Characterization of branching in two *Hevea brasiliensis* clones

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Received 6 October 2003; Accepted 26 January 2004

Abstract

Rubber has been grown for several decades in Africa, notably in Ivory Coast. Although the yields obtained with selected clones are good, some problems with adaptation to edaphic and climatic conditions have yet to be solved. Of these problems, tree breakage due to violent winds during frequent storms is a major handicap. Some clones are more resistant to wind damage. However, this resistance trait remains difficult to measure, and detecting it at an early stage appeared important. As no differences have been found in the physical properties of the wood of different clones, the search for differences between clones displaying resistance and susceptibility to wind damage was switched to architectural structures. Architectural traits were thus studied on two rubber clones with very different resistances to wind. Observations were focused both on young trees and adult trees. Of all the architectural traits observed, a description of branching provided information likely to explain differences in the way the clones being studied developed over time. The clone GT1 which is resistant to wind, developed more lateral branches but they did not grow much in length. On the other hand, fewer axillary branches appeared on the susceptible clone PB235 but they grew longer. Moreover, as some of these traits proved to be similar in both young and adult trees, they could be detected at a sufficiently early stage for use as early prediction traits, if their involvement in susceptibility to wind damage is confirmed.

Key words: Branching, *Hevea brasiliensis*, predictor traits, tree architecture, wind damage.

Introduction

The rubber tree originates from the Amazon forest. The genus *Hevea*, of the family Euphorbiaceae, includes ten species that would seem to have differentiated as the forest evolved in the last hundred thousand years (Clément-Demange et al., 1997). Nowadays, their natural range covers the entire Amazon basin and extends southwards as far as Bolivia and Mato-grosso (Brazil) and westwards to Iquitos in Peru (Compagnon, 1986).

*Hevea brasiliensis*, which is a tall tree that can reach heights of 20–35 m in forests, with a trunk circumference of 1–2 m, has the particularity of producing a latex rich in natural rubber particles. The properties of this product, which have long been known and used by South American Indians, were only discovered by Europeans in the 18th century (Jacob et al., 1994). This species, *Hevea brasiliensis*, which is virtually the only source of natural rubber, is usually grown in clone form.

Rubber is currently grown on 7–8 million hectares of plantations in the humid tropics (Dean, 1987; Clément-Demange et al., 1997). Asia supplies 92% of the world’s production, led by Thailand, Indonesia, and Vietnam. The remaining 8% is produced in Africa (6%), primarily in Ivory Coast and Nigeria, and in South America, the continent of its origin, with only 2% due to a leaf disease (a parasitic fungus: Microcycus).

Plantations currently contain budded clones, i.e. populations of individuals that are all genetically identical, obtained by a vegetative propagation technique known as budding. This technique, which was launched in the 1920s, led to considerable improvement in plot yields, and became the routine practice by 1950 (Dijkman, 1951). The clones used today are the result of so-called recurrent
selection carried out since the beginning of the last century, which consists in selecting the best clones from the progeny of the most efficient clones crossed with each other (Clément-Demange et al., 1995a). Most selections are made within the ‘Wickham’ genetic group, from a survey conducted in 1896 (Sérié, 1993); the genetic base of cultivated populations therefore remains very narrow (Seguin et al., 1995). In order to satisfy the increasing demand for rubber, the main objectives of research today are to improve productivity per hectare and the technological quality of rubber. The factors considered in selection differ depending on the regions, in line with eco-climatic conditions and the phytosanitary problems encountered.

A rubber genetic improvement programme has been under way in Ivory Coast since 1972. As that country does not have any serious phytosanitary problems, selection is primarily geared towards increasing productivity. Some research is therefore concentrated on obtaining higher-yielding clones. The other aim is stand stability. The useful stand density, i.e. the number of trees tapped, tends to decrease with time in plantations. This is mostly due to two factors: the first is a phenomenon known as tapping panel damage, when latex production stops (Jacob et al., 1994), the second is linked to damage caused by wind, uprooting and, especially, trunk snapping. In Ivory Coast, serious damage occurs to rubber plantations during storms (Clément-Demange et al., 1995b).

