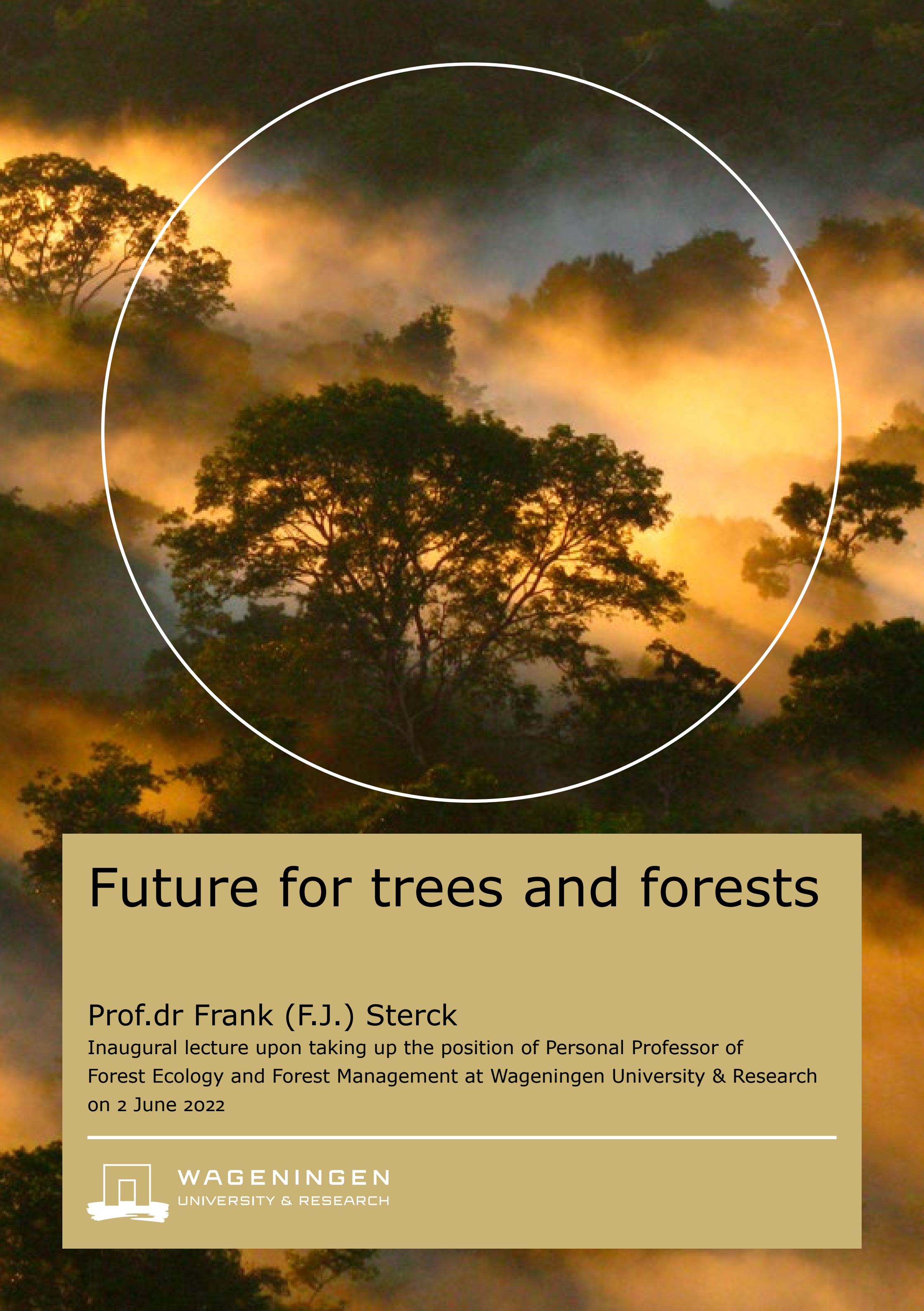

# Future for trees and forests

## Prof.dr Frank (F.J.) Sterck

Inaugural lecture upon taking up the position of Personal Professor of
Forest Ecology and Forest Management at Wageningen University & Research
on 2 June 2022

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# Future for trees and forests

Welcome colleagues, family and friends. I chose the title - “future for trees and forests” - for two reasons. First, as a nature lover, I consider a future with rich and healthy forests a more beautiful and inspiring world. And second, as a scientist, I want to understand the functioning of trees and forests and I want to contribute to a forest-rich world. But before talking about the future, let’s first consider the past.

Where did my fascination for trees and forests start? The seed for this fascination was planted through my love for nature, triggered by my parents taking me and my two sisters regularly to forests and showing us plants and animals. At the age of 18, I felt that I had no other choice but to study Biology. I chose Wageningen University, because it gave the promise of doing exciting field work in the tropics. In 1989, I participated in the canopy raft expedition for studying the tropical forest canopy in French Guyana (Bongers and Sterck 1991). This inspired me to write a NWO proposal for doing a PhD study on the development of trees from seedling to canopy tree in tropical forest.

In the early nineties, I thus started my PhD and climbed trees to study their (crown) development in a tropical rainforest in French Guyana. The forest canopy was considered a so-called new frontier in ecological forest research. Full with life, but difficult to reach, certainly in tropical forests! After a series of postdoc positions, I started as an assistant professor in Wageningen in 2004. I expanded my research on tree crowns with studies on tree stems and roots. I had the ideal study object, another big and new frontier, with many things to be discovered. Recently, I also started a large forest experiment, which serves as a base for my future research on climate smart forests. I will address the research related to this experiment in the second half of my lecture.

I will now briefly introduce the research questions that I will address. In the first half of this lecture, I will illustrate some past studies focussed on growth and mortality patterns of trees, and understanding those phenomena from underlying mechanisms. I will briefly illustrate this work by showing results addressing 2 questions: 1) why do trees grow “like trees”?, and 2) why do trees die? In the second half of this lecture, I will show how to upscale such knowledge on trees to the functioning of forests, with major emphasis on the role of drought and heatwaves for forests. I will present how our research can contribute to so-called climate-smart forest management, aiming at healthy, productive, resilient, and rich forests in the future.

