FuturaGene®



Climate Change Effects on Agriculture and Eucalyptus farms

Climate Change Effects on Agriculture and Eucalyptus farms

Introduction

Based on the scientific literature reviewed for this report, climate change poses a severe and accelerating threat to eucalyptus plantations across South America. Without rapid adaptation, within two decades approximately half of current productive areas may become non-viable economically. Among other agriculture crops, eucalyptus tree-farms face a unique challenge: 7-year growing cycles mean that today's planting decisions must anticipate climate conditions almost a decade into the future, yet, traditional breeding cycles require more than 10 years to develop and deploy improved varieties, creating an adaptation gap at the exact time when unprecedented adaptation is most needed.

Leading tree biotechnology researchers[1] state explicitly:

"…With the growing demand for wood, and the increasing pressure on forests due to climate change and rapidly changing pest populations, it is especially critical that recombinant DNA (rDNA) technologies are integrated in conventional breeding programs…".

They conclude that climate change is *"well known to existentially threaten forests nearly everywhere"* and that *"nothing short of a radical change in regulations, market restrictions, and research investment are warranted"*.

***Material presented here is intended to prompt policy makers, forest and forest product certifiers, industry and other key stakeholders to act urgently, considering the scientific projections on climate change that have been published over the last few years, to avoid catastrophic outcomes in wood supply*.**

This document demonstrates both the severity of climate impacts and the scientific consensus that comprehensive adaptation strategies - including case-by-case evaluation of advanced breeding technologies with appropriate safeguards - are essential to maintain the sustainability mission of forest certifiers, *inter alia*.

---

[1] Boerjan, W. and Strauss, S.H. (2024), Social and biological innovations are essential to deliver transformative forest biotechnologies. New Phytol, 243: 526-536. https://doi.org/10.1111/nph.19855

Climate Threat to Eucalyptus Plantations

Climate change is projected to make **49.2 percent to 56.7 percent of South American Eucalyptus farming areas economically non-viable** due to rising temperatures and an annual water deficit exceeding 500 mm.[2] By the end of the twenty-first century, annual maximum and minimum temperatures in Brazil are predicted to increase by 1.6 to 5.9 °C, along with a 61 percent increase in consecutive dry days under the moderate and severe climate change scenarios (SSP2-4.5 and SSP5-8.5[3])[4]. While eucalyptus production in cooler southern regions may remain viable or show brief gains under moderate scenarios (SSP2-4.5), high-emission pathways (SSP5-8.5) lead to **yield losses and increased disease incidence** across most biomes in Brazil[5,6]. Globally, eucalyptus plantations may be negatively affected in over 89 percent of the earth's surface at 4°C warming[7].

---

2 Martins, F. B., Benassi, R. B., Torres, R. R., & de Brito Neto, F. A. (2022). Impacts of 1.5 C and 2 C global warming on Eucalyptus plantations in South America. Science of The Total Environment, 825, 153820. https://doi.org/10.1016/j.scitotenv.2022.153820.

3 Van Vuuren, D. P., O'Neill, B. C., Tebaldi, C., et al. (2026). The Scenario Model Intercomparison Project for CMIP7 (ScenarioMIP-CMIP7). Geoscientific Model Development, 19(7), 2627-2656. https://doi.org/10.5194/gmd-19-2627-2026. The very high emission scenario SSP5-8.5 (RCP8.5) is no longer considered feasible and will not be used in the modelling for the forthcoming IPCC Seventh Assessment Report (AR7). The issue is not clear-cut, however, comparable '8.5' warming levels can still be reached through lower-emission pathways during periods of this century and when the analysis is extended to 2150. The revised emissions scenarios have not yet been finalized by the IPCC at the time of writing, nor have they been used by modelling teams in assessing climate change impacts.

4 Avila-Diaz, A., Benezoli, V., Justino, F., Torres, R., & Wilson, A. (2020). Assessing current and future trends of climate extremes across Brazil based on reanalyses and earth system model projections. Climate Dynamics, 55(5), 1403–1426. https://doi.org/10.1007/s00382-020-05333-z

5 Abebaw, S. E. (2025). A Global Review of the Impacts of Climate Change and Variability on Agricultural Productivity and Farmers' Adaptation Strategies. Food Science & Nutrition, 13(5), e70260. https://doi.org/10.1002/fsn3.70260

6 Martins, F. B., Benassi, R. B., Torres, R. R., & de Brito Neto, F. A. (2022). Impacts of 1.5 C and 2 C global warming on Eucalyptus plantations in South America. Science of The Total Environment, 825, 153820. https://doi.org/10.1016/j.scitotenv.2022.153820

7 Fagundes, F.F.A., Martins, F.B., Torres, R.R. et al. Global Warming Levels (1.5–4 °C) and Water Availability for Eucalyptus Plantations Based on High-resolution CMIP6 Models. Earth Syst Environ (2025). https://doi.org/10.1007/s41748-025-00916-4

One of the primary climate threats to eucalyptus plantations is water stress, which can develop by two distinct mechanisms. The first is a change in supply, as shifting rainfall patterns leave less water in the soil. The second is a rise in demand, as warmer air draws moisture from leaves and soil faster through evapotranspiration. The two compound, since even where rainfall holds steady the higher demand alone deepens the deficit, and trees that close their stomata to limit water loss take up less carbon dioxide and grow more slowly. Lengthening dry spells sharpen the effect, raising the risk of fire and pushing tropical forests from carbon sinks toward carbon sources[8].

Leading tree physiologists (e.g., Andrew Groover, Rakefet David-Schwartz, and Noel Michele Holbrook) advocate for a collaborative approach in which researchers and forest managers work together to develop solutions for tree-climate adaptation by understanding how genetics and hormonal responses interact with external environmental sensing as temperature rises and water stress increases[9]. Others, such as Sally Aitken, take part in international research initiatives such as CRAAFT (Climate-Ready and Adapted Agroforest and Forests), which develops approaches to help forests and agroforestry systems adapt to rapid climate disruption[10].

Additionally, as documented in a scientific review by the Food and Agriculture Organization of the United Nations on behalf of the International Plant Protection Convention Secretariat, climate change is projected to increase pest and disease pressure in agricultural and forestry ecosystems.[11] The review explicitly identifies the use of host-plant resistance and resistance breeding as a potential solution to reduce dependence on chemical pesticides. Climate-intensified biological

---

8 Gatti, L. V., Basso, L. S., Miller, J. B., Gloor, M., Gatti Domingues, L., Cassol, H. L. G., et al. (2021). Amazonia as a carbon source linked to deforestation and climate change. Nature, 595(7867), 388–393. https://doi.org/10.1038/s41586-021-03629-6

9 Groover, A., Holbrook, N.M., Polle, A., Sala, A., Medlyn, B., Brodersen, C., Pittermann, J., Gersony, J., Sokołowska, K., Bogar, L. and McDowell, N. (2025). Tree drought physiology: critical research questions and strategies for mitigating climate change effects on forests. New Phytologist, 245(5), pp.1817-1832. https://doi.org/10.1111/nph.20326

10 Rozenberg, Philippe, Nils Ferrand, Maria-Elena Fernandez, Alexia Stokes, Henrik Hartmann, Mercy Derkyi, Sally Aitken et al. (2025). "Climate-Ready and Adapted Agroforest and ForesTs (CRAAFT): An international research initiative on adaptation of forest and agroforests to climate change." https://doi.org/10.31219/osf.io/qpm4w_v1

11 IPPC Secretariat. (2021). Scientific review of the impact of climate change on plant pests A global challenge to prevent and mitigate plant pest risks in agriculture, forestry and ecosystems. Rome. FAO on behalf of the IPPC Secretariat. https://doi.org/10.4060/cb4769en

threats (pest and diseases) compound the direct abiotic stresses (drought, heat) documented above, requiring tree genetic improvement strategies to address multiple pressures simultaneously at timescales matched to climate's accelerating pace of change. The rate of change in tree growing conditions due to climate drivers outstrips the evolutionary capacity of both natural forests and tree farms to respond, both in terms of shifting range (location) and genetic characteristics, thus requiring human intervention and the use of full range of the technological tools.

Understanding Climate Change and Agricultural Impacts

Climate change refers to the long-term increase in temperature, and resulting changes in precipitation patterns and other climatological variables, driven by the rise in greenhouse gas concentrations (GHG) in the atmosphere due to human activities. These changes disrupt the stable climatic conditions to which agricultural crops and forests are adapted. As global temperatures rise, shifts in regional hydroclimate, the frequency and intensity of droughts and heatwaves have already, and will increasingly impact plant growth, productivity, and the suitability of different production sites. To systematically explore the impact of potential futures, scientists have used Shared Socio-Economic Pathways (SSPs) of possible GHG emission scenarios, coupled with global climate models. The output from these modeling efforts describe the range of plausible radiative forcing outcomes by the year 2100, indicating the additional energy (Watts) absorbed per square meter (W/m^2) over the earth's surface compared to the pre-industrial era. For instance, SSP2-4.5 represents a scenario with future emissions stabilizing, resulting in an additional forcing of approximately 4.5 W/m^2 by 2100, while SSP5-8.5 represents an extreme, high-emissions pathway leading to 8.5 W/m^2 of additional energy being retained. The retention of additional energy in turn drives changes in the earth's climate. [12]. By linking each SSP with future projections of temperature, precipitation, and water-stress drivers, researchers can assess how ecosystems, including agriculture and forestry, may respond to alternative climate conditions.

---

[12] IPCC, 2021: Summary for Policymakers. In: *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* [Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)]. In Press.

Table 1. Shared Socio-Economic Pathways (SSP) scenarios

Scenario	Full Name	Meaning in Practice (2100)	Typical Future World Description
SSP1-2.6	Low forcing (~2.6 W/m²)	**Very low emissions**; warming limited to ~**1.5–2°C**	Strong climate policies, rapid decarbonization, renewable energy dominates
SSP2-4.5	Intermediate forcing (~4.5 W/m²)	**Moderate emissions**; warming around **2-3°C**	Some climate actions, but not sufficient to stop warming
SSP3-7.0	High forcing (~7.0 W/m²)	**High emissions**; warming approx. **3°C+**	Regional rivalry, slow economic development, limited mitigation
SSP5-8.5	Very High forcing (~8.5 W/m²)	**Very high emissions**; warming could exceed **4°C**	Extreme high-end pathway, now regarded as low-likelihood; High emission, Fossil-fuel–driven development, energy-intensive lifestyle

Plant growth and agricultural crop yields are highly sensitive to climate conditions represented by SSPs scenarios. Modelling studies indicate significant yield losses that accelerate markedly as temperatures rise and water stress intensifies. Wheat, rice, maize, and soybeans provide two-thirds of human caloric intake. Without CO_2 fertilization, effective adaptation and genetic improvement, each Celsius degree increase in global mean temperature would, on average, reduce yields of wheat by 6.0 percent, rice by 3.2 percent, maize by 7.4 percent, and soybean by 3.1 percent averaged globally[13]. A recent study measuring the temperature effect on Brazilian soybean yields found an even greater loss of 6 percent per degree Celsius increase[14]. Under SSP5-8.5, crop model projections suggest that major cereal crops could face yield losses of 10 to 25 percent or more by the end of the century, while under the SSP2-4.5 scenario yield losses are smaller or region-specific gains are possible due to elevated CO_2 fertilization and longer growing seasons[5]. These differential outcomes underscore the critical role of mitigation (lower emissions) and adaptation (adjusted agronomy, species and cultivar choice, irrigation) in securing future food production under climate change. Moreover, evidence indicates that in many cases, climate change will result in increasing yield losses related to problems related to plant health due to diseases, pests, and weed competition, in

13 Zhao, C., Liu, B., Piao, S., Wang, X., Lobell, D. B., Huang, Y., ... & Asseng, S. (2017). Temperature increase reduces global yields of major crops in four independent estimates. Proceedings of the National Academy of sciences, 114(35), 9326-9331. https://doi.org/10.1073/pnas.1701762114

14 Silva, D. S., Arima, E. Y., dos Reis, T. N., & Rattis, L. (2023). Temperature effect on Brazilian soybean yields, and farmers' responses. International Journal of Agricultural Sustainability, 21(1), 2173370. https://doi.org/10.1080/14735903.2023.2173370

managed (e.g., agriculture, horticulture, forestry), semi-managed (e.g., national parks), and presumably also unmanaged ecosystems.

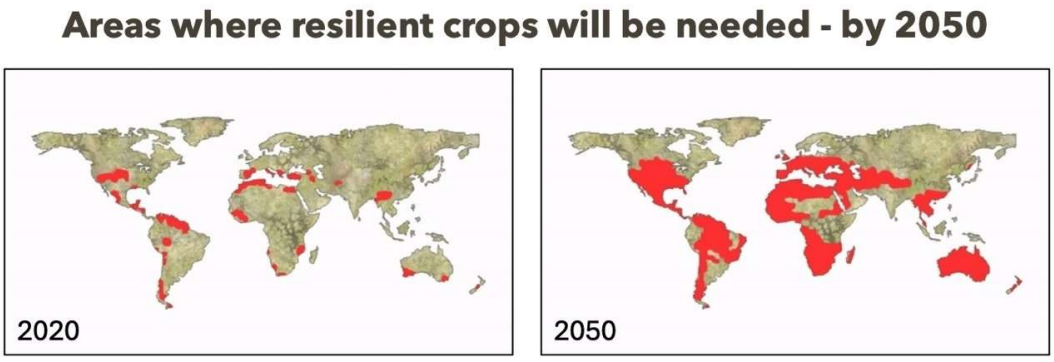


Figure 1. Global distribution of climate change vulnerability zones under projected warming scenarios[15]

Eucalyptus farming is not an exception. A 1.5 - 2°C increase in temperature will make Eucalyptus farming economically unfeasible over 49.2 percent to 56.7 percent of South American areas. Regions in Brazil, such as Maranhão, Tocantins, Piauí and Bahia may become unsuitable for Eucalyptus cultivation due to projected annual water deficits exceeding 500 mm^2. Adaptation options include improvements in breeding programs (genetics, molecular, and conventional), in the operation and management of tree farms, along with shifting plantation locations. Eucalyptus farms located in South and Southeast Brazil are expected to experience yield increases in simulated future scenarios as cold areas warm, while those in Central and North Brazil will experience pronounced yield reductions[16]. Southern and southeastern plantations are projected to maintain or increase productivity across scenarios. Only under the most severe end-of-century scenario does one southern site decline by about 5 percent, while others continue to gain. A recent study involving the mapping of *Eucalyptus urophylla* performance across eight Brazilian states demonstrated that increased temperature and humidity, coupled with elevated diseases and stress incidence, significantly reduce productivity[17].

---

15 Dai, A. (2011). Drought under global warming: a review. Wiley Interdisciplinary Reviews: Climate Change, 2(1), 45-65. https://doi.org/10.1002/wcc.81

16 Elli, E. F., Sentelhas, P. C., & Bender, F. D. (2020). Impacts and uncertainties of climate change projections on Eucalyptus plantations productivity across Brazil. Forest Ecology and Management, 474, 118365. doi.org/10.1016/j.foreco.2020.118365

17 da Costa Oliveira Silva, L., da Rocha, G. N., Jatzek, V. A., Ramos, E., da Silva, P., Lipka, A. E., & Novaes, E. Predicting and Mapping Eucalyptus Urophylla Family Performance Using Large-Scale Environmental

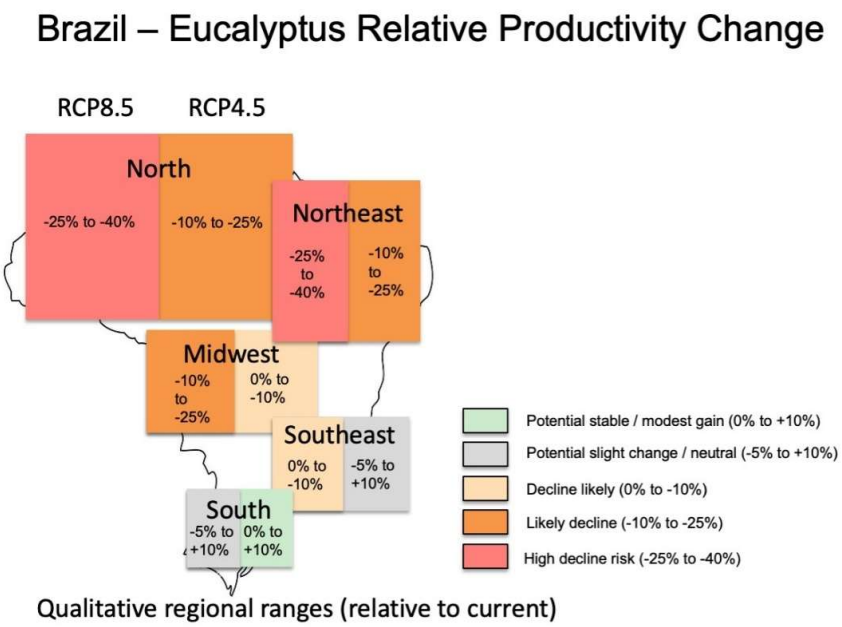


Figure 2. Predictions for eucalyptus productivity changes in Brazil under SSP2-4.5 (right panels) and SSP5-8.5 (left panels) indicate that most of Brazil's areas will experience substantial yield losses. However, cooler regions in the south may still be the only biomes where productivity remains viable (based on Elli et al.[16]).

Driven by a doubling in the earth's energy imbalance (the difference between incoming and outgoing radiation) in recent decades,[18] the rate of warming is itself increasing. Human-induced warming reached about 0.27 C per decade over the 2016 to 2025 period, a rate that is unprecedented in the instrumental record.[19] When sources of natural variation are removed (el Niño, volcanism and solar variation) the rate of warming across five major datasets since 2013/14 shows an increase of 0.37 C per decade.[20] The gap between the pace of change and the pace of adaptation therefore widens with each production cycle.

Covariates for Targeted Deployment. (2025) Available at SSRN 5289714. https://dx.doi.org/10.2139/ssrn.5289714

18 Mauritsen, et al. (2025). Earth's energy imbalance more than doubled in recent decades. AGU Advances, 6, e2024AV001636. https://doi.org/10.1029/2024AV001636

19 Forster, P. M., et al. (2026). Indicators of Global Climate Change 2025: annual update of key indicators of the state of the climate system and human influence. Earth System Science Data, 18(6), 3889-3933. https://doi.org/10.5194/essd-18-3889-2026.

20 Foster, G., & Rahmstorf, S. (2026). Global warming has accelerated significantly. Geophysical Research Letters, 53, e2025GL118804. https://doi.org/10.1029/2025GL118804

Adaptation Pathways for Forest Productivity

The climate threat set out above is severe, broad, and reshaping the conditions eucalyptus must tolerate at a pace without historical precedent. In a situation of this kind the prudent course of action is to continue to reevaluate every adaptation tool available, and not to rule any out. Adaptation draws on four: better site selection, silvicultural management, conventional breeding, and biotechnology. Each is essential, and each has limits as well as value. Better site selection is anticipatory, since it can weigh projected conditions, but it is bounded by physical and land-use constraints such as existing holdings, urban areas, water bodies and protected forests. Adaptive silvicultural management can be applied over shorter periods, yet it offers only limited protection against sustained climate change. Breeding remains the conventional route for most adaptation, which is quantitative and shaped by many genes of small effect, and genomic selection is now sharpening it. Its real constraint is not only speed. Breeding can recombine only the variation that already exists in crossable germplasm, and it must carry a new trait through successive generations before it reaches the clone that is planted. Biotechnology works alongside these tools rather than replacing them, and adds what they cannot: access to traits that lie outside the breeding population, placed directly into the elite genotype that will be planted. The examples below show how:

> The clearest case of a trait that conventional breeding cannot supply is resistance to insect pests conferred by proteins from the soil bacterium Bacillus thuringiensis (Bt). These insecticidal proteins have no counterpart in the eucalyptus gene pool, so they cannot be reached by conventional crossing and have to be introduced directly. Bt traits have been grown in field crops for decades and reduce reliance on chemical insecticides. In eucalyptus, an event expressing three distinct Bt proteins provides high-dose control of the brown looper caterpillar *Thyrinteina arnobia*, a defoliator that can reduce biomass by up to 40 per cent, and was approved by the Brazilian biosafety authority in 2023[21] [22]. Because warming is expanding the range and shortening the generation times of such pests, the value of this protection grows with the climatic conditions it is intended to address. This pressure is

---

21 Pinheiro, A. C., et al. (2024). Genetically engineered eucalyptus expressing pesticidal proteins from Bacillus thuringiensis for insect resistance: a risk assessment evaluation perspective. Frontiers in Bioengineering and Biotechnology, 12, 1322985. https://doi.org/10.3389/fbioe.2024.1322985.

22 de Bortoli, C. P., et al. (2025). Pyramiding of cry genes in high-dose transgenic eucalyptus provides control of Thyrinteina arnobia (Lepidoptera: Geometridae) and reduces the risk of resistance. GM Crops & Food, 16(1), 2604373. https://doi.org/10.1080/21645698.2025.2604373.

rising in Brazil: the eucalyptus area affected by defoliating caterpillars grew from about 58,000 hectares in 2009 to roughly 1.6 million hectares in 2025[23].

The first commercial genetically modified drought-tolerant wheat involved use of transgenic technologies to insert the *HaHB4* gene from Sunflower into wheat showing a 6 percent overall yield advantage (P<0.001) across 37 field environments over nine years, rising to 16 percent under water-stress conditions. The line also showed 9.4 percent higher water use efficiency (P<0.02), and the yield gain tracked an 8 percent increase in grain number per square meter[24,25].

Other ongoing research demonstrates promising outcomes. In one study, scientists introduced a gene called *GolS2* from the Brassicaceae model plant Arabidopsis into poplar trees. The trees carrying this gene showed significantly enhanced drought tolerance in both laboratory and field trials[26].

A second line of biotechnology application works to re-engineer a plant's own metabolism, such as efforts that target photosynthesis itself. The key enzyme in that process, RuBisCO, has a built-in flaw: under heat and other stress it sometimes captures oxygen instead of carbon dioxide. Plants' own efforts to correct this error sets off a wasteful process called photorespiration, which drains energy the plant could otherwise put into growth, and it worsens as temperatures climb. To work around it, researchers engineered a metabolic "bypass", a shortcut that lets the plant avoid most of this waste. In crops, the bypass has already been tested in the open field. Across several crop species, plants carrying the modification produced significant gains in growth and yield, and they also coped better with heat, a benefit that has appeared consistently across these trials [27] [28]. The strategy has been

---

23 IPEF, Instituto de Pesquisas e Estudos Florestais. Occurrence of defoliating caterpillars in eucalyptus plantations in Brazil, 2009 to 2025. Personal communication, 2025.

24 González, F. G., Capella, M., Ribichich, K. F., Curín, F., Giacomelli, J. I., Ayala, F., ... & Chan, R. L. (2019). Field-grown transgenic wheat expressing the sunflower gene HaHB4 significantly outyields the wild type. *Journal of Experimental Botany*, 70(5), 1669-1681. https://doi.org/10.1093/jxb/erz037

25 Gupta, P. K. (2024). Drought-tolerant transgenic wheat HB4®: a hope for the future. *Trends in Biotechnology*, 42(7), 807-809. https://doi.org/10.1016/j.tibtech.2023.12.007

26 Shikakura, Y., Oguchi, T., Yu, X., Ohtani, M., Demura, T., Kikuchi, A., & Watanabe, K. N. (2022). Transgenic poplar trees overexpressing AtGolS2, a stress-responsive galactinol synthase gene derived from Arabidopsis thaliana, improved drought tolerance in a confined field. *Transgenic Research*, 31(4), 579-591. https://doi.org/10.1007/s11248-022-00321-x

27 South, P. F., Cavanagh, A. P., Liu, H. W., & Ort, D. R. (2019). Synthetic glycolate metabolism pathways stimulate crop growth and productivity in the field. Science, 363(6422), eaat9077. https://doi.org/10.1126/science.aat9077

28 Meacham-Hensold, K., Jeong, J., Cavanagh, A. P., & Ort, D. R. (2025). Shortcutting photorespiration: avenues and challenges toward realizing higher-yielding photorespiratory bypass crops. New Phytologist, 249(2), 675–690. https://doi.org/10.1111/nph.70724

extended to forest species: hybrid poplar with this bypass showed up to 53% increased biomass accumulation in controlled environment trials, with field trials currently underway[29].

Varietal development approaches differ in what they can deliver and how soon. Conventional breeding, including marker-assisted selection, recombines genetic variation that already exists within crossable germplasm. Where that variation is present it remains the preferred route, but in a long-lived tree, which flowers only after several years, each round of crossing and selection spans years and a full breeding programme can run well over a decade. A trait absent from the gene pool, however, cannot be obtained by conventional crossing. Genetic transformation removes both limits. It places a defined trait, including one sourced from outside the species, directly into an elite genotype in a single step, without the repeated backcrossing that conventional recovery of that genotype would require. The wheat example above is of this kind: its drought-tolerance trait comes from a sunflower gene, which crossing cannot transfer into wheat. Genome editing alters a gene already present in the elite genotype with precision and without inserting foreign DNA, which leaves the rest of the background unchanged and, in several regulatory systems, is treated separately from transgenic approaches. The practical effect is that biotechnology can act within the relevant plantation decision window, on the genotype that will be planted, while conventional breeding must carry a trait through successive generations before it reaches the field.

Many crop research programs using various biotechnologies are ongoing, with the aim of addressing climate-related stress and yield loss through appropriate modifications. Currently, certification and government regulatory policies have made it very difficult to conduct the research needed to develop climate-resilient trees through genetic modification (engineering or editing), and as a result, tree research lags significantly behind that of major crop species, a lag that is exacerbated by the time scale for implementing new technologies in long-growing species such as trees.

---

29 Tao, Y., Chiu, L. W., Hoyle, J. W., Dewhirst, R. A., Richey, C., Rasmussen, K., Du, J., Mellor, P., Kuiper, J., & Tucker, D. (2023). Enhanced photosynthetic efficiency for increased carbon assimilation and woody biomass production in engineered hybrid poplar. Forests, 14(4), 827. https://doi.org/10.3390/f14040827

Conclusions

This discussion has set out the climate adaptation challenge facing eucalyptus and agriculture, together with the range of tools available to address it. The evidence across climate modelling, forest physiology and breeding points to a clear temporal challenge: climate is changing faster than conventional breeding has historically delivered new varieties, a gap that widens with each planting cycle unless adaptation is pursued deliberately.

Three scientific insights emerge from this synthesis:

1. Tree plantations and forests adaptation face fast growing threats. Climate-stressed trees become more vulnerable to pests and diseases, while warming simultaneously accelerates lifecycles and expands pest and disease range. Adaptation strategies optimized for single stressors, e.g., drought tolerance or pest resistance alone, will prove insufficient.
2. Timing is a real but manageable part of the challenge, not the decisive one. Trees planted today must survive conditions a decade or more ahead, and conventional breeding takes 12 to 16 years to develop and recommend a new variety[30]. The gap is not, however, a simple matter of arithmetic. The warming within a single production cycle is small; a 12 to 16 year adaptation cycle can keep pace if breeding targets are set for tolerance to a future 2 to 3 C temperature rise rather than to the change already observed. The binding constraints are the absence of sustained, climate-targeted breeding to date and specific genetic hurdles. Marker-assisted breeding can shorten the time required for identifying and selecting traits that exist in the gene pool, while genome editing and transgenics introduce traits that crossing cannot, including those from outside the breeding population itself.
3. The scientific consensus has shifted from viewing genetic modification as one tool among many, to recognizing that comprehensive breeding approaches are valuable where conventional breeding alone is unlikely to deliver the required trait in time, in particular for variation that is absent from the breeding population. Boerjan and Strauss1 conclude that "time is not on our side" and that "regulatory relief only for simple forms of gene-editing will be woefully insufficient."

On this basis, biotechnology is best seen as a complement to conventional breeding, site selection and silvicultural management rather than a replacement for them, with its clearest value where a needed trait is difficult or impossible to obtain by conventional crossing. The open question is less whether it should be used than how its deployment, and how it must be governed to safely serve ecological and social sustainability objectives.

---

[30] Rezende, G. D. S. P., de Resende, M. D. V., & de Assis, T. F. (2014). Eucalyptus Breeding for Clonal Forestry. In: Fenning, T. (ed.) Challenges and Opportunities for the World's Forests in the 21st Century. Forestry Sciences, vol 81. Springer, Dordrecht, pp 393–424. https://doi.org/10.1007/978-94-007-7076-8_16

APPENDIX: Scientific Reference | Booklet

We present reference studies that establish the **scientific basis** for the climate challenges outlined in this document.

Collectively, they provide a consistent and robust body of evidence for:

- rising temperatures already **reducing global crop yields**;
- more than half of South America's **eucalyptus plantation** areas being projected to face **significant risk under near-term warming scenarios**;
- current **tree physiology cannot keep pace with accelerating drought stress and pest pressures**.

Across the international forestry research community, adaptation has, therefore, become an urgent priority, and many researchers argue that the full range of tools, including advanced breeding and biotechnology, should be available where conventional approaches fall short.

Selected key studies (full text in the accompanying compendium):

Zhao, C., Liu, B., Piao, S., Wang, X., Lobell, D. B., Huang, Y., ... & Asseng, S. (2017). Temperature increase reduces global yields of major crops in four independent estimates. Proceedings of the National Academy of sciences, 114(35), 9326-9331. https://doi.org/10.1073/pnas.1701762114

Martins, F. B., Benassi, R. B., Torres, R. R., & de Brito Neto, F. A. (2022). Impacts of 1.5 C and 2 C global warming on Eucalyptus plantations in South America. Science of The Total Environment, 825, 153820. https://doi.org/10.1016/j.scitotenv.2022.153820

Groover, A., Holbrook, N.M., Polle, A., Sala, A., Medlyn, B., Brodersen, C., Pittermann, J., Gersony, J., Sokołowska, K., Bogar, L. and McDowell, N. (2025). Tree drought physiology: critical research questions and strategies for mitigating climate change effects on forests. New Phytologist, 245(5), pp.1817-1832. https://doi.org/10.1111/nph.20326

Rozenberg, Philippe, Nils Ferrand, Maria-Elena Fernandez, Alexia Stokes, Henrik Hartmann, Mercy Derkyi, Sally Aitken et al. (2025). "Climate-Ready and Adapted Agroforest and ForesTs (CRAAFT): An international research initiative on adaptation of forest and agroforests to climate change." https://doi.org/10.31219/osf.io/qpm4w_v1 (preprint).

Boerjan, W. and Strauss, S.H. (2024), Social and biological innovations are essential to deliver transformative forest biotechnologies. New Phytol, 243: 526-536. https://doi.org/10.1111/nph.19855

Fagundes, F. F. A., & Martins, F. B. (2026). Global risks and vulnerabilities of Eucalyptus plantations under 1.5 to 4°C global warming levels. Earth Systems and Environment. https://doi.org/10.1007/s41748-026-01319-9

Temperature increase reduces global yields of major crops in four independent estimates

Chuang Zhao[a,1], Bing Liu[b,c,d,e,f,1], Shilong Piao[a,g,h,2], Xuhui Wang[a], David B. Lobell[i], Yao Huang[j], Mengtian Huang[a], Yitong Yao[a], Simona Bassu[k], Philippe Ciais[l], Jean-Louis Durand[m], Joshua Elliott[n,o], Frank Ewert[p,q], Ivan A. Janssens[r], Tao Li[s], Erda Lin[t], Qiang Liu[a], Pierre Martre[u], Christoph Müller[v], Shushi Peng[a], Josep Peñuelas[w,x], Alex C. Ruane[y,o], Daniel Wallach[z], Tao Wang[g,h], Donghai Wu[a], Zhuo Liu[a], Yan Zhu[b,c,d,e], Zaichun Zhu[a], and Senthold Asseng[f,2]

[a]Sino-French Institute for Earth System Science, College of Urban and Environmental Sciences, Peking University, Beijing 100871, China; [b]National Engineering and Technology Center for Information Agriculture, Nanjing Agricultural University, Nanjing, Jiangsu 210095, China; [c]Key Laboratory for Crop System Analysis and Decision Making, Ministry of Agriculture, Nanjing Agricultural University, Nanjing, Jiangsu 210095; [d]Jiangsu Key Laboratory for Information Agriculture, Nanjing Agricultural University, Nanjing, Jiangsu 210095; [e]Jiangsu Collaborative Innovation Center for Modern Crop Production, Nanjing Agricultural University, Nanjing, Jiangsu 210095; [f]Agricultural and Biological Engineering Department, University of Florida, Gainesville, FL 32611; [g]Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100085, China; [h]Center for Excellence in Tibetan Earth Science, Chinese Academy of Sciences, Beijing 100085, China; [i]Department of Earth System Science Center on Food Security and the Environment, Stanford University, Stanford, CA 94305; [j]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China; [k]Desertification Research Centre, University of Sassari, 07100 Sassari, Italy; [l]Laboratoire des Sciences du Climat et de l'Environnement, Le Commissariat à l'Énergie Atomique et aux Énergies Alternatives, CNRS, Université de Versailles Saint-Quentin, Gif-sur-Yvette 91191, France; [m]Unité de Recherche Pluridisciplinaire Prairies et Plantes Fourragères, Institut National de la Recherche Agronomique, CS 80006, 86600 Lusignan, France; [n]University of Chicago Computation Institute, University of Chicago, Chicago, IL 60637; [o]Columbia University Center for Climate Systems Research, Columbia University, New York, NY 10025; [p]Institute of Crop Science and Resource Conservation, University of Bonn, Bonn 53115, Germany; [q]Leibniz Centre for Agricultural Landscape Research, 15374 Müncheberg, Germany; [r]Department of Biology, University of Antwerp, 2610 Wilrijk, Belgium; [s]International Rice Research Institute, Los Baños, 4031 Laguna, Philippines; [t]Agro-Environment and Sustainable Development Institute, Chinese Academy of Agricultural Sciences, Beijing 100081, China; [u]UMR Laboratoire d'Ecophysiologie des Plantes sous Stress Environementaux, Institut National de la Recherche Agronomique, Montpellier SupAgro, 34060 Montpellier, France; [v]Climate Impacts and Vulnerabilities, Potsdam Institute for Climate Impact Research, 14473 Potsdam, Germany; [w]Centre de Recerca Ecològica i Aplicacions Forestals, Cerdanyola del Valles, Barcelona 08193, Catalonia, Spain; [x]Global Ecology Unit CREAF-CSIC-UAB, Consejo Superior de Investigaciones Científicas, Bellaterra, Barcelona 08193, Catalonia, Spain; [y]National Aeronautics and Space Administration Goddard Institute for Space Studies, New York, NY 10025; and [z]UMR 1248 Agrosystèmes et Développement Territorial, Institut National de la Recherche Agronomique, 31326 Castanet-Tolosan Cedex, France

Edited by B. L. Turner, Arizona State University, Tempe, AZ, and approved July 10, 2017 (received for review January 31, 2017)

Wheat, rice, maize, and soybean provide two-thirds of human caloric intake. Assessing the impact of global temperature increase on production of these crops is therefore critical to maintaining global food supply, but different studies have yielded different results. Here, we investigated the impacts of temperature on yields of the four crops by compiling extensive published results from four analytical methods: global grid-based and local point-based models, statistical regressions, and field-warming experiments. Results from the different methods consistently showed negative temperature impacts on crop yield at the global scale, generally underpinned by similar impacts at country and site scales. Without CO_2 fertilization, effective adaptation, and genetic improvement, each degree-Celsius increase in global mean temperature would, on average, reduce global yields of wheat by 6.0%, rice by 3.2%, maize by 7.4%, and soybean by 3.1%. Results are highly heterogeneous across crops and geographical areas, with some positive impact estimates. Multimethod analyses improved the confidence in assessments of future climate impacts on global major crops and suggest crop- and region-specific adaptation strategies to ensure food security for an increasing world population.

climate change impact | global food security | major food crops | temperature increase | yield

Crops are sensitive to climate change, including changes in temperature and precipitation, and to rising atmospheric CO_2 concentration (1, 2). Among the changes, temperature increase has the most likely negative impact on crop yields (3, 4), and regional temperature changes can be projected from climate models with more certainty than precipitation. Meteorological records show that mean annual temperatures over areas where wheat, rice, maize, and soybean are grown have increased by ∼1 °C during the last century (Fig. 1*A*) and are expected to continue to increase over the next century (Fig. 1*B*) —more so if greenhouse gas emissions continue to increase. It is thus necessary to quantify the impact of temperature increase on global crop yields, including any spatial variations, to first assess the risk to world food security, and then to develop targeted adaptive strategies to feed a burgeoning world population (5).

Several methods have been developed to assess the impact of temperature increase on crop yields (6). Process-based crop models characterize crop growth and development in daily time steps and can be used to simulate the temperature response of yield either in areas around the globe defined by grids or at selected field sites or points (1, 7). A third method, statistical modeling, uses observed regional yields and historical weather records to fit regression functions to predict crop responses (8, 9). A fourth method is to artificially warm crops under near-natural field conditions to directly measure the impact of increased

Significance

Agricultural production is vulnerable to climate change. Understanding climate change, especially the temperature impacts, is critical if policymakers, agriculturalists, and crop breeders are to ensure global food security. Our study, by compiling extensive published results from four analytical methods, shows that independent methods consistently estimated negative temperature impacts on yields of four major crops at the global scale, generally underpinned by similar impacts at country and site scales. Multimethod analyses improved the confidence in assessments of future climate impacts on global major crops, with important implications for developing crop- and region-specific adaptation strategies to ensure future food supply of an increasing world population.

Author contributions: C.Z., B.L., S. Piao, D.B.L., F.E., and S.A. designed research; C.Z. and B.L. performed research and analyzed data; C.Z., B.L., S. Piao, D.B.L., and S.A. wrote the paper; and X.W., D.B.L., Y.H., M.H., Y.Y., S.B., P.C., J.-L.D., J.E., F.E., I.A.J., T.L., E.L., Q.L., P.M., C.M., S. Peng, J.P., A.C.R., D. Wallach, T.W., D. Wu, Z.L., Y.Z., and Z.Z. contributed to the interpretation of the results and to the text.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

[1]C.Z. and B.L. contributed equally to this work.

[2]To whom correspondence may be addressed. Email: sasseng@ufl.edu or slpiao@pku.edu.cn.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1701762114/-/DCSupplemental.

Downloaded from https://www.pnas.org by 163.116.224.124 on February 13, 2026 from IP address 163.116.224.124.

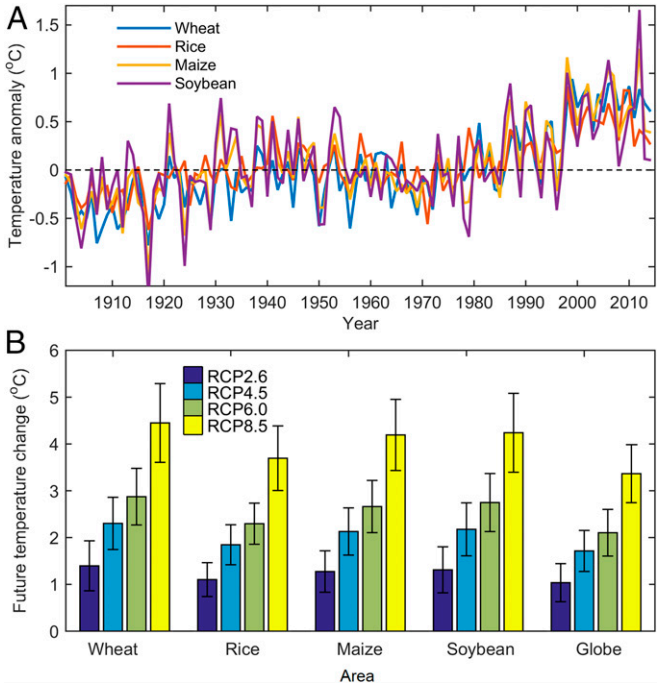


Fig. 1. Mean annual temperature changes over time. (*A*) Historically observed temperature anomalies relative to 1961–1990 for global growing areas of four individual crops. (*B*) Future projected temperature changes (2071–2100 in comparison with 1981–2010 baseline) of four crop-growing areas and the globe (land and sea surface) under four representative concentration pathway (RCP) scenarios of increasing greenhouse gas concentrations. Error bars represent SDs in the climate model results.

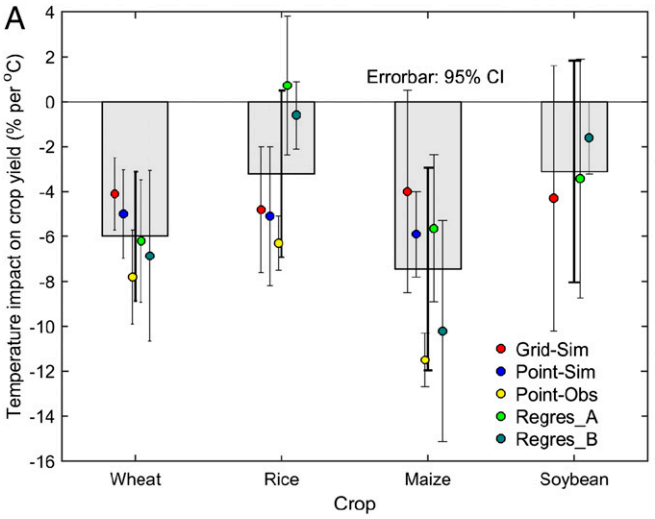
temperatures (4). Here, we combine these four methods, which use disparate data sources, time spans, and upscaling approaches (10), to assess the impact of increasing temperatures on yields of wheat, rice, maize, and soybean. Grid- and point-based simulations from recent international model intercomparison exercises (2, 7, 11, 12) and published results of 13 statistical regression studies and 54 field-warming experiments (*SI Appendix*, Fig. S1) are synthesized (*Materials and Methods*).

Results and Discussion

Fig. 2*A* illustrates the impact of temperature on yields of the four crops at the global scale. The loss in yield for each degree Celsius increase in global mean temperature is largest for maize (with multimethod average ±2 SE) of −7.4 ± 4.5% per degree Celsius. All four methods predict a negative impact for maize, but with varying magnitudes. Mostly the different methods generated similar results at the country scale (Fig. 3*C* and *SI Appendix*, Figs. S2 and S3), but estimates varied between countries. The impact estimates are consistently negative for four major maize producers, together responsible for two-thirds of global maize production—namely, the United States (−10.3 ± 5.4% per degree Celsius), China (−8.0 ± 6.1% per degree Celsius), Brazil (−5.5 ± 4.5% per degree Celsius), and India (−5.2 ± 4.5% per degree Celsius). The estimated impact on maize crops in France, however, is smaller (−2.6 ± 6.9% per degree Celsius), including a small positive estimate (3.8 ± 5.2% per degree Celsius) from statistical modeling (13).

For wheat, the average estimate from all four methods is a 6.0 ± 2.9% loss in global yield with each degree-Celsius increase in temperature (Fig. 2*A*). Results from the four methods agree more closely on the impact on wheat (−7.8 to −4.1% per degree Celsius) than on maize yields (Fig. 2*A*). The results from different methods are also generally consistent for the top five wheat-producing countries (Fig. 3*A*) that harvest >50% of the world's wheat. Spatially, however, the impacts are highly heterogeneous. Estimated wheat yield losses for the United States (−5.5 ± 4.4% per degree Celsius) and France (−6.0 ± 4.2% per degree Celsius) are similar to the global average, while those for India (−9.1 ± 5.4% per degree Celsius) and Russia (−7.8 ± 6.3% per degree Celsius) are more vulnerable to temperature increase. The large yield reductions for Russia are mainly due to the contribution of a markedly higher negative result from the statistical method (−14.7 ± 3.8% per degree Celsius; Fig. 3*A*), which did not account for in-season variations in temperature impact (10). By contrast, for China, the largest wheat producer in the world, the multimethod estimate indicates that only 2.6 ± 3.1% of yield would be lost for each degree-Celsius increase in global mean temperature.

Rice is a main source of calories in developing countries. The analysis from the multimethod ensemble indicates that a global increase in temperature of 1 °C will reduce global rice yield by an average of 3.2 ± 3.7%, much less than for maize and wheat (Fig. 2*A*). Grid- and point-based simulations and field-warming experiments indicate a negative impact of temperature of approximately −6.0% per degree Celsius, but some statistical regressions suggest almost no impact. Similar disparities in estimates between the statistical regressions and other methods are found for several major rice-producing countries (Fig. 3*B*),



B

Scenario	Yield changes (%) due to temperature changes by the end of century				
	Wheat	Rice	Maize	Soybean	Mean
RCP2.6	-6.9	-3.3	-8.6	-3.6	-5.6
	[-15.0, -1.4]	[-9.2, 0.8]	[-18.6, -1.8]	[-11.2,1.7]	[-14.4, -0.1]
RCP4.5	-11.4	-5.5	-14.2	-5.9	-9.2
	[-21.7, -3.9]	[-13.8, 1.0]	[-27.9, -4.9]	[-17.0, 3.1]	[-21.2, -0.3]
RCP6.0	-14.0	-6.8	-17.4	-7.2	-11.3
	[-25.7, -5.1]	[-16.8, 1.3]	[-33.1, -5.8]	[-20.2, 3.6]	[-25.6, 0.1]
RCP8.5	-22.4	-10.8	-27.8	-11.6	-18.2
	[-40.2, -8.5]	[-25.3, 2.4]	[-50.4, -9.7]	[-31.0, 6.0]	[-38.6, -0.7]

Fig. 2. Multimethod estimates of global crop yield changes in response to temperature increase. (*A*) Impacts on crop yields of a 1 °C increase in global temperature in grid-based simulations (Grid-Sim), point-based simulations (Point-Sim), field-warming experiments (Point-Obs), and statistical regressions at the country level (Regres_A) (9) and the global level (Regres_B) (8). Circles, means of estimates from each method or medians for Grid- and Point-Sim. Filled bars, means of the multimethod ensemble. Error bars show 95% CIs for individual methods (gray lines) and the ensemble of methods (black lines). (*B*) Projected changes in yield due to temperature changes by the end of the 21st century. CIs of 95% are given in square brackets.

Downloaded from https://www.pnas.org by 163.116.224.124 on February 13, 2026 from IP address 163.116.224.124.

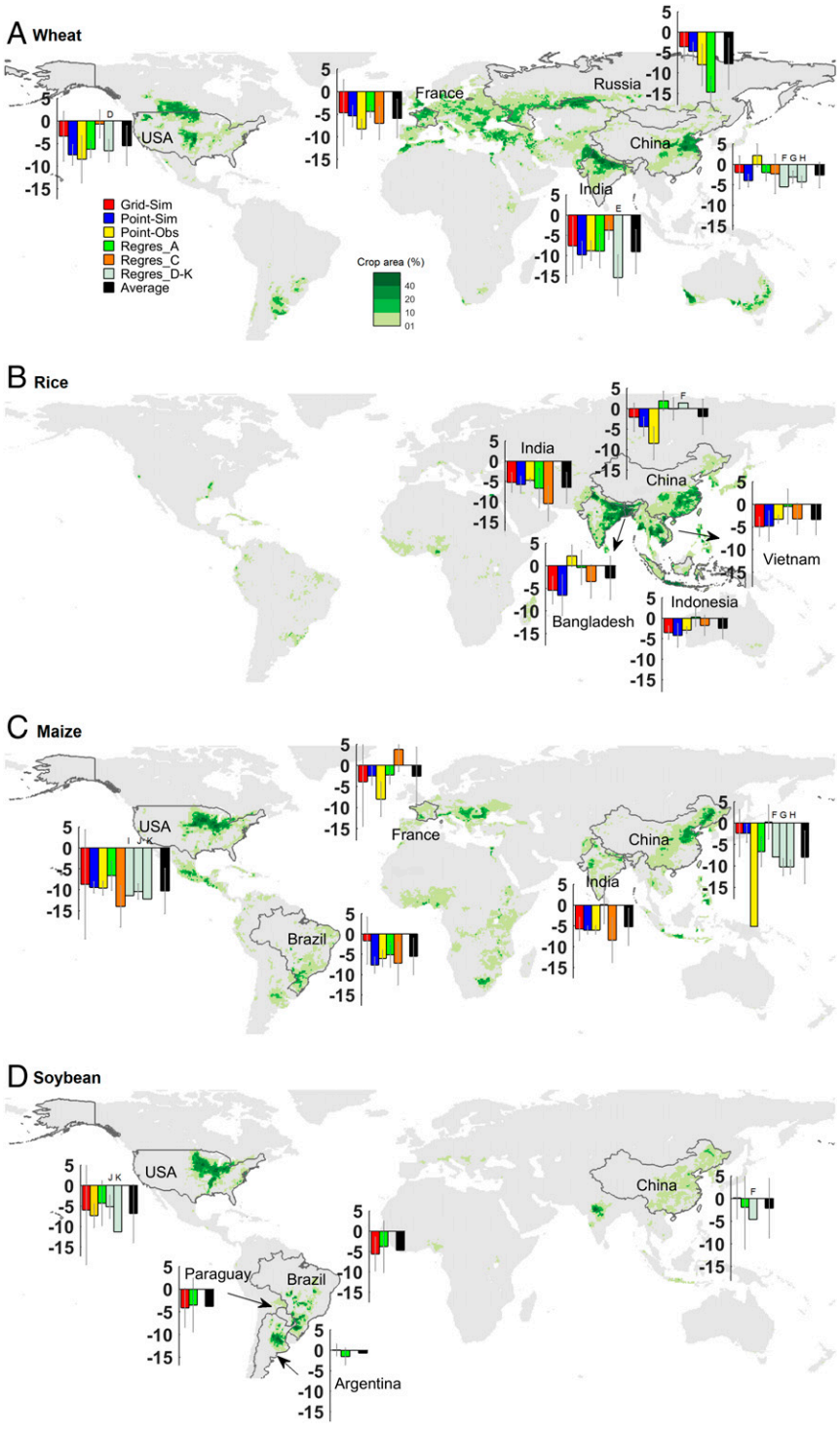


Fig. 3. Multimethod estimates of grain yield changes with a 1 °C increase in global temperature for the five major countries producing each crop. (*A*) Wheat. (*B*) Rice. (*C*) Maize. (*D*) Soybean. Grid-Sim, Point-Sim, Point-Obs, and Regres_A are grid-based simulations, point-based simulations, field-warming experiments, and statistical regressions at the country level (Regres_A) (9), respectively. Regres_C is another regression method used at the country scale (13). Regres_D–K represents various country-level regression analyses used for specific crops or countries shown by individual labels D–K above the bars. Vertical axes show the temperature impact on crop yield in percent per degree Celsius increase. Error bars are 95% CIs. Values for error margins are not available for point-based observations for maize in China.

including China, which produces ∼30% of the world's rice (14). Similar regression methods produce quite different estimates for Indonesia, Bangladesh, and Vietnam, which, when averaged across all methods, lead to small estimated impacts on rice production for each country. For India, however, estimates from all methods predict large temperature impacts, with a multimethod average of −6.6 ± 3.8% per degree Celsius.

Soybean is the fourth most important commodity crop (14). Results of just three studies using only two methods are available for global-scale estimates of the impacts of temperature on soybean yield. The global average reduction in soybean yield is 3.1% per degree-Celsius rise (Fig. 2*A*), but the estimates are not statistically significant due to large uncertainties in each method (the 95% CIs go through zero). Similar effects are estimated with both methods for the United States, Brazil, Argentina, and Paraguay (Fig. 3*D*), which produce 84% of the global soybean harvest (14). The largest expected reduction is −6.8 ± 7.1% per degree Celsius for the United States, the largest soybean producer. The overall results for China, the fourth largest producer, however, do not indicate statistically significant effects of temperature on soybean yield.

We compared different methods for a total of 10 sites and found that method estimates are similar for most site–crop combinations

Downloaded from https://www.pnas.org by 163.116.224.124 on February 13, 2026 from IP address 163.116.224.124.

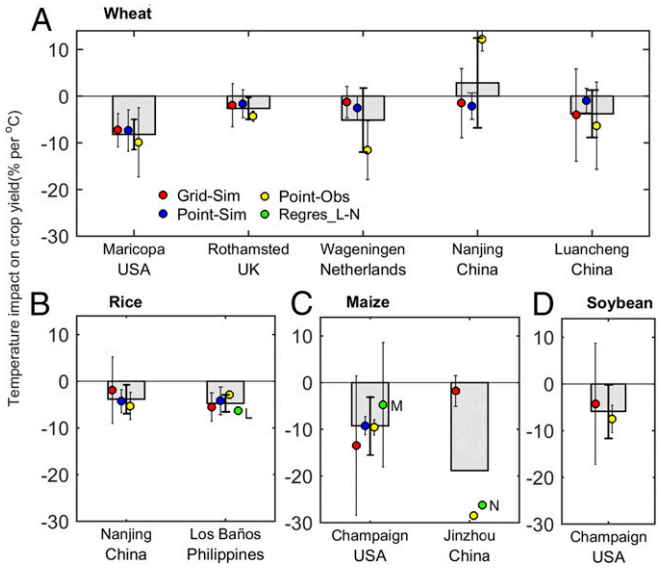


Fig. 4. Site-based multimethod ensemble of crop yield changes with 1 °C of global temperature increase. Site estimates from more than three methods are shown for wheat (*A*), rice (*B*), and maize (*C*) or from two methods for soybean (*D*). Grid-Sim, Point-Sim, and Point-Obs are grid-based simulations, point-based simulations, and field-warming experiments, respectively. Regres_L–N are site-, county- or city-scale regression analyses for specific crops shown by labels L–N next to the mean of the plotted dataset. Error bars are 95% CIs. Error bars for the Jinzhou (China) results for regression L and N were not available.

(Fig. 4). Estimates from grid- and point-based simulations are more similar to each other than to field-warming observations (Fig. 4 and *SI Appendix*, Fig. S4). This is not unexpected, as the two types of simulation have some methodological similarities, such as model structure, assumptions, and parameters. The grid- and point-based models both tend to project greater yield loss with increasing temperature at warmer locations and less yield loss at cooler locations, a distinction not identified in the field experiments (*SI Appendix*, Fig. S4).

Some of the impact differences between simulations and field experiments could be due to the fact that field experiments were only carried out over a few years and might not represent the entire variability of climate at this location, while the simulations represent 30 y. Simulation parameters are also based on the properties of cultivars that differ from those grown in field experiments. For example, the field experiment in Wageningen (The Netherlands) indicated a large negative impact of temperature rise on wheat yield (−11.6% per degree Celsius), but used a spring wheat that is not representative of the region (15). Positive impacts (11.2 ± 1.2% per degree Celsius) were observed in wheat-warming experiments in Nanjing, China, where rising temperatures reduce damage from frost and heat stress during the early and late experimental wheat growing seasons, respectively (16) —factors that are captured less well in crop models (17). For maize grown in Jinzhou (China), a field experiment and a regression analysis produced very large negative estimates of impact, but were not accompanied by margins of error to aid interpretation.

We assumed the temperature response of impact on yield would be linear and multiplied projected temperature changes (Fig. 1*B*) with our multimethod impact estimates to give an average projected decrease in the global crop yields of 5.6% (95% CI, 0.1–14.4%) due to temperature change alone under the scenario of lowest emissions (RCP2.6) going up to 18.2% (95% CI, 0.7–38.6%) under the scenario of highest emissions (RCP8.5) (Fig. 2*B*). The estimated responses in yield are primarily from approximately +2 °C warming simulations, regressions, and experiments (*Materials and Methods*), so the estimates of impact for a global warming scenario near +4 °C (RCP8.5) are likely to be conservative due to the nonlinear impact of rising temperatures in the real world (4, 18). A nonlinear response to temperature has also been suggested in simulations (1, 7, 10).

To prepare for adaptation to climate change, it is necessary to isolate the effects of individual factor for possible impacts on yield, as changes in different factors usually require different adaptation strategies. While elevated atmospheric CO_2 concentration can stimulate growth when nutrients are not limited, it will also increase canopy temperature from more closed stomata (19). Also, changes in precipitation can have an effect on crops, but projections on precipitation change are often uncertain. The focus of our study is on temperature change, one of the most direct negative impacts from climate change on crops, and does not include other possible climate change effects from elevated atmospheric CO_2 concentration or changes in rainfall, and possible deliberate adaptation taken by farmers. Farmers have increased yields through adapting new technologies during the last half-century, but yield has been also lost through increases in temperatures already (9). Yield increase has slowed down or even stagnated during the last years in some parts of the world (20, 21), and further increases in temperature will continue to suppress yields, despite farmers' adaptation efforts.

The direct negative temperature impact on yield could be additionally affected via indirect temperature impacts. For instance, increasing temperature will increase atmospheric water demand, which could lead to additional water stress from increased water pressure deficits, subsequently reducing soil moisture and decreasing yield (22, 23). However, an accelerated phenology from increased temperatures leads to a shorter growing period and less days of crop water use within a cropping season. Such indirect temperature effects are taken into account in each of the methods, but are not explicitly quantified. Other indirect temperature impacts include more frequent heat waves and possible temperature impact on weeds, pests, and diseases (18, 24–26). Increases in management intensity and yield potential could also unintentionally increase yield sensitivity to weather (27).

By combining four different methods, our comprehensive assessment of the impacts of increasing temperatures on major global crops shows substantial risks for agricultural production, already stagnating in some parts of the world (20, 21). However, differences in temperature responses of crops around the world suggest that some mitigation could be possible to substantially affect the magnitude (or even direction) of climate change impacts on agriculture. These impacts will also vary substantially for crops and regions, and may interact with changes in precipitation and atmospheric CO_2, so a reinvigoration of national research and extension programs is urgently needed to offset future impacts of climate change, including temperature increase on agriculture by using crop- and region-specific adaptation strategies.

Materials and Methods

Temperature Data. Historical observed gridded monthly temperature data are from the Climate Research Unit (0.5° × 0.5° grid, CRU TS 3.23; https://crudata.uea.ac.uk/cru/data/temperature/). Future predicted temperature data are from the Coupled Model Intercomparison Project Phase 5 (CMIP5) Earth System Models (ESMs) outputs (1.0° × 1.0° grids; cmip-pcmdi.llnl.gov/cmip5) used in the Intergovernmental Panel on Climate Change (IPCC) Assessment Report 5 (28). According to data availability, the outputs from 15, 20, 11, and 22 ESMs were included in this study for RCP2.6, RCP4.5, RCP6.0, and RCP8.5 scenarios, respectively. However, the calculated temperature changes are very similar to those calculated by using all of the ESMs (IPCC 5). The annual mean temperature over the global growing area of an individual crop was calculated by weighting each grid cell average (0.5° × 0.5° grids) according to the crop growing area within the grid cell (29).

Global Gridded Crop Model Simulations. The Agricultural Model Intercomparison and Improvement Project (AgMIP) (30) and Inter-Sectoral Impact Model Intercomparison Project 1 (31) initiated a fast-track global climate impact assessment for the main global crops in 2012, including wheat, rice, maize, and soybean. Seven global gridded crop models were used to simulate crop yield in 0.5° × 0.5° grid cells over the globe, forced with climate reconstruction for

Downloaded from https://www.pnas.org by 163.116.224.124 on February 13, 2026 from IP address 163.116.224.124.

1980–2099 based on HadGEM2-ES (32) derived from CMIP5. The simulations were carried out under a scenario of constant CO_2 concentration (380 ppm in 2000) and full irrigation, to exclude the possibility of covariance with CO_2 and precipitation. More detailed information about the simulations can be found in refs. 1 and 33. Temperature impact values were calculated from yield changes between 2029 and 2058 (+2 °C of global mean temperature) and 1981–2010 (baseline), which were then halved to give +1 °C of global temperature impact. For global or country results, all of the grids were averaged by weighting the corresponding growing area of each crop (29).

Point-Based Ensemble Simulations. The AgMIP (30) also conducted crop yield simulations at 30, 4, and 4 representative sites around the world (*SI Appendix*, Fig. S1) by using 30 wheat, 13 rice, and 19 maize models, respectively. For wheat, a scenario of +2 °C was created by adjusting each day's temperature by +2 °C relative to the baseline (1981–2010), with other factors being constant. For rice and maize, the +3 °C scenarios were used. Model details about simulations for each crop can be found in refs. 7, 11, and 12. The temperature impact was calculated as the yield change during the warming period relative to the yield during the baseline period normalized to +1 °C impact, assuming the impact showed a linear temperature response. To obtain values for impacts at the country scale, each country was deemed to be similar to one or more representative sites located in said (or nearby) country. As local temperature change can be different from the country mean, the local point-based estimates were scaled up by multiplying each country's temperature factor produced by HagGEM2-ES (28), as in ref. 7. The weighted average temperature impacts over all of the countries were used to estimate the global scale impact, weighted by country-level production (14). It should be noted that the results from only four sites were used to represent all of the rice-/maize-producing countries, which might not encompass all of the uncertainties from diverse production systems and is also one limitation in our analysis. No point-based model-ensemble simulations for soybean were conducted in AgMIP.

