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A Meta-Analysis of Latex Physiology Studies Reveals Limited Adoption and Difficulties to Interpret Some Latex Diagnosis Parameters in *Hevea brasiliensis*

Junaidi[1,2,3,4], Anne Clément-Vidal[1,2], Tri Rini Nuringtyas[3,5], Eric Gohet[7], Siti Subandiyah[3,5,6], Pascal Montoro[1,2*]

[1]*CIRAD, UMR AGAP Institut, Montpellier, France*
[2]*UMR AGAP Institut, Univ Montpellier, CIRAD, INRAE, Institut Agro, Montpellier, France*
[3]*Post Graduate Program, Faculty of Biology, Universitas Gadjah Mada, Yogyakarta, Indonesia*
[4]*Sungei Putih Research Centre, Indonesian Rubber Research Institute, Deli Serdang, Indonesia*
[5]*Research Center for Biotechnology, Universitas Gadjah Mada, Yogyakarta, Indonesia*
[6]*Faculty of Agriculture, Universitas Gadjah Mada, Yogyakarta, Indonesia*
[7]*CIRAD, UMR ABsys, Montpellier, France*

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ABSTRACT

Latex diagnosis is widely adopted in natural rubber-producing countries to optimize the natural rubber production through a physiological-based latex-harvesting system management. This study is the first bibliographical searching and meta-analysis on the variation of latex physiological parameters i.e. sucrose, inorganic phosphorus, thiols, and total solid content. The study used information extracted from 158 scientific papers. Descriptive statistics, agglomerative hierarchical clustering, and principal component analysis were performed to characterize applications of latex diagnosis, how often parameters are used and interpreted as well as the variation of its parameter values. From 158 papers, latex diagnosis parameters were used in 114 agronomy, 22 in physiology, and 22 in breeding papers. The agglomerative hierarchical clustering analysis indicated that sucrose and inorganic phosphorus contents were clustered together and total solid and thiols contents were located in another cluster. The average values of the total solid content, sucrose, inorganic phosphorus and thiols were 43.9%, 9.4 mM, 16.5 mM, and 0.52 mM, respectively. The percentage of interpretation is 63.3% for sucrose, 54.4% for inorganic phosphorus, 47.5% for thiols, and 41.1% for the total solid content. The low interpretation of thiols and total solid contents question their relevance in latex diagnosis. The low adoption of latex diagnosis in breeding could hinder the selection of activities leads to a limitation of selection for long-term high yielding and stress-adapted clones.

1. Introduction

Para rubber (*Hevea brasiliensis*) is the main natural rubber-producing species. It is mainly cultivated in Southeast Asia and some in South Asia, Africa, and Tropical American countries. Natural rubber is a polymer synthesized in derived from the cytoplasm of laticifer cells. The cytoplasm of laticifer cells, called latex, is harvested through the incision of the bark. The latex contains 25–50% dry matter, 95% of which are natural rubber particles (d'Auzac and Jacob 1989; Jacob *et al.* 1993; Bottier 2020). In rubber plantations, the latex production cycle is 25 to 30 years. Sustainability of latex production is imperative for economic viability. To optimize the yield and maintain the lifespan of plantations, the harvesting system implicates some factors, including tapping frequency, ethylene stimulation and panel management.

Tapping frequency depends on the duration of latex regeneration between two tappings wich is related to the laticifer metabolic activity. Ethylene stimulation is required for certain clones to increase the metabolic activity and the latex flow. Panel management combines different factors including cut length and direction of tapping cut. Many scientific studies led to better understand the effect of harvesting systems on latex physiology (for review: d'Auzac *et al.* 1989). Several physiological

* Corresponding Author
E-mail Address: pascal.montoro@cirad.fr

parameters were associated with latex yield and the occurrence of tapping panel dryness (TPD): latex pH, total solid content (TSC), sucrose content (Suc), inorganic phosphorus content (Pi), thiols content (RSH), redox potential (RP), bursting index (BI), magnesium content (Mg^{2+}), etc. (Jacob *et al.* 1985). These knowledge allowed developing latex diagnosis.

As a blood test in humans to check the health status, the latex diagnosis (LD) was introduced to estimate the physiological status at one moment of the tree production. The diagnosis is performed by assessing latex physiological parameters i.e. TSC, Suc, Pi, RSH, BI, RP (Jacob *et al.* 1995). However, in daily practice, only four main parameters (TSC, Suc, Pi, and RSH) are widely used. These parameters represent the latex regeneration level, carbohydrate availability, metabolic activity, and antioxidant status (Escbach *et al.* 1984; Jacob *et al.* 1985; d'Auzac *et al.* 1997). According to Gohet *et al.* (2019), TSC, Suc, and RSH decrease with the increase in stimulation intensity, while Pi exhibits a reverse parabolic pattern. A high Suc and low Pi indicate that the plant is under-exploited; conversely, a low Suc and high Pi indicate high metabolic activities due to tapping and stimulation regimes. The TSC is more used for converting fresh yield to dry yield than for physiological consideration while, the RSH, a parameter for estimating the stress level, in some reports did not represent the stress level received by the plant. Thus, some studies only used two main physiological parameters, Suc and Pi contents, for example in Chantuma *et al.* (2011) and Phearun *et al.* (2016).

At the plantation scale, the LD technology has been adopted in rubber-producing countries. Since it is privately owned by the plantation companies, little is known about LD data, which are mostly not published. Therefore, it is difficult to capture the variation of LD values at the plantation level. The only report in this field is a meta-analysis performed by Gohet *et al.* (2019), in which the authors reported on an LD dataset from rubber plantations in Africa. Besides confirming the positive correlation between RSH and sucrose content, the meta-analysis leads to a hypothesis that RSH and RSH × Pi value could be an indicator for clonal suitability and global stress on the plantation scale. To date, little is known about LD implementation in commercial plantations in the different producing countries.