## Tree growth patterns and underlying mechanisms

The question - why do trees grow "like trees" - may be a bit naive: it sounds circular and is not clearly defined, but for me it was - and is - inspiring. It is the type of question I discussed with my forest colleagues during my PhD study in the rainforest of French Guyana between 1992-1995. Let me introduce this question with the image of a 2-millennia old tree in Patagonia (Figure 1a). This tree shows hardly any sign of senescence. Compared to humans, this tree seems to be  immortal and, like other trees, it looks like a calm, large, well-organized, rigid, immobile 3D-structure. However, such trees are full with physiological action, and we can measure that! Moreover, rather than being rigid, trees are extremely flexible in the way they organise their 3D-structure over decades or centuries of

*Figure 1. a) During a trip in Patagonia I encountered this approximately 2000 year old tree, belonging to the species Fitzroya cupressoides. b) During my PhD, I used alpinist techniques – and sometimes stairs – to study the crown development in large trees in a tropical rainforest in French Guyana (1992-1995).*

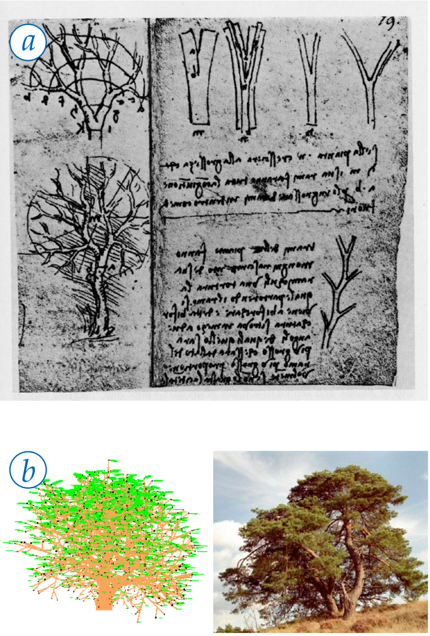
life. For example, in an open field trees often develop thick stems that carry large hemispherical crowns, whereas in forests trees develop more slender stems and crowns that move up by dropping lower branches and leaves (compare the Scots pine trees in Figure 2b). How do trees develop into such big structures, and in the diverse structures adapted to different environments? Trees have no brain centre for dividing tasks over their big body. With my studies, I want to know how trees manage their 3D development, and how this development and the underlying physiological processes contribute to their success (growth, survival and reproduction) or failure (early death).

During my PhD on the development of forest giants in the tropical rainforest of French Guyana, I measured growth responses of shoots, branches and the entire crown and stem for small and large trees (Figure 1b), focussing on the effects of different light conditions. The motto in those days was “meten is weten”, “measuring is knowing”. We thus learned a lot about responses of different organs: from leaves, shoots, branches, and stems. We however lacked an integrative picture of the responses of different organs, and therefore could not explain the 3D tree development over tree life. To obtain that integrative picture, we turned our view from “meten is weten” to “we need a model”.

David and Mona Lisa are examples of famous models, one created by Michelangelo and the other by Leonardo da Vinci around 1500. Pieces of art and models that fascinate, also because they vibrate some essence of humans. But what would be the essence of trees? A first answer was provided by the same Leonardo da Vinci: he developed a model on the structure and functioning of trees (Figure 2a). In the accompanying text, he explains that the branch cross-sections in the crown sum to the same cross-section area at any position in the crown and the stem. He argues that this structure fits the transport of the same amount of water from the stem towards the smallest branches. In other words, with his model he linked the structure of a tree to its functioning.

Inspired by this and other classic model studies, I started working on tree models during a 2-year postdoc at Utrecht University in 1999-2001. This meant building new skills on conceptualizing trees as systems, learning mathematics and computer language coding, and setting up new collaborations with theoretical scientists. The expected holy grail and main ambition was a mechanistic plant model, a model based on biophysical principles. What is so exciting about mechanistic plant models? They bare the promise of generic understanding for all trees across the globe.

For our first model, the goal was to understand the combination of mechanisms that control the flexible 3D-structural development of trees in different forest light



Open field

Forest

*Figure 2. Illustrations of models. a) A tree model developed by Leonardo da Vinci. b) Output from our first mathematical tree model, showing effects of light on tree development and structure (Sterck & Schieving 2007). As real examples, images of Scots pine trees growing in an open area and a forest are shown.*

environments. This is relevant because big forest trees grow under conditions from 1 to 100% light during their life, and they may experience disturbances that cause abrupt changes in light conditions during periods of their life. For illustration, I will show snapshots of trees during their life from seedling to adult tree, one growing in a forest light environment and the other in an open field light environment. You may recognise the forms of a real tree – Scots pine in this case – grown in an open environment and in a forest (Figure 2b). One important insight shown by our model is that trees take fully integrated decisions for their growth, and do not act as a sum of competing branches. To achieve this feat, trees effectively share information over their entire body to make growth decisions. And such decisions allow them to be so flexible and fit under very different light conditions.

In a more general sense, the use of mechanistic plant models allowed us to simulate realistic 3D development from underlying mechanisms (Sterck et al. 2005, Sterck and Schieving 2007), allowing for hypothesis testing on those mechanisms for trees worldwide. In addition, we could predict – but so far only for small trees - growth and survival, as well as species distributions within and across forests in different climates (Sterck et al. 2011, Sterck et al. 2014). Yet, we do not yet fully understand such responses for large, structurally more complex, trees and we require better tree models for predicting their responses to climate variation. In addition we are just starting with integrating root and soil responses in such models (Weemstra et al. 2020, Weemstra et al. 2022), and we require upscaling of these tree responses to entire forests. These challenges receive major attention in my current and future research.