Field-Warming Experiments. We started with all published peer-reviewed studies that applied artificial warming treatments on field crops. To avoid short-term noise, we only selected studies of crops that received all-day warming treatments for >2 mo. Results from laboratory incubators or controlled environments with constant day–night temperature treatment (e.g., 37/29 °C vs. 29/21 °C) were excluded. The studies with temperature change (ΔT) unequal to +1 °C were adjusted to +1 °C impact by dividing the impact value by ΔT, which assumed a linear relationship between impacts and ΔT. The studies that produced temperature impacts of >50% per °C were deemed as outliers and excluded. A total of 46 published studies (available from the corresponding author upon request) and 48 sites (*SI Appendix*, Fig. S1) were therefore included in the following analysis. Most of the sites (41 of 48) had a warming magnitude of 1.5–3.0 °C, similar to the grid- and point-based simulations. The upscaling methods from site to country to global scale are the same as for the point-based model simulations.

Statistical Regressions. Statistical models used regression equations to link historical year-to-year variations in yield to variations in selected climate variables. Different detrending methods were applied in the model to remove the influence of adaptation measures, such as crop management. In the statistical regression studies used here, the global-level results of regressions A and B (Fig. 2*A*) used detrending methods with the inclusion of a quadratic time trend and first differences, respectively, and resulted in more similar temperature impacts than grid- or point-based simulations. A similar result was found for the country-level regressions A and C (the country-level results are in Fig. 3), which used detrending methods with inclusion of a quadratic time trend and first-differences method, respectively. The results from statistical models were from 13 published studies (available from the corresponding author upon request). The interannual fluctuation in temperature over the globe is ∼2 °C (8), similar to the warming magnitude used in other methods. To ensure comparability of results, reported values under local temperature changes were normalized to global surface temperature changes by multiplying the corresponding temperature factor produced by HagGEM2-ES (28).

Multimethod Ensemble. The above four methods constituted the method ensemble that we used to estimate multimethod means and uncertainties. In this study, values from the method ensembles were synthesized at site, country, and global scales. At the country scale, the temperature impacts from regression methods were only reported for the five countries producing each crop; thus, the results mainly focus on the relevant top five countries. The uncertainty for the method ensemble was calculated by using a formula: $\mathrm{var}(Y) = \mathrm{var}(E(Y|\mathrm{method})) + E(\mathrm{var}(Y|\mathrm{method}))$, where the term $\mathrm{var}(E(Y|\mathrm{method}))$ is a measure of the variability between methods, and $E(\mathrm{var}(Y|\mathrm{method}))$ is a measure of the average variability within methods, assuming that this is random sample of approaches from a population of approaches. Confidence intervals (CIs) at 95% were calculated for the multimethod mean as: 95% CI = mean of methods $\pm$ 1.96 $\times\sqrt{\mathrm{var}(Y)}$.

Comparisons Between Methods. A recent study by Liu et al. (2016) (10) compared the temperature impacts on wheat yield estimated by three different methods. We extended the analyses by including a large number of datasets from site-based observations (field-warming experiments) and comparing estimated impacts on yields of wheat, rice, maize, and soybean—the four most important staple crops for humans. At the country scale, different methods were compared across countries. For the regression method, the results were only reported for the five major countries producing each crop, and thus the comparisons only focused on the relevant five countries. At the site scale, grid-based simulations were compared with site-based simulations and field-warming experiments. Grids containing sites of point-based simulations or warming experiments were selected. The comparisons include absolute yield under different temperature scenarios and relative temperature impacts. The baseline and temperature period for each grid was determined when the rolling 30-y annual mean temperature was equal to the baseline and increased temperatures used for point-based simulations and experiments. The temperature impact was calculated as the yield changes relative to the baseline and then adjusted to a +1 °C global temperature impact.

Prediction of Yield Changes by the End of Century. The yield change by the end of century was calculated as the products of the ensemble estimated yield response and projections of global temperature rise from CMIP5. As the yield response (Fig. 2*A*) and predicted temperature change (Fig. 1*B*) both have uncertainties, a bootstrap resampling approach was used to obtain the predicted yield change and its uncertainty. At each instance of bootstrap resampling, one pair of values for yield response and temperature change was sampled, respectively, from their original data to calculate the predicted yield change; this procedure assumes the chosen value is a random sample from a population of values. Repeating the above process 5,000 times gave 5,000 values of predicted yield change, which constitute a new distribution of the predicted yield change. The 2.5th–97.5th percentile was deemed as the boundaries of uncertainty for the predicted yield change.

ACKNOWLEDGMENTS. This study was supported by National Natural Science Foundation of China Grants 41530528 and 41561134016; 111 Project Grant B14001; and the National Youth Top-Notch Talent Support Program in China. We thank the Agricultural Model Intercomparison and Improvement Project (AgMIP). S.A. was supported by the Consultative Group on International Agricultural Research (CGIAR) Research Program on Climate Change, Agriculture and Food Security, and the CGIAR Research Program on Wheat and the Wheat Initiative. B.L. and Y.Z. were supported by National High-Tech Research and Development Program of China Grant 2013AA102404, the 111 Project Grant B16026 and the Priority Academic Program Development of Jiangsu Higher Education Institutions. C.M. was supported by MACMIT (climate mitigation in agricultural production systems through sustainable resource management) Project Grant 01LN1317A, funded through the German Federal Ministry of Education and Research. P.C., I.A.J., and J.P. were supported by European Research Council Synergy Grant ERC-SyG-2013-610028 IMBALANCE-P. P.C. was also supported from the French Agence Nationale de la Recherche (ANR) Convergence Lab Changement climatique et usage des terres (CLAND). F.E. was supported by German Science Foundation Project EW 119/5-1 and by the Joint Programming Initiative for Agriculture, Climate Change, and Food Security Modelling European Agriculture with Climate Change for Food Security Project through German Federal Ministry of Food and Agriculture Grant 2815ERA01J.

1. Rosenzweig C, et al. (2014) Assessing agricultural risks of climate change in the 21st century in a global gridded crop model intercomparison. *Proc Natl Acad Sci USA* 111: 3268–3273.
2. Wheeler T, von Braun J (2013) Climate change impacts on global food security. *Science* 341:508–513.
3. Porter JR, Gawith M (1999) Temperatures and the growth and development of wheat: A review. *Eur J Agron* 10:23–36.
4. Ottman MJ, Kimball BA, White JW, Wall GW (2012) Wheat growth response to increased temperature from varied planting dates and supplemental infrared heating. *Agron J* 104:7–16.

Downloaded from https://www.pnas.org by 163.116.224.124 on February 13, 2026 from IP address 163.116.224.124.

5. Nelson GC, et al. (2010) *Food Security, Farming, and Climate Change to 2050: Scenarios, Results, Policy Options*, IFPRI Research Monograph (International Food Policy Research Institute, Washington, DC).
6. Zhao C, et al. (2016) Plausible rice yield losses under future climate warming. *Nat Plants* 3:16202.
7. Asseng S, et al. (2015) Rising temperatures reduce global wheat production. *Nat Clim Chang* 5:143–147.
8. Lobell DB, Field CB (2007) Global scale climate-crop yield relationships and the impacts of recent warming. *Environ Res Lett* 2:1–7.
9. Lobell DB, Schlenker W, Costa-Roberts J (2011) Climate trends and global crop production since 1980. *Science* 333:616–620.
10. Liu B, et al. (2016) Similar estimates of temperature impacts on global wheat yield by three independent methods. *Nat Clim Chang* 6:1130–1136.
11. Li T, et al. (2015) Uncertainties in predicting rice yield by current crop models under a wide range of climatic conditions. *Glob Change Biol* 21:1328–1341.
12. Bassu S, et al. (2014) How do various maize crop models vary in their responses to climate change factors? *Glob Change Biol* 20:2301–2320.
13. Lobell DB (2007) Changes in diurnal temperature range and national cereal yields. *Agric For Meteorol* 145:229–238.
14. Food and Agriculture Organization of the United Nations (2014) FAOSTAT. Available at www.fao.org/faostat/en/. Accessed August 16, 2016.
15. Van OM, Schapendonk AHCM, Jansen MJH, Pot CS, Maciorowski R (1999) Do open-top chambers overestimate the effects of rising CO_2 on plants? An analysis using spring wheat. *Glob Change Biol* 5:411–421.
16. Tian Y, et al. (2012) Warming impacts on winter wheat phenophase and grain yield under field conditions in Yangtze Delta Plain, China. *Field Crops Res* 134:193–199.
17. Ewert F, et al. (2015) Crop modelling for integrated assessment of risk to food production from climate change. *Environ Model Softw* 72:287–303.
18. Schlenker W, Roberts MJ (2009) Nonlinear temperature effects indicate severe damages to U.S. crop yields under climate change. *Proc Natl Acad Sci USA* 106: 15594–15598.
19. Long SP, Ainsworth EA, Leakey AD, Nösberger J, Ort DR (2006) Food for thought: Lower-than-expected crop yield stimulation with rising CO_2 concentrations. *Science* 312:1918–1921.
20. Brisson N, et al. (2010) Why are wheat yields stagnating in Europe? A comprehensive data analysis for France. *Field Crops Res* 119:201–212.
21. Ray DK, Ramankutty N, Mueller ND, West PC, Foley JA (2012) Recent patterns of crop yield growth and stagnation. *Nat Commun* 3:1293.
22. Asseng S, Foster IAN, Turner NC (2011) The impact of temperature variability on wheat yield. *Glob Change Biol* 17:997–1012.
23. Zhao C, et al. (2016) Field warming experiments shed light on the wheat yield response to temperature in China. *Nat Commun* 7:13530.
24. Porter JR, et al. (2014) *Climate Change 2014: Impacts, Adaptation and Vulnerability: Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, eds Field CB, et al. (Cambridge Univ. Press, Cambridge, UK).
25. Tack J, Barkley A, Nalley LL (2015) Effect of warming temperatures on US wheat yields. *Proc Natl Acad Sci USA* 112:6931–6936.
26. Lesk C, Rowhani P, Ramankutty N (2016) Influence of extreme weather disasters on global crop production. *Nature* 529:84–87.
27. Lobell DB, et al. (2014) Greater sensitivity to drought accompanies maize yield increase in the U.S. Midwest. *Science* 344:516–519.
28. Flato G, et al. (2013) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, eds Stocker TF, et al. (Cambridge Univ Press, Cambridge, UK), pp 741–882.
29. Chad M, Navin R, Foley JA (2008) Farming the planet: 2. Geographic distribution of crop areas, yields, physiological types, and net primary production in the year 2000. *Global Biogeochem Cycles* 22:89–102.
30. Rosenzweig C, et al. (2013) The agricultural model intercomparison and improvement project (AgMIP): Protocols and pilot studies. *Agric For Meteorol* 170:166–182.
31. Warszawski L, et al. (2014) The Inter-Sectoral Impact Model Intercomparison Project (ISI-MIP): Project framework. *Proc Natl Acad Sci USA* 111:3228–3232.
32. Hempel S, Frieler K, Warszawski L, Schewe J, Piontek F (2013) A trend-preserving bias correction–the ISI-MIP approach. *Earth Syst. Dynam.* 4:219–236.
33. Elliott J, et al. (2014) The Global Gridded Crop Model intercomparison: Data and modeling protocols for phase 1 (v1.0). *Geosci. Model Dev. Discuss.* 7: 4383–4427.

Downloaded from https://www.pnas.org by 163.116.224.124 on February 13, 2026 from IP address 163.116.224.124.

Science of the Total Environment 825 (2022) 153820

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Impacts of 1.5 °C and 2 °C global warming on Eucalyptus plantations in South America

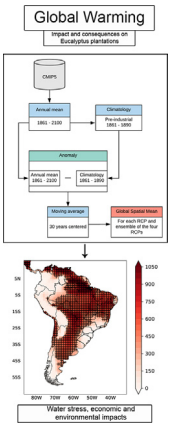
Fabrina Bolzan Martins [a,*], Rafael Bitencourt Benassi [a], Roger Rodrigues Torres [a], Francisco Agustinho de Brito Neto [b]

[a] Natural Resources Institute, Federal University of Itajubá, Unifei, Itajubá, Minas Gerais State, Brazil
[b] Meteorological and Water Resources Foundation of Ceará – FUNCEME, Fortaleza, Ceará State, Brazil

HIGHLIGHTS

- Water availability is analyzed under two global warming thresholds in South America.
- *Eucalyptus* will suffer water availability reductions in large parts of the continent.
- Increases in evapotranspiration and water deficits are projected.
- Traditional areas may become unsuitable for Eucalyptus plantations.
- Unsuitable area for planting Eucalyptus may reach 56.8% of South America at 2 °C.
- Outlining adaptation measures is essential to mitigate reduction in suitable areas.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 14 December 2021
Received in revised form 7 February 2022
Accepted 8 February 2022
Available online 11 February 2022

Editor: Elena PAOLETTI

Keywords:
Paris agreement
Water stress
Forest management
General circulation models
CMIP5

ABSTRACT

Even if the maximum global warming thresholds established by the Paris Agreement (1.5 and 2 °C relative to pre-industrial levels) are not exceeded, part of the climate system impacts resulting from this warming will be unavoidable. Forestry industries may be especially vulnerable, due to water shortages and the inability of growing certain forest species. An important part of the South American economy depends on the forestry sector (between 2 to ~7% of the Gross Domestic Product), mainly products derived from Eucalyptus, and so evaluating water availability considering the temperature thresholds established by the Paris Agreement will be fundamental. This study analyzed increased global average temperatures at 1.5 °C and 2 °C, and the impacts on water availability, using the Climatic Water Balance (CWB), and also studied possible impacts on Eucalyptus plantations in South America. Monthly temperature and precipitation data obtained from a set of simulations and projections of 26 General Circulation Models (GCMs) were used, in four Representative Concentration Pathway (RCP) scenarios. The CWB was calculated for three periods: i) the pre-industrial period (1861–1890), ii) the present period (1975–2005), and iii) the period when temperature projections are expected to reach global average increases of 1.5 °C and 2 °C. Due to changes in the CWB, with increases in actual evapotranspiration, water deficits, and a reduced water surplus, Eucalyptus plantations will be negatively affected and economically unfeasible for about 49.2% to 56.7% of all of South America, including a large part of the Amazon region,

Abbreviations: AE, actual evapotranspiration; AWC, available soil water capacity; CMIP5, Coupled Model Intercomparison Project Phase 5; CMIP6, Coupled Model Intercomparison Project Phase 6; COP21, Conference of the Parties; CWB, Climatic Water Balance; ETc, crop evapotranspiration; GCM, General Circulation Models; Kc, crop coefficient; PET, potential evapotranspiration; PWL, accumulated potential water loss; RCPs, Representative Concentration Pathways; SWHC, soil water holding capacity; SWS, soil water storage; SWSA, soil water storage between two consecutive periods; WD, Water deficit; WS, Water surplus.

* Corresponding author.
E-mail address: fabrina@unifei.edu.br (F.B. Martins).

http://dx.doi.org/10.1016/j.scitotenv.2022.153820
0048-9697/© 2022 Elsevier B.V. All rights reserved.

northern South America, midwestern and northeastern Brazil, western portions of Bolivia, Paraguay, central/northern Argentina, and northern Chile. Only some parts of South America, like the southern and southeastern regions of Brazil, Uruguay, southern Argentina and Chile, Andes Mountain Range, and northwestern South America, will not suffer water deficits, and Eucalyptus plantations will be less impacted in these regions. Large parts of South America will suffer from changes in water availability. The future of the forestry industry, and especially Eucalyptus plantations in these regions, will depend on urgent and effective adaptation measures.

1. Introduction

Eucalyptus is the most widely planted hardwood genus worldwide, covering about 25 million ha (Elli et al., 2020a). In South America, there are more than 10 million ha of cultivated areas. Brazil is the largest Eucalyptus producer, at 7.5 million ha of planted Eucalyptus, while Uruguay has 726 thousand ha planted, Argentina has 350 thousand ha planted, Chile has 200 thousand ha planted, and Ecuador has 164 thousand ha planted (Elli et al., 2020a; Resquin et al., 2020; FAO 2021). Eucalyptus adapts to a wide range of different soils and climatic conditions, and is known for growing quickly, having short rotation periods (commonly about 6–8 years), and is used for various raw materials, e.g., pulp and paper, charcoal, lumber and for civil industry (Martins et al., 2014). Also, Eucalyptus trees provide renewable resources for beekeepers, and help reduce deforestation in native forest areas. These characteristics have driven rapid Eucalyptus adoption in South America (Gonçalves et al., 2013; Martins et al., 2014; Binkley et al., 2017; Elli et al., 2019; Resquin et al., 2020), constituting an important economic resource for these countries.

Despite significant advances in clone adaptation, improvements in management practices, soil preparation and fertilization, and pest and disease control, Eucalyptus productivity is still strongly influenced by climate variability (Gonçalves et al., 2017; Elli et al., 2020a; Resquin et al., 2020). The main limiting factor for Eucalyptus is water scarcity, in the form of prolonged periods or intermittent periods of drought (Martins et al., 2008; Queiroz et al., 2017; Câmara et al., 2020; Elli et al., 2020a, 2020b; Abreu et al., 2022), along with temperature fluctuations outside threshold levels for good Eucalyptus plant development (from 8.5 °C to ~40 °C) (Martins and Streck, 2007; Freitas et al., 2017). Both conditions cause a series of physiological (short to long term), morphological, and anatomical changes and anomalies that can lead to reduced productivity, increased tree mortality, and yield gaps (Bahuguna and Jagadish, 2015; Elli et al., 2020a; Fagundes et al., 2021; Reis et al., 2021). These threats may be even greater in South America, where Eucalyptus plantations continue to expand into less suitable tropical environments where water deficits are more intense, and where higher temperatures prevail (González-Orozco et al., 2016; Elli et al., 2020a; Freitas et al., 2021). Moreover, climate projections point to significant changes in temperature, precipitation, and moisture flow patterns in South America (Torres and Marengo, 2013; Llopart et al., 2020; Penna et al., 2021; Torres et al., 2021), which may modify water availability (Alves et al., 2020; Elli et al., 2020b), and consequently aggravate soil water deficits in some regions (Santos et al., 2017; Resende et al., 2019; Alves et al., 2020).

To reduce risks and impacts to natural ecosystems, the 21st Conference of the Parties (COP21) proposed a new international agreement called the Paris Agreement, which seeks to stabilize average global warming at 1.5 °C and 2.0 °C, relative to pre-industrial levels (Hallegatte et al., 2016; Knutti et al., 2016; IPCC, 2018). Although an exact threshold for climate disruptions cannot be completely projected, temperature increases above the thresholds established at COP21 could severely impact natural ecosystems, species adaptability (Allen et al., 2018; IPCC, 2018; Hoegh-Guldberg et al., 2018; Silva et al., 2019; Lapola et al., 2020), water availability, and suitability for certain crops, like Eucalyptus (e.g., Gonçalves et al., 2013; Elli et al., 2020a), and consequently the sustainability of the agricultural and forestry sectors (Torres et al., 2021).

For these reasons, climate risk assessments on water availability considering the thresholds set at COP21 are very important for Eucalyptus forestry planning, since identifying possible risks, and providing climate-resilient decision-making could help abate these risks. One way of assessing climate risks on water availability is by using future climate projections generated by General Circulation Models (GCMs) for calculating the Climatic Water Balance (CWB) for when 1.5 °C and 2 °C global warming levels are reached (Santos et al., 2017; Alves et al., 2020). The CWB can provide important water availability information for present and future climates, like actual evapotranspiration (AE), water deficit (WD), and water surplus (WS) at the regional level (Sentelhas et al., 2008; Almeida and Sands, 2016; Santos et al., 2017; Alves et al., 2020), providing necessary information for climate risk management practices.

Studies assessing the impacts of the thresholds established in the Paris Agreement are still scarce (Karmalkar and Bradley, 2017; Alfieri et al., 2017; IPCC, 2018; Fu et al., 2018; Chen and Sun, 2019; Torres et al., 2021). Few works have been carried out, and the ones that have, generally focus on analyzing climate temperature and precipitation patterns associated with warming at these thresholds. One example is a study by Torres et al. (2021), who analyzed spatial patterns for warming at 1.5 °C and 2 °C in South America. No studies, however, analyzed impacts on water availability, and the consequences to Eucalyptus plantations. Given the scarcity of studies of this nature, this study seeks to analyze the impacts of increases in global average temperatures at 1.5 °C and 2 °C, relative to pre-industrial levels, on the CWB and on Eucalyptus cultivation in South America, and propose adaptation measures in light of these impacts.

2. Data and methods

2.1. Climate data

This study analyzed climate simulations and projections from a set of GCMs available in the CMIP5 - Coupled Model Intercomparison Project Phase 5 (Taylor et al., 2012), for each continental grid point in South America (Fig. 1). Monthly data on near surface air temperature (°C) and precipitation (mm day^{-1}) were used from a set of historical simulations (1850–2005) and projections (2006–2100) for 26 CMIP5 GCMs (Table 1). Data were provided by the World Climate Research Program, made available via the Earth System Grid data portal, available at https://esgf-data.dkrz.de/search/cmip5-dkrz.

The GCMs have horizontal resolution ranging from 0.8° to 3.8° latitude/longitude (Table 1). The data were interpolated to a regular grid of 1° × 1° latitude/longitude, for comparison's sake, using first-order conservative remapping (Jones, 1999), which is suitable for areal mean values, because it conserves mass by accounting for gradients in the interpolated field (Jones, 1999; Chen and Knutson, 2008; Torres et al., 2021).

CMIP5 climate projections are performed using four emissions scenarios, which are called the Representative Concentration Pathways (RCP) (Moss et al., 2010). In this study, we used RCPs 2.6, 4.5, 6.0, and 8.5, corresponding to approximate radiative forcing by the end of the century at 2.6 W m^{-2} (CO_2 equivalent ≈ 490 ppm), 4.5 W m^{-2} (CO_2 equivalent ≈ 650 ppm), 6.0 W m^{-2} (CO_2 equivalent ≈ 850 ppm), and 8.5 W m^{-2} (CO_2 equivalent ≈ 1370 ppm), relative to pre-industrial levels, respectively (Moss et al., 2010; van Vuuren et al., 2011). The RCPs 2.6, 4.5, 6.0 and 8.5, used 14, 22, 9 and 26 models, respectively, resulting in 71 numerical experiments (Table 1). In this way, uncertainties regarding the different configurations of the GCMs and different trajectories of emissions of greenhouse gases and aerosols are taken into account.

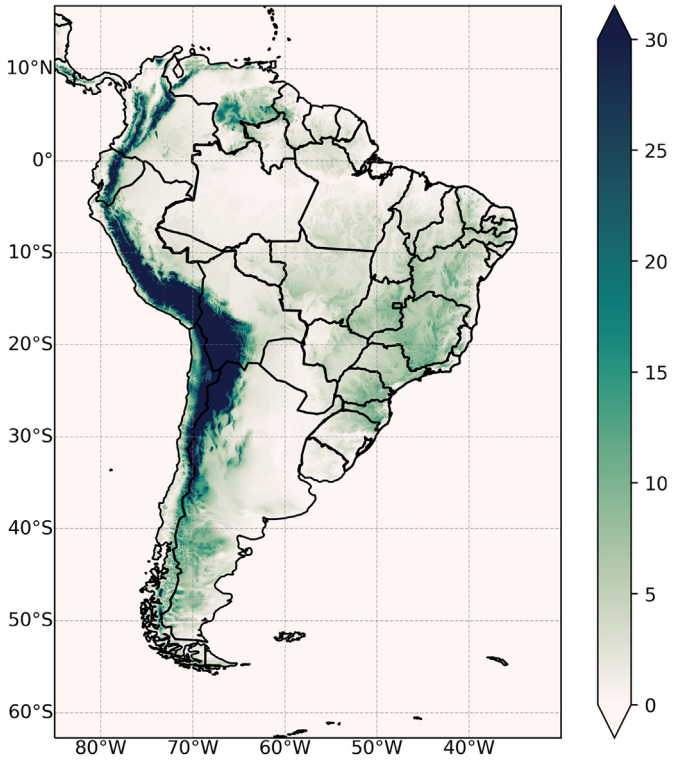


Fig. 1. The topography ($\times 10^2$ m) and domain of the study.

2.2. Steps for calculating the climatic water balance for Eucalyptus

Torres et al. (2021) established warming periods at 1.5 °C and 2 °C, relative to pre-industrial levels, for all of South America, and analyzed monthly spatial temperature and precipitation patterns over the occurrence period for both thresholds. In this study, we used findings from Torres et al. (2021) to calculate the CWB.

To estimate the periods of occurrence and the respective 1.5 °C and 2 °C global warming patterns, in relation to the pre-industrial period (1861–1890), some steps were used as follows. First, the annual mean temperature values were calculated for all GCMs simulations and projections (1861 to 2100). With the annual means series, it was obtained the climatological mean temperature for the pre-industrial period (1861 to 1890) for each GCM. Then, it was calculated an annual series of temperature anomalies, by subtracting the annual value of each GCM from its respective pre-industrial climatology. To remove climate variability on a scale of less than 30 years, a simple 30 years - centered running mean filter was applied in the anomalies series, resulting in annual anomalies smoothed series for the period from 1876 to 2085. To identify the respective years of the global temperature increase by 1.5 °C and 2 °C, a global spatial average was calculated from the series of smoothed annual anomalies, for each GCM and RCP.

For the spatial analysis, an average of all projections available was calculated within each RCP, using the annual series of smoothed anomalies for each GCM in its determined year of reaching the threshold (1.5 °C and 2 °C). Finally, it was averaged the projections for the four RCPs. The procedure for obtaining precipitation patterns was similar to the temperature data, except in the step of calculating the global average, which was not necessary for this variable.

The CWB was calculated for three periods: i) pre-industrial period (1861–1890), ii) present period (1975–2005), and iii) for periods where projections are expected to reach average global warming temperature increases of 1.5 °C and 2 °C (Torres et al., 2021). The present period was the most current period of all the GCMs simulations belonging to the CMIP5, and was used to demonstrate impacts on the CWB that have already occurred, according to the GCMs, and the magnitude of future impacts.

The CWB for Eucalyptus was calculated according to a version of the Thornthwaite and Mather (1955 and 1957) method, which was simplified by Pereira (2005), and later modified by Dourado-Neto et al. (2010). Although this method requires low input data (air temperature, precipitation and evapotranspiration), it is widely used because it supplies accurate and coherent estimates of water balance components, i.e., AE, WD and WS values, on a monthly scale (Dourado-Neto et al., 2010; Santos et al., 2017; Alves et al., 2020; Lima et al., 2021). Additionally, the CWB method used in this study coherently expresses the soil water storage in arid, semi-arid and humid climates, and when there is more than one dry season per year (Dourado-Neto et al., 2010; Alves et al., 2020), which is a common situation in several South American locations. All methodological steps for calculating CWB are demonstrated in Fig. 2. The theoretical background and detailed procedures for calculating the CWB method used in this study can be found in Pereira (2005), Dourado-Neto et al. (2010) and Alves et al. (2020).

The CWB provides soil water availability through regional-scale AE, WD, and WS values (Santos et al., 2017; Alves et al., 2020; Lima et al., 2021). This method requires input data on monthly averages for near-surface air temperature, precipitation, crop evapotranspiration (ETc), calculated for each analyzed period (i, ii, and iii), and for available soil water capacity (AWC, mm). For periods i and ii, climatological monthly averages from 1861 to 1890 and 1975–2005 were used, respectively. For period iii, climatological monthly averages (30 years) were calculated centered on the year when global warming would be 1.5 °C and 2 °C (Torres et al., 2021). To synthesize the results and reduce uncertainties associated with the internal variability of the GCMs and the emission scenarios used (Torres and Marengo, 2013), the average of the variables from the set of all GCMs and RCPs was used to calculate the analyzed CWB.

The ETc was obtained from the product of potential evapotranspiration (PET) and the crop coefficient (Kc). The PET was estimated using a modified version of the Thornthwaite (1948) method proposed by Willmott et al. (1985), which applies adjustments for mean monthly

Table 1
List of models, approximate horizontal resolutions (degrees of latitude/ longitude), simulations (historical period), and projections (RCPs) for the Coupled Model Intercomparison Project Phase 5 (CMIP5) dataset analyzed in this study. The asterisks (dashes) indicate whether the model has (does not have) a respective RCP scenario.

Models	Horizontal resolutions ×	Simulations	RCP			
			2.6	4.5	6.0	8.5
CMCC-CMS	3.7° × 3.8°	*	–	*	–	*
CMCC-CESM	3.4° × 3.8°	*	–	–	–	*
FGOALS-g2	2.8° × 2.8°	*	*	*	–	*
MIROC-ESM	2.8° × 2.8°	*	*	*	*	*
MIROC-ESM-CHEM	2.8° × 2.8°	*	*	*	*	*
CanESM2	2.8° × 2.8°	*	*	–	–	*
GISS-E2-H	2.0° × °2.5°	*	*	*	*	*
GISS-E2-H-CC	2.0° × °2.5°	*	–	*	–	*
GISS-E2-R	2.0° × °2.5°	*	*	*	*	*
GISS-E2-R-CC	2.0° × °2.5°	*	–	*	–	*
IPSL-CM5A-LR	1.9° × 3.8°	*	*	*	*	*
IPSL-CM5B-LR	1.9° × 3.8 °	*	–	*	–	*
CSIRO-Mk3.6.0	1.9° × 1.9°	*	*	*	*	*
MPI-ESM-LR	1.9° × 1.9°	*	*	*	–	*
MPI-ESM-MR	1.9° × 1.9°	*	*	*	–	*
INM-CM4	1.5° × 2.0°	*	–	*	–	*
CNRM-CM5	1.4° × 1.4°	*	*	*	–	*
IPSL-CM5A-MR	1.3° × 2.5°	*	*	–	*	*
ACCESS1.0	1.3° × 1.9°	*	–	*	–	*
ACCESS1.3	1.3° × 1.9°	*	–	*	–	*
HadGEM2-AO	1.3° × 1.9°	*	*	*	*	*
HadGEM2-CC	1.3° × 1.9°	*	–	*	–	*
EC-EARTH	1.1° × 1.1°	*	–	*	–	*
MRI-CGCM3	1.1° × 1.1°	*	*	*	*	*
MRI-ESM1	1.1° × 1.1°	*	–	–	–	*
CMCC-CM	0.8° × 0.8°	*	–	*	–	*

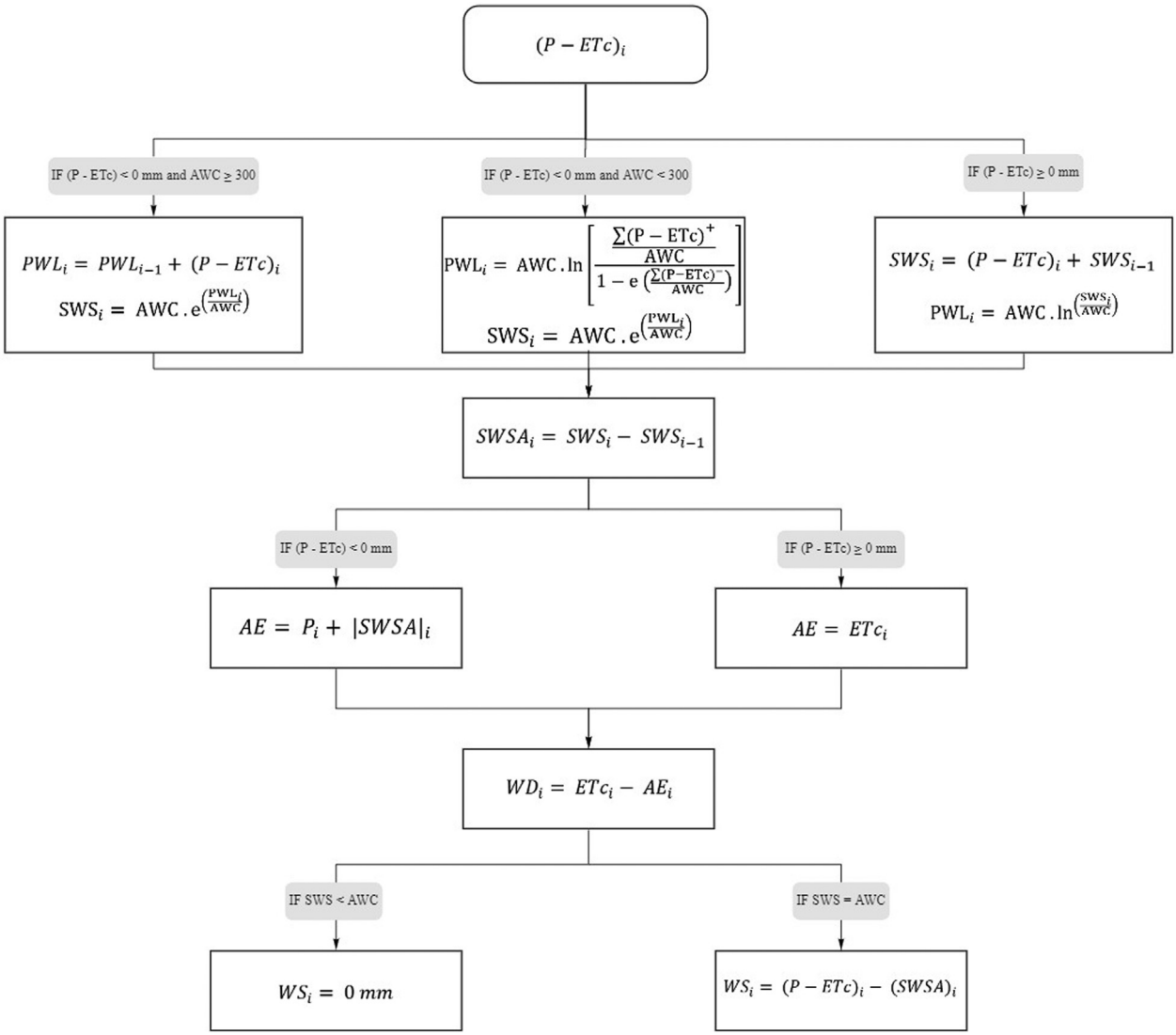


Fig. 2. Step by step to calculate the Climatic Water Balance (CWB) for obtaining actual evapotranspiration (AE, mm), water deficit (WD, mm), and water surplus (WS, mm). AWC = available soil water capacity (mm); ETc = crop evapotranspiration (mm); P = precipitation (mm); PWL = accumulated potential water loss (mm); SWS = soil water storage (mm); SWSA = soil water storage (mm) between the periods i and i-1; + = sum of the positive monthly P- ETc values (wet season); − = sum of the negative monthly P-ETc values (dry season). Since the CWB is calculated on a monthly scale, the i refers to the month of the year (1 = January, 2 = February, …, 12 = December).

air temperature above 26.5 °C and for daylight and month lengths (Aschonitis et al., 2022). Although this PET method is solely based on air temperature, it provides reliable estimates of monthly PET for longer time periods (Oudin et al., 2005; Gharbia et al., 2018). Hence, it is an optimum candidate for large scale PET applications (Willmott et al., 1985; Oudin et al., 2005; Bormann, 2011; Gharbia et al., 2018; Aschonitis et al., 2022), being the most widely used method in CWB studies under present and future climates (Santos et al., 2017; Pirovani et al., 2018; Alves et al., 2020; Lima et al., 2021). The Kc value for Eucalyptus was taken as 1.15 according to Allen et al., 1998; Tatagiba et al. (2015), and Freitas et al. (2020).

The AWC was obtained from the product of the soil water holding capacity (SWHC) and root depth. However, there is a lack of information on SWHC, specific to each soil type in South America, and on root depth for Eucalyptus. Therefore, to account for effects of different SWHC for all locations, we took SWHC = 1.00 mm cm^{-1}, taken from the average of three standard soil types (Elli et al., 2020b; Freitas et al., 2020; Resquin et al., 2020): i) clay soil with high SWHC (1.52 mm cm^{-1}); ii) sandy-clay soil with medium SWHC (0.90 mm cm^{-1}); and iii) sand-loam soil with low SWHC (0.60 mm cm^{-1}). Root depth was taken as 300 cm for the domain, according to Christina et al. (2017), Elli et al. (2020a), and Freitas et al. (2020). The adopted AWC value was 300 mm.

2.3. Impacts of 1.5 °C and 2 °C global warming on Eucalyptus plantations

The impacts of temperature increase on the CWB were analyzed via a representation of spatial annual AE, WD and WS patterns, obtained for each period analyzed, and by taking the difference of the values obtained for these respective periods of global average warming at 1.5 °C and 2 °C minus the pre-industrial period (1861 to 1890), or the present period (1975 to 2005). We chose to analyze the AE, WD and WS spatial pattern values calculated in the warming periods at 1.5 °C and 2 °C, with emphasis on analyzing WD values. Since WD is the leading cause of Eucalyptus yield losses in South American countries (Almeida and Sands, 2016; Elli et al., 2020a, 2020b; Resquin et al., 2020; Freitas et al., 2021; Abreu et al., 2022), we focused on areas with annual WD > 300 mm $year^{-1}$ (>AWC), as regions with water restrictions for Eucalyptus plantations, and therefore may be unsuitable areas for planting Eucalyptus. Regions with WD ≤

300 mm year^{-1} do not have water restrictions and are suitable for planting Eucalyptus.

3. Results and discussion

3.1. Spatial pattern of water balance for the pre-industrial and present periods

The spatial patterns of annual AE, WD and WS values simulated by the GCMs are analogous between the two analyzed periods (pre-industrial and present). However, there was a slight expansion of WD in the present period (Fig. 3). Places with higher AE levels are concentrated in the north Amazon, mainly in Amazonas state, Brazil, while higher WD values are concentrated in the north of northeast Brazil, in the extreme north of South America, northern Chile, and a strip extending from central/northern Argentina towards southern Amazon. Lastly, higher WS values are concentrated in northwestern South America, and extend over the entire Andes Mountain range.

Even with similar spatial patterns between the two periods, areas with higher AE intensity (positive), and WS (negative), and areas with WD > 300 mm year^{-1}, are slightly larger for the present period compared to pre-industrial levels, mainly in the northeast of Brazil. Areas affected by water restrictions are expected to increase more since the GCMs project, on average, warming thresholds reaching 1.5 °C in 2029, and 2 °C in 2044, relative to pre-industrial levels (Torres et al., 2021). Since the CWB patterns are similar between the pre-industrial and present periods, most of the changes, which will be presented in the next section, will occur in the future. We will focus our analysis on anomalies pertaining to the pre-industrial period.

3.2. Water balance under the Paris agreement thresholds

The climatological water balance for Eucalyptus in South America for the period of global average warming at 2 °C, and anomalies with respect to pre-industrial levels are shown in Fig. 4. For brevity's sake, patterns of magnitude and changes for global average warming at 1.5 °C were omitted, since they are very similar to the 2 °C pattern, except for a slight intensification of changes in some regions to 2 °C, like parts of the Amazon, and the extreme north of South America.

Regarding variable AE (Fig. 4A, D), there is an increase in areas with positive values (between ~100 and 500 mm year^{-1}) in a wide range in the northwest direction of South America/southeast Brazil, which extends to the southern regions of Brazil and the Brazilian northeast, Peru, and western Bolivia. The greatest increases are found for northwestern South America (between ~300 and 500 mm year^{-1}). Negative AE values (~−200 to 400 mm year^{-1}) are seen in the southern portion of northeastern Brazil, northern Amazonia, and the extreme north of South America, and less accentuated reductions are seen (~−50 to 100 mm year^{-1}) in northern Paraguay, eastern Bolivia, and south-central western Brazil.

Positive WD values are found for most of South America (Fig. 4B, E), except for northwestern South America, western Bolivia, and southern Brazil. The greatest magnitudes of change (up to 1000 mm year^{-1}) are for the extreme north of South America, most of northeastern Brazil, northern Paraguay, eastern Bolivia, and south-central western Brazil.

WS was the third variable analyzed in the CWB, and shows negative values over most of the territory, exceeding −150 mm year^{-1} (Fig. 4C, F). Places with negative WS values largely coincide with the aforementioned regions of increased AE, except for Peru and Ecuador, which had slight increases (~+100 mm year^{-1}).

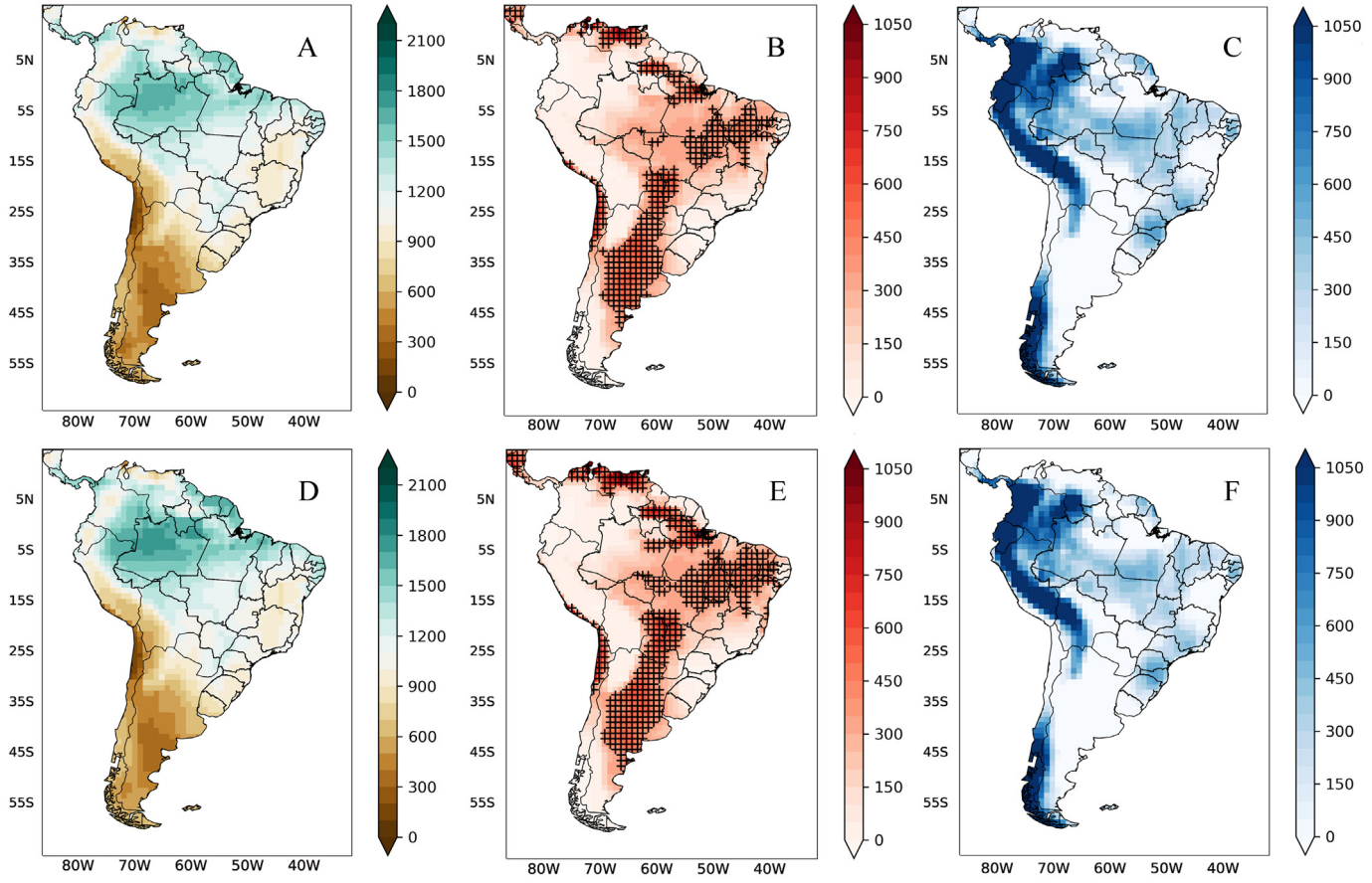


Fig. 3. Climatological water balance (mm year^{-1}) for Eucalyptus in South America: actual evapotranspiration (A, D), water deficit (B, E), and water surplus (C, F). The upper row refers to the pre-industrial period (1861–1890), and the lower row to the present period (1975–2005). Shaded areas in panels B and E indicate regions with water deficits greater than 300 mm year^{-1}.

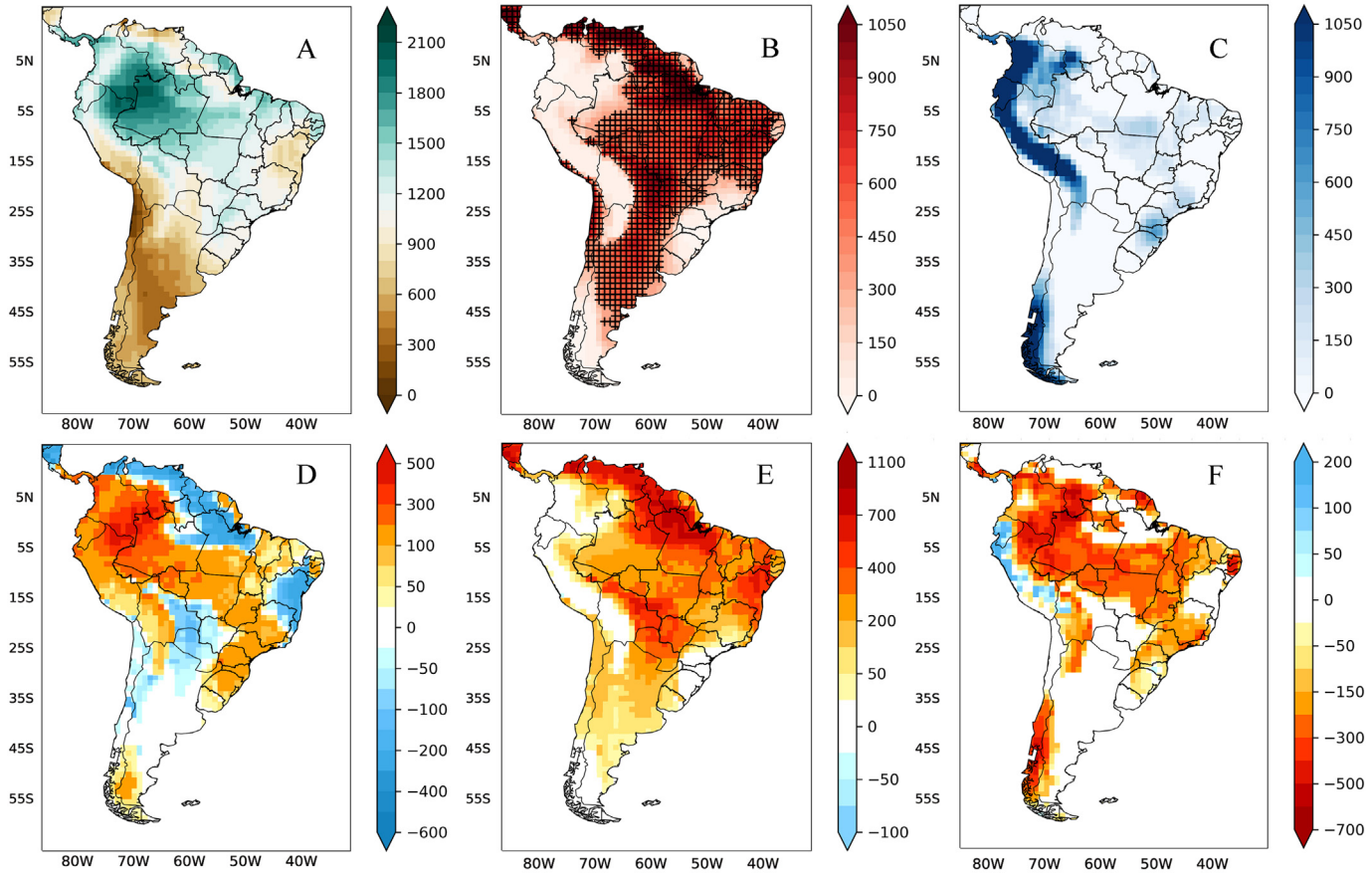


Fig. 4. Climatic water balance (mm year^{-1}) for Eucalyptus in South America for a + 2 °C global warming period (upper row) and anomalies with respect to pre-industrial levels (lower row). Actual evapotranspiration (A, D), water deficit (B, E), and water surplus (C, F). Shaded areas (B) indicate regions with water deficits greater than 300 mm year^{-1}.

Even using a reliable PET method in CWB studies (Willmott et al., 1985; Santos et al., 2017; Pirovani et al., 2018; Alves et al., 2020), it may underestimate the PET and ETc values in arid and semi-arid places (Gharbia et al., 2018; Monteiro et al., 2021), reflecting on the AE, WD and WS values. Thereby, the positive WD, and negative WS values found in this study (Fig. 4) may be even more intensified.

Four coupled patterns for these variables were present in South America, when analyzing variables AE, WD and WS, shown together in this study with temperature and precipitation pattern changes from Torres et al. (2021), for increased global mean temperatures at 2 °C.

The first pattern deals with locations with the highest projected WD increases (i.e., the extreme north of South America, most of northeastern Brazil, northern Paraguay, eastern Bolivia, and south-central western Brazil), which can be explained by reduced precipitation (up to −150 mm year^{-1}, in the far north of South America) and local projected increases in temperature above 2.5 °C, despite reductions in AE and no significant changes in WS.

The second pattern deals with places showing little or no change in WD (i.e., northwestern South America, western Bolivia, and southern Brazil). Increases in AE caused by significant increases in temperature (above 2 °C) are offset by projected increases in precipitation of up to +150 mm year^{-1} at these regions.

The third pattern is for northern Argentina and Uruguay, where small increases in WD (~ 25–50 mm year^{-1}) are projected, resulting from temperature increases above 1.5 °C and slight precipitation increases (~ 25–50 mm year^{-1}), but without significant implications for AE and WS.

Lastly, the fourth identified pattern is located over a large part of midwestern Brazil/southern parts of the Amazon basin, and projects expressive WD increases (~200 mm year^{-1}), which are brought about by a combination of increased temperature (>2.5 °C), increased AE (>75 mm year^{-1}), reduced precipitation (~ 25–75 mm year^{-1}), and reduced WS (150–300 mm year^{-1}).

3.3. Impacts on Eucalyptus plantations in South America

Spatial patterns of the analyzed components of the CWB at both warming thresholds (1.5 °C and 2 °C) indicate that Eucalyptus cultivation will be reduced or restricted to a few regions in South America. The southern region and southernmost part of southeast Brazil, east of Uruguay, Ecuador, Colombia, Peru, and west of the Amazon basin, west of Bolivia, and the northwest of Argentina will not suffer from water restrictions since WD is less than 300 mm year^{-1}. Nevertheless, most of the extreme north of South America and northeast Brazil, the south and east of the Amazon basin, midwestern Brazil, east Bolivia, Paraguay, central/northern Argentina, and northern Chile have water deficits greater than 300 mm year^{-1}. Furthermore, traditional Eucalyptus plantation areas may have cultivation restrictions, or become unsuitable or unfavorable for cultivations, even at the 1.5 °C warming threshold. For example, Minas Gerais, Mato Grosso do Sul, and Bahia States in Brazil, account for 51% of current cultivated Eucalyptus land area in Brazil (Gonçalves et al., 2013, 2017; Freitas et al., 2021), and Argentina currently has 350.00 ha of planted Eucalyptus. In these regions, WD can reach 750 mm year^{-1} with WS reductions at ~200–400 mm year^{-1} (Fig. 4).

Therefore, increased WD and reduced WS occur for practically half of South America, mainly in the tropical and subtropical areas, where there may be significant increases in unsuitable land for cultivating Eucalyptus, reaching ~57% of all of South America (Table 2).

Several studies analyzing precipitation and temperature in South America have already identified that the southern portions of the Amazon

Table 2
Proportions of suitable and unsuitable areas for cultivating Eucalyptus in South America, referring to the pre-industrial period (1861 to 1890), the present period (1975 to 2005), and global average warming at 1.5 °C and 2.0 °C.

Period	Suitable		Unsuitable	
	Percentage	Km² (10^4)	Percentage	Km² (10^4)
Pre-industrial	78.9	1407	21.1	376
Present	70.8	1262	29.2	521
Warming at 1.5 °C	50.8	905	49.2	878
Warming at 2 °C	43.2	769	56.8	1014

basin, the midwest, western Minas Gerais, and central Paraguay, Uruguay and Argentina are persistent climate change hotspots (Torres and Marengo, 2014; Darela Filho et al., 2016; Santos et al., 2017; Llopart et al., 2020; Resquin et al., 2020). Furthermore, these areas may reach the warming thresholds of 1.5 °C and 2 °C earlier (~ in 2030), compared to the rest of the continent (Torres et al., 2021). An additional increase of about 0.5 °C over all of South America, compared to the global average, as per Torres et al. (2021), combined with changes in precipitation patterns, will bring about impacts for Eucalyptus at both the individual and stand levels (Elli et al., 2020a; Resquin et al., 2020; Abreu et al., 2022), and negative effects will be seen throughout South America.

At the individual tree level, water stress induces physiological stresses, triggered by stomatal closure, promoting increases in the photorespiration/photosynthesis ratio and cell maintenance, in addition to reducing transpiration and photosynthetic activities, and changing cell wall synthesis and proteins (Rawal et al., 2015; Resquin et al., 2020; Abreu et al., 2022). As a defense mechanism, the plant reduces cell expansion, leaf expansion, dry matter allocation, and increases senescence and leaf abscission (Martins et al., 2008; Abreu et al., 2015; Resquin et al., 2020; Abreu et al., 2022). These impacts further reduce photosynthesis reactions, and could be minimized by increasing water use efficiency. However, some Eucalyptus species, like *Eucalyptus urophylla*, *Eucalyptus grandis*, *Eucalyptus saligna,* and *Eucalyptus cloeziana*, and hybrid *E. grandis* x *E. camaldulensis*, widely used in plantations in South America, do not change their water use efficiency under water deficit conditions (Martins et al., 2008; Hubbard et al., 2020; Abreu et al., 2022). Thus, these physiological/morphological changes, amplified over time, reduce height and diameter growth, and increase tree mortality, due to the lower competitive capacity of Eucalyptus trees at standing level (Martins et al., 2011; Martins et al., 2014; Rawal et al., 2015). In the medium and long term, all changes lead to reduced mean annual increments, and final productivity at the end of rotations (Elli et al., 2020a; Hubbard et al., 2020), and expand unsuitable areas for Eucalyptus plantations (Booth, 2017; Resquin et al., 2020).

Even with mostly negative impacts, some studies showed positive impacts, with increases in Eucalyptus productivity at specific locations in southern Brazil (Elli et al., 2020a), and little change in the distribution of *Eucalyptus grandis* in Uruguay (Resquim et al., 2020), both due to increased CO_2 concentration. This can be explained by the metabolism of Eucalyptus, which as a C3 plant, depends on atmospheric CO_2 and water availability for photosynthesis reactions (Booth, 2017; Elli et al., 2020a). Both in Southern Brazil and in Uruguay, there are no pronounced increases in WD at the 1.5 °C and 2 °C warming thresholds (Fig. 4), but increases in CO_2 concentration are projected (Moss et al., 2010; Riahi et al., 2017), justifying projections for increased productivity at these regions (Elli et al., 2020a). However, even if not fully known, the positive effects generated by increased CO_2 concentrations can be reduced by limiting the supply of phosphorus, which is commonly found in tropical and subtropical highly weathered soils (Tanner et al., 1998; Goll et al., 2012; Ellsworth et al., 2017). Soils with phosphorus limitations result in complete lacks in trunk, twig and foliage growth, and worsen wood quality (Ellsworth et al., 2017; Gonçalves et al., 2017). Additionally, imbalance in the photosynthesis/photorespiration ratio, caused by extreme temperatures above the proper thresholds for Eucalyptus (from 8.5 °C to ~40 °C) (Martins and Streck, 2007; Booth, 2017; Freitas et al., 2017), and stomatal closure, caused by water stress, are responsible for imbalances between water output (through transpiration) and CO_2 absorption (for photosynthesis) (Martins et al., 2008; Abreu et al., 2015; Abreu et al., 2022), and for a series of phenological anomalies, which promote damage to tree development, wood quality, and Eucalyptus productivity (Booth, 2017; Gonçalves et al., 2017; Elli et al., 2020a).

The future of Eucalyptus plantations in South America will depend on how fast plantations can adjust to the mostly harmful impacts coming from increased WD (AE and temperature), along with more timely and economic adaptation measures. The three adaptation measures that should be considered first, since they require longer execution times and more investments in research are: i) select genotypes (pure species or hybrids) that tolerate increases in air temperature, and have better water use efficiency, especially under water deficit conditions; ii) use interspecific hybrids with other Eucalyptus species, since they are more resilient to water stress (Gonçalves et al., 2013, 2017; Resquin et al., 2020; Abreu et al., 2022); and iii) improve hybridization techniques, or promote revolutions in plant breeding (molecular and conventional) to incorporate desired characteristics.

Improvements will also be needed for seedling production environments at nurseries (i.e., using shades and/or intensified irrigation), in the form of installing, conducting, and managing forest plantations (Gonçalves et al., 2013; Binkley et al., 2017; Hubbard et al., 2020; Fagundes et al., 2021; Reis et al., 2021), along with changing plantation locations (Pirovani et al., 2018; Câmara et al., 2020).

Regarding genotype selection, hybrid seedlings propagated via cloning are more advantageous compared to seed-originated seedlings of pure species (Gonçalves et al., 2013). Although genotypes propagated via cloning have lower genetic diversity and plasticity compared to seed-originated seedlings of pure species, clonal plantations from interspecific hybrids are more tolerant to water deficits (Gonçalves et al., 2013; Câmara et al., 2020; Abreu et al., 2022). The most recommended genotypes for locations with WD between 300 and 400 mm $year^{-1}$ are *E. urophylla* X *E. camaldulensis*, *E. tereticornis* X *E. brassiana*, *E. urophylla* X *E. tereticornis* (Gonçalves et al., 2013), *E. grandis* X *E. camaldulensis* (Hakamada et al., 2020), and the pure species are *E. urophylla* (Câmara et al., 2020; Abreu et al., 2022), *E. tereticornis*, *E. camaldulensis* and *Corymbia citriodora* (formerly known as *E. citriodora*) (Abreu et al., 2015).

When installing and managing forest plantations, planting spacing should be increased mainly in areas with greater WDs, and thinning and pruning should be conducted at shorter intervals (Hakamada et al., 2020; Hubbard et al., 2020; Resquin et al., 2020). Tighter-spaced plantings, for example 2 m × 2 m (with 2500 trees per ha), or 3 m × 2 m (with ~1600 trees per ha), widely employed in Brazil, have higher ETc and higher water consumption (Calder et al., 1997; Xie et al., 2015; Hakamada et al., 2020). Although several studies point to 3 m × 2 m spacing and stockings of 1000 to 1500 trees per ha as being ideal for obtaining volume and generating profit for the energy and pulp industries, only stockings below 1000 trees per ha suffer less water deficit stress (Hakamada et al., 2020) and have lower mortality rates (Martins et al., 2011, 2014). These stockings are achieved by wider spaced planting, at ideally 3.5 m × 3 m (Hakamada et al., 2020), using more intense thinning or at shorter intervals (Martins et al., 2011, 2014; Tateishi et al., 2015).

Several studies have shown that plantation location changes will be necessary (Booth, 2017; Pirovani et al., 2018; Freire et al., 2019; Resquin et al., 2020). Sites with WD < 300 mm $year^{-1}$ will continue to be suitable for plantations, however, sites with WD > 400 mm $year^{-1}$ will be unsuitable for Eucalyptus plantations, since they are economically unfeasible (Gonçalves et al., 2013, 2017). Plantations in locations with WD between 300 and 400 mm $year^{-1}$ should adopt irrigation techniques, mainly in the first months (~18 months) after transplanting the seedlings (Abreu et al., 2015, 2022; Câmara et al., 2020).

Lastly, pests and pathogens may increase with increased WD (and temperature) (Costa and Streck, 2018; Freire et al., 2019), thereby requiring biological controls, exposure to exotic natural agents, or adopting non-environmentally friendly strategies (Garlet et al., 2013;

Machado et al., 2016; Santana et al., 2003; de Santana and Burckhardt, 2007), by applying insecticides like Acetamiprid, Thiacloprid, Tiamethoxam, Lambda-cyhalothrin (Machado et al., 2016; Santana et al., 2003). Some examples of pests that attack Eucalyptus are the bronze bug (*Thaumastocoris peregrinus*) (Machado et al., 2016; Smaniotto et al., 2017), the bluegum chalcid (*Leptocybe invasa*) (Garlet et al., 2013), the redgum lerp psyllid (*Glycaspis brimblecombei*), and the bluegum psyllid (*Ctenarytaina eucalypti*) (Gonçalves et al., 2013).

