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Scaling-up to understand tree–pathogen interactions: A steep, tough climb or a walk in the park?

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Abstract

Plants have proficient tools that allow them to survive interactions with pathogens. Upon attack, they respond with specific countermeasures, which are controlled by the immune system. However, defences can fail and this failure exposes plants to fast-spreading devastation. Trees face similar challenges to other plants and their immune system allows them to mount defences against pathogens. However, their slow growth, longevity, woodiness, and size can make trees a challenging system to study. Here, we review scientific successes in plant systems, highlight the key challenges and describe the enormous opportunities for pathology research in trees. We discuss the benefits that scaling-up our understanding on tree–pathogen interactions can provide in the fight against plant pathogenic threats.

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Keywords

Trees, Model plants, Crops, Plant pathogens.

Trees: Their importance and threats

Trees are among the most valued plants on earth: they provide food and tools, produce oxygen and are major carbon sinks, host and support other organisms, block noise and reduce air pollution, mitigate flooding, provide insights from the past and serve as recreational environments. Therefore, trees are important to food

security, timber trade, climate change mitigation, biodiversity, ecology, landscape interventions, culture and wellbeing [1]. The dramatic rise in observations of tree disease and pest outbreaks [2], both endemic and invasive, have highlighted the importance of pathology research and the need to upskill scientists and develop new approaches to studying tree disease [3]. This needs to address past and current outbreaks (e.g. Dutch elm disease (DED), ash dieback disease (ADD) and acute oak decline (AOD)) as well as future threats (e.g. *Xylella fastidiosa*) that are devastating our keystone broadleaf species. Importantly however, the impact of these pathogens in tree health has also been associated with unfavourable environmental conditions [4], which are mostly linked to climate change. Therefore, future unstable climate conditions have the potential to bring new diseases and to increase severity of current diseases, thus increasing the threat to treescapes and their associated value. Working with trees may benefit from advances in other areas of plant science - the question is, will advancing our knowledge of tree disease be a straightforward walk or is it going to be a tough hike?