In the present study, we carried out a bibliographical searching and meta-analysis using information from 158 scientific papers mentioning latex diagnosis. To our knowledge, this study is the first report on the variation of latex physiological parameters used in *H. brasiliensis* research. We identified the chronological development of the LD application, the frequency of parameter used, the interpreting, variation of LD values, and the relevance of these parameters as well as we address new scientific questions for latex physiology.

2. Materials and Methods

2.1. Strategy to Select Scientific Paper

The scientific papers used in this study were collected from online and printed journals and conference proceedings. Several bibliographic databases were accessed for online searching i.e. Web of Science, Scopus, PubMed, ScienceDirect, Directory of Open Access Journals (DOAJ), Journal Storage (JSTOR), Agris-FAO, Agritrop-CIRAD, and Google Scholar. The keywords used included (*Hevea* or rubber) and (harvesting or tapping or stimulation), (*Hevea* or rubber) and (physiology or latex or diagnosis), (*Hevea* or rubber) and (stress or oxidative or antioxidant), (*Hevea* or rubber) and (sucrose or phosphorus or thiols). Some papers were also obtained directly from authors. The literature searching led identifying 413 papers. A screening procedure, consisting of reading carefully the Materials and Methods section of each paper, was applied and led to select 158 papers that assessed at least one of four main LD parameters i.e., TSC or DRC, Suc, Pi, and RSH.

2.2. Construction of Bibliographical Database and Excel File for Meta-Data Analysis

The 158 selected papers were added to a Mendeley database in order to generate a list of references used in this study (Supplementary data 1). We tagged the papers with the discipline information: "agronomy" for plantation monitoring in order to adjust the tapping system and consequently optimize the yield, "physiology" for studies evaluating the environment and harvesting stresses on various physiological and agronomical parameters, and "breeding" for studies related to the characterization of progenies. The papers were read thoroughly and information was extracted into an MS Excel table: authors, publication year, country, discipline, genotype, tapping system, assessed physiological parameters (Supplementary data 2). Another MS Excel table was prepared to record LD values (TSC (%), Suc (mM), Pi (mM), and RSH (mM)) from each paper (Supplementary data 3).

2.3. Data Analysis

Data summarization was performed using MS Excel and the statistical analysis was performed using the XLSTAT software (Addinsoft Inc., New York, USA). Supplementary data 2 was used for descriptive statistics and the Agglomerative Hierarchical Clustering (AHC) analysis. Supplementary data 3 was used for the descriptive statistic and Principal Component Analysis (PCA).

3. Results

3.1. General Data Description

The literature searching found 413 papers. A careful reading led to select 158 papers published from 1972 to 2020, which assessed at least one of the four main LD parameters: TSC or DRC, Suc, Pi, and RSH (Figure 1). The 158 papers reported studies conducted in 11 countries: Côte d'Ivoire (47 papers), Indonesia (37), China (19), Thailand (18), India (9), Sri Lanka (7), Vietnam (7), Cambodia (5), Malaysia (4), Cameroon (3), and Brazil (2).

With regard to the discipline, the largest number of papers was collected from studies in agronomy (114 papers) compared to breeding (22) and physiology (22). The use of LD parameters, especially in agronomy, increased after 2007 and peaked in 2016 – 2017. The LD parameters were more frequently used in physiological and breeding studies since 2000.

3.2. Significance and Relationship between Latex Physiological Parameters

According to the dataset in Supplementary data 2, early study of latex physiology involved several parameters, including TSC, Suc, Pi, RSH, Mg^{2+}, BI, pH, RP, and enzyme activities (Bealing and Chua 1972; Escbach *et al.* 1984; Escbach *et al.* 1986). The number of latex physiological parameters was reduced to the four most frequent parameters used: TSC, Suc, Pi and RSH. Nonetheless, in the breeding and physiology studies, additional parameters were used to describe physiological traits related to latex yield and the stress defence including initial flow rate, plugging index, proline, peroxidase, superoxide dismutase, and Mg^{2+}. Of the 158 analyzed papers, Suc

