Fruit production and leaf longevity in the tropical shrub *Piper aduncum* L. in Sumatra

Tsuyoshi YONEDA

Faculty of Agriculture, Kagoshima University, 890-0065 Kagoshima, Japan
Tel & Fax: 099–285–8571; E-mail: yoneda@agri.kagoshima-u.ac.jp

ABSTRACT The aggressive reproduction strategy of the naturalized shrub *Piper aduncum* L., introduced from humid Neotropical regions, was studied in Sumatra paying special attention to fruit production and leaf longevity. A single piper shrub produced inflorescences throughout the year and the annual production of a mature inflorescence was estimated at 7.8 ton ha⁻¹ yr⁻¹. It was also shown to consume 100 kg of nitrogen per hectare for annual fruit production on the basis of its crown projection area, while 60% of nitrogen in leaves and branches was reabsorbed with senescence and death. Average leaf longevity was 158 ± 48 days with an average turnover rate of 2.5 ± 0.51 yr⁻¹. This high turnover rate is considered advantageous for continuous fruit production from early growth stages through effective allocation and reabsorption of energy and nutrients. Next, a mathematical model for optimum leaf longevity was proposed taking into account the maintenance costs of a single branch. The model showed that the observed leaf longevity approximately satisfied the expected minimum maintenance cost of a mature branch. A short leaf life span could save stem and branch construction costs through effective leaf production with low biomass. Economical branch structures in terms of energy and nutrient use could allow allocation of more resources to fruit production. This prioritization of fruit production over construction of a durable stem and branches could be evaluated as an adaptive living strategy of this shrubby pioneer species. Based on the proposed model, the adaptive survival strategies of other species were discussed with special reference to the relationship between leaf longevity and branch structure.

Key words: fruit production, leaf longevity, maintenance cost of a single branch, module, piper shrub

INTRODUCTION

The shrub *Piper aduncum* L., introduced from the New World Tropics, has become an aggressive weed in many parts of Malesia (Chew, 1972). In West Sumatra, this species is widely distributed along roadsides, in thickets near areas of cultivation and on forest edges at various altitudes from sea level to around 1000 m. In addition, pure scrubs of a few hectares often cover mountain slopes in the fallow periods of shifting cultivation at 400–600 m above sea level in some regions of this state. It is a rare occurrence to see this species at a big gap in a mature forest at this altitudinal zone. Vigorous precocious *P. aduncum* shrubs bear plentiful inflorescences throughout the year, suggesting that continuous production of a large amount of seeds is advantageous in these habitats, which suffer from frequent disturbances. Halle et al. (1978) suggested Petit's model with regard to the branching pattern of *P. aduncum*, which is characterized by continuous growth of a monopodial trunk and branches. This growth pattern is thought to be one of the reasons why continuous fruit production is seen in this species.

Leaf longevity has evolved through adaptation to various environmental stresses (Chabot & Hicks, 1982; Kikuzawa & Ackerly, 1999); for example, light is one of the environmental factors affecting this trait (Williams et al., 1989; Ackerly & Bazzaz, 1995). Williams et al. (1989) revealed that in a Mexican mature forest, open site Piper species had shorter leaf longevity than those growing in the shady understory. Thus, *P. aduncum* growing in open sites could be expected to have short leaf longevity. How a short leaf life span is related to the continuous and high fruit production of this species is therefore a subject of interest. Kikuzawa (1991) and Reich et al. (1991) analyzed leaf longevity based on the concept of a cost-benefit model, and Kikuzawa and Ackerly (1999) pointed out that construction and maintenance costs of supporting structures influences leaf longevity.

This paper aims to clarify *P. aduncum* fruit production through long-term field observations of
a single shrub, paying particular attention to leaf longevity. Verification of the following was sought: 1) the demography of leaves is advantageous for continuous fruit production through effective allocation of energy and nutrients from leaves from early growth stages, 2) short leaf longevity can save energy for fruit production by decreasing branch maintenance costs through decreasing the weight of a mature branch, and 3) short leaf longevity can save energy for fruit production by decreasing stem and branch construction costs through effective leaf production and low leaf biomass.

**MATERIALS AND METHODS**

**Study site and plant materials**

This study was conducted for six years from November 1993 until November 1999 at the Sumatra Nature Study Center (SNSC: 00°57.106’ N, 100°27.393’ E, altitude: 130 m) of Andalas University, 10 km east of Padang City. This region is highly humid throughout the year, with an average annual rainfall of 4000 mm; during the last 69 years, monthly rainfall has not dropped below 200 mm on average. However, year-to-year changes are large; the drought in 1997 was particularly severe, lasting for 4 months (August-November) with less than 50 mm rainfall/month (Yoneda et al., 2000).