The aerial architecture of the rubber tree was studied by Hallé and Oldeman (1970) and was used as an example to define Rauh’s architectural model: the trunk is a monopode whose rhythmic growth gives the branches a verticillate or sub-verticillate arrangement. Branches are orthotropic and morphologically identical to the trunk. Flowering is always lateral, on the branches and trunk. The rhythmic growth of the meristems follows a 40 d period (Hallé and Martin, 1968). Each portion of the axis between two rest periods in meristem formation is called a growth unit (GU). Each GU can be identified by the existence of morphological markers in the form of scale leaf and assimilating leaf scars alternately distributed along the aerial axes. All axillary branches have a proleptic development; they only develop in the axil of assimilating leaves and, on young trees, their rhythm is synchronous with that of the axis on which they are borne, after which the synchronization gradually alters (Hallé and Oldeman, 1970).

In this study, an attempt is made to provide structural explanations for differences in susceptibility to wind damage. Two clones were chosen, PB235 which is susceptible to wind damage, and GT1 which is reputed to be resistant (Clément-Demange et al., 1995b). As the biomechanical properties of these two clones proved to be very similar (Fourcaud et al., 1998), the architecture of the trees of these two clones was studied to characterize how ‘structure’ affected their reaction to wind.

Materials and methods

Plant material

Two different data sets were used in this study, both of them collected at the Bimbresso experimental station belonging to CNRA (Centre National de Recherche Agronomique) in Ivory Coast. The first observations were carried out in 1990, with a view to modelling the architecture of three Hevea clones (Costes and de Reffye, 1990). Two of them were PB235 and GT1, the two selected clones (Mercyukutty et al., 1995). The trees studied were one year old and two years old, planted in two trials. Forty one-year-old trees and 20 two-year-old trees were described for each clone. In 1997, two 7-year-old trees were described per clone in the same location. This small number of trees per clone resulted from their size and complexity, and from the time required to carry out the architectural descriptions.

Similar cultivation methods were used in the three trials. All the trees were clones that had been budded onto half-sib seedlings (i.e. with a common mother, clone GT1). After budding, the trees were planted in rows 7×2.8 m apart. Tapping began when the trees were between 5- and 7-years-old, depending on their growth. In fact, the trees were tapped once the trunk had reached a girth of 50 cm 1.30 m from the ground. A cut was usually made in the bark to enable rubber collection. Tapping was then carried out 5–10 times per month. Tapping strongly affected tree growth, and was reflected in both the increase in trunk diameter and in overall tree development (Gohet et al., 1996).

Architectural observations

As Hevea growth is rhythmic (Hallé and Martin, 1968), growth units (GU) can be easily identified through scars located at the GU extremities.

In young trees, all the axes were described in terms of GUs and within each GU the number of nodes was counted. Axillary branches were located on the bearing GU by recording the rank of the bearing node. By 1-year-old, the trees had developed two branching orders (order 1 corresponding to the trunk, order 2 to the laterals on the trunk and so on). When they were 3-years-old, the trees consisted of two or three branching orders. Axillary branches were described as the trunk.

When the apical meristem of the trunk died, the branching process was substantially modified. Thus, trees on which such an event was observed were not included in the analysis data. Consequently, only 38 and 32 1-year-old GT1 and PB235 trees, respectively, were used for analysis. Similarly, only 18 2-year-old GT1 trees and 20 PB235 trees were available.

Because of the complexity of the 7-year-old trees, architectural data were organized using the AMAPmod encoding method, which enabled multi-scale description of the trees and made it possible to memorize the topological relationships between tree entities (Godin, 1999). Two scales were considered. On the first scale, the axes were described making a distinction between the trunk, the branches, and the reiterated complexes (Oldeman, 1994). On a finer scale, GUs were considered. For each GU, the length and diameter were measured. To facilitate their description, the trees were first cut down and then described from the bottom to the top.

Data extraction

On young trees, the traits analysed were the percentage of branched GUs on the trunk, the number of axillary branches per GU, and the mean length of axillary branches. The length was measured as the number of nodes, and the mean length was calculated according to the index of the bearing GU, counted from the trunk base.

On adult trees, branching systems located at the tree periphery were studied; their numbers varied from 70 to 210. These branching
systems (which were reiterated complexes; Oldeman, 1994) were selected from the database using 'aml' programming language (Godin et al., 1997). To be selected, the branching systems had to meet two conditions: the apical meristem had to be alive (i.e. they did not have axillary branches on their last GU) and the main axis had to bear at least one axillary shoot.

