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ORIGINAL PAPER

Bridging tradition and technology: comparing growth performances of grafted and tissue cultured RRIM600 *Hevea brasiliensis* trees in West African plantations

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Abstract

The global demand for natural rubber emphasizes the need for increasing yield per hectare as the expansion of planting areas becomes difficult. To overcome some of the limitations related to the propagation of rubber trees through grafting, research has been carried out for years on Hevea clonal plants produced by in vitro tissue culture technology (vitroplants, VP). This study conducts a large-scale evaluation of VP across two rubber estates in Ivory Coast and Ghana. Using VP could significantly reduce the growth time of seedlings in the nursery and provide flexibility in planting schedules independent of seed availability. For 66 months, 14 ha of field trials were monitored to compare growth dynamics, stand uniformity, and trunk conicity of VP with trees from grafted plants (GP) of RRIM600 clone. The findings reveal that VP exhibited superior trunk girth at 66 months, suggesting an earlier readiness for tapping compared to GP with a more conical trunk shape, which may lead to increased latex yield. The differences in growth rates in the field between VP and GP were significantly affected by the developmental stage of the plants at planting, with VP being planted with fully developed leaves and self-rooted systems, while GP were planted with developed rootstocks but dormant buds. This enabled VP to establish more rapidly and thus reach readiness for latex tapping sooner than GP. The study underscores the importance of further research on clonal selection, acclimatization period, rootstock interactions and the yield performances of this novel planting material.

Keywords *Hevea brasiliensis* · Tissue culture · Vitroplants · Growth dynamics · Stand uniformity · Trunk conicity

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Introduction

Rubber is a vital raw material for a variety of industrial products and plays an important role in social and economic development of producing countries. Although rubber can be derived synthetically from natural gas and petroleum, natural rubber (NR) is often preferred over synthetic rubber due to its superior elasticity, tensile strength, biodegradability, and renewability, making it a sustainable choice for the environment [1]. The primary source of NR is the perennial crop *Hevea brasiliensis,* commonly referred to as Hevea, which produces latex retained in specialized cells called laticifers located between the outer bark layers and the inner cambium tissue [2]. The increasing international demand for NR is driving the expansion of industrial-scale and smallholder plantations, with > 2 million ha established during the last decade [3]. Growing areas cannot expand infinitely and rubber growers face agronomic and socio-economic challenges they depend upon. Particularly, natural rubber

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is one of seven commodities covered by the EU Regulation on deforestation-free products. This involves the assurance that raw materials and manufactured goods entering the EU market from 1 st January 2025 onward, were not produced on land deforested or degraded after 31 December 2020 [4].

In the last century, the increase in yield from rubber plantations was made possible by the intensification of tapping systems using ethylene stimulation [5] and by the propagation of high-yielding rubber clones using the grafting technique [6]. Rubber plantations based on grafted clones have made it possible to solve two problems posed by seed-derived plantations: yield heterogeneity between trees and long-term conservation of the genetic resource. Yield variability between seed-derived rubber trees have been documented since Whitby [7] who reported a coefficient of variation (CV) for individual tree yields up to 76%. In this study, 20% of the trees made 50% of the total production. Much later, Combe [8] studied variability in performances of rubber trees from three different clones grafted on rootstocks grown from seeds. The CV for individual tree yields ranged from 20 to 40% depending on tree age, and they found that 50% of the production was made out of 40% of the trees. They also showed that the yield variability between trees was partly related to the variability in trunk girth at 100 cm aboveground at the end of the immature phase, which ranged from 13 to 20% depending on the clone. According to Yao et al. [9], the genetic heterogeneity of the rootstocks is likely a cause of the remaining heterogeneity and yield limitation of grafting-derived rubber tree stands. Although some works were conducted on the effect of rootstocks on graft growth [10, 11], the choice of rootstock is still driven by the availability of a great number of seeds. This indicates the need for significant improvement to achieve a major yield leap.

To overcome some of the limitations related to grafting, research has been carried out for years on Hevea clonal plants produced by tissue culture [12, 13]. Vitroplants (VP) open the way to two innovations for the rubber sector [14]. First, the establishment of a clonal plantation with trees on their own roots, is expected to yield even more homogeneous plants. Second, VP can also be used to produce clonal rootstocks, thus making it possible to breed for root traits like it is done on major fruit tree crops [15]. The development of in vitro propagation methods for Hevea began in the 70 s with the aim of overcoming the problems associated with traditional methods of propagation. Initially, researchers faced challenges in producing plants from mature elite clones, as they failed to produce gravitropic roots [12]. To overcome this issue, researchers discovered that the mature elite varieties had to be rejuvenated through somatic embryogenesis (SE), which is the most efficient method for rejuvenation [16, 17]. This development has opened the way for field trials comparing the behaviour and vigour of VP to grafted plants [18–21]. These studies reported small-scale and short-term trials, which did not really assess the performances of rubber VP stands in terms of growth dynamics and heterogeneity.

This study investigated the comparative performance of vegetatively propagated (VP) and bud-grafted plants. Specifically, the research assessed differences in stem girth (both mean and variance) up to 66 months post-planting, growth dynamics during the juvenile phase, and trunk form, a key factor influencing potential latex yield [14]. The experiment was designed to compare in vitro–propagated plants (VP) as a possible substitute for the present commercial standard bud-grafted seedlings (GP) for extensive rubber plantations. Although in vitro propagation of rootstocks remains an ongoing research activity, the current experiment is aimed at determining the feasibility of self-rooted VP under industrial environments instead of exploring trial grafting combinations. For this reason, a large-scale study was performed with over 7,000 RRIM600 trees planted, covering 14 hectares of trials in Ivory Coast and Ghana. The maturity of the trees is evaluated according to the recommended standard by the Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD), which stipulates that the tree should reach an optimal girth before onset of tapping at regular intervals. The standard tappable girth is about 50 cm, and tapping earlier is not advisable because it restricts the tree's secondary growth [22]. The presented research offers valuable information on the behaviour and performance of VP in comparison to bud-grafted plants, and to evaluate the potential for clonal plant production and breeding for root characteristics. This study will be a valuable resource for the rubber industry to find answers to the challenges faced by rubber plantations and adapt to changing conditions.