## Tree mortality patterns and underlying mechanisms

Let us turn to the second major question: why do trees die? Drought and heatwaves are an important cause of tree mortality (McDowell et al. 2008, Allen et al. 2010). And this mortality risk is increasing due to global warming, and the fact that drought and heatwaves become more severe, and occur more frequently (Dai et al. 2013). Yet, we still do not know the actual cause of, or the mechanism causing, drought-induced tree mortality, making it hard to predict tree mortality (McDowell et al. 2022). I will show results related to this question based on a study in a so-called common garden experiment in Schovenhorst Estate, the Veluwe area in the Netherlands (Song et al. 2021, Song et al. 2022). In this common garden experiment, foresters planted many conifer species originating from different environments across the Northern Hemisphere. They did this to explore the potential of those species for Dutch forestry. For our study, we selected 20 of these conifer tree species. These species included old lineages - including Taxus, Cupressus and Pine species - that evolved for more than 200 million years. We selected trees that were planted before 1970 (study trees were ~50 years or older). We measured functional leaf and stem traits in 2018,  and annual stem growth between 1974 and 2018 from tree rings. We also measured drought-induced mortality risks by scoring the percentage tree death in the populations of these species after the extreme 2018 drought year. Personally, I remember this hot summer well. I tried to write an ambitious research proposal but did not make the deadline. I still blame the >40°C days and my own vulnerability to such heat for this...

The key question we addressed is why trees of some species died following the 2018 drought, while other species did not. We had the perfect experiment for this, because all trees grew under the same conditions. With this study we tested three hypotheses for alternative mechanisms causing such species-specific differences in tree death. The hypotheses we tested are illustrated in Figure 3. The hydraulic safety hypothesis refers to the safety margins that a species achieves. With lower safety margins, the species risks irreversible damage to the water transport system, leading to cell death, crown dieback and ultimately tree death. The leaf legacy hypothesis refers to species differences in leaf lifespan, which varies between half a year to approximately 10 years among our 20 conifer species. We expected that species with shorter leaf life span shed leaves during drought, but rapidly replace them, whereas species with long leaf lifespan may accumulate damage due to drought and heatwaves. Such damage may reduce energy buffers of trees and can cause their mortality. The growth legacy hypothesis refers to species differences in stem

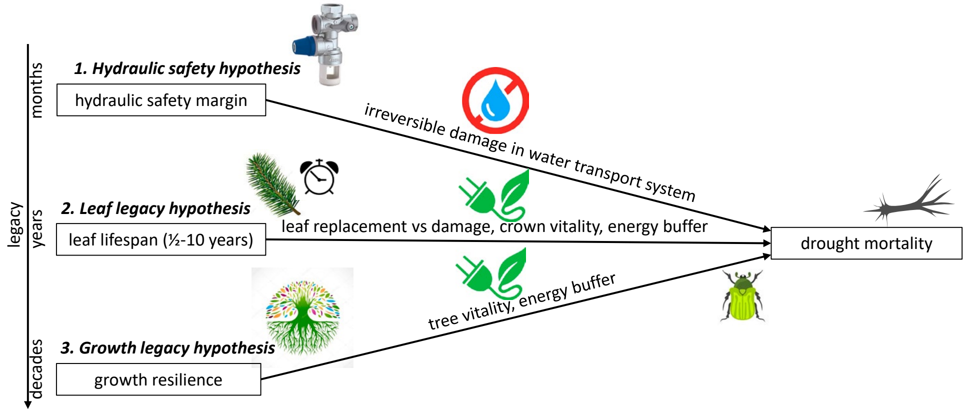


*Figure 3. A visualisation of three alternative mechanisms potentially contributing to drought-induced tree mortality. These mechanisms create legacy effects that operate on different times scales. For explanation, see text.*

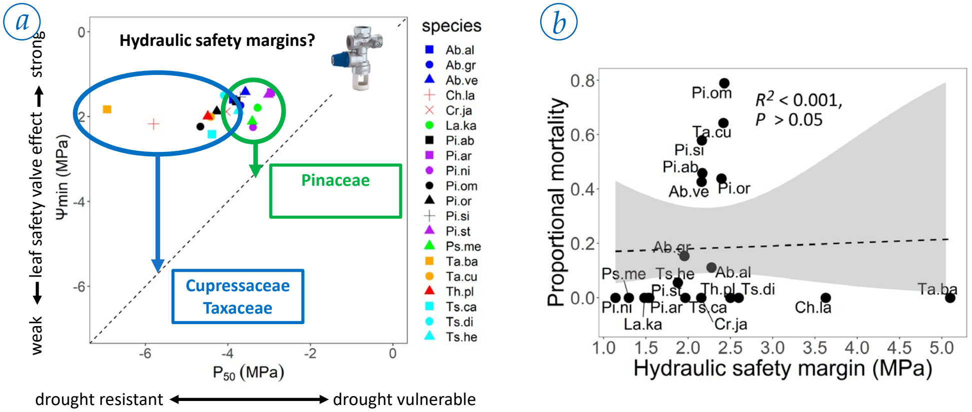


*Figure 4. The hydraulic safety hypothesis. a) The hydraulic safety margins of our 20 study species. b) The result showing that hydraulic safety margins cannot explain species differences in drought-induced mortality. For explanation, see text.*

growth resilience to droughts (between 1974 and 2018), i.e. the droughts before the very extreme 2018 drought that killed many trees. We expected that trees from less resilient species are less vital and thus have lower energy buffers compared to species that are more resilient, and less resilient species will therefore face higher mortality risks. In addition to these three hypotheses, the effects on the hydraulic system and energy budgets can enforce each other, and make trees more vulnerable to pests, such as bark beetles. Compared to one another, these 3 hypotheses reflect different legacy durations or so-called ecological

