



Perspectives and Ongoing Challenges

11

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Abstract

This new Rubber Tree Genome book includes the latest information on the status and application of modern molecular and genomic approaches and resources for natural rubber production, in multiple species, as well as detailed historical information on the origin and development of the current *Hevea brasiliensis* natural rubber industry. Furthermore, it includes new information on rubber particle ontogeny using the analogous species, *Taraxacum kok-saghyz*. In this chapter, I present some perspectives and challenges to our essential supplies of natural rubber, touching on the detailed information in this book and what I believe must be done in the future to ensure continued global rubber security. Also, I discuss some important research directions, rooted in the fundamental biology of rubber production, some of which are currently underdeveloped or largely ignored.

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11.1 Rubber Security

Natural rubber production is a critical agricultural commodity essential to all sectors of manufacturing. Demand continues to increase but many challenges are faced by producers, trying to maintain current supplies and, once prices rise sufficiently, to increase supplies to meet increasing market demands. Disease, political disputes and global warming-induced climate change pose the greatest threats to rubber production. Based on the global spread of fatal tree diseases, it appears inevitable that deadly South American Leaf Blight (SALB, caused by *Microcyclus ulei*) will cross to Southeast Asia, where the industry is yet to introduce resistant trees at scale. Even before this occurs, the current unsustainably low price of natural rubber, which does not provide a living wage to rubber tappers in most producing countries, leads to labor shortages and threatens supplies. The industry is yet to develop effective mechanized production methods, and the current hand tapping latex collection system has changed little, since it was developed by Henry Ridley, Director of the Singapore Botanic Gardens, in 1889 (Wycherley 1958).

Price increase to sustainable levels is now essential because the global moratorium on further deforestation of tropical rain forests prevents planting on newly cleared forest lands in SALB-free regions. Thus, production cannot keep moving to areas with lower labor costs, and

importing cheap immigrant labor has limited the effectiveness when tappers have to live in the production area.

It is possible to increase production from existing plantations, but this is difficult to accomplish. For example, the application of ethephon can increase rubber yields (Abraham et al. 1968; Yew et al. 1998) but this practice has not yet been widely adapted because of the perceived risks associated with ethephon. Even though effective ethephon management practices are now well understood, earlier poor management led to over-application and induced tapping panel dryness (Sivakumaran and Pakianathan 1983). Smallholders have not forgotten this effect, and many remain reluctant to try again. Also, crop management in Indonesia could be significantly improved to bring its production levels up to those achieved in neighboring countries from identical rubber tree clones. However, this requires government investment and training of extension professionals.

Conventional plant breeding is always very slow in tree species; for example, in China, only five *H. brasiliensis* generations have been achieved in 100 years (see Chap. 2), partly because rubber yields from mature trees under regular tapping cycles are very difficult to predict from seedlings or virgin trees. Nonetheless, even though breeding is very time-consuming, the Malaysian Rubber Board's pedigree collection bred in phases since 1928 (Ong et al. 1994) and more recent collections of wild Brazilian germplasm (Adifaiz et al. 2017; Ong and Tan 1987) appear to contain some individual genotypes with outstanding potential. These collections provide an essential source of experimental material for researchers.

The pressure on the rubber supply, coupled with an increasing awareness of rubber supply line insecurity, and price volatility largely caused by futures traders, has led to considerable investment by industry (mostly tire companies) in the development of alternative rubber-producing species in temperate regions to increase the biodiversity of rubber production. The leading species are *T. kok-saghyz* and *Parthenium argenteatum*, and with *H. brasiliensis*, these can

allow rubber to be produced in most parts of the world, not just in specific tropical regions. However, issues of scale remain significant impediments to the alternative crops because small acreages and pilot processing plants cannot produce rubber at the same price as vast acreages of hand-tapped *H. brasiliensis* (Cornish 2017).

11.2 The Biology of Rubber Production

Biology is the foundation of rubber production, and it is the coordinated whole plant system that must be understood to maximize the efficiency of experiments, practices and genetic approaches designed to increase rubber yield.