Material and methods

Study sites

The experiments were set-up in two agro-industrial estates of the SIAT company, the Compagnie Hévéicole de Cavally (CHC) in Ivory-Coast, and the Ghana Oil Palm Development Company (GOPDC) in Ghana. CHC is a rubber estate with a concession of 7700 ha located in the Guiglo department in the Western region of Ivory Coast. GOPDC is an oil palm and rubber plantation with a concession of 14,000 ha located in the Eastern region of Ghana near Kade city (Fig. 1). According to Koppen-Geiger classification (http://koeppen-geiger.vu-wien.ac.at/), both sites are in the Köppen climate classification Aw zone (savanna plains), meaning they have an equatorial climate with a dry season during winter. Rainfall records over the 2015–2021 period showed that GOPDC and CHC displayed the same monthly pattern (Fig. 2) but

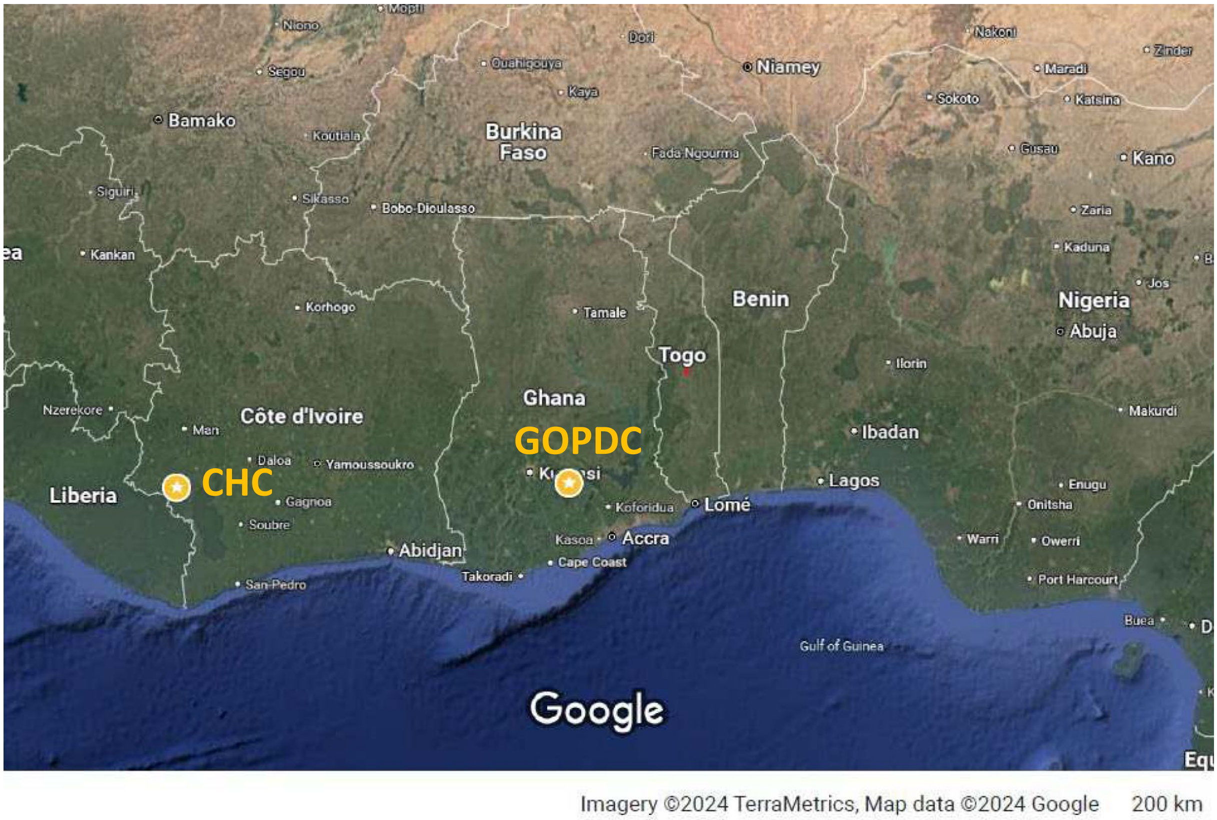
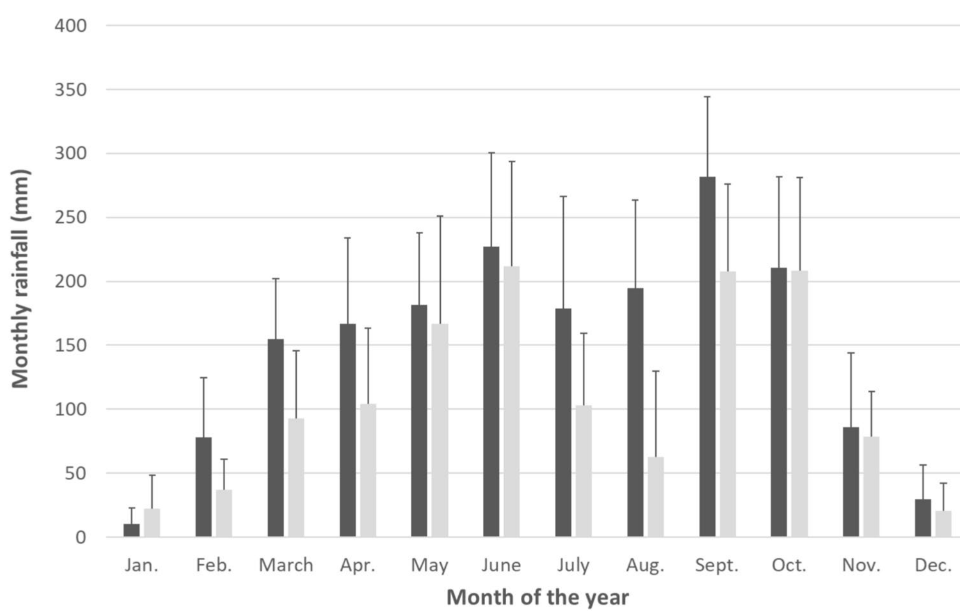


Fig. 1 Geographic location of the study sites in Western Africa. Map illustrating the precise locations of the two rubber estates in Ivory Coast (CHC) and Ghana (GOPDC) where the study was conducted (Google Maps)

Fig. 2 Average monthly rainfall at CHC and GOPDC sites. Bar graph depicting the mean monthly rainfall (dark gray bars for CHC and light gray bars for GOPDC) with standard deviation error bars for the 2015–2021 period



average annual rainfalls were lower at GOPDC (1300 mm on average) compared to CHC (1800 mm on average). Both sites have similar slightly acidic ferric acrisols with a gravel content of about 10%. Terrain is also similar established on gentle slopes not exceeding 5° on average with planting lines oriented east–west in both cases. Previous land use was a rubber plantation at CHC and an oil palm plantation at GOPDC.

Plant material

For this study, we utilized the RRIM600 genotype of *H. brasiliensis*, a clone with a storied legacy as the most extensively planted in the rubber industry's history (far ahead of GT1, PR107, PB217, PB235, PB260, RRIC100, etc.), originating from the Rubber Research Institute of Malaysia with TJIR1 x PB86 parentage and noted for its wide usage since its development (https://rubberclones.cirad.fr/index.php/clones/RRIM600 Cirad, 2011).

The experimental set-up compared traditional bud-grafted seedlings with RRIM600 as scion on an illegitimate GT1 rootstock (grafted plants, GP) with in vitro clonally multiplied RRIM600 plants (vitroplants, VP). Normal operational timings were used in the experiment design, such that both types of plants were field-planted at their normal nursery exit stages and not artificially synchronized. As a consequence, GP were planted at a set stage with dormant buds, whereas VP already have a developed canopy prior to field planting.