To compare the branching process on both young trees and reiterated complexes, a 'relative branching order' was defined in the case of reiterated complexes. The main axis was thus considered as order 1, axillary branches were considered as order 2, etc. The selected branching systems developed two to three relative branching orders.

In adult trees, the characters analysed were the percentage of branched GUs on order 1 axes, the number of axillary branches per GU, and the mean length of the axillary branches. In this case, the length was a metric measurement of GUs per axis and, as for young trees, the mean length was calculated according to the index of the bearing GU.

Data analysis
The extracted traits were compared by analyses of variance to detect any clone effect.

The models used to compare adult clones were placed in hierarchical order in such a way as to take into account the tree effect within the clone effect. In this case, the experimental unit was the branching system.

In young trees, the clone effect was crossed with the age effect (1 year and 2 years). It was, therefore, a two-way analysis of variance model which could be used to test the interaction between these two factors and, thereby, the stability of the traits between one and two years.

The statistical analyses were carried out with SAS software, version 8 (Derr and Everitt, 2002).

Results
Percentage of growth unit branching
In adult trees, considerable uniformity was seen in the average percentage of branched GUs; the percentage was the same for the different trees of the clones studied (Table 1). In young trees, significant differences were detected between clones, along with an interaction between the clone and tree age factors (Table 2). However, tree age as a factor did not have a significant effect on the average percentage of branched GUs. The clone factor effect was then analysed for each age. It was significant when the trees were 1-year-old, though the two clones no longer displayed any significant difference once the trees were 2-years-old.

Figure 1, which shows the percentage of branched GUs depending on the index of the GU from the bottom of the trunk, can be used to interpret this result with greater precision. Indeed, it shows that GUs nearest the ground, i.e. index 1 to 7, were always less branched in PB235 than in GT1, irrespective of tree age. However, beyond the 7th GU, the GUs of clone PB235 branched more often than those of GT1. In other words, a gradual increase in the percentage of branched GUs was seen in both clones. In GT1, the percentage stabilized by the 4th GU, then fluctuated between 40% and 60%. However, in PB235 the

| Table 1. Comparison of the proportion of branching GUs on reiterated complexes located at the periphery of 7-year-old trees of two Hevea clones compared by a hierarchic ANOVA |
|---------------------------------|-----------------|-----------------|
| Clone                          | Mean square     | F   | NS  |
| Tree (clone)                   | 0.033           | 1.41 | NS  |
| GT1                            | 0.003           | 0.13 | NS  |

GT1
<table>
<thead>
<tr>
<th>Tree No.</th>
<th>Mean values</th>
<th>Nb</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.446</td>
<td>204</td>
</tr>
<tr>
<td>2</td>
<td>0.450</td>
<td>125</td>
</tr>
</tbody>
</table>

PB235
<table>
<thead>
<tr>
<th>Tree No.</th>
<th>Mean values</th>
<th>Nb</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.434</td>
<td>210</td>
</tr>
<tr>
<td>2</td>
<td>0.427</td>
<td>70</td>
</tr>
</tbody>
</table>

* F: observed values of the Fisher test; NS: not significant (P value >0.05).

N: Number of GUs.

| Table 2. Proportion of branching GUs along the trunks of young trees of two Hevea clones compared by ANOVA |
|---------------------------------|-----------------|-----------------|
| Clone                          | Mean square     | F   | NS  |
| Tree age                       | 0.03            | 0.93 | NS  |
| Interaction                    | 0.287           | 10.2 | ** |

GT1
<table>
<thead>
<tr>
<th>Mean values</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-year-old</td>
</tr>
<tr>
<td>2-years-old</td>
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</tbody>
</table>

PB235
<table>
<thead>
<tr>
<th>Mean values</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-year-old</td>
</tr>
<tr>
<td>2-years-old</td>
</tr>
</tbody>
</table>

* **, Highly significant (P value <=0.01).

*, Significant (0.01 < P value <0.05).

Fig. 1. Percentage of branching GUs depending on the GU index.
increase continued throughout trunk growth, reaching values of 90–100% at the 12th GU.

Lastly, the tree age effect resulted from a different variation in the percentage of branched GUs with GU index, between the two clones. At adult age, this variation stabilized at around the same value in both clones (Table 1), around 40% of branched GUs, and a clone effect was no longer detected in adult trees.