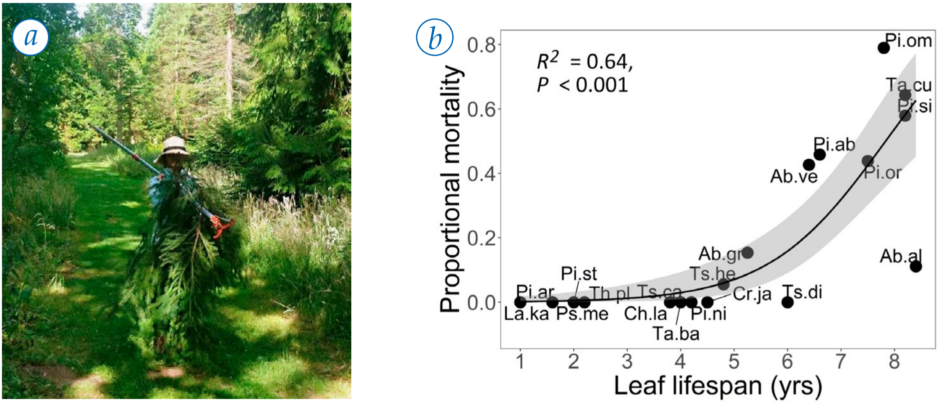


*Figure 5. The leaf legacy hypothesis. a) Yanjun Song carries a branch for structural and physiological measurements during the field work campaign in 2018. b) The result showing that mortality is higher for tree species with longer leaf lifespans. For explanation, see text.*

memory varying from multiple months (for hydraulic safety) to multiple years (leaf legacy) to multiple decades (growth legacy).

First, we tested whether hydraulic safety margins predict the mortality risks of the tree species. Let me introduce the hydraulic safety margin concept with a graph (Figure 4a). On the horizontal (x-)axis we have a measure of drought vulnerability: the water potential in a twig at which 50% of the water transport is lost because of embolism ($P_{50}$ in Figure 4a). Embolism occurs when low water potentials suck air bubbles into water-conducting cells (tracheids for conifers) and impair the water transport. Species located on the right of this axis are thus more vulnerable to drought whereas species on the left are more resistant to drought. On the vertical (y-)axis we put minimum leaf water potential ($\Psi_{min}$): we expect leaves to close the stomata to minimize loss of water at this potential. Leaves can thus act as a kind of valve avoiding too extreme water loss and protect the rest (more proximal part) of the tree body against quick dehydration. The diagonal 1:1 line represents a safety margin of nil, above which trees are supposed to be safe! Different symbols reflect the different species. The safety margins are reflected by the distance to the diagonal: they differ between species, and also between species from different plant families (see the two arrows in Figure 4a). Does that matter for mortality risks? The results show no relationship (Figure 4b): apparently, all conifer species had sufficiently wide margins to survive the 2018 drought. We thus reject the hypothesis that hydraulic safety margins explain conifer species differences in mortality risks.

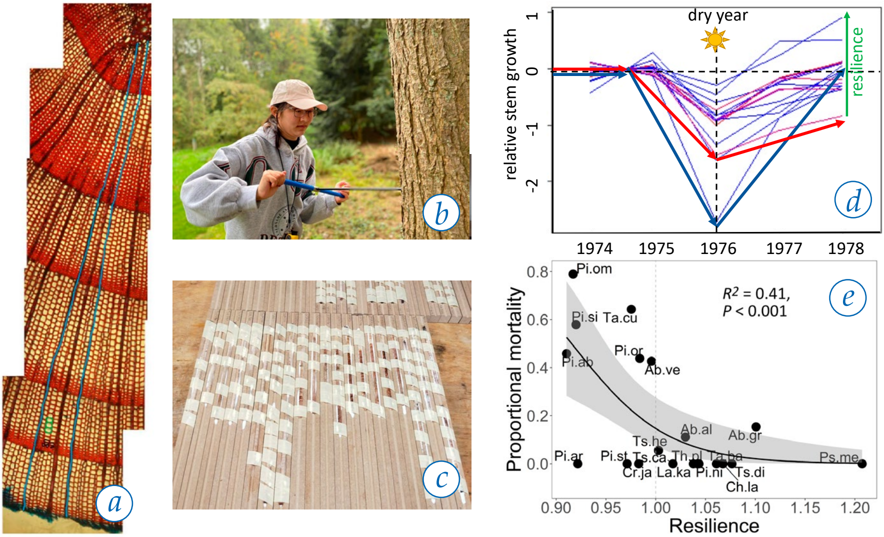


*Figure 6. The growth legacy hypothesis. a) A stem cross section showing tree rings from variations in the sizes of the tracheid cells. b) Yanjun Song coring a tree to obtain a stem core for tree ring analysis. c) Stem core samples glued in wooden frames. d) The concept of stem growth resilience illustrated by tree responses to the dry year 1976. e) The result showing that species that were more resilient to droughts (from 1974-2018) had lower drought-induced mortality risks in response to drought year 2018. For explanation, see text.*

Second, let us turn to the leaf legacy hypothesis, the potential role of leaf lifespan in explaining mortality. To assess leaf life span, branches were sampled (Figure 5a) for all species and the age of the oldest needles was estimated by counting the annual stem rings of the shoots supporting those needles. We observed a higher mortality for tree species with longer leaf lifespan (Figure 5b), which explained 64% of all variation in mortality. The leaf legacy hypothesis is thus supported by our data, suggesting that variation in leaf lifespan can explain species differences in mortality risks.

To test the growth legacy hypothesis, we used tree rings, which appear in stem cross-sections of trees (Figure 6a). Fortunately, we can collect small stem core samples to measure those rings without killing trees (see Figure 6b-c). I will briefly sketch the concept of growth resilience with a graph (Figure 6d). Here the horizontal (x-)axis shows a time window of 5 years, with the drought year 1976 in the middle. Maybe the 50+ people in the audience do remember this dry, hot, sweaty, summer.... On the vertical (y-) axis we put a measure of relative stem growth in each of those years (as observed in dated tree rings). For the years before the dry year 1976, we standardized the average stem growth to 0, highlighted for two species, one represented by a blue arrow and the other by a red one (again Figure 6d). Trees often reduce stem growth during such a dry year, but species may differ a lot in this. And trees usually recover after a dry year, but some species recover better than others. The blue arrow species fully recovers stem growth and is thus fully resilient to the 1976 dry year. But the species represented by the red arrow does not recover stem growth, and is thus less resilient to the 1976 drought. For the stem growth responses of all our species, we observe a lot of variation in growth resilience (see all the other lines in Figure 6d). Tree species that were less resilient show the highest tree mortality (Figure 6e), which is in line with the growth legacy hypothesis.