Production of grafted clones according to the conventional technique took a little over 1 year (see [6] for details and history of this technique). It started with harvesting and germinating GT1 seeds to produce the rootstock with a germination phase and seedling development stage of 8–10 weeks. Subsequently, germinated seeds were transplanted in polyethylene bags (conventional bag nursery) in August 2014. Grafting was done in April–May 2015 and grafted seedlings were planted, using standard methodology, in June 2015 before the bud break of the grafts (dormant bud technique). At planting, the stem of the rootstock was completely pruned to allow the development of the bud.

VP were generated by direct SE of the integument of immature rubber seeds collected in the plantation of CHC, Ivory Coast. The in vitro propagation was performed by Deroose Plants (DRP—Sleidinge Belgium). Genetic conformity was ensured by visual profiling of leaves sampled from the selected trees before collecting immature seeds in the field. The applied SE protocol is based on direct SE from immature seed integuments, followed by micropropagation of shoots in several cycles according to the protocol developed by [23]. According to the DRP methodology, the first step consists of obtaining a clean stock of somatic embryo-derived plantlets, 13 months after initiation. The second step which takes 12 to 18 months focuses on the multiplication by micro-cutting propagation from the clean stock plantlets. The third step consists of rooting for 2.5 months. After rinsing the young roots, plantlets were then placed in plastic jars and sent by express courier to the experimental sites. Upon arrival, the VP were separately potted in 100 cm^3 root trainers. The substrate is made of coco peat. At CHC, VP were grown in a greenhouse for 6–7 weeks under high relative humidity (95%) and low luminosity (15–25%). At this stage, VP had three to four leaves. After this period and for another 7 weeks, VP in root trainers were transferred to a second facility, the shade house, under outside relative humidity and 50% shade. At GOPDC, the acclimatization-hardening procedure was carried out under simplified conditions, in a plastic tunnel located in the pre-nursery shade for palm seeds. During the acclimatization phase, VP received water, fertilization, and fungal protection according to their needs. Once acclimatized, VP were transplanted with the clod into polyethylene bags filled with sieved earth. The plants were retained at the nursery for a minimum of 120 days (or the time corresponding to the development of 2–3 additional leaf clusters) and subsequently put under a top shade net for 30 days. VP were planted in the field at the same time as grafted plants in June 2015.

Experimental design

At CHC, the experimental set-up was a fisher block with 8 treatments each repeated 6 times. In each repetition the 8 treatments were positioned randomly. The first treatment was planted with grafted seedlings (GP). The other 7 treatments were planted with vitroplants (VP). They corresponded to increasing durations of plant development, between 230 and 497 days, from arrival in the plantation's acclimatization greenhouse to planting in the field (SE01). The same planting pattern, equivalent to 510 trees ha^{-1} (7.00×2.80 m spacing), was used for all treatments. Each elementary plot (one repetition of a given treatment) covered 8 lines of 14 trees at planting, meaning one elementary plot encompassed a maximum of 112 trees. Border trees, not included in the experimental design, were separating the elementary plots. In all, the trial at CHC covered 12.11 ha comprising 6177 tree positions.

At GOPDC, the experimental set-up was a complete block design with 2 treatments and 4 repetitions. The first treatment (code GP) was the grafted plants and the second treatment was the vitroplants (code VP) planted in the field after 415–420 days of acclimatization. Planting density was 513 trees.ha^{-1} (7.80 × 2.50 m spacing). Elementary plots were made of 5 lines of 25 trees (125 trees). The total area of the experimental plots including border trees was 1.95 ha.

In both sites, the experimental plots were equally managed, in accordance to the standard field operating procedures of the SIAT company. The interrow spacing between the tree lines was covered by *Pueraria phaseoloides*, a common legume cover crop used in rubber estate. The tree line was slashed twice a month to avoid competition between the young trees and the cover crop. Mineral fertilizers were applied twice a year along the tree line (NPK 12/12/17 at both sites).

Measurements

Stem diameter at 100 cm aboveground of all vitroplants and grafted plants was measured in June and December 2016 with a calliper. From June 2017, beginning of the 3rd year after planting, to December 2020 (5.5 years or 66 months after planting), stem or trunk girth at 100 cm aboveground was measured twice a year (June and December) with a tape ruler. At GOPDC only, the trunk girth was also measured at 25 and 200 cm aboveground to estimate trunk shape.

At the time of planting, girth measurements were not recorded for GP seedlings as they lacked developed scion stems due to the dormant bud technique. Conversely, VP were planted with developed leaves and stems. Therefore, girth measurements at planting were not directly comparable between the two plant types.

Data processing and statistical procedures

The diameter of stem was converted to girth assuming a regular circular shape (Eq. 1).

$$Girth\ (\mathrm{cm}) = Diameter\ (\mathrm{cm}) \times \pi \quad (1)$$

Tree basal area (TBA) was estimated as the area of the circle which girth equalled that of the tree (Eq. 2). Stand basal area (SBA) was obtained by summing the individual basal area of all trees in one plot [24] (Eq. 3).

$$Tree\ Basal\ Area\ \left(\mathrm{cm}^2\right) = \pi \times \frac{Girth^2}{4} \quad (2)$$

$$SBA\ \left(\mathrm{m}^2\ \mathrm{ha}^{-1}\right) = \sum_{i=1}^{n} TBA_i \times plotarea \quad (3)$$

where n is the number of trees per elementary plots (112 at CHC and 125 at GOPDC) and *plotarea* is the surface area of the elementary plots (2196 m^2 at CHC and 2451 m^2 at GOPDC).

The monthly relative growth rate (RGR) was calculated on both individual tree girth and stand basal area values assuming an exponential model [25] (Eq. 4).

$$RGR = \frac{\ln\left(S_{i+1}\right) - \ln\left(S_i\right)}{m_{i+1} - m_i} \quad (4)$$

where S_i and S_{i+1} are the values of the trunk growth indicator (either girth or basal area) measured on month i (mi)and month i + 1 (Y_i + 1).

Trunk shape was described by the parameters a and b of the relationship between trunk girth and the height from the ground derived from the equation given by [26] (Eq. 5).

$$Girth = a \times Height^b \quad (5)$$

We also computed the conicity angle α according to [26]:

$$\propto = \frac{\left(G_{200} - G_{25}\right)}{(200 - 25) \times 2\pi} \quad (6)$$

In order to assess the uniformity of tree girth in every elementary plot, we calculated the kurtosis and skewness of the population distribution, as well as the relative standard deviation (RSD) and interquartile range (IQR). The kurtosis indicates whether a distribution is flat/broad (negative value), or slender/narrow (positive value). The skewness is not directly related to the uniformity of the distribution but tells whether the distribution is asymmetrical with more values inferior to the mean (right-tailed distribution, positive skewness) or with more values superior to the mean (left-tailed distribution, negative skewness).

The effect of treatments on the measured or calculated variables was tested on the elementary plot average values. We used the Wilcoxon test, also called the Mann–Whitney test, due to the small sample size (n = 4 or 6).

All statistical analyses were performed with Xlstat software (2021.1 version, Addinsoft, Paris, France).

