-growth forest plant density was reported for the evergreen broad-leaved forest of north-western Vietnam. Based on these results, we are unable to conclude which type of forest demonstrates a faster rate of plant density regeneration.

This chapter presented a bigger picture of the changes in forest structure during secondary forest succession following shifting cultivation. Comparisons on forest structure among regions and forest types are rarely found in the literature. By reviewing the results from different researches, we can conclude that total above ground biomass, total basal area, canopy height, and plant density do not show a consistent development pathway, which implies that the conditions or characteristics of the forest plays a part in altering the regeneration of forest structure during succession. Chazdon et al. (2007) also highlighted the importance of local species composition on influencing the changes in vegetation, which is seldom mentioned or examined in studies of forest succession. If local or regional characteristics were taken into consideration, in addition to the differences in fallow age, we would be able to better understand the patterns of forest structural changes during secondary succession.

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