Water transport in the plant

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Abstract

Drought-related tree mortality events have been increasing globally for the past few decades and it is feared that this situation will worsen with the increasing risk of heat waves. Understanding the physiological basis of these die-offs can help identify better adapted species or genotypes, but can also improve predictive models of these mortality risks. A drought modifies the hydric and hydraulic functions of a tree, and this more so the more intense the drought is. Beyond a certain intensity, embolism events can occur in the xylem vessels, which can lead to desiccation and then death of the crowns. Vulnerability to embolism thus appears to be a key physiological process in the mortality of plants exposed to drought. It has been studied in detail since the 1980s and work is currently focused on the concept of hydraulic failure risk. This risk integrates the intrinsic vulnerability of the xylem to embolism, but also the water stress undergone by the trees during drought. It is mainly the residual cuticular transpiration of the tree that determines the rate of dehydration and thus the risk of embolism. To assess this risk, all of these physiological processes must be integrated into a model of tree water and hydraulic functioning. The predictions of such models illustrate the key role of xylem vulnerability to embolism and cuticular losses in the mortality process. In particular, a high risk of embolism exists when leaf temperature passes a critical threshold, which could explain the aggravating effect of heat waves. Moreover, the model predicts a very strong increase in the risk of embolism with global warming, and the genetic variability and phenotypic plasticity of forest species seem too low to limit this risk.

1- Introduction: a river runs through it

Trees are capable of a remarkable physical feat: sucking water up to the top of their foliage, often tens of meters above the ground, while the best man-made pumps find their limit at only 10m. The search for this mechanism has been a long scientific epic, well summarized in this article by Cruiziat (2007). Since the seminal work of Dixon (1914), the physical principles of water transport in plants are well established and we will recall the main lines of his theory of "tension-cohesion". What scientists are currently questioning is the capacity of trees to circulate this water in their vascular tissue in a rapidly changing climatic context where drought episodes are increasingly frequent and intense. Can this circulation stop abruptly? Can the hydraulic pump of trees be damaged if the climate becomes too dry? What consequences for the life, or even the survival, of the trees can then be foreseen? Work on the circulation of water in plants carried out in recent years is providing the first answers to these questions. Unfortunately, there is cause for concern.

2- A necessary evil

We are dealing here only with the circulation of raw sap, the upward movement of very diluted water through the sapwood (xylem). We will not deal with the circulation of the elaborated sap, descending, rich in sugar, and taking the phloem pathway. But before going into the physics of the circulation of this sap, let us ask ourselves this question: why do plants

circulate so much water? In summer, the amount of water that circulates in the trunk of a mature tree is hundreds of liters per day. All this water is drawn from the soil by the roots, transported in the vessels of the sapwood, and evaporated by the leaves. Why consume so much water, at the risk of depleting the reserve stored in the soil and quickly becoming water-stressed if the rains fail? The answer to this question is given when we understand the physiological functioning of leaves. Leaves are chemical factories that use solar energy to transform carbon dioxide (CO_2) from the air into sugars through the process of photosynthesis. These sugars are used to cover the plant's energy needs and to ensure its growth, which also makes it possible to store a small part of the fossil CO_2 that we emit each year. The CO_2 molecules enter the leaves through the stomata, tiny holes in the impermeable cuticle that covers the leaves. It is the relatively small concentration gradient between the interior of the leaves and the atmosphere that allows the CO_2 molecules to diffuse. The chemical reaction that transforms CO_2 into sugar takes place in liquid phase, so the CO_2 from the air must first be dissolved in water. This dissolution takes place at the level of the walls of the cells of the lacunar parenchyma of the leaves, which are thus filled with liquid water. The situation is therefore as follows: ambient air is often dry, stomata are wide open to allow CO_2 to diffuse and the internal walls of the leaf cells saturate the air in contact with them with water vapor. The very strong gradient of concentration in water vapor between the leaf and the atmosphere creates a massive diffusion of water molecules towards the atmosphere. This is transpiration. On average, when 1 molecule of CO_2 passes through a stomata, 400 molecules of water escape at the same time to the atmosphere. The plant must therefore let out very large quantities of water to assimilate enough CO_2 to cover its needs. So we can see that transpiration is a "necessary evil" to allow photosynthesis. A plant that consumes a lot of water is a healthy plant that absorbs a lot of CO_2 for optimal growth. We can also see that this transpiration process requires the presence of an efficient hydraulic system to irrigate the leaves and compensate permanently for the water lost through transpiration. If this hydraulic system fails, the leaf risks to dehydrate, even to dry out irremediably. This is why the hydraulic functioning of plants is studied so carefully.