A piper shrub usually consists of several erect stems each with numerous horizontal branches originating from stem nodes; here, this assemblage of a stem is referred to as a shoot (Fig. 1). A single branch has many nodes, each of which produces one internode, one leaf and one inflorescence (spike: bisexual flowers). This modular system, divided by nodes, enables production of these organs to be traced throughout their life spans with nodal order from the branch base or tip. Stems also show a similar modular structure, each node producing one internode, one leaf and one branch. Branch abscission usually occurs at the base where it attaches to the erect stem.

**Demographic observations**

Life spans of all branches, leaves and spikes of one shoot on a single Piper shrub growing in an open site were observed. Branch abscission and the presence of leaves and spikes at each internode of all branches were recorded at each observation. Observations were conducted 17 times during 2.4 years from October 1994 to March 1997 at average intervals of 55 days. The shoot grew from 2.5 to 4.8 cm in diameter at breast height (dbh, 1.3 m above the ground) and from 3.6 to 5.7 m in height (H). Total numbers of observed branches, leaves and spikes were 75, 1522 and 1165, respectively. Average life span of leaves is defined as the average ratio of existing leaves to the annual production rate at each observation period. Turnover time is an inverse value of a life span. Average turnover time is defined as the average ratio. These values for inflorescence are calculated with a loss rate instead of a production rate because of the large variation among observation periods. Average life span of a branch is defined as a ratio of an average existing branches among observation periods to an annual production rate during the whole study period.

Seasonal changes in litter fall rates of a neighboring developed shrub were observed using a 1 m<sup>2</sup> litter trap placed in an open area under the crown (projected area: 11.3 m<sup>2</sup>). The shrub consisted of six shoots sprouting from the stem base. The maximum dbh of the shoots grew from 5.7 to 7.1 cm during the study period of October 1994 to December 1997; crown area showed little change during this period. Litter collection was conducted at intervals of one week (total: 153 times). Collected litter was sorted into four components (leaves, branches, inflorescences and others) then oven-dry weights (80°C) were measured. Carbon and nitrogen concentrations of each component and attached dead branches before falling, sampled from outside of litter-trap’s window, were analyzed using a CHN corder (Yanako MT–3).

**Analysis of growth and branch structures**

Growth processes of each component of a branch module...
Fruit production and branch structure of a piper

were analyzed through changes in oven dry weights at each node. Seventeen branches from the shrub used for litter fall observations were sampled in November 1999. Branches were cut into modules then each was sorted into nodal order from the tip to the base. Modules in each nodal order were separated into internodes, leaves and inflorescences then average dry weights were measured. Carbon and nitrogen concentrations were measured using a CHN-Corder.

Ratios of leaf to total branch weight were observed for all branches of a mature shoot in this area being 6.4 cm in \( \text{dbh} \) and 7.3 m in \( H \). The total number of sampled branches was 48. Oven dry weights of internodes, leaves and inflorescences on each branch were measured, respectively.

The total aboveground dry weight (\( wt \)) and leaf dry weight (\( F \)) of the shoot were calculated from its \( \text{dbh} \) and stem length (\( L \)) with the following allometric relationships obtained from destructive sampling of 12 piper shoots of various sizes in this area:

\[
wt = 0.0837 V^{0.72} \quad (\text{kg, cm}^2 \text{ m}) ; \quad r^2 = 0.981 \quad (1)
\]

\[
F = 0.0312 V^{0.86} \quad (\text{kg, cm}^2 \text{ m}) ; \quad r^2 = 0.831 \quad (2)
\]

where \( V \) represents the \( \text{dbh}^2 \times L \) of a shoot, respectively.

RESULTS AND DISCUSSION

Life spans of branches, leaves and inflorescences

The number of branches of a shoot used for demographic observations was nearly constant at \( 25 \pm 2.0 \), showing balance between production and falling without seasonal changes for the first 2.1 years of the study period before the drought in 1997 (Table 1). The average life span of branches during the study period was 1.0 year; however, the number of branches decreased after defoliation during the 1997 drought. Branches continuously produced new modules throughout their life span and the average production rate was \( 0.079 \pm 0.015 \text{ day}^{-1} \) during active growth periods for the first 150 days. That is, vigorous branches continuously produced a module containing a single leaf, one internode and one inflorescence at intervals of 13-14 days. This rate was not significantly different from the production rate of stem modules (0.072 ± 0.008 day\(^{-1} \)).

