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Metabolic partition between radial vegetative growth and rubber production of *Hevea brasiliensis* clones of different metabolic classes, bled at unstimulated d4 frequency in Côte d'Ivoire

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Abstract
Rubber growing is one of the most important industrial crops in Ivory Coast. In order to achieve a good sustainable rubber crop of *Hevea brasiliensis* in Ivory Coast, the effect of bleeding at unstimulated d4 frequency on radial vegetative growth was evaluated with 16 clones of *Hevea brasiliensis* divided into three classes of vegetative growth and metabolic activity, planted in a completely randomized block pattern. Agronomic (vegetative growth and rubber production) and physiological (sucrose and inorganic phosphorus levels) parameters were assessed over nine years. The results obtained showed that bleeding in d4 had a significant impact on the mean annual increase in circumference of bleeding trees (3.04 $cm.yr^{-1}$) relative to that of non-bleeding trees (5.29 $cm.yr^{-1}$). The reduction in growth expressed as a percentage of the vegetative growth potential was estimated at 42.53%. Mean annual circumference increments of unbleeded trees of clones of active (MAC; 5.46 $cm.yr^{-1}$) and moderate (MMC; 4.96 $cm.yr^{-1}$) vegetative and metabolic growth classes are significantly greater than those of bleeding trees of clones of the same classes (3.00 and 2.80 $cm.yr^{-1}$). On the other hand, the average annual increments of the slow vegetative and metabolic growing clones (SMC) are hardly affected by bleeding. The production and reduction in growth were 58.96 $g.a^{-1}.s^{-1}$, 45.06% for MAC, 56.2 $g.a^{-1}.s^{-1}$ and 43.55% for SMC, and 39.83 $g.a^{-1}.s^{-1}$ and 23.8% for SMC, respectively. A very highly significant polynomial relationship (R^2 = 1) between percent reduction in increment (%RedAcc), rubber production and P/Sac and Pi/Sac ratios was found. The percentage of vegetative growth potential below 50% is a sign that bleeding at the unstimulated d4 frequency is a good indicator for improving the productivity of rubber clones without damaging the physiological state.

Keywords: Vegetative growth, rubber production, bleeding, metabolic activity, *hevea brasiliensis*

1. Introduction
Hevea (*Hevea brasiliensis*) is a plant from the Amazon basin, now Brazil. It is a large tree of the Amazonian forest that can exceed 30 m in height and measure, at man's height, exceptionally more than 3 m in circumference (Compagnon, 1986) [3]. This plant is characterized in plantation by a very strong immature vegetative growth where the average annual growth of circumference is between 9 and 12 $cm.yr^{-1}$ and a moderate mature vegetative growth, with an average annual growth of circumference oscillating between 4 and 7 $cm.yr^{-1}$. Rubber production depends on many factors (Compagnon, 1986) [3] including radial vegetative growth. Indeed, the latter is the process and/or phenological phenomenon during which wood (xylem) and bark are produced by the cambium (libero-linear generative base) (Jacob *et al*., 1995) [9]. Thus, the trunk, which is the most suitable tree compartment, presents a better availability and exploitability of the laticiferous system, in the exploitation of the bark due to the presence of laticiferous coats, specialized and latex-producing cells, which treated gives natural rubber (Jacob *et al*., 1995; Obouayeba *et al*., 2000; Rajagopal *et al*., 2003) [9, 2, 19]. The work of (Obouayeba, 2005; Obouayeba *et al*., 2002) [4, 2] has shown that good vegetative bleeding growth is a good sign for rubber production as it ensures good availability of laticifers, the source of latex and thus rubber. They concluded that the better the vegetative growth, the thicker the bark and the more laticiferous the bark. Such bark is likely to produce more rubber. Hence the appearance of a positive link between laticifer development and vegetative growth. The production of natural rubber inevitably results from