4. Final considerations

Spatial patterns for actual evapotranspiration, water deficit, and water surplus have already undergone minor changes in the present (1975–2005) compared to the pre-industrial period (1861–1890). Even if the limits established in the Paris Agreement are not exceeded, impacts on actual evapotranspiration, water deficit, and water surplus will still affect Eucalyptus plantations in South America, generating vulnerabilities for the sector, or exacerbating vulnerabilities that already exist.

The spatial patterns of the analyzed components of the climatic water balance at both warming thresholds (1.5 °C and 2 °C) indicate that Eucalyptus plantations will be unsuitable and possibly economically unfeasible over about 49.2% to 56.7% of South America. A new agricultural border, known as MATOPIBA, which makes up parts of Maranhão, Tocantins, Piauí, and Bahia States, Brazil, may fail for Eucalyptus cultivation, since projected water deficit values are >500 mm year^{-1} (and water surplus <0).

The future of the forestry sector and Eucalyptus plantations in South America will depend on the speed with which adaptation measures are applied, which will include selecting genotypes that are more tolerant to increased air temperatures and have greater water-use efficiency under water deficit conditions. Adaptation measures should also include improvements to hybridization techniques, or revolutions in breeding programs (molecular and conventional), improvements in the seedling production environment at nurseries, and improved ways of installing, conducting and managing forest plantations, along with shifting plantation locations.

New analyses should be performed with recent state-of-the art GCMs (CMIP6), that have been evaluated in the IPCC Sixth Assessment Report (IPCC AR6), using different socioeconomic pathways (Eyring et al., 2016). Moreover, future studies could take into account additional important meteorological variables for impact evaluations, like soil moisture.

Availability of data and material

The data used in the article will be fully available, in order to contribute to transparency.

Code availability

Not applicable.

CRediT authorship contribution statement

Martins, F·B: Conceptualization, Methodology design, Data analysis, Writing, Review and Editing, Supervision, Project administration, Funding acquisition. **Benassi, R.B.**: Conceptualization, Methodology design, Data analysis, Data curation, Software, Writing and Editing. **Torres, R.R.**: Conceptualization, Methodology design, Data acquisition, Data analysis, Writing, Review and Editing, Funding acquisition. **Brito Neto' F.A.:** Data curation, Software.

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 paper.

Acknowledgements

The second author received support from the Coordination for the Improvement of Higher Education Personnel - CAPES (process number 88882.430040/2019-01). The first and third authors would like to thank the Minas Gerais State Research Support Foundation (FAPEMIG) for funding the APQ-01088-14 and APQ1258-17 projects. The authors also like to thank the Natural Resources Institute at the Federal University of Itajuba for providing subsidies for publishing this article.

References

Abreu, M.C., Martins, F.B., Freitas, C.H., Pereira, R.A.A., Melloni, E.G.P., 2015. Valores limítrofes para transpiração desenvolvimento e crescimento de Corymbia citriodora (Hook) KD Hill and LAS Johnson em resposta à deficiência hídrica no solo. Rev. Árvore 39 (5), 841–852. https://doi.org/10.1590/0100-67622015000500007.

Abreu, M.C., Soares, A.A.V., Freitas, C.H., Martins, F.B., 2022. Transpiration and growth responses by eucalyptus species to progressive soil drying. J. For. Res. 33 (1), 1–15. https://doi.org/10.1007/s11676-021-01448-z.

Alfieri, L., Bisselink, B., Dottori, F., Naumann, G., Roo, A., Salamon, O., Wyser, K., Feyen, L., 2017. Global projections of river flood risk in a warmer world. Earth's Future 5 (2), 171–182. https://doi.org/10.1002/2016EF000485.

Allen, R.G., Pereira, L.S., Raes, D., Smith, M., 1998. Crop evapotranspiration: guidelines for computing crop water requirements. FAO Irrigation and Drainage Paper. 56 Rome, Italy.

Allen, M.R., Dube, O.P., Solecki, W., Aragón-Durand, F., Cramer, W., Humphreys, S., Kainuma, M., Kala, J., Mahowald, N., Mulugetta, Y., Perez, R., Wairiu, M., Zickfeld, K., 2018. Framing and context. In: Masson-Delmotte, V., Zhai, P., Pörtner, H.-O., Roberts, D., Skea, J., Shukla, P.R., Pirani, A., Moufouma-Okia, W., Péan, C., Pidcock, R., Connors, S., Matthews, J.B.R., Chen, Y., Zhou, X., Gomis, M.I., Lonnoy, E., Maycock, T., Tignor, M., Waterfield, T. (Eds.), Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. In Press.

Almeida, A.C., Sands, P.J., 2016. Improving the ability of 3-PG to model the water balance of forest plantations in contrasting environments. Ecohydrology 9, 610–630. https://doi.org/10.1002/eco.1661.

Alves, A.M.M.R., Martins, F.B., Reboita, M.S., 2020. Balanço hídrico climatológico para Itajubá-MG: Cenário atual e projeções climáticas. Rev. Bras. de Climatolol. 26, 712–732. https://doi.org/10.5380/abclima.v26i0.70387.

Aschonitis, V., Touloumidis, D., ten Veldhuis, M.C., Coenders-Gerrits, M., 2022. Correcting Thornthwaite potential evapotranspiration using a global grid of local coefficients to support temperature-based estimations of reference evapotranspiration and aridity indices. Earth Syst. Sci. Data 14, 163–177. https://doi.org/10.5194/essd-14-163-2022.

Bahuguna, R.N., Jagadish, K.S.V., 2015. Temperature regulation of plant phenological development. Environ. Exp. Bot. 111, 83–90. https://doi.org/10.1016/j.envexpbot.2014.10.007.

Binkley, D., Campoe, O.C., Alvares, C., Carneiro, R.L., Cegatta, Í., Stape, J.L., 2017. The interactions of climate, spacing and genetics on clonal eucalyptus plantations across Brazil and Uruguay. For. Ecol. Manag. 405, 271–283. https://doi.org/10.1016/j.foreco.2017.09.050.

Booth, T.H., 2017. Impacts of climate change on eucalypt distributions in Australia: an examination of a recent study. Aust. For. 80, 208–215. https://doi.org/10.1080/00049158.2017.1365402.

Bormann, H., 2011. Sensitivity analysis of 18 different potential evapotranspiration models to observed climatic change at German climate stations. Clim. Chang. 104, 729–753. https://doi.org/10.1007/s10584-010-9869-7.

Calder, I.R., Rosier, P.T., Prasanna, K.T., Parameswarappa, S., 1997. Eucalyptus water use greater than rainfall input-possible explanation from southern India. Hydrol. Earth Syst. Sci. 1 (2), 249–256. https://doi.org/10.5194/hess-1-249-1997.

Câmara, A.P., Vidaurre, G.B., Oliveira, J.C.L., Picoli, E.A.T., Almeida, M.N.F., Roque, R.M., Filho, M.T., Souza, H.J.P., Oliveira, T.R., Campoe, O.C., 2020. Changes in hydraulic architecture across a water availability gradient for two contrasting commercial Eucalyptus clones. For. Ecol. Manag. 474 (15), e118380. https://doi.org/10.1016/j.foreco.2020.118380.

Chen, C.T., Knutson, T., 2008. On the verification and comparison of extreme rainfall indices from climate models. J. Clim. 21 (7), 1605–1621. https://doi.org/10.1175/2007JCLI1494.1.

Chen, H., Sun, J., 2019. Increased population exposure to extreme droughts in China due to 0.5 C of additional warming. Environ. Res. Lett. 14 (6), 064011. https://doi.org/10.1088/1748-9326/ab072e.

Christina, M., Nouvellon, Y., Laclau, J.P., Stape, J.L., Bouillet, J.P., Lambais, G.R.Le, Maire, G., 2017. Importance of deep water uptake in tropical eucalypt forest. Funct. Ecol. 31, 509–519. https://doi.org/10.1111/1365-2435.12727.

Costa, D.B., Streck, N.A., 2018. Duração da fase de muda em eucalipto simulada em cenários de aumento de temperatura. Ciênc. Florestal 28 (3), 1263–1279. https://doi.org/10.5902/1980509833378.

Darela Filho, J.P., Lapola, D.M., Torres, R.R., Lemos, M.C., 2016. Socio-climatic hotspots in Brazil: how do changes driven by the new set of IPCC climatic projections affect their relevance for policy? Clim. Chang. 136, 413–425. https://doi.org/10.1007/s10584-016-1635-z.

de Santana, D.L.Q., Burckhardt, D., 2007. Introduced Eucalyptus psyllids in Brazil. J. For. Res. 12 (5), 337–344. https://doi.org/10.1007/s10310-007-0035-7.

Dourado-Neto, D., de Jong van Lier, Q., Metselaar, K., Reichardt, K., Nielsen, D.R., 2010. General procedure to initialize the cyclic soil water balance by the Thornthwaite and Mather method. 67 (1), 87–95. https://doi.org/10.1590/S0103-90162010000100013.

Elli, E.F., Sentelhas, P.C., Freitas, C.H., Carneiro, R.L., Alvares, C.A., 2019. Intercomparison of structural features and performance of eucalyptus simulation models and their ensemble for yield estimations. For. Ecol. Manag. 450, e106325. https://doi.org/10.1016/j.foreco.2019.117493.

Elli, E.F., Sentelhas, P.C., Bender, F.D., 2020a. Impacts and uncertainties of climate change projections on eucalyptus plantations productivity across Brazil. For. Ecol. Manag. 474, e118365. https://doi.org/10.1016/j.foreco.2020.118365.

Elli, E.F., Sentelhas, P.C., Huth, N., Carneiro, R.L., Alvares, C.A., 2020b. Gauging the effects of climate variability on eucalyptus plantations productivity across Brazil: a process-based modelling approach. Ecol. Indic. 114, e118365. https://doi.org/10.1016/j.ecolind.2020.106325.

Ellsworth, D.S., Anderson, I.C., Crous, K.Y., Anderson, I.C., Crous, K.Y., Cooke, J., Drake, J.E., Gherlenda, A.N., Gimeno, T.E., Macdonald, C.A., Medlyn, B.E., Powell, J.R., Tjoelker, M.G., Reich, P.B., 2017. Elevated CO2 does not increase eucalypt forest productivity on a low-phosphorus soil. Nat. Clim. Chang. 7, 279–282. https://doi.org/10.1038/nclimate3235.

Eyring, V., Bony, S., Meehl, G.A., Senior, C., Stevens, B., Stouffer, R.J., Taylor, K.E., 2016. Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) experimental design and organization. Geosci. Model Dev. 9, 1937–1958. https://doi.org/10.5194/gmd-9-1937-2016.

Fagundes, F.F.A., Reis, Y.F.S., Martins, F.B., 2021. A model for predicting the initial development of two native forest species under current and future climates. Environ. Exp. Bot. 192, 104662. https://doi.org/10.1016/j.envexpbot.2021.104662.

FAO, O. Food and Agriculture Organization of the United Nations. Faostat: database – crop production.Available at: http://faostat.fao.org/ Accessed on: Oct. 12 2021.

Freire, J.A., Rodrigues, G.C., Tomé, M., 2019. Climate change impacts on Pinus pinea L. silvicultural system for cone production and ways to contour those impacts: a review complemented with data from permanent plots. Forests 10 (2), 169–198. https://doi.org/10.3390/f10020169.

Freitas, C.H., Martins, F.B., Abreu, M.C., 2017. Cardinal temperatures for the leaf development of Corymbia citriodora and Eucalyptus urophylla seedlings. Pesq. Agrop. Brasileira 52 (5), 283–292. https://doi.org/10.1590/S0100-204X2017000500001.

Freitas, C.H., Elli, E.F., Sentelhas, P.C., Carneiro, R.L., Alvares, C.A., 2020. Adaptation, calibration and evaluation of a simple agrometeorological model for wood eucalyptus productivity estimation. Eur. J. For. Res. 139 (5), 759–776. https://doi.org/10.1007/s10342-020-01283-7.

Freitas, C.H., Elli, E.F., Sentelhas, P.C., 2021. On-farm assessment of eucalyptus yield-gaps – a case study for the producing areas of the state of Minas Gerais, Brazil. Int. J. Biometeorol. 65, 1659–1673. https://doi.org/10.1007/s00484-021-02120-1.

Fu, Y.-H., Lu, R.-Y., Guo, D., 2018. Changes in surface air temperature over China under the 1.5 and 2.0 C global warming targets. Adv. Clim. Chang. Res. 9 (2), 112–119. https://doi.org/10.1016/j.accre.2017.12.001.

Garlet, J., Costa, E.C., Boscadin, J., Deponti, G., Shwengher, C.R., Machado, L.M., 2013. Leptocybe invasa em Eucalyptus sp. no estado do Rio Grande Do SulBrasil. Ciênc. Rural 43 (2), 2175–2177. https://doi.org/10.1590/S0103-84782013001200009.

Gharbia, S.S., Smullen, T., Gill, L., Johnston, P., Pilla, F., 2018. Spatially distributed potential evapotranspiration modeling and climate projections. Sci. Total Environ. 633, 571–592. https://doi.org/10.1016/j.scitotenv.2018.03.208.

Goll, D.S., Brovkin, V., Parida, B.R., Reick, C.H., Kattge, J., Reich, Peter, B., van Bodegom, P.M., Niinemets, U., 2012. Nutrient limitation reduces land carbon uptake in simulations with a model of combined carbon, nitrogen and phosphorus cycling. Biogeosciences 9, 3547–3569. https://doi.org/10.5194/bg-9-3547-2012 2012.

Gonçalves, J.D.d.M., Alvares, C.A., Higa, A.R., Silva, L.D., Alfenas, A.C., Stahl, J., Ferraz, S.F.B., Lima, W.P., Brancalion, P.H.S., Hubner, A., Bouillet, J.P.D., Laclau, J.P., Nouvellon, Y., Epron, D., 2013. Integrating genetic and silvicultural strategies to minimize abiotic and biotic constraints in Brazilian eucalypt plantations. 301, 6–27. https://doi.org/10.1016/J.FORECO.2012.12.030.

Gonçalves, J.L., Alvares, C.A., Rocha, J.H., Brandani, C.B., Hakamada, R., 2017. Eucalypt plantation management in regions with water stress. South. For. J. For. Sci. 79, 169–183. https://doi.org/10.2989/20702620.2016.1255415.

González-Orozco, C.E., Pollock, L.J., Thornhill, A.H., Mishler, B.D., Knerr, N., Laffan, S.W., Miller, J.T., Rosauer, D.F., Faith, D.P., Nipperess, D.A., Kujala, H., Linke, S., Butt, N., Kullheim, C., Crisp, M., Gruber, B., 2016. Phylogenetic approaches reveal biodiversity threats under climate change. Nat. Clim. Chang. 6, 1110–1114. https://doi.org/10.1038/nclimate3126.

Hakamada, R.E., Hubbard, R.M., Stape, J.L., Lima, W.P., Moreira, G.G., Ferraz, S.F.B., 2020. Stocking effects on seasonal tree transpiration and ecosystem water balance in a fast-growing *Eucalyptus* plantation in Brazil. For. Ecol. Manag. 466, 118149. https://doi.org/10.1016/j.foreco.2020.118149.

Hallegatte, S., Rogelj, J., Allen, M., Clarke, L., Edenhofer, O., Field, C.B., Stocker, T.F., van Vuuren, D.P., 2016. Mapping the climate change challenge. Nat. Clim. Chang. 67, 663–668. https://doi.org/10.1038/nclimate3057.

Hoegh-Guldberg, O., Jacob, D., Taylor, M., Bindi, M., Brown, S., Camilloni, I., Diedhiou, A., Djalante, R., Ebi, K., Engelbrecht, F., et al., 2018. Chapter 3: impacts of 1.5 °C global warming on natural and human systems. Intergovernmental Panel on Climate Change (IPCC) Special Report on the Impacts of Global Warming of 1.5 °C above Pre-industrial Levels and Related Global Greenhouse Gas Emission Pathways, in the Context of Strengthening the Global Response to the Threat of Climate Change, Sustainable Development, and Efforts to Eradicate Poverty. World Meteorological Organization, Geneva, Switzerland.

Hubbard, R.M., Carneiro, R.L., Campoe, O., Alvares, C.A., Figura, M.A., Moreira, G.G., 2020. Contrasting water use of two eucalyptus clones across a precipitation and temperature gradient in Brazil. For. Ecol. Manag. 475, e118407. https://doi.org/10.1016/j.foreco.2020.118407.

IPCC, 2018. In: Masson-Delmotte, V., Zhai, P., Pörtner, H.-O., Roberts, D., Skea, J., Shukla, P.R., Pirani, A., Moufouma-Okia, W., Péan, C., Pidcock, R., Connors, S., Matthews, J.B.R., Chen, Y., Zhou, X., Gomis, M.I., Lonnoy, E., Maycock, T., Tignor, M., Waterfield, T. (Eds.), Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. In Press.

Jones, P.W., 1999. First- and second-order conservative remapping schemes for grids in spherical coordinates. Mon. Weather Rev. 127 (9), 2204–2210. https://doi.org/10.1175/1520-0493(1999)127<2204:FASOCR>2.0.CO;2.

Karmalkar, A.V., Bradley, R.S., 2017. Consequences of global warming of 1.5°C and 2°C for regional temperature and precipitation changes in the contiguous United States. PLoS One 12 (1), e0168697. https://doi.org/10.1371/journal.pone.0168697.

Knutti, R., Rogelj, J., Sedlácek, J., Fischer, E.M., 2016. A scientific critique of the two-degree climate change target. Nat. Geosci. 9 (1), 13–18. https://doi.org/10.1038/ngeo2595.

Lapola, D.M., Silva, J.M.C., Braga, D.R., Carpigiani, L., Ogawa, F., Torres, R.R., Barbosa, L.C.F., Ometto, J.P.H.B., Joly, C.A., 2020. A climate-change vulnerability and adaptation assessment for Brazil's protected areas. Conserv. Biol. 34 (2), 427–437. https://doi.org/10.1111/cobi.13405.

Lima, R.F., Aparecido, L.E.O., Lorençone, J.A., Lorençone, K.C.M., Moraes, J.R.S.C., Rolim, G.S., 2021. Climate change in Brazil: future scenarios classified by Thornthwaite (1948). Theor. Appl. Climatol. 146, 1367–1386. https://doi.org/10.1007/s00704-021-03803-w.

Llopart, M., Reboita, M.S., Rocha, R.P., 2020. Assessment of multi-model climate projections of water resources over South America CORDEX domain. Clim. Dyn. 54, 99–116. https://doi.org/10.1007/s00382-019-04990-z.

Machado, D.N., Costa, E.C., Garlet, J., Boscardin, J., Pedron, J., Perini, C.R., Bolzan, L., 2016. Avaliação de inseticidas no controle de Thaumastocoris peregrinus (Hemiptera: Thaumastocoridae) percevejo-bronzeado em condições de laboratório. Floresta Ambiente 23 (2), 245–250. https://doi.org/10.1590/2179-8087.144415.

Martins, F.B., Streck, N.A., 2007. Aparecimento de folhas em mudas de eucalipto estimado por dois modelos. Pesq. Agrop. Brasileira 42 (8), 1091–1100. https://doi.org/10.1590/S0100-204X2007000800005.

Martins, F.B., Streck, N.A., Silva, J.C., Morais, W.W., Susin, F., Navroski, M.C., Vivian, M.A., 2008. Deficiência hídrica no solo e seu efeito sobre transpiração, crescimento e desenvolvimento de mudas de duas espécies de eucalipto. Rev. Brasileira Ciênc. Solo 32 (3), 1297–1306. https://doi.org/10.1590/S0100-06832008000300037.

Martins, F.B., Soares, C.P.B., Leite, H.G., de Souza, A.L., Castro, R.V.O., 2011. Índices de competição em árvores individuais de eucalipto. Pesq. Agrop. Brasileira 46 (9), 1089–1098. https://doi.org/10.1590/S0100-204X2011000900017.

Martins, F.B., Soares, C.P.B., Silva, G.F.da, 2014. Individual tree growth models for eucalyptus in northern Brazil. 71 (3), 212–225. https://doi.org/10.1590/S0103-90162014000300006.

Monteiro, A.F.M., Martins, F.B., Torres, R.R., Almeida, V.H.M., Abreu, M.C., Mattos, E.V., 2021. Intercomparison and uncertainty assessment of methods for estimating evapotranspiration using a high-resolution gridded weather dataset over Brazil. Theor. Appl. Climatol. 146, 583–597. https://doi.org/10.1007/s00704-021-03747-1.

Moss, R.H., Edmonds, J.A., Hibbard, K.A., Manning, M.R., Rose, S.K., Van Vuuren, D.P., Carter, T.R., Emori, S., Kainuma, M., Kram, T., Meehl, G.A., Mitchell, J.F.B., Nakicenovic, N., Riahi, K., Smith, S.J., Stouffer, R.J., Thomson, A.M., Weyant, J.P., Wilbanks, T.J., 2010. The next generation of scenarios for climate change research and assessment. Nature 463 (7282), 747–756. https://doi.org/10.1038/nature08823.

Oudin, L., Hervieu, F., Michel, C., Perrin, C., Andréassian, V., Anctil, F., Loumagne, C., 2005. Which potential evapotranspiration input for a lumped rainfall–runoff model?: part 2 - towards a simple and efficient potential evapotranspiration model for rainfall–runoff modelling. J. Hydrol. 303, 290–306. https://doi.org/10.1016/j.jhydrol.2004.08.026.

Penna, A.C., Torres, R.R., Garcia, S.R., Marengo, J.A., 2021. Moisture flows on Southeast Brazil: present and future climate. Int. J. Climatol. 41, E935–E951. https://doi.org/10.1002/joc.6738.

Pereira, A.R., 2005. Simplificando o balanço hídrico de Thornthwaite-Mather. Bragantia 64 (2), 311–313. https://doi.org/10.1590/S0006-87052005000200019.

Pirovani, D.B., Pezzopane, J.E.M., Xavier, A.C., Pezzopane, J.R.M., Júnior, W.C.J., Machuca, M.A.H., Santos, G.M.A.D.A., Silva, S.F., Almeida, S.L.H., Peluzio, T.O., Eugenio, F.C., Moreira, T.R., Alexandre, R.S., Santos, A.R., 2018. Climate change impacts on the aptitude area of forest species. Ecol. Indic. 95, 405–416. https://doi.org/10.1016/j.ecolind.2018.08.002.

Queiroz, T.B., Rocha, S.M.G., Fonseca, F.S.A.da, Alvarenga, I.C.A., Martins, E.R., 2017. Efeitos do déficit hídrico no cultivo de mudas de Eucalipto. Irriga 22 (4), 659–674. https://doi.org/10.15809/irriga.2017v22n4p659-674.

Rawal, D.S., Kasel, S., Keatler, M.R., Nitschke, C.R., 2015. Climatic and photoperiodic effects on flowering phenology of select eucaliptus from south-eastern Australia. Agric. For. Meteorol. 214/215 (15), 231–242. https://doi.org/10.1016/j.agrformet.2015.08.253.

Reis, F.Y.S., Martins, F.B., Torres, R.R., Florêncio, G.W.L., Casemiro, J.M., Monteiro, V.F.C., de Cássia Ferreira, M., 2021. Climate change impact on the initial development of tropical forest species: a multi-model assessment. Theor. Appl. Climatol. 145, 533–547. https://doi.org/10.1007/s00704-021-03646-5.

Resende, N.C., Miranda, J.H., Cooke, R., Chu, M.L., Chou, S.C., 2019. Impacts of regional climate change on the runoff and root water uptake in corn crops in Parana,Brazil. Agric. Water Manag. 221 (20), 556–565. https://doi.org/10.1016/j.agwat.2019.05.018.

Resquin, F., Duque-Lazo, J., Acosta-Muñoz, C., Rachid-Casnati, C., Carrasco-Letelier, L., Navarro-Cerrillo, R.M., 2020. Modelling current and future potential habitats for plantations of Eucalyptus grandis Hill ex Maiden and E. dunnii Maiden in Uruguay. Forests 11 (9), 948. https://doi.org/10.3390/f11090948.

Riahi, K., van Vuuren, D.P., Kriegler, E., Edmonds, J., et al., 2017. The shared socioeconomic pathways and their energy, land use, and greenhouse gas emissions implications: an

overview. Glob. Environ. Chang. 42, 153–168. https://doi.org/10.1016/j.gloenvcha.2016.05.009.
Santana, D.L.Q. de, Menezes Junior, A., Silva, H.D.da, Bellote, A.F.J., Favaro, R.M., 2003. O Psilídeo-de-concha (Glycaspis brinblecombei) em eucalipto. Embrapa Florestas, Colombo Comunicado Técnico n° 105. Available at: https://core.ac.uk/download/pdf/15427903.pdf.
Santos, D.F., Martins, F.B., Torres, R.R., 2017. Impacts of climate projections on water balance and implications on olive crop in Minas Gerais. Rev. Bras. Engenharia Agríc. Ambient. 21 (2), 77–82. https://doi.org/10.1590/1807-1929/agriambi.v21n2p77-82.
Sentelhas, P.C., Santos, D.L., Machado, R.E., 2008. Water deficit and water surplus maps for Brazil, based on FAO Penman-Monteith potential evapotranspiration. Ambiente Água Interdiscip. J. Appl. Sci. 3 (3), 29–42. https://doi.org/10.4136/ambi-agua.59.
Silva, J.M.C.da, Rapini, A., Barbosa, L.C.F., Torres, R.R., 2019. Extinction risk of narrowly distributed species of seed plants in Brazil due to habitat loss and climate change. PeerJ. 7, e7333. https://doi.org/10.7717/peerj.7333.
Smaniotto, M.A., Silva, A., Cunha, U.S., Garcia, M.S., 2017. Biologia de Thaumastocoris peregrinus carpinteiro e Dellapé (Hemiptera: Thaumastocoridae) em dez espécies de eucalipto. Ciênc. Rural 27 (2), 679–685. https://doi.org/10.5902/1980509827752.
Tanner, E.V.J., Vitousek, P.M., Cuevas, E., 1998. Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. Ecology 79 (1), 10–22. https://doi.org/10.1890/0012-9658(1998)079[0010:EIONLO]2.0.CO;2.
Tatagiba, S.D., Xavier, T.M.T., Torres, H., Pezzopane, J.E.M., Cecílio, R.A., Zanetti, S.S., 2015. Determinação da máxima capacidade de retenção de água no substrato para produção de mudas de eucalipto em viveiro. Floresta 45 (4), 745–754. https://doi.org/10.5380/rf.v45i4.38334.
Tateishi, M., Xiang, Y., Saito, T., Otsuki, K., Kasahara, T., 2015. Changes in canopy transpiration of Japanese cypress and Japanese cedar plantations because of selective thinning. Hydrol. Process 29 (24), 5088–5097. https://doi.org/10.1002/hyp.10700.
Taylor, K.E., Stouffer, R.J., Meehl, G.A., 2012. An overview of CMIP5 and the experiment design. Bull. Am. Meteorol. Soc. 93 (4), 485–498. https://doi.org/10.1175/BAMS-D-11-00094.1.
Thornthwaite, C.W., 1948. An approach toward a rational classification of climate. Geogr. Rev. 38 (1), 55–94. https://doi.org/10.2307/210739.
Thornthwaite, C.W., Mather, J.R., 1955. The Water Balance. 8, n.1. Johns Hopkins University, Laboratory in Climatology Publications in Climatology.
Thornthwaite, C.W., Mather, J.R., 1957. Instructions and Tables for Computing Potential Evapotranspiration and the Water Balance. 10, n.3. Johns Hopkins University, Laboratory in Climatology Publications in Climatology.
Torres, R.R., Marengo, J.A., 2013. Uncertainty assessments of climate change projections over South America. Theor. Appl. Climatol. 112, 253–272. https://doi.org/10.1007/s00704-012-0718-7.
Torres, R.R., Benassi, R.B., Martins, F.B., Lapola, D.M., 2021. Projected impacts of 1.5 and 2°C global warming on temperature and precipitation patterns in South America. Int. J. Climatol., 1–15 https://doi.org/10.1002/joc.7322.
Torres, R.R., Marengo, J.A., 2014. Climate change hotspots over South America: From CMIP3 to CMIP5 multi-model datasets. Theor. Appl. Climatol. 117, 579–587. https://doi.org/10.1007/s00704-013-1030-x.
Van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G.C., Kram, T., Krey, V., Lamarque, J.F., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S.J., Rose, S.K., 2011. The representative concentration pathways: an overview. Clim. Chang. 109 (1), 5–31. https://doi.org/10.1007/s10584-011-0148-z.
Willmott, C.J., Rowe, C.M., Mintz, Y., 1985. Climatology of the terrestrial seasonal water cycle. J. Climatol. 5, 589–606. https://doi.org/10.1002/joc.3370050602.
Xie, H., Zhu, X., Yuan, D.Y., 2015. Pan evaporation modelling and changing attribution analysis on the TibetanPlateau (1970–2012). Hydrol. Process. 29 (9), 2164–2177. https://doi.org/10.1002/hyp.10356.

Check for updates

New Phytologist

Forum

Viewpoint

Tree drought physiology: critical research questions and strategies for mitigating climate change effects on forests

Summary

Droughts of increasing severity and frequency are a primary cause of forest mortality associated with climate change. Yet, fundamental knowledge gaps regarding the complex physiology of trees limit the development of more effective management strategies to mitigate drought effects on forests. Here, we highlight some of the basic research needed to better understand tree drought physiology and how new technologies and interdisciplinary approaches can be used to address them. Our discussion focuses on how trees change wood development to mitigate water stress, hormonal responses to drought, genetic variation underlying adaptive drought phenotypes, how trees 'remember' prior stress exposure, and how symbiotic soil microbes affect drought response. Next, we identify opportunities for using research findings to enhance or develop new strategies for managing drought effects on forests, ranging from matching genotypes to environments, to enhancing seedling resilience through nursery treatments, to landscape-scale monitoring and predictions. We conclude with a discussion of the need for co-producing research with land managers and extending research to forests in critical ecological regions beyond the temperate zone.

Introduction

Climate change is associated with periods of drought and heat that are increasing in frequency and severity, resulting in forest mortality and decreased tree growth (Breshears *et al.*, 2005; Brodribb *et al.*, 2020). Given the central role forests play in the carbon cycle, drought-related changes in tree growth and mortality have implications for carbon cycle–climate feedback on a global scale (Paschalis *et al.*, 2024). At local and regional levels, drought-related mortality affects forest community structure and function, with cascading effects on other trophic levels including the diversity of plants, animals, and microbes found within forest ecosystems. Drought-related forest mortality also has major impacts on society through increased wildfire, economic losses to traditional forest industries and tourism, and the myriad other ecological and societal benefits associated with forests (Cheng *et al.*, 2024). An example of the impacts of drought on forests in the Northern Hemisphere is given by forest mortality and associated wildfires in California (Fig. 1), with estimated annual economic losses averaging $117 M per year between 2017 and 2021 (Paci *et al.*, 2023).

Currently, we lack critical elements needed to understand how trees respond to and mitigate drought-related stress that are needed to meet forest management goals under drought scenarios. Tree drought physiology describes the biological processes underlying responses to drought from the cellular level to forest levels, including how trees ultimately die or survive (Choat *et al.*, 2018; Brodribb *et al.*, 2020; McDowell *et al.*, 2022a,b). As long-lived perennials, trees experience environmental changes at sub-hourly to millennial time scales. Tree physiological responses to drought mirror those timescales and range from rapid responses such as stomatal closure, to annual changes in wood development, to responses that can take decades to manifest in mortality (Cailleret *et al.*, 2017), and to the eventual mismatch in long-lived trees whose genotypes and adaptive traits no longer match contemporary conditions (Ledig & Kitzmiller, 1992). Legacy effects of a current year's drought on future years' growth (Anderegg *et al.*, 2015) is but one example of the many complexities involved in understanding drought physiology in trees without direct parallels in better studied model annual plants.

In a practical sense, managed forests are typically grown on heterogeneous landscapes with minimal cultivation or irrigation, limiting direct agronomic interventions. Strategies promoting drought resilience thus rely on landscape-scale interventions such as the selection of resilient species or genotypes, nursery practices that increase the survival of outplanted seedlings, and silvicultural practices. The most challenging of all is to understand and manage the diversity among the thousands of tree species of interest including angiosperm and gymnosperm species separated by 300 million years (Myr) of evolution, and the various strategies they exhibit to mitigate drought effects.

The complex biological responses of trees to drought are at best partially described, which limits innovation and the translation of research findings into effective strategies for forest conservation and management. Encouragingly, new technologies, an increasing base of knowledge, and opportunities for integrative research can enable significant advances. Here, we present ideas developed during a workshop 'Forest Tree Drought Physiology Research Innovation Group' held at the Arnold Arboretum, with the goals of identifying key research questions that, if addressed, might enable new transformative approaches for forest management under drought. The participants of the workshop were varied in approach and scope, and we thus are a broad but incomplete representation of the many research and management needs posed by drought. The topics selected for discussion here reflect the expertise of the authors and areas we believe are strategic for new discoveries that can be translated to forest management. While many of the

© 2024 The Author(s).
New Phytologist © 2024 New Phytologist Foundation.
This article has been contributed to by U.S. Government employees and their work is in the public domain in the USA.

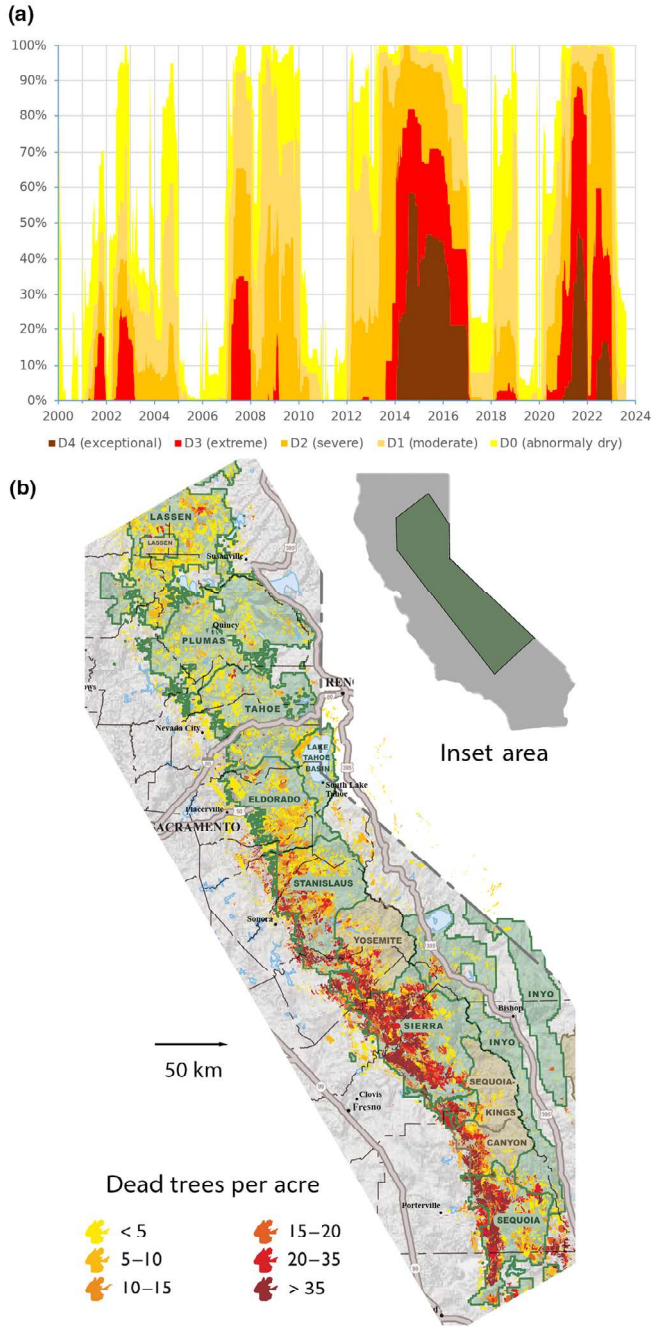


Fig. 1 Drought impacts on forest mortality in California. (a) California is characterized by a Mediterranean climate that experiences seasonal droughts. Drought severity is shown as percent area affected for 2000–2024, including exceptional drought from 2014 to 2017. (b) Tree mortality is shown for the Sierra Nevada of California from 2014 to 2017. (a) US Drought Monitor https://droughtmonitor.unl.edu/, (b) adapted from US Forest Service Forest Health Protection.

concepts and problems discussed are applicable to different forest types, our examples are drawn primarily from temperate forests, and do not adequately address the additional complexities of tropical and boreal forests. We also acknowledge that our discussion of molecular and genetic regulation of drought response skewed toward model angiosperm trees supported by genomic and gene function studies (notably *Populus* and *Eucalyptus*), despite the ecological and environmental importance of coniferous species.

In the first section of this paper, we highlight basic research knowledge gaps and opportunities to address them. In the second section, we then examine ways to translate research findings to enhance or even develop new strategies for forest management and conservation under climate change and drought. In the conclusion, we provide perspectives on practical research issues, as well as broader societal and ecological issues.

The concepts and approaches discussed in the paper are presented in Fig. 2.

From cells to forests: critical research questions for tree drought physiology

Below, we discuss missing information about the basic biology of drought response in trees that, if addressed, would enable new insights and approaches for forest management. This section is not intended to be a review of all tree drought physiology research, but rather to highlight examples of what are now tractable problems that can produce transformative insights.

How do trees adjust wood development and physiology to avoid hydraulic failure?

The anatomy and related physiology of tree stems play a major role in how trees respond to and potentially succumb to drought (Rodriguez-Zaccaro & Groover, 2019; Anfodillo & Olson, 2021; Olson *et al.*, 2023), including embolism resistance and regulation of osmotic potential. Tree stems are composed of secondary vascular tissues (wood and inner bark) produced by the cambium meristem. Wood evolves as a complex, heterogeneous tissue containing both dead and living cells (Olson, 2023), which collectively are responsible for water conduction, mechanical support, transport of signaling molecules, carbohydrate storage, and mineral nutrient transport (Carlquist, 2013).

The movement of water through nonliving tracheary elements in wood is explained by a cohesion-tension mechanism in which transpiration from leaves creates negative pressure that is transmitted down the water column to 'pull' water from roots through the stem to the canopy. Under drought, transpiration leads to increasingly low xylem pressures within tracheary elements potentially causing the formation and spread of air embolisms that disrupt the transport of water. The propagation of air embolisms can cause hydraulic failure and the irreversible desiccation of downstream tissues, which if widespread can lead to whole tree mortality (Choat *et al.*, 2018; Arend *et al.*, 2021; Lens *et al.*, 2022).

Wood development and subsequent anatomy undergo striking changes under drought, although direct functional relationships between anatomy and drought resistance are not always clear and have been debated in the literature (Olson *et al.*, 2023). In north-temperate conifers, embolism resistance is associated with narrow, thick-walled tracheids and small pit aperture diameters that hold across different species (Pittermann *et al.*, 2006; Delzon *et al.*, 2010). In woody angiosperms, narrower vessel diameter and increased pit membrane thickness have been implicated in

© 2024 The Author(s).
New Phytologist © 2024 New Phytologist Foundation.
This article has been contributed to by U.S. Government employees and their work is in the public domain in the USA.

14698137, 2025, 5, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.20326 by Capes, Wiley Online Library on [09/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

14698137, 2025, 5, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.20326 by Capes, Wiley Online Library on [09/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

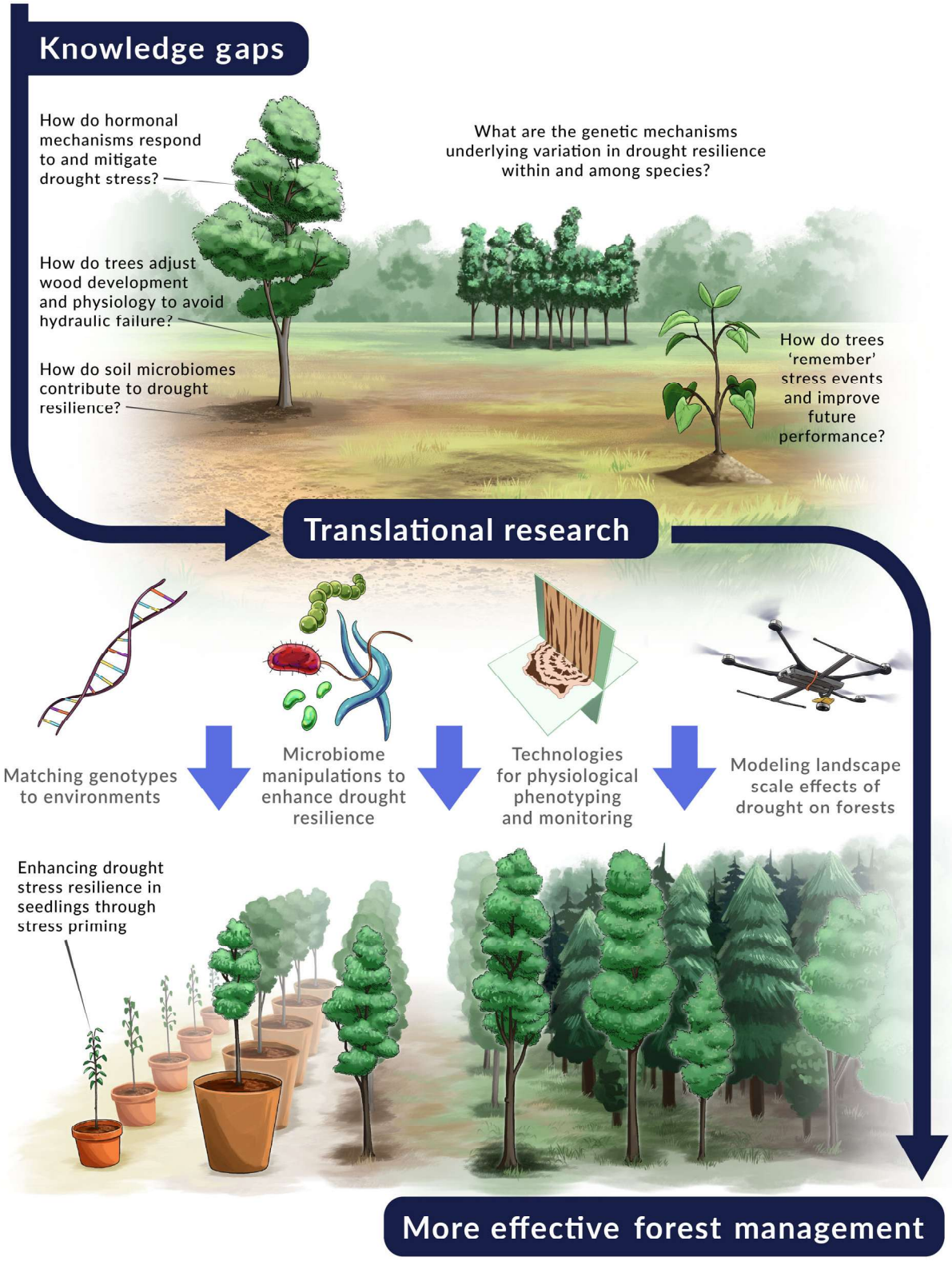


Fig. 2 Examples of knowledge gaps and how addressing them can enable translation to new approaches for forest management under drought. While not intended to be comprehensive, examples of key knowledge gaps of tree drought physiology are highlighted that, if rigorously addressed by research, have potential to translate into new applications for more effective forest management under drought scenarios.

© 2024 The Author(s).
New Phytologist © 2024 New Phytologist Foundation.
This article has been contributed to by U.S. Government employees and their work is in the public domain in the USA.

embolism resistance, but the causative factors are unclear (Hacke *et al.*, 2017; Lemaire *et al.*, 2021; Levionnois *et al.*, 2021; Lens *et al.*, 2022; Isasa *et al.*, 2023). Fibers have thick secondary cell walls that act as mechanical support in wood and increase vessel resistance to implosion (Jacobsen *et al.*, 2005; Janssen *et al.*, 2020). Fibers can also act as reservoirs of water that can be used during water transport under drought stress (Jupa *et al.*, 2016; Knipfer *et al.*, 2017; Ziemińska *et al.*, 2020). These roles of fibers and variation in fiber development under drought are understudied. The degree of plasticity for key hydraulic traits such as pit membrane thickness that ultimately determine embolism resistance has been evaluated in Arabidopsis (Thonglim *et al.*, 2021). Similar studies are needed for trees to resolve the regulation and functional consequences of wood anatomy changes under drought. Furthermore, homologies and unique attributes among wood hydraulic traits in angiosperm vs gymnosperm tree species separated by over 300 Myr of evolution can now be explored using functional genomics.

The cellular and molecular processes driving drought response in woody tissue are a promising area for physiology research in forest trees and could provide insights useful for applications such as monitoring and predicting mortality, or breeding for drought resilience. Living cells within secondary xylem can concentrate solutes (sugars, organic acids, etc.) to lower water potential and reach equilibrium with the xylem (Ozturk *et al.*, 2021). Such osmoregulation occurs over hours or days and prevents water loss from living cells to the vessels. When present, xylem parenchyma appears to be involved in mitigating embolism, presumably because the parenchyma stores water and solutes, and can offer an osmotic means of regulating water potential (Pratt *et al.*, 2021). Some highly specialized parenchyma cells known as vessel-associated cells (VACs; also referred to as contact cells) are in direct contact with vessel elements via contact pits and are responsible for transport of water, sugars, amino acids, and possibly proteins, lipids, and surfactants into and out of vessel elements (Słupianek *et al.*, 2021, 2024). Molecular exchange between xylem parenchyma and vessels is highly regulated under drought, and VACs may facilitate embolism recovery (Brodersen & McElrone, 2013; Brodersen *et al.*, 2020). However, knowledge of the underlying molecular mechanisms and cellular processes is incomplete, including how ray parenchyma cells facilitate the exchange of water and solutes between xylem and phloem, and how movement of sugars from the phloem to the xylem is regulated to increase conduit resistance to embolism.

How do hormonal mechanisms respond to and mitigate drought stress?

Hormonal regulation is central to tree drought physiology, involving primary and interacting effects of multiple hormones (Table 1) that mediate acclimation of the hydraulic system to drought. The phytohormone abscisic acid (ABA) is arguably the best studied and plays a direct role in drought sensing, triggering known protective measures such as stomatal closure (Raghavendra *et al.*, 2010) and changes in wood development, including production of smaller diameter and more interconnected vessels

Table 1 Phytohormones with documented roles in plant drought response.

Phytohormone	Roles in drought response and key references
Abscisic acid (ABA)	Stomatal regulation (Munemasa *et al.*, 2015; Kuromori *et al.*, 2018); suppression of lateral root formation in air (i.e. 'xerobranching'; Mehra *et al.*, 2022); putative role in xylem development (Arend & Fromm, 2007; Yu *et al.*, 2021); drought-induced leaf senescence (Zhao *et al.*, 2016)
Auxin (IAA and IBA)	Lateral root formation/root branching in response to water (i.e. 'hydropatterning'; Bao *et al.*, 2014); leaf senescence and abscission (Jin *et al.*, 2015; Ma *et al.*, 2021); putative role in vessel diameter and patterning (Hacke *et al.*, 2017; Johnson *et al.*, 2018); crosstalk with ABA (Sharma *et al.*, 2023)
Brassinosteroids (BR)	Root development and architecture (Wei & Li, 2016); stomatal development (with ABA; Serna, 2014); crosstalk with numerous other hormones (Choudhary *et al.*, 2012)
Cytokinins (CK)	Crosstalk with SL (Li *et al.*, 2019); with IAA re : root : shoot ratio (Kurepa & Smalle, 2022); and with ABA (Li *et al.*, 2016)
Ethylene (ET)	Root development and leaf senescence (Baharudin & Osman, 2023); crosstalk with ABA in stomatal regulation (Kazan, 2015) and with JA in root growth (Song *et al.*, 2014); reactive oxygen species (ROS) defense (Depaepe *et al.*, 2021)
Gibberellins (GA)	Root growth and crosstalk with JA (Koo *et al.*, 2020)
Jasmonates (JA, JA-Ile)	Stomatal closing, root physiology and cross talk with ABA (Kazan, 2015); root growth and crosstalk with ET and GB (Song *et al.*, 2014)
Salicylic acid (SA)	Osmotic stress and ROS response (Koo *et al.*, 2020); crosstalk with ABA and JA (Muñoz-Espinoza *et al.*, 2015); crosstalk with BR (Choudhary *et al.*, 2012)
Strigolactones (SL)	Indirectly implicated via roles in shoot branching inhibition (e.g. for reduced transpirational demand; Gomez-Roldan *et al.*, 2008; Umehara *et al.*, 2008) and root architecture (Koltai, 2011)

(Yu *et al.*, 2021), but ABA sensitivity varies among tree species (Brodribb & McAdam, 2013) and how ABA affects wood growth and physiology is only recently being revealed at the molecular level. Basic questions include whether living cells in wood directly sense drought and respond through ABA production or whether wood primarily responds to signals from other drought-sensing tissues (notably roots). Grafting experiments in Arabidopsis between root stocks of ABA-deficient mutants and wild-type scions did not impair stomatal response to water stress, while reciprocal grafts were impaired, suggesting that ABA signals from stems are necessary and sufficient for stomatal response (Christmann *et al.*, 2007). In trees, comparative phytohormone profiling in the immature xylem from drought-stressed and control poplars showed a drastic increase in ABA levels, which was much greater than in leaves and roots (Yu *et al.*, 2021). Transcripts for the homologs to all ABA biosynthetic enzymes were detected in immature xylem (Yu *et al.*, 2021). In drought-stressed immature xylem, the transcript abundances of putative ABA exporter genes, as well as of the key genes for ABA biosynthesis, were increased (Yu *et al.*, 2021). These changes were accompanied by phenotypic shifts from thin- to thick-walled fiber cells, and from large to smaller and

© 2024 The Author(s).
New Phytologist © 2024 New Phytologist Foundation.
This article has been contributed to by U.S. Government employees and their work is in the public domain in the USA.

14698137, 2025, 5, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.20326 by Capes, Wiley Online Library on [09/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

more frequent vessels. Similar anatomical changes in the xylem were found in many drought studies (Polle *et al.*, 2019) and can be induced locally by the application of ABA to the stem of poplars (Arend & Fromm, 2007). However, direct experimental validation demonstrating ABA production in wood is missing.

Abscisic acid signaling initiates changes in development to produce anatomy more suited to water stress (Yu *et al.*, 2021), but how ABA connects with the other hormones affecting wood development remains poorly defined. The control of cell division in the cambium and subsequent cell differentiation can involve auxin, cytokinin, brassinosteroids, jasmonates, and gibberellin (Table 1). In developing xylem of drought-stressed poplars, some of these hormones show significant changes in response to drought (Table 1). Vessel expansion and patterning depend on cambial auxin concentrations and transport processes (Schrader *et al.*, 2003; Junghans *et al.*, 2004; Johnson *et al.*, 2018), and there is accumulating evidence for the interaction of ABA and auxin signaling in plants (Ortiz-García *et al.*, 2023). Cytokinin concentrations modulate the sensitivity of the cambium to auxin and thereby affect radial growth (Immanen *et al.*, 2016). Auxins also contribute to drought response by altering root development to maximize water acquisition, adjusting the root : shoot ratio in response to water demand and availability (Bao *et al.*, 2014), and regulating leaf shedding (Jin *et al.*, 2015). How ABA affects other hormonal signaling pathways to affect wood development and physiological changes is a promising area for the development of new drought-resistant genotypes or applications such as stress priming (discussed below) and could provide new diagnostic tools for evaluating drought stress in forests.

How do soil microbiomes contribute to drought resilience?

Understanding how microbes impact tree drought physiology could facilitate the development of climate- or site-specific inocula that could improve tree performance as climates change. Soil microbiota can improve leaf water potential and photosynthetic rates in drought-stressed seedlings (Kannenberg & Phillips, 2017). Their benefits can be locally adapted, as microbes from dry, hot, or cold sites can improve tree seedling survival when faced with the same stressors (Allsup *et al.*, 2023). Leaf endophytes, too, can improve conifer seedling survival and photosynthesis under drought (Aghai *et al.*, 2019). Microbial effects on plant drought response can depend on the time scale on which the drought is imposed (Ulrich *et al.*, 2019), and on the variety of microbial interactions that a plant can engage in (e.g. arbuscular mycorrhizal vs ectomycorrhizal host plants) (Allsup *et al.*, 2023). Ectomycorrhizal symbiosis alters tree response, both locally and systemically, to abiotic cues such as water limitation (de Freitas Pereira *et al.*, 2023), a process which is mediated by ABA and other key drought-responsive hormones detailed above.

Hormones can all be impacted by or modulate microbial interactions (Kim *et al.*, 2012; Foo *et al.*, 2019), but it remains difficult to predict which microbial strains or consortia have particular effects. Adding complexity, microbial communities themselves respond strongly to drought stress (Baldrian *et al.*, 2023), potentially changing their impacts on drought-stressed plants by shifting the density or behavior of mutualistic or pathogenic organisms. This balance between helpful and harmful microbes in the microbiome may be controlled, in part, by plant genetics. Drought-tolerant genotypes of *Populus trichocarpa* support more beneficial microbes than drought-susceptible genotypes (Kristy *et al.*, 2022). Molecular interactions between tree roots and beneficial microbes can impact plant drought response. Ectomycorrhizal networks facilitate the exchange of nonstructural carbohydrates and impact drought tolerance-related traits in *Pinus ponderosa* (Sapes *et al.*, 2021). Ectomycorrhizal fungi can increase tree production of ABA and salicylic acid, potentially priming the plant to better endure drought stress (Kebert *et al.*, 2023), while fungi can enhance tree drought tolerance by improving plant antioxidant function and enhancing mitogen-activated protein kinase (MAPK) signaling cascades linked to drought tolerance (Wang *et al.*, 2023). However, the drivers of microbial communities, adaptive traits of microbes, and interactions with tree genotypes within the context of drought resilience are not well understood presently.

Current questions in microbiome research for forest tree drought physiology reflect a shift from correlative observations to descriptions of causative biological mechanisms and processes. Ongoing advances in nucleic acid, protein, and metabolite analysis are being used to explore mechanisms of and physiological responses to microbial associations by employing 'multi-omic' approaches to reveal the specific organisms and biochemicals involved in tree-microbe interactions (de Freitas Pereira *et al.*, 2023; Nosenko *et al.*, 2023). Although often employed in isolation, combining sequencing with fine-scale biochemical analyses will be an important step toward developing a predictive framework of how microbes impact tree drought response, and expand our understanding beyond seedlings to encompass adult trees in field contexts. Identifying the mechanisms involved will also require growth chamber experiments whose design can be guided by correlative multi-omic datasets, allowing for the isolation of specific microbes and compounds responsible for shifts in tree drought response. Questions that can be addressed with such methods include whether trees actively select or recruit microbes suited for drought conditions, the role tree genotypic variation might play in microbiome assemblage, the degree to which variation in microbial traits contributes to drought-relevant phenotypes (Allsup *et al.*, 2023), and what genes and mechanisms are associated with drought resistance and resilience during the interaction of trees and microbes under drought. Importantly, studies describing the population-level variation in functional traits of soil microbes associated with drought could provide the foundations for effective microbiome treatments, which would also be informative for assisted migration applications.

What are the genetic mechanisms underlying variation in drought resilience within and among species?

Identifying and harnessing natural genetic variation for tree drought response underpins forest conservation under climate change. Variation among and within species for drought response is observed, but the ability to relate resilience to specific genes remains

© 2024 The Author(s).
New Phytologist © 2024 New Phytologist Foundation.
This article has been contributed to by U.S. Government employees and their work is in the public domain in the USA.

14698137, 2025, 5, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.20326 by Capes, Wiley Online Library on [09/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

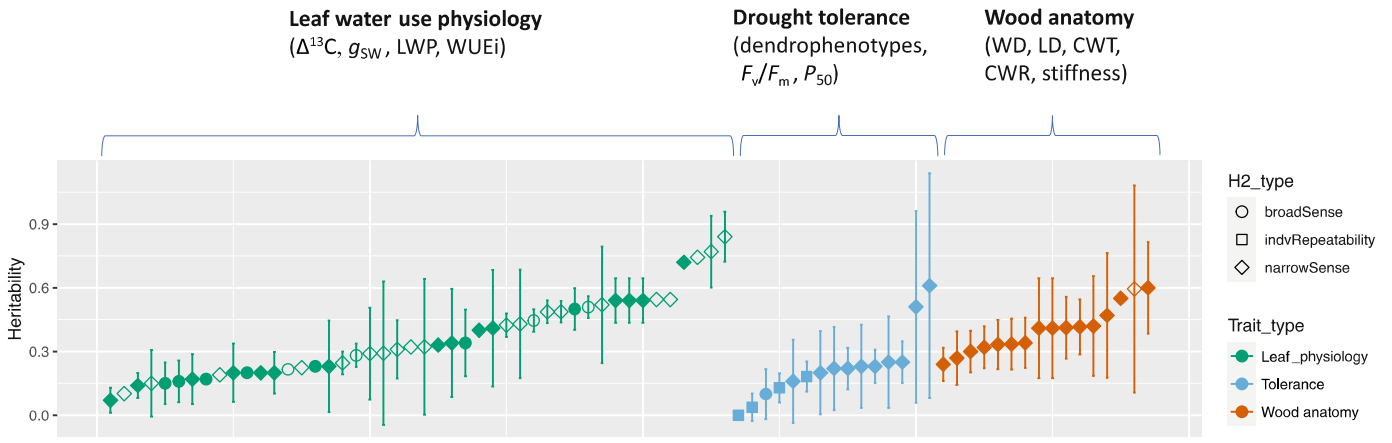


Fig. 3 Within-species genetic variation for forest tree drought response. Values shown are heritabilities (i.e. the proportion of phenotypic variance attributed to genetic effects) estimated from common garden or provenance trial experiments, displayed in order of increasing magnitude along the *x*-axis for different classes of drought-related traits. Symbol shapes denote the type of heritability estimate (narrow-sense, broad-sense, or individual repeatability). Filled symbols are for coniferous trees, while open symbols are estimates from angiosperm trees. Values represent a nonexhaustive sampling of 26 studies reporting natural genetic variation in drought response traits across 14 tree species. Estimates are means ± 95% CI, when reported. CWR, cell wall reinforcement; CWT, cell wall thickness; dendrophenotypes, tree-ring derived growth traits in response to drought; F_v/F_m, maximum efficiency of Photosystem II; g_{sw}, stomatal conductance; LD, lumen diameter; LWP, leaf water potential; P_{50}, pressure at 50% loss of xylem hydraulic conductance; stiffness, wood stiffness measured by acoustic velocity; WD, wood density; WUEi, instantaneous water use efficiency; $\Delta^{13}C$, carbon isotope discrimination. Further details are available in Supporting Information Table S1.

challenging for both technical and biological reasons. The inherent capacity to tolerate drought reflects complex, polygenic mechanisms that are highly responsive to the environment and present challenges for traditional genetic analysis where experimental variation reduces the power to detect quantitative genetic effects. A major technical challenge is to establish phenotyping methods that both measure complex physiological phenotypes and can scale to the large numbers of genotypes required for genomic studies. Typical experimental approaches for tree genomic studies require hundreds or thousands of trees and include field trials and common garden studies that permit phenotyping under quasi-natural conditions (Jaramillo-Correa *et al.*, 2015; de Villemereuil *et al.*, 2016), and glasshouse-based studies that permit manipulation of environmental conditions and application of experimental treatments. Advances in sequencing technologies have largely removed the technical challenge of extending genomic approaches to tree species and allow experimental designs with large sample sizes, but the technical hurdle to identify and accurately measure relevant physiological traits in large numbers of trees remains. To date, phenotyping in genome-wide association studies (GWAS) has been largely limited to water use efficiency since the isotopic ratio of carbon ^{13}C : ^{12}C can be used as a proxy for a time-integrated measure of water use efficiency due to plant carbon isotope discrimination (CID) (Farquhar *et al.*, 1989). CID can be estimated using mass spectrometry on either leaf or woody tissue and is feasible for large sample sizes (González-Martínez *et al.*, 2008; Cumbie *et al.*, 2011). While water use efficiency displays extensive plasticity in response to soil water availability, there is also evidence for natural genetic variation, with GWAS of CID in a variety of conifer and broad-leaved tree species returning a wide range of heritabilities, from 0.07 to 0.84 (mean = 0.36; Fig. 3). However, these measures reflect an amalgam of component traits contributing to water use efficiency. Only recently, there is some progress in describing metabolic mechanisms underlying ^{13}C signatures (Wieloch *et al.*, 2024). More problematic is that, to date, only a fraction of observed phenotypic variation for any drought-related traits can be explained based on genetic predictions.

