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LETTER TO THE EDITOR

WILEY Global Change Biology

Plant cuticle under global change: Biophysical implications

The climatic stressors that modify the chemical composition of plant tissues have been recently reviewed by Suseela and Tharayil (2018). In particular, the authors stated that the response of plants to global change effects (*viz.* increasing temperatures and frequent drought periods) can induce important modifications in plant cuticles such as an increase of the main cuticle components (cutin and polysaccharides), a preponderance of cutan, heavier wax loads, and changes in the chemical composition of waxes, mainly the accumulation of longer aliphatic compounds. In this letter, we would like to emphasize the biophysical consequences that this new scenario involves and how it would affect plant performance.

Plant cuticles are composite interfaces between the aerial organs and the atmosphere, playing many biological roles (Figure 1) related to avoiding massive water loss, defense against pathogens, harmful UV radiation, xenobiotics, etc. (Martin & Rose, 2014). In the above-mentioned context, hydric, thermal, and mechanical properties of plant cuticles are expected to be significantly modified. Main biophysical consequences to global change effects are summarized in Table 1. The glass transition temperature, T_g, is an important thermodynamic parameter of amorphous polymers like cutin. It is the temperature where a reversible transition between a rigid behavior and a rubber-like state occurs. When $T > T_g$ polymer chains increase their molecular mobility, changing the viscosity, stiffness, and heat capacity of the entire macromolecule. In the case of plant cuticles, the T_g is ~23°C for cutin and *ca.* −33°C for cutan (Chen, Li, Guo, Zhu, & Schnoor, 2008; Domínguez, Heredia-Guerrero, & Heredia, 2011). Interestingly, the heat capacity (the amount of heat necessary to increase by 1°C the temperature of a material) increases at temperatures above the T_g and, hence, also the thermoregulatory role of plant cuticles. For instance, the heat capacity of cutin shifts from ~2.0 J g^{-1}°C^{-1} for $T < T_g$ to ~3.0 J g^{-1}°C^{-1} for $T > T_g$, while the heat capacity of cellulose (the main component of cell walls) is constant with a value of ~1.5 J g^{-1}°C^{-1} (Domínguez, Heredia-Guerrero, 2011). In this sense, the higher amounts of cutin and/or cutan as well as of natural fillers (i.e., intracuticular waxes, specifically longer aliphatic waxes that can reduce the interactions between cutin polymer chains, decreasing the T_g) associated with increasing temperatures can have an indirect effect, improving plant protection. The decrease of T_g (see Table 1) would allow plants to fine-tune their heat capacity.

Another important aspect is the hydrodynamic of plant cuticles, mainly water permeability and hydrophobicity. Both increased temperatures and drought play a direct effect on cuticle membranes increasing their water permeability. However, temperature, low relative humidity and drought also induce an increase in cuticle components, especially waxes, thus reducing water permeability (Schuster, Burghardt, & Riederer, 2017). It is known that waxes play a major role as water barrier but they also affect hydrophobicity (Fernández et al., 2017). The wettability of a surface depends on its chemical nature and roughness. In plant cuticles, both factors are governed by epicuticular waxes. Therefore, although the increase in cutin and polysaccharides would not be primary involved, the increase of waxes is expected to result in a better wax coverage and, hence, to higher hydrophobicity. The accumulation of longer aliphatic waxes can have