bleeding (Serres *et al*., 1994; Jacob *et al*., 1995; Gohet *et al*., 1996; Obouayeba *et al*., 2000; Rajagopal *et al*., 2003; Obouayeba, 2005) [9, 2, 19, 5]. This consists of making an incision, a cut in the bark (Webster and Paardekooper, 1989; Jacob *et al*., 1995) [9, 24] and occurs at the physiological maturity of the tree determined at 6 years after planting (Obouayeba *et al*., 2000 and 2002; Obouayeba, 2005) [2, 5]. However, the exploitation of the tree for latex production has a negative impact on the vegetative growth of trees (Gooding 1952, Pardekooper 1989, Gohet 1996, Silpi *et al*., 2006) [7, 24, 5, 21]. Since bleeding is an action that involves a series of processes that can affect the vegetative growth of the plant, through the production of latex, a secondary metabolism of latex regeneration. This artificially created metabolism leads to competition between growth and production metabolisms for the use of photosynthesis and energy. For these two metabolisms, this competition is all the more harmful as bleeding is early and the latex harvesting system is intensive (Gohet, 1996; Obouayeba *et al*., 2000; Silpi *et al*., 2006; Soumahin *et al*., 2010) [5, 2, 21, 22]. In addition, radial vegetative growth of logged trees is generally reduced by 50% compared to non-harvested trees (Gohet, 1996; Obouayeba *et al*., 2000; Silpi *et al*., 2006) [5, 2, 21]. However, the purpose of rubber tree bleeding is to produce rubber in a sustained manner, without significant damage to the trees, a state reflected, among other things, by good vegetative growth during bleeding. Therefore, maintaining the balance between tree vegetative growth and latex production is an important challenge to ensure good rubber tree productivity in the long term. To achieve this, it makes sense to identify, understand, explain and quantify the antagonism between vegetative growth and rubber production, or to determine the behaviour of the radial vegetative growth of rubber trees bled and only bled to the exclusion of all other factors, including exogenous hormonal stimulation. Since the variations in this parameter, linked to the corresponding latex production, make it possible to quantify and estimate the characteristics of the distribution of photosynthetic assimilates and energy towards the primary and secondary biomass of rubber plants (Gohet, 1996) [5].

The aim of this work is to study the effect of bleeding on the vegetative growth of 16 rubber clones, divided into three classes. The importance of the reduction in vegetative growth associated with bleeding at frequency d4 will be assessed according to the radial vegetative growth and metabolic activity classes of *Hevea brasiliensis* clones.

2. Study environment

The study was conducted in the region of San-Pedro in south-western Ivory Coast, precisely in the industrial plantations of the Southwestern Agricultural Civil Society (SCASO) located between 6°30' and 6°50' north latitude and 5°00' and 5°20' west longitude (Figure 1). This region is characterized by an annual rainfall varying between 1200 and 1800 mm, with an annual insolation of 1500 hours (Brou, 2005) [1]. The average annual temperature of this region is about 25.6°C. The San Pedro region is subject to four seasons: a large dry season from December to February, followed by a long rainy season from March to June; a small dry season from July to August and a short rainy season from September to November. The relief is characterized by vast plateaus surmounted in places by a few elevations. The soil profile is ferralitic, relatively altered and varies in texture from clayey silt to silty sand. Deep and permeable, these soils are generally well adapted to all types of food and industrial crops (Ministry of Planning and Development, 2015) [12].

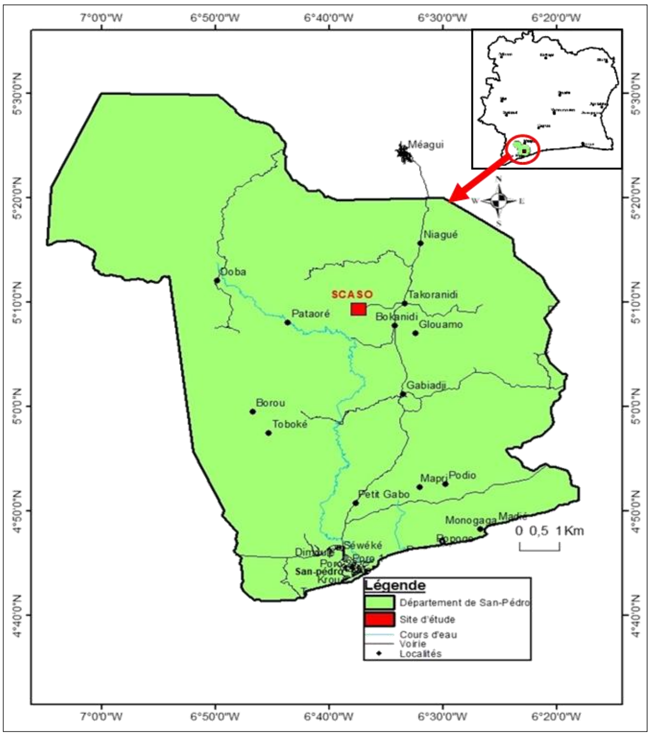

Fig 1: Location of Study Site (Konan, 2019)

3. Plant material

The plant material (Table I) used in this study consists of 16 clones of *Hevea brasiliensis* (Muel. Arg., Euphorbiaceae), divided into three classes of vegetative growth and metabolic activity (Jacob *et al*., 1988; Obouayeba *et al*., 2000; Chapuset *et al*., 2001; Obouayeba, 2005) [8, 2, 5]. The choice of these clones was based on their hardiness and the fact that they are more or less used in the country.