These genetic predictions could be useful for understanding water relations in trees, but relatively few studies have addressed these linkages to more direct physiological and anatomical traits associated with mortality because of additional phenotyping challenges (Brodribb *et al.*, 2020). For example, xylem vulnerability to embolism can be estimated from dose–response curves that determine the pressure at which xylem is embolized (P_x), which corresponds closely to lethal water potential (ψ lethal) in trees (Liang *et al.*, 2021). High-precision methods for estimating xylem vulnerability curves involve the use of optical techniques or high-speed centrifugation (e.g. 'Cavitrons'), but are time-intensive to collect and not easily adapted for population-level or genomic studies (Plomion *et al.*, 2016). As previously discussed, wood anatomical traits are correlated with hydraulic failure, but are time consuming to assay through traditional histology. Genetic studies in poplar identified significant heritabilities, quantitative trait loci, and candidate genes for vessel traits associated with drought resilience in a large pedigree carrying induced chromosomal lesions (Rodriguez-Zaccaro *et al.*, 2021, 2024). Such studies could be expanded and made much more informative if higher throughput methods for phenotyping were available.

An important question for trees is how genotypes respond to variation in drought stress across many years of growth, including the basis for plasticity in drought responses. The response to past drought stress can be derived from tree rings ('dendrophenotypes') sampled from trees growing in established provenance trials

© 2024 The Author(s).
New Phytologist © 2024 New Phytologist Foundation.
This article has been contributed to by U.S. Government employees and their work is in the public domain in the USA.

14698137, 2025, 5, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.20326 by Capes, Wiley Online Library on [09/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

14698137, 2025, 5, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.20326 by Capes, Wiley Online Library on [09/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

(Housset *et al.*, 2018). Such time-series data can be used to estimate the climatic sensitivity of different genotypes and provenances and to derive measures of resistance, resilience, and recovery in response to drought (Depardieu *et al.*, 2020). Drought response in dendrophenotypes measured from tree rings showed low to moderate, but often significant heritabilities (Fig. 3), suggesting the presence of plasticity, but also some promise for genetic mapping of responses to naturally occurring drought episodes in the field. Applying this approach in white spruce (*Picea glauca*) using GWAS on dendrophenotypes spanning a natural drought event revealed strong associations identifying a suite of candidate genes and mechanisms (Depardieu *et al.*, 2021).

How do trees 'remember' stress events and improve future performance?

Given that trees have long lifespans, they must adjust their physiological responses at different time scales to increase resilience to repeated stress and drought. Epigenetics is emerging as a key mechanism by which forest trees respond to environmental stresses including drought (Bräutigam *et al.*, 2013; Amaral *et al.*, 2020). The epigenome, which is a proxy for stress memory in plants, is increasingly seen as a key point of regulation of drought-responsive genes and associated mechanisms (Lämke & Bäurle, 2017; Balao *et al.*, 2018; Sadhukhan *et al.*, 2022; Gallusci *et al.*, 2023). Histone modifications and DNA methylation are epigenetic marks known to be dynamic in response to environmental changes in plants (Gallusci *et al.*, 2023). These marks are modified in individual trees in response to stress and, in some cases, can be transmitted across generations (Zolfaghari *et al.*, 2022). For instance, induced drought stress for 12 yr in *Quercus ilex* was correlated with an increase in hypermethylated loci and a decrease in fully methylated loci (Rico *et al.*, 2014). Do Nascimento *et al.* (2022) pre-exposed genetically identical trees raised from somatic embryos of *Pinus radiata* to either a control or heat stress and found that prestressed trees later had improved drought response that was correlated with DNA methylation. A direct relationship between epigenetic modifications and drought response was observed in transgenic poplars, where suppressing DNA methylation using RNAi resulted in increased drought tolerance (Sow *et al.*, 2021). A recent study on poplar (*Populus tomentosa*) demonstrated a connection between DNA methylation, structural changes, and gene expression in response to drought (Zhou *et al.*, 2023). This study also showed cross-generational epigenetic changes, which is challenging to address in organisms as long-lived as forest trees. A mechanism for Histone H3 lysine-4 methylation activation of drought-responsive genes has also been identified recently in poplar (Zhang *et al.*, 2024).

Progress in describing the functional relationships between epigenetics and drought physiology is being made and the above-mentioned studies demonstrate general correlations among chromatin marks and drought response, but the specific molecular mechanisms and target genes connecting drought perception, epigenetic changes, and downstream physiological and developmental changes remain uncertain. Further extending knowledge of evolutionarily conserved epigenetic mechanisms from model herbaceous species to trees is an obvious area of opportunity to advance this field. How to effectively manipulate epigenetic variation within the framework of operational forestry genetics, nursery, or management context is largely unaddressed, but could open exciting opportunities for drought preconditioning (e.g. see stress priming below).

Translating research to applications for mitigating climate effects on forests

The current pace of climate change is causing increasing frequency and severity of drought within the lifetimes of individual trees, and the rate of natural dispersal is far slower than the rate of warming (Aitken *et al.*, 2008). Thus, a question increasingly discussed among tree biologists working at the intersections of physiology, genetics, conservation, and forest health is, how to facilitate adaptation of forests to future climate (Isabel *et al.*, 2019)?

Translating advances in tree drought physiology into effective applications for land managers is part of the answer, but there are significant challenges to address. Long generation times and inefficient phenotyping of drought traits of relevance to forest management make the development of new drought-resistant genotypes a slow and costly enterprise. Rotation ages measured in decades translate into long periods with limited options for changes in management strategies or interventions. However, there are significant opportunities for research advances in drought physiology that enable more effective strategies for forest management. Below, we discuss examples of enhanced or new applications for forest management under drought that would take advantage of new research findings, including those discussed in the previous section. We first consider how land managers can anticipate and monitor drought impacts to guide silvicultural practices, and then outline areas for management interventions including nursery practices for reforestation, microbiome manipulations, and selection of genotypes for future climates. These examples are not intended to be exhaustive of all existing or potential applications, but rather to present some promising avenues toward effective mitigation of practical problems faced by land managers on large scales.

Predicting and monitoring landscape-scale effects of drought on forests

Forest managers need the ability to assess current and predict future conditions when making decisions about reforestation and silvicultural treatments. The development of predictive process-based models of tree mortality is a very active area of research, drawing heavily on new insights from tree physiology (McDowell *et al.*, 2022a,b). For instance, physiological studies have shown that hydraulic failure is involved in many drought-related mortality events (Adams *et al.*, 2017), but is not universal (Körner, 2019). Many modelling groups have incorporated a representation of the hydraulic pathway and the processes leading up to embolism, to enable use of thresholds of xylem embolism as a predictor for tree mortality (McDowell *et al.*, 2013; Xu *et al.*, 2016, 2023; Mencuccini *et al.*, 2019). This suite of

© 2024 The Author(s).
New Phytologist © 2024 New Phytologist Foundation.
This article has been contributed to by U.S. Government employees and their work is in the public domain in the USA.

hydraulic processes can be usefully characterized by a small number of plant traits, particularly the P_{50} or xylem water potential for 50% loss of hydraulic conductivity (MPa) (Brodribb, 2017; Venturas *et al.*, 2017). This threshold appears to vary systematically among species and provenances depending on their climate of origin (e.g. Larter *et al.*, 2017; Li *et al.*, 2018). Knowledge of variation in hydraulic thresholds among genotypes is advancing our capacity to predict species-level differences in drought vulnerability (De Kauwe *et al.*, 2022), with the ultimate goal of matching species or populations to future climates. However, challenges remain including how to accurately capture whole soil–plant hydraulic vulnerability, particularly in mature large trees, and/or where along the soil–plant–atmosphere continuum the most relevant thresholds are, and which respective physiological processes prevent or delay reaching these thresholds.

Additionally, interacting physiological characteristics are also needed to predict risk of mortality (Trugman *et al.*, 2021). Studies of the relationship between stomatal behavior and hydraulic thresholds suggest that in many woody species, stomatal closure is coordinated with the onset of xylem embolism (Li *et al.*, 2018), and models link these two sets of processes (e.g. Sperry *et al.*, 2017). Predictions of the time to mortality are also sensitive to the representation of processes occurring after the point of stomatal closure, particularly the rate of water loss via cuticles and incomplete sealing of stomatal pores g_{min} (Duursma *et al.*, 2019). This conductance appears to be variable with environmental conditions, and in particular increases significantly at high temperatures (Cochard, 2021). This increase in conductance exacerbates hydraulic failure under heatwaves and be a mechanism by which hot droughts drive mortality (Hammond *et al.*, 2022).

A deeper, preferably quantitative, physiological description of drought legacies is thus a priority if we are to predict the long-term impacts of drought stress. Drought stress can also cause long-term legacy effects on tree health and forest functioning (Anderegg *et al.*, 2015) relevant to long-term management strategies. Mechanistic and predictive models of recovery from drought stress and the effects of repeated droughts are growing research areas. Recovery from drought requires rebuilding of canopy foliage, root biomass, carbohydrate stores, and xylem conduits (Gauthey *et al.*, 2022). The recovery rate of wood growth can last decades and trees that do not recover wood growth are more likely to die than those that fully recover (Cailleret *et al.*, 2017). The recovery rate of carbohydrate stores after drought is short in angiosperms but long in gymnosperms (Piper & Paula, 2020) and depletion of stored carbohydrates reduce osmoregulation capacity (Sapes *et al.*, 2021). Ultimately, there is little evidence that trees in nature die directly of carbon starvation during drought by reaching zero carbohydrate concentrations, but the interaction of carbohydrate stores and plant water relations are fundamentally intertwined and can affect long-term growth and recovery (McDowell *et al.*, 2022a,b).

While predictive models can potentially assist in targeting management interventions, broad-scale monitoring of drought stress impacts is critical to evaluate such models. However, quantifying these impacts at scales relevant for land management remains a significant challenge (Hartmann *et al.*, 2018). Ground-based forest inventory methods can be too infrequent and too sparse to assess and attribute impacts of drought. Satellite remote sensing offers high temporal and spatial coverage, but detecting mortality remains difficult due to high spatial heterogeneity in mortality rates and the problem of how to interpret the remote sensing signal (Yan *et al.*, 2024). Greenness can often recover rapidly following a drought stress event, but this may reflect the recovery of understory or weeds rather than overstorey trees. Nonetheless, several promising approaches are in development. Airborne LiDAR can be used to map biomass at high spatial resolution and identify tree mortality at scales of individual trees (Stovall *et al.*, 2019). High-resolution satellite optical imagery, capable of distinguishing individual tree crowns, is also becoming available, and machine learning approaches trained on airborne LiDAR show promise for large-scale tree detection (Dixon *et al.*, 2013). These methods have the potential to deliver regular monitoring of tree mortality, although ground-based inventory data will continue to remain essential for ground-truthing such approaches.

Technologies for physiological phenotyping and monitoring

Measuring physiological traits that describe drought response and resilience remains a key challenge for both high-throughput/high-precision phenotyping required for genomic studies, and for evaluation of landscape-scale studies (e.g. common gardens) and informing management strategies. High-resolution imaging data (e.g. spectral, hyperspectral, Chl fluorescence, and infrared) has the potential for widespread use for precision phenotyping of drought response in trees, as recently demonstrated for crops (Al-Tamimi *et al.*, 2022). Recent work by Castillo-Argaez *et al.* (2024) and Sapes *et al.* (2024) show that both drought stress and disease can be monitored with remote sensing technology for more rapid assessment of large forest tracts, and the ability to detect stress before visual symptoms appear. For field studies, image-based phenotyping of plant stress has the capacity for high-throughput measurements suitable to common gardens, provenance trials using ground vehicles or unmanned aerial vehicles (D'Odorico *et al.*, 2020). Glasshouse-based studies that can incorporate precisely applied experimental treatments are supported by automated high-throughput phenotyping platforms capable of precision phenotyping of plant stress responses that are non-destructive and that permit repeated measurements of the temporal dynamics of drought response with high temporal resolution (Bian *et al.*, 2022). An example is the Advanced Plant Phenotyping Laboratory (APPL; Department of Energy, Oak Ridge National Lab) designed for capturing detailed image-based tree phenotypes utilizing multiple sensors to estimate features of plant water balance, stress response and stomatal regulation on hundreds of samples over short time intervals within an automated glasshouse (Fig. 4). This facility now enables functional 'omic' studies integrating genome, gene expression, proteomic and metabolic data to ultimately provide mechanistic understanding and predictions of tree drought phenotypes.

© 2024 The Author(s).
New Phytologist © 2024 New Phytologist Foundation.
This article has been contributed to by U.S. Government employees and their work is in the public domain in the USA.

14698137, 2025, 5, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.20326 by Capes, Wiley Online Library on [09/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

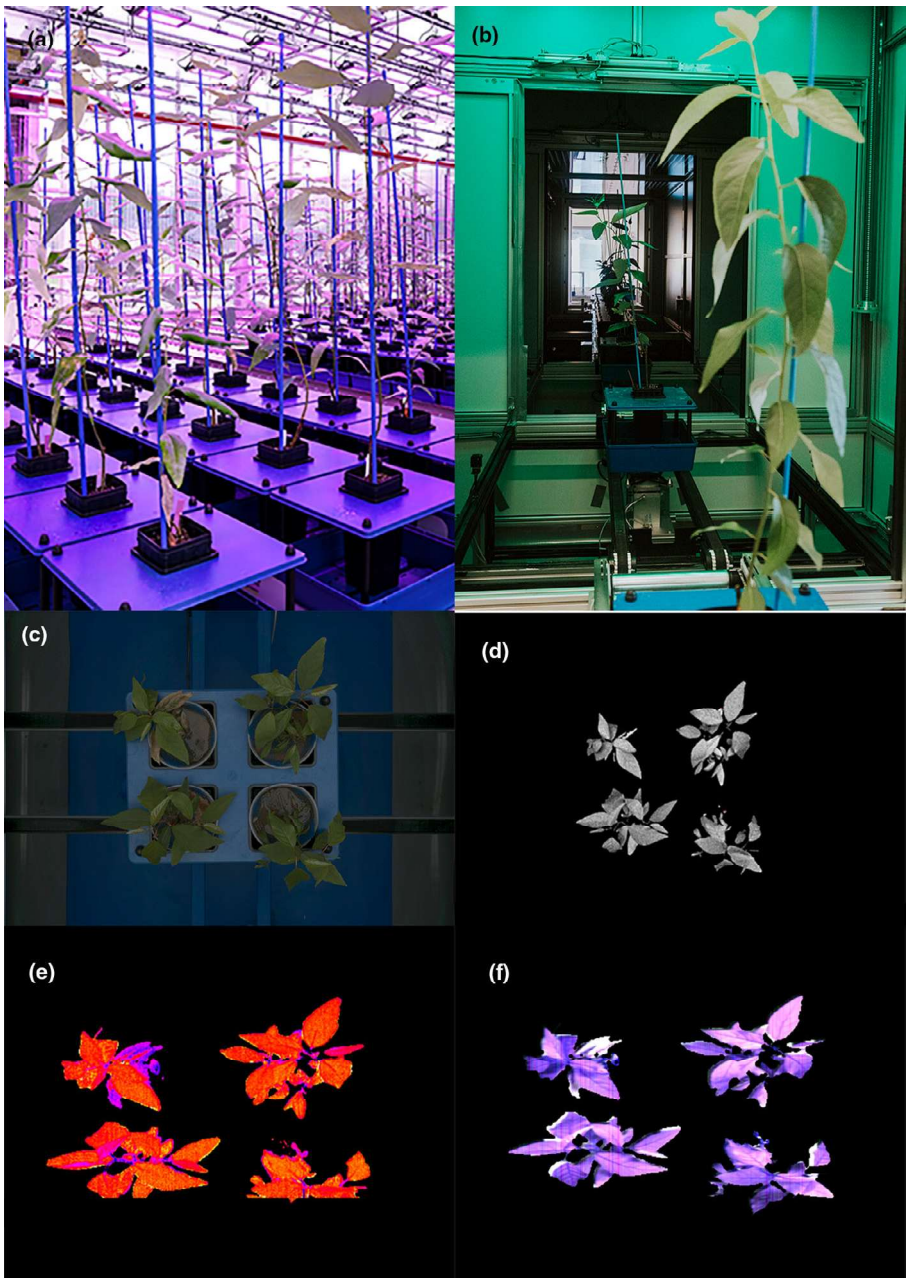


Fig. 4 Automated precision phenotyping platform for poplar growth and physiological studies. The Advanced Plant Phenotyping Laboratory (APPL) at Oak Ridge National Laboratory was established to conduct high-throughput plant physiological, morphological, and spectral characterization using multimodal phenotyping stations. Photographs show (a) *Populus trichocarpa* genotypes from a genome-wide association study being grown under precise water and nutrient regimes, and (b) individual plants sequentially entering a series of phenotyping cabinets. Other photographs show trays of four plants for greater capacity as imaged by four different modalities, including (c) red, green blue (RGB) for plant size and morphology, (d) chlorphyll fluorescence for estimations of photosynthetic efficiency, (e) visible to near-infrared (VNIR) hyperspectral signatures in the 400–900 nm range, such as Normalized Difference Vegetation Index (NDVI), and (f) short wave infrared (SWIR) for spectral signatures in the 900–1700 nm range for the detection of water content or chemical composition. Images (c–f): courtesy of Larry York, Jun Lee, and David Weston.

Matching genotypes to environments

Given the highly polygenic nature of tree drought responses and the long breeding cycle for most tree species, selecting genotypes and breeding for drought tolerance is a challenging prospect. Genomic selection (GS), in which a genomic relatedness matrix and trait measurements on potential parents is used to predict offspring trait values, has proven a valuable strategy that can shorten the breeding cycle (Resende *et al.*, 2012). For example, in white spruce (*P. glauca*), GS was used to predict components of drought response impacting radial growth following natural drought episodes in a large breeding trial (Laverdière *et al.*, 2022). A persistent challenge for GS is that prediction accuracies are often reduced under novel environments (Resende *et al.*, 2012), although recent developments incorporating multi-site phenotyping and G × E into models are promising in this regard (Crossa *et al.*, 2022). An important consideration of using GS for breeding stress-tolerant genotypes arises from potential genetic correlations with other traits due to pleiotropy, which constrains breeding targets due to tradeoffs with other desirable traits, such as growth and productivity (Sebastian-Azcona *et al.*, 2018). Additionally, the genetic architecture of drought tolerance and growth is likely to be species-specific (Csilléry *et al.*, 2020; Compton *et al.*, 2023).

While genomics holds promise for accelerating breeding for drought response, this approach may not be possible or efficient for many species due to constraints of generation time and/or availability of resources in noncommercial species. Alternatively, if

© 2024 The Author(s).
New Phytologist © 2024 New Phytologist Foundation.
This article has been contributed to by U.S. Government employees and their work is in the public domain in the USA.

14698137, 2025, 5, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.20326 by Capes, Wiley Online Library on [09/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

existing drought-tolerant genotypes or populations can be identified from natural stands on the landscape and prioritized for underplanting or reforestation in regions where they are preadapted to future climate, it is possible to mitigate losses due to maladaptation (Williams & Dumroese, 2013). Such a strategy forms the basis for assisted migration – the intentional translocation of individuals to facilitate adaptation. Depending on the specific context, assisted migration can refer to movement within the current range (also known as assisted gene flow) or movement beyond the current range (assisted range expansion) (Aitken & Whitlock, 2013). Implementing assisted migration is a topic of much debate and still faces several uncertainties, but it is increasingly being discussed as an important management option for climate change adaptation (Palik *et al.*, 2022). Provenance trials and seedling common gardens are providing some answers to the question of how survival and growth are impacted by climate transfer distance (i.e. the difference in climate between source and planting site) (Risk *et al.*, 2021; Park & Rodgers, 2023), with maximal fitness often attained in sites most similar to a genotype's source climate (Wang *et al.*, 2010; but see Browne *et al.*, 2019). Field trials of assisted migration in three North American conifer species showed tree populations moved northward or upward in elevation had good productivity (Sáenz-Romero *et al.*, 2021), providing initial support for the rationale that pairing source genotypes or populations with landscape location(s) that minimize transfer distance under future climate can provide useful targets for assisted migration. Indeed, the mismatch between local genetics and need for assisted migration may already be present for some species and not just a future consideration. In a study on two species of North American oaks, climate warming over the last century is evident as adaptation lags, whereby selection at northern sites favors trait values expressed by southern ecotypes (Etterson *et al.*, 2020).

Confidence in assisted migration as a strategy to combat future maladaptation to drought requires more empirical tests, particularly ones that address the impact of episodic or extreme events of temperature or drought stress that can critically determine long-term success (Park & Rodgers, 2023). An example of the latter comes from a long-term provenance trial in lodgepole pine (*Pinus contorta*) that spanned a severe drought episode (Montwé *et al.*, 2016; Isaac-Renton *et al.*, 2018). Lodgepole pine provenances in the northern part of the range showed persistent growth reductions indicating physiological maladaptation to drought, with reduced stomatal responsiveness and thinner-walled tracheids less resistant to xylem embolism. In comparison, provenances from the southern range edge had thick-walled, drought-resistant tracheids, and recovered growth more quickly following drought (Montwé *et al.*, 2016; Isaac-Renton *et al.*, 2018). Given the maladaptation of northern provenances under a drier climate, assisted migration of southern genotypes northward could help increase resilience to future drought, although this must be weighed against the potential susceptibility of southern genotypes to risk from freezing damage (Montwé *et al.*, 2016, 2018). These and other studies serve as a reminder that assisted migration must be approached cautiously and after consideration of genetic and physiological tradeoffs between tolerance to different types of stressors and components of climate adaptation (e.g. cold and drought stress) (Schreiber *et al.*, 2013; Sebastian-Azcona *et al.*, 2018; Sang *et al.*, 2021). It should also be kept in mind that a major limitation of the assisted migration approach is the focus almost exclusively on climate, while ignoring biotic interactions (Bucharova, 2017). More studies are needed to ascertain whether translocating genotypes to minimize climate offset has net fitness benefits when taking both beneficial (e.g. soil microbiome) and negative (e.g. exposure to new insect pest or pathogens) biotic interactions into account.

Enhancing drought stress resilience in seedlings through stress priming

The seedling stage is especially vulnerable to heat and drought conditions because seedlings have a limited root system and reserves. Improving nursery practices to enhance seedling resilience is an obvious target for increasing reforestation success. While nursery managers have long used practices to 'drought harden' tree seedlings before planting through controlled water stress exposure, a recent meta-analysis (Puértolas *et al.*, 2024) found little evidence for significant increase in outplanting survival and growth across all studies examined. However, within the many species and approaches examined, there were successes, and research in crop species suggests these practices can be significantly improved. Stress priming methods involve controlled exposure of seed or seedlings to stress or chemical surrogates followed by recovery, which enables more robust and effective responses to future exposure to stress in the field for crops (Liu *et al.*, 2022; Saha *et al.*, 2022). The mechanisms responsible for stress priming and subsequent stress 'memory' and enhanced resilience are complex, and involve the interplay of physiology, gene expression, epigenetics, and other factors (Hilker & Schmülling, 2019).

The nursery setting represents the rare opportunity in forestry to apply treatments enhancing stress resilience to large numbers of seeds or seedlings. Initial research to establish effective stress priming treatments could be performed in controlled nursery conditions and overlayed with the production of genomic, imaging, and other data types to describe physiological responses and underlying mechanisms in a critical forest management setting. Such data can be used to rigorously evaluate treatment effects and correlated with seedling performance after outplanting in operational reforestation settings. While actual drought and heat stress can be directly applied as priming agents, beneficial priming has also been achieved using the application of chemical surrogates, including hormones, reactive oxygen species, and different synthetic compounds that promote priming, often with protection against multiple types of stress (Savvides *et al.*, 2016). In one example, treatment of containerized oaks with paclobutrozol (an inhibitor of gibberellin biosynthesis) resulted in higher recovery rates after drought treatment (Percival & AlBalushi, 2007). Other priming agents, such as glycine betaine, affect stress resilience through the manipulation of antioxidant and osmotic compounds (Giri, 2011). Seed pretreatments before sowing include osmo-priming, which involves hydrating seed in a low osmotic solution followed by dehydrating before sowing (Lutts *et al.*, 2016).

© 2024 The Author(s).
New Phytologist © 2024 New Phytologist Foundation.
This article has been contributed to by U.S. Government employees and their work is in the public domain in the USA.

14698137, 2025, 5, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.20326 by Capes, Wiley Online Library on [09/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

14698137, 2025, 5, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.20326 by Capes, Wiley Online Library on [09/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Microbiome manipulations to enhance drought resilience

Similar to stress priming, microbiome treatments can be applied *en masse* to nursery seedlings before outplanting. In a practical sense, it has been known for many decades that soil microbes are essential for forest tree growth and health (Baldrian *et al.*, 2023), but the practical challenges of cultivating the growth of beneficial microbes in nursery settings are significant (Hagh-Doust *et al.*, 2022). Some challenges include sourcing and cultivating appropriate microbes and successfully encouraging their growth in nursery soils and conditions. While some microbes, such as mycorrhizal fungi, are known to be beneficial or even essential for tree growth, there is now increasing evidence for the idea that, like the trees themselves, these microbes are adapted to specific environmental conditions and can impart drought and heat resilience to trees (Allsup *et al.*, 2023). With sequencing technologies, it is now possible to perform landscape genetic surveys of forest mycorrhizal fungi and other microbes, pairing these with common garden studies to obtain functional information about what microbes and genotypes of microbes impart resilience to drought and stress.

In a practical sense, after the fundamental work of identifying sources of beneficial microbial communities has matured, the next challenge will be to develop methods to source inocula for nursery applications and to encourage the growth of those microbes in nursery soils. In agriculture, various formulations with arbuscular mycorrhizal fungal and beneficial bacteria are commercially available. However, when and under which environmental conditions these inocula afford beneficial effects on yield is not fully understood and is currently an expanding field of active research (Lutz *et al.*, 2023). In forestry, this area is understudied. Environmental DNA sequencing of soils can be used to guide and evaluate nursery methods for encouraging the growth of such beneficial microbial communities within operational nursery settings, and at the same time identify the presence of potential soil pathogens.

Implementing translational physiology to co-produce research questions

Translational ecology describes a creative approach to applied research (Enquist *et al.*, 2017). In this practice, scientists collaborate with various partners who are invested in the forest to co-create research questions and agendas. Within the United States, the Northern Institute of Applied Climate Science and the regional Climate Adaptation Science Centers are examples of organizations that coordinate interactions among research, land management, and tribal organizations. A corollary approach of 'Translational Physiology' could similarly be informed by collaborations between physiologists and landowners, foresters, silviculturists, indigenous land managers, or fire management teams to optimize management practices. Specific research questions would be co-produced by the collaborative team to move forward with both basic and applied research.

Importantly, forests cover a third of the Earth's land, forest types are ecologically highly diverse, and the utilization and societal values associated with forests vary dramatically. The effects of drought disproportionately harm regions, countries, and individuals that are economically vulnerable, inflicting damage that is exacerbated by social inequality (Salvador *et al.*, 2023). To be the most effective, tree drought research and the associated research community should thus recognize and reflect these realities. Focusing research on regions that stand to lose the most as forests succumb to drought stress, and on applications and technologies that can improve outcomes in those regions, would be a productive way forward. In general, ethnic minorities are currently underrepresented in ecology and evolution-related fields in the United States (O'Brien *et al.*, 2020). Increased inclusion and support of new researchers from underrepresented regions and communities affected by drought and forest mortality is thus one obvious step.

Conclusions

There remain many other fundamental questions not discussed here that should be addressed to not only provide new insights into the basic biology of tree drought physiology, but also to develop effective new applications to increase forest resilience to drought and heat stress. Such questions include the following. How do trees perceive water and heat stress? What are the signaling mechanisms that link stress perception and complex physiological responses? How does drought stress predispose trees to subsequent insect or pathogen susceptibility? While past research has provided insights, for the most part these and other critical questions remain largely unanswered.

Despite the importance of this field to addressing climate change effects on forests, the size of the research community and available research funding arguably do not match the scope of research and management needs, or the magnitude of environmental, societal, and economic impacts. Thus, effective collaboration within the research community, cross-disciplinary research, and advocacy are all critical activities. Even more challenging is the translation of research findings to new effective applications, including the ones discussed here. This will require increased interaction among researchers and nursery practitioners, silviculturists, and land managers. For translation of research to application, infrastructure for forest management must be supported, including nurseries, tree breeding, and propagation facilities and associated staff. In recognition of how forests impact climate, ecosystems, and societies across the planet, the field of forest tree physiology must engage and encourage participation from the diverse geographic regions, societies, and people affected by drought and forest mortality to help prioritize research and link them to effective forest management.

Acknowledgements

This work was organized by attendees of the 'Forest Tree Drought Physiology Research Innovation Group' workshop at the Arnold Arboretum, funded by the New Phytologist Trust. Research support for this work for AG is from the US Forest Service and DOE BER Interagency (agreement no.:

© 2024 The Author(s).
New Phytologist © 2024 New Phytologist Foundation.
This article has been contributed to by U.S. Government employees and their work is in the public domain in the USA.

89243022SSC0000). NM was supported by the National Science Foundation and the Department of Energy's Next Generation Ecosystem Experiment-Tropics. The contribution of TJT for this work is supported by the Center for Bioenergy Innovation (CBI), US Department of Energy, Office of Science, Biological and Environmental Research Program (award no.: ERKP886). JG was supported by USDA NIFA (grant no.: 1029588) and NSF ORCC (grant no. 2222348). SK was supported by NSF-IOS (award no.: 1856450).

Competing interests

None declared.

ORCID

Laura Bogar https://orcid.org/0000-0001-6121-2224
Craig Brodersen https://orcid.org/0000-0002-0924-2570
Rakefet David-Schwartz https://orcid.org/0000-0001-5923-8636
Jessica Gersony https://orcid.org/0000-0003-2619-3851
Andrew Groover https://orcid.org/0000-0002-6686-5774
N. Michele Holbrook https://orcid.org/0000-0003-3325-5395
Stephen Keller https://orcid.org/0000-0001-8887-9213
Nate McDowell https://orcid.org/0000-0002-2178-2254
Belinda Medlyn https://orcid.org/0000-0001-5728-9827
Jarmila Pittermann https://orcid.org/0000-0003-1880-1888
Andrea Polle https://orcid.org/0000-0001-8697-6394
Yakir Preisler https://orcid.org/0000-0001-5861-8362
Anna Sala https://orcid.org/0000-0003-4090-6758
Katarzyna Sokołowska https://orcid.org/0000-0001-7971-6113
Timothy J. Tschaplinski https://orcid.org/0000-0002-9540-6622

Andrew Groover[1,2]*, N. Michele Holbrook[3]*, Andrea Polle[4], Anna Sala[5], Belinda Medlyn[6], Craig Brodersen[7], Jarmila Pittermann[8], Jessica Gersony[9], Katarzyna Sokołowska[10], Laura Bogar[11], Nate McDowell[12,13], Rachel Spicer[14], Rakefet David-Schwartz[15], Stephen Keller[16], Timothy J. Tschaplinski[17] and Yakir Preisler[3,18]

[1]USDA Forest Service Northern Research Station, Burlington, VT 05446, USA;
[2]Institute of Forest Genetics, USDA Forest Service Pacific Southwest Research Station, Placerville, CA 95667, USA;
[3]Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA;
[4]Forest Botany and Tree Physiology, University of Göttingen, Büsgenweg 2, 37077, Göttingen, Germany;
[5]Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA;
[6]Hawkesbury Institute for the Environment, Western Sydney University, Locked Bag 1797, Penrith, NSW, 2751, Australia;
[7]School of the Environment, Yale University, New Haven, CT 06511, USA;
[8]Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95060, USA;
[9]Department of Biological Sciences, Smith College, Northampton, MA 01060, USA;
[10]Department of Plant Developmental Biology, Faculty of Biological Sciences, University of Wrocław, Kanonia 6/8, 50-328, Wrocław, Poland;
[11]Department of Plant Biology, University of California Davis, Davis, CA 95616, USA;
[12]Atmospheric, Climate, and Earth Sciences, Pacific Northwest National Laboratory, Richland, WA 99352, USA;
[13]School of Biological Sciences, Washington State University, Pullman, WA, 99164-4236, USA;
[14]Department of Botany, Connecticut College, New London, CT 06320, USA;
[15]Institute of Plant Sciences, Agricultural Research Organization – Volcani Institute, 68 HaMaccabim Road, Rishon Lezion, 7505101, Israel;
[16]Department of Plant Biology, University of Vermont, Burlington, VT 05405, USA;
[17]Biosciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 38731, USA;
[18]Agriculture Research Organization – Volcani Institute, 68 HaMaccabim Road, Rishon Lezion, 7505101, Israel
(*Authors for correspondence: email andrew.t.groover@usda.gov (AG); holbrook@oeb.harvard.edu (NMH))

References

Adams HD, Zeppel MJB, Anderegg WRL, Hartmann H, Landhäusser SM, Tissue DT, Huxman TE, Hudson PJ, Franz TE, Allen CD *et al.* 2017. A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nature Ecology & Evolution* **1**: 1285–1291.

Aghai MM, Khan Z, Joseph MR, Stoda AM, Sher AW, Ettl GJ, Doty SL. 2019. The effect of microbial endophyte consortia on *Pseudotsuga menziesii* and *Thuja plicata* survival, growth, and physiology across edaphic gradients. *Frontiers in Microbiology* **10**: 1353.

Aitken SN, Whitlock MC. 2013. Assisted gene flow to facilitate local adaptation to climate change. *Annual Review of Ecology, Evolution, and Systematics* **44**: 367–388.

Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications* **1**: 95–111.

Allsup CM, George I, Lankau RA. 2023. Shifting microbial communities can enhance tree tolerance to changing climates. *Science* **380**: 835–840.

Al-Tamimi N, Langan P, Bernád V, Walsh J, Mangina E, Negrão S. 2022. Capturing crop adaptation to abiotic stress using image-based technologies. *Open Biology* **12**: 210353.

Amaral J, Ribeyre Z, Vigneaud J, Sow MD, Fichot R, Messier C, Pinto G, Nolet P, Maury S. 2020. Advances and promises of epigenetics for forest trees. *Forests* **11**: 976.

Anderegg WRL, Schwalm C, Biondi F, Camarero JJ, Koch G, Litvak M, Ogle K, Shaw JD, Shevliakova E, Williams AP *et al.* 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science* **349**: 528–532.

Anfodillo T, Olson ME. 2021. Tree mortality: testing the link between drought, embolism vulnerability, and xylem conduit diameter remains a priority. *Frontiers in Forests and Global Change* **4**: 704670.

Arend M, Fromm J. 2007. Seasonal change in the drought response of wood cell development in poplar. *Tree Physiology* **27**: 985–992.

© 2024 The Author(s).
New Phytologist © 2024 New Phytologist Foundation.
This article has been contributed to by U.S. Government employees and their work is in the public domain in the USA.

14698137, 2025, 5, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.20326 by Capes, Wiley Online Library on [09/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Arend M, Link RM, Patthey R, Hoch G, Schuldt B, Kahmen A. 2021. Rapid hydraulic collapse as cause of drought-induced mortality in conifers. *Proceedings of the National Academy of Sciences, USA* **118**: e2025251118.

Baharudin NF, Osman NI. 2023. Plant development, stress responses, and secondary metabolism under ethylene regulation. *Plant Stress* 7: 100146.

Balao F, Paun O, Alonso C. 2018. Uncovering the contribution of epigenetics to plant phenotypic variation in Mediterranean ecosystems. *Plant Biology* **20**: 38–49.

Baldrian P, López-Mondéjar R, Kohout P. 2023. Forest microbiome and global change. *Nature Reviews Microbiology* **21**: 487–501.

Bao Y, Aggarwal P, Robbins NE II, Sturrock CJ, Thompson MC, Tan HQ, Tham C, Duan L, Rodriguez PL, Vernoux T *et al.* 2014. Plant roots use a patterning mechanism to position lateral root branches toward available water. *Proceedings of the National Academy of Sciences, USA* **111**: 9319–9324.

Bian L, Zhang H, Ge Y, Čepl J, Stejskal J, El-Kassaby YA. 2022. Closing the gap between phenotyping and genotyping: review of advanced, image-based phenotyping technologies in forestry. *Annals of Forest Science* **79**: 1–21.

Bräutigam K, Vining KJ, Lafon-Placette C, Fossdal CG, Mirouze M, Marcos JG, Fluch S, Fraga MF, Guevara MÁ, Abarca D *et al.* 2013. Epigenetic regulation of adaptive responses of forest tree species to the environment. *Ecology and Evolution* **3**: 399–415.

Breshears DD, Cobb NS, Rich PM, Price KP, Allen CD, Balice RG, Romme WH, Kastens JH, Floyd ML, Belnap J *et al.* 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences, USA* **102**: 15144–15148.

Brodersen C, McElrone A. 2013. Maintenance of xylem network transport capacity: a review of embolism repair in vascular plants. *Frontiers in Plant Science* **4**: 108.

Brodersen C, McElrone A, Choat B, Matthews M, Shackel K. 2020. The dynamics of embolism repair in xylem: *in vivo* visualizations using high-resolution computed tomography. *Plant Physiology* **154**: 1088–1095.

Brodribb T. 2017. Progressing from 'functional' to mechanistic traits. *New Phytologist* **215**: 9–11.

Brodribb T, McAdam S. 2013. Abscisic acid mediates a divergence in the drought response of two conifers. *Plant Physiology* **162**: 1370–1377.

Brodribb TJ, Powers J, Cochard H, Choat B. 2020. Hanging by a thread? Forests and drought. *Science* **368**: 261–266.

Browne L, Wright JW, Fitz-Gibbon S, Gugger PF, Sork VL. 2019. Adaptational lag to temperature in valley oak (*Quercus Lobata*) can be mitigated by genome-informed assisted gene flow. *Proceedings of the National Academy of Sciences, USA* **116**: 25179–25185.

Bucharova A. 2017. Assisted migration within species range ignores biotic interactions and lacks evidence. *Restoration Ecology* **25**: 14–18.

Cailleret M, Jansen S, Robert EMR, Desoto L, Aakala T, Antos JA, Beikircher B, Bigler C, Bugmann H, Caccianiga M *et al.* 2017. A synthesis of radial growth patterns preceding tree mortality. *Global Change Biology* **23**: 1675–1690.

Carlquist S. 2013. *Comparative wood anatomy.* Berlin, Heidelberg, Germany: Springer.

Castillo-Argaez R, Sapes G, Mallen N, Lippert A, John GP, Zare A, Hammond WM. 2024. Spectral ecophysiology: hyperspectral pressure–volume curves to estimate leaf turgor loss. *New Phytologist* **242**: 935–946.

Cheng Y, Oehmcke S, Brandt M, Rosenthal L, Das A, Vrieling A, Saatchi S, Wagner F, Mugabowindekwe M, Verbruggen W *et al.* 2024. Scattered tree death contributes to substantial forest loss in California. *Nature Communications* **15**: 641.

Choat B, Brodribb TJ, Brodersen CR, Duursma RA, López R, Medlyn B. 2018. Triggers of tree mortality under drought. *Nature* **558**: 531–539.

Choudhary SP, Yu J, Yamaguchi-Shinozaki K, Shinozaki K, Tran LP. 2012. Benefits of brassinosteroid crosstalk. *Trends in Plant Science* **17**: 594–605.

Christmann A, Weiler EW, Steudle E, Grill E. 2007. A hydraulic signal in root-to-shoot signalling of water shortage. *The Plant Journal* **52**: 167–174.

Cochard H. 2021. A new mechanism for tree mortality due to drought and heatwaves. *Peer Community Journal* **1**: e36.

Compton S, Stackpole C, Dixit A, Sekhwal MK, Kolb T, De la Torre AR. 2023. Differences in heat tolerance, water use efficiency and growth among Douglas-fir families and varieties evidenced by GWAS and common garden studies. *AoB Plants* **15**: lad008.

Crossa J, Montesinos-López OA, Pérez-Rodríguez P, Costa-Neto G, Fritsche-Neto R, Ortiz R, Martini JWR, Lillemo M, Montesinos-López A, Jarquin D *et al.* 2022. Genome and environment based prediction models and methods of complex traits incorporating genotype × environment interaction. *Methods in Molecular Biology* **2467**: 245–283.

Csilléry K, Buchmann N, Fady B. 2020. Adaptation to drought is coupled with slow growth, but independent from phenology in marginal silver fir (*Abies alba* Mill.) populations. *Evolutionary Applications* **13**: 2357–2376.

Cumbie WP, Eckert A, Wegrzyn J, Whetten R, Neale D, Goldfarb B. 2011. Association genetics of carbon isotope discrimination, height and foliar nitrogen in a natural population of *Pinus taeda* L. *Heredity* **107**: 105–114.

D'Odorico P, Besik A, Wong CYS, Isabel N, Ensminger I. 2020. High-throughput drone-based remote sensing reliably tracks phenology in thousands of conifer seedlings. *New Phytologist* **226**: 1667–1681.

De Kauwe M, Sabot M, Medlyn B, Pitman A, Meir P, Cernusak L, Gallagher R, Ukkola A, Rifai S, Choat B. 2022. Towards species-level forecasts of drought-induced tree mortality risk. *New Phytologist* **235**: 94–110.

Delzon S, Douthe C, Sala A, Cochard H. 2010. Mechanism of water-stress induced cavitation in conifers: bordered pit structure and function support the hypothesis of seal capillary-seeding. *Plant, Cell & Environment* **33**: 2101–2111.

Depaepe T, Hendrix S, Janse van Rensburg HC, Van den Ende W, Cuypers A, Van Der Straeten D. 2021. At the crossroads of survival and death: the reactive oxygen species–ethylene–sugar triad and the unfolded protein response. *Trends in Plant Science* **26**: 338–351.

Depardieu C, Gérardi S, Nadeau S, Parent GJ, Mackay J, Lenz P, Lamothe M, Girardin MP, Bousquet J, Isabel N. 2021. Connecting tree-ring phenotypes, genetic associations and transcriptomics to decipher the genomic architecture of drought adaptation in a widespread conifer. *Molecular Ecology* **30**: 3898–3917.

Depardieu C, Girardin MP, Nadeau S, Lenz P, Bousquet J, Isabel N. 2020. Adaptive genetic variation to drought in a widely distributed conifer suggests a potential for increasing forest resilience in a drying climate. *New Phytologist* **227**: 427–439.

Dixon DJ, Zhu Y, Brown CF, Jin Y. 2013. Satellite detection of canopy-scale tree mortality and survival from California wildfires with spatio-temporal deep learning. *Remote Sensing of Environment* **298**: 113842.

Do Nascimento AMM, Montalbán IA, Llamazares De Miguel D, Goicoa T, Ugarte MD, Moncaleán P. 2022. High temperature and water deficit cause epigenetic changes in somatic plants of *Pinus radiata* D. Don. *Plant Cell, Tissue and Organ Culture (PCTOC)* **151**: 107–121.

Duursma RA, Blackman CJ, Lopéz R, Martin-StPaul NK, Cochard H, Medlyn BE. 2019. On the minimum leaf conductance: its role in models of plant water use, and ecological and environmental controls. *New Phytologist* **221**: 693–705.

Enquist CA, Jackson ST, Garfin GM, Davis FW, Gerber LR, Littell JA, Tank JL, Terando AJ, Wall TU, Halpern B *et al.* 2017. Foundations of translational ecology. *Frontiers in Ecology and the Environment* **15**: 541–550.

Etterson JR, Cornett MW, White MA, Kavajecz LC. 2020. Assisted migration across fixed seed zones detects adaptation lags in two major North American tree species. *Ecological Applications* **30**: e02092.

Farquhar GD, Ehleringer JR, Hubick KT. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* **40**: 503–537.

Foo E, Plett JM, Lopez-Raez JA, Reid D. 2019. Editorial: the role of plant hormones in plant–microbe symbioses. *Frontiers in Plant Science* **10**: 1391.

de Freitas Pereira M, Cohen D, Auer L, Aubry N, Bogeat-Triboulot M-B, Bure C, Engle NL, Jolivet Y, Kohler A, Novák O *et al.* 2023. Ectomycorrhizal symbiosis prepares its host locally and systemically for abiotic cue signaling. *The Plant Journal* **116**: 1784–1803.

Gallusci P, Agius DR, Moschou PN, Dobránszki J, Kaiserli E, Martinelli F. 2023. Deep inside the epigenetic memories of stressed plants. *Trends in Plant Science* **28**: 142–153.

Gauthey A, Peters JMR, Lòpez R, Carins-Murphy MR, Rodriguez-Dominguez CM, Tissue DT, Medlyn BE, Brodribb TJ, Choat B. 2022. Mechanisms of xylem hydraulic recovery after drought in *Eucalyptus saligna*. *Plant, Cell & Environment* **45**: 1216–1228.

Giri J. 2011. Glycinebetaine and abiotic stress tolerance in plants. *Plant Signaling & Behavior* **6**: 1746–1751.

Gomez-Roldan V, Fermas S, Brewer PB, Puech-Pagès V, Dun EA, Pillot J, Letisse F, Matusova R, Danoun S, Portais J *et al.* 2008. Strigolactone inhibition of shoot branching. *Nature* **455**: 189–194.

© 2024 The Author(s).
New Phytologist © 2024 New Phytologist Foundation.
This article has been contributed to by U.S. Government employees and their work is in the public domain in the USA.

14698137, 2025, 5, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.20326 by Capes, Wiley Online Library on [09/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

González-Martínez SC, Huber D, Ersoz E, Davis JM, Neale DB. 2008. Association genetics in *Pinus taeda* L. II. Carbon isotope discrimination. *Heredity* **101**: 19–26.

Hacke UG, Spicer R, Schreiber SG, Plavcová L. 2017. An ecophysiological and developmental perspective on variation in vessel diameter. *Plant, Cell & Environment* **40**: 831–845.

Hagh-Doust N, Färkkilä SMA, Hosseyni Moghaddam MS, Tedersoo L. 2022. Symbiotic fungi as biotechnological tools: methodological challenges and relative benefits in agriculture and forestry. *Fungal Biology Reviews* **42**: 34–55.

Hammond W, Williams A, Abatzoglou J, Adams H, Klein T, López R, Sáenz-Romero C, Hartmann H, Breshears D, Allen C. 2022. Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests. *Nature Communications* **13**: 1761.

Hartmann H, Moura CF, Anderegg WRL, Ruehr NK, Salmon Y, Allen CD, Arndt SK, Breshears DD, Davi H, Galbraith D *et al.* 2018. Research frontiers for improving our understanding of drought-induced tree and forest mortality. *New Phytologist* **218**: 15–28.

Hilker M, Schmülling T. 2019. Stress priming, memory, and signalling in plants. *Plant, Cell & Environment* **42**: 753–761.

Housset JM, Nadeau S, Isabel N, Depardieu C, Duchesne I, Lenz P, Girardin MP. 2018. Tree rings provide a new class of phenotypes for genetic associations that foster insights into adaptation of conifers to climate change. *New Phytologist* **218**: 630–645.

Immanen J, Nieminen K, Smolander O-P, Kojima M, Alonso Serra J, Koskinen P, Zhang J, Elo A, Mähönen AP, Street N *et al.* 2016. Cytokinin and auxin display distinct but interconnected distribution and signaling profiles to stimulate cambial activity. *Current Biology* **26**: 1990–1997.

Isaac-Renton M, Montwé D, Hamann A, Spiecker H, Cherubini P, Treydte K. 2018. Northern forest tree populations are physiologically maladapted to drought. *Nature Communications* **9**: 5254.

Isabel N, Holliday JA, Aitken SN. 2019. Forest genomics: advancing climate adaptation, forest health, productivity, and conservation. *Evolutionary Applications* **13**: 3–10.

Isasa E, Link RM, Jansen S, Tezeh FR, Kaack L, Sarmento Cabral J, Schuldt B. 2023. Addressing controversies in the xylem embolism resistance–vessel diameter relationship. *New Phytologist* **238**: 283–296.

Jacobsen AL, Ewers FW, Pratt RB, Paddock WA, Davis SD. 2005. Do xylem fibers affect vessel cavitation resistance? *Plant Physiology* **139**: 546–556.

Janssen TA, Hölttä T, Fleischer K, Naudts K. 2020. Wood allocation trade-offs between fiber wall, fiber lumen, and axial parenchyma drive drought resistance in neotropical trees. *Plant, Cell & Environment* **43**: 965–980.

Jaramillo-Correa JP, Prunier J, Vázquez-Lobo A, Keller S, Moreno-Letelier A. 2015. Molecular signatures of adaptation and selection in forest trees. *Advances in Botanical Research* **74**: 265–306.

Jin X, Zimmermann J, Polle A, Fischer U. 2015. Auxin is a long-range signal that acts independently of ethylene signaling on leaf abscission in *Populus*. *Frontiers in Plant Science* **6**: 634.

Johnson D, Eckart P, Alsamadisi N, Noble H, Martin C, Spicer R. 2018. Polar auxin transport is implicated in vessel differentiation and spatial patterning during secondary growth in *Populus*. *American Journal of Botany* **105**: 186–196.

Junghans U, Langenfeld-Heyser R, Polle A, Teichmann T. 2004. Effect of auxin transport inhibitors and ethylene on the wood anatomy of poplar. *Plant Biology* **6**: 22–29.

Jupa R, Plavcová L, Gloser V, Jansen S. 2016. Linking xylem water storage with anatomical parameters in five temperate tree species. *Tree Physiology* **36**: 756–769.

Kannenberg SA, Phillips RP. 2017. Soil microbial communities buffer physiological responses to drought stress in three hardwood species. *Oecologia* **183**: 631–641.

Kazan K. 2015. Diverse roles of jasmonates and ethylene in abiotic stress tolerance. *Trends in Plant Science* **20**: 219–229.

Kebert M, Kostić S, Stojnić S, Čapelja E, Markić AG, Zorić M, Kesić L, Flors V. 2023. A fine-tuning of the plant hormones, polyamines and osmolytes by ectomycorrhizal fungi enhances drought tolerance in pedunculate oak. *International Journal of Molecular Sciences* **24**: 7510.

Kim Y-C, Glick BR, Bashan Y, Ryu C-M. 2012. Enhancement of plant drought tolerance by microbes. In: Aroca R, ed. *Plant responses to drought stress: from morphological to molecular features*. Berlin, Heidelberg, Germany: Springer, 383–413.

Knipfer T, Cuneo I, Earles M, Reyes C, Brodersen C, McElrone A. 2017. Storage compartments for capillary water rarely refill in an intact woody plant. *Plant Physiology* **175**: 1649–1660.

Koltai H. 2011. Strigolactones are regulators of root development. *New Phytologist* **190**: 545–549.

Koo YM, Heo AY, Choi HW. 2020. Salicylic acid as a safe plant protector and growth regulator. *Plant Pathology Journal* **36**: 1–10.

Körner C. 2019. No need for pipes when the well is dry – a comment on hydraulic failure in trees. *Tree Physiology* **39**: 695–700.

Kristy B, Carrell AA, Johnston E, Cumming JR, Klingeman DM, Gwinn K, Syring KC, Skalla C, Emrich S, Cregger MA. 2022. Chronic drought differentially alters the belowground microbiome of drought-tolerant and drought-susceptible genotypes of *Populus trichocarpa*. *Phytobiomes Journal* **6**: 317–330.

Kurepa J, Smalle JA. 2022. Auxin/cytokinin antagonistic control of the shoot/root growth ratio and its relevance for adaptation to drought and nutrient deficiency stresses. *International Journal of Molecular Sciences* **23**: 1933.

Kuromori T, Seo M, Shinozaki K. 2018. ABA transport and plant water stress responses. *Trends in Plant Science* **23**: 513–522.

Lämke J, Bäurle I. 2017. Epigenetic and chromatin-based mechanisms in environmental stress adaptation and stress memory in plants. *Genome Biology* **18**: 124.

Larter M, Pfautsch S, Domec J, Trueba S, Nagalingum N, Delzon S. 2017. Aridity drove the evolution of extreme embolism resistance and the radiation of conifer genus *Callitris*. *New Phytologist* **215**: 97–112.

Laverdière J-P, Lenz P, Nadeau S, Depardieu C, Isabel N, Perron M, Beaulieu J, Bousquet J. 2022. Breeding for adaptation to climate change: genomic selection for drought response in a white spruce multi-site polycross test. *Evolutionary Applications* **15**: 383–402.

Ledig FT, Kitzmiller JH. 1992. Genetic strategies for reforestation in the face of global climate change. *Forest Ecology and Management* **50**: 153–169.

Lemaire C, Quilichini Y, Brunel-Michac N, Santini J, Berti L, Cartailler J, Conchon P, Badel É, Herbette S. 2021. Plasticity of the xylem vulnerability to embolism in *Populus tremula x alba* relies on pit quantity properties rather than on pit structure. *Tree Physiology* **41**: 1384–1399.

Lens F, Gleason SM, Bortolami G, Brodersen C, Delzon S, Jansen S. 2022. Functional xylem characteristics associated with drought-induced embolism in angiosperms. *New Phytologist* **236**: 2019–2036.

Levionnois S, Jansen S, Wandji RT, Beauchêne J, Ziegler C, Coste S, Stahl C, Delzon S, Authier L, Heuret P. 2021. Linking drought-induced xylem embolism resistance to wood anatomical traits in Neotropical trees. *New Phytologist* **229**: 1453–1466.

Li W, Herrera-Estrella L, Tran LP. 2016. The Yin–Yang of cytokinin homeostasis and drought acclimation/adaptation. *Trends in Plant Science* **21**: 548–550.

Li W, Herrera-Estrella L, Tran LP. 2019. Do cytokinins and strigolactones crosstalk during drought adaptation? *Trends in Plant Science* **24**: 669–672.

Li X, Blackman C, Choat B, Duursma R, Rymer P, Medlyn B, Tissue D. 2018. Tree hydraulic traits are coordinated and strongly linked to climate-of-origin across a rainfall gradient. *Plant, Cell & Environment* **41**: 646–660.

Liang X, Ye Q, Liu H, Brodribb TJ. 2021. Wood density predicts mortality threshold for diverse trees. *New Phytologist* **229**: 3053–3057.

Liu H, Able A, Able J. 2022. Priming crops for the future: rewiring stress memory. *Trends in Plant Science* **27**: 699–716.

Lutts S, Benincasa P, Wojtyla L, Kubala S, Pace R, Lechowska K, Quinet M, Garnczarska M. 2016. Seed priming: new comprehensive approaches for an old empirical technique. In: Balestrazzi A, ed. *New challenges in seed biology – basic and translational research driving seed technology*. London, UK: InTech. doi: 10.5772/64420.

Lutz S, Bodenhausen N, Hess J, Valzano-Held A, Waelchli J, Deslandes-Hérold G, Schlaeppi K, van der Heijden MGA. 2023. Soil microbiome indicators can predict crop growth response to large-scale inoculation with arbuscular mycorrhizal fungi. *Nature Microbiology* **8**: 2277–2289.

Ma C, Jiang C, Gao J. 2021. Regulatory mechanisms underlying activation of organ abscission. *Annual Plant Reviews Online* **4**: 27–56.

McDowell NG, Ball M, Bond-Lamberty B, Kirwan ML, Krauss KW, Megonigal JP, Mencuccini M, Ward ND, Weintraub MN, Bailey V. 2022a. Processes and

© 2024 The Author(s).
New Phytologist © 2024 New Phytologist Foundation.
This article has been contributed to by U.S. Government employees and their work is in the public domain in the USA.

14698137, 2025, 5, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.20326 by Capes, Wiley Online Library on [09/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

mechanisms of coastal woody-plant mortality. *Global Change Biology* **28**: 5881–5900.

McDowell NG, Fisher RA, Xu C, Domec JC, Hölttä T, Mackay DS, Sperry JS, Boutz A, Dickman L, Gehres N *et al.* 2013. Evaluating theories of drought-induced vegetation mortality using a multimodel–experiment framework. *New Phytologist* **200**: 304–321.

McDowell NG, Sapes G, Pivovaroff A, Adams HD, Allen CD, Anderegg WRL, Arend M, Breshears DD, Brodribb T, Choat B *et al.* 2022b. Mechanisms of woody-plant mortality under rising drought, CO_2 and vapour pressure deficit. *Nature Reviews Earth & Environment* **3**: 294–308.

Mehra P, Pandey BK, Melebari D, Banda J, Leftley N, Couvreur V, Rowe J, Anfang M, De Gernier H, Morris E *et al.* 2022. Hydraulic flux–responsive hormone redistribution determines root branching. *Science* **378**: 762–768.

Mencuccini M, Manzoni S, Christoffersen B. 2019. Modelling water fluxes in plants: from tissues to biosphere. *New Phytologist* **222**: 1207–1222.

Montwé D, Isaac-Renton M, Hamann A, Spiecker H. 2016. Drought tolerance and growth in populations of a wide-ranging tree species indicate climate change risks for the boreal north. *Global Change Biology* **22**: 806–815.

Montwé D, Isaac-Renton M, Hamann A, Spiecker H. 2018. Cold adaptation recorded in tree rings highlights risks associated with climate change and assisted migration. *Nature Communications* **9**: 1574.

Munemasa S, Hauser F, Park J, Waadt R, Brandt B, Schroeder JI. 2015. Mechanisms of abscisic acid-mediated control of stomatal aperture. *Current Opinion in Plant Biology* **28**: 154–162.

Muñoz-Espinoza VA, López-Climent MF, Casaretto JA, Gómez-Cadenas A. 2015. Water stress responses of tomato mutants impaired in hormone biosynthesis reveal abscisic acid, jasmonic acid and salicylic acid interactions. *Frontiers in Plant Science* **6**: 997.

Nosenko T, Zimmer I, Ghirardo A, Köllner TG, Weber B, Polle A, Rosenkranz M, Schnitzler J-P. 2023. Predicting functions of putative fungal sesquiterpene synthase genes based on multiomics data analysis. *Fungal Genetics and Biology* **165**: 103779.

O'Brien LT, Bart HL, Garcia DM. 2020. Why are there so few ethnic minorities in ecology and evolutionary biology? Challenges to inclusion and the role of sense of belonging. *Social Psychology of Education* **23**: 449–477.

Olson ME. 2023. Imperforate tracheary element classification for studies of xylem structure-function relations. *IAWA Journal* **44**: 439–464.

Olson ME, Pace MR, Anfodillo T. 2023. The vulnerability to drought-induced embolism-conduit diameter link: breaching the anatomy-physiology divide. *IAWA Journal* **43**: 335–354.

Ortiz-García P, Ortega-Villaizán AG, Onejeme FC, Müller M, Pollmann S. 2023. Do opposites attract? Auxin-abscisic acid crosstalk: new perspectives. *International Journal of Molecular Sciences* **24**: 3090.

Ozturk M, Turkyilmaz Unal B, García-Caparrós P, Khursheed A, Gul A, Hasanuzzaman M. 2021. Osmoregulation and its actions during the drought stress in plants. *Physiologia Plantarum* **172**: 1321–1335.

Paci J, Newman M, Gage T. 2023. *The economic, fiscal, and environmental costs of wildfires in California.* Palo Alto, CA, USA: Gordon and Betty Moore Foundation. [WWW document] URL https://www.moore.org/docs/default-source/default-document-library/the-economic-fiscal-and-environmental-costs-of-wildfires-in-ca.pdf?sfvrsn=1b1b620c_0 [accessed 1 June 2024].

Palik BJ, Clark PW, D'Amato AW, Swanston C, Nagel L. 2022. Operationalizing forest-assisted migration in the context of climate change adaptation: examples from the Eastern USA. *Ecosphere* **13**: e4260.

Park A, Rodgers J. 2023. Provenance trials in the service of forestry assisted migration: a review of North American field trials and experiments. *Forest Ecology and Management* **537**: 120854.

Paschalis A, De Kauwe MG, Sabot M, Fatichi S. 2024. When do plant hydraulics matter in terrestrial biosphere modelling? *Global Change Biology* **30**: e17022.

Percival G, AlBalushi A. 2007. Paclobutrazol-induced drought tolerance in containerized English and evergreen oak. *Arboriculture and Urban Forestry* **33**: 397–409.

Piper F, Paula S. 2020. The role of nonstructural carbohydrates storage in forest resilience under climate change. *Current Forestry Reports* **6**: 1–13.

Pittermann J, Sperry JS, Wheeler JK, Hacke UG, Sikkema EH. 2006. Mechanical reinforcement of tracheids compromises the hydraulic efficiency of conifer xylem. *Plant, Cell & Environment* **29**: 1618–1628.

Plomion C, Bartholomé J, Bouffier L, Brendel O, Cochard H, de Miguel M, Delzon S, Gion J-M, Gonzalez-Martinez SC, Guehl J-M *et al.* 2016. Understanding the genetic bases of adaptation to soil water deficit in trees through the examination of water use efficiency and cavitation resistance: maritime pine as a case study. *Journal of Plant Hydraulics* **3**: e008.

Polle A, Chen S, Eckert C, Harfouche A. 2019. Engineering drought resistance in forest trees. *Frontiers in Plant Science* **9**: 1875.