Results

For the CHC site, the results of the VP treatment presented in Tables 1 and 2 and in Figs. 3, 4 and 5 are based on data of the VP with the same acclimatization time of the VP used at GOPDC site (i.e. 415 to 426 days). A summary of the growth performances of the seven different VP acclimatization groups at CHC are presented in the supplementary material SE01.

Stand characteristics 5.5 years (66 months) after planting

The term"stand"typically denotes a group of trees considered as a unit for management or measurement purposes. After 66 months of growth in the field, VP exhibited a significantly higher average girth than GP at both sites (Table 1 and Fig. 3). VP had a similar average girth at GOPDC and CHC while GP were significantly bigger at GOPDC (47.0 cm) than in CHC (43.0 cm). Hence, VP demonstrated a superior growth performance at CHC compared to GP (+ 16%) than in GOPDC (+ 9%). On both sites, the girth average of VP was marginally above the standard girth for initiating harvesting latex, i.e. 50 cm at 1 m above the ground. According to this standard, the VP plots were ready for tapping with more than 50% trees having a girth higher than 50 cm at 1 m above the ground (Table 1), as also indicated by the median

Table 1 Stand characteristics at 66 months after planting of vitroplants (VP) and grafted plants (GP) at CHC and GOPDC

Variable	Site	Vitroplants	Grafted plants	Wilcoxon test (5% threshold)
Girth average	GOPDC	51.1 cm	47.0 cm	**Significant (α = 0.014)**
	CHC	50.0 cm	43.0 cm	**Significant (α = 0.001)**
Stand basal area	GOPDC	10.4 $m^2.ha^{-1}$	8.9 $m^2.ha^{-1}$	**Significant (α = 0.014)**
	CHC	10.0 $m^2.ha^{-1}$	7.6 $m^2.ha^{-1}$	**Significant (α = 0.001)**
% Tappable trees (G > 50 cm)	GOPDC	54%	24%	**Significant (α = 0.014)**
	CHC	53%	17%	**Significant (α = 0.001)**
Girth minimum	GOPDC	36.0 cm	34.9 cm	Not tested
	CHC	27.3 cm	19.1 cm	Not tested
Girth maximum	GOPDC	65.2 cm	61.9 cm	Not tested
	CHC	61.6 cm	58.9 cm	Not tested
Girth RSD	GOPDC	12%	11%	**Significant (α = 0.014)**
	CHC	12%	18%	**Significant (α = 0.002)**
Girth IQR	GOPDC	8.3	6.1	**Significant (α = 0.014)**
	CHC	6.8	9.4	**Significant (α = 0.002)**
Girth distribution kurtosis (average)	GOPDC	− 0.36	0.74	**Significant (α = 0.014)**
	CHC	2.77	1.00	**Significant (α = 0.002)**
Girth distribution skewness (average)	GOPDC	0.01	0.24	Non-significant (α = 3.430)
	CHC	− 1.14	− 0.74	**Significant (α = 0.032)**

Each value is the average of 6 elementary plots of 112 trees at CHC, and 4 elementary plots of 125 trees ay GOPDC except for minimum and maximum

RSD relative standard deviation, *IQR* inter-quartile range

Table 2 Comparison of annual relative growth rate (RGR) of vitroplants (VP) and grafted plants (GP) at CHC and GOPDC

		RGR calculation intervals (months)				
		12–24	24–36	36–48	48–60	60–66
CHC	RGR GP	**0.841**	0.508	**0.394**	**0.284**	**0.106**
	RGR VP	**0.628**	0.528	**0.359**	**0.225**	**0.083**
	alpha value (Wilcoxon test)	**0.001**	0.242	**0.032**	**0.001**	**0.013**
GOPDC	RGR GP	**0.862**	**0.514**	0.289	0.303	**0.041**
	RGR VP	**0.794**	**0.491**	0.277	0.300	**0.036**
	alpha value (Wilcoxon test)	**0.014**	**0.014**	0.100	0.171	**0.014**

Each value is the average of 6 elementary plots of 112 trees at CHC, and 4 elementary plots of 125 trees ay GOPDC. Data in bold show significant differences between VP and GP growing in the same site

girth of VP being above the reference line in Fig. 3. The GP were far from this threshold with 17% and 24% tappable trees at CHC and GOPDC respectively.

On both sites, the mortality rate was low, less than 2% of the tree number at planting, and was not significantly different between the treatments (data not shown). Consequently, stand basal area (SBA) values reflected the differences in tree girth: VP treatments had a comparable SBA slightly over 10 $m^2\ ha^{-1}$, significantly different from SBA of GP particularly at GOPDC (8.90 $m^2\ ha^{-1}$) compared to CHC (7.62 $m^2\ ha^{-1}$).

The statistical indicators of the tree girth distribution between the two sites were notably distinct (Table 1). At CHC, the VP stand displayed greater uniformity than the GP stand with a significantly lower RSD (12% vs 18%) and interquartile range (6.8 cm against 9.4 cm), and a significantly higher kurtosis (2.77 vs 1.00). The skewness values were also significantly different. Both were negative indicating a left-tailed distribution. These differences are well represented by the frequency histograms (SE01). At GOPDC, the GP stand appeared more uniform than VP's one but with slightly less differences. The VP stand at GOPDC was the only one with a negative kurtosis indicating a broad distribution with a much lower peak than the other distribution (Fig. 4). Unlike CHC, both VP and GP stands of GOPDC have a right-tailed distribution with a positive skewness (Table 1).

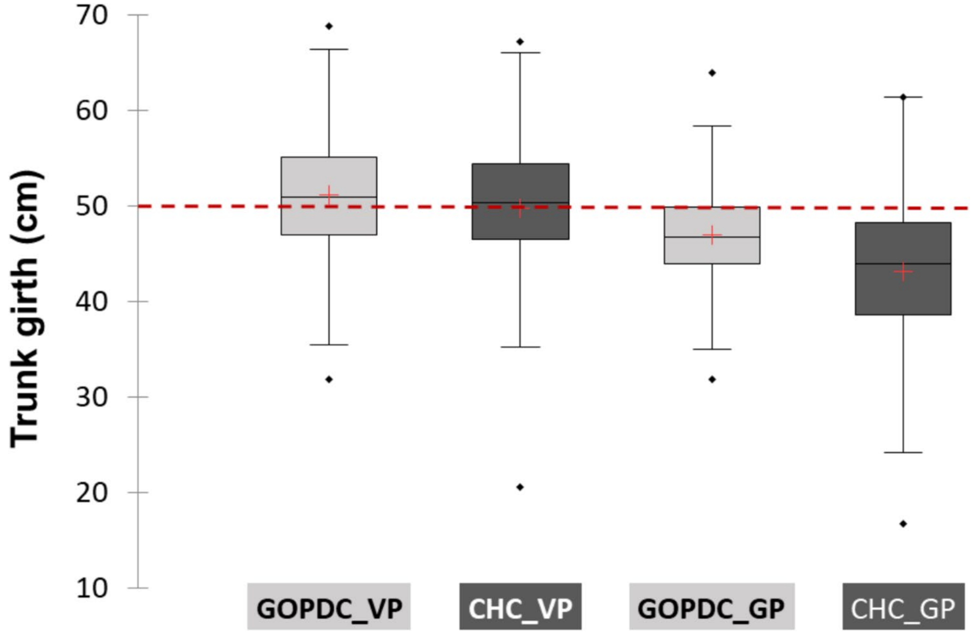


Fig. 3 Distribution of trunk girth of trees grown from vitroplants (VP) and grafted seedlings (GP) 66 months after planting at CHC (dark gray box, n = 672) and GOPDC (light gray box, n = 500). Box lower and upper edges correspond to the 1 st and 3rd quartile; red crosses and vertical black lines are median and mean values respectively; whiskers are the 5th and 95th percentiles; symbols show the min and max values. The red dash line indicates the threshold (50 cm) to start tapping when 50% of the trees have reached this girth