We thus have learned that hydraulic traits cannot explain conifer tree mortality, but legacies from leaves and stem growth can! Moreover, such legacies can enforce each other and better explain tree mortality together. What conclusions can we draw in general? First, there is increasing evidence that drought and heatwaves play an important role. That poses a challenge, since we know that drought and heatwaves become more severe with climate change. Second, long-term legacy or memory effects are important to consider for explaining tree mortality risks. Third, tree ring information showing weaker growth resilience in 1976 can predict mortality risks after 2018, more than 40 years later. Tree rings can thus provide early warning signals for long-term drought-mortality risks! Fourth, these tree species were planted to test their potential for wood production. Adaptation of exotic trees, to other climates, may thus have unexpected implications for their growth and survival in a new environment. Fifth, we showed results for a common garden experiment, which has its own limitation; the actual importance of such mechanisms in explaining tree mortality in natural temperate and tropical forests remains to be tested. And finally, we will need models that integrate different features (hydraulics, legacies and 3D structure) that operate at different scales but jointly cause overall growth and mortality responses of trees to climate.

## Studying forest dynamics: new opportunities and challenges

So far I presented some results and conclusions from past studies on 2 major questions for trees, i.e. (1) why do trees grow “like trees”? and (2) why do trees die? The results and conclusions of these and other studies help in understanding the dynamics of forests in a changing world. For my current research, I consider the development of new technologies and the expansion of interdisciplinary collaborations with scientists and forest users crucial in addressing the challenges that forests face in the future. The new technologies include a multitude of new tools to measure and monitor trees and forests (for examples, Figure 7). For trees, sensors are available to measure diel and seasonal responses in stem growth and water conditions of trees (Steppe et al. 2015). An example of such a sensor is the dendrometer,

*Figure 7. Examples of the equipment toolbox. a) Lidar images quantifying 3D forest structure, b) a dendrometer showing stem growth and shrinkage (proxy for water deficit) at 10 minute resolution, c) satellites and d) drones for monitoring forest dynamics from remote.*

which measures changes in stem diameter at small (e.g. 10 minute) time resolution (Figure 7b). The measurements of such sensors are nowadays downloaded instantly and thus allow for almost real-time monitoring of stem growth (for diel trends, (see Zweifel et al. 2021)), and for seasonal trends, (Etzold et al. 2022)) and stem shrinkage, which is a measure of water deficit in trees (Zweifel et al. 2007, Salomón et al. 2022). For forests, other tools are nowadays available. An example is LIDAR (from "LIght Detection of Lasar Imaging And Ranging", image Figure 7a) using laser pulses to digitize trees (Van Der Zee et al. 2021) and forests (Sterck et al. 2022), which bares the potential to evaluate, for example, the effects of crown shape on the resilience of trees to drought and heatwaves. Other examples include the rapid developments in the analysis of DNA and RNA, used to identify fungi and bacterial communities and their role in the carbon, nutrient and/or water cycles in forest soils (Sterck et al. 2021) and dead wood (Yang et al. 2022). And, finally, by equipping satellites (Reiche et al. 2016) and drones (D'Odorico et al. 2021) with ever improving sensors, promising steps are set to improve our ability to monitor the dynamics and drought stress of forests at local and regional scales (Figure 7c-d). The expansion of interdisciplinary collaborations with scientists allow for applying and integrating these new technological tools to better understand forest responses to ongoing global changes. Moreover, the expansion of collaborations with forest users contributes to translating the new scientific insights into climate-smart forest management, aiming at productive, resilient and carbon-storing forests. We jointly aim at providing a better "future for trees and forests", because trees and forests are important but their future is highly uncertain.

Forests are important for many reasons. First, they are responsible for 45% of the terrestrial carbon stocks and 50% of the terrestrial carbon production (Bonan 2008). They play a central role in the climate change policy debate, since carbon sequestration by forests mitigates atmospheric $CO_2$ rise and warming (Luyssaert et al. 2018). Second, forests recycle and transpire a lot of water. They, for example, contribute to 30% or more of rain fall across continents (Sheil et al. 2018), and can cool areas by several degrees (Shukla et al. 1990). Third, they are important for good soil fertility since they recycle nutrients effectively (for example >90% for nitrogen and phosphorous, (Chapin et al. 2002)). They thus maintain soil nutrient stocks and forest productivity in the long term. Fourth, forest, are important for biodiversity. They are recently estimated to harbour globally >70.000 tree species (Cazzolla Gatti et al. 2022) and provide habitats for many other plant species, as well as numerous animal species.

However, the future of trees and forests is at stake. One of the main reasons is that drought and heatwaves will occur more frequently, and more severely, in the future (Dai 2013, Masson-Delmotte et al. 2021). Droughts and heatwaves lead to slower growth and higher mortality risks of trees worldwide, and this is particularly true for large trees (Bennett et al. 2015). As an example, the 2018 drought and heatwave year lead to huge tree losses across Europe, with mortality rates taking dramatic forms with over 100 million m3 of dead trees in Europe after that summer (Nabuurs et al. 2019). For tropical forests, drought and heat effects may ultimately transform the tall and diverse tropical forests into lower and less diverse woodlands or savannahs, and turn tropical forests into carbon sources, not sinks, in the long term (Hirota et al. 2011). There are more global challenges. The increasing world population creates larger demands on forests, for example for wood and the use of biomass as a source of renewable energy (Mantau et al. 2010, Nabuurs et al. 2015). Forests therefore become more frequently disturbed by human action. And last but not least, nitrogen deposition causes soil acidification and reduces soil fertility, with negative implications for long-term forest productivity (de Vries et al. 2021). All these threats culminate in an uncertain future for forests.

## Towards climate-smart forests

This brings me to my personal ambitions for the coming years: I address the question "how do forests respond to these global changes". And I consider forests from the perspective of their carbon, water and nutrient economy, and their role in maintaining biodiversity. I address this question by looking into the mechanistic understanding of such forest responses in research and teaching, and by capacity building. And I contribute to using mechanistic insights for creating solutions by developing strategies for climate-smart forestry (CSF), e.g. by developing CSF tools within broad consortia.