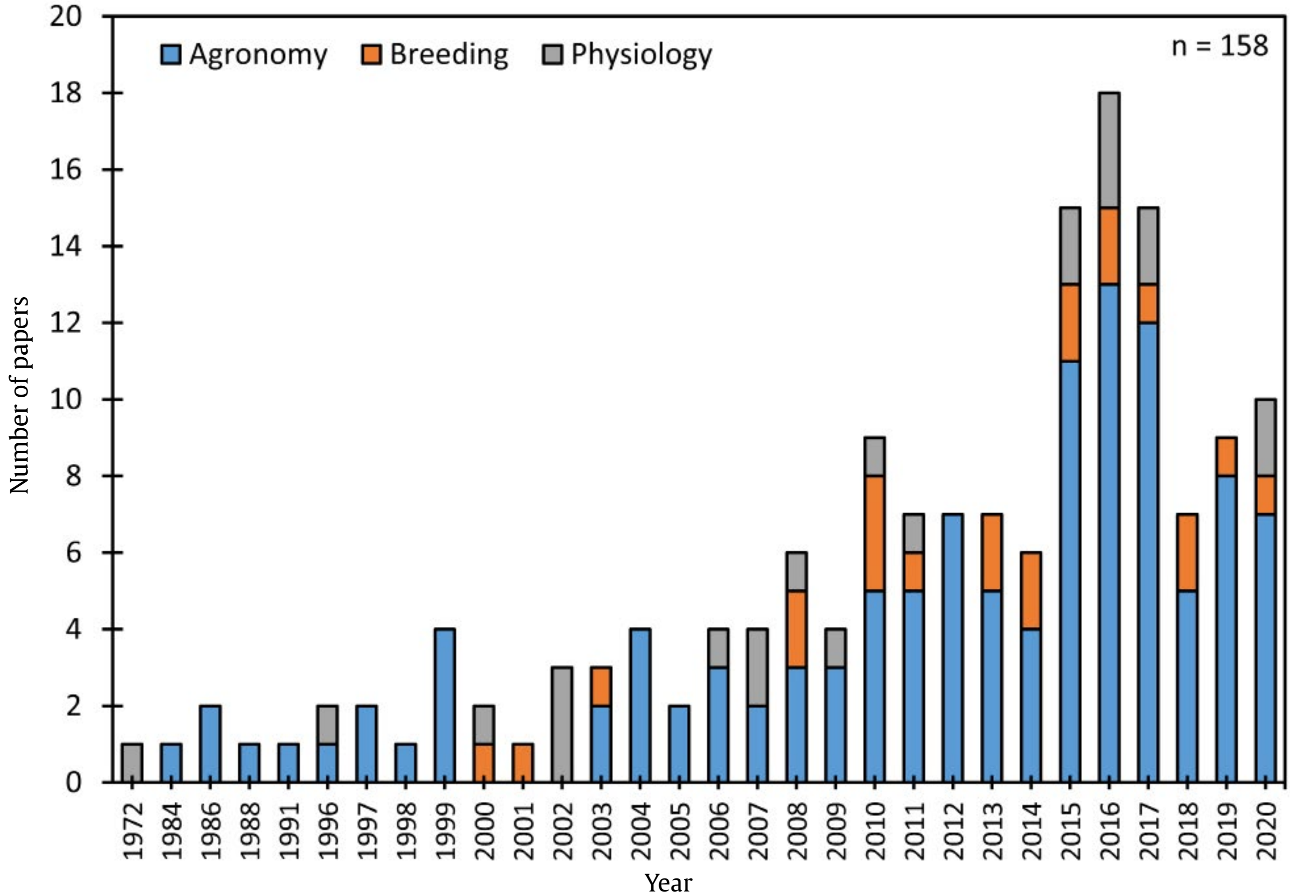

Figure 1. Number of literature by year published and discipline used for statistical analysis

was assessed in 152 papers (96.2%), Pi in 142 papers (89.9%), RSH in 131 papers (82.9%), while TSC and DRC were assessed in 116 papers (73.4%). The other parameters were assessed in less than 15% of cases.

An Agglomerative Hierarchical Clustering (AHC) analysis was performed to identify the proximity of the latex physiological parameters. Nine parameters were selected when they were studied in more than five papers. The AHC analysis was conducted on criteria 'Assessed' and 'Not assessed' for each parameter. The result indicated that these parameters were grouped in 3 clusters: one for Suc and Pi, one for RSH and TSC and one for all other parameters (Figure 2). This later cluster consisted of numerous parameters that were less frequently assessed i.e. latex pH, BI, Mg^{2+}, initial flow and plugging index.

3.3. Variability of LD Parameters in the World

The average TSC was 43.9% with the minimum value was 15.6% in Soumahin *et al.* (2016) and the maximum was 71.4% in Soumahin *et al.* (2009) (Figure 3A.). The minimum value of Suc was around 0.4 mM in Putranto *et al.* (2015) and the non-outlier maximum observation was 20.2 mM with an average of 9.2 mM. The highest outlier value was 46.3 mM in Obouayeba *et al.* (2016) (Figure 3B.). We omitted the data from Setiono *et al.* (2015), Attanayake *et al.* (2018), and Syaher *et al.* (2020), which consisted of extraordinary values up to 150.0 mM. For the Pi, the minimum value was 0.15 mM (Anushka *et al.* 2020) and the maximum was 36.3 mM, the average was 16.3 mM (Figure 3C.). The observations from Obouayeba *et al.* (2009), Obouayeba *et al.* (2015), and Kudaligama *et al.* (2017) were excluded due to their overly high values up to 118.0 mM. Non-outlier RSH values ranged from 0.11 mM (Guo *et al.* 2016; Lacote *et al.* 2019) to 1.03 mM (Lubis *et al.* 2020) with an average value was 0.51 mM, while the outliers reached 1.50 mM in Wei *et al.* (2015) (Figure 3D.). The observation from Anushka *et al.* (2020) was omitted due to its extremely low values up to 0.008 mM, while the observations from Commère *et al.* (1988), Obouayeba *et al.* (2016), and Sumarmadji and Tistama (2004) were excluded due to their overly high value up to 2.02 mM. The Suc exhibited the highest variation among LD parameters (coefficient variation was 72.9%), while TSC had the lowest coefficient variation (19.6%). The Pi and RSH also showed a high variation, coefficient variation 45.1% and 41.6%, respectively.

The principal component analysis (PCA) was conducted on a set of data from papers in which TSC, Suc, Pi and RSH were assessed together. The result showed that the first two principal components accounted for 65.38% of the variance in the original dataset. For the first principal component (F1), all four parameters were well represented with factor loadings 0.494 to 0.694. The TSC, Suc and RSH were positively correlated. For the second principal component (F2), the TSC and Pi (factor loadings 0.562 and 0.615 respectively) were positively associated, while Suc and RSH (factor loadings -0.445 and -0.530) were negatively correlated (Figure 4). The correlation matrix showed a small correlation between RSH/Suc and TSC/Pi.

3.4. Interpreting of LD Parameters

Of the 158 scientific papers included in our database, Suc was the most frequently analysed parameter (96.2%) followed by Pi (89.9%), and RSH (82.9%), and whilst TSC was the least frequently analysed (73.4%) (Figure 5). Following a thoughtful reading, we identified the authors' interpretation for each LD parameter such as the effect of genotypes, harvesting systems or environmental conditions. The TSC was interpreted in 56.0% of the papers, Suc 63.8%, Pi 60.6%, and RSH 42.8%. According to our assessment, Suc was the most frequently interpreted parameter, while the RSH was poorly interpreted.

