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Abstract

Terrestrial ecosystem dynamics are strongly modified by stresses associated with climate change, impacting plant growth and development, mortality, and ecological succession. Here we highlight the potential role of plant cell wall esters to link changes in cell wall structure/function with biosphere-atmosphere fluxes of methanol, acetic acid, carbon dioxide, and water.

Main text

Terrestrial ecosystem dynamics, including carbon stocks and biosphere-atmosphere fluxes of carbon dioxide (CO₂), water (H₂O), and volatile organic compounds (VOCs) are dramatically changing in response to climate factors such as trends in surface warming and a higher frequency and intensity of large-scale droughts and associated insect infestation epidemics [1]. Understanding the mechanisms that drive forest responses to climate change is vital for predicting

how the structure and function of natural and managed ecosystems will react to environmental change including alterations in carbon and H₂O cycling, and the ecosystem services and products provided. Therefore, understanding the underlying biochemical, physiological, and ecological processes including plant growth and development, abiotic and biotic stress responses, mortality, and ecological succession and forest recovery are critical for accurately predicting the future of forest structure and function.

Increased abiotic and biotic disturbances threaten the ability of terrestrial ecosystems to maintain a net carbon sink and consequently mitigate anthropogenic climate effects in the atmosphere. For example, reductions in net primary productivity (NPP), decreases in biomass gains, increased vegetation mortality, and shortening of carbon residence times have been linked to drought and warming anomalies across numerous ecosystems [1]. However, mortality-linked generation of forest gaps can lead to the release of suppressed understory trees and increased rates of early successional species recruitment. Thus, forest regrowth can counterbalance carbon losses and contribute to accelerated forest dynamics with the majority of tree biomass being in the form of **plant cell walls** (80-95%; see glossary). Here, we highlight cell wall-derived emissions of methanol and acetic acid, along with associated changes in cell wall structure and function as a common thread among the processes that underlie ecosystem responses to climate change (**Fig. 1**).

Methanol is the most abundant non-methane volatile in the atmosphere with emissions from terrestrial vegetation the largest global source. High methanol emissions, often dominating ecosystem release of VOCs, have been reported from agricultural crops and temperate, boreal, and tropical forests. Methanol emissions are closely associated with plant growth, stress, and senescence processes attributed to physicochemical changes in cell walls [2]. While field observations are rare, acetic acid is also an important volatile emitted by terrestrial ecosystems [3] and like methanol was recently suggested to derive primarily from cell walls [4]. Methanol emissions tightly correlate with leaf expansion rates and young expanding leaves emit substantially higher amounts of both methanol and acetic acid than mature leaves. Moreover, leaf methanol emissions more than double for each 10 °C increase in leaf temperature [5]. Furthermore, leaves undergoing age-related senescence show elevated emissions of methanol and acetic acid [6], while detached leaves undergoing desiccation release large pulses of methanol and acetic acid [4]. These findings suggest that methanol and acetic acid emissions increase together with NPP during forest growth and recovery processes, but diverge during high temperature and drought stress with stimulated emissions of methanol and acetic acid and suppressed NPP. Thus, if terrestrial forests are becoming more dynamic, gap-phase processes play a critical role in determining carbon stocks, residence times and biosphere-atmosphere fluxes of VOCs, CO₂, and H₂O.

The **primary cell wall**, which surrounds all plant cells, provides shape, strength and flexibility. It consists of a complex structure composed of **hemicellulose** and cellulose microfibrils embedded in a gel-like matrix composed of **pectin**. In addition to providing structure, the cell wall is dynamic, facilitating numerous interactions within the extracellular matrix including cell adhesion, migration, and growth, and exchange of macromolecules, nutrients, metabolites and hormones. Such dynamic responses are facilitated by chemical modifications that can significantly alter

physicochemical, mechanical, and biological properties. The cell wall is the first line of defense against many stresses, and cell wall remodeling is a common stress response. While cell wall structure and function are controlled to a large extent by the polysaccharide composition, which varies with tissue type, developmental stage, and plant species, more rapid secondary chemical modifications can occur in response to environmental or developmental cues. For example, non-cellulosic cell wall polysaccharides can be extensively modified with methyl and/or O-acetyl esters [7],[8]. The removal of esters via enzymatic hydrolysis leads to rapid physicochemical changes in the cell wall and the release of methanol and acetic acid, which can then be transported in the transpiration stream and emitted to the atmosphere as a VOC or feed into central carbon and energy metabolism (**Fig. 2**). Changes in cell wall esters during stress induce signaling via damage-associated molecular patterns, which in turn activate immunity responses [9]. This suggests that cell wall-derived methanol and acetic acid are involved in signaling and immune responses as an essential component of plant monitoring systems.

Once released from the cell wall, acetic acid and methanol may be efficiently integrated into central carbon and energy metabolism[10]. Following activation to acetyl-CoA, acetic acid can participate in numerous catabolic and anabolic processes whereas methanol initiates the C₁ pathway integrating into photosynthesis/photorespiration via formaldehyde/formate/CO₂ and the universal C₁ donor **5,10-CH₂-THF**. Given that high temperature and drought stress suppresses stomatal conductance and photosynthesis and accelerates photorespiration, enhanced release of cell wall-derived methanol and acetic acid may play important roles in thermal tolerance by **1)** providing an alternative carbon source for glycine methylation in photorespiration thereby potentially reducing glycine decarboxylation, **2)** enhancing CO₂ concentrations within chloroplasts for photosynthesis, and **3)** producing key C₂ intermediates (e.g., acetyl-CoA) used in lipid and secondary metabolite biosynthesis, energy generation during mitochondrial respiration, and regulation of biopolymer function via acetylation. However, little is known about the quantitative significance of cell wall ester metabolism to plant carbon and energy requirements during stress.