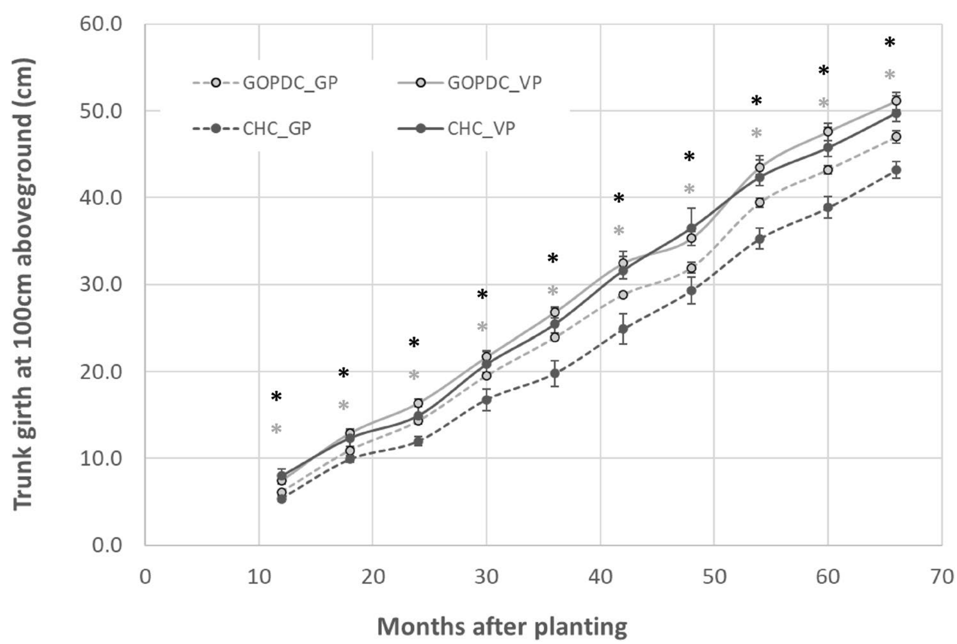


Fig. 4 Trunk girth dynamic from 12 to 66 months after planting of vitroplants (solid line) and grafted plants (dashed line) at CHC (dark gray) and GOPDC (light gray). Each symbol is the average of 6 elementary plots of 112 trees each at CHC, 4 plots of 125 trees each at GOPDC. The error bars represent the standard deviation of the 6 plots. The stars indicate the significant differences between the means of VP and GP per site and per date

Finally, the experimental design at CHC facilitated to compare VP trees with different time of acclimatization before planting, from 230 up to 497 days (SE02). All the 7 VP treatments (T2 from T8) had a significant higher average girth than the GP treatment (T1). The highest average girth was reached by VP with 405–426 days of acclimatization, i.e. T3 and T4 treatments, T3 being the reference treatment for comparison with GOPDC site. The lowest VP girth was obtained with the shortest (T8, 230 days) acclimatization time. However, there were no significant differences between VP treatments. All VP treatments also showed better stand uniformity than the GP's as commented above.

Comparative analysis of trunk girth growth between vitroplants and grafted plants over time

Diameter and girth measurements at 100 cm from the ground taken every 6 months between 12 and 66 months after planting showed that the VP consistently maintained a larger average girth than the GP (Fig. 4). However, we observed a steady decrease in the ratio of VP's girth to

GP's at both sites. At CHC, VP girth was 49% larger than GP's 12 months after planting (MAP) and remained notably higher but dropped to 16% at 66 MAP. At GOPDC, the decrease was from 21% at 12 MAP to a still significant 9% at 66 MAP. This result suggests that GP girth increased more rapidly than VP's but the initial growth advantage of VP was maintained. That assumption was confirmed by the calculation of the annual relative growth rate (RGR) that is the ratio of the annual girth increment to the girth of the tree at the beginning of the year (Table 2). For both planting material at both sites, the RGR steadily decreased from the first to the fifth year after planting. The RGR of grafted plants were larger than the VP every year on both sites, except during the 3rd year (24–36 MAP) at CHC. The differences were statistically significant 4 years out of 5 at CHC, and 3 years out of 5 at GOPDC (Table 2). At CHC site, the differences were the largest between the 1st and the 2nd year after planting (+ 34%), and after the 4th year (+ 27%). At GOPDC, the differences were much less, from 5 to 13%, the maximum being observed after the 5th year. These differences in GP and VP vigor were also observed during the first 9 months after planting. At this stage, we monitored the growth in height of the stem because GP seedlings were too small to measure girth at 100 cm aboveground. At the time of planting, VP seedlings measured between 165 and 152 cm high, at CHC and GOPDC respectively, whereas GP seedlings were transplanted with fully developed rootstocks but had not developed a scion stem yet. After nine months, height increment since planting was 161 and 289 cm for GP, respectively at CHC and GOPDC, while it was 168 and 196 cm for VP (data not shown).

Uniformity of tree girth also changed with time between 12 and 66 months after planting (Fig. 5). In all situations (treatments x sites), girth RSD was the highest at 12 MAP indicating that the stand uniformity improved with time (RSD decrease). The change was stronger for GP stands than for VP stands, which suggests that VP stands were relatively uniform from the beginning. At CHC for instance, girth RSD decreased from 24 to 18% (27% change) for GP while it decreased from 14 to 12% (17% change) only for VP emphasizing the consistency of VP performance. In other words, it means that the difference in stand uniformity between VP and GP decreased with time. At GOPDC, GP stands exhibited lower uniformity than VP 12 MAP (20% vs 16% RSD) but demonstrated slightly higher uniformity at 66 MAP (11% vs 12% RSD).