A walk in the park: Successes in plant–pathogen interaction studies

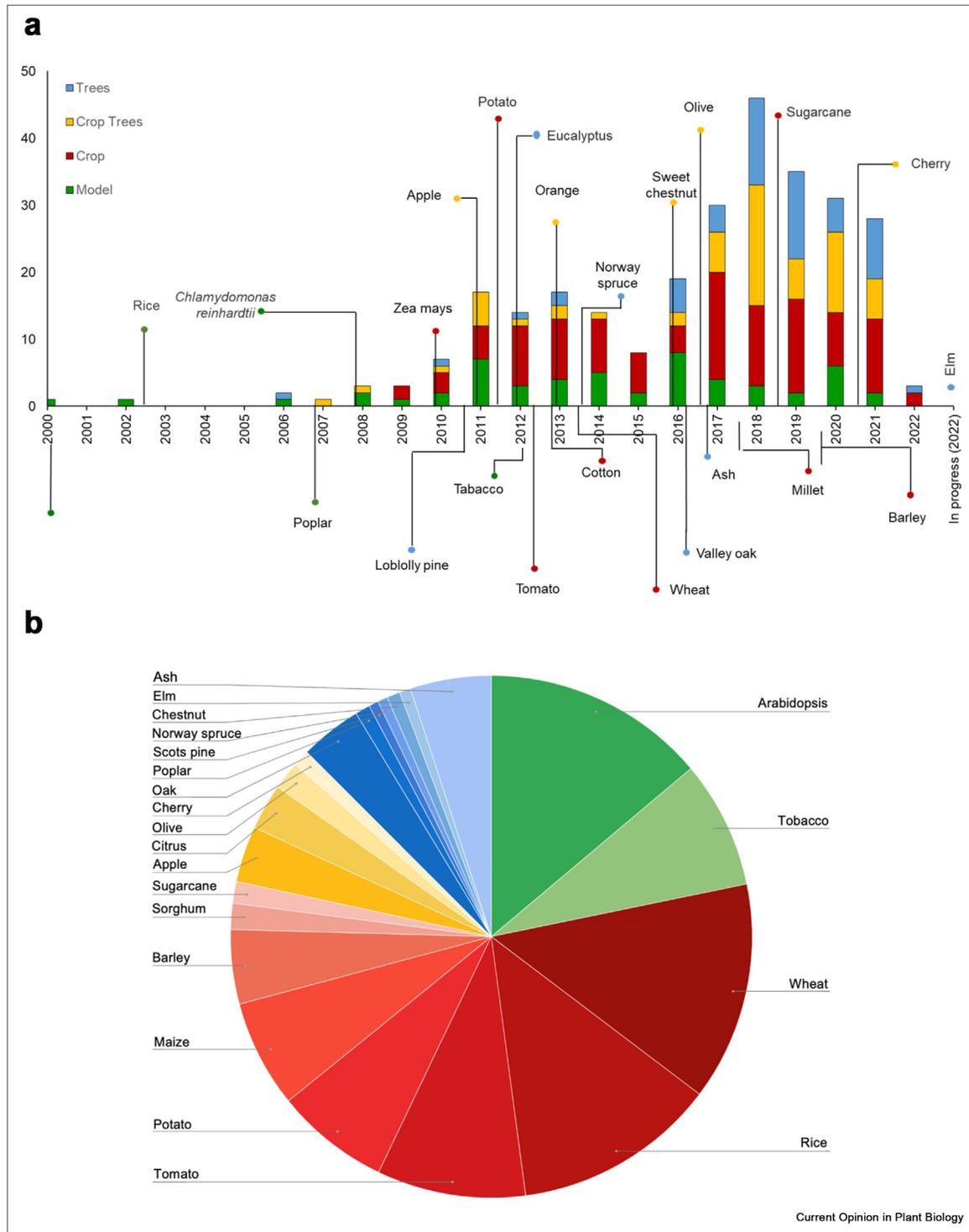
Carrying out research in plant–microbe interactions has been driven by the development of model systems that enabled the creation of a suite of tools for study. This has been a challenging process but is now a mature field and provides the opportunity to transfer and innovate in new plant systems, including trees (Table 1). For example, genome sequence availability has provided prodigious tools for the detailed understanding of plant–pathogen interactions at the genetic and genomic level. Whereas the last few decades have been focussed on the sequencing of model and crop plants, genome sequence availability in tree species has improved in the last few years (Figure 1a). Specific gene families that play important roles in disease resistance through recognition of pathogen-derived molecules have been identified in many model and crop systems [5]. These include both large-effect (qualitative) disease resistance (R) genes and smaller effect (quantitative) QTLs. To date over three hundred plant R genes have been cloned [6].

Table 1

Successes in models, crops and trees and the challenges of trees.