Leaves rapidly grew up to a mature size of 15-18 cm in length and ca. 5 cm wide within 10-20 days after emergence, and inflorescences continuously increased their volume throughout their entire life span. Inflorescences bloomed 40-45 days after emergence, and on average, formed mature fruits after a further 30-35 days. A mature spike was 0.65 ± 0.21 g in dry weight, 11-16 cm long and 0.45-0.55 cm in diameter, containing about 1500 seeds. Few mature inflorescences were found on the ground under the crown during the study period, suggesting that they were scavenged by animals and/or birds before or immediately after falling.

Numbers of leaves and inflorescences on a single shoot tended to be constant through equilibrium of production and loss, without clear seasonal changes during the first 2.1 years (Table 1). During the study period, the total number of lost spikes was 1042, representing 79% of the total number of fallen leaves. Thus, on average, the shoot produced 1.4 spikes and about 2000 seeds per day. Average leaf longevity during the first 2.1 years was estimated as 158 ± 48 days. The average life span of an inflorescence was estimated as 78 ± 20 days, half the length of leaf longevity. Average turnover rates of a leaf and inflorescence were 2.5 ± 0.51 and 5.0 ± 1.3 yr\(^{-1} \), respectively.

Leaf and fruit production rates

Litter fall rates of leaves and branches showed weak positive correlations with the cumulated rainfall over 30 days before each collection day; coefficients of correlation (\( r \)) were 0.21 (\( P < 0.01 \)) for leaf litter and 0.28 (\( P < 0.001 \)) for branch litter. Average rates of these two components during the first 2.1 years were significantly higher than rates during the drought in 1997 (Table 2). The average fall rate of inflorescences during the entire study period was only 8% of that of leaf litter. Most inflorescences

<table>
<thead>
<tr>
<th>Organ</th>
<th>Total number produced (2.1 yr(^{-1} ))</th>
<th>Total number lost (2.1 yr(^{-1} ))</th>
<th>Average number (shoot(^{-1} ))</th>
<th>Average life span (days)</th>
<th>Average turnover rate (yr(^{-1} ))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Branch</td>
<td>53</td>
<td>48</td>
<td>25 ± 2.0</td>
<td>358</td>
<td>1.02</td>
</tr>
<tr>
<td>Leaf</td>
<td>1296 (100%)</td>
<td>1318 (100%)</td>
<td>247 ± 36</td>
<td>158 ± 48</td>
<td>2.5 ± 0.51</td>
</tr>
<tr>
<td>Inflorescence</td>
<td>1028 (79%)</td>
<td>1042 (79%)</td>
<td>98 ± 13</td>
<td>78 ± 20</td>
<td>5.0 ± 1.3</td>
</tr>
</tbody>
</table>

Table 1. Average life spans and turnover rates of each organ on a single piper shoot growing in an open site in Padang, West Sumatra. Values are estimates from data obtained over 2.1 years before the drought in 1997. Values in parentheses represent ratios to the values for leaf.
collected in the litter trap were immature, and fall rates tended to be higher during periods of drought. The average annual rate of leaf litter fall was $6.08 \pm 3.13$ ton ha$^{-1}$ yr$^{-1}$ for the first 2.1 years, while the rate during the drought in 1997 was only 78% of this. The average leaf and aboveground biomasses of the observed shoot during the study period were 1.9 and 15.7 ton ha$^{-1}$ based on Eqs. (1) and (2), respectively.

Average dry weights of a single mature inflorescence and fallen mature leaf were 0.65 and 0.40 g, respectively. By applying these values under the assumptions of all lost inflorescences being mature, the annual production rate of inflorescences during the first 2.1 years before the drought was calculated as 7.8 ton ha$^{-1}$ yr$^{-1}$ ($6.08 \times 0.79 \times 0.65/0.40$), accounting for 48% of the total production rate (16.3 ton ha$^{-1}$ yr$^{-1}$ in dry matter) of fine litter (8.50 ton ha$^{-1}$ yr$^{-1}$) and inflorescences (Table 3). This inflorescence production rate is equivalent to consumption of 99 kg nitrogen (N) ha$^{-1}$ yr$^{-1}$, 72% of the total annual nitrogen consumption for fine litter and fruit production. Thus, a piper shrub uses large amounts of nitrogen on inflorescence production, distributing most of its allocation outside the crown area through feeding of mature fruits rich in nitrogen.