Pratt RB, Tobin MF, Jacobsen AL, Traugh CA, De Guzman ME, Hayes CC, Toschi HS, MacKinnon ED, Percolla MI, Clem ME *et al.* 2021. Starch storage capacity of sapwood is related to dehydration avoidance during drought. *American Journal of Botany* **108**: 91–101.

Puértolas J, Villar-Salvador P, Andivia E, Ahuja I, Cocozza C, Cvjetković B, Devetaković J, Diez JJ, Fløistad I, Ganatsas P *et al.* 2024. Die-hard seedlings. A global meta-analysis on the factors determining the effectiveness of drought hardening on growth and survival of forest plantations. *Forest Ecology and Management* **572**: 122300.

Raghavendra AS, Gonugunta VK, Christmann A, Grill E. 2010. ABA perception and signalling. *Trends in Plant Science* **15**: 395–401.

Resende MDV, Resende MFR Jr, Sansaloni CP, Petroli CD, Missiaggia AA, Aguiar AM, Abad JM, Takahashi EK, Rosado AM, Faria DA *et al.* 2012. Genomic selection for growth and wood quality in *Eucalyptus*: capturing the missing heritability and accelerating breeding for complex traits in forest trees. *New Phytologist* **194**: 116–128.

Rico L, Ogaya R, Barbeta A, Peñuelas J. 2014. Changes in DNA methylation fingerprint of *Quercus ilex* trees in response to experimental field drought simulating projected climate change. *Plant Biology* **16**: 419–427.

Risk C, McKenney DW, Pedlar J, Pengxin L. 2021. A compilation of North American tree provenance trials and relevant historical climate data for seven species. *Scientific Data* **8**: 29.

Rodriguez-Zaccaro FD, Groover A. 2019. Wood and water: how trees modify wood development to cope with drought. *Plants, People, Planet* **1**: 346–355.

Rodriguez-Zaccaro FD, Henry I, Groover A. 2021. Genetic regulation of vessel morphology in *Populus*. *Frontiers in Plant Science* **12**: 705596.

Rodriguez-Zaccaro FD, Lieberman M, Groover A. 2024. A systems genetic analysis identifies putative mechanisms and candidate genes regulating vessel traits in poplar wood. *Frontiers in Plant Science* **15**: 1375506.

Sadhukhan A, Prasad SS, Mitra J, Siddiqui N, Sahoo L, Kobayashi Y, Koyama H. 2022. How do plants remember drought? *Planta* **256**: 7.

Sáenz-Romero C, O'Neill G, Aitken SN. 2021. Assisted migration field tests in Canada and Mexico: lessons, limitations, and challenges. *Forests, Trees and Livelihoods* **12**: 9.

Saha D, Choyal P, Mishra UN, Dey P, Bose B, Prathibha MD, Gupta NK, Mehta BK, Kumar P, Pandey S *et al.* 2022. Drought stress responses and inducing tolerance by seed priming approach in plants. *Plant Stress* **4**: 100066.

Salvador C, Nieto R, Vicente-Serrano S, Garcia-Herrera R, Gimeno L, Vicedo-Cabrera AM. 2023. Public health implications of drought in a climate change context: a critical review. *Annual Review of Public Health* **44**: 213–232.

Sang Z, Hamann A, Aitken SN. 2021. Assisted migration poleward rather than upward in elevation minimizes frost risks in plantations. *Climate Risk Management* **34**: 100380.

Sapes G, Demaree P, Lekberg Y, Sala A. 2021. Plant carbohydrate depletion impairs water relations and spreads via ectomycorrhizal networks. *New Phytologist* **229**: 3172–3183.

Sapes G, Schroeder L, Scott A, Clark I, Juzwik J, Montgomery RA, Guzmán QJA, Cavender-Bares J. 2024. Mechanistic links between physiology and spectral reflectance enable previsual detection of oak wilt and drought stress. *Proceedings of the National Academy of Sciences, USA* **121**: e2316164121.

Savvides A, Ali S, Tester M, Fotopoulos V. 2016. Chemical priming of plants against multiple abiotic stresses: mission possible? *Trends in Plant Science* **21**: 329–340.

Schrader J, Baba K, May ST, Palme K, Bennett M, Bhalerao RP, Sandberg G. 2003. Polar auxin transport in the wood-forming tissues of hybrid aspen is under simultaneous control of developmental and environmental signals. *Proceedings of the National Academy of Sciences, USA* **100**: 10096–10101.

Schreiber SG, Ding C, Hamann A, Hacke UG, Thomas BR, Brouard JS. 2013. Frost hardiness vs. growth performance in trembling aspen: an experimental test of assisted migration. *Journal of Applied Ecology* **50**: 939–949.

© 2024 The Author(s).
New Phytologist © 2024 New Phytologist Foundation.
This article has been contributed to by U.S. Government employees and their work is in the public domain in the USA.

14698137, 2025, 5, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.20326 by Capes, Wiley Online Library on [09/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Sebastian-Azcona J, Hamann A, Hacke UG, Rweyongeza D. 2018. Survival, growth and cold hardiness tradeoffs in white spruce populations: implications for assisted migration. *Forest Ecology and Management* **433**: 544–552.

Serna L. 2014. The role of brassinosteroids and abscisic acid in stomatal development. *Plant Science* **225**: 95–101.

Sharma A, Gupta A, Ramakrishnan M, Ha CV, Zheng B, Bhardwaj M, Tran LP. 2023. Roles of abscisic acid and auxin in plants during drought: a molecular point of view. *Plant Physiology and Biochemistry* **204**: 108129.

Słupianek A, Dolzblasz A, Sokołowska K. 2021. Xylem parenchyma-role and relevance in wood functioning in trees. *Plants* **10**: 1247.

Słupianek A, Myśkow E, Kasprowicz-Maluśki A, Dolzblasz A, Żytkowiak R, Turzańska M, Sokołowska K. 2024. Seasonal dynamics of cell-to-cell transport in angiosperm wood. *Journal of Experimental Botany* **75**: 1331–1346.

Song S, Qi T, Wasternack C, Xie D. 2014. Jasmonate signaling and crosstalk with gibberellin and ethylene. *Current Opinion in Plant Biology* **21**: 112–119.

Sow MD, Le Gac A-L, Fichot R, Lanciano S, Delaunay A, Le Jan I, Lesage-Descauses M-C, Citerne S, Caius J, Brunaud V *et al.* 2021. RNAi suppression of DNA methylation affects the drought stress response and genome integrity in transgenic poplar. *New Phytologist* **232**: 80–97.

Sperry J, Venturas M, Anderegg WRL, Mencuccini M, Mackay DS, Wang Y, Love DM. 2017. Predicting stomatal responses to the environment from the optimization of photosynthetic gain and hydraulic cost. *Plant, Cell & Environment* **40**: 816–830.

Stovall AEL, Shugart H, Yang X. 2019. Tree height explains mortality risk during an intense drought. *Nature Communications* **10**: 4385.

Thonglim A, Delzon S, Larter M, Karami O, Rahimi A, Offringa R, Keurentjes J, Balazadeh S, Smets E, Lens F. 2021. Intervessel pit membrane thickness best explains variation in embolism resistance amongst stems of *Arabidopsis thaliana* accessions. *Annals of Botany* **128**: 171–182.

Trugman AT, Anderegg LDL, Anderegg WRL, Das AJ, Stephenson NL. 2021. Why is tree drought mortality so hard to predict? *Trends in Ecology & Evolution* **36**: 520–532.

Ulrich DEM, Sevanto S, Ryan M, Albright MBN, Johansen RB, Dunbar JM. 2019. Plant–microbe interactions before drought influence plant physiological responses to subsequent severe drought. *Scientific Reports* **9**: 249.

Umehara M, Hanada A, Yoshida S, Akiyama K, Arite T, Takeda-Kamiya N, Magome H, Kamiya Y, Shirasu K, Yoneyama K *et al.* 2008. Inhibition of shoot branching by new terpenoid plant hormones. *Nature* **455**: 195–200.

Venturas MD, Sperry JS, Hacke UG. 2017. Plant xylem hydraulics: what we understand, current research, and future challenges. *Journal of Integrative Plant Biology* **59**: 356–389.

de Villemereuil P, Gaggiotti OE, Mouterde M, Till-Bottraud I. 2016. Common garden experiments in the genomic era: new perspectives and opportunities. *Heredity* **116**: 249–254.

Wang T, O'Neill GA, Aitken SN. 2010. Integrating environmental and genetic effects to predict responses of tree populations to climate. *Ecological Applications* **20**: 153–163.

Wang S, Ren Y, Han L, Nie Y, Zhang S, Xie X, Hu W, Chen H, Tang M. 2023. Insights on the impact of Arbuscular Mycorrhizal symbiosis on *Eucalyptus grandis* tolerance to drought stress. *Microbiology Spectrum* **11**: e04381-22.

Wei Z, Li J. 2016. Brassinosteroids regulate root growth, development, and symbiosis. *Molecular Plant* **9**: 86–100.

Wieloch T, Holloway-Phillips M, Yu J, Niittylä T. 2024. New insights into the mechanisms of plant isotope fractionation from combined analysis of intramolecular ^{13}C and deuterium abundances in *Pinus nigra* tree-ring glucose. *bioRxiv*. doi: 10.1101/2024.02.21.581384.

Williams MI, Dumroese RK. 2013. Preparing for climate change: forestry and assisted migration. *Journal of Forestry* **111**: 287–297.

Xu C, Christoffersen B, Robbins Z, Knox R, Fisher RA, Chitra-Tarak R, Slot M, Solander K, Kueppers L, Koven C *et al.* 2023. Quantification of hydraulic trait control on plant hydrodynamics and risk of hydraulic failure within a demographic structured vegetation model in a tropical forest (FATES–HYDRO v.1.0). *Geoscientific Model Development* **16**: 6267–6283.

Xu X, Medvigy D, Powers J, Becknell J, Guan K. 2016. Diversity in plant hydraulic traits explains seasonal and inter-annual variations of vegetation dynamics in seasonally dry tropical forests. *New Phytologist* **212**: 80–95.

Yan Y, Piao S, Hammond WM, Chen A, Hong S, Xu H, Munson SM, Myneni RB, Allen CD. 2024. Climate-induced tree-mortality pulses are obscured by broad-scale and long-term greening. *Nature Ecology & Evolution* **8**: 912–923.

Yu D, Janz D, Zienkiewicz K, Herrfurth C, Feussner I, Chen S, Polle A. 2021. Wood formation under severe drought invokes adjustment of the hormonal and transcriptional landscape in poplar. *International Journal of Molecular Sciences* **22**: 9899.

Zhang B, Wang Z, Dai X, Gao J, Zhao J, Ma R, Chen Y, Sun Y, Ma H, Li S *et al.* 2024. A COMPASS histone H3K4 trimethyltransferase pentamer transactivates drought tolerance and growth/biomass production in *Populus trichocarpa*. *New Phytologist* **241**: 1950–1972.

Zhao Y, Chan Z, Gao J, Xing L, Cao M, Yu C, Hu Y, You J, Shi H, Zhu Y *et al.* 2016. ABA receptor PYL9 promotes drought resistance and leaf senescence. *Proceedings of the National Academy of Sciences, USA* **113**: 1949–1954.

Zhou J, Xiao L, Huang R, Song F, Li L, Li P, Fang Y, Lu W, Lv C, Quan M *et al.* 2023. Local diversity of drought resistance and resilience in *Populus tomentosa* correlates with the variation of DNA methylation. *Plant, Cell & Environment* **46**: 479–497.

Ziemińska K, Rosa E, Gleason SM, Holbrook NM. 2020. Wood day capacitance is related to water content, wood density, and anatomy across 30 temperate tree species. *Plant, Cell & Environment* **43**: 3048–3067.

Zolfaghari R, Dalvand F, Fayyaz P, Solla A. 2022. Maternal drought stress on Persian oak (*Quercus brantii* Lindl.) affects susceptibility to single and combined drought and biotic stress in offspring. *Environmental and Experimental Botany* **194**: 104716.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Table S1 References and data used to produce Fig. 3.

Please note: Wiley is not responsible for the content or functionality of any Supporting Information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.

Key words: climate change, drought, forest management, forests, physiology.

Received, 6 September 2024; accepted, 18 November 2024.

Disclaimer: The New Phytologist Foundation remains neutral with regard to jurisdictional claims in maps and in any institutional affiliations.

© 2024 The Author(s).
New Phytologist © 2024 New Phytologist Foundation.
This article has been contributed to by U.S. Government employees and their work is in the public domain in the USA.

14698137, 2025, 5, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.20326 by Capes, Wiley Online Library on [09/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Climate-Ready and Adapted Agroforest and ForesTs (CRAAFT): An international research initiative on adaptation of forest and agroforests to climate change

Philippe Rozenberg[1], Nils Ferrand[2], Maria-Elena Fernandez[3], Alexia Stokes[4], Henrik Hartmann[5], Mercy Afua Adutwumwaa Derkyi[6], Sally Aitken [7], Sabas Barima[8], Amy Duchelle[9], Bruno Fady[10], Oliver Gailing[11], Jessica Halofsky[12], Carole Kerdelhué[13], Kostya Krutovsky[14], Georges Kunstler[15], Donald Midoko Iponga[16], Arthur Perroton[17], Markus Mueller[18], Annabel Porté[19], Suzanne Mary Prober[20], Silvio Schueler[21], Ivan Scotti[22], Susan Stein[23], Eshetu Yirdaw[24], Claire Depardieu[25,*]

[*]Corresponding author: Claire Depardieu, email: calimaclaire@outlook.com.

[1] UMR 0588 BIOFORA, INRAE Val de Loire, Cedex, Orleans, France; [2] Ingénierie de participation et décision, UMR G-EAU, INRAE, CIRAD, IRD, Agroparistech, Institut Agro, BRGM,Université de Montpellier, Montpellier, France; [3] Instituto de Innovación para la Producción Agropecuaria y el Desarrollo Sostenible (IPADS Balcarce INTA -CONICET). Tandil office: General Rodríguez 370, (B7000) Tandil, Argentina;[4] AMAP, University of Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France; [5] Max Planck Institute for Biogeochemistry, Jena, Germany; [6] Department of Forest Science, University of Energy and Natural Resources, Sunyani, Ghana; [7] Forest and Conservation Sciences, University of British Columbia, Vancouver, British Columbia, Canada; [8] Laboratory of Tropical Biodiversity and Ecology, Environmental Training and Research Unit, Jean Lorougnon Guédé University, BP 150, Daloa, Cote d'Ivoire; [9] Food and Agriculture Organization of the United Nations (FAO), Viale delle Terme di Caracalla, 00153, Rome, Italy; [10] INRAE, Ecologie Des Forêts Méditerranéennes (URFM), Avignon, France; [11] Forest Genetics and Forest Tree Breeding, University of Göttingen, Göttingen, Germany; [12] USDA Forest Service, Pacific Northwest Research Station, Western Wildland Environmental Threat Assessment Center, Olympia, Washington, USA; [13] UMR CBGP, INRAE, CIRAD, IRD, Institut Agro, Université Montpellier, Montpellier, France; [14] Department of Forest Genetics and Forest Tree Breeding, Faculty of Forest Sciences and Forest Ecology, Georg-August University of Göttingen, Büsgenweg 2, 37077 Göttingen, Germany; [15] Université Grenoble Alpes, LESSEM, INRAE, Grenoble, France; [16] Institut de Recherche en Ecologie Tropicale (IRET), Centre National de la Recherche Scientifique et Technologique (CENAREST), BP 9882, Libreville, Gabon; [17] CIRAD, UR Forêts et Sociétés, Campus international de Baillarguet, 34398 Montpellier, France; [18] School of Engineering, University of Edinburgh, Edinburgh EH9 3JL, United Kingdom; [19] BIOGECO, University of Bordeaux, INRAE, Cestas, France; [20] CSIRO Environment, Canberra, ACT 2601, Australia; [21] Department of Forest Growth, Silviculture & Genetics, Austrian Research Centre for Forests BFW, Vienna, Austria; [22] NRAE-URFM, Domaine Saint Paul, Avignon, France; [23] U.S. Department of Agriculture, Pacific Northwest Research Station, Western Wildland Environmental Threat Assessment Center, Olympia, Washington, USA; [24] Viikki Tropical Resources Institute (VITRI), Department of Forest Sciences, University of Helsinki,Helsinki, Finland; [25] Institut de biologie intégrative et des systèmes, 1030 Ave. de la Médecine, Université Laval, Québec, QC, G1V 0A6, Canada.

This concept note was produced as part of the International Union of Forest Research Organizations (IUFRO) Task Force on Forest Living Labs for Sustainable Climate Adaptation (FORLIVS).

Abstract

Climate change is rapidly disrupting forest and agroforest ecosystems, with rising temperatures, extreme events, and species shifts threatening their health and resilience. Proactive management strategies are crucial to ensuring the continued provision of essential ecosystem services. Despite significant progress in forest-climate research, gaps remain in integrating monitoring data, modeling future conditions, and developing context-specific adaptation strategies. International cooperation is essential, as climate impacts and ecological processes transcend national borders. The Climate-Ready and Adapted Agroforests and Forests initiative (CRAAFT) aims to enhance knowledge and develop tools for adaptive forest management. By integrating biological, ecological, economic, and social sciences, CRAAFT focuses on improving resilience through international collaboration, data sharing, and the use of innovative technologies. The initiative promotes transformative adaptation strategies that balance biodiversity conservation, ecosystem service provision, and sustainable resource use. Through a global research strategy, CRAAFT aims to improve forecasting, develop operational frameworks, and foster knowledge exchange to deliver actionable solutions for forest adaptation.

Context and scope considerations

The acceleration of climate change over the past few decades has had major impacts on forests globally, with decreased forest health and increased tree mortality in many forest and agroforest ecosystems. Along with general warming, the frequency of extreme events such as severe droughts and heatwaves is increasing. Species ranges of trees and their biotic stressors are shifting geographically, and biotic interactions are changing. It remains unclear whether naturally regenerating forests can adapt to new conditions through selection, tolerate climatic changes through plasticity, or even continue to regenerate. Where trees are planted, seed sources or species that are currently already adapted to new conditions may offer promising solutions for climate-resilient forests. To maintain the critical ecosystem services and contributions that forests and agroforests provide to people, research is needed to improve the knowledge base required for adaptive and transformative forest management approaches (see box 1). This concept note outlines key research areas and novel approaches that, combined with new technologies and a better understanding of social-ecological systems, will inform adaptive and transformative forest management. The ultimate goal of these approaches is to increase the resilience and resistance of forests to climate change in ways that maintain ecosystem services and are acceptable to the people who depend on them.

The international research initiative CRAAFT "Climate-Ready and Adapted Agroforest and ForesTs" is one of six INRAE "*Programmes Prioritaires Internationaux*" (PPI[1]). It covers forest and agroforest ecosystems (see box 1 for a definition) and other forest entities that may or may not be managed, are naturally regenerated or planted, have variable size, harbour pure or mixed stands, or integrate crops or cattle in agroforestry farming systems. Of particular importance among the objectives of this initiative are tools and research approaches that support the international scientific community in addressing adaptation to climate change: long-lasting tools to foster large-scale international communication and collaboration, improvements in the collection, scope, relevance and sharing of data, and global improvement of the efficiency and reach of international research on forest and agroforest adaptation to climate.

[1] The International Priority Programs (or International Research Initiative) (PPI, or IRI in English) are part of INRAE's European and International Strategy. Their aim is to incubate, launch and support large-scale international research initiatives in a number of priority areas, to structure sustainable networks of international partnerships and to develop shared research agendas at the global level. https://www.inrae.fr/en/priority-projects-international-scope

Forest ecosystems support high levels of biodiversity and play a key role in regulating climate at local, regional and global scales-directly through their influence on the water cycle and the albedo effect, and indirectly through their carbon fixation and storage (Popkin 2019). Forest and agroforestry ecosystems also contribute to a wide range of other ecosystem services (Brockerhoff et al. 2017) including biomass production, soil formation, water supply and purification, pollination, regulation of arthropod pest populations, and provision of both material (e.g. food, shelter, fuel wood, timber and non-timber products, pharmaceutical compounds) and immaterial resources (e.g. well-being, sense of place, social cohesion through collective identification to a given landscape). Furthermore, human societies live with and within forests, and are part of multiple feedback loops that have major and decisive effects on forest ecosystems and societies themselves. Most forests and all agroforestry systems include humans and should be conceptualized as social-ecological systems (See box 1 for definition).

Trees are the foundation species of forest and agroforest ecosystems. Their potential ranges correspond to the maximum potential geographical distribution of each species as determined by abiotic tolerances, particularly climate and soil (Walthert et Meier 2017; Woodward et Williams 1987). The characteristics of particular species also interact with the biotic components of the environment to determine their realised climatic niches and actual ranges. These ranges can be reduced, extended or restored following natural processes (e.g. wildfires, floods) and human interventions (namely deforestation, afforestation and reforestation). Competition, predation, mutualism, facilitation and parasitism represent primary biotic interactions with other living constituents which, combined with physical selection pressures, can affect evolutionary trajectories and should be considered.

Climatic fluctuations across space and time affect forest and agroforest health, productivity and geographic distribution (Martin et Canham 2020), with local dynamics variously affected by climate gradients and extreme events (Svenning et Skov 2007). During the last 650 000 years, seven successive ice ages, separated by warmer interludes, periodically reshaped the distribution of tree species and the composition of forest ecosystems (Whitlock et al. 2018). The rapid end of the last glaciation ~12000 years ago represents the start of the current climate age, and coincides with the beginning of the modern human era and the adoption of agriculture. Long before that, forests were already affected by controlled burnings practiced by forager populations. Since then, the ever-growing interaction between humans and forests was soon followed by what can be regarded as the first steps of forest management (Gulev et al. 2021). Although global climate has frequently changed in the past, there is wide scientific agreement today over the particular conditions of the current global climate change and the fact that: 1. Climate is warming faster than ever and the frequency and severity of extreme weather events are increasing (Eyring et al. 2021), 2. the main cause of the warming is the increase of atmospheric greenhouse gases resulting from human activities[2] (Reidmiller et al. 2018; Graham, Turner, et Dale 1990), and 3. forest ecosystems show clear signs of responses to these changes in climate, observed since the beginning of the 1990's (Allen, Breshears, et McDowell 2015; McDowell et al. 2020; Anderegg et al. 2019). The first notable response observed was a growth increase related to both moderate warming, nitrogen deposition and atmospheric CO_2 increase (Bréda et Peiffer 2014). However, this observation was soon followed by numerous reports of declines and diebacks, mostly attributed to drought and pests (Anderegg et al. 2015; Hubau et al. 2020; Lewis et al. 2011), and wildfires and windstorms (Esquivel-Muelbert et al. 2020). Moreover, many biotic and abiotic threats and hazards affecting forests and agroforests are climate-related and are often exacerbated by climate change (Arias et al. 2021).

Forests subjected to a rapidly changing climate respond at the level of individual trees which aggregate into species, populations, communities and ecosystems. Individual trees respond in the short term through phenotypic plasticity (which includes acclimation, but can also be maladaptive), while

[2]According to the IPCC, in 2019, about 79% of global greenhouse gas emissions came from energy, industry, transport and buildings sectors and 22% from agriculture, forestry and other land use.

populations and species adapt -or fail to adapt- over the longer term through evolution by natural selection. An individual or evolutionary response is considered adaptive when it increases mean *fitness*, where fitness encompasses both survival and reproductive success. In this context, *adaptation* refers to a set of natural processes that enable populations to minimize fitness loss under new environmental -particularly climatic- conditions (see box 1 for definitions). To some extent, climate change-induced mortality may promote evolutionary adaptation to the new climatic conditions via selection (Kuparinen, Savolainen, et Schurr 2010), provided that enough offspring survive to compensate for deaths-a process known as *evolutionary rescue*. Another component of evolution is migration, which occurs when naturally dispersed genotypes, i.e., seeds, arrive in, test, and, if successful, colonize new environments. Tree breeding and assisted migration programs support these natural processes, generating faster and more efficient nature-based solutions to adaptation challenges, as well as sounder wood production trade-offs than for example indiscriminate harvesting. Research programs targeting these objectives, and the solutions they consider, must also consider biotic interactions, both with symbionts and antagonistic species. However, once a given mortality threshold is crossed, adaptation is no longer possible and populations of some forest tree species may decline in abundance or health permanently, or be locally or completely extirpated from ecosystems.

The term adaptation is also often used in the context of forestry, distinct from evolutionary adaptation, to refer to the full range of human actions (e.g. forest planning, silviculture, tree breeding, assisted migration, risk management) aimed at helping tree populations and components of forest and agroforestry ecosystems cope with emerging conditions while conserving their services throughout the value chain. To avoid confusion arising from the dual meaning of the word “adaptation”, we use the term “climate adaptation management” rather than simply “adaptation” when referring to human interventions intending to facilitate adaptation to climate. Furthermore, climate adaptation management in forests is not only an ecological issue, it also encompasses economic, social and cultural resilience.

Forest resilience refers to how well forest communities and ecosystems recover from variations in disturbance regimes, such as those associated with climate change (Box 1). Resilience is crucial for maintaining forest and agroforest ecosystems themselves and the key ecosystem services that they provide to humanity. Resilience is a function of evolutionary adaptation and phenotypic plasticity of species, species interactions, and properties of the social-ecological system (e.g. species diversity, forest complexity and functional diversity found at local, regional and landscape scales) (Oliver et al. 2015). As with plasticity, resilience must be defined relative to the social-ecological system, the function in question (and its associated set of variables -phenotypic, economic, social…-), and the type of disturbance considered (i.e., resilience of what to what?). Diversity influences the capacity of a social-ecological system to reorganize fundamental structures and maintain both fitness and functions (Scheffer 2020). There are complex interactions between ecosystem level functions and evolutionary adaptation of each individual species (Lavergne et al. 2010). However, when climatic conditions or climate-induced disturbances (extreme drought, wildfires, high-intensity windstorms or flooding) exceed certain thresholds, forests can reach a tipping point and shift to another type of ecosystem (Scheffer et al. 2001).

Forty years of accelerated climate change is a short time interval relative to the long lifespan of most tree species. This implies that, although the direct and indirect effects of climate change are felt within a single tree generation, the long-term consequences of forest planning and management can only be achieved over multiple tree and human generations, spanning up to several centuries.Given the uncertainties of projected climatic scenarios, particularly concerning extreme climatic events, it is challenging to predict and project future consequences and the actions to take (Petr et al. 2019). Accounting for such long-time frames and their inherent large uncertainties calls for new, complementary and demanding approaches.

Within past decades, forest and ecosystem research has made groundbreaking progress in understanding and predicting effects of climate change on trees and forests ecosystems (i.e. modeling forest species distribution and ecosystem services, understanding drivers of disturbances, etc.) as well as in developing

and testing forest adaptation measures (i.e. thinning, assisted migration, etc.). Also, next generation sequencing and bioinformatics have revealed clearer pictures of the genetic basis of the capability of forest trees and forest communities to adapt. At the same time, terrestrial and remote forest monitoring systems have delivered an increasing amount of data ranging from single-tree growth and vitality data up to forest fluxes into neighboring ecosystems and the atmosphere. However, the increasing understanding of the natural science basis has not yet resulted in comprehensive actions to adapt forest and agroforest ecosystems to climate change. This is mainly due to: 1) need for greater transdisciplinary engagement among biophysical, social and economic actors to define management objectives and desired ecosystem services under changing conditions; 2) deficient integration of monitoring data and model outcomes across disciplines for reliable and trustful predictions as a basis for communication of climate change outcomes, natural adaptation and potential climate adaptation management; 3) incomplete systemic understanding of climate change and adaptation outcomes across biological (genes, species, ecosystems) and socioeconomic (i.e. landowner, local communities, wood and paper industries) levels; 4) poor understanding of interactions between climate change, climate adaptation management and the global decline of biodiversity and its needs for conservation and restoration of habitats; 5) deficient balance in the understanding and available knowledge of different forest biomes with the predominance of studies from the Global North, and scarce knowledge from social-ecosystems of the Global South.

Thus, innovative approaches should consider the multiple consequences of climate change for biodiversity, the economic use of wood and non-timber forest and agroforest products, and the non-commercial services of forest ecosystems, including their roles in reducing social vulnerability to climate change (Pramova et al. 2012).

This international research initiative (IRI) addresses natural adaptation and its natural mechanisms as well as adaptive management by considering economic, human and social sciences along with biology and ecology. The IRI proposes to explore *transformative* strategies (Fedele et al. 2019) as well as coping or incremental strategies, and to help decision-makers avoid insufficient, maladaptive or unsustainable options. The IRI will not directly address forest and agroforest potential to mitigate climate change, but will be involved in research dealing with forest-climate interactions, particularly, the consequences of climate change on forests and agroforests—and their products and services—and how to increase their adaptability.

Multiple aspects of how forests function and of how they react to disturbance still escape us, and this will be a major challenge for any forest research program of the 21st century, particularly in the context of a rapidly changing world. In particular, we still lack a clear understanding of the complex interactions among the different components of forest systems, particularly when they are non-linear and/or change non-linearly with time and disturbance intensity (e. g., tipping points). We also lack a precise understanding of the role played by the different levels of biodiversity (ecosystem; species; genetic diversity) in system stability; and finally, we do not fully grasp the behavior of non-equilibrium systems, for which the identification of the key parameters (and of their values) is hard to obtain, and which may display chaotic trajectories (Chaos theory; that is, system trajectory heavily depends on initial conditions). These are overarching questions that we pressingly need to address to fully disclose the way forest systems work. Major methodological breakthroughs may be required to solve these puzzles; and we may need to appeal to many research fields outside the usual boundaries of forestry and forest biology—such as multiple branches of mathematics; artificial intelligence; physics—to operate such breakthroughs. We will also need to make decisions on research directions in appropriate social-ecological contexts to ensure inclusion of multiple values and avoid perverse outcomes. These are likely to be gloomy times for the global preservation of life on Earth and forest systems in particular; but they can and must be exciting times to open new ways for forestry research.

Research on the natural mechanisms of adaptation and on the transformative climate adaptation management solutions in forest species and ecosystems could benefit from increased and improved

international collaboration and could lead rapidly to more efficient nature-based solutions to adaptation problems. The international dimension of this program is essential because:

- Current and future tree species ranges and the geographical distribution of climate do not follow country borders
- Disturbances as well as patterns and processes of biological invasions, either voluntary or otherwise, affect forests and agroforests irrespective of country borders
- The local ecological, economic and social opportunities for and constraints to adaptation can differ among countries, requiring a broad set of study contexts to enable generalization of research outcomes and generation of a suitable range of possible adaptation paths
- International collaboration gives access to study models (forests and species), human and technical resources not necessarily available locally while increasing the power and the significance of experimentation
- Some adaptive actions are more advanced in other countries and the level of challenges and threats calls for extensive exchange of knowledge, innovation and solutions among regions and countries
- Forests and agroforests, their definitions and their management are the object of international treaties and conventions, international certifications, and international power struggles. These international conventions and treaties must be explored in relation to local social practices and national issues.

Research Issues

The members of the IRI working group strive to address the forest adaptation challenge by elaborating a global research strategy based on a common integrated vision, from local and regional issues to any geographical scale. To generate their vision, they will tackle the global research context shown above with specific research questions.

We are currently elaborating a list of research frontiers, which will address, among others, the following action items:

a. **Improve the knowledge base**: Gain new basic knowledge of the forest-climate relationships and of the natural mechanisms of adaptation and resilience to climate change in forest species and ecosystems, by improving our ability to monitor, and better communicate and share observations and data about the different types of responses, whether favorable or unfavorable, on forests and agroforests and the consequences for their products and services.
b. **Develop conceptual and operational frameworks and tools for social-ecological systems**: Bring together actors of forest social-ecological systems, facilitate the search for science-based, economically feasible and more collective and consensual adaptation solutions that consider conflicts of interest. Identify the direct and indirect feedbacks between social dynamics, environmental dynamics and the variation of social-ecological resilience.
c. **Improve forecasting:** Quantify uncertainty and manage the major discrepancy between the long-time scale of forest biology and forest planning and management and the speed and uncertainties of climate change, to eventually improve the accuracy and ecological, economic, social and cultural relevance of predictive models and of decision-support tools. To do so, interdisciplinary self-learning and AI-driven multi-model simulation environments, like digital twins, will be developed and continuously improved by the constant data streams that are generated by other activities within the IRI.
d. **Study feedback mechanisms:** Investigate the link between adaptation to climate change and forest biodiversity, measured at different levels of organization and considering both taxonomic and functional criteria, as well as between forest biodiversity and strategies of reduction and prevention of broad-scale mortality.

e. **Self-assessment:** Generate evidence for effectiveness of ecological, social and economic interventions proposed to facilitate climate adaptation, as a basis for modelling, future decision making and refining intervention options in forest and agroforestry systems.

Existing or new tools and research approaches have to be developed, improved, tested, validated and deployed to help the international scientific community address the above research issues. From this point of view, the priority is to create long-lasting tools that will allow us to foster large-scale international communication and collaboration, to improve the collection, scope, relevance and sharing of data, and globally to enhance the efficiency and reach of international research on forest adaptation to climate. In particular some are (in no particular order) 1. Networking of people and experiments, for enhanced communication, to broaden the context of results, to share experiences and outcomes, and for promoting student and staff exchanges; 2. Transnational databases maintained in the long term; 3. Technical devices and facilities to measure, digitize, transfer, store and share standardized environmental and biological observations, associated with demonstrator projects and reference sites; 4. Approaches and methods, including participative process, for converting research results into decision support tools.

One major international initiative emerging from this work—and potentially CRAAFT's first high-priority operational objective—is the creation of an international network of living lab approaches for adapting forests and agroforests to climate change. The aims of such an international living lab network may include (non-exhaustive list):

i) To evaluate, develop and validate shared tools, particularly those used to observe the responses of agroforestry and forest socio-ecosystems to climate change

ii) To share technical, experimental and human resources by pooling certain efforts

iii) To exchange, communicate, train, and openly discuss and share ideas, objectives, approaches, protocols, results, and solutions

In this context a forestry living lab is an organization located in a territory defined by its own socio-ecosystem, with its human and non-human populations, its associated functions and the network of their relationships and interactions. Each living lab operates within a defined geographic area and includes a science-society consortium comprising research laboratories and local stakeholders (owners, managers, sectors and their organizations and companies, public authorities, citizens and communities, whether organized or not...). Each organization is necessarily autonomous, with its own legal status, objectives and resources.

An international network of forest living labs sharing the same goal, i.e. the adaptation of forests and agroforests to climate change, effectively brings together and synthesizes the priority objectives identified in this concept note. Within this framework, the federated Living Labs are familiar with one another, can communicate, and may act in concert when mutually beneficial. Approaches and tools can be shared across ecosystems, communities, or methodological frameworks. A first for forests, this initiative is inspired by others in agriculture and agri-food, such as the International Forum of Living Laboratories in Agroecosystems.

This consensus, reached by CRAAFT's international group of experts, is now being shared with national and international scientific partners and institutions, with the goal of translating it into a research program and a strategic agenda.

This strategic research agenda will be presented to research funding organizations in order to seek support for the whole program or specific components- and enhance international visibility and research on adaptation. The goal is to collaborate in identifying and securing sufficient funding for ambitious, large-scale projects that no single participant could undertake at the national level.

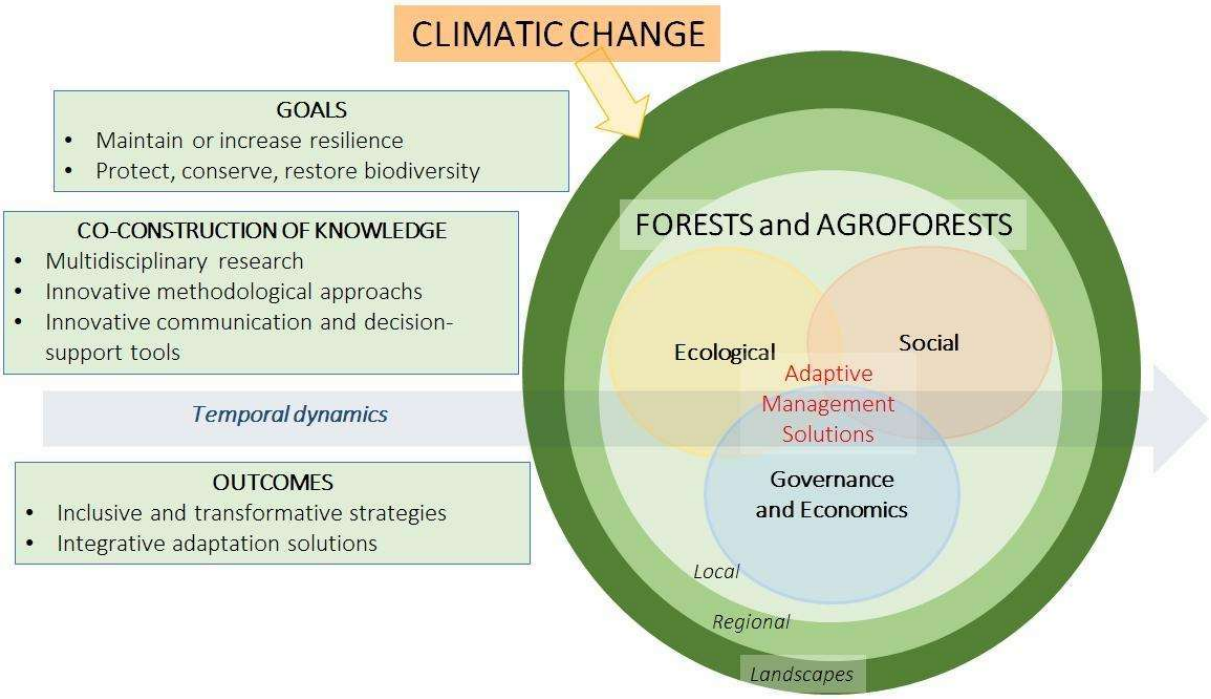


Figure 1: Interdisciplinary framing emphasizing the central role of ecological, social as well as governance and economics components at local, regional and landscapes scales and the need to consider the interaction among them in forest management.

Box 1 - Definitions

Forest: according to the FAO, a forest is "…a plant formation consisting of trees with a minimum adult height of 5 m, with a crown projection covering at least 10% of the ground area, this area being at least 0.5 ha with a minimum width of 20 m". According to World Agroforestry (ICRAF, www.worldagroforestry.org) "Agroforestry is the interaction of agriculture and trees, including the agricultural use of trees".

Resilience: the definition of resilience varies depending on whether one is looking at it from the perspective of the humanities and social sciences or of the natural sciences: "the degree to which an ecosystem function can resist or recover rapidly from environmental perturbations, thereby maintaining function above a socially acceptable level (Oliver et al. 2015)", or "Resilience is broadly defined as the capacity of an ecosystem, community or individual to recover after disturbance and regain its pre-disturbance structure and function (Scheffer et al. 2001; Folke et al. 2004)". Resilience describes systems in an undesirable regime, where overcoming unsustainable practices is impeded due to the system's resilience. Resilience approaches focus on the process of responding to disturbances, and building adaptive capacity to cope with unknown shocks and stressors.

Social-ecological system: governance networks hold promise for managing forest landscapes as social-ecological systems (Fischer 2018). In general, social-ecological systems are ecosystems that are analysed considering human interventions. Beyond this point of view, the system could be analysed as a whole, where socio-economic decisions and ecosystem dynamics interact in all directions in feedback loop mechanisms. The different parts of the system (the society, the biodiversity, etc.) are not separate compartments anymore, and when analyzing a particular compartment, the others are not considered as black boxes. The complexity added to the analysis is necessary to reach a better level of integration in the study of forest (social-ecological-) systems.

Adaptation: 1. Set of natural processes allowing populations to minimize fitness loss despite new environmental conditions (e.g. evolutionary adaptation, adaptive plasticity). Natural adaptation. 2. Human actions aimed at helping forest and agroforest ecosystems to deal with emerging new conditions

while conserving their services all along the value chain (e.g. forest planning, silviculture, tree breeding, assisted migration, risk management). Climate adaptation management.

Transformative strategies: strategies designed to create transformative change, which involves a fundamental shift in the functioning and dynamics of forest-landscape systems. To cite a few examples, transformative adaptation can potentially be achieved by restoring natural ecosystems (e.g., grassland, wetlands, or abandoned land), establishing sustainable land management practices (e.g., agroforestry, prescribed fires, selective logging, and replanting), and creating new income sources (e.g., through ecotourism, Payment for Ecosystem Services).

References

Allen, Craig D., David D. Breshears, et Nate G. McDowell. 2015. « On Underestimation of Global Vulnerability to Tree Mortality and Forest Die-off from Hotter Drought in the Anthropocene ». *Ecosphere* 6 (8): art129. https://doi.org/10.1890/ES15-00203.1.

Anderegg, William R. L., Leander D. L. Anderegg, Kelly L. Kerr, et Anna T. Trugman. 2019. « Widespread Drought-Induced Tree Mortality at Dry Range Edges Indicates That Climate Stress Exceeds Species' Compensating Mechanisms ». *Global Change Biology* 25 (11): 3793-3802. https://doi.org/10.1111/gcb.14771.

Anderegg, William R. L., Jeffrey A. Hicke, Rosie A. Fisher, Craig D. Allen, Juliann Aukema, Barbara Bentz, Sharon Hood, et al. 2015. « Tree Mortality from Drought, Insects, and Their Interactions in a Changing Climate ». *New Phytologist* 208 (3): 674-83. https://doi.org/10.1111/nph.13477.

Arias, Paola A., Nicolas Bellouin, Erika Coppola, Richard G. Jones, Gerhard Krinner, Jochem Marotzke, Vaishali Naik, et al. 2021. « Technical summary ». In *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, édité par Valérie Masson-Delmotte, Panmao Zhai, Anna Pirani, Sarah L. Connors, C. Péan, Sophie Berger, Nada Caud, et al. Cambridge University Press.

Bréda, Nathalie, et Marianne Peiffer. 2014. « Vulnerability to Forest Decline in a Context of Climate Changes: New Prospects about an Old Question in Forest Ecology ». *Annals of Forest Science* 71 (6): 627-31. https://doi.org/10.1007/s13595-014-0411-3.

Brockerhoff, Eckehard G., Luc Barbaro, Bastien Castagneyrol, David I. Forrester, Barry Gardiner, José Ramón González-Olabarria, Phil O'B. Lyver, et al. 2017. « Forest Biodiversity, Ecosystem Functioning and the Provision of Ecosystem Services ». *Biodiversity and Conservation* 26 (13): 3005-35. https://doi.org/10.1007/s10531-017-1453-2.

Esquivel-Muelbert, Adriane, Oliver L. Phillips, Roel J. W. Brienen, Sophie Fauset, Martin J. P. Sullivan, Timothy R. Baker, Kuo-Jung Chao, et al. 2020. « Tree Mode of Death and Mortality Risk Factors across Amazon Forests ». *Nature Communications* 11 (1): 5515. https://doi.org/10.1038/s41467-020-18996-3.

Eyring, Veronika, Nathan P. Gillett, Krishna M. Achutarao, Rondrotiana Barimalala, Marcelo Barreiro Parrillo, Nicolas Bellouin, Christophe Cassou, et al. 2021. « Human influence on the climate system ». In *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, édité par Valérie Masson-Delmotte, Panmao Zhai, Anna Pirani, Sarah L. Connors, C. Péan, Sophie Berger, Nada Caud, et al. Cambridge University Press.

Fedele, Giacomo, Camila I. Donatti, Celia A. Harvey, Lee Hannah, et David G. Hole. 2019. « Transformative Adaptation to Climate Change for Sustainable Social-Ecological Systems ». *Environmental Science & Policy* 101 (novembre): 116-25. https://doi.org/10.1016/j.envsci.2019.07.001.

Fischer, Alexandra Paige. 2018. « Forest Landscapes as Social-Ecological Systems and Implications for Management ». *Landscape and Urban Planning* 177 (septembre): 138-47. https://doi.org/10.1016/j.landurbplan.2018.05.001.

Folke, Carl, Steve Carpenter, Brian Walker, Marten Scheffer, Thomas Elmqvist, Lance Gunderson, et C. S. Holling. 2004. « Regime Shifts, Resilience, and Biodiversity in Ecosystem Management ». *Annual Review of Ecology, Evolution, and Systematics* 35: 557-81.

Graham, Robin Lambert, Monica G. Turner, et Virginia H. Dale. 1990. « How Increasing CO2 and Climate Change Affect Forests ». *BioScience* 40 (8): 575-87. https://doi.org/10.2307/1311298.

Gulev, Sergey K., Peter W. Thorne, Jinho Ahn, Frank J. Dentener, Catia M. Domingues, Sebastian Gerland, Daoyi Gong, et al. 2021. « Changing state of the climate system ». In *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, édité par Valérie Masson-Delmotte, Panmao Zhai, Anna Pirani, Sarah L. Connors, C. Péan, Sophie Berger, Nada Caud, et al. Cambridge University Press.

Hubau, Wannes, Simon L. Lewis, Oliver L. Phillips, Kofi Affum-Baffoe, Hans Beeckman, Aida Cuní-Sanchez, Armandu K. Daniels, et al. 2020. « Asynchronous Carbon Sink Saturation in African and Amazonian Tropical Forests ». *Nature* 579 (7797): 80-87. https://doi.org/10.1038/s41586-020-2035-0.

Kuparinen, Anna, Outi Savolainen, et Frank M. Schurr. 2010. « Increased mortality can promote evolutionary adaptation of forest trees to climate change ». *Forest Ecology and Management* 259 (5): 1003-8. https://doi.org/10.1016/j.foreco.2009.12.006.

Lavergne, Sébastien, Nicolas Mouquet, Wilfried Thuiller, et Ophélie Ronce. 2010. « Biodiversity and Climate Change: Integrating Evolutionary and Ecological Responses of Species and Communities ». *Annual Review of Ecology, Evolution, and Systematics* 41 (1): 321-50. https://doi.org/10.1146/annurev-ecolsys-102209-144628.

Lewis, Simon L., Paulo M. Brando, Oliver L. Phillips, Geertje M. F. van der Heijden, et Daniel Nepstad. 2011. « The 2010 Amazon Drought ». *Science* 331 (6017): 554-554. https://doi.org/10.1126/science.1200807.

Martin, Patrick H., et Charles D. Canham. 2020. « Peaks in Frequency, but Not Relative Abundance, Occur in the Center of Tree Species Distributions on Climate Gradients ». *Ecosphere* 11 (6): e03149. https://doi.org/10.1002/ecs2.3149.

McDowell, Nate G., Craig D. Allen, Kristina Anderson-Teixeira, Brian H. Aukema, Ben Bond-Lamberty, Louise Chini, James S. Clark, et al. 2020. « Pervasive shifts in forest dynamics in a changing world ». *Science* 368 (6494): eaaz9463. https://doi.org/10.1126/science.aaz9463.

Oliver, Tom H., Matthew S. Heard, Nick J. B. Isaac, David B. Roy, Deborah Procter, Felix Eigenbrod, Rob Freckleton, et al. 2015. « Biodiversity and Resilience of Ecosystem Functions ». *Trends in Ecology & Evolution* 30 (11): 673-84. https://doi.org/10.1016/j.tree.2015.08.009.

Petr, M., G. Vacchiano, D. Thom, P. Mairota, M. Kautz, L. M. S. Goncalves, R. Yousefpour, S. Kaloudis, et C. P. O. Reyer. 2019. « Inconsistent Recognition of Uncertainty in Studies of Climate Change Impacts on Forests ». *Environmental Research Letters* 14 (11): 113003. https://doi.org/10.1088/1748-9326/ab4670.

Popkin, Gabriel. 2019. « How Much Can Forests Fight Climate Change? » *Nature* 565 (7739): 280-82. https://doi.org/10.1038/d41586-019-00122-z.

Pramova, Emilia, Bruno Locatelli, Houria Djoudi, et Olufunso A. Somorin. 2012. « Forests and Trees for Social Adaptation to Climate Variability and Change ». *WIREs Climate Change* 3 (6): 581-96. https://doi.org/10.1002/wcc.195.

Reidmiller, David R., Christopher W. Avery, David R. Easterling, Kenneth E. Kunkel, Kristin L.M. Lewis, Thomas K. Maycock, et Brooke C. Stewart. 2018. « Report-in-Brief. Impacts, Risks, and Adaptation in the United States: The Fourth National Climate Assessment, Volume II ». U.S. Global Change Research Program. https://doi.org/10.7930/NCA4.2018.RiB.

Scheffer, Marten. 2020. *Critical Transitions in Nature and Society*. Princeton University Press.

Scheffer, Marten, Steve Carpenter, Jonathan A. Foley, Carl Folke, et Brian Walker. 2001. « Catastrophic Shifts in Ecosystems ». *Nature* 413 (6856): 591-96. https://doi.org/10.1038/35098000.

Svenning, Jens-Christian, et Flemming Skov. 2007. « Ice Age Legacies in the Geographical Distribution of Tree Species Richness in Europe ». *Global Ecology and Biogeography* 16 (2): 234-45. https://doi.org/10.1111/j.1466-8238.2006.00280.x.

Walthert, Lorenz, et Eliane Seraina Meier. 2017. « Tree Species Distribution in Temperate Forests Is More Influenced by Soil than by Climate ». *Ecology and Evolution* 7 (22): 9473-84. https://doi.org/10.1002/ece3.3436.

Whitlock, Cathy, Daniele Colombaroli, Marco Conedera, et Willy Tinner. 2018. « Land-Use History as a Guide for Forest Conservation and Management ». *Conservation Biology* 32 (1): 84-97. https://doi.org/10.1111/cobi.12960.

Woodward, F. I., et B. G. Williams. 1987. « Climate and Plant Distribution at Global and Local Scales ». *Vegetatio* 69 (1): 189-97. https://doi.org/10.1007/BF00038700.

Check for updates

Viewpoints

Social and biological innovations are essential to deliver transformative forest biotechnologies

Summary

Forests make immense contributions to societies in the form of ecological services and sustainable industrial products. However, they face major challenges to their viability and economic use due to climate change and growing biotic and economic threats, for which recombinant DNA (rDNA) technology can sometimes provide solutions. But the application of rDNA technologies to forest trees faces major social and biological obstacles that make its societal acceptance a 'wicked' problem without straightforward solutions. We discuss the nature of these problems, and the social and biological innovations that we consider essential for progress. As case studies of biological challenges, we focus on studies of modifications in wood chemistry and transformation efficiency. We call for major innovations in regulations, and the dissolution of method-based market barriers, that together could lead to greater research investments, enable wide use of field studies, and facilitate the integration of rDNA-modified trees into conventional breeding programs. Without near-term adoption of such innovations, rDNA-based solutions will be largely unavailable to help forests adapt to the growing stresses from climate change and the proliferation of forest pests, nor will they be available to provide economic and environmental benefits from expanded use of wood and related bioproducts as part of an expanding bioeconomy.

With the recent launch of the new section of *New Phytologist* on 'transformative plant biotechnology (Halpin *et al.*, 2023)', it is an apt time to consider what is needed for transformative leaps that can enhance forest tree biotechnology. By biotechnology, we mean modification by recombinant DNA (rDNA) in the form of gene-editing (i.e. targeted modification of native DNA) or gene insertion, not applications such as genomic selection that can accelerate conventional breeding. We are both biotechnologists who have conducted basic and applied research on genomic and molecular biology of trees, including field trials of prototype-modified trees in the United States and Europe (e.g. reviewed in Pilate *et al.*, 2002; Strauss *et al.*, 2016; Chanoca *et al.*, 2019; De Meester *et al.*, 2022b). We have experience in research, translation, and interaction with legal and market systems, as well as engagement with the general public.

We believe there are urgent needs for both social and biological innovations if biotechnology is to have a significant and beneficial impact on the productivity and quality of tree plantations or other types of forests. First, we need to create a regulatory and market environment that is conducive to innovation, rather than one that poses tremendous impediments; the latter is the rule throughout most of the world today. This is especially critical in the context of today's reality of rapid climate change, where genetic improvements of all sorts must occur as rapidly as possible if they are to help the ongoing adaptation of tree plantations and other forests to changing climates and pathogen pressures (Jacobs *et al.*, 2023). Second, there is a critical need for accelerated research, both fundamental studies such as the analysis of basic processes underlying plant regeneration and wood development, and technology advancements to make genetic modification more efficient and reliable in multiple tree species and genotypes. Third, it is essential that rDNA methods are well-integrated with conventional and genomic breeding, though many technical and social obstacles make this difficult. This would include extensive field research, as most results from laboratory or glasshouse experiments have limited relevance to field environments due to the very different stresses and other aspects of tree ecophysiology in the field vs indoor conditions (Viswanath *et al.*, 2012; Khaipho-Burch *et al.*, 2023). Field research is also important for public education about the true benefits and risks of modified trees. Finally, there are a number of larger contextual issues related to rDNA-modified forests, including questions of how to evaluate risks from rDNA technology vs that from other forms of breeding and management in a climate change world, and when and where rDNA methods should be applied. We believe that the primary uses will be in intensively managed, short-rotation clonal plantations, for which wood products have distinct industrial uses, but that there are also important opportunities to help with the protection or restoration of wild or feral forests. We will discuss each of these areas, giving examples from our own research and experience.

Social innovation

Perhaps the most impactful social constraint is the implicit or explicit legal presumption of guilt due to the use of rDNA methods, with only minor exceptions for gene-edited plants that are similar or identical to those that could be produced from conventional breeding (Strauss *et al.*, 2010, 2022). By contrast, conventional breeding methods – whether they involve species transfer among continents, production of novel hybrids, clonal deployment, or radiation/chemical mutagenesis – have no such presumption of guilt. Some exceptions exist in the form of strict regulations on some exotic species that are known to be highly invasive and

© 2024 The Authors
New Phytologist © 2024 New Phytologist Foundation

damaging. This dichotomy is true essentially everywhere, including in the United States, where it is inherent to both the US Department of Agriculture (USDA) and Environmental Protection Agency (EPA) regulatory systems. However, the recently enacted USDA SECURE regulatory system is a modest exception; though regulation is triggered by the use of rDNA methods, regulatory decisions are intended to focus exclusively on whether there is a plausible risk that an rDNA-modified plant will cause or exacerbate a pest problem. It also has a means for rapid deregulation decisions, and exemptions for simple types of gene-edited plants. We regard this system, with its trait focus and options for exemptions and rapid decisions, as a first step in the right direction (Goralogia *et al.*, 2021). There are now also regulatory exemptions for simple gene-edits in the regulatory systems of many other countries around the globe (Smyth, 2019; Turnbull *et al.*, 2021).

We are also encouraged by the mostly growing acceptance of rDNA-based methods by the public. The 'eco'vandalism of recent decades against rDNA trees, whether due to concerns about violation of trees that are perceived as 'natural' or concerns about corporate control of forests, appears to have abated internationally. In addition, the sensational and highly derogatory headlines about rDNA crops, particularly in Europe, have become extremely rare. Although concerns about the safety of 'GMO food' have risen in the United States in the last decade and are shared by approximately half of the public, many view GMOs as a 'necessary evil' given their perceived value for helping to 'feed the world' amidst growth in population and standards-of-living (Funk, 2020). Likewise, social media messages have become distinctly less negative in recent years (Evanega *et al.*, 2022). Unfortunately, scientifically false statements, mostly negative ones, are still very common in mainstream print and online media, with a rate of 9% and considerably higher in Africa (*c.* 20%) during 2019–2021 (Lynas *et al.*, 2022).

On the other hand, the US EPA continues to increase its regulatory coverage in what seems far beyond its original mandate to protect the public and environment from pesticide harms; it now covers growth-improved plants and pest-resistant plants that do not involve pesticide use at all, but engage natural resistance mechanisms. This is a very effective deterrent for the use of pest-resistant trees, and indeed even the blight-resistant American chestnut, which involves no novel pesticides, has been held up in regulatory limbo there for years. The US EPA's 'exemption' for gene-editing is also very limited, still requiring safety data and proof that the edit is already present in a sexually compatible relative (Stokstad, 2023). It appears that congressional action will be needed if this regulatory overreach is to be reversed. A similar sentiment was reflected in a recent US Senate report; it highlighted the need for regulatory discipline if biotechnology innovations are to flourish (National Security Commission on Emerging Biotechnology, 2023).

In contrast to most of the regulatory systems world-wide, for decades, scientists have called for a science-based regulatory system that focuses on the comparative risk associated with the presence vs non-presence of the trait, not with the method employed, and that would allow a broad array of rDNA-modified varieties to be planted and commercialized unless there are tangible, major risks associated with the novel trait (e.g. National Academies of Sciences Engineering and Medicine, 2016). Such risks could include novel disease resistance mechanisms that might substantially impact wild or feral populations, or the generation of herbicide-resistant plants that will compromise plantation or weed management. A system focused on trait-based risk would also not preclude all gene flow during field research and breeding, thus allowing rDNA-modified plants to be readily deployed alongside conventionally bred plants during field trials unless they pose a tangible risk at the relevant rates of gene flow (normally very low in research/breeding trials) compared with potential benefits; this is critical for the expanded use of field trials as discussed below.

We note that a change to a trait-based system would not imply that all gene flow is risk-free, only that society will tolerate low levels and their impacts, just as it does for conventional breeding and agricultural production of the large majority of crop species, in exchange for the benefit of accelerated innovation to help cope with climate change and social stresses on food and fiber production systems. Of course, regulations that define what 'tangible risk at the relevant rates of gene flow compared to potential benefits' would look like is complex and beyond the scope of this paper to explore in depth; but, we imagine a system similar to the Canadian rDNA regulatory system (Lassoued *et al.*, 2020) in that it would apply to both rDNA and conventional breeding. The new USDA SECURE system, which tries to define 'plausible plant pest risk', faces similar challenges in definition (no surprise given biological and ecological complexity and diversity). A biological framework for such a system, which might be based on changes in native genes and their expression as familiar vs modifications that impart truly novel and exogenous trait mechanisms (e.g. new pest resistance toxins), and whether the trait is a domesticating one or likely to exacerbate weediness, was described more than two decades ago (Strauss, 2003). Due to extensive global trade in food and forest products, such a change to a trait-based system would ultimately need to occur at an international level, presumably through modifications to the Cartagena Protocol. Thus, it will require strong international leadership at the highest political levels.

In addition to regulatory considerations, the market also provides major constraints to rDNA innovation. Most importantly, the now widespread forest certification systems impose a complete ban on the use of rDNA-modified trees in production forests (Strauss *et al.*, 2019). This ban has been long-standing, and recent efforts by the Forest Stewardship Council (FSC) to lift the ban, or to at least allow joint research projects with developers of rDNA-modified trees, have failed due to its controversial nature within the FSC. This ban has discouraged investment in biotechnology throughout most of the globe – as our personal experience working with forestry companies has clearly shown. Regulatory revisions notwithstanding, until such bans are broadly and permanently lifted, most companies will continue to be unwilling to undertake significant investments in rDNA biotechnology.

Science and technology innovation

Informed by genomic databases and a growing understanding of the genes and pathways that control plant physiology and growth, the opportunities and the efficiency of trait modification have

© 2024 The Authors
New Phytologist © 2024 New Phytologist Foundation

14698137, 2024, 2, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.19655 by Capes, Wiley Online Library on [10/02/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

expanded rapidly. Innovations such as basic gene transfer and regeneration methods, which were first developed in model plants (Barton *et al.*, 1983; De Block *et al.*, 1984) and then applied to crop plants, found their way into forest trees very soon after, first in the model tree poplar (Fillatti *et al.*, 1987) and then in horticultural tree crops, such as apple (James *et al.*, 1989), followed by the more difficult to transform conifers (Ellis *et al.*, 1989). Gene silencing (or RNA interference (RNAi)) was first observed in the model plant petunia (Napoli *et al.*, 1990), and once its mechanism was revealed and its application was optimized, it was widely applied to modify a diversity of traits in forest trees, from flowering (Rottmann *et al.*, 2000) to wood chemistry (Van Doorsselaere *et al.*, 1995). Gene-editing methods using for instance zinc fingers were rapidly applied to forest trees (Lu *et al.*, 2016), and soon replaced by CRISPR, which has ever since been widely used to study tree physiology, flowering, and wood chemistry (Fan *et al.*, 2015; Zhou *et al.*, 2015; Elorriaga *et al.*, 2018; Sulis *et al.*, 2023). It is clear that the power and precision of rDNA methods will continue to grow, providing a further motivation for breeders to start taking advantage of its capabilities. We describe two areas of economic importance, in which rDNA innovations have been growing, as examples.