**Number of lateral branches per branched GU**

The number of axillary branches was counted on branched GUs only, then the clones were compared for the different tree ages.

In adult trees (Table 3), the two clones displayed significantly different numbers of lateral branches: on average, GT1 developed more lateral branches than PB235.

In young trees (Table 4), the clone effect was significant, as were the tree age effect and the interaction between those two factors. However, the clone effect was much greater than the tree age effect and the interaction effect. A separate analysis of the 1-year-old and 2-year-old trees showed that the number of lateral branches differed significantly between the two clones in the 1-year-old trees, but not in the 2-year-old trees. As before, this apparent contradiction resulted from an inversion of the average numbers of lateral branches per GU beyond the 7th GU; for GU indexes 1–7, PB235 developed fewer lateral branches, but on GU indexes over 7, branching appeared to be much more active in PB235 than in GT1 (Fig. 2). In adult trees, the reiterated systems on which the analysis focused had developed 4–5 GUs on average (Milet, 2001). The average numbers of axillary branches borne were therefore comparable to those found in young trees for similar GU indexes.

**Length of lateral branches**

Once axillary branches appeared, their growth was itself subject to variation, depending on both the index of the bearing GU and the clone. The metric length of axillary branches on adult trees was compared for the two clones, according to the number of GUs on the axillary branches. In addition, the length of axillary branches was analysed in terms of the number of GUs, grouping axillary branches according to the insertion index of the GU on which they were borne, starting from the top. This analysis was carried out on both adult and young trees.

In adult trees, the metric length of the lateral branches was always significantly greater for PB235, irrespective of the number of GUs on the branches considered. (Fig. 3). In both young and adult trees, the number of GUs on the branches gradually increased in line with the insertion index of the bearing GU starting from the top. In adult trees, above three GUs from the top, the axillary branches of PB235 developed a larger average number of GUs than those of GT1 (Fig. 4). At six GUs from the top, the axillary branches developed 3.5 GUs on average in PB235, whereas they had fewer than 3 in GT1. In young trees, the lateral branches inserted on the first three indexes had substantially the same number of GUs in both clones.

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**Table 3. Mean number of axillary branches per GU of reiterated complexes located at the periphery of 7-year-old trees of two Hevea clones compared by ANOVA**

<table>
<thead>
<tr>
<th>Clone</th>
<th>Mean square</th>
<th>F</th>
<th>**</th>
</tr>
</thead>
<tbody>
<tr>
<td>GT1</td>
<td>596.34</td>
<td>16.12</td>
<td>**</td>
</tr>
<tr>
<td>PB235</td>
<td>64.44</td>
<td>1.84</td>
<td>NS</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Tree no.</th>
<th>Mean values</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>GT1 1</td>
<td>6.17</td>
<td>210</td>
</tr>
<tr>
<td>GT1 2</td>
<td>6.83</td>
<td>70</td>
</tr>
<tr>
<td>PB235 1</td>
<td>4.96</td>
<td>204</td>
</tr>
<tr>
<td>PB235 2</td>
<td>3.79</td>
<td>125</td>
</tr>
</tbody>
</table>

**Table 4. Mean number of axillary branches along the trunks of 1-year-old and 2-year-old trees compared by ANOVA**

<table>
<thead>
<tr>
<th>Clone</th>
<th>Mean square</th>
<th>F</th>
<th>**</th>
</tr>
</thead>
<tbody>
<tr>
<td>GT1</td>
<td>89.58</td>
<td>37.23</td>
<td>**</td>
</tr>
<tr>
<td>PB235</td>
<td>10.93</td>
<td>4.3</td>
<td>*</td>
</tr>
<tr>
<td>Interaction</td>
<td>12.5</td>
<td>4.92</td>
<td>*</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Mean values</th>
<th>1-year-old</th>
<th>2-years-old</th>
</tr>
</thead>
<tbody>
<tr>
<td>GT1</td>
<td>3.40</td>
<td>4.45</td>
</tr>
<tr>
<td>PB235</td>
<td>2.46</td>
<td>4.80</td>
</tr>
</tbody>
</table>

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Fig. 2. Number of lateral branches per GU depending on GU rank.