Table 1: Origin and characteristics of the 16 Hevea clones investigated

Clones	Geographical origin	Genetic origin	Production	Activity class
IRCA 109	Ivory Coast	PB5/51 x IR22	High production	Medium
IRCA 111	Ivory Coast	PB 5/51 X RRIM 605	High producer	Fast
IRCA 130	Ivory Coast	PB 5/51 X IR 22	High producer	Fast
IRCA 18	Ivory Coast	PB 5/51 x RRIM605	High production	Fast
IRCA 209	Ivory Coast	GT1 x PB5/51	High production	Fast
IRCA 230	Ivory Coast	GT1 x PB5/51	Very high production	Medium
PB 255	Ivory Coast	PB5/51 x PB32/36	Very good initial productions	Fast

PB 260	Malaysia	PB 5/51 X PB 49	High producer	Fast
PB 280	Malaysia	PB 5/54 et PB 32/36	Good production	Fast
PB 310	Malaysia	PB5/51 x RRIM600	Quite productive	Very fast
PB 330	Malaysia	PB 5/51 X PB 32/36	Good production	Fast
GT 1	Indonesia		Very high production	Medium
BPM 24		GT 1 X Avros 1734	Good production	Medium
RRIM 712		RRIM605 x RRIM71	Quite productive	Medium
PB 217	Malaysia	PB 5/51 X PB 6/9	High producer	Slow
PR 107	Malaysia	Clone primitif	High productivity	Slow

4. Study method

4.1. Trial conduct and data collection

To study the partition between vegetative growth and rubber production during bleeding at frequency d4, circumference measurements were made on trees of *Hevea brasiliensis* clones per class of vegetative growth and metabolic activity planted at a density of 510 trees/ha, i.e. a spacing of 7m x 2.80m in a completely randomized block system. During this study, elementary plots consisting of about 100 trees were established. Measurements were carried out in the elementary plots every year on unbleached trees (control treatment) and bleeding trees. The bleeding was carried out according to the descending half-spiral system. It was done every four days, six days a week with one day of rest per week for 12 months (S/2 d4 6d/7 12 m/12), i.e. 78 bloodlettings per year. Rubber production from the bled trees was recorded per clone during the experimental period. The data collected represent an average of nine years of exploitation.

4.2. Data processing

During this study, different parameters were evaluated.

4.2.1. Circumference increase

In this study, the average annual circumference increase was determined from measuring the circumference of the trunk of rubber trees using a tape measure. Thus, the average annual increase in circumference was obtained according to the formula of:

$$\mathbf{Acc_n\ (cm/an) = Circ_n - Circ_{n-1}}$$

Acc_n: Annual circumference increase; **$Circ_n$:** Circumference of trees from the current season; **$Circ_{n-1}$:** Circumference of trees from the previous season.

The reduction in growth, expressed as a percentage of growth potential, was determined according to Gohet's (1996) [5] formula:

$$\mathbf{RedAcc\ (\%) = 100 \times (Acc_{NS} - Acc_S) / (Acc_{NS})}$$

Acc_{NS}= Average annual mean increase (cm/year) in unbled treatment; **Acc_S**= Average annual mean increase (cm/year) in unstimulated bled treatment; **RedAcc (%)**: reduction in increase, expressed as a percentage of growth potential

4.2.1. Dry rubber production

Rubber production was carried out every 4 weeks. It was determined after bleeding. Thus, after bleeding, the rubber in the cups was weighed and made up the fresh weight (Pf). A sample of each treatment was then crimped and made up the Crimped Weight (Pc) and oven-dried at 80°C for 24 hours and then reweighed (Dry Weight). Creping consisted of crushing the coagulum between two metal rollers rotating in opposite directions. The flattened coagulum is easier to dry. This process removed much of the water contained in the coagulum. The production of dry rubber was obtained from the conversion of fresh weight to dry weight by the processing coefficient (CT) formulated as follows:

$$\mathbf{CT = (Pc / Pf) \times 100}$$

CT: Coefficient of transformation, **Pc:** Crepe weight, Pf: fresh weight

The processing coefficient determined was used to evaluate the dry weight (Ps) of the rubber produced. It was calculated according to the following formula:

Ps: Dry weight

$$\mathbf{Ps = CT \times Pf}$$

Rubber production is expressed in grams per tree per bleed ($g.a^{-1}.s^{-1}$). This gives a precision on the amount of rubber a tree produces during a bleeding.