4. Discussion

This study gathered and analyzed 158 papers from 1972 to 2020, in which latex physiological parameters were determined. These papers are associated with studies on agronomy, physiology and breeding. The number of physiological parameters analysed was drastically reduced from to 16 to 4 main parameters in the recent years, sucrose and inorganic phosphorus contents being well interpreted to describe the latex metabolic status of rubber trees. These results raise several questions with regard to the application of latex diagnosis and its limited use

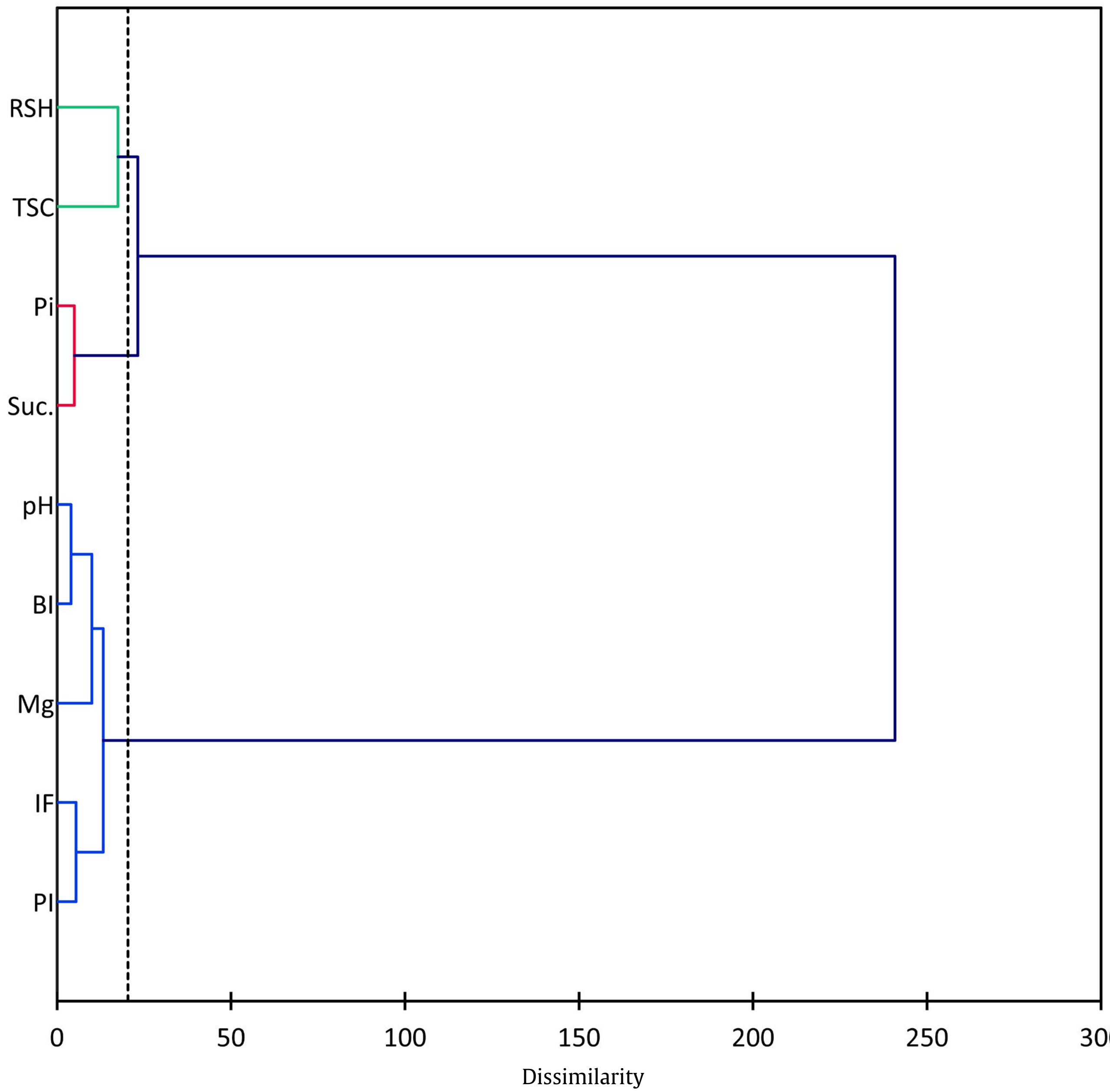

Figure 2. Hierarchical clustering parameters used in latex physiological assessment (RSH: reduced thiols, TSC: total solid content, Pi: inorganic phosphorus, Suc: sucrose, pH: latex pH, BI: bursting index, Mg: magnesium content, IF: initial latex flow, PI: plugging index)