Fig. 3. Mean number of lateral branches per GU depending on GU rank.
However, the number of GUs on lateral branches inserted beyond 3 GUs from the top increased much more quickly in PB235 than in GT1 (Fig. 4). At seven GUs from the top, the axillary branches had 3.7 GUs on average in PB235 trees, whereas they had fewer than 3 in GT1. These results confirm those found in adult trees, the greater length of lateral branches in PB235 resulted from the development of a larger number of GUs.

Discussion

Three branching traits were observed: the percentage of branched growth units (GU), the number of lateral branches per branched GU, and the length of the lateral branches. These observations were carried out on two clones with a different architectural habit, PB235 and GT1, on trees aged 1 year, 2 years, and 7 years. It was thus possible to explain differences in structure between these two clones.

The percentage of branched GUs changed depending on the insertion index of the bearing GUs, and with the age of the tree, and did not distinguish between adult tree clones. However, the number of axillary branches per GU and the length of the branches proved to be stable over time, although changing with the index of the bearing GU. These results show that GT1 developed more lateral branches, but they did not grow much in length. On the other hand, fewer axillary branches appeared on PB235, but they grew longer.

In terms of resistance to wind damage, these results suggest that the crowns of PB235 trees develop more in width than those of GT1. This widthways development of the crowns can also be seen in the diagrams of the two clones studied (Fig. 5). GT1 has a growth habit sometimes known as a 'paintbrush', whereas PB235 has a more outspread growth habit.

The results obtained on these two clones with opposite reactions, GT1 resistant to wind damage and PB235 highly susceptible, suggest that wind damage could be linked to the shape of the trees, rather than to the physical properties of the wood. Indeed, no significant difference has been found in wood density or elasticity (Fourcaud et al., 1998), whilst the architectural study of these clones found differences in branching explaining the differences in shape. In terms of structural stability, wind susceptible architectures are characterized by a greater trunk–crown imbalance, due to both more abundant and/or more developed peripheral branched systems, and crowns with greater wind interception. The way reiterated complexes along trunks affect swaying of the structure was studied using a biomechanical model and computerized mock-ups of trees (Rogier et al., 1993). More generally, crown development is a factor in tree instability which is naturally compensated for by specific reactions brought into play during cambium growth (Spatz et al., 1999; Niklas, 2000), such as the formation of reaction wood zones, stimulation of cambium growth by the wind, and thickening at the bottom of the trunk.

In the case of Hevea, it has been shown that tapping strongly affects tree development (Gohet et al., 1996). The changes induced by tapping, with a reduction in the radial growth of the tree whilst vertical growth is not modified, contributes towards an imbalance between the trunk and the crown, which could also make trees more susceptible to wind damage. Increased susceptibility due to tapping could, therefore, be combined with a natural tendency for some genotypes to develop a trunk–crown imbalance.

Analyses on the peripheral branched systems of the trees showed that some branching traits seemed to be well-conserved during development. Indeed, for each clone the

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**Fig. 3.** Mean length of lateral branches depending on the number of GUs.

**Fig. 4.** Mean number of GUs per branch depending on insertion rank.
number of axillary branches per GU and length of these branches were similar in adult trees and in trees aged 1 year and 2 years, which should make it possible to predict certain aspects of the structure of adult trees from measurements taken on young trees.

However, several points remain to be confirmed. Indeed, this study only involved two clones and, for adult trees, only a small number of individuals since it was necessary to fell the trees to examine the architecture of adult trees closely. This practice, which is costly for the farmer, cannot be generalized, but it did make it possible to show that an analysis of peripheral branched systems, which correspond to reiterated complexes, can be used to compare the development of young and adult trees.

In future studies, thought will have to be given to sampling procedures, so that more trees and a larger number of clones can be observed. This will need to take into account architectural gradients, such as the increase in the number of axillary branches per GU along the trunks of young trees, or the length of axillary branches depending on their insertion index from the top of the bearing GU. In addition, the relationship between the shoot architecture of young and adult trees, and the implication of branching differences in resistance to wind damage, will have to be confirmed on a wider range of clones.

Acknowledgements

This work was funded by CIRAD interorganizational thematic research project ATP 97/60. We should like to thank the organizations associated with this study, notably CNRA Ivory Coast. We acknowledge also Mr Peter Biggins for the translation.

References


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Fig. 5. Diagrams of two 7-year-old rubber trees featuring PB235 (left, 10 m high) and GT1 (right 9 m high). Enlarged views indicate details about peripheral reiterated complexes.
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