4.2.3. Physiological parameters

The physiological analysis of rubber latex called Micro-Diagnostic Latex (MDL) was carried out annually on the most important physiological parameters of latex. For this purpose, latex was collected by pricking under the bleeding notch (descending bleeding) using the Micro-Diagnostic Latex method (Jacob *et al*., 1988) [8]. Sucrose (Sac) and inorganic phosphorus (Pi) were the physiological parameters evaluated. They were determined from the solution obtained after coagulation of the latex in trichloroacetic acid (TCA). Latex sucrose was determined by the anthrone method developed by Ashwell (1957). Inorganic phosphorus was determined by the ammonium molybdate/ammonium vanadate method developed by Taussky and Shorr (1953).

4.3. Statistical analysis of the data

The collected data were subjected to analysis of variance (Anova) using SAS 9.3 software. The Newman-Keuls test at the 5% threshold was used to compare means when there were significant differences between the variables studied.

5. Results

5.1 Effect of bleeding at frequency d4 on radial vegetative growth of *Hevea brasiliensis*

5.1.1. All the clones studied

The mean annual increase in trunk circumference of *Hevea brasiliensis* trees varied significantly ($p<0.0001$) depending on whether or not it was bled (Table II). Thus, the unbleached trees of *Hevea brasiliensis* had a statistically higher average annual increase in trunk circumference (5.29

cm.yr^{-1}) than the bleeding trees (3.04 cm.yr^{-1}) (Table II). The associated reduction in increment (RedAcc) was estimated at 2.25 cm.yr^{-1}; equivalent to 42.53% of the vegetative growth of unbleeded trees of all clones combined.

Table 2: Mean annual increase in trunk circumference of unbled and bled trees of all clones during nine years of experimentation

Treatment	Average annual increase (cm.yr^{-1})
Not bled	5,29 a
Bled	3,04 b
MG	4,16
Pr > F	<0,0001
CV (%)	28,82
RedAcc (cm.yr^{-1})	2,25
RedAcc (%)	42,53

Values followed by the same letter in the same column are not significantly different in the Newman-Keuls Test at the 5% threshold.
RedAcc (%): reduction in growth expressed as a percentage of growth potential (% Acc_{NS})
RedAcc (cm.yr^{-1}): reduction of the increase expressed in cm per year
MG (cm.yr^{-1}): General average of the annual average increase in circumference, expressed in centimeters per year.
CV (%): Coefficient of variation, expressed as a percentage

5.1.2. In relation to the radial vegetative growth and metabolic activity classes of the clones studied

Analysis of data on mean annual trunk circumference growth of *Hevea brasiliensis* trees showed a highly significant difference (p<0.0001) between bled and non-bled trees for the class of clones with vegetative growth and rapid or active and moderate metabolic activity (MMA and MMC; Table III). No significant effects were observed for the class of clones with slow vegetative growth and metabolic activity (SMC; p > 0.05) as presented in Table III.

Unbleached trees of the MAC and MMC clones (Table III) showed statistically higher mean annual increases in circumference (5.46 and 4.96 cm.yr-1) than those of bleeding trees (3.00 and 2.80 cm.yr^{-1}).

The analysis (Table III) showed that bleeding at d4 significantly influenced the mean annual mean tree circumference growth of clones with rapid and moderate radial vegetative growth and metabolic activity (p < 0.0001). While bleeding had no effect on the mean annual increase in tree circumference of clones with radial vegetative growth and slow metabolic activity (p > 0.05).

Table 3: Mean annual increase in trunk circumference of unbled and bled trees according to the class of metabolic activity of the clone during 9 years of experimentation

Treatment	Average annual increment (cm.yr^{-1})		
	MAC	MMC	SMC
No bleeding	5,46 a	4,96 a	4,79 a
Bleeding	3,00 b	2,80 b	3,66 a
MG	4,23	3,88	4,23
Pr > F	< 0,0001	< 0,0001	0,0844
CV (%)	26,29	22,92	42,66

Values followed by the same letter in the same column are not significantly different in the Newman-Keuls Test at the 5% cut-off.
MAC: Active Metabolism Clones or Clones of the Rapid Metabolic Activity Class
MMC: Moderate Metabolism Clones or Clones of the moderate metabolic activity class
SMC: Slow Metabolism Clones or Clones of the Slow Metabolic Activity class
CV (%): Coefficient of variation, expressed as a percentage
MG (cm.yr-1): General average of the annual average increase in circumference, expressed in centimetres per year.