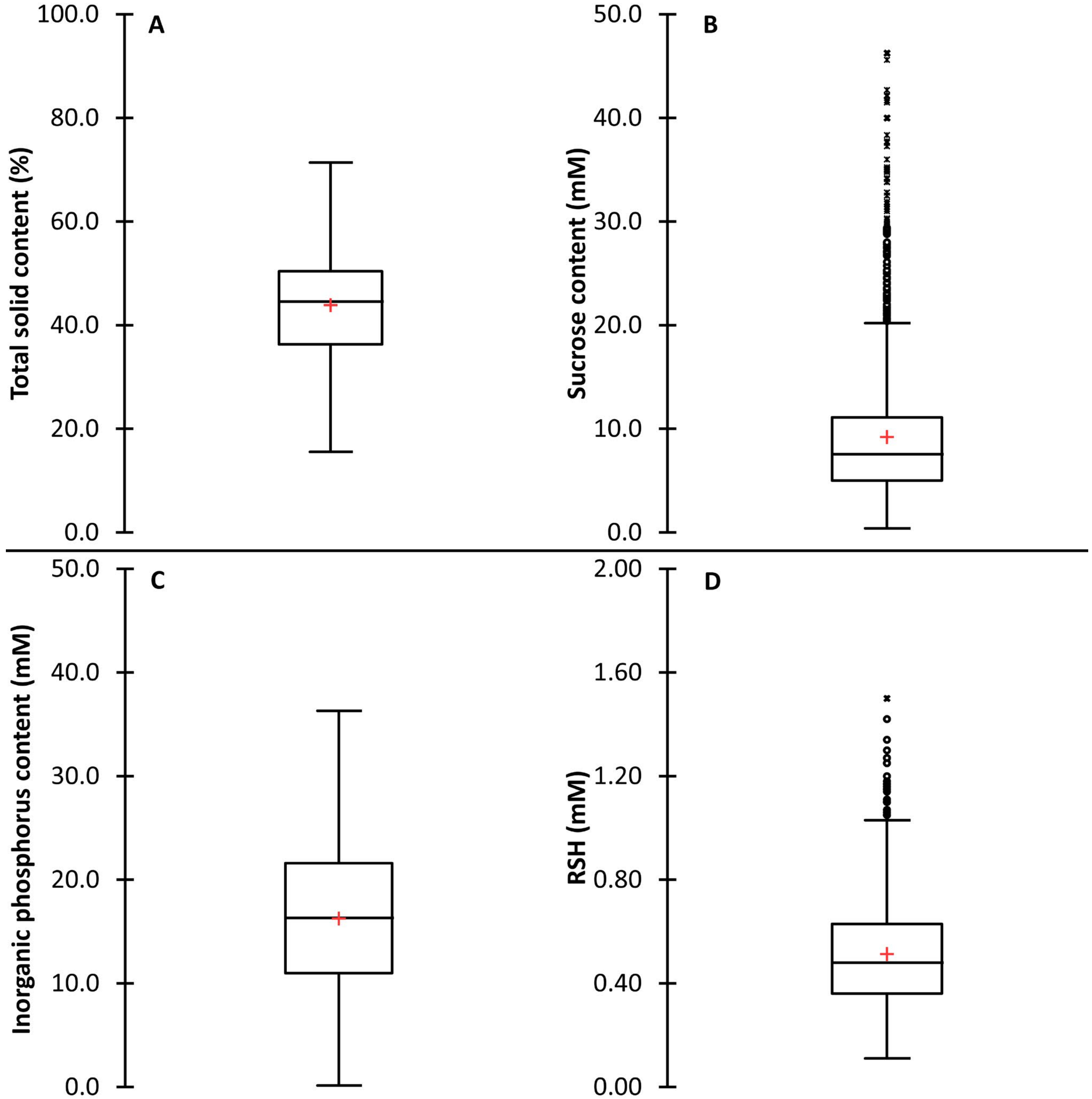

Figure 3. Box plot representative of the variability of four main latex physiological parameters, (A) total solid content, (B) Sucrose content, (C) Inorganic phosphate content, and (D) Thiols (RSH) content