Regeneration and transformation

Large improvements in transformation efficiency are essential for biotechnology to address the wide diversity of germplasm in tree breeding programs. In crop plants, genetic transformation methods have taken great steps forward in the last decade, largely the result of the use of developmental or morphogenic regulator (*DEV*) genes such as *WUSCHEL* and *BABY BOOM*. The benefits have been the greatest in monocots (cereal crops), which, combined with decades of research to develop embryogenic propagation systems, have led to transformation protocols that work in a wide variety of species and explant types (Gordon-Kamm *et al.*, 2019; Wang *et al.*, 2023). Similar progress is now being made for dicot species, including poplar, though these appear to often require different types of *DEV* genes or delivery systems that fit with their biology. For example, Ryan (2022) reported that the success of using the recently popular GRF-GIF types of *DEV* genes in poplar and eucalypts was highly genotype- and construct-dependent, requiring substantial gene customization and refinement of transformation protocols for successful use. Many woody species, both dicots and most notably conifers, also have distinct reproductive biology and/or regeneration systems compared with commonly studied, seed-propagated annual plants. In addition, the epigenetically 'mature' clonal tissues usually employed have distinct and highly variable levels of totipotency, which appear to affect their potential for embryogenesis or organogenesis. As discussed earlier (Strauss *et al.*, 2022), transformation and gene-editing systems for forest trees will require substantial further innovation and refinement for *DEV* genes to help mitigate the transformation bottleneck.

The very limited budgets for research in forest tree regeneration and transformation have prompted most researchers to simply try the genes and *Agrobacterium* strains available from agricultural crops – rather than to seek to understand the fundamental causes of

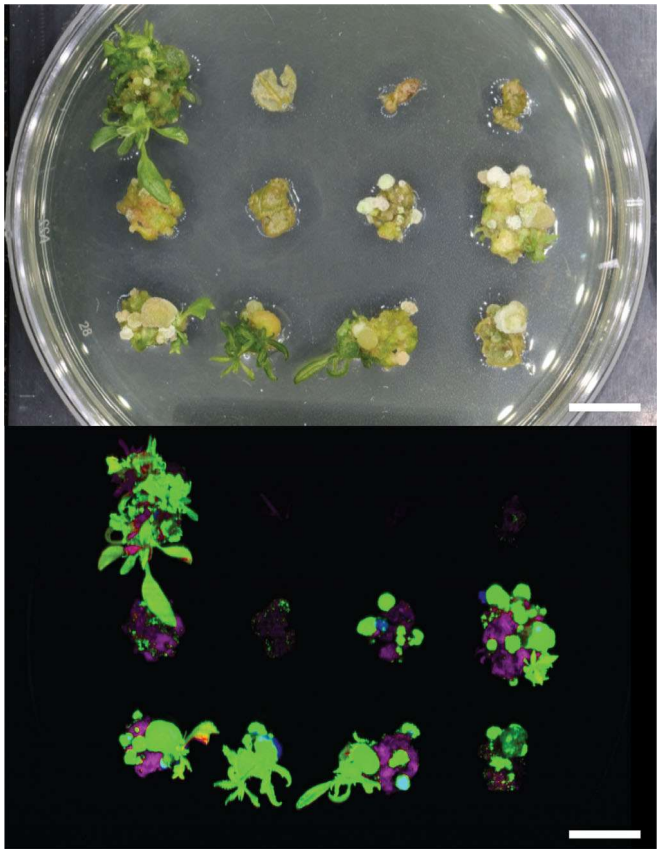


Fig. 1 New phenomic systems enable more precise and rapid means for scientific research and technology development. Here, new imaging and machine vision methods facilitated genome wide association studies (GWAS) of transformation. A hyperspectral imaging system, combined with machine learning, was used to quantify transformation rate as part of a GWAS of its biological basis in *Populus trichocarpa* (Nagle *et al.*, 2024a). Brightfield image above, and false color image below showing *GFP*-expressing tissues in green, and non-transgenic, chlorophyll-containing tissues in magenta. Bars: 1 cm.

recalcitrance to standard transformation methods. However, it is likely that significant inroads could be made by taking a fresh look at the distinct biology of trees and their development first. For example, recent genome wide association studies (GWAS) facilitated by new phenomic methods (Fig. 1) have shown that there are numerous genes involved with amenability to regeneration or transformation, and very few of these appear to be identical to those that have been effective in aiding transformation in crops (Nagle *et al.*, 2023, 2024a, b). In addition, the massive immune response, extreme genetic diversity, and strong epigenetic/ontogenetic variation discussed above warrant investigation into their biological mechanisms and variability. Finally, some of the basic technologies required for advanced rDNA-based modification, such as that of gene excision, appear to work very poorly or not at all in trees, likely a reflection of the extensive DNA methylation that accompanies recombinase induction (Liu *et al.*, 2021). The desire to remove any transformation-promoting genes from the genome to avoid pleiotropy, or to remove gene-editing reagents to ease regulatory acceptance and reduce off-target mutagenesis, will require smarter excision systems as well as much improved transformation

© 2024 The Authors
New Phytologist © 2024 New Phytologist Foundation

14698137, 2024, 2, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.19655 by Capes, Wiley Online Library on [10/02/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

14698137, 2024, 2, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.19655 by Capes, Wiley Online Library on [10/02/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

technologies. There are also promising editing systems that rely solely on transient expression or viral inoculation (e.g. Huang *et al.*, 2023; Sun *et al.*, 2024), thus not requiring gene excision. However, transient systems may be very difficult to apply in species that are already highly recalcitrant to transformation. Although wide host range viral systems that can carry out transient editing, such as tomato spotted wilt virus, are known (Liu *et al.*, 2023), to our knowledge, their infectiousness, potential for systemic spread, and rate of editing have not been established for any forest trees.

Wood chemistry and structure

One of the biggest markets for wood is the pulp and paper industry. Wood is largely composed of cellulose, hemicellulose, and lignin, but the lignin fraction needs to be extracted from wood chips in order to obtain high-quality pulp. The extraction of lignin is costly, as it requires the use of harsh chemicals at high temperature. Reducing lignin content or altering its chemical composition in trees would increase pulp yield and, thus, reduce the area of planted trees needed to supply pulp mills. A developing market for wood is in the biorefinery sector, in which lignocellulosic material is enzymatically converted to fermentable sugars to feed the bioeconomy. Also here, lignin is a main hurdle that limits the efficiency of biomass processing – although extracted lignin can also be an energy source or a feedstock for the synthesis of chemicals and materials (Brienza *et al.*, 2024). According to the Food and Agriculture Organization (FAO), the consumption of primary processed wood products is predicted to grow by 37% by 2050 in a business-as-usual scenario and will increase even more in a bioeconomy scenario (FAO, 2022). Clearly, the expected increase in wood consumption will put further pressure on the available space for plantation forestry, justifying rDNA-based efforts to improve the efficiency of wood productivity and processing.

Glasshouse and short-term confined field trials have demonstrated that strong improvements in wood processing efficiency can be achieved using rDNA technologies (reviewed by Chanoca *et al.*, 2019; De Meester *et al.*, 2022b; Li *et al.*, 2024; Zhu & Li, 2024). For example, downregulation of *CSE* in poplar by RNAi reduced lignin content by 25% and increased saccharification by 80–90% in glasshouse-grown trees (Saleme *et al.*, 2017), and 8-month-old, field-grown poplar CRISPR-edited in *CSE* showed a reduced lignin content by 29%, resulting in a 25% increase in saccharification efficiency (Jang *et al.*, 2021). Although these trees could provide obvious environmental benefits, including less chemical use and more pulp per acre of planted forest, the wood products derived from such trees cannot receive an FSC or other forest certification label simply because of the rDNA method used to engineer them, as discussed above (Strauss *et al.*, 2019).

Lignin has many important physiological functions for sustaining upward growth, stem rigidity, and water conduction under tension in the xylem. Thus, strong modification in lignin content may lead to compromised tree health, especially under stressful environmental conditions, limiting the extent to which wood chemistry and physical properties can be productively modified (De Meester *et al.*, 2022b). One means to reduce or eliminate the negative impact of lignin modification is to target lignin modification to specific tissues and cell types. For example, targeted downregulation of lignin biosynthesis in xylem fibers, while keeping vessel lignification intact, largely alleviates the negative effect on tree health while wood processing efficiency is still significantly improved (Gui *et al.*, 2020; De Meester *et al.*, 2021). Using gene-editing, a variety of strong and weak alleles can be created, allowing further 'fine-tuning' of lignin modification. Indeed, while poplar trees with a bi-allelic (full) knockout of the lignin biosynthesis gene *CCR2* could barely survive, CRISPR-based engineering of one knockout *CCR2* allele in combination with a leaky *CCR2* allele resulted in healthy trees with a 25–41% improved wood processing efficiency (De Meester *et al.*, 2020). A recent development is the engineering of lignin types that are entirely new by directing the biosynthesis of alternative lignin monomers in wood cells. These new monomers will be incorporated into the lignin polymer, facilitating biomass deconstruction (Wilkerson *et al.*, 2014; Mottiar *et al.*, 2016; Sibout *et al.*, 2016; Oyarce *et al.*, 2019; Hoengenaert *et al.*, 2022). Such new lignin structures may also improve the valorization of the lignin fraction itself, making lignin easier to fractionate into basic building blocks for the chemical industry (Van den Bosch *et al.*, 2015; de Vries *et al.*, 2021). Multiplex gene-editing or stacking of genes involving wood quality traits (e.g. lignin and wood density) with genes known to improve biomass yield (e.g. for pest resistance (Klocko *et al.*, 2014) or nitrogen metabolism (Jing *et al.*, 2004)), possibly combined with sterility genes to help in the management of gene flow (Strauss *et al.*, 2017), may help to promote a more sustainable wood products industry (Chang *et al.*, 2018; Sulis *et al.*, 2023).

Integration of breeding and rDNA methods

Genetic improvements to adapt trees to new environments or to improve economically important traits depend on the presence of genetic variation in the breeding germplasm (Fig. 2). Forest trees are in the earliest stages of domestication and harbor a great deal of genetic and phenotypic diversity that can be exploited by conventional breeding. For example, in wild *Populus trichocarpa*, lignin content varies from 15.5% to 27.9%, indicating that major gains in wood processing efficiency can be made by conventional breeding alone (Studer *et al.*, 2011). In addition, rare defective alleles for lignin biosynthesis genes (and probably many other traits) are naturally present in the wild germplasm (MacKay *et al.*, 1997; Marroni *et al.*, 2011; Yamamoto *et al.*, 2020), and they can have a large effect on the trait if made homozygous (Vanholme *et al.*, 2013). However, forest tree breeding takes many decades, inbreeding is difficult (dioecious species such as poplar are mostly impossible to self-pollinate), and new sexual crosses to integrate such rare alleles into the genome of elite clones will break up the clone's genetic constitution, thus requiring extra generations of breeding (Vanholme *et al.*, 2013).

In contrast to conventional breeding, rDNA methods such as RNAi or gene-editing are not limited to standing genetic variation; they make it possible to create or insert alleles as homozygous or dominant forms in any elite line without shuffling their genotypes as in conventional breeding. Moreover, they can be introduced in

© 2024 The Authors
New Phytologist © 2024 New Phytologist Foundation

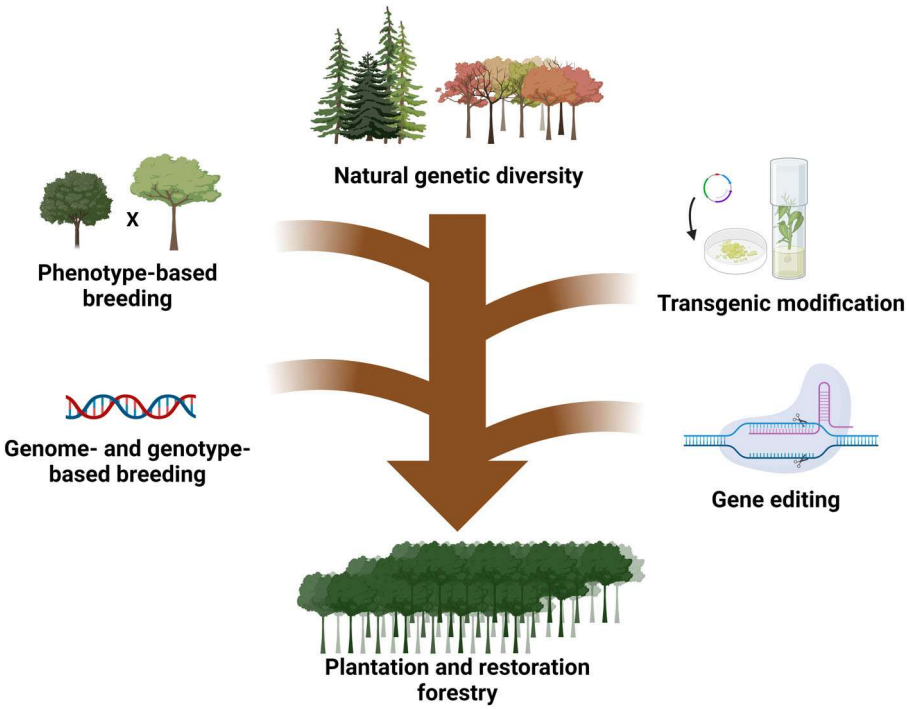


Fig. 2 Overview of methods for genetic improvement of forest trees. To accelerate genetic improvement, conventional and new breeding methods need to be fully integrated, as suggested by the central arrow. Genetic improvement starts by exploiting phenotypic diversity from natural trees and provenances by conventional breeding (sexual crossing followed by phenotypic selection). Current advances in genome sequencing and genotyping allow conventional breeders to accelerate the use of natural genetic diversity using strategies such as genomic selection. A variety of rDNA tools, including transformation (constitutive or tissue-specific overexpression or downregulation using transgenes) and gene-editing (to genetically modify native genes by insertion, deletion, translocation, or inversion), can insert or create desirable alleles for inclusion in breeding populations to modify high-value traits. Figure created with Biorender.com.

multiple parental lines of the breeding germplasm provided that broadly effective transformation technologies are available, as discussed above. rDNA technologies also allow weak alleles to be generated (i.e. not just knockouts or strong overexpression), and these can be readily edited at multiple loci, giving a wide variation of effects that would be sorted out during field studies as part of conventional breeding. Thus, rDNA modification should not be regarded as an alternative to conventional breeding, but rather as a co-developed, complementary tool for generating diversity that is directed at specific traits of interest.

Genetic variation in most traits of economic importance, including yield, crown form, and overall stress tolerance, is controlled by hundreds to thousands of genes. For such traits, conventional breeding, in some cases aided by genomic selection, is the method of choice to improve these highly polygenic traits (Fig. 3). rDNA methods, which require knowledge of specific genes and their roles in the control of valuable traits, are currently best suited for physiologically simpler, mostly qualitative traits such as changes to plant chemistry, sexual fertility, and resistance to selected pests and pathogens that are controlled by a few genes (Strauss *et al.*, 2022). However, successful engineering of ecophysiologically complex traits, such as abiotic stress tolerance or yield, has been demonstrated numerous times in the glasshouse and field, and achieved to a limited extent in commercial agricultural crops such as wheat and maize (Simmons *et al.*, 2021; Gupta, 2024). With the advent of multiplex editing and advanced phenomic methods, the division between traits suitable for rDNA-based modification and conventional breeding may weaken over time.

With the growing demand for wood, and the increasing pressure on forests due to climate change and rapidly changing pest populations, it is especially critical that rDNA technologies are integrated in conventional breeding programs in a manner that does not slow conventional breeding. Most important is the early evaluation of rDNA-modified trees in the field (Fig. 4), preferably at several locations and over several years that approach a harvest cycle, and that the trait is introduced in multiple genotypes of the target commercial species. Currently, most rDNA-based research in forest trees is conducted in laboratories and glasshouses but is rarely further translated through field trials. Contained, indoor studies work well for fundamental research directed toward understanding biological processes and gene function; a well-controlled environment enhances the capacity for the detection of biological effects from a specific genetic modification. However, trees grown in the field experience daily and seasonal differences in weather conditions, including exposure to periods of drought, rain, frost, high UV radiation, wind, and pathogens. Furthermore, they undergo the seasonal cycles of growth and dormancy that have major effects on wood structure and stress tolerance, and also undergo a transition from juvenility to maturity, only starting to flower after several years. This maturation also affects the structure of wood and the expression of most other traits, including tolerance to stresses and pathogens. It is therefore no surprise that the phenotypes of field-grown trees, including their basic chemical composition (Viswanath *et al.*, 2012), are very different from those of glasshouse-grown trees, and that phenotypic differences observed for rDNA-modified trees grown in greenhouse conditions are often not maintained in the field (e.g. Lu *et al.*, 2015; Van Acker *et al.*, 2017; De Meester *et al.*, 2022a, b; Derba-Maceluch *et al.*, 2023). Indeed, conventional breeding, including the statistical model development needed for genomic selection, relies almost exclusively on field results for the same reasons.

Under current regulations and research programs, rDNA-based modifications are usually made in a single model genotype that is

© 2024 The Authors
New Phytologist © 2024 New Phytologist Foundation

14698137, 2024, 2, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.19855 by Capes, Wiley Online Library on [10/02/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

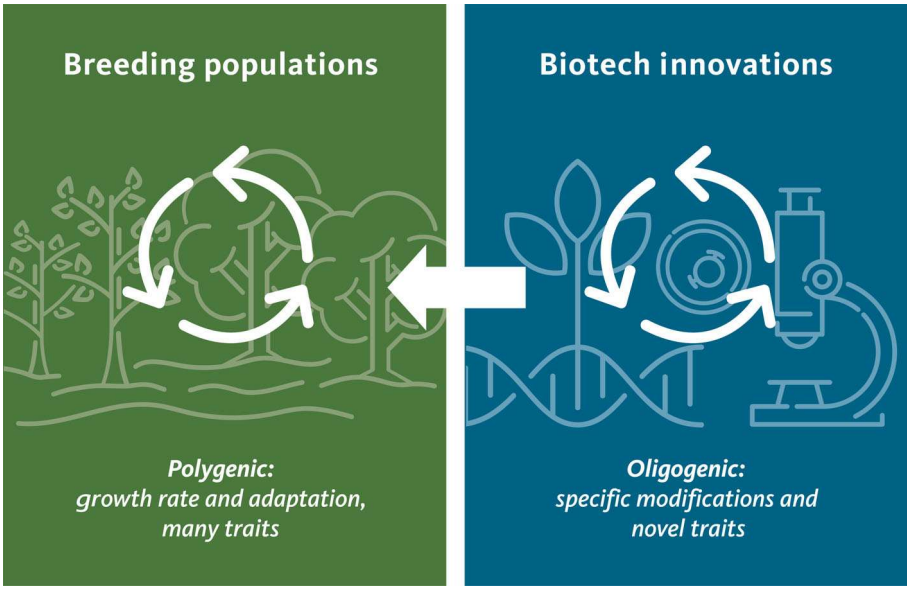


Fig. 3 Integration of rDNA-based modification and conventional breeding. rDNA-based modification is today focused on traits under single gene or oligogenic control and provides qualitative trait modifications (blue box, circular arrows). Conventional and genomic breeding focuses on complex traits that are under polygenic control, resulting in quantitative trait modification (green box, circular arrows). Both forms needs to be efficiently integrated so as not to slow conventional breeding progress. The horizontal arrow represents rDNA trees that enter the breeding program.

easily transformed; thus, rDNA-modified trees are evaluated completely independent of breeding populations. For integration into breeding, the rDNA-based modifications would first need to be recreated in appropriate germplasm and then re-evaluated in field studies in parallel (i.e. as breeding continues to improve germplasm). If the transformation of relevant germplasm and field testing could be readily undertaken as part of initial rDNA concept testing, the real-world value and pleiotropy from rDNA-based modifications could be evaluated much more rapidly (Khaipho-Burch *et al.*, 2023). Successful rDNA-based modifications could then be ready for inclusion in breeding programs soon after, and further tested as part of its crossing and field evaluations.

Early testing is also important because these novel rDNA-based modifications require scrutiny; most have not previously been subjected to multi-generational natural selection as have the highly polymorphic alleles in wild gene pools (Burdon & Walter, 2001).

The few early field studies that have been conducted indeed support their value for rapid evaluation of useful rDNA-based traits. For example, when a variety of RNAi constructs and insertion events were explored in the field with the intent of modifying the xylan content of poplar wood to aid saccharification, several constructs and events were identified that led to favorable results without compromising productivity, whereas others did not result in any improvements (Derba-Maceluch *et al.*, 2023). These

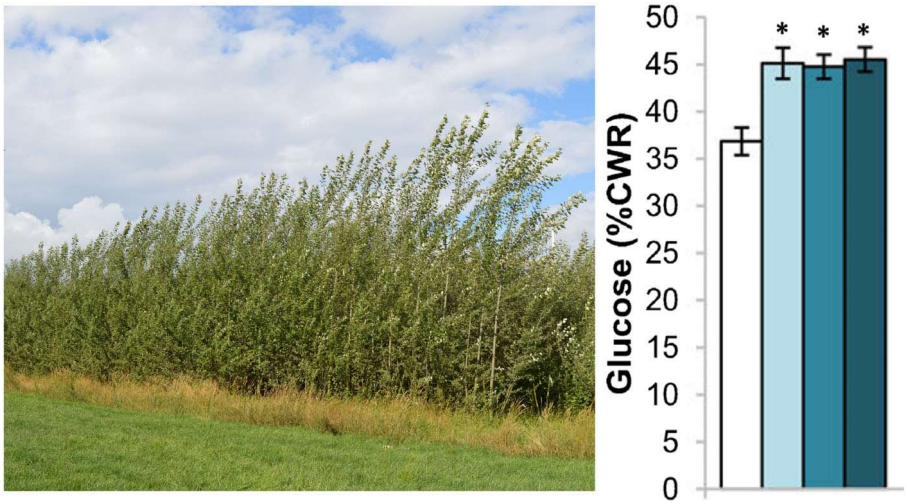


Fig. 4 Field studies of rDNA trees are essential for the integration of rDNA and breeding. Shown is a field trial and saccharification analysis of wild-type (WT) and transgenic *Populus tremula* × *P. alba* with altered lignin composition. Left, trees grown for 2 yr after coppicing. Right, wood from three transgenic lines (blue bars) was found to be easier to deconstruct with cell wall-degrading enzymes as compared to that from WT trees (white bar). Shown is the amount of glucose released as percentage of cell wall residue (CWR). Bars represent means ± SD. Asterisks show that all transgenic lines were significantly different from the WT ($P < 0.05$ for a two-way ANOVA with Dunnett's *post hoc* test). $n = 18$ for WT and all three transgenic lines. Data are from De Meester *et al.* (2022a).

© 2024 The Authors
New Phytologist © 2024 New Phytologist Foundation

14698137, 2024, 2, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.19655 by Capes, Wiley Online Library on [10/02/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

New Phytologist

events could not have been predicted from laboratory studies alone. In a field experiment with poplars intended to identify transgenes that could elevate productivity by modification of active gibberellin levels, only one of several constructs was found to be successful, and would be a logical candidate for further testing and breeding (Lu *et al.*, 2015). Two field trials with transgenic poplar downregulated for *CAD* and with altered lignin demonstrated that the level of *CAD* downregulation is important to balance wood modification with normal growth; modest downregulation resulted in improved wood quality and normal growth, whereas strong downregulation resulted in a strong yield penalty (Pilate *et al.*, 2002; De Meester *et al.*, 2022a). The latter trees had shown no-yield penalty when grown in a well-controlled glasshouse, it was only observed in the field (Van Acker *et al.*, 2017). A similar phenomenon was seen with poplars downregulated for *CCR2* (Leplé *et al.*, 2007; Van Acker *et al.*, 2014).

Putting opportunities and risks in context

Plantation and 'natural forest' biotechnology

Although intensive plantation forestry is likely to be the main focus for rDNA innovations, wild and feral 'natural' trees (including those in forests affected by humans in the past or present) continue to be subject to devastating pathogens and insects for which, in some cases, there is limited innate resistance. This, coupled with the slowness of traditional tree breeding, especially when resistant germplasm is rare, creates a demand for new solutions, potentially including that of rDNA technologies. The most famous case is that of the American chestnut, which was devastated throughout its natural range by an exotic Asian fungal pathogen unintentionally imported to the United States via shipments of plant materials. Despite recent setbacks (Grandoni, 2023) and continuing regulatory obstacles, a transgenic, fully, or partially blight-resistant American chestnut appears likely to be the first rDNA-modified tree used for wild plantings (Newhouse & Powell, 2021). rDNA-based solutions for ecosystem repair beyond the chestnut have been very few, and we know of none that are in advanced field research, which is, to our opinion, due to several factors, including the following: (1) the extensive genetic diversity in forest tree germplasm, which therefore usually includes resistant germplasm, (2) the challenges and costs of transformation technology for most species, (3) the lack of in-depth knowledge of resistance mechanisms and the genes that are needed to support gene-editing or RNAi approaches, and (4) most importantly, the social obstacles in the form of regulatory and market blockages, as discussed above, which severely impede investments in research that could lead to rDNA-based solutions.

Field trials as communication tools

In addition to their essential role in rDNA trait evaluation, field trials are also excellent means for communicating with the public about the science surrounding rDNA-modified trees. Seeing trees in the field – where they generally look like, well, trees!—provides a stark contrast to the caricatured, demonizing picture often painted by activists. Unfortunately, regulations that require strict laboratory and glasshouse containment are the rule throughout most of the world – and make casual viewing of rDNA trees problematic. In some regions, companies are able to establish useful field trials; however, they are not usually open to the public due to proprietary and 'eco'vandalism concerns. Public–private partnerships are likely to be important to enable wider use of field trials for the goals of trusted public education and dialog (May *et al.*, 2024).

Activist concerns about rDNA-modified trees

As forest tree biotechnology causes skepticism among some sectors of the public and the scientific community, it is important to recognize that – similar to tree breeding and other forestry research (White *et al.*, 2007) – assessment of its value and impact will occur incrementally over many years and locations as part of the common forestry practice of 'adaptive management' (e.g. Bolte *et al.*, 2009); the large majority of forest lands and species will see no significant applications of rDNA technologies at all for the foreseeable future. This is a result of the realities of scale-up and replacement of other types of trees and crops as they reach harvest age; the technical and social constraints discussed above; and of the fact that rDNA methods are today mainly suitable for a few intensively grown and clonal plantation species, such as eucalypts and poplars, and a very short list of wild species that are under serious biotic or abiotic threats, such as the American chestnut as discussed above. The realm for gene-editing in forest trees is likewise expected to be very limited for many years, as discussed in depth by Strauss *et al.* (2022). Thus, risks of rDNA use in forest systems will be highly focused, and there will be literally decades for impacts to be assessed and changes in technology or use made if needed. In addition, any risks from rDNA modification will occur along with the growing use and risks from a variety of novel breeding and planting approaches, including assisted migration and species replacement (Gömöry *et al.*, 2020), that are being forced by increasing climate impacts and pest stresses. The risks and benefits of rDNA-modified trees, as well as the risks from their non-use, must be considered in proportion to these very large new risks.

Unlike some activists that regularly emphasize 'genetic contamination' of forests by rDNA trees (e.g. Smolker & Petermann, 2019), we do not consider this, in general, to be a major biological issue. This does not mean that it would not be wise to use genetic containment means (sterility) at scale when socially or ecologically prudent, such as to avoid the spread of herbicide resistance where it would compromise weed control, avoid the spread of an unsafe protein into a food-producing forest tree such as chestnut, or to avoid further spread from exotic forest species that are known to be invasive (Strauss *et al.*, 2017). However, the use of rDNA-based methods *per se* does not, in our view, constitute a sufficient risk to require strict containment, and particularly not at the level of field research and breeding. When rDNA-modified trees could promote environmental values such as stress or disease resistance and thus are potentially critical to sustaining forests, we believe that the risks from some low-level spread into wild or feral trees must be considered acceptable. Indeed, during conventional breeding and ornamental horticulture, genes are continuously

© 2024 The Authors
New Phytologist © 2024 New Phytologist Foundation

14698137, 2024, 2, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.19655 by Capes, Wiley Online Library on [10/02/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Box 1 Key requirements for rDNA-based innovations to enhance forest productivity and adaptation

(**1**) Removal of strong regulatory and marketplace impediments to field research and commercial activities;
(**2**) Expanded investment in basic and applied research, including transformation and gene-editing technology;
(**3**) Early integration with breeding programs, including publicly visible and scientifically vetted field studies.

'leaked' from test plantations, generally without significant impact. Of course, until laws and market standards change, the spread of recombinant genes or propagules will present serious legal or market risks and thus severely constrain research.

Conclusions

Forests, both planted and natural, are immense sources of ecological services and sustainable industrial products throughout much of the world. Plantations, the main focus of efforts to employ rDNA technologies, are superior to other forest communities when wood production is the primary goal (Hua *et al.*, 2022), and thus can relieve pressure on native forests for intensive harvesting.

For rDNA biotechnology to help increase forest productivity and adaptation to ongoing rapid climate change, however, it must have a similar freedom to innovate and be deployed to that of conventional breeding. Climate change is well known to existentially threaten forests nearly everywhere, and research in crops suggests that rDNA biotechnology may help in adaptation (Anderson *et al.*, 2020). We are unable to conceive of any of the often-stated risks from biotechnology that are on a par with the risks of doing little to nothing due to the current obstructive social environment. We therefore firmly believe that nothing short of a radical change in regulations, market restrictions, and research investment is warranted (Box 1).

There remain substantial gaps in the technical capacity for efficient use of rDNA technologies in forest trees. This primarily results from the very limited investment from either private or public sources in technology and variety development, including necessary field evaluations, a result that we believe is caused by the daunting social constraints discussed above. Thus, we must have social innovation first if we are to make substantial scientific and technical progress. We therefore should not wait for technology to mature to convince society of the case for strong investments and regulatory relief.

Finally, although acceptance of rDNA technologies in food and forest systems is clearly a 'wicked' problem (Durant & Legge Jr, 2006), we believe that substantial social innovations to regulations and market restrictions are not impossible to achieve. Some of these have in fact occurred in recent years, such as those embodied in the USDA Secure system (Hoffman, 2021) and the new UK Genetic Technology (Precision Breeding) Bill (Caccamo, 2023). Relaxations of regulation are occurring through these new policies, and throughout the world for basic gene-editing, and even the EU is seriously considering revision of its GMO regulatory policies to exempt some categories of gene-edited and cisgenic plants (Nature Plants, 2023). However, we believe that regulatory relief only for simple forms of gene-editing will be woefully insufficient to meet most of the major threats that forests face; a much fuller set of rDNA biotechnologies will need to be included. For example, transgenes or edits that enhance weed management, pest control, pollution reduction, and wood quality have already been demonstrated to provide substantial benefits in pilot field studies (discussed in Strauss *et al.*, 2022). We will need these technologies, closely integrated with conventional breeding in all its forms, to have a chance of significantly mitigating the effects of climate stress on forest health and survival. We also will need to act expeditiously, as the extraordinary pace of climate change in recent years has shown us that time is not on our side. As has been said many times and in many ways (Council for Agricultural Science and Technology, 2013), we believe that today's precaution with regard to rDNA technologies is not to be found in the lengthy delays typically associated with the Precautionary Principle, but in extensive innovation and field research that can provide new options for production and adaptation.

Acknowledgements

SHS thanks several sources for support of his laboratory in recent years, including members of the GREAT TREES Research Cooperative at Oregon State University (grant Z0019C), the NSF Plant Genome Research Program (grant IOS1546900), and the USDA National Institute of Food and Agriculture Biotechnology Research Assessment Grants Program (grant 2020-02922). WB is indebted to the Energy Transition Funds (ETF) projects ADV_BIO and AD-LIBIO, to the interuniversity BOF project Next-BIOREF, and to the ERC-Advanced-Grant POPMET (grant No. 834923). We thank Dr. Annick Bleys for critically reading the manuscript and helping with the submission.

Competing interests

None declared.

Author contributions

WB and SHS both conceived and wrote the article. WB and SHS contributed equally to this work.

ORCID

Wout Boerjan https://orcid.org/0000-0003-1495-510X
Steven H. Strauss https://orcid.org/0000-0001-9670-3082

Wout Boerjan[1,2†*] and Steven H. Strauss[3†*]

[1]Department of Plant Biotechnology and Bioinformatics, Ghent University, Technologiepark 71, 9052, Ghent, Belgium; [2]Center for Plant Systems Biology, VIB, Technologiepark 71, 9052, Ghent, Belgium;

© 2024 The Authors
New Phytologist © 2024 New Phytologist Foundation

14698137, 2024, 2, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.19655 by Capes, Wiley Online Library on [10/02/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

[3]Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA
(*Authors for correspondence: email wout.boerjan@psb.vib-ugent.be (WB); steve.strauss@oregonstate.edu (SHS))
[†]These authors contributed equally to this work.

References

Anderson R, Bayer PE, Edwards D. 2020. Climate change and the need for agricultural adaptation. *Current Opinion in Plant Biology* **56**: 197–202.

Barton KA, Binns AN, Matzke AJ, Chilton M-D. 1983. Regeneration of intact tobacco plants containing full length copies of genetically engineered T-DNA, and transmission of T-DNA to R1 progeny. *Cell* **32**: 1033–1043.

Bolte A, Ammer C, Löf M, Nabuurs G-J, Schall P, Spathelf P. 2009. Adaptive forest management: a prerequisite for sustainable forestry in the face of climate change. *Managing Forest Ecosystems* **19**: 115–139.

Brienza F, Cannella D, Montesdeoca D, Cybulska I, Debecker DP. 2024. A guide to lignin valorization in biorefineries: traditional, recent, and forthcoming approaches to convert raw lignocellulose into valuable materials and chemicals. *RSC Sustainability* **2**: 37–90.

Burdon RD, Walter C. 2001. Perspectives on risk in transgenic forest plantations in relation to conventional breeding and use of exotic pines and eucalypts: Viewpoints of practicing breeding and transformation scientists. In: Strauss SH, Bradshaw HD, eds. *Proceedings of the first international symposium on ecological and societal aspects of transgenic plantations.* Corvallis, OR, USA: College of Forestry, Oregon State University, 124–137.

Caccamo M. 2023. New precision-breeding law unlocks gene editing in England. *Nature Biotechnology* **41**: 752–753.

Chang S, Mahon EL, MacKay HA, Rottmann WH, Strauss SH, Pijut PM, Powell WA, Coffey V, Lu H, Mansfield SD *et al.* 2018. Genetic engineering of trees: progress and new horizons. *In Vitro Cellular & Developmental Biology - Plant* **54**: 341–376.

Chanoca A, de Vries L, Boerjan W. 2019. Lignin engineering in forest trees. *Frontiers in Plant Science* **10**: 912.

Council for Agricultural Science and Technology. 2013. Impact of the precautionary principle on feeding current and future generations. In: *Issue Paper 52.* Ames, IA, USA: Council for Agricultural Science and Technology (CAST), 1–20.

De Block M, Herrera-Estrella L, Van Montagu M, Schell J, Zambryski P. 1984. Expression of foreign genes in regenerated plants and in their progeny. *EMBO Journal* **3**: 1681–1689.

De Meester B, Madariaga Calderón B, de Vries L, Pollier J, Goeminne G, Van Doorsselaere J, Chen M, Ralph J, Vanholme R, Boerjan W. 2020. Tailoring poplar lignin without yield penalty by combining a null and haploinsufficient *CINNAMOYL-CoA REDUCTASE2* allele. *Nature Communications* **11**: 5020.

De Meester B, Van Acker R, Wouters M, Traversari S, Steenackers M, Neukermans J, Van Breusegem F, Déjardin A, Pilate G, Boerjan W. 2022a. Field and saccharification performances of poplars severely downregulated in *CAD1*. *New Phytologist* **236**: 2075–2090.

De Meester B, Vanholme R, de Vries L, Wouters M, Van Doorsselaere J, Boerjan W. 2021. Vessel-and ray-specific monolignol biosynthesis as an approach to engineer fiber-hypolignification and enhanced saccharification in poplar. *The Plant Journal* **108**: 752–765.

De Meester B, Vanholme R, Mota T, Boerjan W. 2022b. Lignin engineering in forest trees: from gene discovery to field trials. *Plant Communications* **3**: 100465.

Derba-Maceluch M, Sivan P, Donev EN, Gandla ML, Yassin Z, Vaasan R, Heinonen E, Andersson S, Amini F, Scheepers G *et al.* 2023. Impact of xylan on field productivity and wood saccharification properties in aspen. *Frontiers in Plant Science* **14**: 1218302.

Durant RF, Legge JS Jr. 2006. "Wicked problems," public policy, and administrative theory: lessons from the GM food regulatory arena. *Administration and Society* **38**: 309–334.

Ellis D, Roberts D, Sutton B, Lazaroff W, Webb D, Flinn B. 1989. Transformation of white spruce and other conifer species by *Agrobacterium tumefaciens*. *Plant Cell Reports* **8**: 16–20.

Elorriaga E, Klocko AL, Ma C, Strauss SH. 2018. Variation in mutation spectra among CRISPR/Cas9 mutagenized poplars. *Frontiers in Plant Science* **9**: 594.

Evanega S, Conrow J, Adams J, Lynas M. 2022. The state of the 'GMO' debate - toward an increasingly favorable and less polarized media conversation on ag-biotech? *GM Crops & Food* **13**: 38–49.

Fan D, Liu T, Li C, Jiao B, Li S, Hou Y, Luo K. 2015. Efficient CRISPR/Cas9-mediated targeted mutagenesis in populus in the first generation. *Scientific Reports* **5**: 12217.

FAO. 2022. *Consumption of primary processed wood products predicted to grow 37 percent by 2050.* [WWW document] URL https://www.fao.org/newsroom/detail/consumption-of-primary-processed-wood-products-predicted-to-grow-37-percent-by-2050/en#:~:text=Consumption%20of%20primary%20processed%20wood%20products%20predicted%20to%20grow%2037%20percent%20by%202050,-FAO%20publishes%20Global&text=Rome%20%E2%80%93%20Overall%20consumption%20of%20primary,United%20Nations%20(FAO)%20said [accessed 16 May 2024].

Fillatti JJ, Sellmer J, McCown B, Haissig B, Comai L. 1987. *Agrobacterium* mediated transformation and regeneration of *Populus*. *Molecular and General Genetics* **206**: 192–199.

Funk C. 2020. *About half of U.S. adults are wary of health effects of genetically modified foods, but many also see advantages.* [WWW document] URL https://www.pewresearch.org/short-reads/2020/03/18/about-half-of-u-s-adults-are-wary-of-health-effects-of-genetically-modified-foods-but-many-also-see-advantages/ [accessed 16 May 2024].

Gömöry D, Krajmerová D, Hrivnák M, Longauer R. 2020. Assisted migration vs. close-to-nature forestry: what are the prospects for tree populations under climate change? *Central European Forestry Journal* **66**: 63–70.

Goralogia GS, Redick TP, Strauss SH. 2021. Gene editing in tree and clonal crops: progress and challenges. *In Vitro Cellular & Developmental Biology - Plant* **57**: 683–699.

Gordon-Kamm B, Sardesai N, Arling M, Lowe K, Hoerster G, Betts S, Jones AT. 2019. Using morphogenic genes to improve recovery and regeneration of transgenic plants. *Plants* **8**: 38.

Grandoni D. 2023. *Genetic engineering was meant to save chestnut trees. Then there was a mistake. The Washington Post.* [WWW document] URL https://www.washingtonpost.com/climate-environment/2023/12/24/chestnut-tree-genetic-engineering-mistake/ [accessed 16 May 2024].

Gui J, Lam PY, Tobimatsu Y, Sun J, Huang C, Cao S, Zhong Y, Umezawa T, Li L. 2020. Fibre-specific regulation of lignin biosynthesis improves biomass quality in *Populus*. *New Phytologist* **226**: 1074–1087.

Gupta PK. 2024. Drought-tolerant transgenic wheat HB4®: a hope for the future. *Trends in Biotechnology* S0167-7799(23)00346-3.

Halpin C, Lennon S, Pinfield-Wells H, Hetherington AM. 2023. Introducing transformative plant biotechnology. *New Phytologist* **237**: 5–6.

Hoengenaert L, Wouters M, Kim H, De Meester B, Morreel K, Vandersyppe S, Pollier J, Desmet S, Goeminne G, Ralph J *et al.* 2022. Overexpression of the scopoletin biosynthetic pathway enhances lignocellulosic biomass processing. *Science Advances* **8**: abo5738.

Hoffman NE. 2021. Revisions to USDA biotechnology regulations: the SECURE rule. *Proceedings of the National Academy of Sciences, USA* **118**: e2004841118.

Hua F, Bruijnzeel LA, Meli P, Martin PA, Zhang J, Nakagawa S, Miao X, Wang W, McEvoy C, Peña-Arancibia JL *et al.* 2022. The biodiversity and ecosystem service contributions and trade-offs of forest restoration approaches. *Science* **376**: 839–844.

Huang X, Jia H, Xu J, Wang Y, Wen J, Wang N. 2023. Transgene-free genome editing of vegetatively propagated and perennial plant species in the T0 generation via a co-editing strategy. *Nature Plants* **9**: 1591–1597.

Jacobs DF, Dumroese RK, Brennan AN, Campbell FT, Conrad AO, Delborne JA, Fitzsimmons S, Flores D, Giardina CP, Greenwood L *et al.* 2023. Reintroduction of at-risk forest tree species using biotechnology depends on regulatory policy, informed by science and with public support. *New Forests* **54**: 587–604.

James DJ, Passey AJ, Barbara DJ, Bevan M. 1989. Genetic transformation of apple (*Malus pumila* Mill.) using a disarmed Ti-binary vector. *Plant Cell Reports* **7**: 658–661.

Jang H-A, Bae E-K, Kim M-H, Park S-J, Choi N-Y, Pyo S-W, Lee C, Jeong H-Y, Lee H, Choi Y-I *et al.* 2021. CRISPR-knockout of *CSE* gene improves

© 2024 The Authors
New Phytologist © 2024 New Phytologist Foundation

14698137, 2024, 2, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.19655 by Capes, Wiley Online Library on [10/02/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

saccharification efficiency by reducing lignin content in hybrid poplar. *International Journal of Molecular Sciences* **22**: 9750.

Jing ZP, Gallardo F, Pascual MB, Sampalo R, Romero J, De Navarra AT, Cánovas FM. 2004. Improved growth in a field trial of transgenic hybrid poplar overexpressing glutamine synthetase. *New Phytologist* **164**: 137–145.

Khaipho-Burch M, Cooper M, Crossa J, de Leon N, Holland J, Lewis R, McCouch S, Murray SC, Rabbi I, Ronald P *et al.* 2023. Genetic modification can improve crop yields—but stop overselling it. *Nature* **621**: 470–473.

Klocko AL, Meilan R, James RR, Viswanath V, Ma C, Payne P, Miller L, Skinner JS, Oppert B, Cardineau GA *et al.* 2014. Bt-Cry3Aa transgene expression reduces insect damage and improves growth in field-grown hybrid poplar. *Canadian Journal of Forest Research* **44**: 28–35.

Lassoued R, Macall DM, Smyth SJ, Phillips PWB, Hesseln H. 2020. How should we regulate products of new breeding techniques? Opinion of surveyed experts in plant biotechnology. *Biotechnology Reports* **26**: e00460.

Leplé J-C, Dauwe R, Morreel K, Storme V, Lapierre C, Pollet B, Naumann A, Kang K-Y, Kim H, Ruel K *et al.* 2007. Downregulation of cinnamoyl-coenzyme A reductase in poplar: multiple-level phenotyping reveals effects on cell wall polymer metabolism and structure. *Plant Cell* **19**: 3669–3691.

Li W, Lin Y-CJ, Chen Y-L, Zhou C, Li S, De Ridder N, Oliveira DM, Zhang L, Zhang B, Wang JP *et al.* 2024. Woody plant cell walls: fundamental and utilization. *Molecular Plant* **17**: 112–140.

Liu Q, Zhao C, Sun K, Deng Y, Li Z. 2023. Engineered biocontainable RNA virus vectors for non-transgenic genome editing across crop species and genotypes. *Molecular Plant* **16**: 616–631.

Liu R, Long Q, Zou X, Wang Y, Pei Y. 2021. DNA methylation occurring in Cre-expressing cells inhibits loxP recombination and silences loxP-sandwiched genes. *New Phytologist* **231**: 210–224.

Lu H, Klocko AL, Dow M, Ma C, Amarasinghe V, Strauss SH. 2016. Low frequency of zinc-finger nuclease-induced mutagenesis in *Populus*. *Molecular Breeding* **36**: 121.

Lu H, Viswanath V, Ma C, Etherington E, Dharmawardhana P, Shevchenko O, Strauss SH, Pearce DW, Rood SB, Busov V. 2015. Recombinant DNA modification of gibberellin metabolism alters growth rate and biomass allocation in *Populus*. *Tree Genetics & Genomes* **11**: 127.

Lynas M, Adams J, Conrow J. 2022. Misinformation in the media: global coverage of GMOs 2019-2021. *GM Crops & Food*: 1–10. doi: 10.1080/21645698.2022.2140568.

MacKay JJ, O'Malley DM, Presnell T, Booker FL, Campbell MM, Whetten RW, Sederoff RR. 1997. Inheritance, gene expression, and lignin characterization in a mutant pine deficient in cinnamyl alcohol dehydrogenase. *Proceedings of the National Academy of Sciences, USA* **94**: 8255–8260.

Marroni F, Pinosio S, Di Centa E, Jurman I, Boerjan W, Felice N, Cattonaro F, Morgante M. 2011. Large-scale detection of rare variants via pooled multiplexed next-generation sequencing: towards next-generation Ecotilling. *The Plant Journal* **67**: 736–745.

May M, Hirsch S, Abramson M. 2024. Transformation of plantation forestry productivity for climate change mitigation and adaptation. *Cold Spring Harbor Perspectives in Biology* **16**: a041670.

Mottiar Y, Vanholme R, Boerjan W, Ralph J, Mansfield SD. 2016. Designer lignins: harnessing the plasticity of lignification. *Current Opinion in Biotechnology* **37**: 190–200.

Nagle MF, Yuan J, Kaur D, Ma C, Peremyslova E, Jiang Y, Goralogia GS, Magnuson A, Li JY, Muchero W *et al.* 2024a. Genome-wide association study and network analysis of *in vitro* transformation in *Populus trichocarpa* support key roles of diverse phytohormone pathways and cross talk. *New Phytologist* **242**: 2059–2076.

Nagle MF, Yuan J, Kaur D, Ma C, Peremyslova E, Jiang Y, Niño de Rivera A, Jawdy S, Chen J-G, Feng K *et al.* 2024b. GWAS supported by computer vision identifies large numbers of candidate regulators of *in planta* regeneration in *Populus trichocarpa*. *G3: Genes, Genomes, Genetics* **14**: jkae026.

Nagle MF, Yuan J, Kaur D, Ma C, Peremyslova E, Jiang Y, Zahl B, Niño de Rivera A, Muchero W, Fuxin L *et al.* 2023. GWAS identifies candidate genes controlling adventitious rooting in *Populus trichocarpa*. *Horticulture Research* **10**: uhad125.

Napoli C, Lemieux C, Jorgensen R. 1990. Introduction of a chimeric chalcone synthase gene into petunia results in reversible co-suppression of homologous genes *in trans*. *Plant Cell* **2**: 279–289.

National Academies of Sciences Engineering and Medicine. 2016. *Genetically engineered crops: experiences and prospects*. Washington, DC, USA: The National Academies Press.

National Security Commission on Emerging Biotechnology. 2023. *New Report December 2023*. [WWW document] URL https://www.biotech.senate.gov/press-releases/interim-report/ [accessed 16 May 2024].

Nature Plants. 2023. EU rethinks genome editing. *Nature Plants* **9**: 1169–1170.

Newhouse AE, Powell WA. 2021. Intentional introgression of a blight tolerance transgene to rescue the remnant population of American chestnut. *Conservation Science and Practice* **3**: e348.

Oyarce P, De Meester B, Fonseca F, de Vries L, Goeminne G, Pallidis A, De Rycke R, Tsuji Y, Li Y, Van den Bosch S *et al.* 2019. Introducing curcumin biosynthesis in *Arabidopsis* enhances lignocellulosic biomass processing. *Nature Plants* **5**: 225–237.

Pilate G, Guiney E, Holt K, Petit-Conil M, Lapierre C, Leplé J-C, Pollet B, Mila I, Webster EA, Marstorp HG *et al.* 2002. Field and pulping performances of transgenic trees with altered lignification. *Nature Biotechnology* **20**: 607–612.

Rottmann WH, Meilan R, Sheppard LA, Brunner AM, Skinner JS, Ma C, Cheng S, Jouanin L, Pilate G, Strauss SH. 2000. Diverse effects of overexpression of *LEAFY* and *PTLF*, a poplar (*Populus*) homolog of *LEAFY/FLORICAULA*, in transgenic poplar and *Arabidopsis*. *The Plant Journal* **22**: 235–245.

Ryan NW. 2022. *Overexpression of the GROWTH REGULATING FACTOR 4-GRF-INTERACTING FACTOR 1 Transcription Factor Chimera Modifies Transformation and Regeneration Efficiency in Populus and Eucalyptus*. [WWW document] URL https://ir.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/s4655q40j [accessed 16 May 2024].

Saleme MLS, Cesarino I, Vargas L, Kim H, Vanholme R, Goeminne G, Van Acker R, Fonseca FCA, Pallidis A, Voorend W *et al.* 2017. Silencing *CAFFEOYL SHIKIMATE ESTERASE* affects lignification and improves saccharification in poplar. *Plant Physiology* **175**: 1040–1057.

Sibout R, Le Bris P, Legée F, Cézard L, Renault H, Lapierre C. 2016. Structural redesigning arabidopsis lignins into alkali-soluble lignins through the expression of *p*-coumaroyl-CoA:monolignol transferase PMT. *Plant Physiology* **170**: 1358–1366.

Simmons CR, Lafitte HR, Reimann KS, Brugière N, Roesler K, Albertsen MC, Greene TW, Habben JE. 2021. Successes and insights of an industry biotech program to enhance maize agronomic traits. *Plant Science* **307**: 110899.

Smolker R, Petermann A. 2019. *The GMO American chestnut*. [WWW document] URL https://portside.org/2019-08-10/gmo-american-chestnut [accessed 16 May 2024].

Smyth SJ. 2019. Global status of the regulation of genome editing technologies. *CABI Reviews* **14**: 1–6.

Stokstad E. 2023. *EPA decision to tighten oversight of gene-edited crops draws mixed response. Scienceinsider.* [WWW document] URL https://www.science.org/content/article/epa-decision-tighten-oversight-gene-edited-crops-draws-mixed-response [accessed 16 May 2024].

Strauss SH, Boerjan W, Chiang V, Costanza A, Coleman H, Davis JM, Lu MZ, Mansfield SD, Merkle S, Myburg A *et al.* 2019. Certification for gene-edited forests. *Science* **365**: 767–768.

Strauss SH, Jones KN, Lu H, Petit JD, Klocko AL, Betts MG, Brosi BJ, Fletcher RJ Jr, Needham MD. 2017. Reproductive modification in forest plantations: impacts on biodiversity and society. *New Phytologist* **213**: 1000–1021.

Strauss SH, Kershen DL, Bouton JH, Redick TP, Tan H, Sedjo RA. 2010. Far-reaching deleterious impacts of regulations on research and environmental studies of recombinant DNA-modified perennial biofuel crops in the United States. *Bioscience* **60**: 729–741.

Strauss SH, Ma C, Ault K, Klocko AL. 2016. Lessons from two decades of field trials with genetically modified trees in the USA: biology and regulatory compliance. *Forestry Sciences* **82**: 101–124.

Strauss SH, Slavov GT, DiFazio SP. 2022. Gene-editing for production traits in forest trees: challenges to integration and gene target identification. *Forests* **13**: 1887.

Strauss SS (2003) Genetic technologies. Genomics, genetic engineering, and domestication of crops. *Science* **300**: 61–62.

© 2024 The Authors
New Phytologist © 2024 New Phytologist Foundation

14698137, 2024, 2, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.19855 by Capes, Wiley Online Library on [10/02/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Studer MH, DeMartini JD, Davis MF, Sykes RW, Davison B, Keller M, Tuskan GA, Wyman CE. 2011. Lignin content in natural *Populus* variants affects sugar release. *Proceedings of the National Academy of Sciences, USA* **108**: 6300–6305.

Sulis DB, Jiang X, Yang C, Marques BM, Matthews ML, Miller Z, Lan K, Cofre-Vega C, Liu B, Sun R *et al.* 2023. Multiplex CRISPR editing of wood for sustainable fiber production. *Science* **381**: 216–221.

Sun S, Han X, Jin R, Jiao J, Wang J, Niu S, Yang Z, Wu D, Wang Y. 2024. Generation of CRISPR-edited birch plants without DNA integration using *Agrobacterium*-mediated transformation technology. *Plant Science* **342**: 112029.

Turnbull C, Lillemo M, Hvoslef-Eide TAK. 2021. Global regulation of genetically modified crops amid the gene edited crop boom – a review. *Frontiers in Plant Science* **12**: 630396.

Van Acker R, Déjardin A, Desmet S, Hoengenaert L, Vanholme R, Morreel K, Laurans F, Kim H, Santoro N, Foster C *et al.* 2017. Different routes for conifer- and sinapaldehyde and higher saccharification upon deficiency in the dehydrogenase CAD1. *Plant Physiology* **175**: 1018–1039.

Van Acker R, Leplé J-C, Aerts D, Storme V, Goeminne G, Ivens B, Légée F, Lapierre C, Piens K, Van Montagu MCE *et al.* 2014. Improved saccharification and ethanol yield from field-grown transgenic poplar deficient in cinnamoyl-CoA reductase. *Proceedings of the National Academy of Sciences, USA* **111**: 845–850.

Van den Bosch S, Schutyser W, Vanholme R, Driessen T, Koelewijn S-F, Renders T, De Meester B, Huijgen WJJ, Dehaen W, Courtin C *et al.* 2015. Reductive lignocellulose fractionation into soluble lignin-derived phenolic monomers and dimers and processable carbohydrate pulps. *Energy & Environmental Science* **8**: 1748–1763.

Van Doorsselaere J, Baucher M, Chognot E, Chabbert B, Tollier MT, Petit-Conil M, Leplé JC, Pilate G, Cornu D, Monties B *et al.* 1995. A novel lignin in poplar trees with a reduced caffeic acid/5-hydroxyferulic acid *O*-methyltransferase activity. *The Plant Journal* **8**: 855–864.

Vanholme B, Cesarino I, Goeminne G, Kim H, Marroni F, Van Acker R, Vanholme R, Morreel K, Ivens B, Pinosio S *et al.* 2013. Breeding with rare defective alleles (BRDA): a natural *Populus nigra* HCT mutant with modified lignin as a case study. *New Phytologist* **198**: 765–776.

Viswanath V, Albrectsen BR, Strauss SH. 2012. Global regulatory burden for field testing of genetically modified trees. *Tree Genetics & Genomes* **8**: 221–226.

de Vries L, Guevara-Rozo S, Cho M, Liu L-Y, Renneckar S, Mansfield SD. 2021. Tailoring renewable materials via plant biotechnology. *Biotechnology for Biofuels* **14**: 167.

Wang N, Ryan L, Sardesai N, Wu E, Lenderts B, Lowe K, Che P, Anand A, Worden A, van Dyk D *et al.* 2023. Leaf transformation for efficient random integration and targeted genome modification in maize and sorghum. *Nature Plants* **9**: 255–270.

White TL, Adams WT, Neale DB. 2007. *Forest genetics*. London, UK: CAB International.

Wilkerson CG, Mansfield SD, Lu F, Withers S, Park J-Y, Karlen SD, Gonzales-Vigil E, Padmakshan D, Unda F, Rencoret J *et al.* 2014. Monolignol ferulate transferase introduces chemically labile linkages into the lignin backbone. *Science* **344**: 90–93.

Yamamoto M, Tomiyama H, Koyama A, Okuizumi H, Liu S, Vanholme R, Goeminne G, Hirai Y, Shi H, Nuoendagula *et al.* 2020. A century-old mystery unveiled: Sekizaisou is a natural lignin mutant. *Plant Physiology* **182**: 1821–1828.

Zhou XH, Jacobs TB, Xue L-J, Harding SA, Tsai C-J. 2015. Exploiting SNPs for biallelic CRISPR mutations in the outcrossing woody perennial *Populus* reveals 4-coumarate:CoA ligase specificity and redundancy. *New Phytologist* **208**: 298–301.

Zhu Y, Li L. 2024. Wood of trees: Cellular structure, molecular formation, and genetic engineering. *Journal of Integrative Plant Biololgy* **66**: 443–467.

Key words: field trials, forestry, gene-editing, lignin, *Populus*, regeneration, regulation, transgenes.

Received, 1 February 2024; accepted, 30 April 2024.

© 2024 The Authors
New Phytologist © 2024 New Phytologist Foundation

14698137, 2024, 2, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.19655 by Capes, Wiley Online Library on [10/02/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Earth Systems and Environment
https://doi.org/10.1007/s41748-026-01319-9

ORIGINAL ARTICLE

Global Risks and Vulnerabilities of Eucalyptus Plantations Under 1.5 to 4 °C Global Warming Levels

Flávia Fernanda Azevedo Fagundes[1] · **Fabrina Bolzan Martins**[1]

Received: 2 April 2026 / Revised: 30 June 2026 / Accepted: 3 July 2026
© The Author(s) 2026

Abstract

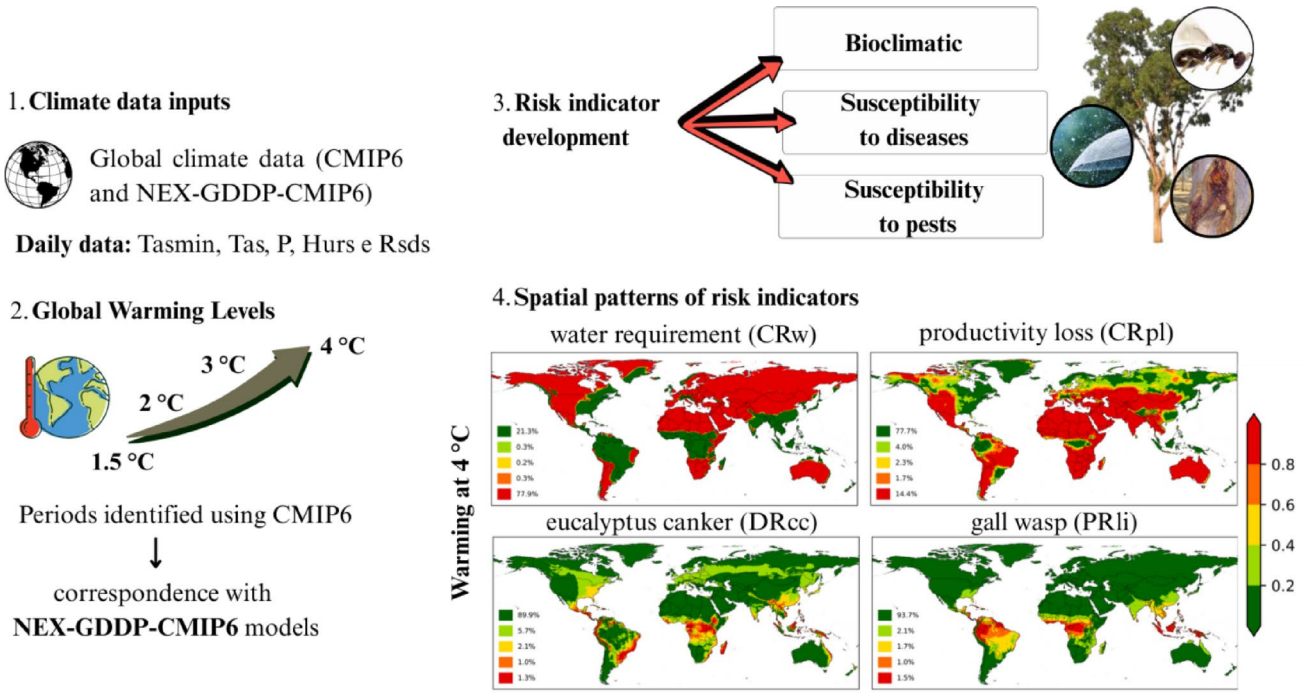
The vulnerability of forest plantations to climate change threatens global forest production, particularly as current climate commitments are unlikely to limit global warming to 1.5 °C. Developing risk indicators is essential to quantify vulnerabilities and anticipate potential losses in Eucalyptus plantations. This study developed and applied twenty-one Eucalyptus-specific bioclimatic, pests and diseases risk indicators across four global warming levels (GWLs, 1.5 °C to 4 °C). The analysis was based on high-resolution simulations (1995–2014) and projections (2015–2100) from 23 General Circulation Models from the NASA Earth Exchange Global Daily Downscaled Projections (NEX-GDDP-CMIP6), under Shared Socioeconomic Pathways SSP2-4.5 and SSP5-8.5. Daily near-surface air temperature, accumulated precipitation, relative humidity, and global solar radiation were used to calculate all indicators for a control period (1995–2014) and for time slices corresponding to each warming level. Indicators were subsequently classified into five risk levels ranging from very low to very high. Climate-driven changes in temperature, precipitation, humidity, and radiation produced broadly similar risk types across regions, differing in magnitude and spatial extent. Globally, the highest risks were associated with productivity loss (77.7–80.2% of the global area), water requirement (~78%), water stress (~8.5%), gall wasp infestation (~3%), and eucalyptus canker (~1.3%). Although phytosanitary risks affected smaller areas, they were concentrated in major eucalyptus-producing regions across South America, Africa, Asia, Europe, and Oceania. These findings underscore the need to integrate climate risk into forest planning and management and to strengthen genetic improvement and biological control strategies to enhance resilience under progressive warming.