Although many hemicellulose and pectin polysaccharides can be heavily O-acetylated, only pectin is thought to be substantially methyl esterified. Pectin provides both mechanical and adhesive properties within the cell wall, properties which can be dramatically altered through de-esterification. Newly synthesized pectin is exported to the cell wall in a highly methyl and O-acetyl esterified state. Once positioned in the cell wall, pectin methyl and acetyl esterases can selectively hydrolyze these esters. For example, following de-methylation, the generation of carboxylate anion side chains can bind Ca⁺² cations in an **egg-box structure**, increasing cell wall rigidity. Alternatively, the de-methylated pectin can be targeted for degradation by polygalacturonases. De-methylated pectin is suggested to be an essential component of plant response to heat stress through its role in controlling cell wall mechanical properties [11] and is deemed vital for stomatal function [7]. Enriched levels of methyl esterified pectin in stomatal guard cell walls lead to a reduced dynamic range of conductance which in turn impacts transpiration and evaporative cooling as well as photosynthesis and growth.

Recently it has been reported that acetyl groups on **xylan**, a major component of the **secondary cell wall**, are essential for proper xylem structure and function through facilitation of xylan-cellulose interactions [12]. Consequently, mutations in several genes associated with acetylation

of xylose residues during xylan biosynthesis lead to the collapse of xylem vessels and dramatically reduced transpiration rates [8]. Additionally, O-acetylation of pectins and hemicelluloses is essential for maintaining the structural integrity of leaf epidermis [13]. Additionally, a global stress response was activated, including a marked upregulation in ROS detoxification. These findings support an emerging view of the interacting roles of cell wall esters and ROS in sensing and signaling pathways involved in cell wall remodeling in response to stress [14].

Conclusions

While little is known about the functions of cell wall ester modifications in trees, evidence from model plant systems like *Arabidopsis thaliana* suggests that they may be highly dynamic, playing central roles in cell growth, tissue development and function, participating in sensing and signaling pathways involved in cell wall remodeling in response to stress, and integrate into primary C₁₋₃ metabolism. Although the reservoirs and fluxes of carbon through acetylated and methylated cell wall polysaccharides are potentially large, they remain poorly characterized. Methanol and acetic acid products of cell wall de-esterification may be transported over large distances within the plant and enter central metabolism in distant tissues or be emitted into the atmosphere as gases, but plant and ecosystem emissions studies investigating this are rare. Thus, interdisciplinary studies linking cell wall biochemistry and metabolism with plant physiology and biosphere-atmosphere gas exchange will lead to better predictive understanding of the mechanisms through which cell wall esters facilitate forest response to climate extremes. Of particular interest are high latitude forests responding to rapid warming through expansion of deciduous broadleaf trees and commensurate declines in evergreen conifer trees [15]. These distinct plant functional types vary in their leaf phenological cycles and cell wall composition, with deciduous trees undergoing seasonal leaf emergence and senescence while conifer trees retain their needles over the winter months. This may impact the timing, spatial distribution, and magnitude of biosphere-atmosphere fluxes of VOCs, CO₂, and H₂O in such changing forests in the future.

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Figures

Figure 1: Acceleration of forest dynamics and biosphere-atmosphere interactions associated with cell wall-derived methanol and acetic acid emissions under future predictions in surface warming, droughts, and biotic stress. The size of the arrows representing emissions of methanol and acetic acid are indicative of the relative strength of these emissions. Methanol is emitted in greater quantities than acetic acid, and emissions of both increase under stress. Figure created using Biorender.com.

Figure 2: Integration of cell wall methyl and O-acetyl esters with atmospheric emissions and primary carbon metabolism. Created using Biorender.com and FigShare (<https://doi.org/10.6084/m9.figshare.7398800.v1>)

Glossary box

5,10-CH₂-THF: 5,10-Methylenetetrahydrofolate, the universal one carbon (C₁) donor.

Egg-box structure: Calcium-induced association of two parallel pectic galacturonan chains with a pattern of specific de-esterified galacturonic acid monomers ionically bound via Ca²⁺ ions.

Hemicellulose: Plant polysaccharides that contain a β-(1→4) linked backbone, traditionally characterized by alkaline extraction. Hemicelluloses include xylan, arabinoxylan, xyloglucan, glucomannan, and mannan.

Pectin: A component of the plant primary cell wall. Pectic polysaccharides are characterized by a galacturonic acid-enriched backbone. There are four major pectic domains: homogalacturonan, xylogalacturonan, rhamnogalacturonan I and rhamnogalacturonan II.

Plant cell wall: Plant cells are surrounded by a cell wall which provides shape and strength. Cell walls consist of polysaccharides, including cellulose, hemicellulose, and pectin, proteins, and lignin.

Primary cell wall: A thin cell wall that surrounds all cells. It consists of cellulose, hemicellulose and pectin. It provides structure while retaining the flexibility and extensibility necessary to allow cell expansion.

ROS: Reactive oxygen species such as hydrogen peroxide, singlet oxygen, superoxide anion, and the hydroxyl radical.

Secondary cell wall: The secondary cell wall is deposited after the cell stops growing, and provides more strength and rigidity. The secondary cell wall contains mainly cellulose, lignin and hemicellulose. The secondary cell wall accounts for the majority of plant biomass.

Xylan: A hemicellulosic component of the cell wall, it is a polysaccharide with a β -1,4 linked xylose backbone, which carries various chemical substitutions.

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