Success	Models/crops	Trees	Challenges for tree studies
Tools and cloning R genes	Tools in Arabidopsis Tomato Pto Tomato Cf9 Wheat LR64, LR34 Wheat Sr50 Wheat STB6 Tools in rice Maize Hm1	Tools in poplar Tools in apple Tools in citrus	Long-lived, slow growth, complex woody tissues and root systems
Breeding	Wheat wild relative introgression Tobacco, oil seed rape male sterile lines Maize heterosis and haploid induction	Poplar wild relative introgression Poplar male sterile lines	Limited genetic quantitative traits, genome sequence data and longevity
Genomes, QTL mapping/ genomic prediction	Wheat spot blotch resistance Chickpea ascochyta blight Maize rough dwarf disease Rice blast, sheath blight and bacterial leaf blight Tomato bacterial canker	Apricot bacterial canker Ash dieback Norway spruce to stem and root rot disease Eucalyptus to foliar fungal pathogens	Genome sequence availability and longevity
Other omics	Tomato metabolomics for ABA signaling Microbiome of wheat and tomato affecting disease Transcriptomics in wheat and tomato Proteomics in wheat, tomato, and grapes for post-harvest diseases	White pine blister rust in sugar pine Poplar metabolomics for ABA signaling Microbiome of poplar, horse chestnut and oak affecting disease Transcriptome of oak in response to powdery mildew Proteomics in Pinus–Fusarium interaction	Metabolite and gene dataset availability, large genomes, extractions from different tissue types
Genetic transformation	Maize protoplast/inmature embryo Arabidopsis and tobacco Ti plasmid Rice TALENS Wheat and grapevine CRISPR Onion and wheat gold-particle bombardment	Pine protoplast/inmature Embryo Poplar, wild cherry, walnut Ti Plasmid Poplar CRISPR Norway spruce and scot pine gold-particle bombardment	Tissue biochemistry and structure, longevity, late reproduction
Gene reporter assays	Arabidopsis, Soy/Medicargo GUS reporter Arabidopsis and tobacco luminescence Arabidopsis, tobacco, tomato, potato virus-induced gene silencing (VIGS)	Apple and poplar GUS reporter Poplar luminescence Apple, pear, and walnut virus-induced gene silencing (VIGS)	Unstable expression of transgenes, long life cycles, absence of sexual propagation in field and commercial deployment
Plant–microbe interactions	Use of suppressive soils for take-all disease of wheat and barley Use of biocontrol for powdery mildew on wheat and barley and Fusarium crown rot of wheat	Use of suppressive soils for Panama disease of banana Use of biocontrol for powdery mildew of apple	Diverse, complex, and seasonal microbial communities associated to trees

Figure 1



a) Timeline showing dates of approximate number of species with available sequenced genomes according to web search performed using 3 principal resources [43–45]. **b)** Total number of plant–microbe interaction publications by plant species. Data collected from Web of Science search “((((ALL = (plant–microbe interactions)) or ALL = (pathogens)) or ALL = (immunity)) or ALL = (resistance)) or ALL = (defence)) and ALL = (*species name*)”. Pie chart slices represent number of search results on Web of science database on 8/3/2022. Green slices represent model plants, red: crops, yellow: crop trees and blue: trees.

This gigantic effort spanning more than 25 years now provides enough insight to begin to understand their mechanistic function. Moreover, this knowledge now enables us to entertain the idea of designing novel R genes, that can be trialled as new resistance tools [7,8].

Spanning from this, a powerful tool to study plant–pathogen interactions is the use of genetically modified lines [9]. Gain of function, over-expressor and knock-out lines are examples of the molecular techniques that have successfully been implemented over decades (Table 1). This is possible thanks to the availability of genomes from model organisms and successful experimental protocols (Figure 1a). For instance, in *Arabidopsis*, agrobacterium floral-dip transformation results in an effective and high-throughput method that allows for transformants to be obtained within weeks from flower buds [10].

Beyond the identification, transformation and characterisation of R genes, modern advancement of -omics tools such as transcriptomics, proteomics and metabolomics has facilitated major progress in our knowledge of the molecular basis of plant–microbe interactions. They have provided insights into genes, proteins, metabolites and enriched pathways for the understanding of resistant and susceptible responses, as well as revealing pathogen infection mechanisms and lifestyle (Table 1) [11]. Crucially, all these techniques rely strongly on available databases (genomes, proteins and metabolites), which are limited in non-model systems, therefore compromising robust marker identifications in other plant species [12].

All these powerful techniques used to unravel major discoveries are based on model organisms such as *Arabidopsis* or tobacco, herbaceous plants with quick generation spans, small genomes and high adaptability to hostile conditions (Table 1). So far, the number of scientific articles focused on the molecular aspects of forest trees is quite limited, and only represent about 12.5% of all articles published in plant–microbe interactions (Figure 1b). This is simply due to the challenges that these higher plants bring and ultimately the limited funding that this type of high-risk, long-term research obtains.