**Nitrogen metabolism of branches and shoots**

Amounts of nitrogen per leaf rapidly increased after emergence, achieving nearly the same content as a mature leaf at the second or third internode from the branch tip; however, the amount of carbon continued to increase until the seventh order (Fig. 2). With increasing order over the seventh node, nitrogen content per leaf linearly decreased, and the amount seen in senescent leaves was 4 mg N leaf$^{-1}$, only 50% of the maximum content. The average content seen in dead leaves collected by the litter trap was 3 mg leaf$^{-1}$, which indicates that piper shrubs reabsorb around 60% of the nitrogen seen in mature leaves through senescence and defoliation.

The amount of nitrogen in the inflorescences linearly increased throughout growth, reaching 7.5 mg inflorescence$^{-1}$ at the eighth node during mature conditions. This was nearly equivalent to the content of a mature leaf. Carbon rapidly increased from the fourth order, reaching 265 mg inflorescence$^{-1}$ at the final order (1.5–1.8 times that of a single leaf).

The maximum number of nodes on the 17 sampled branches was 26. Nitrogen concentrations of internodes decreased from 2.6 to 0.35% with increasing order, and those of attached dead branches before falling ranged from 0.19 to 0.22%. The nitrogen concentration of fallen branches in the litter trap was 0.17%. These differences suggest that the nitrogen in an internode is reabsorbed through senescence and death. Based on these concentrations, the total nitrogen content of 26 internodes on a single branch was estimated as

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**Table 2.** Average litter fall rates (ton ha$^{-1}$ yr$^{-1}$) of a piper shrub during three different time periods. Letters in bold show significant differences between pre-drought (1994–1996) and drought (1997) periods.

<table>
<thead>
<tr>
<th>Period</th>
<th>Number of samples</th>
<th>Leaves</th>
<th>Branches</th>
<th>Inflorescences</th>
<th>Others</th>
<th>Total</th>
<th>Total minus inflorescences</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oct. 1994-Dec. 28'97</td>
<td>151</td>
<td>5.67 ± 2.91</td>
<td>1.69 ± 1.86</td>
<td>0.43 ± 0.49</td>
<td>0.48 ± 0.54</td>
<td>8.28 ± 4.14</td>
<td>7.84 ± 4.01</td>
</tr>
<tr>
<td>Oct. 1994-Dec. 6'96</td>
<td>104</td>
<td>6.08 ± 3.13$^*$</td>
<td>1.99 ± 2.12$^*$</td>
<td>0.36 ± 0.36$^*$</td>
<td>0.43 ± 0.52</td>
<td>8.87 ± 4.44$^{**}$</td>
<td>8.50 ± 4.33$^*$</td>
</tr>
<tr>
<td>Jan. 10'97-Dec. 28'97</td>
<td>47</td>
<td>4.75 ± 2.07$^*$</td>
<td>1.02 ± 0.70$^*$</td>
<td>0.60 ± 0.67$^*$</td>
<td>0.59 ± 0.55</td>
<td>6.98 ± 2.96$^{**}$</td>
<td>6.38 ± 2.67$^*$</td>
</tr>
</tbody>
</table>

$^*$: P < 0.01 and $^{**}$: P < 0.05.

**Table 3.** Concentrations of carbon and nitrogen in a piper shrub, and estimated proportions of each litter fraction in terms of dry matter, carbon content and nitrogen content. Values represent litter fall rates during a pre-drought period before 1997. Values in parentheses represent ton ha$^{-1}$ yr$^{-1}$.

<table>
<thead>
<tr>
<th>Litter Fraction</th>
<th>Carbon concentration (%)</th>
<th>Nitrogen concentration (%)</th>
<th>Dry matter content (%)</th>
<th>Carbon content (%)</th>
<th>Nitrogen content (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaves</td>
<td>31</td>
<td>0.55</td>
<td>37</td>
<td>29</td>
<td>24</td>
</tr>
<tr>
<td>Branches</td>
<td>46</td>
<td>0.17</td>
<td>12</td>
<td>14</td>
<td>2</td>
</tr>
<tr>
<td>Inflorescences</td>
<td>44</td>
<td>1.27</td>
<td>48</td>
<td>54</td>
<td>72</td>
</tr>
<tr>
<td>Others</td>
<td>31</td>
<td>0.55</td>
<td>3</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Total</td>
<td>-</td>
<td>-</td>
<td>100 (16.3)</td>
<td>100 (6.4)</td>
<td>100 (0.14)</td>
</tr>
</tbody>
</table>
22, 10 and 8 mg under each of these three conditions, respectively. Reabsorbed nitrogen (14 mg), which was nearly equivalent to the content of two mature spikes, accounted for about 60% of the content of a single living branch. That is, the same resorption proficiency seen in leaves was seen here.