5.2. Evaluation of the reduction in circumference increase and rubber production of the trees of bleeding clones by metabolic activity class

Table IV shows the mean production values and the rate of reduction in growth according to the metabolic activity of the clones studied during nine years of experimentation.

The reduction in circumference increase and rubber production of the clones relative to the class of metabolic activity were significantly different (p < 0.0001). Thus, reductions in percent growth potential (% RedAcc) in trees of the fast (45.06%) and moderate (43.55%) radial vegetative growth and metabolic activity clones were statistically identical and greater than those of the slow growing radial vegetative growth and metabolic activity clones (23.8%).

Similarly, tree rubber yields from clones with rapid (58.96 g.a^{-1}.s^{-1}) and moderate (56.20 g.a^{-1}.s^{-1}) radial vegetative growth and metabolic activity were statistically identical and higher than those from clones with radial vegetative growth and slow metabolic activity (39.83 g.a^{-1}.s^{-1}).

Table 4: Reduction in growth (%) and average rubber production (g.a^{-1}.s^{-1}) by class of metabolic activity of clones bled at frequency d4 for nine years.

Metabolic class	RedAccr (%)	Prod (g.a^{-1}.s^{-1})
MAC	45,06 a	58,96 a
MMC	43,55 a	56,2 ab
SMC	23,8 b	39,83 b
MG	41,4	55,9
p-value	0,0413	0,0002
CV (%)	22,88	31,91

Values followed by the same letter in the same column are not significantly different in the Newman-Keuls Test at the 5% cut-off.
MAC: Active Metabolism Clones or Clones of the Rapid Metabolic Activity Class
MMC: Moderate Metabolism Clones or Clones of the moderate metabolic activity class
SMC: Slow Metabolism Clones or Clones of the Slow Metabolic Activity class
MG: Overall mean of the parameters studied
CV (%): Coefficient of variation, expressed as a percentage
RedAcc (%): reduction in growth, expressed as a percentage of growth potential (%Acc_{NS})
Prod (g.a^{-1}.s^{-1}): Average rubber production, expressed in grams per tree per bleed.

5.3. Relationship between the reduction in growth expressed as a percentage of growth potential and the ratios P/Sac and Pi/Sac and rubber production

Figures 2, 3 and 4 represent the polynomial relationship between the reduction in increment (RedAcc (%)), P/Sac and Pi/Sac ratios and rubber production, all metabolisms combined.

Figure 2 shows that the reduction in the mean annual increase in circumference is very closely related (R^2 = 1) to the Pi/Sac ratio of the clones studied by a polynomial function. Its analytical expression is RedAcc (%) = -84.871 $(Pi/Sac)^2$ + 292.44 Pi/Sac - 195.34.

The reduction in circumference increase is very significantly related to the P/Sac ratio (R^2 = 1; Figure 3). The analytical expression describing this relationship is RedAcc (%) = -2.6124 (P/Sac) ^{2}+ 27.101 P/Sac - 23.897.

Figure 4 shows that rubber production (g.a^{-1}.s^{-1}) is in a very highly significant polynomial relationship (R^2 = 1) with the reduction in the mean annual circumference increase of bled trees, all classes of metabolic activity of the clones studied. The analytical expression describing this relationship is RedAcc (%) = -0.0471 P^2 (g.a^{-1}.s^{-1}) + 5.7778 P - 131.77. The reduction in average annual rubber production (g.a^{-1}.s^{-1}) is all the more important as is the reduction in the average annual increase in circumference.

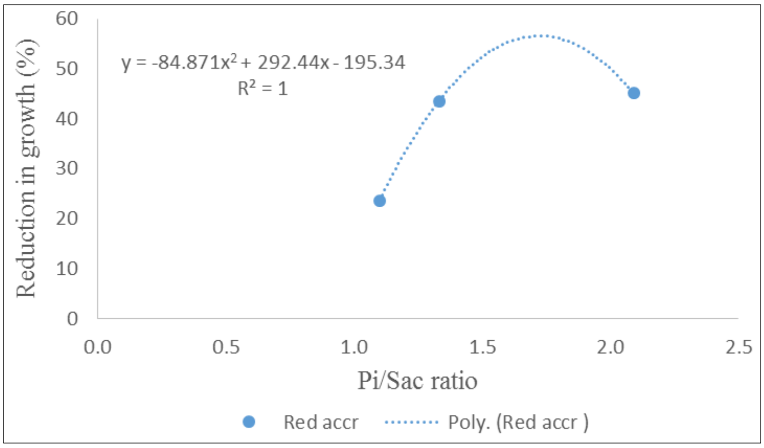

Fig 2: Polynomial relationship between the reduction in circumference increase (%) and the Pi/Bag ratio for the three classes of metabolic activity of the clones studied.