✉ Fabrina Bolzan Martins
fabrina@unifei.edu.br

[1] Natural Resources Institute, Federal University of Itajubá, Itajubá 37500-903C.P. 50, Minas Gerais, Brazil

Published online: 15 July 2026

Graphical Abstract



The graphical abstract presents the global risks and vulnerabilities of eucalyptus plantations under four global warming levels (GWLs). The study first identified the years at which each GWL was reached using CMIP6 General Circulation Models (GCMs). These years were subsequently linked to their high-resolution counterparts from the NEX-GDDP-CMIP6 dataset. A total of 21 indicators were developed and analyzed to quantify climate and phytosanitary risks to eucalyptus plantations at the global scale across all GWLs (1.5 °C to 4 °C). In addition, key adaptation measures were identified to mitigate these risks based on high-resolution climate projections. The results indicate that the greatest risks were associated with productivity loss (77.7–80.2% of the area), water requirement (~78%), water stress (~8.5%), gall wasp infestation (~3%), and eucalyptus canker (~1.3%). Although phytosanitary risks affected smaller areas, they were concentrated in major eucalyptus-producing regions across South America, Africa, Asia, Europe, and Oceania. These findings underscore the need to integrate climate risk into forest planning and management and to strengthen genetic improvement and biological control strategies to enhance resilience under progressive warming.

Highlights

- Proposal of 21 bioclimatic, pest and disease risk indicators for Eucalyptus.
- Assessment of 21 risk indicators across four global warming levels (1.5 to 4 °C).
- Productivity loss and water requirement pose the highest bioclimatic risks (~77.8% worldwide).
- *Chrysoporthe cubensis* poses the highest disease susceptibility risk (~1.5% worldwide).
- *Leptocybe invasa* poses the highest pest susceptibility risk (~1.3% worldwide).

Keywords Paris agreement · NEX-GDDP-CMIP6 · Risk indicators · Eucalyptus diseases · Eucalyptus pests

Abbreviations

AE	Actual evapotranspiration
AWC	Available soil water capacity
BECCS	Bioenergy with carbon capture and storage
CMIP5	Coupled model intercomparison project phase 5
CMIP6	Coupled model intercomparison project phase 6
CP	Control period
CRbt	Basal temperature indicator
CRfrost	Frost stress indicator
CRpl	Productivity loss indicator
CRw	Water requirement indicator
CRws	Water stress indicator
DRcc	Eucalyptus canker susceptibility indicator
DRce	Leaf spot susceptibility indicator for

	Cryptosporiopsis eucalypti
DRcf	Leaf spot susceptibility indicator for Ceratocystis fimbriata
DRcy	Leaf spot susceptibility indicator for Cylindrocladium spp
DRns	Pink disease susceptibility indicator
DRpp	Eucalyptus rust susceptibility indicator
DRqe	Leaf spot susceptibility indicator for Quambalaria eucalypti
DRtm	Leaf spot susceptibility indicator for Teratosphaeria sp. and Mycosphaerella spp
ETc	Crop evapotranspiration
ETo	Reference evapotranspiration
FAO	Food and agriculture organization
GCM	General circulation models
GLDAS-2	Global land data assimilation system version 2
GWL	Global warming levels
Hurs	Near-surface relative humidity
Kc	Crop coefficient
Ky	Water stress sensitivity index
LAI	Leaf area index
LDAS	Land data assimilation system
NCCS	NASA center for climate simulation
NEX-GDDP	NASA earth exchange global daily downscaled projections
P	Accumulated precipitation
P_{annual}	Annual accumulated precipitation
P_{month}	Month accumulated precipitation
PRbo	Eucalyptus shoot psyllid susceptibility indicator
PRce	Eucalyptus psyllid susceptibility indicator
PRgb	Red gum lerp psyllid susceptibility indicator
PRgp	Eucalyptus weevil susceptibility indicator
PRli	Gall wasp susceptibility indicator (Leptocybe invasa)
PRmp	Autumn gum moth susceptibility indicator
PRom	Gall wasp susceptibility indicator (Ophelimus maskelli)
PRtp	Bronze bug susceptibility indicator
Riskn	Normalized value of the indicator
Rsds	Global solar radiation
SSP	Shared socioeconomic pathways
SWB	Soil water balance
SWHC	Soil water holding capacity
Tas	Mean near-surface air temperature
Tasmin	Minimum near-surface air temperature
WD	Water deficit
WD_{annual}	Annual accumulated water deficit
Zr	Root depth

1 Introduction

Climate change poses a threat to forest ecosystems, including *Eucalyptus* spp. plantations, which represent the most relevant genus for the global forest sector due to their rapid growth, relative edaphoclimatic adaptability, and broad economic versatility (Florêncio et al. 2022; Martins et al. 2022; Fagundes et al. 2025). Beyond their central role in timber, pulp, and paper production, Eucalyptus plantations have also emerged as a strategic source of biomass for Bioenergy with Carbon Capture and Storage (BECCS) systems, for mitigating greenhouse gas emissions (Bacani et al. 2024). Consequently, Eucalyptus plays an important role in the global bioeconomy, particularly in countries with extensive plantation areas, such as Brazil (~8.1 million hectares; IBÁ 2025), China (~5.5 million ha; Xu et al. 2019), India (~4.3 million ha; Hoogar et al. 2019), and Australia (~1.6 million ha; National Forest Inventory Steering Committee, 2019).

The wide geographic distribution of Eucalyptus plantations, combined with the increase in global mean temperature of 0.99 °C (0.84–1.10 °C) since the pre-industrial period (IPCC 2021), and changes in precipitation patterns, solar radiation, and moisture fluxes (Almazroui et al. 2020a, b; Penna et al. 2021; Ruv Lemes et al. 2023), make the genus particularly vulnerable to climate change, amplifying risks to cultivation across diverse regions worldwide.

Despite advances in silvicultural practices and phytosanitary control, Eucalyptus productivity remains intrinsically constrained by climate variability (Gonçalves et al. 2017; Florêncio et al. 2022; Martins et al. 2022). Prolonged water stress when coupled with temperatures exceeding suitable physiological thresholds (8.5 °C to ~40 °C) (Florêncio et al. 2022), reduces growth potential (Elli et al. 2020; Martins et al. 2022) and increases susceptibility to diseases and pests, potentially leading to mortality (Mota et al. 2022). For example, under global warming scenarios, the relative abundance of forest pests may triple (Delgado-Baquerizo et al. 2020), while also favoring the emergence and spread of pathogenic organisms (Deidda et al. 2016; Mota et al. 2023; Silva and Asiegbu 2023).

Among the most damaging Eucalyptus diseases worldwide are eucalyptus canker, eucalyptus rust, leaf spot and pink disease (Alfenas et al. 2009). Major insect pests include bronze bug, gall wasps, eucalyptus weevils, red gum lerp psyllids, autumn gum moths, eucalyptus psyllid and eucalyptus shoot psyllid (Lemes et al. 2021; Mota et al. 2023).

The economic and productive impacts of these threats are already evident across major eucalyptus-producing countries. In Brazil, eucalyptus rust can reduce annual increment by up to 30% (Auer et al. 2010). In parts of Europe, severe defoliation caused by eucalyptus weevils has resulted in timber losses exceeding 80% in heavily affected stands, with associated economic impacts of ~US$ 251.45 million per year (Ayuga-Téllez et al. 2022). In Asia and North America, psyllids and gall wasps have caused leaf area loss and growth reduction, leading to economic losses exceeding US$ 20 million, and in countries like Israel, Thailand, and China, to the interruption of *Eucalyptus camaldulensis* cultivation (Santana et al. 2005; Kulkarni 2010; Petro et al. 2015).

Given the high vulnerability of Eucalyptus plantations to climate change, which is expected to intensify under increasing Global Warming Levels (GWLs), the development of tools capable of anticipating risks and supporting adaptation measures is imperative. Risk indicators provide a robust framework for characterizing the magnitude, spatial distribution, severity, and temporal evolution of risks (Walsh et al. 2020; Dias et al. 2024; Xavier et al. 2026), and are typically designed based on the specific requirements of each crop (Dias et al. 2024; Ferreira et al. 2021; Xavier et al. 2026). For Eucalyptus plantations, however, such indicators have not yet been established. Their development should integrate bioclimatic constraints along with susceptibility to diseases and pests, which are key drivers of economic losses and are strongly modulated by climatic conditions (Dias et al. 2024).

The need for eucalyptus-specific risk indicators is further underscored by the temperature targets established under the Paris Agreement, which aims to limit global warming to 1.5–2 °C above pre-industrial levels (UNFCCC 2015). Warming beyond these thresholds may compromise forest resilience, intensify phytosanitary pressures, and reduce the adaptive capacity of commercially important *Eucalyptus* species (Torres et al. 2021; Fagundes et al. 2025). In this context, the GWL framework provides a standardized approach for assessing climate change impacts across different warming thresholds and supporting adaptation planning in the global forestry sector (Betts et al. 2018).

For these reasons, assessing risks to Eucalyptus across different GWLs (1.5 °C to 4 °C) is essential to support climate-resilient forest planning and to underpin adaptation measures aimed at reducing vulnerabilities and economic losses. Despite its importance, the impacts of the GWLs established under the Paris Agreement have not yet been assessed using risk indicators tailored to eucalyptus plantations. Existing studies have focused primarily on temperature, precipitation, or water availability under different GWLs (Mba et al. 2018; Yaduvanshi et al. 2019; Martins et al. 2022; Fagundes et al. 2025), with most analyses relying on projections from the Coupled Model Intercomparison Project Phase 5 (CMIP5). Only a limited number of studies have employed CMIP6 datasets, and none has assessed eucalyptus-specific climatic and phytosanitary risks using high-resolution climate models such as the NASA Earth Exchange Global Daily Downscaled Projections (NEX-GDDP-CMIP6). These datasets provide an improved representation of regional climate variability and enable a more detailed assessment of spatial risk patterns (Fagundes et al. 2025). Against this background, this study seeks to fill knowledge gaps by testing the hypothesis that progressive increases in GWLs may amplify risks and vulnerabilities, leading to heterogeneous impacts across major eucalyptus-producing regions. Accordingly, the aims of this work were to (i) propose and analyze indicators to quantify climate and phytosanitary risks to eucalyptus plantations at the global scale across GWLs (1.5 °C to 4 °C), and (ii) identify the key adaptation measures to address these risks by integrating specific indicators with high-resolution GCMs (NEX-GDDP-CMIP6).

2 Data and Methods

2.1 Climate Data and Obtaining Global Warming Thresholds

Daily near-surface minimum (Tasmin, °C) and mean (Tas, °C) air temperature, accumulated precipitation (P, mm day^{-1}), near-surface relative humidity (Hurs, %), and global solar radiation (Rsds, MJ m^{-2} day^{-1}) were obtained from ensemble simulations for the control period (CP, 1995–2014) and projections (2015–2100) from 23 high-spatial-resolution GCMs (0.25° latitude × longitude) from the NEX-GDDP-CMIP6 (Table S1). Although this spatial resolution is relatively high for global climate model projections, it may still be insufficient to accurately represent microclimatic conditions and climate refugia in mountainous regions and areas with complex topography (Thrasher et al. 2022). These GCMs were selected following Fagundes et al. (2025) based on two criteria: (i) availability of daily data for all required variables, and (ii) adoption of a standard 365-day calendar (no leap years), ensuring temporal consistency. These data are provided by the Climate Analytics Group and the NASA Ames Research Center and are made available by the NASA Center for Climate Simulation (NCCS) at: https://www.nccs.nasa.gov/services/data-collections/land-based-products/nex-gddp-cmip6.

The NEX-GGDP-CMIP6 GCMs are derived from the CMIP6 outputs with a statistical downscaling approach (Thrasher et al. 2022), forced by combined socioeconomic

Table 1 Bioclimatic ranges used in each eucalyptus risk indicator

Category	Indicator	Scientific name	Abbreviation	Bioclimatic ranges	References
Bioclimatic	Water requirement		CRw	Number of years with: $P_{annual} \leq 900$ mm year^{-1}	Flores et al. (2016)
	Water stress		CRws	Number of years with: $WD_{annual} > 330$ mm year^{-1}	Fagundes et al. (2025)
	Basal temperature stress		CRbt	Number of days with: Tas ≤ 8.5 °C or Tas ≥ 38. °C	Martins and Streck (2007); Florêncio et al. (2022)
	Frost stress		CRfrost	Number of days with: Tasmin ≤ 4.0 °C	Dias et al. (2024)
	Productivity loss		CRpl	Productivity loss (between 0 and 1), obtained by Eq. (1)	Rao et al. (1988); Ferreira et al. (2021); Dias et al. (2024)
Susceptibility to diseases	Eucalyptus canker	*Chrysoporthe cubensis* (Bruner) Gryzenhout & M.J. Wingf.	DRcc	Number of days with: 27 °C ≤ Tas ≤ 33 °C	Souza et al. (2010)
				Hurs ≥ 75%	Soares et al. (2018)
	Eucalyptus rust	*Puccinia psidii* Winter	DRpp	Number of days with: 18 °C ≤ Tas ≤ 25 °C	Alfenas et al. (2009)
				Hurs ≥ 75%	Dias et al. (2024)
	Leaf spot diseases	*Teratosphaeria* sp. and *Mycosphaerella* spp.	DRtm	Number of days with: 15 °C ≤ Tas ≤ 25 °C	Alfenas et al. (2009)
				Hurs ≥ 75%	Jacome et al. (1991)
		Cryptosporiopsis eucalypti Sankaran & B. Sutton	DRce	Number of days with: 23 °C ≤ Tas ≤ 30 °C	Old et al. (2002)
				Hurs ≥ 75%	
		Cylindrocladium spp.	DRcy	Number of days with: 20 °C ≤ Tas ≤ 30 °C	Sharma and Mohanan (1991)
				Hurs ≥ 75%	
		Quambalaria eucalypti (M.J. Wingf., Crous & W.J. Swart) J.A. Simpson	DRqe	Number of days with: 20 °C ≤ Tas ≤ 30 °C	Alfenas et al. (2009)
				Hurs ≥ 75%	Pegg et al. (2009)
		Ceratocystis fimbriata Ellis & Halsted	DRcf	Number of days with: 20 °C ≤ Tas ≤ 25 °C	Piveta 2013
				Hurs ≥ 70%	Ahmad et al. (2022)
	Pink disease	*Necator salmonicolor* (Berk. & Broome) K.H. Larss.	DRns	Number of days with: 20 °C ≤ Tas ≤ 28 °C	Akrofi et al. (2014) Nomi et al. (2000)
				Hurs ≥ 75%	
Susceptibility to pests	Bronze bug	*Thaumastocoris peregrinus* Carpintero & Dellapé	PRtp	Number of days with: 18 °C ≤ Tas ≤ 25 °C	Barbosa et al. (2019)
				Hurs ≥ 70%	
	Gall wasps	*Leptocybe invasa* Fisher & LaSalle	PRli	Number of days with: 18 °C ≤ Tas ≤ 30 °C	Garlet el al. (2013)
				Hurs ≥ 65%	Puretz et al. (2015)
		Ophelimus maskelli (Ashmead)	PRom	Number of days with: 24 °C ≤ Tas ≤ 26 °C	Protasov et al. (2007)
				Hurs ≥ 65%	
	Eucalyptus weevil	*Gonipterus platensis* Marelli and *Gonipterus pulverulentus* Lea	PRgp	Number of days with: 20 °C ≤ Tas ≤ 25 °C	Souza et al. (2021)
				Hurs ≥ 70%	
	Red gum lerp psyllid	*Glycaspis brimblecombei* Moore	PRgb	Number of days with: 22 °C ≤ Tas ≤ 26 °C	Lemes et al. (2021)
				Hurs ≤ 65%	

Table 1 (continued)

Category	Indicator	Scientific name	Abbreviation	Bioclimatic ranges	References
	Autumn gum moth	*Mnesampela privata* (Guenée)	PRmp	Number of days with: 24 °C ≤ Tas ≤ 30 °C	Steinbauer et al. (2004)
				Hurs ≥ 70%	Walker and Allen (2011)
	Eucalyptus psyllid	*Ctenarytaina eucalypti* (Maskell)	PRce	Number of days with: 20 °C ≤ Tas ≤ 25 °C	Purvis et al. (2002)
				Hurs ≥ 70%	Azevedo and Figo (1979)
	Eucalyptus shoot psyllid	*Blastopsylla occidentalis* Taylor	PRbo	Number of days with: 20 °C ≤ Tas ≤ 25 °C	Künast et al. (2021)
				Hurs ≥ 70%	Queiroz et al. (2020)

CRw = water requirement indicator (dimensionless); P_{annual} = annual accumulated precipitation (mm $year^{-1}$); CRws = water stress indicator (dimensionless); WD_{annual} = annual water deficit (mm $year^{-1}$); CRbt = basal temperature indicator (dimensionless); Tas = daily mean air temperature (°C); CRfrost = frost stress indicator (dimensionless); Tasmin = daily minimum air temperature (°C); CRpl = productivity loss indicator (dimensionless); DRcc = eucalyptus canker susceptibility indicator; DRpp = eucalyptus rust susceptibility indicator; DRtm = leaf spot susceptibility indicator for *Teratosphaeria* sp. and *Mycosphaerella* spp.; DRce = leaf spot susceptibility indicator for *Cryptosporiopsis eucalypti*; DRcy = leaf spot susceptibility indicator for *Cylindrocladium* spp.; DRqe = leaf spot susceptibility indicator for *Quambalaria eucalypti*; DRcf = leaf spot susceptibility indicator for *Ceratocystis fimbriata*; and DRns = pink disease susceptibility indicator; Hurs = near-surface relative humidity (%); PRtp = bronze bug susceptibility indicator; PRli and PRom = gall wasp susceptibility indicator; PRgp, eucalyptus weevil susceptibility indicator; PRgb = red gum lerp psyllid susceptibility indicator; PRmp = autumn gum moth susceptibility indicator; PRce = eucalyptus psyllid susceptibility indicator and PRbo = eucalyptus shoot psyllid susceptibility indicator

and radiative forcing scenarios (called Shared Socioeconomic Pathways, SSPs) (Thrasher et al. 2022). In this study, two SSPs were used: SSP2-4.5 ("middle of the road") and SSP5-8.5 ("fossil-fueled development"). SSP2-4.5 is an intermediate scenario assuming stabilization of emission rates relative to pre-industrial levels, resulting in a radiative forcing of 4.5 W m^{-2} and an atmospheric CO_2 concentration of ~600 ppm by 2100 (Riahi et al. 2017; Nazarenko et al. 2022). In contrast, SSP5-8.5 is a pessimistic scenario in which mitigation efforts are largely neglected, leading to a fossil-fuel-driven socioeconomic trajectory with a radiative forcing reaching 8.5 W m^{-2} and a CO_2 concentration of ~1100 ppm by 2100 (Riahi et al. 2017; Nazarenko et al. 2022).

Fagundes et al. (2025) established global warming periods from 1.5 °C to 4 °C relative to pre-industrial levels. In this study, these warming periods were adopted to calculate Eucalyptus risk indicators. Accordingly, each indicator used in this study (described in Sect. 2.2) was calculated for two periods: (i) the CP (1995–2014); and (ii) the periods in which projections reached the four GWLs (1.5–4 °C) under each SSP (SSP2-4.5 and SSP5-8.5).

It is important to note that the NEX-GDDP-CMIP6 GCMs do not include simulations for the pre-industrial period (1850–1900) and do not provide global coverage (e.g., absence of data for latitudes > 60°S). For this reason, GWLs were determined using the corresponding 23 CMIP6 GCMs and subsequently associated with their respective NEX-GDDP-CMIP6 GCMs. This approach follows the recommendations of Samuel et al. (2023) and Fagundes et al. (2025).

To identify the periods corresponding to the occurrence of the 1.5 °C to 4 °C GWLs relative to the pre-industrial period (1850–1900), a sequence of steps described in Fagundes et al. (2025) was followed. First, annual mean air temperature time series were calculated from daily air temperature data for each GCM and SSP over the period 1850–2100. Second, a climatological mean for the pre-industrial period (1850–1900) was calculated for each GCM, and annual temperature anomalies were obtained by subtracting the respective pre-industrial climatology from the annual values of each GCM. To remove short-term climate variability, a centered 21-year moving average was applied to the anomaly series, resulting in smoothed anomalies spanning 1860–2090. Finally, the years in which each GWL (1.5 °C, 2 °C, 3 °C, and 4 °C) was reached were identified by computing a global spatial mean of the smoothed annual anomaly series for each GCM and SSP.

For the spatial analysis, the ensemble mean of all available projections within each SSP was calculated using the smoothed annual anomaly series for each GCM in the year when the respective GWL was reached, and subsequently an ensemble mean of the projections for the two SSPs (SSP2-4.5 and SSP5-8.5) was obtained.

Spatial patterns of Tasmin, P, Hurs, and Rsds were also analyzed, as these variables serve as inputs for the Eucalyptus risk indicators (described in Sect. 2.2). The same procedure described above was applied, except for the calculation of the global mean, which is unnecessary for these variables, as described in Torres et al. (2021) and Fagundes et al. (2025).

Table 2 Water stress sensitivity index (Ky, dimensionless) values for the eucalyptus

Ky values (dimensionless)	
Months	Average Ky values
1	1.4
10	1.3
30	1.7
60	1.3
84	1.0

* Adapted from Freitas et al. (2020). Ky values were obtained from the arithmetic mean across eucalyptus clones reported by Freitas et al. (2020)

2.2 Development of Risk Indicators for Eucalyptus Plantations

A total of 21 risk indicators were developed, based on three categories: (i) bioclimatic indicators, including water requirement (CRw), water stress (CRws), basal temperature stress (CRbt) and frost stress (CRfrost), and productivity loss (CRpl); (ii) disease susceptibility indicators, including eucalyptus canker (DRcc), eucalyptus rust (DRpp), leaf spot diseases (DRtm, DRce, DRcy, DRqe, DRcf), and pink disease (DRns); and (iii) pest susceptibility indicators, including bronze bug (PRtp), gall wasps (PRli and PRom), eucalyptus weevil (PRgp), red gum lerp psyllid (PRgb), autumn gum moth (PRmp), eucalyptus psyllid (PRce), and eucalyptus shoot psyllid (PRbo). All threshold ranges for each indicator were defined based on an extensive literature review (Table 1).

All indicators, except CRw, CRws, and CRpl, were calculated on a daily basis for two periods: (i) the CP (1995–2014); and (ii) the periods in which the projections reached the four GWLs (1.5–4 °C) under each SSP (SSP2-4.5 and SSP5-8.5), as described in Sect. 2.1. The CRw, CRws, and CRpl indicators were obtained on an annual basis. For period (ii), the mean central warming year of each GWL (Table S2) was considered, obtained by averaging the years of occurrence across the 23 GCMs from both SSPs, along with a ± 10-year time window centered on this central year. The CRpl indicator provides productivity loss due to soil water deficit (Dias et al. 2024), provided by (Rao et al. 1988):

$$\mathrm{CRpl} = 1 - \prod {}^{\mathrm{n}}_{\mathrm{i}=1} \left[1 - \mathrm{Ky}^{*} \left(1 - \frac{\mathrm{AE}}{\mathrm{ETc}} \right) \right] \quad (1)$$

Where: CRpl = productivity loss indicator (dimensionless), ∏ = product operator, i= months of the control period (CP, 1995–2014) and the periods (central year ± 10 years) in which the projections reached each GWL (1.5–4 °C), from January (1st month) to December (12th month); n = total eucalyptus rotation length (84 months); Ky = eucalyptus-specific water stress sensitivity index (Table 2) (dimensionless), AE = monthly actual evapotranspiration (mm month^{-1}) and ETc = monthly crop evapotranspiration (mm month^{-1}). ETc and AE values were obtained from the soil water balance (described in Sect. 2.3).

2.3 Soil Water Balance and Crop Evapotranspiration

The soil water balance (SWB) was calculated using the modified version of the Thornthwaite and Mather (1955, 1957) method, adopting the initial soil water storage conditions proposed by Dourado-Neto et al. (2010). This method quantifies actual evapotranspiration (AE) and water deficit (WD), which are subsequently used in the risk indicators (Table 1 and Eq. 1), under different climatic conditions (arid, semi-arid, and humid), and in regions with more than one dry season per year (Dias et al. 2024; Fagundes et al. 2025; Xavier et al. 2026).

The application of this method requires information on soil available water capacity (AWC, mm) and monthly accumulated precipitation ($P_{month;}$ mm month^{-1}) and crop evapotranspiration (ETc, mm month^{-1}).

AWC was obtained by the multiplying root depth (Zr, cm) by soil water holding capacity (SWHC, mm cm^{-1}) (described in Sect. 2.4). Root depth for eucalyptus varies along the growth stages (I = age, in months), being obtained by Freitas et al. (2020):

$$\mathrm{Zr} = \begin{cases} 10, & until\ I = 1st\ month \\ 85.264\ .\ln(\mathrm{I}) + 10, & for\ 1 < I \leq 30 \\ 300, & for\ 30 < I \leq 84 \end{cases} \quad (2)$$

Monthly precipitation and ETc were obtained from daily values and subsequently accumulated on a monthly basis for the CP and for the periods in which projections reached each GWL (1.5–4 °C). Here, these values were calculated for the mean central warming year of each GWL (across the 23 GCMs and SSPs; Table S1), using a ± 10-year time window centered on this central year. Detailed steps for calculating the SWB are provided in Dias et al. (2024).

Daily ETc was obtained by multiplying reference evapotranspiration (ETo, mm day^{-1}) and the crop coefficient (Kc) (Allen et al. 1998; Freitas et al. 2020). ETo was calculated using the Turc method (Turc 1961) (Eq. 3), due to its good performance across different regions worldwide, including Brazil (Monteiro et al. 2021), the United States (Lu et al. 2005), the Western Balkans (Trajkovic and Kolakovic 2009), China (Xu et al. 2012), India (Pandey et al. 2016), and Iran (Ahmadi and Javanbakht 2020), and because it requires input variables (Tas, Hurs, and Rsds) that are consistently available across the 23 NEX-GDDP-CMIP6 GCMs used in this study.

$$\mathrm{ETo} = (0.3107{*}\mathrm{Rsds} + 0.65) * \frac{\mathrm{Tas}{*}\mathrm{at}}{\mathrm{Tas} + 15}, \begin{cases} \mathrm{at} = 1 \text{ if Hurs} \geq 50\% \text{ or} \\ \mathrm{at} = 1 + \frac{50-\mathrm{Hurs}}{70} \text{ if Hurs} < 50\% \end{cases} \quad (3)$$

Where: ETo = reference evapotranspiration (mm day^{-1}); Rsds = global solar radiation (MJ m^{-2} day^{-1}); Tas = mean near-surface air temperature (°C); and Hurs = near-surface relative humidity (%).

The Eucalyptus Kc values vary according to growth stage, being obtained by (Freitas et al. 2020):

$$\mathrm{Kc} = \begin{cases} 0.5, & when \;\; LAI < 1.5 \\ 0.2011 \times \; LAI - 0.0075, & when \; LAI \geq \; 1.5 \end{cases} \quad (4)$$

Where: LAI = leaf area index = LAI = $\begin{cases} \frac{6.079071}{(1+(79.9335\,\exp(-0.29 \times \mathrm{I})))}, & I < 30\; month \\ 0.0006 \times \mathrm{I}^2 - 0.1191 \times I + 9.0042, & I \geq \; 30\; month \end{cases}$, I = age (in months).

2.4 Soil Water Holding Capacity Data

Soil water holding capacity (SWHC, mm cm^{-1}) data were obtained from soil texture information provided by the NASA Global Land Data Assimilation System Version 2 (GLDAS-2) through the Land Data Assimilation System (LDAS) portal. These data have a horizontal resolution compatible with the NEX-GDDP-CMIP6 GCMs (0.25° latitude/longitude) and encompass the 12 soil texture classes defined by the Food and Agriculture Organization of the United Nations (FAO), as well as organic matter, rock, and other categories. Soil texture classes were grouped into three main categories to represent different SWHC values (Abdu et al. 2008; Kadyampakeni and Morgan 2017; Dias et al. 2024): (i) clay soils with high SWHC (1.50 mm cm^{-1}); (ii) sandy-clay soils with intermediate SWHC (1.00 mm cm^{-1}); and (iii) sand-loam soils with low SWHC (0.60 mm cm^{-1}).

2.5 Normalization and Assessment of Risk Indicators Under Different Global Warming Levels

For evaluation and intercomparison purposes, all risk indicators, except CRfrost and CRpl, were normalized (Eq. 5), resulting in values ranging from 0 to 1 (Ferreira et al. 2021; Dias et al. 2024). Normalized values close to 0 indicate low risk, whereas values close to 1 indicate high risk, reflecting adverse conditions for eucalyptus plantations. CRfrost was not normalized because frost occurrence, especially during the first two years of the cycle (24 months), represents a high risk for eucalyptus (Freitas et al. 2020). CRpl was not normalized because its values range from 0 (no yield loss) to 1 (maximum yield loss).

$$\mathrm{Riskn_{ij}} = \frac{\mathrm{nd_{ij}} - \mathrm{n_{min}}}{\mathrm{n_{max}} - \mathrm{n_{min}}} \quad (5)$$

Where: $\mathrm{Riskn_{ij}}$ = normalized value of indicator *i* at the *j*-th grid cell (dimensionless and from 0 to 1), $\mathrm{nd_{ij}}$ = value of indicator *i* at the *j*-th grid cell, $\mathrm{n_{min}}$ = minimum possible value of indicator *i* (best situation = lowest risk), and $\mathrm{n_{max}}$ = maximum possible value of indicator *i* (worst situation = highest risk). The values of $\mathrm{nd_{ij}}$, $\mathrm{n_{min}}$ and $\mathrm{n_{max}}$ were obtained for the CP and for GWLs from 1.5 °C to 4 °C, considering the mean year of occurrence across the 23 GCMs and the two SSPs, and ± 10-year time window centered on this central year.

Normalized risk values were classified as (Dias et al. 2024; Xavier et al. 2026): very low risk when $\mathrm{Riskn_{ij}} \leq 0.2$; low risk when $0.2 < \mathrm{Riskn_{ij}} \leq 0.4$; moderate risk when $0.4 < \mathrm{Riskn_{ij}} \leq 0.6$; high risk when $0.6 < \mathrm{Riskn_{ij}} \leq 0.8$, and very high risk when $\mathrm{Riskn_{ij}} > 0.8$.

The assessment of projected changes in Eucalyptus risk indicators was conducted in two steps. First, the global spatial patterns of the NEX-GDDP-CMIP6 variables used as inputs for the indicators (Table 1) were evaluated: Tasmin, Tas, Tasmax, P, Hurs and Rsds. Second, global spatial patterns of each normalized risk indicator were analyzed for the CP and for the periods in which the four GWLs were reached. For spatial analysis, an integrated approach was adopted considering the ensemble mean of the SSPs (SSP2-4.5 and SSP5-8.5) and the GCMs that reached each GWL (Torres et al. 2021; Fagundes et al. 2025).

3 Results

3.1 Patterns of Changes in Input Variables Under Four GWLs

The analysis of changes in Tasmin and Tas relative to the CP indicates that under the 1.5 °C and 2 °C GWLs (Fig. 1a1–b2), increase from +0.5 °C to +2 °C occurs in localized areas of Brazil, large parts of the United States and Canada, northern and southern Africa, southern Europe, and much of Asia, extending to Australia under the 2 °C GWL. Under the 3 °C and 4 °C GWLs, these regions may experience substantially higher warming, with increases from +2.5 °C to +6 °C in Tasmin and Tas, particularly across the northern

high latitudes (>60 °N), including Alaska, Canada, Greenland, and extensive areas of northern Russia (Fig. 1a1–d2).

Spatial patterns of changes in annual accumulated precipitation (P_{annual}), Hurs, and Rsds reveal an increase of negative and positive anomalies under the 3 °C and 4 °C GWLs compared to the 1.5 °C and 2 °C GWLs (Fig. 1a3–d5). Although the overall spatial patterns remain broadly similar across GWLs, their magnitude increases substantially at higher warming levels. Negative P_{annual} changes (>−100 mm year^{-1}) are predominantly concentrated in tropical and subtropical regions, including portions of Central and South America, southern Europe, northern and southern Africa, and parts of Australia (Fig. 1a3–d3). Positive P_{annual} changes (>+150 mm year^{-1}) are projected mainly for high-latitude regions, including northern North America, Europe, and Asia, as well as Central Africa, the southern Asian regions influenced by the Asian monsoon system, and parts of Oceania, particularly Papua New Guinea and New Zealand (Fig. 1c3–d3).

Changes in Hurs generally mirror the responses observed for P_{annual}. Negative Hurs anomalies (>−4%) intensify in subtropical regions, particularly across South America, Central America and southern North America, northern and southern Africa, and south-central Europe, whereas positive anomalies (>+1%) occur mainly in humid tropical and

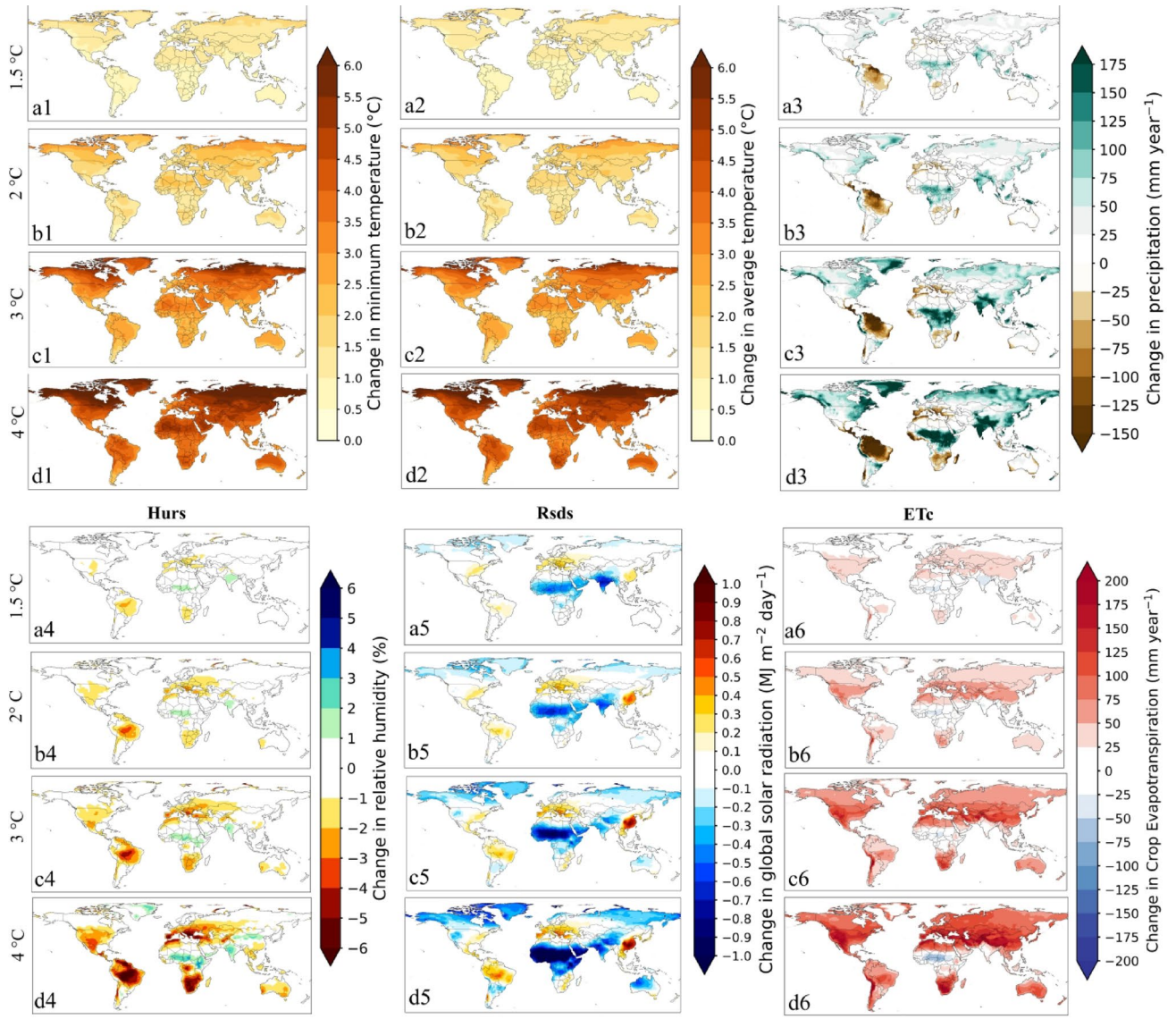


Fig. 1 Ensemble mean patterns of changes in minimum temperature (°C, panels **a1**–**d1**) and mean air temperature (°C, panels **a2**–**d2**), annual accumulated precipitation (mm year^{-1}, panels **a3**–**d3**), near-surface relative humidity (%, panels **a4**–**d4**), global solar radiation (MJ m^{-2} day^{-1}, panels **a5**–**d5**), and crop evapotranspiration (mm year^{-1}, panels **a6**–**d6**) for global warming levels of 1.5 °C (panels **a1**–**a6**), 2 °C (panels **b1**–**b6**), 3 °C (panels **c1**–**c6**), and 4 °C (panels **d1**–**d6**) relative to the control period (CP, 1995–2014). Ensemble mean was calculated using all GCMs that reached each warming threshold under the two socioeconomic scenarios (SSPs 2-4.5 and 5-8.5)

monsoon regions, including southern Asia and parts of Central Africa (Fig. 1a4–d4).

Regarding Rsds, heterogeneous changes are also observed, with more intense negative Rsds anomalies (>-1 MJ m^{-2} day^{-1}) across much of Africa (excluding the far north and southern Africa) and the Arabian Peninsula (Saudi Arabia, Yemen, and Oman) (Fig. 1d5), and less intense anomalies (between -0.1 and -0.4 MJ m^{-2} day^{-1}) occur in high-latitude regions of North America, Europe, and Asia, as well as in parts of South America, southwestern Asia, and Oceania. Positive Rsds anomalies ($>+0.2$ MJ m^{-2} day^{-1}) are projected primarily for tropical and subtropical regions, including north-central South America, eastern North America, south-central Europe, Southeast Asia, and parts of Australia, particularly under the 3 °C and 4 °C GWLs (Fig. 1d5).

Finally, areas exhibiting positive changes in ETc ($+25$ to $+125$ mm $year^{-1}$) expand progressively as GWLs increase from 1.5 °C to 4 °C (Fig. 1a6–d6), encompassing nearly the entire globe, except Greenland and central regions of Africa and India. Increases exceeding $+150$ mm $year^{-1}$ are predominantly observed in arid and semi-arid regions, including western North America, the Andes, northern and southern Africa, and southwestern Asia. Conversely, negative ETc changes (up to -75 mm $year^{-1}$) are restricted to a small area in central Africa, spanning from eastern Mali to central-western Sudan (Fig. 1d6).

The spatial patterns of ETc changes closely resemble the positive patterns of Tasmin, Tas, and Rsds, and the negative patterns of P_{annual} and Hurs, indicating that surface energy, in terms of Tasmin, Tas, and Rsds, drives water output through evapotranspiration, which is counterbalanced by reduced P_{annual} and Hurs. The projected warming patterns and the heterogeneous responses of P_{annual}, Hurs, and Rsds, are consistent with previous studies based on CMIP5 and CMIP6 GCMs and regional climate models (Bartók et al. 2017; Torres et al. 2021; IPCC 2022; Almazroui et al. 2020a, b, 2021; Douville and Willett 2023). However, comparable analyses for Tasmin and ETc remains scarce, rendering the results presented here novel for both variables.

3.2 Spatial Patterns of Risk Indicators Under Four Global Warming Levels

Figures 2 and 3, and 4 show the spatial patterns of bioclimatic risk indicators (CRw, CRws, CRbt, CRfrost, and CRpl), disease susceptibility indicators (DRce, DRcf, DRcy, DRpp, DRqe, DRtm, and DRns), and pest susceptibility indicators (PRbo, PRce, PRgb, PRgp, PRli, PRmp, PRom, and PRtp), respectively, for the CP and the four GWLs. These figures integrate mean values of SSP2-4.5 and SSP5-8.5, rather than assessing the scenarios separately.

In the CP, the bioclimatic indicators posing the highest risk to Eucalyptus cultivation are, in order of severity: CRpl, with very high risk ($Riskn \geq 0.8$) in ~81% of the globe (Fig. 2a5), followed by CRw, in ~77% (Fig. 2a1), and CRws in ~8% (Fig. 2a2). These percentages refer to the global spatial domain considered in this study and should not be interpreted as the proportion of currently cultivated Eucalyptus plantations exposed to risk. Conversely, CRbt (Fig. 2a3) and CRfrost (Fig. 2a4) exhibit low to very low risk ($Riskn \leq 0.4$) in ~83% of the globe, and high to very high risk ($Riskn \geq 0.6$) in only 11.8% (CRbt) and 12.7% (CRfrost), mainly located at high latitudes ($>+60°$), including Mongolia, southwestern China, and along the Andes (Fig. 2a3 and a4). As GWLs increase, areas of elevated risks associated with CRbt and CRfrost tend to decrease (from 5% under 1.5 °C to 2.6% under 4 °C GWL; Fig. 2; Table 3). Despite the increase in Tas under the GWLs, Tas values are expected to remain within 8.5 °C to 38.7 °C, considered optimal range for Eucalyptus growth. Additionally, the number of days conducive to frost formation is expected to decline (Meehl et al. 2004), as warming reduces the occurrence of $Tasmin \leq 4$ °C (Dias et al. 2024), rendering this threshold increasingly unlikely to be reached across different GWLs. Nevertheless, isolated late-frost events may still occur and cause severe damage, particularly in young Eucalyptus plantations (Vitasse et al. 2025), indicating that a reduction in the mean frequency of frost events does not eliminate the risks associated with extreme cold events.

With progressive warming from 1.5 °C to 4 °C, the bioclimatic risks (CRw and CRws) intensify slightly in magnitude at localized areas (Fig. 2). CRpl remains the main threat to Eucalyptus plantations, although the area of highest risk slight decreases from 80.2% of the globe at the 1.5 °C to 77.7% at the 4 °C) (Fig. 2b5–e5). This reduction occurs mainly at latitudes $>60°$ N, where eucalyptus is not currently cultivated, leaving the risk over major production regions largely unchanged. Consequently, risks linked to CRpl, CRw, and CRwd remain predominantly high ($Riskn \geq 0.6$).

The location of high-risk areas ($Riskn \geq 0.6$) for CRw and CRws is largely consistent between the CP and the GWLs in the Southern Hemisphere, while exhibiting slightly shifts in the Northern Hemisphere. In the Southern Hemisphere, this high risk areas are concentrated in South America (northeastern Brazil, large parts of Argentina and Chile, and western coast of Peru), Africa (a continuous belt extending from northern Africa to Eritrea, encompassing parts of Ethiopia, Djibouti, Somalia, Kenya, central Tanzania, Zambia, as well as southern and western Angola, South Africa, Namibia, Botswana, and Zimbabwe), and Oceania (most of Australia). In the Northern Hemisphere, high-risk areas are located in northern Mexico and the central-western United

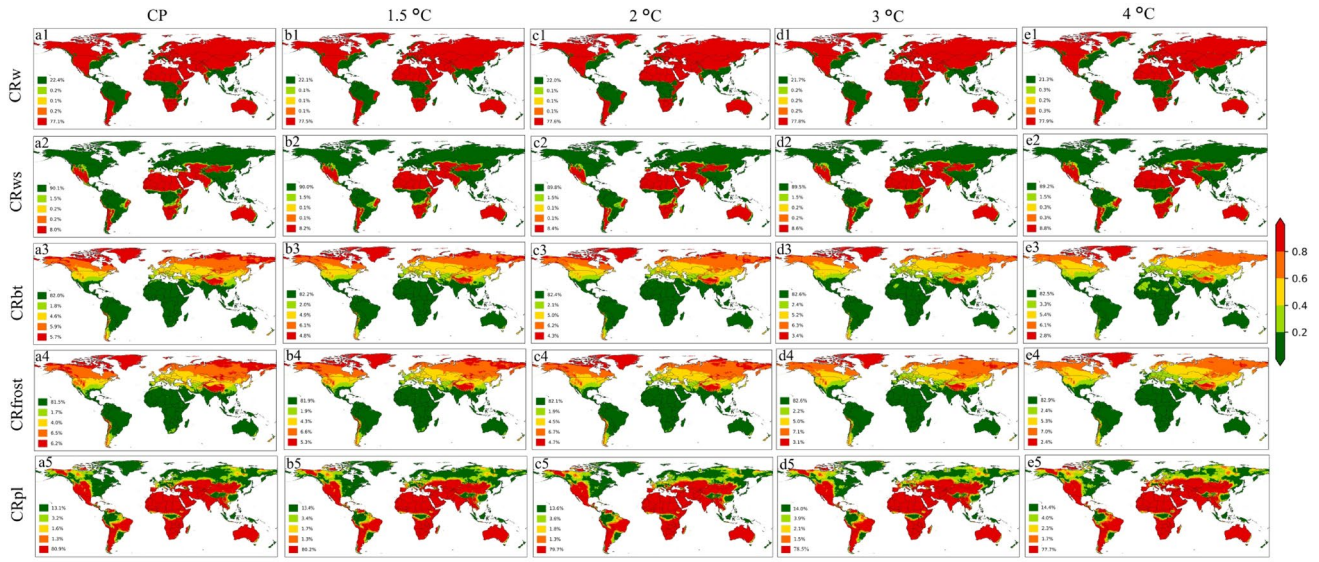


Fig. 2 Spatial distribution of bioclimatic risks for Eucalyptus (shown on the x-axis) for the control period (CP, 1995–2014) (Panels **a1**–**a5**), and for the periods in which global warming levels (GWLs) of 1.5 °C (Panels **b1**–**b5**), 2 °C (Panels **c1**–**c5**), 3 °C (Panels **d1**–**d5**), and 4 °C (Panels **e1**–**e5**) are reached (shown on the y-axis). The indicators were calculated using the ensemble mean central warming year (± 10-year time window) across the 23 NEX-GDDP-CMIP6 GCMs and SSPs that reached each GWL. CRw = water requirement indicator, CRws = water stress indicator, CRbt = basal temperature indicator, CRfrost = frost stress indicator, CRpl = productivity loss indicator. Percentage values (%) represent the area at risk within each class

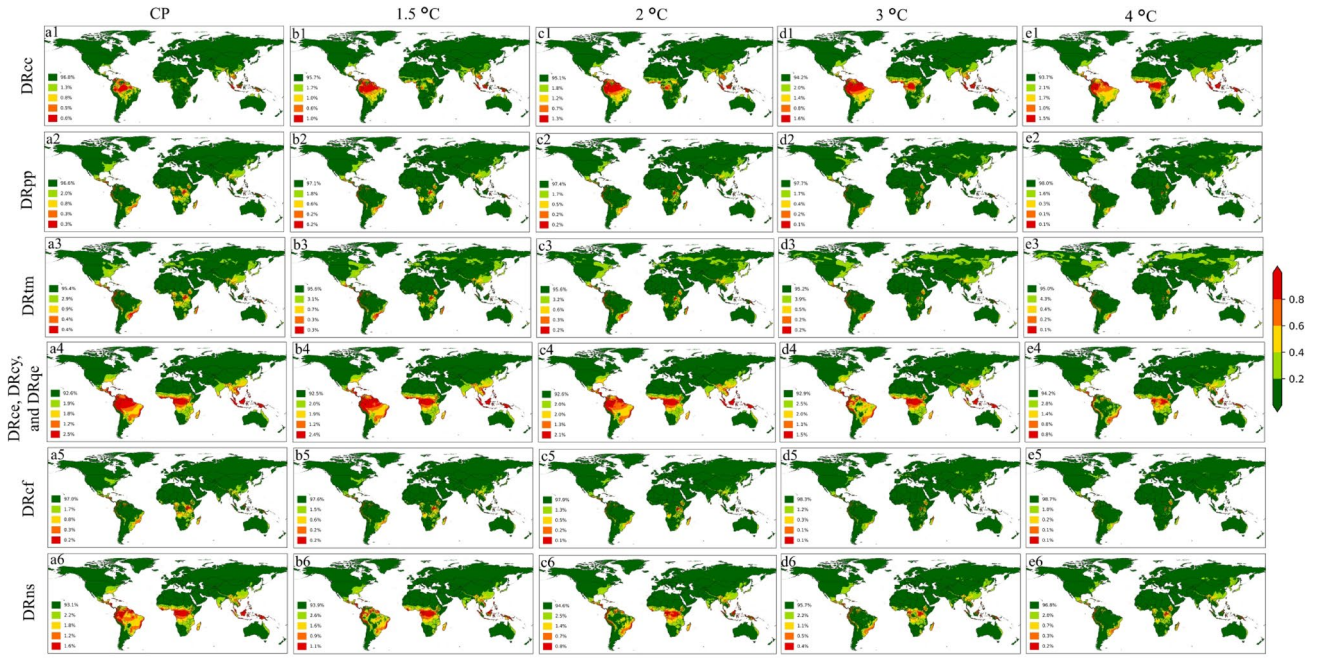


Fig. 3 Spatial distribution of disease susceptibility risks for Eucalyptus (shown on the x-axis) for the control period (CP, 1995–2014) (Panels **a1**–**a5**), and for periods in which global warming levels (GWLs) of 1.5 °C (Panels **b1**–**b5**), 2 °C (Panels **c1**–**c5**), 3 °C (Panels **d1**–**d5**), and 4 °C (Panels **e1**–**e5**) are reached (shown on the y-axis). The indicators were calculated using the ensemble mean central warming year (± 10-year time window) across the 23 NEX-GDDP-CMIP6 GCMs and SSPs that reached each GWL. DRcc = eucalyptus canker susceptibility indicator, DRpp = eucalyptus rust susceptibility indicator, leaf spot susceptibility indicators such as DRtm = *Teratosphaeria* sp. and *Mycosphaerella* spp., DRce = *Cryptosporiopsis eucalypti*, DRcy = *Cylindrocladium* spp., Drqe = *Quambalaria eucalypti*, DRcf = *Ceratocystis fimbriata* and DRns = pink disease susceptibility indicator. Percentage values (%) represent the area at risk within each class

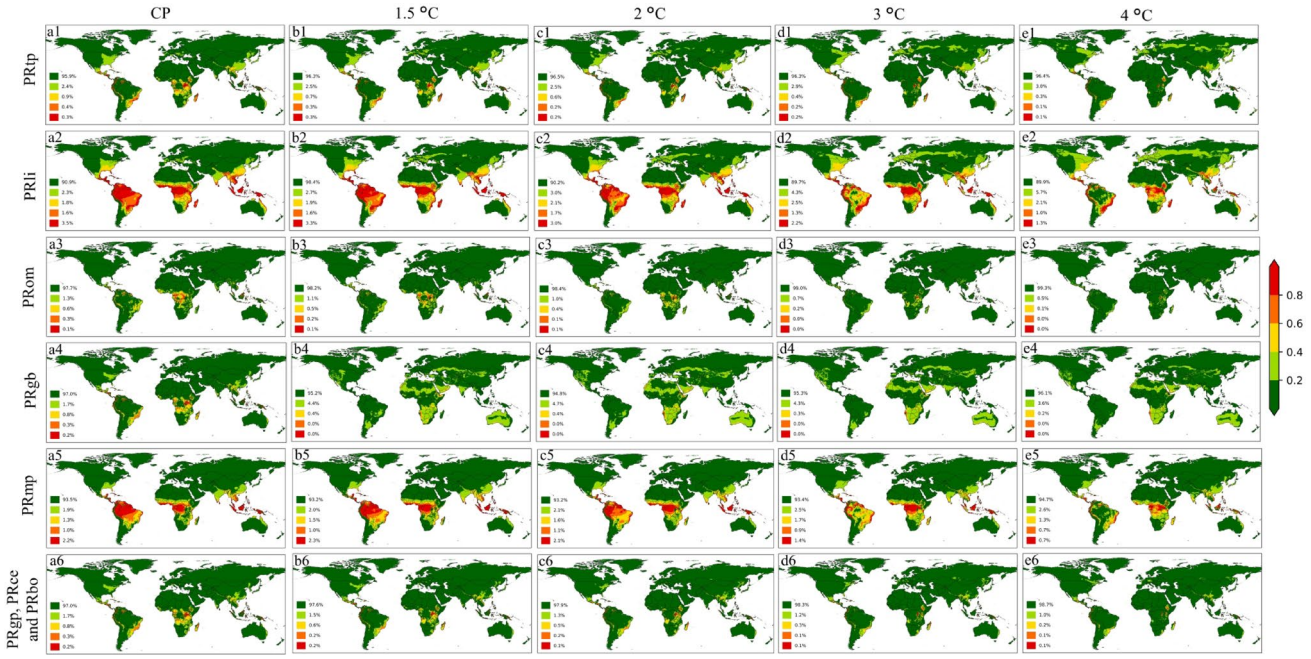


Fig. 4 Spatial distribution of pest susceptibility risks for Eucalyptus (shown on the x-axis) for the control period (CP, 1995–2014) (Panels **a1**–**a5**), and for periods in which global warming levels (GWLs) of 1.5 °C (Panels **b1**–**b5**), 2 °C (Panels **c1**–**c5**), 3 °C (Panels **d1**–**d5**), and 4 °C (Panels **e1**–**e5**) are reached (shown on the y-axis). The indicators were calculated using the ensemble mean central warming year (±10-year time window) across the 23 NEX-GDDP-CMIP6 GCMs and SSPs that reached each GWL. PRtp = bronze bug (*Thaumastocoris peregrinus*), PRli = gall wasp (*Leptocybe invasa*), Prom = gall wasp (*Ophelimus maskelli*), PRgb = red gum lerp psyllid (*Glycaspis brimblecombei*), PRmp = autumn gum moth (*Mnesampela privata*), PRgp = eucalyptus weevil (*Gonipterus platensis* and *Gonipterus pulverulentus*), PRce = eucalyptus psyllid (*Ctenarytaina eucalypti*) and PRbo = eucalyptus shoot psyllid (*Blastopsylla occidentalis*). Percentage values (%) represent the area risk area within each class

States, Portugal, Spain, and Turkey, as well as in two extensive belts: one extending from Southwest Asia to India and another from Kazakhstan and Mongolia to northern China. The highest risks are driven by increases in Tasmin and Tas (up to +2.5 °C), reductions in P_{annual} (up to −150 mm year^{-1}), and increases in ETc (between +25 and +125 mm year^{-1}) (Fig. 1).

Regarding CRw, the spatial distribution of high to very high risk (Riskn ≥ 0.6) exhibits a broad global coverage. Exceptions, i.e., low-risk areas (Riskn ≤ 0.4), are concentrated in specific regions of South America (from Venezuela to southern Brazil, Uruguay, northeastern Argentina, Guyana, Suriname, and French Guiana), a small area of North America (southeastern and northeastern United States and the extreme southeastern Canada), central Africa, small parts of Europe (extreme northern Portugal, western Spain, United Kingdom, and a strip from eastern France to Montenegro and Norway), southern Asia (from India to Vietnam, including southeastern China and Indonesia), and Oceania (e.g., Papua New Guinea). These areas coincide with projections of P_{annual} increases of up to +150 mm year^{-1}, except in Brazil and central-southern Europe (Fig. 1).

With respect to CRpl, areas with high risk (Riskn ≥ 0.6) encompass large portion of the globe, including extensive regions of South America (most of Argentina, Brazil, Bolivia, Chile, northern Paraguay, western Peru, and northern Venezuela), Central America (Nicaragua, Honduras, and El Salvador), North America (Mexico, much of the central-western United States, southern and northwestern Canada, and western Alaska), most of Africa, southern Europe (Portugal, Spain, and a belt from southern Italy to Turkey), parts of southwestern and southern Asia (from Turkey to northern China, and from Saudi Arabia to Vietnam), and Oceania (most of Australia). These regions include major eucalyptus-producing areas, as demonstrated by Fagundes et al. (2025). In other words, the highest risks associated with CRw, CRws, and CRpl occur precisely where warming of +0.5 °C (1.5 °C GWL) to +2.5 °C (4 °C GWL) coincides with increased ETc (up to +125 mm year^{-1}), and reduced P_{annual} (up to −150 mm year^{-1}) (Fig. 1).

Furthermore, the spatial patterns of heightened risk identified under the CP are consistent with historical reports of water stress, productivity losses, and localized mortality in commercial Eucalyptus plantations. For example, in southwestern Australia, mortality events in young *E. globulus* plantations have been linked to limited soil water-holding capacity and the recurrent occurrence of seasonal droughts (Harper et al. 2009).