A steep, tough climb: The challenges of working with trees

Trees have many characteristics that distinguish them from most model herbaceous plants and bring challenges to progress in plant–pathogen interaction studies (Table 1). However, in our opinion, two bring the biggest challenges for the study of tree–pathogen interactions: their size/slow growth and their woody tissue. Tree size and complexity prohibits experimental work in controlled growth conditions. To

overcome this challenge, many studies use tree seedlings [13], but this can have complications. For example, for some tree species such as ash, sweet chestnut and hawthorn, germination can take weeks, months or even years. Conversely, some tree species such as oak germinate quickly but their recalcitrant seed nature means that long-term storage is very difficult. Thus, experiments using seedlings require extensive planning. In addition, some trees of different ages can exhibit variations in susceptibility/resistance/tolerance [14]. This can be due to differences in pathogen strategies and/or increased susceptibility of seedlings driven by age-related resistance [15], which has been reported in many tree species, including pines [16] and apple trees [17]. Importantly however, there are some tree diseases, like AOD, that mostly affect mature trees [18]. Current efforts by our research groups and others focus on developing a system to study AOD in seedlings, however optimisation is still taking place, which leaves the field of research relying on bacterial growth in artificial systems such as logs [19]. Therefore, seedlings may be inappropriate in different settings when trying to reproduce disease symptoms and researchers should ensure that reliable and accurate information is collected [20]. Another strategy to work with mature trees relies on investigating disease changes on specific branches, through detachment or by branch isolation within the tree. These strategies can be useful, but also entails problems when translating results from a part of the tree to the entire organism. This is because tree ageing can also lead to intra-tree genetic variation arising through mitotic divisions in the stem cells of apical meristems, something that occurs often, as described by Plomion et al. (2018) in oak trees [21]. Therefore, this study clearly raises a question about the reliability of using different parts of the tree for experimental work on the characterisation of susceptibility and resistance genotypes.

There are difficulties while studying host–pathogen interactions in woody tissue. This is partly because the infection route in many cases remains unknown. For some diseases, insect vectors are behind woody tissue infection by *Ophiostoma novo-ulmi* (Dutch elm disease) [22] and *X. fastidiosa* in olive, citrus and grapevine [23]. However, in other pathosystems such as AOD, the role of a bark-feeding beetle in infection remains unclear [18]. To achieve infections in woody systems scientists develop bioassays that bypasses the natural infection route (e.g. the use of logs, detached shoots and saplings) [19,24]. However, these shortcuts have also posed problems for introducing pathogens into the woody tissue and reproducibility with natural conditions [15]. These problematic assays have strongly hampered the prompt and timely study of tree diseases that affect woody tissue.