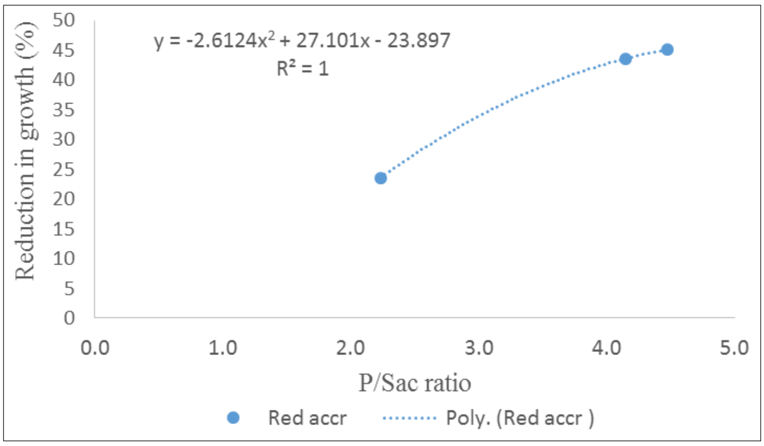

Fig 3: Polynomial relationship between the reduction in circumference increase (%) and the P/Sac ratio for the three classes of metabolic activity of the clones studied.

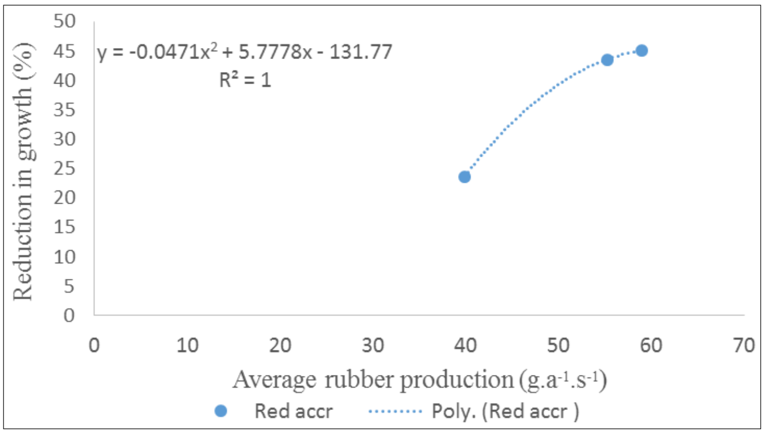

Fig 4: Relationship between reduction in growth expressed as a percentage of growth potential (%) and rubber production (g.a^{-1}.s^{-1})

6. Discussion

Evaluation of the effect of bleeding at frequency d4, without exogenous hormonal stimulation, on the vegetative growth of trees of *Hevea brasiliensis* clones showed that the mean annual increase in circumference of unbleached trees was significantly higher than that of bleeding trees. This difference would illustrate that bleeding for rubber production would have a significant negative impact on the primary metabolism which is the vegetative growth of the tree as already shown by several authors (Gohet, 1996; Obouayeba *et al.*, 2002; Obouayeba, 2005) [5, 16, 17]. This would logically result in a decrease in vegetative growth, which would be reflected in a slowing down of the biosynthesis of the primary biomass indispensable to the life of the plant. This slowing would be related to the decrease in the sucrose content of latex, starch and total sugars throughout the tree trunk (Lacrotte, 1991) [10]. This could be explained by the fact that the latex regeneration activity induced and following bleeding would be fuelled by a transfer of sucrose from the storage tissues to the drained area, the area of the tree bark impacted by bleeding (Patrick, 1990; Gohet, 1996) [18, 5].