3- Hanging on a wire
To understand the mechanism of the ascent of the raw sap in summer, we need some notions of anatomy. The raw sap circulates in the sapwood, a tissue formed by tiny pipes (vessels), filled with water, which connect the leaf evaporation sites to the root absorption sites. There is thus a hydraulic continuum between the leaves and the roots, provided by columns of water suspended from the leaves by capillary forces. Transpiration is the engine of the ascent of the raw sap. It generates capillary tensions in the leaves that "pull" on the water columns of the vessels. Because of the cohesion of the water molecules between them, these tensions are transmitted to the roots which can then absorb water from the soil, setting the whole water column in motion. Dixon (1914) was the first to formalize this mechanism, to which he gave the name "tension-cohesion". The singularity of this mechanism is that the water is under tension (a negative pressure), i.e. in a physically metastable state. The greater the transpiration, the drier the soil, the greater these tensions. We typically measure tensions of the order of several megapascals (or tens of bars), much higher than that created by vacuum (0.1 MPa or 1 bar). The plants live suspended from a wire and under the permanent risk of a sudden vaporization of the sap by a phenomenon called "cavitation".
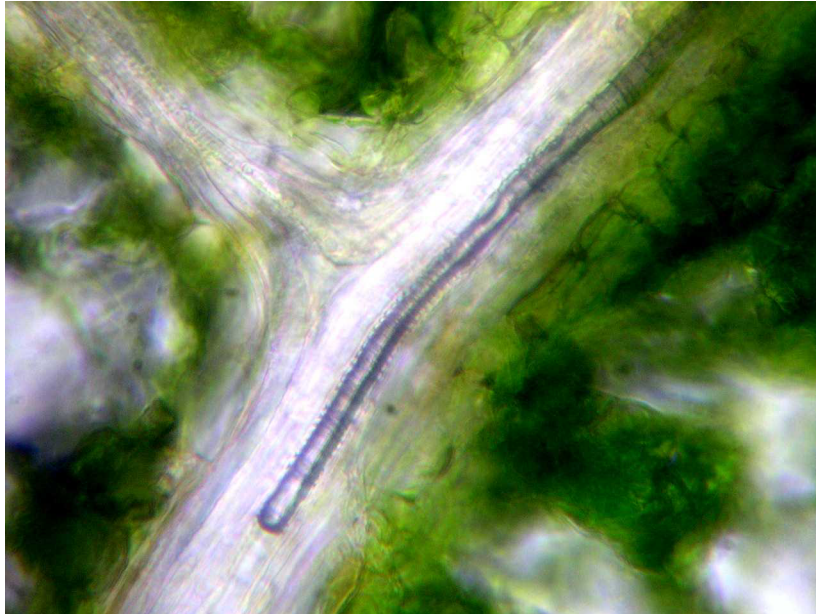
Figure 1: Presence of an air bubble in a vein of a walnut leaf. The bubble creates a gas embolism which blocks the circulation of the sap.

4- Circulation accident

As with a suction pump, the entry of air into the hydraulic circuit is the Achilles heel of the water circulation mechanism in the plant because it breaks the hydraulic continuity essential for the ascent of the sap (figure 1). Dixon himself had clearly identified this limitation to his theory. However, it was not until the 1960s, with the development of techniques to measure the functionality of the sapwood, that this risk of dysfunction could be quantified. We now know that this risk is real, that it is not linked to a cavitation phenomenon in the precise sense of the physicists, but to a capillary rupture of a meniscus located on the vessel wall. This meniscus is most probably located at the level of the pits, these holes in the wall which allow the passage of the sap from one vessel to another. The stability of this meniscus follows Young-Laplace's law, so there is a threshold sap tension beyond which an air bubble is sucked through a pore of these pits. This critical pressure is all the higher that the porosity of the pit is low. Once sucked in, the air bubble spreads until it occupies the entire lumen of the vessel. This creates a gas embolism, a thrombosis that irreversibly blocks the flow of sap in this vessel. How can plants limit this risk of embolism?