11.2.1 A Consideration of Root Stocks

Commercial rubber trees are produced by grafting buds harvested from high yielding clonal trees onto seedling root stocks and, once sufficiently established, the original shoot is excised. However, it should not be forgotten that latex production is a product of biology and is strongly influenced by the physiology of the intact tree. It is likely that different performance among identical clones, and among disparate soils and environments, reflects the root stock variation which, despite a limited ancestry, is still genetically and physiologically heterogeneous.

Inbred lines of *H. brasiliensis* are not yet available and not likely to be achieved through conventional inbreeding of this tree species. However, reciprocal grafts could easily be done by obtaining seeds generated from clonal plants. Also, since *H. brasiliensis* is amenable to tissue culture, it is feasible to generate cloned plants from new germplasm, and hence cloned root stocks from different genotypes. Both methods could be very useful tools to investigate the influence of root stock genetics, physiology and biochemistry on latex yield in the above ground laticifers. For example, rubber yield and molecular weight are strongly affected by the

concentration of monomeric (isopentenyl pyrophosphate, IPP) and initiating (farnesyl pyrophosphate, FPP) rubber polymer substrates in the laticifer but are even more sensitive to the concentration of the essential magnesium cation activator in the laticifer cytoplasm (da Costa et al. 2004, 2006; Scott et al. 2003). Magnesium is taken up from the soil in which the tree is grown and so is dependent upon the efficiency of the magnesium transmembrane transporters in the root cell plasmalemma and then the internal transporters in the vasculature and laticifers. Cytoplasmic magnesium concentration can be changed by differential expression of magnesium transporters, and also very probably by the concentration of soluble magnesium in the soil which, in turn, can be changed by fertilizers and chelators. I find it surprising that the effect of root stock and magnesium continue to be largely ignored by the rubber production industry when both are readily addressable research questions.

11.2.2 Molecular Resources, Approaches and the Biochemistry of Rubber Biosynthesis

Molecular resources have only recently been developed for rubber-producing species, and several genomes, transcriptomes and proteomes are now available for *H. brasiliensis* and other species (Chow et al. 2007; Dai et al. 2013; Lau et al. 2016; Lin et al. 2017; Luo et al. 2017; Mantello et al. 2014; Ponciano et al. 2012; Rahman et al. 2013; Stonebloom and Scheller 2019; Tang et al. 2016; Tong et al. 2017; Wahler et al., 2012; Wang et al., 2015). However, the *H. brasiliensis* genome is large and contains more than 70% repeat sequences (Tang et al. 2016). Additional resources include chloroplast and mitochondrial genome sequences (Shearman et al. 2014; Tangphatsornruang et al. 2011; Zhang et al. 2017). Chloroplasts and mitochondria are important producers of IPP and can export excess IPP into the cytoplasm where it supplements the IPP pool available for rubber polymerization. The high $K_m^{\text{IPP-Mg}}$ of all rubber

transferases (RT-ases) characterized to date means that rubber is only made when IPP is accumulated to concentrations non-limiting to all the other IPP-requiring enzymes present in the cytosol (Cornish 2001a, b). New technologies, such as CRISPR/Cas9 gene editing have also been used in rubber-producing plants (Iaffaldano et al. 2016).

Rubber production requires complex developmental regulation (Chow et al. 2012). For example, an important yield determinant in laticiferous species is the number of laticifers per unit cross-sectional area. This was made very clear in the investigation of rubber particle ontogeny and laticifer development in *Taraxacum kok-saghyz* (Abdul Ghaffar and Cornish 2019). The genetics of laticifer ontogeny are not well understood (Sando et al. 2009) but, since rubber particles appear before laticifers in *T. kok-saghyz*, it seems possible that rubber particles may trigger laticifer development. The induction of more rubber particles may concomitantly lead to the induction of more laticifers. Similarly, the creation of rubber particles may be triggered by the expression of all or some of the subunits making up the RT-ase complex (Berthelot et al. 2014; Cherian et al. 2019; Collins-Silva et al. 2012; Cornish et al. 2018; Dai et al. 2017; Lakusta et al. 2019; Yamashita et al. 2016). Overexpression of a critical subunit might lead to expression of the other components or all these processes may be controlled by a key transcription factor. Transcription factors certainly operate in *H. brasiliensis* (Li et al. 2016). The available genomic resources now make it possible to address some of these questions.