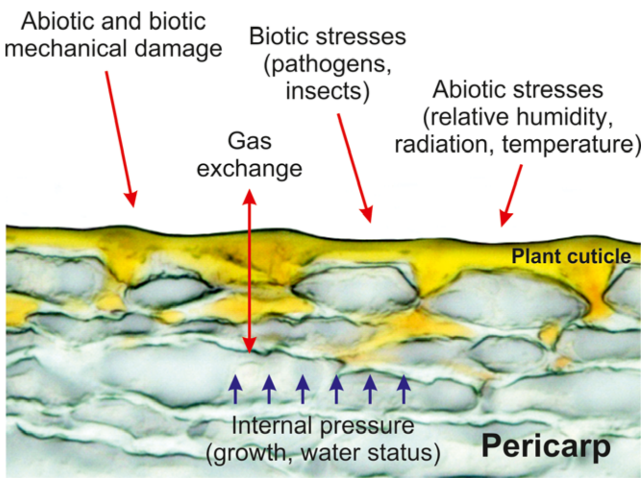

FIGURE 1 Light microscopy image of a cross-section of tomato fruit pericarp. The plant cuticle is the outermost composite membrane (yellow colored) that covers the epidermis. It is composed of cutin (a polyester formed by condensed hydroxylated fatty acids), polysaccharides from the epidermal cell wall, waxes on the top (epicuticular waxes) and distributed throughout the cuticle (intracuticular waxes), and phenolic compounds. Some species may contain an alternative lipid polymer named cutan (a chemically inert polymer matrix that consists of an ether-linked network of methylene chains, double bonds, and carboxyl groups) that may partially or completely substitute cutin. A detailed description of the fine structure and chemical composition of the plant cuticle can be found elsewhere (Domínguez, Heredia-Guerrero, 2011; Jeffree, 2006). As the interface between the plant and the atmosphere, plant cuticles regulate gas exchange, interacts with pathogens and insects and are exposed to different environmental stresses such as mechanical damage from abiotic (wind, heavy rain) or biotic (herbivores, insects and fungi) sources as well as severe changes in relative humidity, light intensity and quality (e.g., harmful UV radiation), and temperature. In addition, cuticles are also subjected to the hydrostatic pressure exerted by internal tissues, which varies depending on the growth stage and water status [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Effects of global change in the hydric, thermal, and mechanical properties of plant cuticles. Direct effects relate to those exerted on already synthesized cuticles, whereas indirect refers to those occurring to the cuticle during the period of growth and development

			Biophysical outcome		
Global change	Effect	Cuticle changes	Thermodynamics	Biomechanics	Hydrodynamics
Rise in temperature	Direct	–	Structural changes if $T > T_g$	Viscoelasticity	Higher water permeability
Drought	Direct	–	No changes in T_g	Higher stiffness	Higher water permeability
Temperature and/or drought	Indirect	More cutin and polysaccharides	Presumably not related to modifications of T_g	Presumably higher stiffness	Not related to water permeability or hydrophobicity
		Increased amount of cutan	Predominance of a lower T_g	Higher stiffness	Presumably higher hydrophobicity
		Higher wax load	Presumably lower T_g	Higher stiffness	Higher hydrophobicity and lower permeability[a]
		Longer waxes	Presumably lower T_g	Presumably higher stiffness	Higher hydrophobicity and lower permeability[a]

[a]It could vary depending on the nature of the waxes/Assuming a higher load of long chain aliphatic waxes.

a double effect. They are less polar than their shorter aliphatic homologs, while they can also induce the formation of bigger wax crystals, increasing surface roughness and, hence, hydrophobicity. Collaterally, such bigger wax crystals could improve protection against harmful UV radiation by increasing its reflection. Finally, the presumably less polar chemical structure of cutan could produce small regions of increased hydrophobicity in surface areas not covered by waxes.

Temperature and water also directly affect the biomechanical properties of plant cuticles. In fact, higher temperatures induce viscoelasticity, while drought stiffens the cuticle (Domínguez, Cuartero, & Heredia, 2011). In general, expected cuticle modifications induced by global climate changes should increase stiffness. Higher amounts of cuticle material, especially cuticular waxes, which have been reported to “fix” strain and increase stiffness (Khanal, Grimm, Finger, Blume, & Knoche, 2013), are expected to increase plant rigidity. We consider that this effect could become more pronounced for longer aliphatic waxes, since their interaction with cutin would be stronger. Cutan has also been associated with a rigidizing effect of the cuticle (Takahashi, Tsubaki, Sakamoto, Watanabe, & Azuma, 2012).

To conclude, plant cuticles are likely to respond to global environmental changes by becoming heavier, stiffer and physicochemically more inert, thus improving plant protection. This new scenario at the plant surface could have ecophysiological consequences altering the interaction with other organisms (e.g., bacteria, fungi, insects, herbivores, etc.). Cuticle stiffening could create new challenges for agriculture, given the role of the cuticle and epidermis in controlling organ growth. During plant growth the cuticle remains viscoelastic to accommodate increases in size and only stiffens at the end of the growing period. A higher rigidity during growth could negatively influence yield, forcing to address the effects of global change with new strategies.

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CONFLICT OF INTEREST

There are no conflicts of interests.

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