5- To starve or die of thirst

As we have just seen, the risk of embolism is linked to the fine anatomy of the vessels on the one hand and to the state of tension of the sap in these vessels on the other. Therefore, there are two possibilities for plants to limit the risk of embolism. The first is to modify the anatomy of the vessel walls. For a long time, it was thought that this possibility was excluded because the vessels are dead cells, without cytoplasm. But recent work (Sorek et al 2021) shows that some plants appear to be able to adjust the embolism resistance of a vessel over the course of a season. The second option available to plants to reduce the risk of embolism is to control sap tension by reducing transpiration. Over the course of a day, there is a fairly linear relationship between leaf transpiration and sap tension, reflecting the existence of a constant hydraulic resistance on this time scale. Therefore, if the stomata close, transpiration decreases

and sap tension is also reduced, which can keep it below the critical embolism threshold. However, if the stomata close to limit the outflow of water vapor, CO_2 no longer penetrates the leaf, which may eventually affect its carbon status. In periods of water stress, plants are faced with a dilemma: to starve or to die of thirst. Recent work, synthesized by Adams et al (2017), suggests that the risk of hydraulic failure outweighs the risk of carbon starvation, even though this carbon problem may exacerbate the risk of mortality. There is a critical threshold of embolism rate beyond which the damage inflicted on the plant's hydraulic circuit is irreversible, inevitably leading to its death. This threshold seems to be quite variable according to the species and located between 50 and 95% of embolism. Clearly, in periods of intense hydric stress, the plants die of thirst by lack of water supply linked to a hydraulic rupture of the system of circulation of the ascending sap.

6- On the razor's edge
What is the risk of hydraulic rupture for a plant? This risk depends mainly on two parameters: 1) the intrinsic vulnerability of vessels to embolism, and 2) the degree of exposure to drought. Let us first look at the vulnerability to embolism of species. Thanks to the introduction of innovative phenotyping methods, the spectrum of embolism resistance of species is well known and remarkably broad. The most vulnerable species are completely embolized at voltages of 1MPa while the most resistant are able to withstand tensions of 18MPa. This variability is not randomly distributed, with species in arid environments being much more resistant to embolization than those in humid environments. In an arid environment, having a vascular system highly resistant to embolism seems to be an adaptive character. In a humid environment it seems on the contrary maladaptive, because all species in this environment are vulnerable. This illustrates the notion of functional tradeoffs. Dryland species also have very dense woods, and reduced growth capacities. When placed in a moist environment they are less competitive than more vulnerable species that grow faster and acquire resources more quickly. Are species that are highly resistant to embolism in dry environments less exposed to the risk of embolism? This brings us to the second aspect, that of exposure to risk. In a dry environment, the tensions exerted on the sap columns of the vessels are naturally much greater than in a humid environment. Therefore, one cannot assess the risk of embolism only by considering the intrinsic vulnerability of the vessels, one must calculate the hydraulic safety margin, the difference between the embolism threshold sap tension and the sap tension experienced by the plant in its environment. Choat et al (2012) calculated these hydraulic safety margins for a large number of species from very different environments. They made the remarkable finding that these safety margins are relatively small (on the order of 2MPa on average) and mostly constant between environments. It is not much higher in a Mediterranean forest than in a tropical rainforest. This convergence of functioning also suggests the existence of the physiological compromise mentioned above with an optimum degree of resistance to embolism for each ecological niche, or even each type of ecosystem. In their natural environment, plants thus seem to live on the razor's edge of the risk of hydraulic rupture. The direct consequence of this functional convergence is that the risk of embolism increases in all environments as soon as it becomes abnormally dry. With global warming, we can therefore expect to see dieback affecting all forest ecosystems on the planet. Ongoing inventories already seem to confirm this trend (Allen et al 2010).
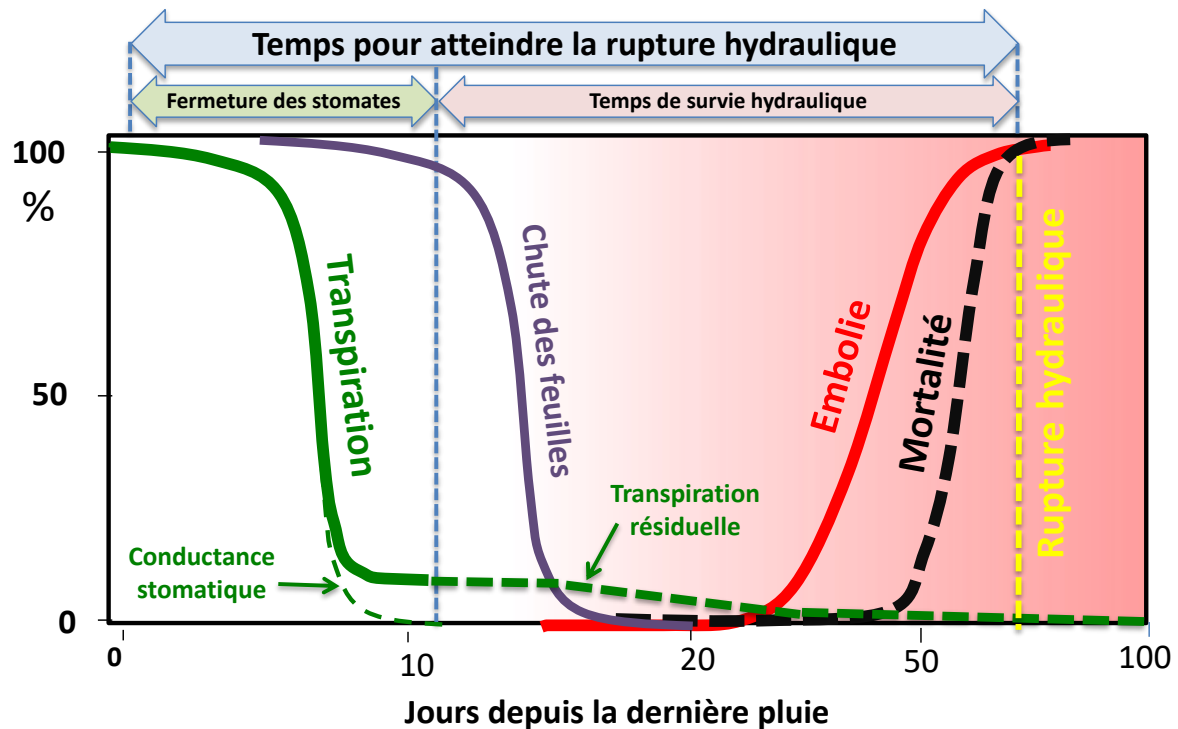
Figure 2: Conceptual diagram of the temporal dynamics of key physiological processes that will lead to plant mortality by hydraulic failure upon exposure to extreme drought.