Trunk shape and bark area

At GOPDC, we measured the girth of the tree at 20, 100 and 200 cm above the ground at 66 months after planting to assess the shape of the trunk. VP had a significant larger girth than grafted plants at all height but the differences decreased with height from + 8 cm (+ 15%) at 25 cm above ground to + 2 cm (+ 5%) at 200 cm (Fig. 6). The trunk of the VP displayed a more conical shape than the grafted plants with a 16 cm girth difference between 20 and 200 cm, while it was only 10 cm for the grafted. The visual observation was confirmed by the conicity models fitted to the experimental data. The a and b coefficients were significantly different between VP (a = 97.4 cm and b = − 0.14) and grafted plants (a = 73.0 cm and b = − 0.09). The a coefficient represents the theoretical girth at the ground level, and the b coefficient the curvature of the model (the lower the most curved). We used these coefficients to simulate the shape of VP and grafted

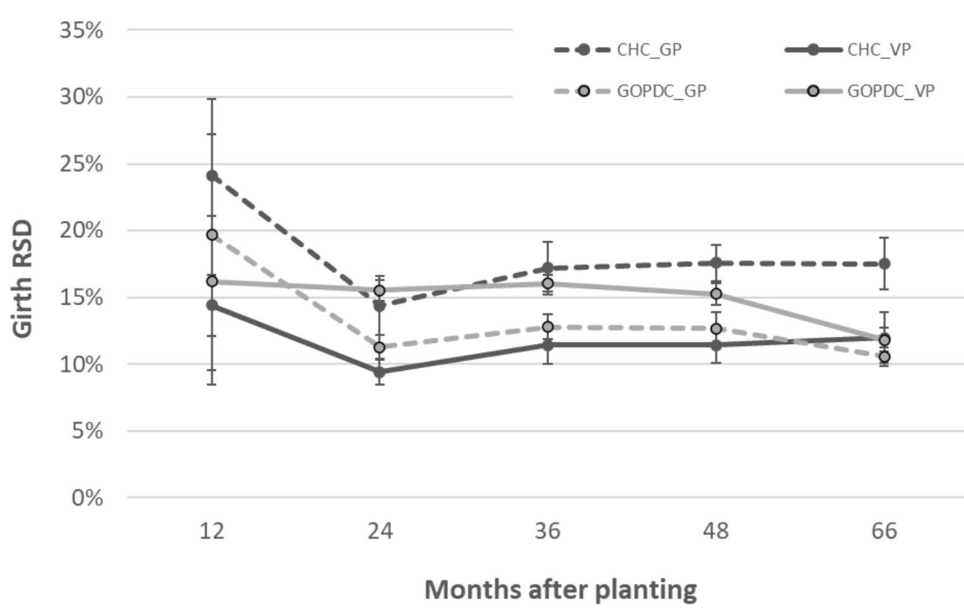


Fig. 5 Dynamic of stand heterogeneity from 12 to 66 months after planting of vitroplants (solid line) and grafted plants (dashed line) at CHC (dark gray) and GOPDC (light gray). Each symbol is the mean relative standard deviation (RSD) of individual trunk girth in the 6 and 4 elementary plots of CHC and GOPDC respectively

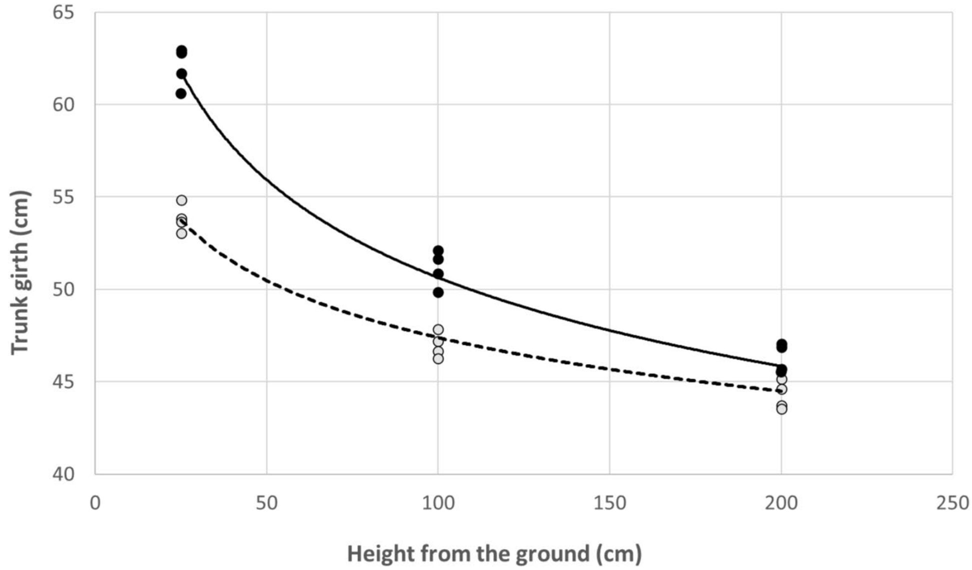


Fig. 6 Trunk girth profiles of vitroplants (VP, dark gray symbols) and grafted plants (GP, light gray symbols) at 66 months on the GOPDC site. Each symbol represents the average trunk girth of 125 trees**.** Lines represent the best fit line for the power function $Girth = a \times Height^b$ (Eq. 5)

trees having reached 50 cm girth at 100 cm above ground, that is the norm for starting the tapping of latex (Fig. 7). It showed that the VP has a greater girth than the grafted below 100 cm, and the reverse above 100 cm. But the girth difference is larger below 100 cm (+ 4.4 cm for VP à 20 cm aboveground) than above (+ 1.2 cm for GP at 180 cm). Based on these data, we calculated the bark area between 20 and 180 cm aboveground, i.e. the available bark for tapping, assuming the trunk is a regular truncated cone-shape. The results gave a + 9% greater bark area of the VP tree (nearly 9200 cm^2) compared to the grafted tree (nearly 8500 cm^2).

Discussion

To our knowledge, this paper is the first published study to report long-term large-scale (6 years) field observations of self-rooted rubber tree produced in-vitro (vitroplants, VP) grown in multiple locations (2 sites, Ghana and Ivory Coast) in large-scale trials (1.95 and 12.11 ha respectively). Previously, Carron et al. [14] reported the results of trials carried out in 3 countries (Nigeria, Ivory Coast and Thailand), but these trials were small-scale experiments with less than 100 trees per treatment. Mayati et al. [20] in Malaysia and Xiongting et al. [21] in China also set-up small-scale trials with 8 to 101 trees per treatment and 9 to 75 trees per treatment respectively. In our experimental designs, elementary plots included 112 and 125 trees repeated 6 and 4 times