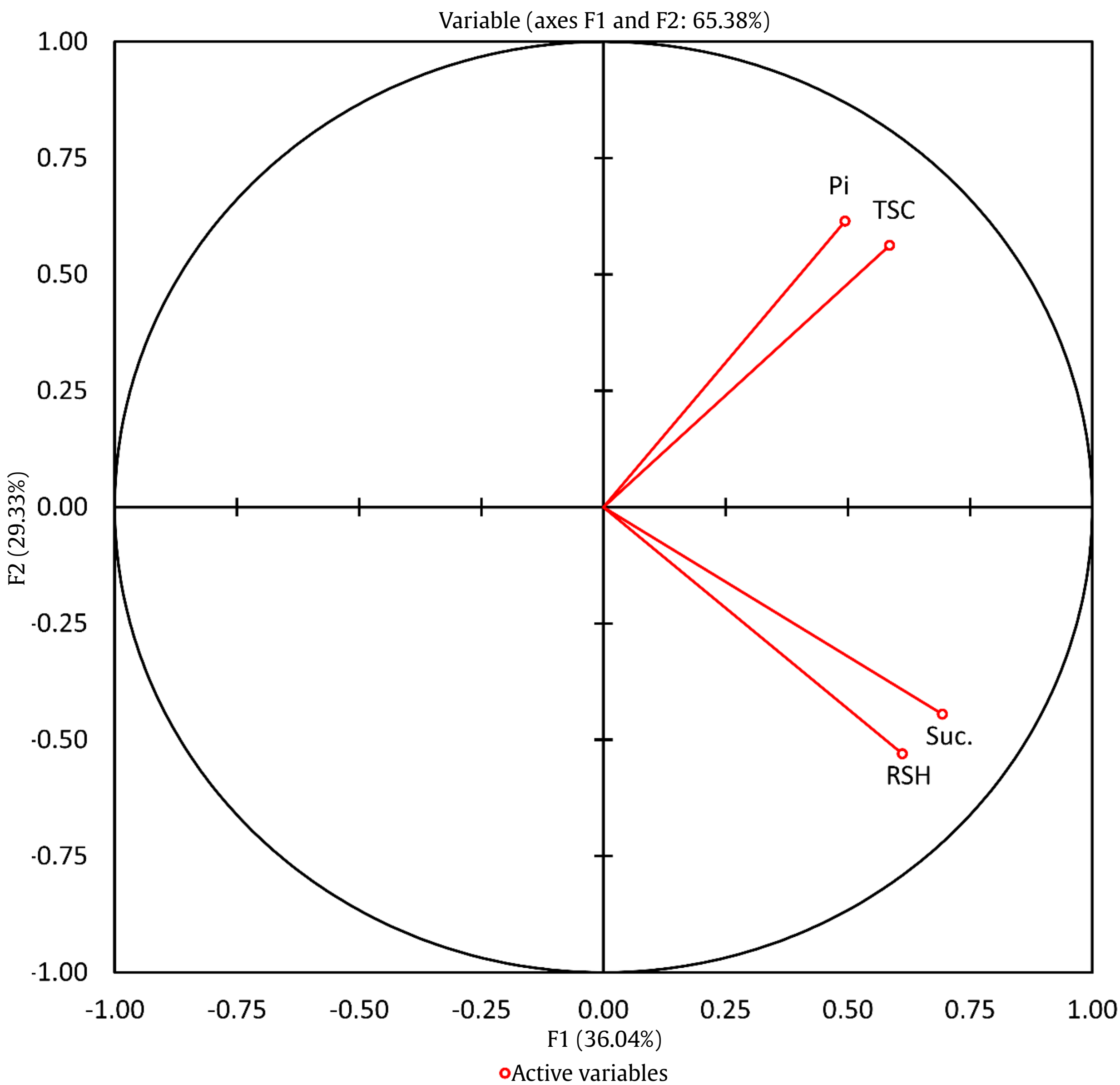

Figure 4. Principal component analysis (PCA) axes F1 and F2 of four main LD parameters values (TSC: total solid content, Suc: sucrose; Pi: inorganic phosphorus; RSH: reduced thiols)

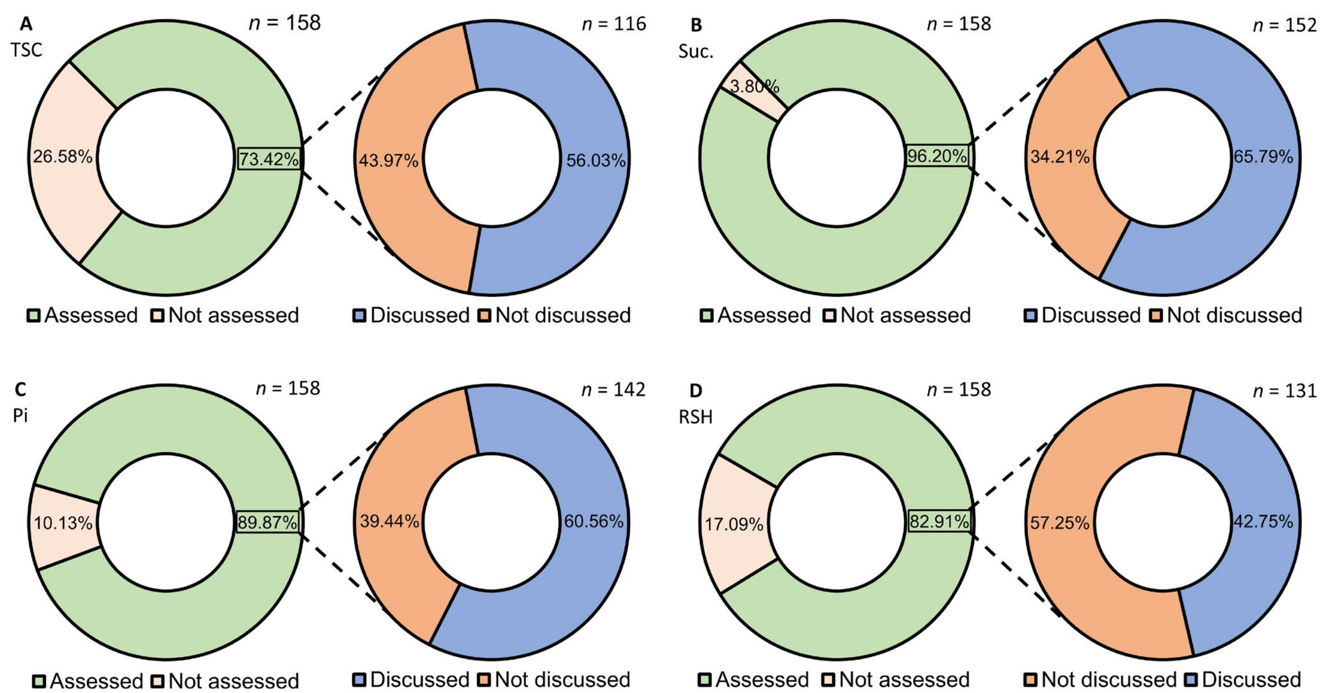

Figure 5. The proportion of the paper listed and interpreted by the authors for TSC (A), Suc (B), Pi (C), and RSH (D)

in breeding program. They also reveal the essential role of two main latex diagnosis parameters and the inconsistency of RSH.

4.1. Application of Latex Diagnosis in Rubber Plantations and Research Stations

The present work showed that latex physiology analysis is used in different studies, including agronomy, physiology, and breeding.

In agronomy works, latex diagnosis application was mainly for yield optimization. The increase in the number of publications using LD parameters occurred since 2003–2013 when studies searched for a new tapping system to optimize clonal yield potential, for example, the use of double cutting (Chantuma *et al.* 2011) and ultrasound (She *et al.* 2013). The number of publications remained high after 2013, even reached a peak in 2015–2017 (Supplementary data 2). The experiments of low-frequency tapping accompanied by stimulation modification, for example, the works by Sainoi *et al.* (2017), Atsin *et al.* (2014), and Phearun *et al.* (2019), contributed to a significant report on LD application. These typical studies might be a response to the low natural rubber price in order to reduce the tapping cost.