7- Taking risks

The knowledge acquired on the circulation of water in plants now allows us to propose a conceptual model that offers the possibility of understanding their response and resistance to a drought. This model can be represented in the form of a graph showing the temporal evolution during a drought of some key physiological variables of the plant functioning (figure 2). When soil water is still fully available, stomata are wide open, transpiration is high, sap tension is low and photosynthesis and growth are optimal. This is the water comfort zone of plants sought in agriculture for example. When the soil water content is depleted (typically below 40% of its useful reserve), the hydraulic properties of the soil are affected, stomata close, which reduces transpiration and keeps sap tension below the embolism threshold. Photosynthesis and growth are also reduced, but the plant can quickly return to optimum functioning at this stage once the water stress is lifted. If the drought persists, the stomata close completely but the plant continues to dehydrate at a much slower rate as water evaporates from the soil directly and mainly due to residual water losses through the leaf cuticles. A lot of attention is currently paid to these cuticular losses because they will determine what happens next. It has been shown, for example, that these losses are very sensitive to temperature, with threshold effects that could explain the deleterious impact of heat waves on tree mortality. A number of species lose their leaves during a drought episode. This mechanism further reduces the residual transpiration of the plant, which is then limited to water losses through the bark of the branches and trunk. But this strategy has a high metabolic cost for the plant, probably already marking the entry into a survival zone. If the drought persists, the embolism will eventually form and when it reaches a critical threshold, a point of no return is reached, resulting in the death of part of the crown or the entire tree.

It is therefore clear that the time between the arrival of the last rainfall and the death of the tree due to hydraulic failure will depend on a large number of parameters, including the characteristics of the conductive tissue, the stomatal function, the properties of the cuticles and, of course, the local pedoclimatic conditions. Taking all these parameters into consideration is a challenge. One way to meet this challenge is to integrate them into a numerical model of the plant's hydric and hydraulic functioning.