Moreover, the results of this study show that the reduction in circumference increase expressed as a percentage of growth potential (% Acc_{NS}) is below 50% in a general case. This result contradicts those of several authors (Gohet, 1996; Obouayeba *et al*., 2000; Silpi *et al*., 2006) [5, 2, 21]. The latter showed that radial vegetative growth of logged trees is generally reduced by 50% compared to non-harvested trees. Although it has been shown that bleeding significantly affects tree growth, it is worth recalling that this could be related to the early bleeding and especially the intensification of the latex harvesting system (Gohet, 1996; Obouayeba *et al*., 2000; Silpi *et al*., 2006; Soumahin *et al*., 2010) [5, 16, 2, 22]. Thus, the lower growth reduction reflects the effectiveness of bleeding at the d4 frequency on the growth of all clones. This could be explained by the small deviation of metabolites and energy related to bleeding at the d4 frequency for rubber production of all clones in our study. Indeed, there would be strong competition, for photosynthetic assimilates and energy, between vegetative growth and rubber yield, as Templeton, (1969) [23] had shown. Thus, for trees harvested at a reduced frequency d4, photosynthetic assimilates and energy would, due to the relatively long time between two consecutive bleedings, be more sufficient to ensure rubber yield and vegetative growth (Jacob *et al*., 1995; Obouayeba *et al*., 2000; Soumahin *et al*., 2010) [9, 16, 22]. With respect to the class of metabolic activity of the clones, our results show that bleeding at frequency d4, without exogenous hormonal stimulation, has, globally and significantly, more affected the vegetative growth of rubber trees of clones with active and moderate metabolism than those of the class of slow metabolic activity. This result would mean that the response to bleeding is variable depending on the metabolism of the clones. Thus, the absence of significant differences between unbled and bled trees in clones of the radial vegetative growth and slow metabolic activity classes would result in a low incidence of d4 bleeding on the vegetative growth of trees in this group of clones. This low incidence could be related to a small deviation of assimilates and energy towards secondary biomass biosynthesis, resulting in a less pronounced drop in the carbohydrate reserves available for the other pathways of general metabolism, particularly vegetative growth metabolism, as shown by some authors (Patrick, 1990; Lacrotte, 1991; Gohet, 1996) [18, 10, 5]. This would result in a reduction in growth expressed as a percentage of the lower growth potential for this group of clones. On the other hand, the difference in growth observed in the other two groups of clones highlights the extent of bleeding on their vegetative growth. This would be explained by the fact that the bark of the trees of these two groups of clones would have drained a greater amount of photosynthetic assimilates and energy subsequently inducing a greater drop in the level of non-constituent sugar contents within the tree trunk despite the relatively long period between two consecutive bleedings due to the frequency d4 (Jacob *et al*., 1995; Obouayeba *et al*., 2000; Soumahin *et al*., 2010) [9, 16, 22]. These would have been preferentially oriented towards the latex regeneration pathway to the detriment of that of vegetative growth linked to primary biomass (Patrick, 1990; Lacrotte, 1991; Gohet *et al*., 1991) [18, 10, 4]. Hence a less impetuous increase reduction for these two classes of metabolic activity. The results obtained in this study show, as indicated by Patrick (1990) [18], that the reduction in increment follows a positive gradient in the activation of laticigene metabolism.