The regulation of rubber biosynthesis is somewhat distinct from the machinery required for synthesis. By this I mean that although rubber obviously cannot be made in species without RT-ases, laticifers are not always used to make rubber particles (*Parthenium argentatum* is the best characterized non-laticiferous rubber-producing species). Also, even when sufficient RT-ase complexes are present to support higher rubber synthetic rate, molecular studies, which alter rubber particle protein composition or substrate availability and lead to increased amounts of

rubber in seedlings, have yet to maintain such gains in field crops (Dong et al. 2013; Hillebrand et al. 2012; Placido et al. 2019; Stolze et al. 2017). Clearly, feedback loops are acting in rubber plants which prevent a perceived overproduction of rubber, presumably because of some adverse effect on primary metabolism, possibly due to substrate deficits or accumulation of toxic byproducts. Such feedback clearly changes under different environmental conditions, because rubber biosynthetic rates change with environmental factors (Benedict et al. 2008; Cornish and Backhaus 2003; Ji et al. 1993; Kreuzberger et al. 2016). Thus, a fundamental understanding of the genetic and biochemical regulation of rubber biosynthesis is required to inform effective molecular modification to predictably increase rubber yield.

In-depth molecular and metabolomic investigation of plants within individual species with naturally large differences in rubber content will certainly improve our fundamental understanding of rubber biosynthesis. In addition to the issues raised in the previous paragraph, these plants perhaps have even more value in the development of selectable molecular markers, quantitative trait loci and molecular maps—all of which may be used to inform selection and molecular approaches, and be applicable to seedlings without requiring initial phenotyping of mature plants (Luo et al. 2017; Mantello et al. 2014; Rosa et al. 2018; Shearman et al. 2015). The Malaysian collection may also be sufficiently diverse to permit meaningful genome-wide association mapping approaches. These germplasm sources would become even more powerful if homozygous lines could be developed from high and low rubber yielding parents. Haploid induction from germ cells, or by manipulation of *cen* genes (Britt and Koppu 2016; Karimi-Ashtiyani et al. 2015; Ravi and Chan 2010) followed by chromosome doubling via colchicine poisoning (Luo et al. 2018), are two potential avenues to achieve this goal.

Interspecific approaches have already yielded considerable fundamental biochemical and genetic information about rubber biosynthesis and can expand on what may be provided from a

single species, especially a tree such as *H. brasiliensis*. The rubber and rubber particle composition produced by *T. kok-saghyz* are very similar to those produced by *H. brasiliensis* (Cornish et al. 2015) indicating either strong conservation of the rubber biosynthetic machinery or strong convergent evolution. In all species investigated so far, the basic rubber particle structure has been highly conserved within the Eudicots, where all higher plant rubber-producing plants are classified (Metcalf 1967). Rubber particles are always made in the cytosol, are often moved into vacuolar storage, have a uni-lamellar membrane (although the membrane lipid and protein composition may differ), have a membrane-bound RT-ase complex, use the same substrates and cofactors, and compartmentalize the rubber polymers into the particle interior (Cornish 2001a, b; Cornish et al. 1999; Siler et al. 1997; Singh et al. 2003). However, the details of rubber production differ among plants and these differences may be exploited to improve yield or quality in other species. This potential has become extremely important as additional rubber-producing species enter the agricultural arena and contribute their own newly developed genomic resources.

11.3 Conclusions

The information in this book provides a consolidated foundation of rubber genome resources currently available and some of the associated studies currently published, focused primarily on *H. brasiliensis*. However, comparative genomic studies are becoming increasingly informative in identifying key pathways and genes associated with or key to rubber biosynthesis and yield, and there are many fascinating research questions still awaiting elucidation. As alternative rubber-producing crops are introduced, it is important to maintain polymer quality so that the needs of the rubber manufacturing industry continue to be met. In addition, premium niche applications must be identified to permit these crops to be scaled up—they have a very long way to go before they can become a rubber commodity

producer like *H. brasiliensis*. Nonetheless, biodiversity of the global natural rubber supply is essential to rubber security and interdisciplinary research on multiple rubber-producing species is needed to achieve this goal. Natural rubber is, and will continue to be, a major contributor to the circular bioeconomy and sustainable production is essential.

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