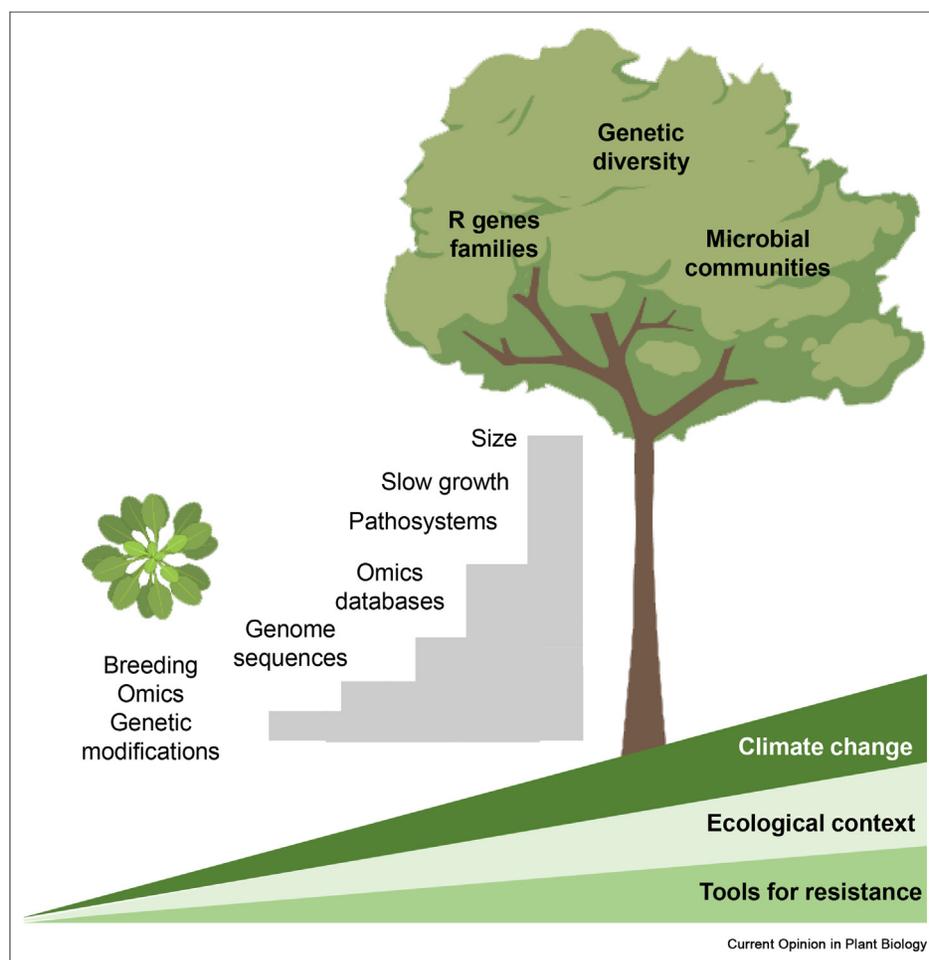
Are these challenges too difficult to overcome? Maybe, the truth is that there is not much we can do about the size of a 200-year-old oak tree or about other characteristics such as the gigantic genome size of some species (e.g. conifers) that hinder genome sequencing (Figure 1a). Similar thoughts went through the minds of wheat scientists years ago when they faced the need to perform genomic studies in a polyploid species with a genome size of 17 GB [25]. In the same way that wheat scientists did, our guess is that the appropriate question to ask ourselves would be, is it worth it?

Testing out new boots: The opportunities of tree systems

Some of the key successes in the plant–pathogen interaction field are often not able to be translated into trees due to the challenges that they bring (Table 1, Figure 2). This results in a dearth of knowledge and a

major fundamental knowledge gap for most tree species. Despite the difficulties, advances in omics have given us a rapid understanding of genetic diversity of gene contents and enabled us to identify homologous signaling pathways from other model plants (Table 1) [26,27]. For instance, receptor-like protein (RLP), receptor-like kinase (RLK) and nucleotide-binding leucine-rich repeat (NLR) R gene families are vastly expanded in trees compared to those in short-lived herbaceous species. In the recently sequenced *Quercus robur* (oak) genome, a comparison of just under 600 gene families in oak relative to 15 other dicot species found RLKs, RLPs, and NLRs to be amongst the most expanded and diversified of all gene families [21], suggesting that oak trees have a higher number of tools to defend themselves against diseases. It has been speculated that a large repertoire of highly diversified defence-related genes may be a genomic signature of long-lived trees, providing

Figure 2



Representation of the model system successes and the challenges and opportunities in forest trees. Schematic of the relevance that scaling-up to understand tree–pathogen interactions can have for key outputs: identification and exploitation of tools to fight pathogens, inclusion of the ecological context to be able to look beyond individual plants and in the fight against climate change. Created with BioRender.com.

resistance against the plethora of pathogens encountered over their centuries-long lifetimes [28]. Increasing our understanding of the role of those R genes could provide a source of tools to use in other plant species and for existing and emerging plant pathogens.