The reduction in circumference increase expressed as a percentage of growth potential (%Acc_{NS}) is all the more important as the metabolism of rubber production is also important (Patrick, 1990) [18]. This is illustrated by the results obtained highlighting two groups of clones relative to the impact of bleeding alone at frequency d4, of bleeding intensity (50%), on their vegetative growth in this study. The first group consists of clones of the radial vegetative growth and active and moderate metabolic activity classes (IRCA 109; IRCA 111; IRCA 18; IRCA 130; IRCA 230; IRCA 209; PB 280; PB 330; PB 310; PB 255; PB 260 and GT 1; RRIM 712; BPM 24). The second group consists of clones of the radial vegetative growth and slow metabolic activity classes (PB 217 and PR 107). These different groups are distinguished by their intrinsic (initial) energy. The first group of clones with rapid and moderate metabolic activity have high and medium intrinsic energy. The second group of clones with slow metabolic activity have low energy (Jacob *et al*., 1988 and 1995; Gohet *et al*., 1991) [8, 9, 4]. Given that unstimulated rubber production is closely related to this energy (Gohet *et al*., 1991; Serres *et al*., 1994; Jacob *et al*., 1995; Gohet *et al*., 1996; Lacrote *et al*., 2010) [4, 9, 5], then the difference in productivity of the 3 classes of metabolic activity of the clones in our work is understandable. In addition, our results show a very strong link between rubber production and the reduction in circumference increase. To the high rubber productivity ($58.96\ g.a^{-1}.s^{-1}$) relative to the first class is associated the very high growth reduction (45.06%) giving the low average annual increase in circumference (3.00 against $5.46\ cm.yr^{-1}$). For a relatively moderate rubber productivity ($56.2\ g.a^{-1}.s^{-1}$) of the 2nd class is added the reduction of moderate increase in circumference (43.55 %) leading to an equally moderate average annual increase in circumference (2.8 against 4.96 $cm.yr^{-1}$). The low rubber productivity ($39.83\ g.a^{-1}.s^{-1}$) of the 3rd class is related to the very small reduction in circumference increase (23.8%) leading to the highest average annual circumference increase statistically comparable to that of unstimulated trees (3.66 vs. 4.79 $cm.yr^{-1}$). We deduce that the bleeding of the rubber trees in our work creates an antagonism between radial vegetative growth and rubber production. Our conclusions corroborate those of numerous works (Templeton, 1986; Obouayeba et Boa, 1993; Gohet, 1996, Obouayeba *et al*., 2000) [5, 16]. The competition thus created is all the stronger as the intrinsic metabolic energy is also strong. Indeed, as the results of this study indicate, the group of clones with active and moderate laticigene metabolism with more initial energy produced more rubber than the last group of clones with slower laticigene metabolism with less initial energy. This resulted in a large significant effect on the radial vegetative growth of the first group and a small non-significant effect on the radial vegetative growth of the second group. This result illustrates Patrick's (1990) [18] assertion that the faster or more active the metabolism of the clones, the greater the diversion of metabolites and energy, the greater the rubber production and the greater the reduction in mean annual increment.

The evolution of the reduction in growth due to bleeding as a function of the P/Sac and Pi/Sac ratios and rubber production (P) resulted in a very significant polynomial relationship. This result highlights the very close link between the reduction in vegetative growth (primary biomass) and the functioning of the laticigenic tissue that competitively synthesizes latex (secondary biomass). Thus the P/Sac or Pi/Sac ratios would reflect the overall energy mobilized by the regeneration process within each class of metabolic activity of the clones (Patrick, 1990; Gohet *et al.*, 1991) [18, 4]. Indeed, the higher the ratios, the greater the reduction in increase due to bleeding at the d4 frequency. Comparison of the production levels of actively or moderately metabolizing clones with those of slowly metabolizing clones shows that higher initial sucrose content and lower intrinsic energy within the drained area coincide with less growth reduction. Hence the existence of variability in the intensity of growth reduction according to the class of vegetative growth and metabolic activity of *Hevea brasiliensis* clones. Moreover, the antagonism between growth and rubber production seems to be all the more reduced as the availability of sugars within the latex, defining the strength of the laticigenic well, is important and vice versa, as Gohet's work (1996) [5] has shown. This weaker antagonism determined by the reduction of growth below 50% could also be explained by the relatively long period between two consecutive d4 bleedings due to the frequency of d4 bleeding, which allowed photosynthetic assimilates and energy to be less limiting for rubber production and vegetative growth.

7. Conclusion

The assessment of the extent of metabolite diversion and energy diversion associated with rubber tree bleeding was based on the comparison of mean annual increases in circumference of unbleached and bleeding trees of rubber tree clones according to their class of radial vegetative growth and metabolic activity. This study showed that bleeding at frequency d4 has a significant impact on the mean annual circumference increase of clones of the radial vegetative growth and rapid and moderate metabolic activity class. The reduction in increment, expressed as a percentage of the vegetative growth potential, was relatively large for these two groups of clones. While clones in the radial vegetative growth and slow metabolic activity class were unaffected by bleeding at d4. The latter clones consequently expressed a relatively smaller percentage reduction in circumference increase than that observed in the other classes. This reduction from bleeding would be all the more important as the metabolism of the lactic acid system is active with more initial energy. A very close link appears between the reduction in circumference increase and rubber production of clones of different classes of metabolic activity during bleeding coupled with latex physiological parameters. This suggests an important balance between sucrose concentration, intrinsic metabolic energy and the carbohydrate reserves needed to maintain the tree's vegetative growth. The clones in the vegetative growth and slow metabolic activity class illustrate this balance by the high concentration of sucrose obtained at their level and acceptable production. In addition, the percentage of growth potential below 50% is a sign that bleeding at the d4 frequency is a good indicator in improving the productivity of rubber clones without damaging the physiological state.

8. Conflict of interest

The authors do not declare any conflict of interest.

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