To meet these ambitions I started the so-called climate-smart forestry project with a consortium of scientists from different disciplines and a large group of forest users. Our first aim is to quantify and better understand the effects of drought and forest management on forest productivity, forest resilience, and carbon storage in trees and soils. This creates the scientific basis to address the second aim, which is to develop "climate-smart" forest management tools and make them operational for students and foresters to develop better management in a drier and warmer future.

A consequence of the increasing demands on forests for certain resources, such as timber, is that many forests will be used for harvesting trees. An important question is, what is the best mode of tree harvesting? In traditional forest practice, forests are thinned and at some point in time the whole stand is cut. After that, the whole forest succession cycle has to start again. I think that it might be better to maintain forests by harvesting trees at low intensity and not apply final harvest. In such a selection-cut system young trees benefit

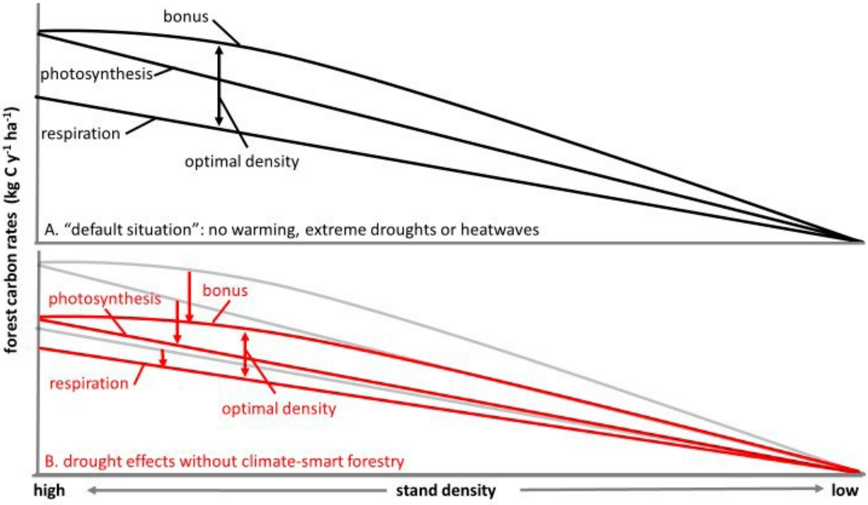


*Figure 8. A hypothesis for stand density and drought effects on forest functioning and, in turn, on forest productivity, resilience and carbon storage. For explanation, see text.*

from open spots and replace the harvested trees. In the long-term, this will result in uneven-aged and structurally more complex forests. While this idea is not new, the question what harvest regime will maximize productivity, resilience, carbon storage and/or biodiversity remains urgent and unanswered, certainly in the context of the extremer droughts and heatwaves as predicted for this century.

I will briefly sketch a hypothesis and then turn to the approach that we use to tackle this hypothesis. We start from the idea that we can manage forests for any stand density between an (unmanaged), dense and closed forest and a very open forest. That is the horizontal (x-)axis in this Figure 8. On the vertical (y-) axis, I show the implications for the major forest carbon uptake and loss rates. Such carbon rates are important because trees thus exchange carbon with the atmosphere. Moreover, they use the acquired carbon to grow in biomass, which consists of 50% carbon mass. Let me first introduce the “default situation”, in which there is no warming and no extreme drought periods and/or heatwaves (Figure 8a). First, forests fix carbon by photosynthesis: if trees are equal, forest photosynthesis decreases linearly with decreasing stand density, a lower number of trees. Second, forests respire (or consume carbon and emit carbon dioxide) to maintain all kinds of living cell functions. If all trees are equal, forest respiration also decreases linearly with lower stand density, a lower number of trees. Third, there is a bonus effect because trees are in fact not equal with decreasing stand density. Compared to closed forest, trees in forests with some openings capture more light and can acquire more carbon, nutrients and water because there are fewer neighbouring trees competing for the same resources. However, at too low density, the remaining trees cannot increase the bonus anymore since the extra light is not intercepted and falls on the soil, and the water and nutrients in open spots are out of reach for their roots. The potential maximum forest growth is expected when carbon gain minus carbon costs are largest. The expectation is that at that density the productivity, resilience and carbon uptake are then also maximal. This is illustrated by the double headed arrow between bonus and respiration (costs) line (Figure 8a).

But what happens in the long run with more drought (see for this Figure 8b)? First, photosynthesis goes down, since tree close stomata to reduce water loss, which comes at the cost of lower uptake of carbon, or lower photosynthesis. Second, respiratory costs can be reduced, but this may come at the cost of weaker protection against herbivory insects by, for example, lower resin production protecting against bark beetles in many conifers. Third, the bonus still exists, but operates at a lower level. Fourth, there will also be an optimal density that maximizes forest growth and related forest services, but it is difficult to predict whether the optimal density moves along the axis of stand density. Overall, I hypothesize such an optimum to occur at relatively low levels of tree harvest, with >60% of tree biomass (relative to the closed forest) maintained (Sohn et al. 2016, Sterck et al. 2021), and that the actual optimal density will differ between tree species and change with climate change.

## A new forest experiment

To test this hypothesis, we started a large, new, forest experiment (Figure 9). The ideas for this experiment started with brainstorm sessions with Jan den Ouden, Wim de Vries and others, which resulted in an NWO/STW proposal. This proposal did not get granted. Fortunately, the year after, Marleen Vos got inspired and she largely integrated the planned forest experiment into her PhD proposal. This proposal did get granted. We could ultimately start our ambitious plans. Then Ciska Veen and I developed the climate-smart forest project with many other scientists and forest users. Again good news: also this project got supported (see (Sterck et al. 2022).