Early maturation of leaves in carbon and nitrogen contents would be caused by the prior allocation for high primary production throughout their life spans to inflorescences as a non-photosynthetic organ showing gradual growth. Annually, a piper shrub allocates 99 kg N ha\(^{-1}\) to inflorescences, while 39 kg N ha\(^{-1}\) is returned to the forest floor as fine litter on the basis of its crown projection area. About 60% of the nitrogen is reabsorbed from mature leaves and branches through senescence and falling, and the total amount allocated to these organs, including inflorescences, was 197 kg N ha\(^{-1}\) yr\(^{-1}\) = 99 + 39/0.4. Therefore, a piper shrub could effectively allocate 1.4 times the total consumed nitrogen (138 kg = 99 + 39 kg) to construction of these organs. A large amount of reabsorbed nitrogen from leaves and branches with short life spans would largely contribute to nitrogen metabolism of inflorescences with high turnover rates. The nitrogen consumption rate of a piper shrub, 138 kg N ha\(^{-1}\) yr\(^{-1}\), was shown to be almost identical to the annual nitrogen flow of litter fall in a tropical rain forest (201 kg ha\(^{-1}\) yr\(^{-1}\), Nye, 1961; and 123 kg ha\(^{-1}\) yr\(^{-1}\), Yoda & Kira, 1982). Furthermore, the amount allocated to inflorescence production was equivalent to the annual N uptake by an evergreen oak forest in a warm-temperate region of Japan (Katagiri et al., 1978). Almost all mature inflorescences were removed from the crown projection area by animals and/or birds; therefore, the nitrogen content of the habitat will gradually decrease unless a good external supply is provided.

**Structure of a mature piper branch**

Demographic observations revealed that a mature piper branch consists of 28 internodes (558 x 0.079), 12 leaves (158 x 0.079) and 6 inflorescences (78 x 0.079), based on the production rate of new modules and the life span of each organ. The average age of a branch was one year.

The weight ratio of one leaf (L) to one internode (I) was directly observed using the 17 branches used for observations of nitrogen metabolism (Fig. 2). The maximum nodal order was 26, showing the size of a mature branch. Carbon and dry matter weights of a leaf tended to be constant at above the seventh nodal order, while internode values increased gradually until the maximum order; the L/I ratio constantly decreased with increasing nodal order. The average L/I ratio of a single branch was 1.86 in dry matter when assessed using average values of whole leaves and internodes from the 17 branches.

Figure 3 shows the vertical distributions of branch dimensions in a mature piper shoot 6.4 cm in dbh and 7.3 m in height. Branch volume increased from the top to the base of the shoot, growing to the mature size of 100 cm\(^3\) at around the middle of the crown; 12 branches over 100 cm\(^3\) in the lower crown were defined as mature based on their vertical distribution patterns (Fig 3). The average
The optimal L/I and B/we ratios satisfying the minimum maintenance cost of a mature piper branch were also examined using a mathematical model. Referring to the growth traits of a piper shrub, the model branch continuously grows according to a modular system of one internode and one leaf (Fig. 4). It was assumed that the existing number of leaves on an entire branch is always constant (c) at maturity with internodes over c in number, since older leaves fall when new leaves are formed. It was also assumed that the life span of a branch is one year with constant total investment during its entire life span (t). These relationships can be shown by the following equations:

\[ p_c = (L + D) \cdot t \]  
\[ B_{mat} = w_c + I_t \]  
\[ = c \cdot L + I_t \]  

where \( B_{mat} \) and \( t \) are the weight of a mature branch and the annual production rate of a module, \( t \) [yr\(^{-1}\)], respectively. From Eqs. (3) and (4), relationship between \( B_{mat} \) and \( t \) can be shown by:

\[ B_{mat} = c \cdot p_c / t - c \cdot I_t + I_t \]  

The minimum maintenance cost of a mature branch was defined as the minimum value of \( B_{mat} \) having close correlation with total maintenance cost of a branch through its whole stage from emergence to a mature stage. The \( t \) value producing the minimum branch weight, the optimum rate of \( t \) (\( t_{opt} \)), can be obtained under conditions of \( \partial B_{mat} / \partial t = 0 \) using Eq. (5). By differentiating Eq. (5) with respect to \( t \), \( t_{opt} \) can be presented by:

\[ t_{opt} = \sqrt{c \cdot p_c / I_t} \]  

and Eq. (3) at \( t = t_{opt} \) is:

\[ p_c = (L + D) \cdot t_{opt} \]  