In physiology studies, LD parameters were used for physiological mechanism understanding, environmental stress adaptation, and tapping stress mitigation. The researchers investigated the seasonal variation of physiological parameters (Sreelatha *et al.* 2011; Nguyen *et al.* 2016), rubber tree physiological maturity (Rachmawan and Sumarmadji 2007; Obouayeba *et al.* 2012), environmental stress impacts (Alam *et al.* 2003; Kudaligama *et al.* 2017), and free radical and the scavengers' production on account of TPD extent (Kudaligama *et al.* 2017; Tistama *et al.* 2019). The studies had two main objectives: first, to establish more suitable tapping system to optimize the latex yield, and second, to monitor the stress level in laticifers to prevent TPD.

The breeding works involved LD parameters for growth and yield-related traits investigation (Vinod *et al.* 2000; Rattanawong *et al.* 2008), progenies evaluation (Sayurandi and Daslin 2011; Woelan *et al.* 2014; Syafaah *et al.* 2015; Phearun *et al.* 2016), and performance assessment of rubber clones (Woelan *et al.* 2013; Cardoso *et al.* 2014). The LD was also used for clonal typology characterization, grouping the rubber clones based on the latex physiological characteristic (Escbach *et al.* 1984; Thanh and Thuy 2003; Gohet *et al.* 2015). The typology was then used as the foundation for the determination of the exploitation system by agronomists in plantations (Gohet *et al.* 2008).

Interestingly, this meta-analysis reveals that the adoption of the LD method in physiology and breeding works (reported in 22 papers for each discipline) is lower than the agronomy discipline (assessed in 114 papers). Breeding activities still rely on histology (such as bark tissue and laticifers characteristics) and agronomy traits (especially initial growth and yield) in the screening process, indicating that a dissatisfactory link occurs between breeding and physiological works. In the case of LD adoption, the agronomy works took more advantages than breeding. Given the robustness of some LD parameters such as of Suc and Pi, these parameters should be better adopted this deserves further investigations to promote better and more efficient use of LD by breeders.

Most of the publications analysed in this paper came from scientific experiments (Supplementary Data 1). The connexion with research institutions is a key factor for the adoption of LD by the private sector. Determination and analysis of LD require both laboratory facilities, lab-skill and expertise in data analysis. In rubber plantation, the adoption of the technology is mainly by well-established companies which have access to research institutions and able to build a laboratory. However, The data from the companies are rarely published. In our database, only Nang *et al.* (2015) and Gohet *et al.* (2019) reported LD data from rubber companies in communication. On the other hand, the adoption in smallholding plantations is still limited. Some papers, such as Gohet and Chantuma (2003), Obouayeba *et al.* (2008), and Kudaligama *et al.* (2017) included the LD parameters in the harvesting system experiments in smallholding plantations, yet not particularly for the physiological evaluation. The smallholding plantation, which is characterized by limited land tenure and in some cases with low technology adoption, dominates the proportion of the total world rubber cultivated area. Thus, the diffusion LD technology may be a breakthrough for yield improvement on a global scale. Although the LD method has been introduced for more than three decades, the utilization of the technology is still limited to partial research discipline and type of rubber plantation and calls for the development of a high throughput and easy-to-use methodology.

4.2. Limited Use of Latex Diagnosis in Breeding Program

The standard 45-50 cm of girth for open-tapping of rubber tree may be reached in 4-8 years, depending on the clones, agro-climate and agronomical practices applied (Obouayeba *et al.* 2012). Due to a long immature period, the conventional breeding program led to select clones for early tapping and high early production, so-called quick starter clones. This type of clones, for example, PB 235, PB 260, RRIM 911, and IRCA 130, possesses the characteristics of low-medium sugar loading and high metabolic activity of the laticifers (Jacob *et al.* 1995; Gohet *et al.* 2019). The high yield emanates from the effectiveness of the latex regeneration and flow. However, the quick starter clones were reported to have a weak response to ethylene stimulation (Gohet *et al.* 1996; Jetro and Simon 2007; Lacote *et al.* 2010). Some studies also showed that the quick starter clones are susceptible to tapping panel dryness (Gohet *et al.* 1997; Okoma *et al.* 2011; Putranto *et al.* 2015).

The harvesting system in rubber plantations is shifting toward low-frequency tapping system (up to d6) combined with high stimulation intensity (up to 78/year) (Supplementary data 2). This approach is adopted in response to increasing labour costs and skilled-tapper shortage. Although some studies showed that quick starter clones have a low response to ethylene stimulation and consequently are less suitable to the low-frequency tapping (Atsin *et al.* 2014; Atsin *et al.* 2017), some new quick-starter clones may be more responsive to ethylene application. On the other hand, several studies showed that high sugar loading clones were able to amplify the benefit of low-frequency tapping (Gohet *et al.* 1996; Soumahin *et al.* 2009; Lacote *et al.* 2010; Diarrassouba *et al.* 2012). High sugar-loading clones are also more resistant to TPD due to the abundant availability of latex and antioxidant material (Jacob *et al.* 1995; Gohet *et al.* 1997, 2019). This capability is crucial in terms of climate change that increases environmental stress. Based on these considerations, the breeding program needs to switch the direction from high metabolic clones to high sugar loading clones. Various sucrose-related genes were characterized in *H. brasiliensis*, such as sucrose synthase (HbSus) gene family (Xiao *et al.* 2014), efflux transporter (HbSWEET) genes (Sui *et al.* 2017), and sucrose transporter (HbSUT) genes (Dusotoit-Coucaud *et al.* 2009; Long *et al.* 2019). Interestingly, Klaewklad *et al.* (2017) suggested that the expression of SUT3 gene may be used in the early selection of high-yielding rubber clones.