Unlike crops, most trees have not undergone a century of targeted breeding efforts. As such, forest trees have not gone through the genetic bottleneck associated with breeding programs, thus retaining higher levels of genetic diversity at the population level [29]. This wealth of diversity presents a tremendous opportunity from a breeders perspective, especially where the R genes underlying such resistance are known [15,30–32]. Fortunately, the rapid generation of high-quality genomes and other -omics datasets, makes the cloning and characterization of R genes in trees now feasible. For example, fully annotated reference genomes are now available for key tree species such as oak, poplar, pine, and eucalyptus (Figure 1a), enabling genotyping-by-sequencing (GBS) approaches for more effective QTL mapping and association analysis. This allows both qualitative and quantitative resistance traits to be more easily identified. GBS has already been used to great effect in Poplar to identify three RLK type R-genes likely important for defence against the fungal pathogen *Sphaerulia musiva* [33]. The population level diversity of forest trees may even stretch to so-called exapted resistance, rare resistance in a native host population to an invasive pathogen to which the host is otherwise evolutionarily naïve [34]. Identifying and selectively breeding for genes underlying exapted resistance may be vital in protecting keystone forest species from invasive diseases.

Importantly, a specific defence mechanism of woody plants is the production of secondary metabolites that accumulate in the xylem to serve as physical barriers against pathogens, which has been described as a highly potent defence mechanism [35]. Compartmentalization of Damage/Dysfunction in Trees (CODIT) models have highlighted the benefits of understanding this defence system [36] as it brings studies into defence mechanisms to a plant holistic level linking the roles of carbohydrates and the hydraulic system.

Going to big sky country: Scaling-up our understanding

Trees clearly offer new opportunities to increase our understanding of plant–pathogen interactions, but there is yet another level to exploit: the ecological context. Because trees are long-lived organisms, over their lifetime they can assemble a community of organisms to help them succeed. Microbial communities have a profound effect on plant and tree diversity functional relationships [37], which has been linked to four key ecological processes: selection (i.e. change in

species composition), drift (i.e. change in population size), dispersal (i.e. change in location) and speciation (i.e. creation of new species) [38,39]. We still lack a clear understanding of how disturbance of these communities can lead to the development of disease. However, there are many clear examples that demonstrate microbes (e.g. mycorrhizal fungi) are essential for the health and well-being of long-lived trees [40]. This has also been clearly demonstrated for environmental stress by Allsup and Lankau (2019) who showed that the migration of drought-adapted microbial species can promote drought tolerance [41]. Therefore, by studying these communities in trees we can use ecology to scale-up our understanding of tree–microbe interactions.

Crucially, as our climate continues to change rapidly, it has been already demonstrated that both the trees and the microorganisms associated with them are already being impacted [42]. Studying the trees in isolation with their pathogens may only provide limited insights into what makes a tree vulnerable to a particular disease and will not address the impact of climate change. By scaling-up our studies, taking into account the wider ecology of a forest (e.g. species diversity, climate) and combining this with molecular plant pathology, we anticipate making advances not only in the genes that underpin tree immunity but also our understanding of what constitutes a “healthy” forest community in a changing environment.

Conclusion

Considering the information described here, we strongly believe that, even when the challenges of working with trees are big, the opportunities to advance our knowledge on not just the trees but also their communities are bigger. For instance, exploiting the knowledge developed through omics approaches in trees (Table 1) into enhancing mechanistic understanding would provide concrete strategies in the fight against tree pathogens. Given the importance of these communities in supporting our health, climate and wellbeing, we consider this path, even when challenging, very much worth the effort.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this article.

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They sequenced, assembled and annotated the oak (*Quercus robur*) genome and discovered different characteristics that mediate tree longevity. The authors demonstrate the accumulation and transmission of somatic mutations and unravel the expansion of R gene families that could explain tree adaptation to different stresses.

This paper uses powerful genomic tools to identify genes that mediate resistance to the fungal pathogen *Sphaerulina musiva* in poplar trees. These findings could accelerate identification in other tree species to develop breeding programs.

This article studies potential genetic resistance to two exotic pathogens in oak (*Quercus robur*) and demonstrates that oak has Quantitative Trait Loci (QTLs) associated with the resistance of one of them

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This article demonstrate the importance between microbiota, soil characteristics and trees. They observed that when soil microbes that are introduced are drought adapted, they can provide tree tolerance to dry conditions.