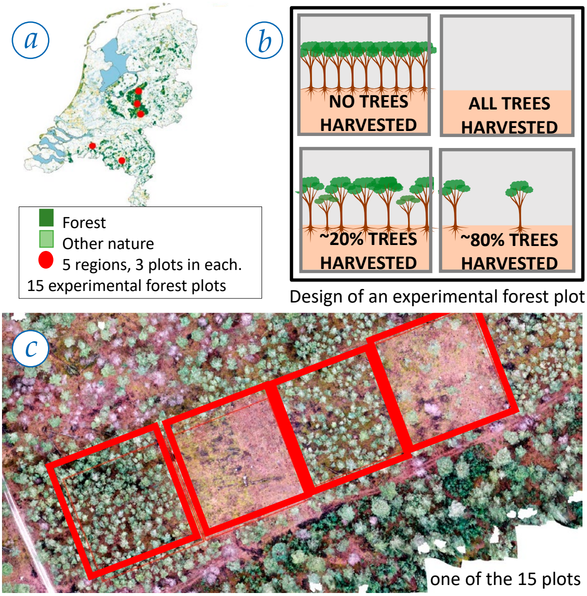


*Figure 9. A new large scale forest experiment for studying effects of forest management on forest productivity, resilience, carbon storage and diversity. a) The 5 regions with 3 plots per region, b) The stand density treatment, as established in each of the 15 plots, c) A top view on one plot, Scots Pine in National Park the Hoge Veluwe. For explanation, see text.*

After long preparations, we started the implementation of the forest experiment in February & March 2019: 6 weeks in a row, 15 people working non-stop, on establishing 15 forest experiment plots (Figure 9). Parallel to this, Marleen lead another team to measure harvested trees for their fresh biomass in the field, and later dry biomasses and nutrient concentrations in the lab. We established three plots in 5 regions in the Netherlands, resulting in a total of fifteen 1-ha plots (Figure 9a). Within each plot, we established four tree harvest intensity levels in 4 subplots: a control forest with nothing removed, a high-thinning forest with ~20% of trees removed, a shelterwood

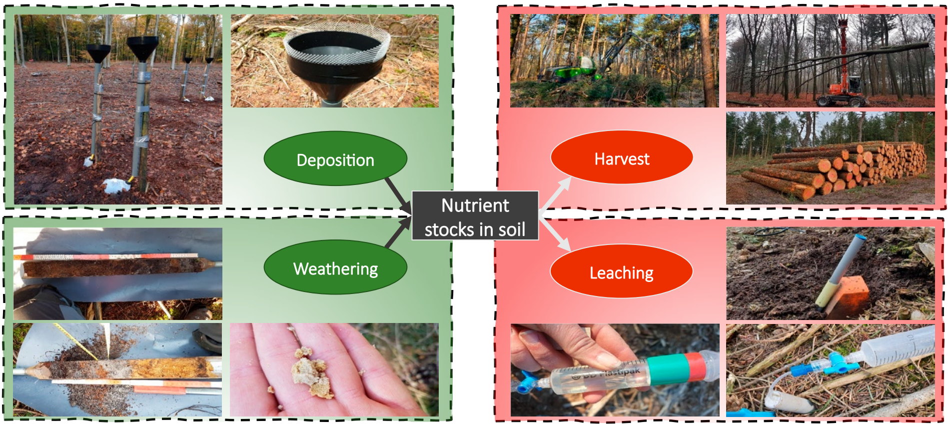


*Figure 10. Illustration of field work to quantify the 4 main nutrient input and output fluxes in the forest experiment. These fluxes drive the dynamics in nutrient stocks in forest soils. For explanation, see text.*

system with ~80% removed, and a clear-cut (Figure 9b). In addition, two sub-plots treatments were added (not shown in Figure 9). First, traditional stem-only harvest versus whole-tree harvest was added. In the latter approach, crowns of cut trees are not left in the forest but removed to be used as fuel for energy plants, thus providing a form of bioenergy. And second, flail mulching (in Dutch "klepelen") was added, a soil surface treatment to mix and smash the topsoil and promote seedling establishment. We did the same treatments for forests dominated by three different species, common beech, Douglas fir and Scots pine. A drone-made top view of one of the plots shows - from the left to the right - the control forest, clear-cut, high-thinning and shelterwood system (Figure 9c).

So far I discussed the implications of forest management for trees. An important part of our work was – and is - however on soils. This is important since more than 80% of the forests occurs on poor soils in the Netherlands, and approximately 50% in Central Europe. This is because often the best soils are kept for agriculture. Soil nutrient availability in soils is thus expected to limit forest growth and recovery, in addition to dry and hot periods.
To quantify the possible nutrient-limitations for forest growth and recovery limitations, we measured and quantified the nutrient budgets in these forests in the different treatment combinations. Next, we quantified the four main fluxes into and away from the forest (Figure 10). These fluxes consist of: 1) Nutrient losses by tree harvest; 2) Nutrient losses by leaching, the leaking of soil water with nutrients to deeper levels in the soil out of reach of roots; 3) Nutrient inputs by deposition from air flow; and 4) Nutrient inputs by weathering of the mineral soils. These four fluxes were quantified in the project of Marleen, with support from

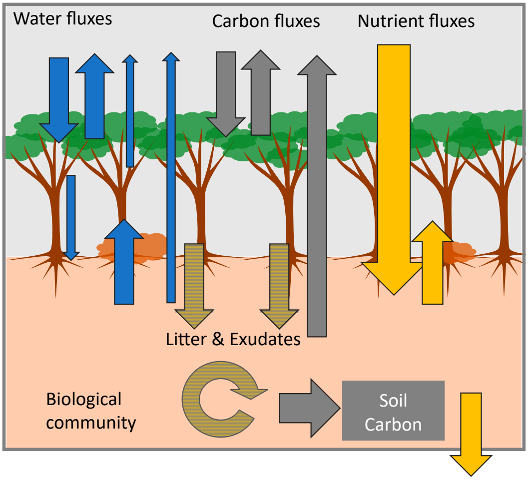


*Figure 11. An illustration of the major nutrient, water and carbon fluxes measured in our forest experiment, for better understanding forest management effects on forests (adapted from Sterck et al. 2021 and 2022). For explanation, see text.*

Leo Goudzwaard and Henk van Roekel for the intensive fieldwork campaigns. This work will show us the limits for using forests – by harvesting and removing trees – from the perspective of the nutrient stocks in the soil.