8- The worst is yet to come

The hydric and hydraulic functioning of a plant is based on thermodynamic principles that have been known for a long time. It is therefore quite easy to put these principles into equations and integrate them into a mechanistic structure-function model of the plant. Many such models exist, but none of them described in detail the key processes that lead to hydraulic breakdown beyond the point of stomatal closure. We have developed such a model recently (SurEau model, Cochard et al 2021). The model is based on a simplified architecture of the plant and describes all the physical and physiological processes that will allow us to predict the risk of hydraulic breakage according to the local pedoclimatic conditions. The model has, for example, allowed for a better understanding of the necessary coordination between the stomatal and hydraulic functioning of plants (Martin StPaul et al 2017). A sensitivity analysis of this type of model also allows us to identify the key parameters, those that will have a major impact on the risk of hydraulic failure and therefore those on which we should focus our measurements and analyses.

The model is also useful for predicting the risk of hydraulic failure induced by climate change. This is a major issue that will determine the stability of plant ecosystems and their ability to sequester part of our CO_2 emissions. We have carried out such a modeling exercise on a lowland oak forest (Cochard et al 2021). For the historical part (1950-2020), the model predicts low embolism rates (<10%) in average years, but a higher rate in particularly hot and dry years (1976, 2003, 2018-2020), years also marked by significant dieback. This confirms that embolism is a rare physiological event that occurs only under extreme climatic conditions and can be associated with dieback. The projections for the period 2020-2100 obviously depend on the climate scenarios that we will experience (Figure 3).