By substituting Eq. (3) for Eq. (6),

\[ t_{opt} = c \cdot (L/I + 1) \]  

and from the definition of leaf longevity (s), \( s = c / t \), \( s \) at \( t_{opt} \) (\( s_{opt} \)) is given by:

\[ s_{opt} = c / t_{opt} = 1 / (X + 1) \]  

where \( X \) is \( L/I \). Therefore, Eq. (7) represents the \( s_{opt} \) - \( L/I \) relationship satisfying the minimum \( B_{mat} \) value. By substituting Eq. (4) at \( t = t_{opt} \) for Eq. (6), the relationship between \( s_{opt} \) and \( B_{mat} / we \) is:

\[ s_{opt} = (Y - 2) / (Y - 1) \]  

where \( Y \) is \( B_{mat} / we \).
Fig. 5. Relationship between optimum leaf longevity (s_{opt}) and the L/I ratio of a module obtained from Eq. (11). L, I and n represent the weights of a leaf and internode, and the turnover rate (years) of a branch, respectively. The two arrows show gradients of the relationship according to the L/I ratio (succession) and n values (resources), respectively.

Table 4. Average leaf longevity of a piper shrub and three tropical rain forests. HPPB and PIN are secondary (Yoneda et al., 2000) and well developed forests (Yoneda et al., 1994), respectively, in the study area, West Sumatra, and Pasoh is a mature lowland tropical rain forest in Peninsular Malaysia (Kira, 1987).

<table>
<thead>
<tr>
<th></th>
<th>Piper shrub (this study)</th>
<th>HPPB</th>
<th>PIN</th>
<th>Pasoh</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aboveground biomass (ton ha^{-1})</td>
<td>15.7*</td>
<td>161</td>
<td>414</td>
<td>431</td>
</tr>
<tr>
<td>Leaf biomass, F (ton ha^{-1})</td>
<td>1.9*</td>
<td>2.8</td>
<td>6.8</td>
<td>7.8</td>
</tr>
<tr>
<td>Fruit &amp; seed production (ton ha^{-1} yr^{-1})</td>
<td>7.8</td>
<td>0.87**</td>
<td>0.66**</td>
<td>0.38**</td>
</tr>
<tr>
<td>Leaf litter-fall, Lf (ton ha^{-2} yr^{-1})</td>
<td>6.1</td>
<td>5</td>
<td>5.8</td>
<td>7</td>
</tr>
<tr>
<td>Leaf longevity, s = F /Lf (yr)</td>
<td>0.31</td>
<td>0.56</td>
<td>1.17</td>
<td>1.11</td>
</tr>
</tbody>
</table>

*: estimated based on the crown projection area using the allometric relationships in the text; **: estimated using the litter trap method.
without such systems have a longer leaf life span of over 5 years (Tadaki, 1991). Williams et al. (1989) suggested that in a Mexican lowland tropical forest, leaf longevity is negatively correlated with daily photosynthetic photon-flux density (PFD) in about nine species of Piper. Equation (11) could explain this relationship since PFD is one factor controlling the annual investment to a branch. Kempf & Pickett (1981) showed that later successional shrubs allocated more to longer branches than early successional shrubs in order to avoid self-shading of leaves under lower light conditions. This shows some biological meanings about a gradient of L/I values along the environmental resources, though their leaf longevities were not observed in the study. Ackerly & Bazzaz (1995) revealed that the leaf longevity of a tropical pioneer species is negatively related to PFD and nitrogen resources, and is influenced by self-shading conditions. Equation (11) suggests that these changes in leaf longevity could be achieved by intra and interspecific plasticity of modular structure.

CONCLUSION

A single piper shrub, Piper aduncum L., produced inflorescences throughout the year and the annual production of a mature inflorescence accounted for 52% and 72% of total litter production in carbon and nitrogen amounts, respectively. This aggressive reproduction was managed by effective utilization of energy and nutrient through their high turnover rates of leaves, 2.5 ± 0.51 yr⁻¹, producing high reabsorption of nitrogen from leaves, low maintenance costs of a mature branch, and low construction costs of a stem and branches of a shoot. Basing on these results, a model was proposed for relationships between leaf longevity and branch structure with parameters being secondary sere and resources.

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