Before the start of our climate-smart forest study, we already have a strong base established for the forest density effects on the main nutrient fluxes (Figure 11). Within the CSF project, several PhD students and postdocs will explore the consequences of climate-smart forestry on different environmental and biological aspects. PhD student Eva Meijers will quantify the density effects on water and carbon fluxes. PhD student Steven de Goede will quantify the implications for the activities of biological life and their role in carbon storage in soils. Post-Doc Jorad de Vries will show what that means for the entire forest: he will integrate and upscale the tree and soil processes in a new forest model. In addition, the forest experiment serves as a supersite for testing remote information. PhD student Sietse van der Woude will test remote methods from satellites for the detection of different levels of forest disturbance, caused by natural tree mortality or logging. And PhD student Arjen Mulder will test how remote methods can detect the vitality and physiological stress of trees under drought, using drones and satellites. Ultimately, we aim at using these measurements from new technologies to calibrate and test a mechanistic forest model for the forest experimental supersite, and from this aim at upscaling the forest model predictions and satellite information from our supersite to forests at continental scale.

## Ambitions for the coming years

Let me end this presentation with a summary of my ambitions for the coming years. First, this experiment will allow us to test our hypothesis (Figure 8, Sterck et al. 2021)) and thus better understand drought and stand density effects on trees, soils and forests. Second, we will develop, validate and promote two CSF-products for forest managers. The first product is a CSF-learning-app to train foresters and students in making CSF decisions.

With the app, they will be able to evaluate effects of tree harvest scenarios (by virtually removing trees) for the future economic and ecological value of forests under different drought scenarios. The second product is a CSF-proof decision support system, which provides predictions on stand density effects – as controlled by management - on forest productivity, forest resilience to drought, and carbon storage below and above ground. We will develop these tools with Dutch forest managers, but also introduce, validate, and implement our CSF products across Europe.

But there are more ambitions – and new projects - to be realised, particularly focussing on opportunities for increasing the health and potential of forest growth, resilience, and carbon storage with global change (Figure 12). First, a long term monitoring programme for our current forest experiment will allow for better analyses of the long-term perspective of uneven-aged, structurally complex forest, which are in my view also prettier than even-aged and single-species dominated forests. Second, such a monitoring programme needs to be expanded with experiments that allow for evaluating the positive (or negative) effects of combining different tree species in the same forest. And third and lastly, we want to set up comparative measurement protocols for unmanaged forests to show the roles of our future “jungles” for carbon storage, biodiversity and resilience to drought. I aim at developing new research projects and new collaborations in line of these three main ambitions, because they are all required for better balancing forest management and nature conservation at national and continental scales. Such new initiatives will be required to fully address our key ambition: contribute to a scientific base for climate-resilient, healthy and rich forests. And thus contribute to some of the current political ambitions, as recently formulated in the global Paris Agreement, European Green Deal, and the Dutch Climate Agreement and National Forest Strategy.

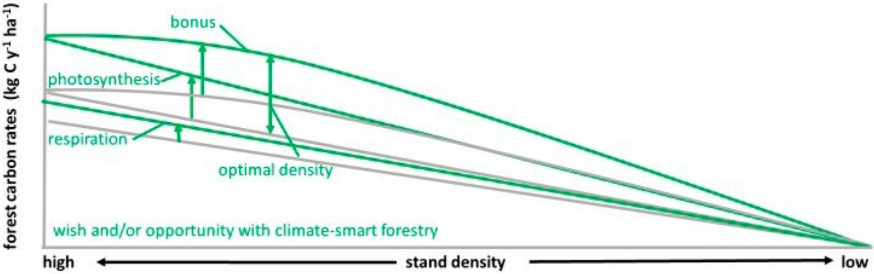


*Figure 12. The hypothesis for stand density and drought effects revisited (compare with Figure 8). The green arrows and lines reflect a possible mechanism allowing for revitalizing forests, since increased carbon gain (the length of the double headed arrow) could improve the production, resilience, carbon storage and biodiversity of forests. The question is how we can achieve this promise of climate-smart forestry. For explanation, see text.*

## A word of thanks

Finally, let my express some words of thanks. I am privileged to work on these ambitions with an ever increasing research team, with so many nice, enthusiastic, and skilled colleagues. And I feel equally privileged to collaborate with such an interested, dedicated, and positive-minded group of forest users, nationally and internationally. I like to thank my colleagues from the Forest Ecology and Forest Management Group for the ever great atmosphere and joy during office hours and critical and constructive comments that contributed to developing ideas. I consider two colleagues particularly important, as they acted as a kind of mentor during the past: Frans Bongers, who taught me how to do good science during my PhD, and later as a colleague he showed me all corners of scientific work, including how to collaborate and manage small and large projects; Feike Schieving, whose brilliance, originality and scientific mindset inspired me to keep on working on mechanistic tree and forest models. Thanks to my family for everything, and our shared love for nature; and friends, for enjoying all pleasures of life outside forest and university; and the Grand Hotel Kleinhesselink-Jansen, for their hospitality catering my stay in Wageningen over the past 20 years; and my partner Mirjam and daughter Donna with partner Michael, also for everything, and for sharing so much joy on a daily basis.

This brings me to my first and last slide. I started my talk saying that – as a nature lover – I consider a future with healthy and rich forests a more beautiful and inspiring world. With this lecture, I have shown you how I – as a scientist – try to contribute to such a forest-rich world with ongoing global changes.

Beste ma, ik hoop dat jij er ook van genoten hebt, het is tijd om te stoppen met praten.

Ik heb gezegd

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*Franks research focusses on the effects of climate on trees and forests. He recently started a large-scale forest experiment to calibrate forest management to the responses of trees and soil to increased drought. Frank leads the partnership of scientists and forest managers who collect data in this forest experiment and who develop forest models to use the new insights for the creation of "climate-smart" forests. This work is a unique test case for increasing the productivity, resilience, biodiversity and/or carbon storage of forests with ongoing climate change.*

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