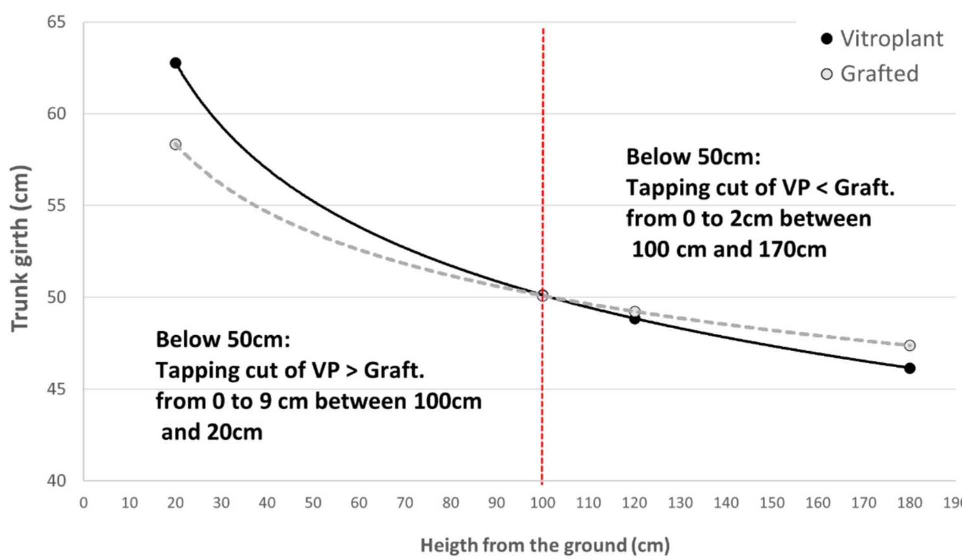


Fig. 7 Trunk girth profiles of trees with a girth of 50 cm at a height of 100 cm simulated with models adjusted to measured data for vitroplants (VP, dark gray) and grafted plants (GP, light gray) at GOPDC. Due to their greater conicity, VP trees have wider trunks below 1 m and therefore more bark surface available for downward tapping

respectively, making a total of 672 and 600 trees used for collecting data in each treatment. The trials were set-up in industrial estates and were managed following the standards operating procedures of the commercial plots, which enabled us to assess the behaviour of self-rooted VP and the conventional GP planting material. The use of VP rootstock with a grafted scion was not considered because it combines the drawbacks of both techniques—increased cost of in vitro rootstock production and grafting challenge—and is considered an unsuitable choice for mass deployment at this point. This paper focuses on the immature period of rubber stand. It does not include any data on dry rubber output from tapping the trees that would be essential for comparing VP and GP actual yield potential. Nevertheless, studying the immature period is important for understanding the effect of the planting material on the number of tappable trees, one of the two main yield components of a rubber stand along with the rubber yield per tree. In this regard, we believe this paper brings valuable insights on this topic by proposing a detailed analysis of tree and stand characteristics that are important to consider the contribution of the immature phase (growth increment, stand heterogeneity, trunk conicity) to the yield performances of the rubber plantation.

Growth performance of vitroplants versus grafted plants

Previous studies showed that the growth of trees from VP was equal or superior to that of GP. In the study of Xiongting et al. [21], the girth of VP trees was + 32% greater than that of GP at the end of the immature period. Trials conducted in Ivory Coast [18, 19] showed a 10 to 16% increase in tree size of VP from clones PB260, IRCA18 and BPM24 compared to GP, while they didn't find any differences between VP and GP for clones RRIM600 (clone used in our study) and PR107. Mayati et al. [20] also observed no differences in the tree size of VP compared to GP for clones RRIM600 and RRIM2025, 12 years after planting. Taken as a whole, these data suggest a strong Genotype X Environment effect on the vigour of VP. They also show that VP exhibit a consistent growth performance in the field, even if they do not always outperform the GP trees. Our results align with those findings, with girth data at 66 months, or 5.5 years after planting, indicating a robust growth of VP trees compared to GP trees. Trunk girth of VP was 9 to 16% greater than that of GP. In both experiments, at least 50% of the VP trees had attained an average trunk girth at 100 cm aboveground slightly higher than 50 cm, girth threshold used in rubber plantations as the standard to decide the beginning of tapping operations. In comparison, only 17% (at CHC) and 24% (at GOPDC) of GP trees had attained this minimum girth requirement.

However, analysis of growth dynamics showed that the differences between VP and GP at 66 months were attributable to the more advanced leaf bearing development stage of VP at planting. It is important to note that girth measurements at GP planting were not recorded due to the developmental differences between VP and GP seedlings. GP seedlings were planted with undeveloped scion stems, making girth measurements at that stage not feasible or comparable to VP, which had developed stems. GP trees were planted as polybag green buddings without any development of the scions (dormant bud planting) while the VP trees the VP trees were planted with a more developed scion structure, having at least two fully developed leaf whorls. Differences in trunk girth between VP and GP trees were larger 12 months after planting than 66 months after (+ 21% vs 9% and + 49% vs 16% for VP at GOPDC and CHC respectively). GP growth caught up with that of VP, which was evident from the average relative growth rate between 12 and 66 months (0.427 for GP vs 0.365, + 17%, at CHC; 0.402 vs 0.380, + 6%, at GOPDC). Sherperd et al. [28] cited in details by [29] reported 2–15-month extension of the immature period according to the development of the scion of bud-grafted stumps or polybags. Our results are consistent with this study, GP trees were 6 to 12 months behind VP trees at GOPDC and CHC respectively. Our observations do not support the hypothesis of better immature growth of RRIM600 VP trees compared to bud-grafted trees during the growing period after planting.

Interestingly, VP demonstrated consistent growth performance both at CHC and GOPDC, despite the differences in annual rainfall. This consistent performance suggests that VP might have a greater potential of adaptability and resilience, making them a valuable asset for rubber cultivation in diverse climates.

Early growth differences between VP and GP wher the result of their innate propagation characteristics. Whereas VP were planted with leaves developed, GP were planted prior to bud break following standard plantation practice. Prolonging GP nursery duration to equalize VP development would not only change industry practice but also negate the possible advantage of VP, i.e., earlier establishment and reduced time to tapping readiness. The production of polybag grafted seedlings takes approximately 360 days, from seed nursery preparation to grafting and planting. In our analysis the GOPDC and CHC trials, the VP were planted roughly 420 days after their arrival at the plantations, which is 60 days longer in nursery growth compared to the GP. To achieve the same developmental stage in GP as the VP at planting, specifically with two fully developed leaf stages, nearly 90 additional days of nursery growth would be necessary. This would result in a total of about 450 days, considering the growth rate of rubber tree growth units is 40–45 days per leaf stage [30]. Additionally, the CHC trial revealed that

VP planted just 230 days after their arrival at the plantation exhibited a growth advantage over the GP. This analysis therefore shows that the use of VP could significantly reduce the growth time of seedlings in the nursery. In addition to the potential cost advantage of a shorter nursery phase, the use of VP offers a wider time frame for planting. In fact, with GP, the planting window is tightly controlled and closely linked to that of seed production by the trees, due to the rapid loss of germination capacity of the seeds after harvesting. In Ivory Coast and Ghana, seeds can be harvested only in July–August, making planting possible in June-July for plants with dormant buds, or in September–October for plants with two leaf stages, the following year. With VP, planting is possible at any time of year, depending on climatic conditions, by adjusting both the date the plants are received at the plantation and the time they spend acclimatizing and maturing in the nursery. Such insights are invaluable for understanding the holistic impacts of plant preparation methods on the growth dynamics, latex production readiness, and the overall adaptability of *H. brasiliensis* in varying environmental conditions.