The rubber breeding cycle consists of F1 seedling evaluation, primary selection, small-scale clone trial, and multilocation trial that takes at least 33 years from the crossing to improved clones release (Gireesh *et al.* 2017). This conventional procedure is still the main method to select desired superior clones. To date, the rubber breeding program is mainly dedicated to yield and growth characteristics, while physiological traits are rarely assessed. Although some works have involved the LD parameters in the early assessment of the progenies (Phearun *et al.* 2016), our present observation suggesting that the LD parameters are still infrequently adopted in the breeding discipline, only found in 22 out of 158 selected papers. Further investigations are necessary to better understand the limitations of LD applications in *Hevea* breeding.

4.3. Two Latex Diagnosis Parameters Widely Represented

Latex flow and in situ regeneration between two tappings are the main limiting factors in latex production of *H. brasiliensis*. Parameters linked to the latex flow are TSC, BI, RSH, and Mg^{2+}. Parameters linked with latex regeneration including TSC, Suc, pH, Pi, Mg^{2+}, RSH, and RP (Jacob *et al.* 1989). Those parameters were the basis of latex diagnosis at the early period when this method was introduced (Jacob *et al.* 1985; Jacob *et al.* 1995). Progressively, LD was based on only four main parameters (TSC, Suc, Pi and RSH) to monitor rubber plantations. These parameters represent the latex regeneration level, carbohydrate availability, metabolic activity, and antioxidant status, respectively, in laticifers (Eschbach *et al.* 1984; Jacob *et al.* 1985; d'Auzac *et al.* 1997).

The papers in this work came from various countries, disciplines, plant age, clone, and tapping systems so that the LD values showed a high variation (coefficient variation of 19.6-72.9%). Among the four main parameters used in latex diagnosis, Suc and Pi were the most used and interpreted in the scientific papers. Sucrose content indicates carbohydrate availability, a carbon source for rubber biosynthesis and a source of energy in the laticifers (Tupy 1985; Jacob *et al.* 1995). The energy is required for various metabolic pathways, including enzymes biosynthesis and antioxidant regeneration, which are pivotal for resilience to oxidative stress. The principal component analysis (PCA) revealed that Suc had higher correlation with RSH than other LD parameters. The Pi parameter shows the metabolic activity level in the laticifers. High Pi in latex indicates that the plant has spent much energy on latex regeneration. In the context of climate change, we can question the role of latex metabolism in clone adaptation. Nguyen and Dang (2016) showed that the latex yield of a high-metabolic rubber clone PB 235 was more affected by temperature fluctuation than a medium metabolic clone GT1.

Variability of Suc and Pi is a genetic component and can be used for early rubber clonal selection (Phearun *et al.* 2016). In breeding, they are combined with anatomy and agronomy parameters for progenies evaluation and clonal metabolism identification. They are also used in the environmental stress assessment by collaborating with other stress markers. Indeed, Suc and Pi are the most considered parameters by agronomists in settling the harvesting system.

4.4. Role of Antioxidants

The latex harvesting practice, by mechanical artificial wounding and exogenous ethylene application, induces the reactive oxygen species (ROS) accumulation beside the natural production by cellular metabolism and environmental stress (Tian *et al.* 2015; Putranto *et al.* 2015). Over-exploitation and over-stimulation are known as the main factors of the TPD, a physiological disorder due to over-accumulation of ROS (Yusof *et al.* 1995; Gohet *et al.* 1997; Das *et al.* 2002; Putranto *et al.* 2015). Antioxidants and ROS-scavenging enzymes are essential to maintain the redox homeostasis and prevent cellular damage. The function of latex main antioxidants (thiols, ascorbate, and tocotrienol) and detoxifying enzymes such as superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPX), and glutathione S-transferase (GST) was reviewed in Zhang *et al.* (2017).

Thiols, the organo-sulphur compounds that contain a carbon-bonded sulfhydryl group (R–SH) (Rouhier *et al.* 2015), plays important role in the stress responses of plants due to its redox properties. In latex, up to 90% of RSH consists of glutathione and cysteine (Mc Mullen 1960). Low RSH content indicates that the plant is either under minimum stress, which not require antioxidant synthesis, or high antioxidant oxidation due to exceeding stress. A rubber tree with high RSH is expected to have the ability for neutralizing oxidative stress and maintaining the yield level. Total RSH content in latex is around 0.5-0.9 mM (Jacob *et al.* 1984). Our meta-analysis showed that the RSH values ranged from 0.11-1.50 mM with the mean was 0.51 mM. The variability may reflect the clonal effect, plant age, agro-climatic, harvesting regime, and measurement methodology.

According to our dataset, RSH is still low-interpreted both in plantation monitoring and research disciplines. RSH was interpreted only in 42.8% of the 131 papers. Some RSH values were not associated with the level of stress leading authors to limit the interpretation of their data. For example, in Herlinawati and Kuswanhadi (2012) and She *et al.* (2013), the content of the RSH remained constant whilst the stress increased. Some papers mentioned that Suc and Pi might be a better stress indicator

(Gohet *et al.* 2019; Tistama *et al.* 2019). The low interpreting of RSH questions whether this parameter is relevant in LD and calls for the development of a new parameter.

The reduced form of antioxidant carries the antioxidant power. When ROS are generated, the reduced form neutralizes ROS and is transformed into oxidized form (Tausz *et al.* 2003). Some studies detected the alteration in the proportion of reduced and oxidized antioxidants in response to environmental stress (Noctor *et al.* 2012; Marok *et al.* 2013). The ratio revealed the capacity of regeneration of antioxidant power through the ascorbate-glutathione cycle. This ratio could be a better indicator than total antioxidant content only. This approach offers an opportunity to improve the LD method.

Our study indicated that the better use of LD in breeding can improve selection for long-term high-yielding and stress-adapted clones. Clone adaptation is needed and a better understanding of redox metabolism should allow identifying better biomarkers related to stress tolerance (Zhang *et al.* 2019). The development of a simple and robust LD technology is also a challenge for sustainable rubber production.

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