Under the assumption of the most pessimistic scenario (RCP8.5), exceptional climatic conditions such as those of 2003 or 2018 will become daily at the end of the century and the annual risk of hydraulic failure will reach 30%. In other words, 1 year out of 3 the trees will be exposed to a lethal risk. This is obviously incompatible with the maintenance of oak forestry in the plains of France in 2100. Only the scenario that respects the agreements of the COP21 in Paris (RCP2.6) seems to allow the maintenance of the survival of oak in the plains by 2100. These simulations do not take into account the genetic variability of the species, nor their capacity to acclimatize to climate change. The model allows us to explore these aspects in a rather theoretical way, as experimental data on these variabilities are still very partial. The simulations suggest that, under RCP8.5, the degree of variation in the various physiological traits required to maintain optimal functioning of the oak in the plains is much greater than the variability currently existing within the populations. Furthermore, the number of generations between now and the end of the century is probably too low to allow genetic adaptation of this species to climate change. It is therefore to be feared that if the worst-case climate scenario occurs, oak forests will disappear from the French plains by the end of the century.
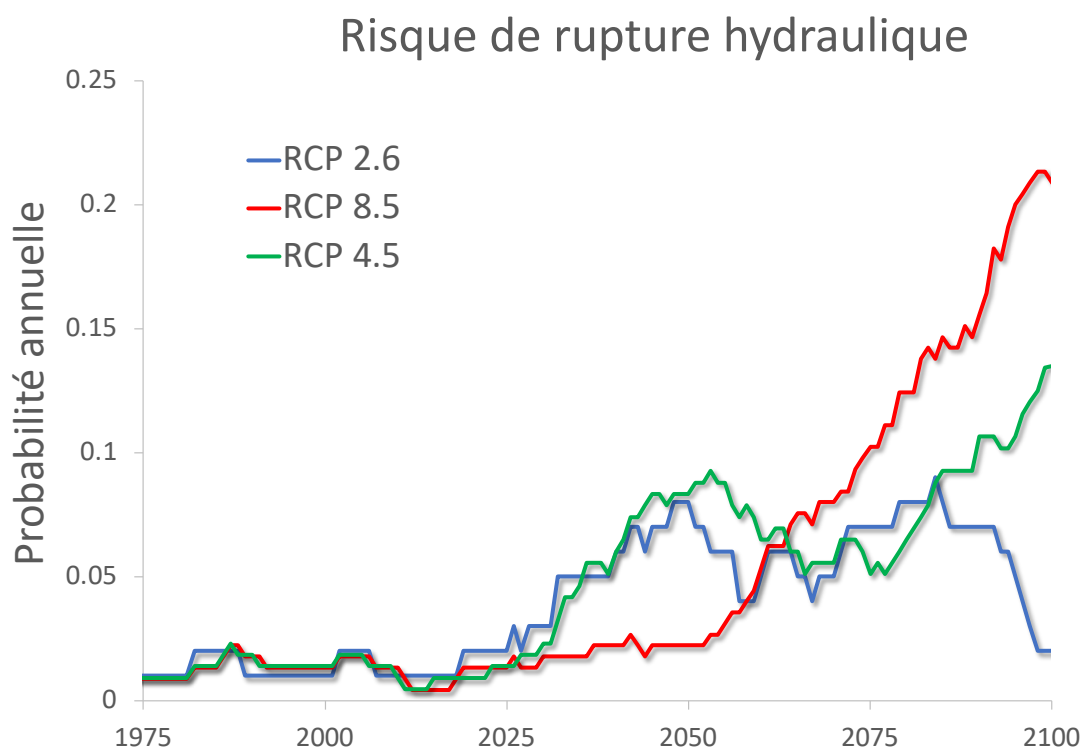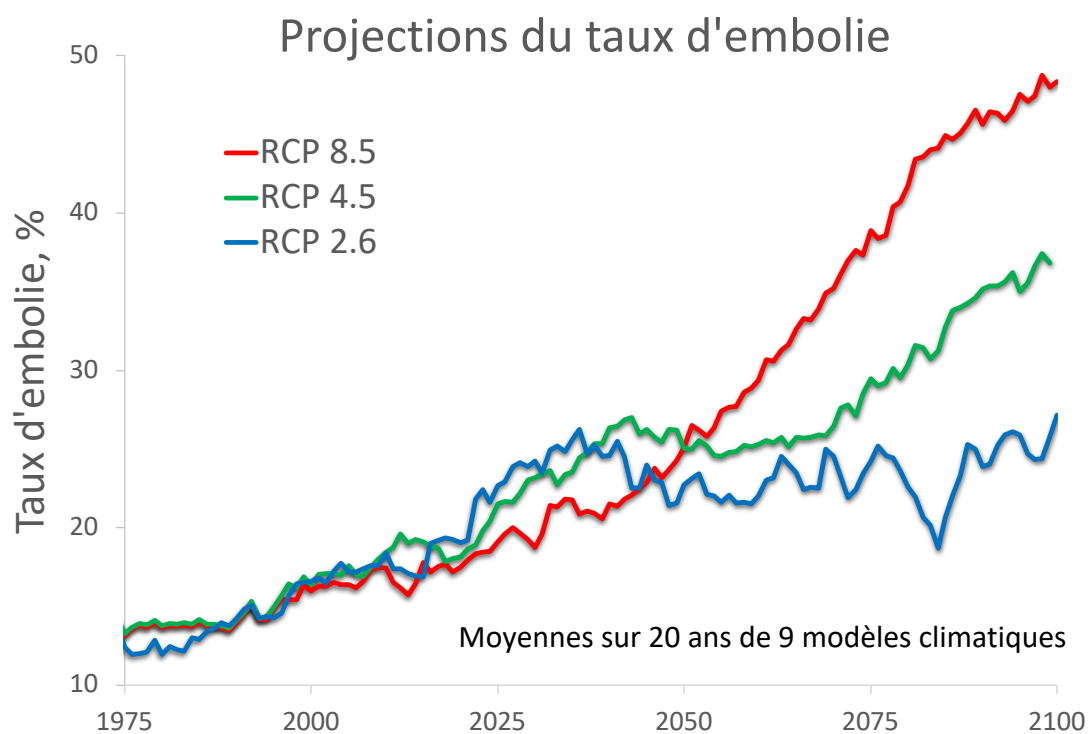
Figure 3: Example of the use of the mechanistic model SurEau to predict the rate of embolism (top) and the annual risk of hydraulic failure (bottom) for a lowland oak forest according to three climate scenarios.

9- Conclusion

The circulation of water in the plant first questioned physicists and physiologists, which allowed them to understand the mechanism and to identify its weak point, the risk of hydraulic rupture. These relatively fundamental scientific advances now provide keys to propose robust, mechanistic models of plant functioning and to predict and anticipate the effects of global warming on the stability of ecosystems, particularly forests. Efforts remain to be made to improve our knowledge of the hydric and hydraulic functioning of plants, to refine our predictions and provide solutions to adapt our crops and forests to the climatic challenges they will face in the future.

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