Impact of vitroplants on the uniformity of rubber stands

Stand uniformity improves the productivity of monospecific tree plantation [31, 32]. In rubber, the highest productivity of bud-grafted clonal stands compared to seedling stands is mainly due to much lower heterogeneity in tree size and individual yields [6, 33]. Gener [34] observed a relative standard deviation of trunk girth between 24 and 31% for seedlings and only 10 to 15% for bud-grafted trees of clone GT1 4 years after planting. Self-rooted clonal rubber trees obtained through CIV are expected to further improve the uniformity of tree stands as it is reported on other tree species [35]. In our study, the girth RSD of VP stands ranged between 9 to 13%, which matches the lowest values reported for GP stands in previous studies [8, 33]. While VP stands were indeed more uniform with a slender left-tailed distribution at CHC, this is not the case at GOPDC where GP stands were slightly more uniform with a better distribution than VP stands. Moreover, as concluded above on growth data, the dynamic of girth RSD suggests that the development stage of the planting material had a strong impact on stand uniformity. One year after panting, GP stands always had a much higher girth RSD than VP stands. This observation is consistent with the studies carried out by Sherperd et al. [28] by Webster [29] to compare the effect of different planting materials on rubber stand development. Planting plantlets containing developed scions, from the grafted buds (or VP treatments in our experiment), enables control of the uniformity of the plantlets prior to field planting while this control is not possible with dormant bud material (GP treatments in our experiment). However, as observed for growth, the difference between the uniformity of GP and VP stands decreased over time on our two experimental sites. At GOPDC, the uniformity of GP stands was even equal to or slightly greater than that of VP. It is noteworthy from Fig. 5 that the uniformity of VP stands followed the same trend as that of GP stands. This is further evidence that VP trees can be used successfully to produce commercial rubber stands.

These results on tree growth and stand uniformity suggest that the genetic make-up of the root system, clonal self-rooted system versus illegitimate rootstock, and the propagation technique, grafting versus tissue culture, of aerial part did not have strong effects on rubber tree development in our experiments. The observed differences were mainly due to the development stage of the scion at planting. This is a surprising result given the accumulated knowledge about the effect of rootstocks on the phenotype of scions in many woody species [15]. In the case of rubber, even if rootstocks stem out from illegitimate seeds, significant effects of the rootstock mother parentship on growth and latex yield of bud-grafted clones were reported in several studies [9, 10, 36, 37]. However, the effect of the rootstock varies according to the grafted clone. Nouy and Nicolas [10] reported that the clone RRIM600 was the least responsive of the four clones they tested with no significant effect of the rootstock family on tree girth. Martins et al. [37] also observed that clones grafted on different rootstock families had the lowest growth with rootstock from RRIM600 seeds. These results may explain the absence of differences in the behaviour of self-rooted RRIM600 VP trees compared with RRIM600 grafted onto GT1 rootstock. This conclusion is consistent with the studies of Dibi et al. [19] and Mayati et al. [20], which also did not show better VP growth in the field compared to GP with RRIM600 clone. Further insights can be drawn if similar field trials were initiated on other rubber clones that are more likely to show interactions between rootstock and the development of the aerial system.

Trunk conicity: a positive trait for the productivity of rubber plantations

The trunk shape is critical in rubber cultivation as it influences the area available for tapping and consequently, the yield of latex; a more conical shape, is associated with a larger bark area conducive to higher latex productivity. Our results confirm previous observations on the differences in trunk shape between VP and GP trees [6, 19]. In most cases, the architecture and anatomy of the trunk of VP are similar to those of trees grown from seed, whereas GP have the characteristics of a branch. Ferwerda [38] made the same observations when comparing clones grafted from scions taken from the main axis of young plants, which he called juvenile-type scions, with clones from scions taken from a wood garden, called secondary or mature-type scions. In particular, he showed that the trunk conicity of trees grown from juvenile grafts was significantly higher than that of trees grown from mature grafts (+79%), but lower than that of seedlings (−30%). Dibi [26] obtained similar results when comparing VP, GP and seedling trees from the same family.

The conicity of VP can have two advantages for the productivity of rubber plantations. Firstly, it is a trait that can contribute to better resistance to wind breakage, thus limiting losses of productive trees linked to this disturbance [39]. The model proposed by Engonga Edzang et al. [40] to assess the sensitivity of rubber trees to wind shows that resistance is proportional to the power of 4 of the diameter or girth of the trunk section at the base of the tree. Our results show that for a similar girth 2 m above-ground, the girth of the VP at the base of the trunk was nearly 10 cm greater than that of the GP (Fig. 6a). Secondly, higher trunk conicity increases the surface area of bark over the height of the trunk that can be exploited for tapping. This bark surface is an essential factor in rubber tree productivity, as it translates into a longer tapping cut length and therefore greater yield potential [40]. In the long term, the management of tapping panels can be optimised to make the most of this available bark [42, 43].

Conclusion

The extensive field trials conducted in West Africa to compare the growth performance of RRIM600 VP and GP have yielded illuminating insights on the potential of in vitro propagation methods in enhancing rubber plantation efficacy. This study, encompassing over 7000 trees across 14 hectares in Ivory Coast and Ghana, meticulously measured trunk girth at various stages post-plantation to assess growth dynamics, uniformity, and trunk conicity—factors pivotal for latex production efficiency. Our findings indicate that VP exhibit a consistently superior trunk girth compared to grafted plants 66 months post-plantation. This advantage was evident despite the variations in acclimatization durations for VP, underscoring their robustness and adaptability. The initial growth advantage of VP can be attributed to their advanced developmental stage at planting, characterized by the presence of well-developed leaf whorls, in contrast to GP that were planted shortly after grafting, lacking developed clonal buds on the grafted rootstock. This disparity in initial development stages facilitated a more accelerated growth for VP, enabling them to be ready for tapping operations sooner than their grafted counterparts. The comparison with bud-grafted trees of the same clone did not allow us to conclude that this new type of material is superior in terms of tree growth after planting and stand homogeneity.

Adopting VP in rubber plantations could play a pivotal role in plantation sustainability and productivity, ultimately contributing to the fulfilment of the increasing global demand for natural rubber. We therefore recommend that this comparison be carried out on other clones that are more likely to show interactions between the origin of the root system and the phenotype of the above-ground part. Our observations confirm that VP have a different trunk shape to GP, and that this could result in higher tapping productivity. Future works should examine this aspect and assess the value of VP in terms of ancillary income from the sale of wood at the end of the cycle, or from higher carbon stocks in the standing biomass.

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Author Contributions Conceptualization of the experiment: RI, LV; Investigation and data acquisition: RI, SS, JB, RL; Data curation: RI, SS, FG; Formal analysis of data: FG; Manuscript writing: FG, FV, RI, LV; Project administration: JB, RI.

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Data availability The data supporting the conclusions of this study are not publicly available for reasons of confidentiality and can be obtained from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethical approval Ethical approval was not sought for this research because it did not involve the use of sensitive data or material.

Informed consent This research did not involve human subjects.

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