Table 3 Area proportions for each Eucalyptus risk indicator for the control period (CP, 1995–2014) and global warming levels (GWLs) of 1.5 °C, 2 °C, 3 °C, and 4 °C, as well as differences between each GWL and the CP

Indicator	Risk	CP	1.5 °C	2 °C	3 °C	4 °C	1.5 °C – CP	2 °C – CP	3 °C – CP	4 °C – CP
Bioclimatic										
CRw	**very low**	22.4	22.1	22	21.7	21.3	-0.3	-0.4	-0.7	-1.1
	low	0.2	0.2	0.1	0.2	0.3	0	-0.1	0	0.1
	moderate	0.1	0.2	0.1	0.2	0.2	0.1	0	0.1	0.1
	high	0.2	0.2	0.1	0.2	0.3	0	-0.1	0	0.1
	very high	77.1	77.5	77.6	77.8	77.9	0.4	0.5	0.7	0.8
CRws	**very low**	90.1	90	89.8	89.5	89.2	-0.1	-0.3	-0.6	-0.9
	low	1.5	1.5	1.5	1.5	1.5	0	0	0	0
	moderate	0.2	0.1	0.1	0.2	0.3	-0.1	-0.1	0	0.1
	high	0.2	0.1	0.1	0.2	0.3	-0.1	-0.1	0	0.1
	very high	8	8.2	8.4	8.6	8.8	0.2	0.4	0.6	0.8
CRbt	**very low**	82	82.2	82.4	82.6	82.5	0.2	0.4	0.6	0.5
	low	1.8	2	2.1	2.4	3.3	0.2	0.3	0.6	1.5
	moderate	4.6	4.9	5	5.2	5.4	0.3	0.4	0.6	0.8
	high	5.9	6.1	6.2	6.3	6.1	0.2	0.3	0.4	0.2
	very high	5.7	4.8	4.3	3.4	2.8	-0.9	-1.4	-2.3	-2.9
CRfrost	**very low**	81.5	81.9	82.1	82.6	82.9	0.4	0.6	1.1	1.4
	low	1.7	1.9	1.9	2.2	2.4	0.2	0.2	0.5	0.7
	moderate	4	4.3	4.5	5	5.3	0.3	0.5	1	1.3
	high	6.5	6.6	6.7	7.1	7	0.1	0.2	0.6	0.5
	very high	6.2	5.3	4.7	3.1	2.4	-0.9	-1.5	-3.1	-3.8
CRpl	**very low**	13.1	13.4	13.6	14	14.4	0.3	0.5	0.9	1.3
	low	3.2	3.4	3.6	3.9	4	0.2	0.4	0.7	0.8
	moderate	1.6	1.7	1.8	2.1	2.3	0.1	0.2	0.5	0.7
	high	1.3	1.3	1.3	1.5	1.7	0	0	0.2	0.4
	very high	80.9	80.2	79.7	78.5	77.7	-0.7	-1.2	-2.4	-3.2
Diseases										
DRcc	**very low**	96.8	95.7	95.1	94.2	93.7	-1.1	-1.7	-2.6	-3.1
	low	1.3	1.7	1.8	2	2.1	0.4	0.5	0.7	0.8
	moderate	0.8	1	1.2	1.4	1.7	0.2	0.4	0.6	0.9
	high	0.5	0.6	0.7	0.8	1	0.1	0.2	0.3	0.5
	very high	0.6	1	1.3	1.6	1.5	0.4	0.7	1	0.9
DRpp	**very low**	96.6	97.1	97.4	97.7	98	0.5	0.8	1.1	1.4
	low	2	1.8	1.7	1.7	1.6	-0.2	-0.3	-0.3	-0.4
	moderate	0.8	0.6	0.5	0.4	0.3	-0.2	-0.3	-0.4	-0.5
	high	0.3	0.2	0.2	0.2	0.1	-0.1	-0.1	-0.1	-0.2
	very high	0.3	0.2	0.2	0.1	0.1	-0.1	-0.1	-0.2	-0.2
DRtm	**very low**	95.4	95.6	95.6	95.2	95	0.2	0.2	-0.2	-0.4
	low	2.9	3.1	3.2	3.9	4.3	0.2	0.3	1	1.4
	moderate	0.9	0.7	0.6	0.5	0.4	-0.2	-0.3	-0.4	-0.5
	high	0.4	0.3	0.3	0.2	0.2	-0.1	-0.1	-0.2	-0.2
	very high	0.4	0.3	0.2	0.2	0.1	-0.1	-0.2	-0.2	-0.3
DRce	**very low**	92.6	92.5	92.6	92.9	94.2	-0.1	0	0.3	1.6
DRcy DRqe	**low**	1.9	2	2	2.5	2.8	0.1	0.1	0.6	0.9
	moderate	1.8	1.9	2	2.0	1.4	0.1	0.2	0.2	-0.4
	high	1.2	1.2	1.3	1.1	0.8	0	0.1	-0.1	-0.4
	very high	2.5	2.4	2.1	1.5	0.8	-0.1	-0.4	-1	-1.7
DRcf	**very low**	97	97.6	97.9	98.3	98.7	0.6	0.9	1.3	1.7
	low	1.7	1.5	1.3	1.2	1	-0.2	-0.4	-0.5	-0.7
	moderate	0.8	0.6	0.5	0.3	0.2	-0.2	-0.3	-0.5	-0.6
	high	0.3	0.2	0.2	0.1	0.1	-0.1	-0.1	-0.2	-0.2
	very high	0.2	0.2	0.1	0.1	0.1	0	-0.1	-0.1	-0.1

Table 3 (continued)

Indicator	Risk	CP	1.5 °C	2 °C	3 °C	4 °C	1.5 °C – CP	2 °C – CP	3 °C – CP	4 °C – CP
DRns	**very low**	93.1	93.9	94.6	95.7	96.8	0.8	1.5	2.6	3.7
	low	2.2	2.6	2.5	2.2	2	0.4	0.3	0	-0.2
	moderate	1.8	1.6	1.4	1.1	0.7	-0.2	-0.4	-0.7	-1.1
	high	1.2	0.9	0.7	0.5	0.3	-0.3	-0.5	-0.7	-0.9
	very high	1.6	1.1	0.8	0.4	0.2	-0.5	-0.8	-1.2	-1.4
Pests										
PRtp	**very low**	95.9	96.3	96.5	96.3	96.4	0.4	0.6	0.4	0.5
	low	2.4	2.5	2.5	2.9	3	0.1	0.1	0.5	0.6
	moderate	0.9	0.7	0.6	0.4	0.3	-0.2	-0.3	-0.5	-0.6
	high	0.4	0.3	0.2	0.2	0.1	-0.1	-0.2	-0.2	-0.3
	very high	0.3	0.3	0.2	0.1	0.1	0	-0.1	-0.2	-0.2
PRli	**very low**	90.9	90.4	90.2	89.7	89.9	-0.5	-0.7	-1.2	-1
	low	2.3	2.7	3	4.3	5.7	0.4	0.7	2	3.4
	moderate	1.8	1.9	2.1	2.5	2.1	0.1	0.3	0.7	0.3
	high	1.6	1.6	1.7	1.3	1	0	0.1	-0.3	-0.6
	very high	3.5	3.3	3	2.2	1.3	-0.2	-0.5	-1.3	-2.2
PRom	**very low**	97.7	98.2	98.4	99	99.3	0.5	0.7	1.3	1.6
	low	1.3	1.1	1	0.7	0.5	-0.2	-0.3	-0.6	-0.8
	moderate	0.6	0.5	0.4	0.2	0.1	-0.1	-0.2	-0.4	-0.5
	high	0.3	0.2	0.1	0	0	-0.1	-0.2	-0.3	-0.3
	very high	0.1	0.1	0.1	0	0	0	0	-0.1	-0.1
PRgb	**very low**	97	95.2	94.8	95.3	96.1	-1.8	-2.2	-1.7	-0.9
	low	1.7	4.4	4.7	4.3	3.6	2.7	3	2.6	1.9
	moderate	0.8	0.4	0.4	0.3	0.2	-0.4	-0.4	-0.5	-0.6
	high	0.3	0	0	0	0	-0.3	-0.3	-0.3	-0.3
	very high	0.2	0	0	0	0	-0.2	-0.2	-0.2	-0.2
PRmp	**very low**	93.5	93.2	93.2	93.4	94.7	-0.3	-0.3	-0.1	1.2
	low	1.9	2	2.1	2.5	2.6	0.1	0.2	0.6	0.7
	moderate	1.3	1.5	1.6	1.7	1.3	0.2	0.3	0.4	0
	high	1	1	1.1	0.9	0.7	0	0.1	-0.1	-0.3
	very high	2.2	2.3	2.1	1.4	0.7	0.1	-0.1	-0.8	-1.5
PRgp	**very low**	97	97.6	97.9	98.3	98.7	0.6	0.9	1.3	1.7
PRce	**low**	1.7	1.5	1.3	1.2	1	-0.2	-0.4	-0.5	-0.7
PRbo	**moderate**	0.8	0.6	0.5	0.3	0.2	-0.2	-0.3	-0.5	-0.6
	high	0.3	0.2	0.2	0.1	0.1	-0.1	-0.1	-0.2	-0.2
	very high	0.2	0.2	0.1	0.1	0.1	0	-0.1	-0.1	-0.1

Regarding diseases, only the DRcc indicator, caused by eucalyptus canker, shows an increase in risk (in area and magnitude) across the GWLs, whereas the other disease indicators exhibit progressively reduced risk as warming intensifies. The largest reduction is observed for DRns (Fig. 3a6–e6, Table 3), with decreases of ~0.8% (1.5 °C GWL), 1.3% (2 °C GWL), 1.9% (3 °C GWL), and 2.3% (4 °C GWL) in areas classified as high and very high risk. Reductions in high-risk areas for DRce, DRcy, and DRqe range from ~0.2% (1.5 °C and 2 °C GWLs) to 2.1% (4 °C GWL) (Table 3). A similar but less pronounced pattern is observed for DRcf (~0.1–0.3%), DRpp (~0.2–0.4%), and DRtm (~0.2–0.5%) across the GWLs (Table 3).

This reduction is mainly associated with declining patterns of Hurs and P as warming intensifies. Nevertheless, DRce, DRcy, DRqe, and DRns exert greater risk to eucalyptus under the CP and the 1.5 °C GWL, reaching high to very high (Risk$n \geq 0.6$) over ~3.7% (Fig. 3a4 and b4) and 2.8% of the globe (Fig. 3a6 and b6). The most critical areas for leaf spots (caused by *C. eucalypti*, *Cylindrocladium* spp., *Q. eucalypti*) and *N. salmonicolor* are primarily concentrated in the Americas, encompassing most of South America (except Argentina, Chile, northern Paraguay, much of Bolivia, and western Peru), Central America (from Panama to Guatemala), and southern North America. In Africa, the highest risk occurs in the central regions (belt from Liberia to southern Central African Republic, including Uganda, the Democratic Republic of the Congo, northern Angola, Congo, Gabon, and Equatorial Guinea). In Asia, high-risk areas covers northeastern India, northern Myanmar, southern China, Laos, Vietnam, Malaysia, and Indonesia, as well

as localized areas in Oceania, mainly in Papua New Guinea and the eastern coast of Australia.

The fungi *C. eucalypti*, *Cylindrocladium spp.* and *Q. eucalypti* are favored under conditions of 20 °C ≤ Tas ≤ 30 °C and Hurs ≥ 75% (Sharma et al., 1991; Old et al. 2002; Alfenas et al. 2009; Pegg et al. 2009), which enhance mycelial growth, spore germination and foliar infection rates, leading to increased infestation severity. Leaf spots caused by these fungi cause premature defoliation and the emergence of foliar lesions that reduce radiation interception area, impair photosynthesis, and compromise tree growth and wood quality (Andrade et al. 2007; Alfenas et al. 2009; Cheewangkoon et al. 2010). Leaf damage of ~ 20% can reduce *E. globulus* growth by 4–17% (Balmelli et al. 2013).

For *N. salmonicolor*, the highest risks occur under combined conditions of 20–28 °C and Hurs ≥ 75%, typical of tropical and subtropical regions (Nomi et al. 2000; Akrofi et al. 2014). This pathogen forms pink mycelial growth on bark, causing girdling lesions on branches and trunks that disrupt sap flow and lead to progressive branch dieback (Alfenas et al. 2009), ultimately compromising tree structure and development.

Furthermore, occurrence records available from the Global Biodiversity Information Facility (GBIF) indicate that these diseases (*C. cubensis*, *C. eucalypti*, *Cylindrocladium* spp., *Q. eucalypti*, and *N. salmonicolor*) are already distributed across major eucalyptus-producing regions, including South America, Mexico, Africa, China, India, Thailand, Vietnam, and Australia (Fig. S1 and Table S1).

Other disease indicators (DRpp, DRtm, and DRcf) exhibit low to very low risk (Riskn ≤ 0.4) across most of the globe (~ 98.4%) during the CP and all GWLs (98.7% to 99.7%). High-risk areas, although limited, are spatially consistent and concentrated in coastal Brazil, northeastern Peru and Venezuela, western Colombia and Guyana, parts of Central America (Nicaragua and Honduras), central Africa (northeastern Democratic Republic of the Congo, Uganda, Rwanda, Burundi, Ethiopia and Madagascar, southern Asia, such as southern Thailand, Cambodia, Vietnam, Malaysia and Indonesia and Papua New Guinea. In Brazil, such risks are particularly relevant, as *P. psidii* can reduce Eucalyptus mean annual increment by up to 30% (Auer et al. 2010).

Finally, pests indicators (PRtp, PRli, PRom, PRgb, PRmp, PRgp, PRce, and PRbo) exhibit a similar pattern to diseases indicators, with a progressive reduction in high to very high risk (Riskn ≥ 0.6) as warming intensifies. However, this apparent reduction in risk may be attributable to the fact that, particularly under higher GWLs, some regions experience Tas values that exceed the upper thermal thresholds for the development of specific pests and diseases (Table S3). Consequently, the increased frequency of Tas exceeding the favorable thermal ranges under the + 3 °C and + 4 °C GWLs may reduce the climatic suitability for these organisms. Under such conditions, increasing Tas ceases to be a favorable factor and instead becomes a limiting factor for their development, survival, reproduction, or infection potential. Therefore, the reduction observed in this study should not be interpreted solely as a decrease in biotic pressure, but also as a potential consequence of Tas exceeding the optimum thermal range for certain species.

The most significant risks (in area and magnitude) for eucalyptus plantations are PRli and PRmp, affecting ~ 5.1% and ~ 3.2% of the globe during the CP and under 1.5 °C, respectively, declining to ~ 1.3–1.4% under 4 °C (Fig. 4). Notably, the spatial patterns of high-risk areas are highly similar between these indicators, encompassing nearly all of South America (except for the western coastal belt, Uruguay, and large parts of Argentina), Central America (from Panama to Guatemala), the southern portion of North America, and the central region of Africa (extending from Sierra Leone to southern South Sudan and encompassing Equatorial Guinea, Gabon, the Republic of the Congo, northern Angola, the Democratic Republic of the Congo, Burundi, Rwanda, Uganda, Kenya, northern and northeastern Tanzania, eastern Mozambique, and Madagascar), several countries in Asia (Bangladesh, Myanmar, Laos, Thailand, Cambodia, Vietnam, southern and southeastern China and India, Malaysia, and Indonesia), as well as Papua New Guinea and the eastern coast of Australia.

Furthermore, occurrence records available from the GBIF indicate that *L. invasa* is widely distributed across major eucalyptus-producing regions, including Brazil, Africa, China, and Southeast Asian countries such as Thailand and Vietnam (Fig. S2 and Table S2). By contrast, the native range of *M. privata* is restricted to Australia. Moreover, studies based on climate projections have reported a potential decline in the invasion risk of this pest in Brazil by 2070 (Mota et al. 2023), consistent with the risk reduction projected in the present study.

The remaining pest indicators (PRtp, Prom, PRgb, PRgp, Prce, and Prbo) are mostly classified as low and very low risk across ~ 97.1% and 99.2% worldwide (Fig. 4). High to very high risk (Riskn ≥ 0.6) is restricted to southern and southeastern Brazil (South America), Guatemala and Honduras (Central America), localized areas in Mexico (North America), eastern Democratic Republic of the Congo, Uganda, Ethiopia, Rwanda, Burundi, northern Tanzania, Madagascar, and specific areas in northern Angola, Congo, and Cameroon (Africa).

The coupled of the 21 risk indicators (bioclimatic, disease, and pest) reveals that different regions exhibit distinct vulnerability levels depending on the dominant risk types. Overall, Eucalyptus-growing areas in tropical regions, such as central South America, Central America, and parts of

Oceania, are more vulnerable to bioclimatic risks associated with productivity losses, increased susceptibility to leaf spots diseases, and higher pest incidence, especially the gall wasp and the autumn gum moth (Figs. 2 and 3, and 4). Thus, the adoption of efficient and environmentally sound adaptation measures will be essential in these regions to mitigate adverse impacts and ensure the long-term sustainability of eucalyptus plantations under global warming.

However, it is important to emphasize that the dynamics of forest diseases and pests are shaped by the interaction among favorable climatic conditions, host characteristics, inoculum availability, and management practices (Szyniszewska et al. 2024; Farda et al. 2026; Silva et al. 2026; Xavier et al. 2026). Therefore, the bioclimatic indicators employed in this study should be interpreted as representations of climatic suitability for disease and pest development rather than as direct predictors of outbreaks. The occurrence, establishment, and severity of these phytosanitary agents depend on additional factors operating at local and regional scales. Thus, future studies are needed to validate and refine these indicators using observational and experimental data, while incorporating information on host distribution, inoculum pressure, genetic variability, silvicultural practices, and ecophysiological responses, thereby improving phytosanitary risk assessments under different GWLs.

4 Discussion

By jointly analyzing the spatial patterns of risk (Figs. 2 and 3, and 4; Table 3), four main findings emerge: (i) risk magnitudes differ among the 21 indicators, although, overall, most exhibit a slight reduction over the different GWLs, mainly those related to diseases and pests; (ii) the greatest vulnerabilities to eucalyptus cultivation are driven by bioclimatic factors, especially productivity losses associated with water stress (CRpl and CRw); (iii) there is a consistent spatial pattern of overlapping vulnerabilities in specific locations; and (iv) the most vulnerable regions are concentrated in the central South and Central America, as well as specific areas of Africa, Asia, and Oceania.

Despite the gradual reduction in areas classified as high to very high risk (Riskn $\geq$ 0.6) with increasing global warming, the spatial patterns of the 21 indicators at the 1.5 °C and 2 °C GWLs remain very similar to those the CP. This persistence is a concern, as it shows that impacts of increasing global mean temperature are already evident at or even beyond the 1.5 °C threshold, with a rapid progression toward 2 °C. Projections from the IPCC (2021) and Fagundes et al. (2025) indicate that the 2 °C threshold is likely to be exceeded around 2041 (ensemble mean of 30 CMIP6 GCMs), with model-dependent variations ranging from 2023 to 2052 (under SSP5.8-5). I.e., increases of 0.5 °C and 1 °C relative to the CP are already underway, with risk patterns closely aligned with spatial patterns of increasing temperature and decreasing precipitation and air humidity (Fig. 1).

Overall, most indicators exhibited relatively gradual or near-linear responses across the different GWLs, with a progressive intensification of risk from 1.5 °C to 4 °C. This behavior is likely attributable to the structure of the indicators, which are primarily based on continuous climatic variables and predefined climatic thresholds, including temperature, precipitation, and relative humidity. Because these variables tend to change progressively as warming levels increase, the indicators likewise tend to exhibit smoother transitions among risk classes. Although some indicators showed slightly more pronounced reductions, particularly under higher GWLs (3 °C and 4 °C), no abrupt tipping points or clear disproportionate shifts were identified, with most responses remaining predominantly gradual across the different GWLs (Table 2).

Several previous studies analyzing precipitation and temperature using CMIP5 and CMIP6 models have already identified regions in South America (Brazil, Paraguay, Ecuador, Colombia, and Venezuela) (Florêncio et al. 2022; Torres et al. 2021), Central America, North America (mainly the southeastern portion) (Almazroui et al. 2021), southern Europe (from Portugal to Turkey) (Fagundes et al. 2025), southern Asia (including India and China) (Shi et al. 2018; Yaduvanshi et al. 2019; Zhang et al. 2021), and parts of Oceania (including Papua New Guinea and Australia) (Alexander and Arblaster 2017) as persistent climate change hotspots. Furthermore, in these areas, eucalyptus cultivation is likely to be adversely affected by changes in ETc, AE, and WD patterns combined with temperature increases of 0.5 °C to 3 °C relative to the global mean, alongside heterogeneous precipitation changes (reduction and increase) (Florêncio et al. 2022; Martins et al. 2022; Yang et al. 2023; Fagundes et al. 2025).

These findings are consistent with the results of this study, in which the highest risks (in area and magnitude) are associated with bioclimatic indicators, especially CRpl, CRw, and CRws for most of the globe, whereas risks related to CRbt and CRfrost prevail in the Northern Hemisphere, particularly in regions where Tas < 8.5 °C (Martins and Streck 2007; Florêncio et al. 2022). Water stress, represented by CRw, CRws, and CRpl, triggers a cascade of physiological stresses, beginning with stomatal closure, which increases the photorespiration/photosynthesis ratio and cellular maintenance costs, in addition to reducing transpiration, photosynthetic efficiency, and altering cell wall and protein synthesis (Abreu et al. 2022). As a defensive response, plants reduce cell and leaf expansion dry matter allocation, and intensify leaf senescence and abscission (Martins et

al. 2008; Abreu et al. 2015, 2022). Consequently, reduced CO_2 uptake into chloroplasts further constrains photosynthesis (Nievola et al. 2017; Dias et al. 2024), reducing carbon assimilation and therefore leaf expansion and tissue development, with direct negative impacts on biomass accumulation and productivity (Martins et al. 2022, 2023). Furthermore, under severe and prolonged water stress ($WD_{anual} \geq 330$ mm year^{-1}; Fagundes et al. 2025), hydraulic failure due to xylem embolism can occur, leading to vascular collapse and, ultimately, plant mortality (Chen et al. 2020; Yang et al. 2023).

Regarding thermal stress (CRbt and CRfrost), temperatures outside the optimal threshold for Eucalyptus (≤8.5 °C and ≥38.7 °C) (Martins and Streck 2007; Florêncio et al. 2022; Martins et al. 2023) trigger a series of reactions that generate cascading effects capable of compromising molecular integrity and physiological performance (Ruelland and Zachowski 2010; Nievola et al. 2017). In locations with higher CRfrost risk, such as the western United States and south-central China, exposure to low (or freezing) temperatures can inhibit or delay development and cause irreversible damage and/or cell death (Martins et al. 2022, 2023; Fagundes et al., 2024). Conversely, in locations where CRbt is higher, exposure to elevated temperatures (gradual or abrupt) negatively affects the molecular (proteins and DNA) and supramolecular (membranes and chromosomes) structures, causes physiological stress (Ruelland and Zachowski 2010; Nievola et al. 2017), and disrupts plant carbon balance (Ruelland and Zachowski 2010; Florêncio et al. 2022; Fagundes et al. 2024). In both cases, these processes constrain Eucalyptus growth and productivity in high-thermal-risk environments, with stemwood production declining by ~10% per 1 °C increase (Binkley et al. 2017).

When combined, water and heat stresses exert cumulative effects that can amplify risks to the sustainability of Eucalyptus plantations, including increased susceptibility to diseases and pest attacks under severe stress conditions (Herms and Mattson 1992; Barradas et al. 2018; Solís et al. 2025). Under these conditions, plants prioritize resource allocation toward maintenance, reducing investment in defense mechanisms (Barradas et al. 2018; Solís et al. 2025). The findings of Barradas et al. (2018) demonstrated this trade-off in *E. globulus*, showing that plants subjected to water stress exhibited greater susceptibility to fungal diseases, with extensive lesion development, leaf senescence symptoms, and a 66% reduction in survival rate. In natural systems, different stressors commonly interact synergistically, producing combined effects that exceed their individual impacts. Regions where water stress, disease, and pest risks overlap may experience even greater risks to eucalyptus productivity than those observed by each indicator. Although these interactions were not incorporated into the methodology of this study, future research may consider them in developing integrated risk indicators.

Despite the overall reduction in disease and pest risks across the four GWLs (Figs. 2 and 3), persistent (and localized) areas of susceptibility remain in some parts worldwide. In many cases, the reduction in overall risk magnitude is associated with the contraction of climatically suitable areas under the different GWLs. Nevertheless, several major eucalyptus-producing regions remain highly vulnerable or even exhibit localized increases in risk. E.g., the disease susceptibility indicators DRpp, DRce, DRcy, DRqe, DRcf, and DRns show an overall decline in global risk magnitude, such as Ethiopia, South Africa, and Spain, still exhibit small increases in areas classified as very high risk (Riskn > 0.8). Furthermore, the pest susceptibility indicator PRli shows an expansion of areas with very high risk (Riskn > 0.8) in Chile, Ethiopia, Portugal, South Africa, Spain, and Uruguay, whereas PRgp, PRce, and PRbo indicators exhibit localized increases primarily in Ethiopia. Detailed information on risk percentages for all indicators and GWLs evaluated across the major eucalyptus-producing countries is available in the Zenodo (https://zenodo.org/records/18462820).

These persistent patterns of vulnerability are primarily associated with eucalyptus canker caused by *C. cubensis*, leaf spots caused by *C. eucalypti*, *Cylindrocladium spp.* and *Q. eucalypti*, and pink disease, occurring along a belt extending from northwestern South America to Central America, central Africa, and from southern China to Papua New Guinea. Similarly, the gall wasp and autumn gum moth exhibit slightly broader distributions over Brazil. These patterns reflect the persistence of climatic conditions favorable to pathogens across all GWLs. Especially in tropical regions, eucalyptus canker remains one of the most severe diseases affecting commercially cultivated Eucalyptus species (Rodas et al. 2005; Pham et al. 2025), causing necrotic lesions and stem cracking at different heights, potentially girdling tissues and leading to mortality in young trees (Alfenas et al. 2009; Pham et al. 2025). Infections also reduce wood quality, with pulp yield losses of ~1% for every 10% of wood affected (Ferrari et al. 1984; Guimarães et al. 2010).

Leaf spots primarily attack foliage, causing defoliation and lesion formation, whereas pink disease mainly attacks the bark of branches and stems, producing lesions that can girdle tissues (Andrade et al. 2007; Alfenas et al. 2009; Cheewangkoon et al. 2010). In Brazil, defoliation caused by *Cylindrocladium spp.* resulted in a 27.6% reduction in total wood volume per hectare (Krügner et al. 1990).

The pests with the largest areas of severe risk are *L. invasa* and *M. privata*. *L. invasa* thrives under conditions of 18 °C ≤ Tas ≤ 30 °C and Hurs ≥ 65% (Garlet et al. 2013; Puretz et al. 2015). Under these conditions, *L. invasa* females lay 80 to 100 eggs, and the emerging larvae induce

Table 4 Key adaptation measures to minimize bioclimatic risks, susceptibility to diseases and pests in global eucalyptus plantations

Risk indicator	Adaptation measure	Technical purpose	References	Countries*
Water requirement (CRw) and Water stress (CRws)	Increased spacing (~3 × 3–4 m), thinning and pruning at shorter intervals, use of mulch, and no-tillage planting	Reduces competition for water and nutrients; reduces ETc, atmospheric demand, and water consumption; conserves soil water content under WD conditions, and enhances soil organic matter conservation and soil water-holding capacity	Gonçalves et al. (2017), Florêncio et al. (2022), Martins et al. (2022), Bose et al. (2025), Santos and Reichert (2022)	Argentina, Australia, Bolivia, Brazil, Chile, China, Colombia, Ecuador, Ethiopia, India, Mexico, Pakistan, Paraguay, Peru, Portugal, South Africa, Spain, United States, Uruguay, and Venezuela.
Water stress (CRws)	Selection of drought-tolerant genotypes	Reducing water-stress effects through the selection of more tolerant genotypes such as: *E. urophylla x E. camaldulensis*, *E. tereticornis* x *E. brassiana*, *E. tereticornis*, *E. camaldulensis*, *C. torelliana x C. citriodora*, *E. brassiana*, and *C. maculata*	Fagundes et al. (2025)	Argentina, Australia, Bolivia, Brazil, Chile, China, Colombia, Ecuador, Ethiopia, India, Mexico, Pakistan, Paraguay, Peru, Portugal, South Africa, Spain, United States, Uruguay, and Venezuela.
Productivity loss (CRpl)	Selection of genotypes, soil fertility correction, application of agricultural gypsum ($CaSO_4.2H_2O$), use of remote sensing and vegetation indices	Promotes the use of high-productivity genotypes under thermal and water stress; removes chemical constraints to growth and improves water and nutrient uptake; enhances soil structure, promotes deeper rooting, and increases water-use efficiency; enables identification, mapping, and monitoring of low-vigor eucalyptus areas using, e.g., the Normalized Difference Vegetation Index (NDVI)	Martins et al. (2022), Hutapea et al. (2023)	Argentina, Australia, Bolivia, Brazil, Chile, China, Colombia, Ecuador, Ethiopia, India, Mexico, Pakistan, Paraguay, Peru, Portugal, South Africa, Spain, Thailand, United States, Uruguay, Vietnam, and Venezuela.
Basal temperature stress (CRbt)	Selection of heat-tolerant genotypes	Minimizes physiological, morphological, and anatomical alterations caused by temperatures exceeding optimal thresholds by selecting genotypes with greater tolerance to thermal extremes, such as *E. camaldulensis*, *E. urophylla*, *E. tereticornis*, *E. grandis*, *E. saligna*, *C. citriodora*, *E. urophylla* × *E. grandis*, *E. urophylla* × *E. camaldulensis*, and *E. urophylla* × *E. tereticornis*	Teulières et al. (2007), Queiroz et al. (2020)	Argentina, Bolivia, Brazil, Chile, China, India, Pakistan, Peru, and United States
Frost stress (CRfrost)	Selection of cold-tolerant genotypes; adjustment of planting sites	Minimizes foliar damage and frost-induced mortality through the selection of cold-tolerant genotypes, such as *E. benthamii*, *E. viminalis*, and *E. dunnii*	Oberschelp et al. (2020), Tomé et al. (2021), Tambarussi et al. (2023), Aparecido et al. (2025)	Argentina, Bolivia, Brazil, Chile, China, Ecuador, India, Pakistan, Peru, and United States
Eucalyptus canker (DRcc)	Avoidance of susceptible species (e.g., *E. grandis* and *E. saligna*), biological control with *Cleruchoides noackae* and *Stethynium* spp., application of systemic fungicides (carboxamides and benzimidazoles), and removal of severely infected trees	Reduces intrinsic stand susceptibility to the pathogen; lowers inoculum pressure through biological control of disease-associated agents, limiting direct damage; suppresses fungal development in plant tissues via systemic action, reducing disease severity and inoculum production; and eliminates active inoculum sources, interrupting the pathogen cycle and limiting spread to healthy plants	Alfenas et al. (2009), Dias (2010)	Bolivia, Brazil, Colombia, Ecuador, India, Mexico, Peru, Thailand, Venezuela and Vietnam

Table 4 (continued)

Risk indicator	Adaptation measure	Technical purpose	References	Countries*
Leaf spot caused by *Cryptosporiopsis eucalypti* (DRce)	Biological control using actinomycetes, and Gram-positive saprophytic bacteria	Reduces inoculum pressure through biological control of disease-associated agents, thereby limiting direct damage	Himaman et al. (2016)	Bolivia, Brazil, Colombia, Ecuador, Mexico, Peru, Thailand, Venezuela and Vietnam
Leaf spot caused by *Cylindrocladium* spp. (DRcy)	Biological control with *Trichoderma spp*., application of systemic fungicides from the triazole group (epoxiconazole and tebuconazole) and the triazole + strobilurin mixture (epoxiconazole + pyraclostrobin)	Reduces inoculum pressure through biological control of disease-associated agents, limiting direct damage; suppresses fungal development in plant tissues via systemic action, reducing disease severity and inoculum production	Ferreira et al. (2006), Alfenas et al. (2009), Maciel et al. (2012)	
Leaf spot caused by *Quambalaria eucalypti* (DRqe)	Application of systemic fungicides from the triazole group (epoxiconazole and tebuconazole) and the triazole + strobilurin mixture (epoxiconazole + pyraclostrobin)	Controls fungal development in plant tissues through systemic action, reducing disease severity and inoculum production	Ferreira et al. (2008)	
Pink disease (DRns)	Biological control with *Trichoderma* spp., application of copper-based fungicides or sulfur-based paste, and pruning during the dry season	Reduces inoculum pressure through biological control via microbial antagonism; prevents infection and pathogen development in plant tissues through contact fungicides; and limits disease spread by pruning during dry periods, which are unfavorable to infection	Castro-Toro and Rivillas-Osorio (2012), Pradhanang (1994)	Bolivia, Brazil, Colombia, Ecuador, Peru, Venezuela and Vietnam
Gall wasp (*Leptocybe invasa*, PRli)	Biological control using *Aprostocetus* sp., *Megastigmus* sp. and *Quadrastichus mendeli*	Reduces pest populations through parasitism, limiting gall formation and associated damage to plant development	Garlet et al. (2013), Yousuf et al. (2020)	Argentina, Australia, Bolivia, Brazil, China, Colombia, Ecuador, Ethiopia, India, Mexico, Paraguay, Peru, Portugal, South Africa, Thailand, Uruguay, Venezuela and Vietnam
Autumn gum moth (*Mnesampela privata*, PRmp)	Biological control using *Telenomus* sp. (egg parasitoid), Ichneumonidae, Braconidae, and Tachinidae species (larval parasitoids), and natural predators (spiders and predatory bugs)	Reduces pest populations through egg and larval parasitism and natural predation, decreasing defoliation intensity, population pressure, and negative impacts on growth and productivity	Rapley et al. (2004)	Bolivia, Brazil, Colombia, Ecuador, Mexico, Peru, Thailand, Venezuela and Vietnam

* Country-level affected areas (%) for each indicator are available at: https://zenodo.org/records/18462820

gall formation, leading to branch deformation, reduced height and diameter growth (Petro et al. 2015), and consequent reduction in productivity and wood quality (Alfenas et al. 2009; Garlet et al. 2013). Similarly, *M. privata* lays 100 to 200 eggs under conditions of 24 °C ≤ Tas ≤ 30 °C and Hurs ≥ 70% (Steinbauer et al. 2004; Walker and Allen 2011). The larvae penetrate the cambium and excavate galleries that disrupt sap flow, causing branch dieback, delayed development, reduced productivity, and increased vulnerability to other pests and diseases (Steinbauer et al. 2001). As the life cycles of both species range from 80 to 130 days, increasing Tas (across the 4 GWLs) is expected to shorten development cycles and increase the number of generations per year (Florêncio et al. 2022; Mota et al. 2023).

From an economic perspective, *L. invasa* infestations have already resulted in losses of USD20 million in India (Kulkarni 2010; Petro et al. 2015), led to the interruption of *E. camaldulensis* cultivation in Israel, Thailand, and China (Petro et al. 2015), and reduced growth by ~40% in *E. grandis* and *E. saligna* in Tanzania (Petro et al. 2015). *M. privata*, has caused severe defoliation in *E. nitens* and *E. globulus* plantations in Tasmania (Australia), resulting in reductions of ~94 m^3 ha^{-1} in commercial volume in trees experiencing 90% defoliation (Rapley et al. 2009). According to Pizzi (2016), successive defoliations in Eucalyptus clones resulted in productivity losses, with a reduction of 48% to 60% in wood biomass, reaching up to 80% in more sensitive clones.

A consistent and well-localized spatial pattern of overlapping risks among the 21 indicators across the GWLs, indicating that Eucalyptus plantations are particularly vulnerable in these locations. These overlaps are concentrated in large parts of South America, encompassing southeastern to northern Brazil, Argentina, Chile, northern Paraguay, Bolivia, eastern Peru, Ecuador, Colombia, and Venezuela; portions of Central America (Panama, Guatemala, southern Mexico); south-central Africa, including Angola, Congo, Ethiopia, the Democratic Republic of Congo, Rwanda, Uganda, Mozambique, and Madagascar; as well as specific parts of Asia and Oceania, mainly along the belt connecting southern India and China to Papua New Guinea; and parts of southern Europe (Portugal, Spain, Italy, and Turkey). These spatial risk patterns encompass the world's major eucalyptus-producing regions.

Although the percentages presented throughout this study refer to the global spatial domain analyzed rather than to the area currently planted with Eucalyptus, complementary risk estimates for the major eucalyptus-producing countries are available at Zenodo (https://zenodo.org/records/18462820). Of the 19 countries with the largest current Eucalyptus plantation areas (in descending order: Brazil, China, India, Australia, Chile, Portugal, Uruguay, Spain, South Africa, Thailand, Argentina, Vietnam, Ecuador, Colombia, Paraguay, United States of America, New Zealand, Pakistan, and Ethiopia, https://zenodo.org/records/13328650) (Martins et al. 2022; Aparecido et al. 2025; Fagundes et al. 2025), 13 are located precisely within these overlapping risk zones.

Recent studies further reinforce the vulnerability patterns identified here. Fagundes et al. (2025), analyzing temperature, precipitation, and water stress patterns in relation to cultivated eucalyptus genotypes, identified that the highest vulnerabilities occur in central-western and northeastern Brazil, southern Europe, and parts of Africa (and Australia), where species and hybrids with low to moderate tolerance, such as *E. globulus*, *E. grandis*, *E. nitens*, *E. dunnii*, *E. benthamii* and *E. urophylla* vs. *E. grandis* predominate. Martins et al. (2022) projected that 49.2% to 56.7% of South America may become economically unviable for Eucalyptus cultivation by the end of the 21st century due to $WD_{annual} \geq 330$ mm year^{-1}. In Brazil, 15% to 47% of the territory is expected to become restricted or unsuitable for Eucalyptus cultivation (Florêncio et al. 2022), with productivity losses of ~40% (Palma et al. 2021) by 2100. In South Africa, suitable areas for *E. dunnii* and *E. grandis* may be reduced by ~25% and 30%, respectively, at GWL=2 °C (Warburton and Schulze 2008), while in Portugal and Spain, areas suitable for *E. globulus* may decline by up to 51% by 2070 (Deus et al. 2022).

The future of Eucalyptus plantations, particularly in the aforementioned regions, will depend on the implementation of assertive adaptation measures to minimize risks associated with patterns generated by GWLs.

4.1 Adaptation Measures to Deal with the Impacts of Global Warming

In general, the main cross-cutting adaptation measures applicable across multiple production contexts include (Florêncio et al. 2022; Martins et al. 2022; Mota et al. 2022; Aparecido et al. 2025; Fagundes et al. 2025): (i) selection of genotypes (pure species or hybrids)with greater tolerance to thermal and water stress and higher water-use efficiency; (ii) adjustments in silvicultural management practices; (iii) adoption of soil water conservation practices; (iv) strengthening early-warning systems and integrated pest and disease management; and (v) diversification of production systems through agroforestry arrangements.

Since the 21 risk indicators exhibit distinct spatial patterns and vary in area and magnitude, adaptation measures must be tailored to the specific conditions of each producing region (Table 4).

Furthermore, increases in the frequency and intensity of wildfires are expected (Tomé et al. 2021; Hutapea et al. 2023). Therefore, in locations with high wildfires occurrence (in descending order) like Australia, Brazil, the United States, Portugal, Spain, Chile, South Africa, Argentina, Bolivia, China, India, Mexico, and Paraguay (Reddy et al. 2019; Bowman et al. 2021; Hutapea et al. 2023; Fagundes et al. 2025), it is recommended to reduce plantation connectivity through firebreaks, non-flammable vegetation strips, or open buffer zones (Fagundes et al. 2025), and to integrate fire monitoring and suppression technologies (Tomé et al. 2021; Hutapea et al. 2023; Fagundes et al. 2025). Additionally, selecting less flammable genotypes, such as *E. urophylla*, *E. pellita*, *E. dunnii* and *E. grandis* vs. *E. urophylla* is advisable compared to highly flammable species such as *E. globulus* (van Groeningen et al. 2019; Modarres et al. 2024).

Adopting these alternative species introduces important industrial trade-offs, particularly regarding kraft pulping efficiency. Species and hybrids better adapted to high temperatures, water deficit, or frost events, such as *E. camaldulensis*, *E. saligna*, *E. grandis*, *E. viminalis*, and *E. benthamii*, generally exhibit lower pulp yields, often below 48% compared to *E. globulus*, thereby increasing specific wood consumption (Magaton et al. 2009; Neiva et al. 2015). Thus, the transition toward genetically more resilient materials to global warming may impose significant economic and operational challenges on the forestry sector.

Finally, these integrated approaches, combined with climate-resilience policies, financial support, and improved access to forest insurance, will be crucial to reducing risks

to Eucalyptus plantations under GWLs. However, it is important to emphasize that this study represents a generalized average across major commercial *Eucalyptus* species and does not account for species- and genotype-specific climatic requirements, which may lead to distinct responses across different regions. Therefore, future studies incorporating species-specific parameters are recommended to improve the accuracy of vulnerability assessments. Furthermore, future research employing machine learning–based approaches may contribute to more accurate and dynamic predictions of pest and disease outbreaks, as well as productivity losses, under different climate change scenarios.

5 Conclusions

Air temperature (minimum and mean) increases across the four global warming levels (GWLs 1.5 °C to 4 °C), ranging from +0.5 °C to +6 °C, while precipitation, relative humidity, global solar radiation, and crop evapotranspiration exhibit heterogeneous spatial patterns. These changes will be more intense in Brazil, central and southern Africa, southern Europe (Portugal, Spain, Italy, Greece, Turkey), Morocco, Saudi Arabia, India, China, and Australia, and less intense in Argentina, northern Europe, Russia, Thailand, Vietnam, and Indonesia.

Spatial patterns and risk magnitudes differ among the 21 indicators, with a general tend toward reduced risk severity across the four GWLs, particularly for disease- and pest-related indicators. Despite this slight reduction, spatial patterns at the 1.5 °C and 2 °C GWLs remain very similar to the control period.

The greatest vulnerabilities in Eucalyptus cultivation are associated with bioclimatic categories, especially productivity losses driven by water stress (CRpl and CRw). High to very high risks are observed across ~ 79% of the globe in the control period, ~ 78.7% at 1.5 and 2 °C GWLs, and ~ 78% at 3 and 4 °C GWLs, mainly in South America (Brazil, Argentina, Bolivia, Chile, Paraguay, and Peru), North America (Mexico and the southwestern United States), much of Africa, southern Europe (Portugal, Spain, Italy, Greece, and Turkey), extensive portions of Asia (from Saudi Arabia to India and northern China), and Australia.

Moreover, a consistent and spatially well-defined overlap of risks among the 21 indicators is evident across the GWLs, indicating heightened vulnerability of eucalyptus plantations in central South America and Central America, as well as in specific regions of Africa, Asia, and Oceania. These high-risk areas encompass major eucalyptus-producing countries, including Brazil, China, India, Australia, Chile, Portugal, Spain, Thailand, Argentina, Ecuador, Colombia, Paraguay, New Zealand, Pakistan, and Ethiopia.

Adapting Eucalyptus plantations to global warming requires region-specific measures. In general, these include selecting genotypes (pure species or hybrids) with greater tolerance to thermal and water stress and high water-use efficiency, adjusting silvicultural management practices, implementing soil water conservation techniques, strengthening early-warning systems and integrated pest and disease management, diversifying production systems through agroforestry arrangements, and controlling key diseases (*Chrysoporthe cubensis*, *Cryptosporiopsis eucalypti*, *Cylindrocladium* spp., *Quambalaria eucalypti* and *Necator salmonicolor*) and pests (*Leptocybe invasa* and *Mnesampela private*). These actions should be implemented in an integrated manner to effectively reduce risks to eucalyptus plantations across the GWLs. The 21 risk indicators developed in this study may support spatial planning tools and help identify areas with lower climatic and phytosanitary risk for future Eucalyptus plantations.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s41748-026-01319-9.

Acknowledgements The authors thank the Minas Gerais Research Support Foundation (FAPEMIG), for financially supporting the project APQ 01511-24, the Coordination for the Improvement of Higher Education Personnel (CAPES, process number 88887.825319/2023-00), for granting scholarships to the 1st author, and the National Council for Scientific and Technological Development (CNPq, process numbers 306845/2021-0 and 305799/2024-0) for the research fellowship granted to the 2nd author. We also thank the study group NEX-GDDP-CMIP6 for providing high-resolution GCMs.

Funding The Article Processing Charge (APC) for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614). This research was funded by the Minas Gerais Research Support Foundation (FAPEMIG), the Coordination for the Improvement of Higher Education Personnel (CAPES) and National Council for Scientific and Technological Development (CNPq). This study was financed in part by the CAPES- Brasil - finance code 001.

Data Availability The data generated during the study are available from the corresponding author upon reasonable request.

Declaration

Competing Interest The authors assert the absence of any conflicts of interest.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended

use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Abdu H, Robinson DA, Seyfried M, Jones SB (2008) Geophysical imaging of watershed subsurface patterns and prediction of soil texture and water holding capacity. Water Resour Res 44:e2008WR007043. https://doi.org/10.1029/2008WR007043

Abreu MC, Martins FB, Freitas CH, Pereira RAA, Melloni EGP (2015) Valores limítrofes para transpiração, desenvolvimento e crescimento de *Corymbia citriodora* (Hook.) K D Hill & L A S Johnson em resposta à deficiência hídrica no solo. Rev Árvore 39:841–852. https://doi.org/10.1590/0100-67622015000500007

Abreu MC, Soares AAV, Freitas CH, Martins FB (2022) Transpiration and growth responses by eucalyptus species to progressive soil drying. J Res 33:1–15. https://doi.org/10.1007/s11676-021-01448-z

Ahmad T, Zeng Q, Zheng Y, Moosa A, Nie C, Liu Y (2022) First record of Ceratocystis fimbriata causing quick wilt of Calotropis gigantea in Pakistan. Plant Dis 106:1755. https://doi.org/10.1094/PDIS-08-21-1786-PDN

Ahmadi SH, Javanbakht Z (2020) Assessing the physical and empirical reference evapotranspiration (ETo) models and time series analyses of the influencing weather variables on ETo in a semi-arid area. J Environ Manage 276:111278. https://doi.org/10.1016/j.jenvman.2020.111278

Akrofi AY, Amoako-Atta I, Assuah M, Kumi-Asare E (2014) Pink disease caused by *Erythricium salmonicolor* (Berk. & Broome) Burdsall: an epidemiological assessment of its potential effect on cocoa production in Ghana. J Plant Pathol Microbiol 5:1000215. https://doi.org/10.4172/2157-7471.1000215

Alexander LV, Arblaster JM (2017) Historical and projected trends in temperature and precipitation extremes in Australia in observations and CMIP5. Weather Clim Extrem 15:34–56. https://doi.org/10.1016/j.wace.2017.02.001

Alfenas AC, Zauza EAV, Mafia RG, Assis TF (2009) Clonagem e doenças do eucalipto. Universidade Federal de Viçosa, Viçosa

Allen RG, Pereira LS, Raes D, Smith M (1998) Crop evapotranspiration: guidelines for computing crop water requirements. FAO, Rome

Almazroui M, Saeed S, Islam MN, Ismail M (2020a) Projections of precipitation and temperature over the South Asian countries in CMIP6. Earth Syst Environ. https://doi.org/10.1007/s41748-020-00157-7

Almazroui M, Saeed F, Saeed S, Islam MN, Ismail M, Klutse NAB, Haroon M (2020b) Projected change in temperature and precipitation over Africa from CMIP6. Earth Syst Environ 4:455–475. https://doi.org/10.1007/s41748-020-00161-x

Almazroui M, Islam MN, Saeed F, Saeed S, Ismail M, Ehsan MA, Diallo I, O'Brien E, Ashfaq M, Martínez-Castro D, Cavazos T, Cerezo-Mota R, Tippett MK, Gutowski WJ Jr, Alfaro EJ, Hidalgo HG, Vichot-Llano A, Campbell JD, Kamil S, Rashid IU, Sylla MB, Stephenson T, Taylor M, Barlow M (2021) Projected changes in temperature and precipitation over the United States, Central America, and the Caribbean in CMIP6 GCMs. Earth Syst Environ 5:1–24. https://doi.org/10.1007/s41748-021-00199-5

Andrade GCG, Alfenas AC, Mafia RG, Zauza EAV, Couto MMF, Maffia LA (2007) Características culturais e severidade da mancha foliar de *Quambalaria eucalypti* sob diferentes regimes de temperatura, luz e período de molhamento foliar. Fitopatol Bras 32:329–334. https://doi.org/10.1590/S0100-41582007000400007

Aparecido LEO, Torsoni GB, Lima RF, Rolim GS, Mesquita DZ (2025) Redefining eucalyptus cultivation in South America: adaptive strategies under future climate scenarios. New For 56:36. https://doi.org/10.1007/s11056-025-10106-9

Auer CG, Santos AF, Bora KC (2010) A ferrugem do eucalipto na região Sul do Brasil. Embrapa Florestas, Colombo

Ayuga-Téllez E, García-Iruela A, Causí Rielo J, González-García C (2022) Actions for monitoring the *Gonipterus* pest in eucalyptus on the Cantabrian Coast. Agronomy 12:1692. https://doi.org/10.3390/agronomy12071692

Azevedo F, Figo ML (1979) *Ctenarytaina eucalypti* Maskell (Homoptera, Psyllidae). Bol Sanid Veg Plagas 5:41–46

Bacani VM, Silva BHM, Sato AASA, Sampaio BDS, Cunha ER, Vick EP, Oliveira VFR, Decco HF (2024) Carbon storage and sequestration in a eucalyptus productive zone in the Brazilian Cerrado using the Ca-Markov/Random Forest and InVEST models. J Clean Prod 444:141291. https://doi.org/10.1016/j.jclepro.2023.141291

Balmelli G, Simeto S, Altier N, Marroni V, Diez JJ (2013) Long-term losses caused by foliar diseases on growth and survival of Eucalyptus globulus in Uruguay. New For 44:249–263. https://doi.org/10.1007/s11056-012-9314-z

Barbosa LR, Santos FD, Soliman EP, Rodrigues AP, Wilcken CF, Campos JM, Zanuncio AJV, Zanuncio JC (2019) Biological parameters, life table and thermal requirements of *Thaumastocoris peregrinus* (Heteroptera: Thaumastocoridae) at different temperatures. Sci Rep 9:10174. https://doi.org/10.1038/s41598-019-45663-5

Barradas C, Pinto G, Correia B, Castro BB, Phillips AJL, Alves A (2018) Drought × disease interaction in *Eucalyptus globulus* under *Neofusicoccum eucalyptorum* infection. Plant Pathol 67:87–96. https://doi.org/10.1111/ppa.12703

Bartók B, Wild M, Folini D et al (2017) Projected changes in surface solar radiation in CMIP5 global climate models and in EURO-CORDEX regional climate models for Europe. Clim Dyn 49:2665–2683. https://doi.org/10.1007/s00382-016-3471-2

Betts RA, Alfieri L, Bradshaw C, César J, Feyen L, Friedlingstein P, Gohar L, Koutroulis A, Lewis K, Morfopoulos C, Papadimitriou L, Richardson KJ, Tsanis I, Wyser K (2018) Changes in climate extremes, fresh water availability and vulnerability to food insecurity projected at 1.5°C and 2°C global warming with a higher-resolution global climate model. Philos Trans R Soc A 376:20160452. https://doi.org/10.1098/rsta.2016.0452

Binkley D, Campoe OC, Alvares C, Carneiro RL, Cegatta Í, Stape JL (2017) The interactions of climate, spacing and genetics on clonal eucalyptus plantations across Brazil and Uruguay. Ecol Manag 405:271–283. https://doi.org/10.1016/j.foreco.2017.09.050

Bose T, Roux J, Titshall L, Dovey SB, Hammerbacher A (2025) Mulching of post-harvest residues and delayed planting improves fungal biodiversity in South African Eucalyptus plantations and enhances plantation productivity. Appl Soil Ecol 210:106091. https://doi.org/10.1016/j.apsoil.2025.106091

Bowman DMJS, Williamson GJ, Gibson RK, Bradstock RA, Keenan RJ (2021) The severity and extent of the Australia 2019–20 Eucalyptus forest fires are not the legacy of forest management. Nat Ecol Evol 5:1003–1010. https://doi.org/10.1038/s41559-021-01415-4

Castro-Toro AM, Rivillas-Osorio CA (2012) *Trichoderma* spp.: modos de acción, eficacia y usos en el cultivo de café. Federación Nacional de Cafeteros de Colombia/Cenicafé, Chinchiná

Cheewangkoon R, Groenewald JZ, Verkley GJM, Hyde KD, Wingfield MJ, Gryzenhout M, Summerell BA, Denman S, Toanun C, Crous PW (2010) Re-evaluation of *Cryptosporiopsis eucalypti* and *Cryptosporiopsis*-like species occurring on Eucalyptus leaves. Fungal Divers 44:89–105. https://doi.org/10.1007/s13225-010-0041-5

Chen X, Zhao P, Ouyang L, Zhu L, Ni G, Schäfer KV (2020) Whole-plant water hydraulic integrity to predict drought-induced Eucalyptus urophylla mortality under drought stress. Ecol Manag 468:118179. https://doi.org/10.1016/j.foreco.2020.118179

Deidda A, Buffa F, Linaldeddu BT, Pinna C, Scanu B, Deiana V, Satta A, Franceschini A, Floris I (2016) Emerging pests and diseases threaten Eucalyptus camaldulensis plantations in Sardinia. Italy iForest 9:883–891. https://doi.org/10.3832/ifor1805-009

Delgado-Baquerizo M, Guerra CA, Cano-Díaz C, Egidi E, Wang JT, Eisenhauer N, Singh BK, Maestre FT (2020) The proportion of soil-borne pathogens increases with warming at the global scale. Nat Clim Chang 10:550–554. https://doi.org/10.1038/s41558-020-0759-3

Deus E, Silva JS, Vicente JR, Catry FX (2022) Eucalypt recruitment and invasion potential in protected areas of the Iberian Peninsula under current and future climate conditions. Forests 13:1199. https://doi.org/10.3390/f13081199

Dias ACR (2010) Controle químico de doenças de Eucalyptus spp. em viveiros e seus efeitos morfo-fisiológicos. Dissertação (Mestrado em Ciência Florestal). Universidade Estadual Paulista Júlio de Mesquita Filho, Botucatu

Dias CG, Martins FB, Martins MA (2024) Climate risks and vulnerabilities of the Arabica coffee in Brazil under current and future climates considering new CMIP6 models. Sci Total Environ 907:167753. https://doi.org/10.1016/j.scitotenv.2023.167753

Dourado-Neto D, de Jong Q, Metselaar K, Reichardt K, Nielsen DR (2010) General procedure to initialize the cyclic soil water balance by the Thornthwaite and Mather method. Sci Agric 67:87–95. https://doi.org/10.1590/S0103-90162010000100013

Douville H, Willett KM (2023) A drier than expected future, supported by near-surface relative humidity observations. Sci Adv 9:ade6253. https://doi.org/10.1126/sciadv.ade6253

Elli EF, Sentelhas PC, Bender FD (2020) Impacts and uncertainties of climate change projections on eucalyptus plantation productivity across Brazil. Ecol Manag 474:118365. https://doi.org/10.1016/j.foreco.2020.118365

Fagundes FFA, Martins FB, Torres RR, Marrafon VHA (2025) Global warming levels (1.5–4°C) and water availability for eucalyptus plantations based on high-resolution CMIP6 models. Earth Syst Environ, pp 1–18. https://doi.org/10.1007/s41748-025-00916-4

Farda B, Sabbi E, Fares R, Djebaili R, Mignini A, Mitra D, Pellegrini M (2026) Shifting disease dynamics: effect of climate change on plant pathogens and their management in field crops. J Plant Biochem Biotechnol, pp 1–23. https://doi.org/10.1007/s13562-026-01042-6

Ferrari MP, Krügner TL, Couto HTZ (1984) Avaliação de perdas em rendimento de madeiras devido ao cancro do Eucalyptus causado por *Chryphonectria cubensis*. IPEF 27:9–15

Ferreira EM, Alfenas AC, Maffia LA, Mafia RG (2006) Eficiência de fungicidas sistêmicos para o controle de *Cylindrocladium candelabrum* em eucalipto. Fitopatol Bras 31:485–491. https://doi.org/10.1590/0100-41582006000500006

Ferreira EM, Alfenas AC, Maffia LA, Mafia RG, Mounteer AH (2008) Effectiveness of systemic fungicides in the control of *Quambalaria eucalypti* and their effects on production of eucalypt mini-cuttings for rooting. Crop Prot 27:161–170. https://doi.org/10.1016/j.cropro.2007.05.001

Ferreira NCR, Martins M, Tavares PST, Chou SC, Monteiro A, Gomes L, Santana A (2021) Assessment of crop risk due to climate change in São Tomé and Príncipe. Reg Environ Change 21:22. https://doi.org/10.1007/s10113-021-01746-6

Florêncio GWL, Martins FB, Fagundes FFA (2022) Climate change on eucalyptus plantations and adaptive measures for sustainable forestry development across Brazil. Ind Crops Prod 188:115538. https://doi.org/10.1016/j.indcrop.2022.115538

Flores TB, Alvares CA, Souza VC, Stape JL (2016) Eucalyptus no Brasil. IPEF, Piracicaba

Freitas CH, Elli EF, Sentelhas PC, Carneiro RL, Alvares CA (2020) Adaptation, calibration and evaluation of a simple agrometeorological model for wood eucalyptus productivity estimation. Eur J Res 139:759–776. https://doi.org/10.1007/s10342-020-01283-7

Garlet J, Costa EC, Boscardin J, Deponti G, Shwengber CR, Machado LM (2013) *Leptocybe invasa* em Eucalyptus sp. no estado do Rio Grande do Sul, Brasil. Cienc Rural 43:2175–2177

Gonçalves JL, Alvares CA, Rocha JH, Brandani CB, Hakamada R (2017) Eucalypt plantation management in regions with water stress. South For 79:169–183. https://doi.org/10.2989/20702620.2016.1255415

Guimarães LMS, Resende MDV, Lau D, Rosse LN, Alves AA, Alfenas AC (2010) Genetic control of *Eucalyptus urophylla* and *E. grandis* resistance to canker caused by *Chrysoporthe cubensis*. Genet Mol Biol 33:525–531. https://doi.org/10.1590/S1415-47572010005000069

Harper RJ, Smettem KRJ, Carter JO, McGrath JF (2009) Drought deaths in *Eucalyptus globulus* (Labill.) plantations in relation to soils, geomorphology and climate. Plant Soil 324:199–207. https://doi.org/10.1007/s11104-009-9948-1

Herms DA, Mattson WJ (1992) The dilemma of plants: to grow or defend. Q Rev Biol 67:283–335

Himaman W, Thamchaipenet A, Pathom-Aree W, Duangmal K (2016) Actinomycetes from Eucalyptus and their biological activities for controlling eucalyptus leaf and shoot blight. Microbiol Res 188–189:42–52. https://doi.org/10.1016/j.micres.2016.04.011

Hoogar R, Malakannavar S, Sujatha HT (2019) Impact of eucalyptus plantations on groundwater and soil ecosystem in dry regions. J Pharmacogn Phytochem 8:2929–2933

Hutapea FJ, Weston CJ, Mendham D, Volkova L (2023) Sustainable management of *Eucalyptus pellita* plantations: A review. Ecol Manag 537:120941. https://doi.org/10.1016/j.foreco.2023.120941

IBÁ (2025) Indústria Brasileira de Árvores: Relatório 2025. IBÁ, São Paulo

IPCC (2021) Climate change 2021: the physical science basis. Cambridge University Press, Cambridge

IPCC (2022) Summary for policymakers. In: Pörtner H-O, Roberts DC, Poloczanska ES, Mintenbeck K, Tignor M, Alegría A, Craig M, Langsdorf S, Löschke S, Möller V, Okem A, Rama B (eds) Climate change 2022: impacts, adaptation and vulnerability. Cambridge University Press, Cambridge. https://doi.org/10.1017/9781009325844.001

Jacome LH, Schuh W, Stevenson RE (1991) Effect of temperature and relative humidity on germination and germ tube development of *Mycosphaerella fijiensis* var. difformis. Phytopathology 81:1480–1485

Kadyampakeni DM, Morgan KT (2017) Irrigation scheduling and soil moisture dynamics influence water uptake by Huanglongbing-affected trees. Sci Hortic 224:272–279. https://doi.org/10.1016/j.scienta.2017.06.037

Krügner TL, Guerrini IA, Auer CG (1990) Surto epidêmico da mancha foliar causada por *Cylindrocladium* spp. e sua relação com o crescimento de espécies/procedências de Eucalyptus na região de Tucuruí, PA. IPEF 43–44:74–78

Kulkarni HD (2010) Screening Eucalyptus clones against *Leptocybe invasa* Fisher & La Salle (Hymenoptera: Eulophidae). Karnataka J Agric Sci 23:87–90

Künast TBS, Queiroz DL, Burckhardt D, Andrade EA, Barreto MR (2021) Efeito da temperatura no desenvolvimento e na reprodução de *Blastopsylla occidentalis* (Hemiptera: Aphalaridae) em condições de laboratório. Cienc Florest 31:440–455. https://doi.org/10.5902/1980509843846

Lemes PG, Nascimento DN, Costa RF, Matos MF, Soares IJA (2021) Glycaspis brimblecombei. In: Lemes PG, Zanuncio JC (eds) Novo manual de pragas florestais brasileiras. Instituto de Ciências Agrárias, Universidade Federal de Minas Gerais, Montes Claros, pp 824–839

Lu J, Sun G, McNulty SG, Amatya DM (2005) A comparison of six potential evapotranspiration methods for regional use in the southeastern United States. J Am Water Resour Assoc 41:621–633. https://doi.org/10.1111/j.1752-1688.2005.tb03759.x

Maciel CG, Lazarotto M, Mezzomo R, Poletto I, Muniz MFB, Lippert DB (2012) Trichoderma spp. no biocontrole de *Cylindrocladium* candelabrum em mudas de Eucalyptus saligna. Rev Árvore 36:833–841. https://doi.org/10.1590/S0100-67622012000500004

Magaton AS, Colodette JL, Gouvêa AFG, Gomide JL, Muguet MCS, Pedrazzi C (2009) Eucalyptus wood quality and its impact on kraft pulp production and use. Tappi J 8(8):32–39

Martins FB, Streck NA (2007) Aparecimento de folhas em mudas de eucalipto estimado por dois modelos. Pesq Agropec Bras 42:1091–1100. https://doi.org/10.1590/S0100-204X2007000800005

Martins FB, Streck NA, Silva JC, Morais WW, Susin F, Navroski MC, Vivian MA (2008) Deficiência hídrica no solo e seu efeito sobre transpiração, crescimento e desenvolvimento de mudas de duas espécies de eucalipto. Rev Bras Cienc Solo 32:1297–1306. https://doi.org/10.1590/S0100-06832008000300037

Martins FB, Benassi RB, Torres RR, Brito Neto FA (2022) Impacts of 1.5°C and 2°C global warming on eucalyptus plantations in South America. Sci Total Environ 825:153820. https://doi.org/10.1016/j.scitotenv.2022.153820

Martins FB, Florêncio GWL, Ferreira MC, Fagundes FFA, Freitas CH (2023) Predicting seedling development for two commercial forest species under current and future climates: a multi-model assessment. Ecol Manag 537:120929. https://doi.org/10.1016/j.foreco.2023.120929

Mba WP, Longandjo GNT, Moufouma-Okia W, Bell JP, James R, Vondou DA, Haensler A, Fotso-Nguemo TC, Guenang GM, Tchotchou ALD, Kamsu-Tamo PH, Takong RR, Nikulin G, Lennard C, Dosio A (2018) Consequences of 1.5°C and 2°C global warming levels for temperature and precipitation changes over Central Africa. Environ Res Lett 13:055011. https://doi.org/10.1088/1748-9326/aab048

Meehl GA, Tebaldi C, Nychka D (2004) Changes in frost days in simulations of twenty-first century climate. Clim Dyn 23:495–511. https://doi.org/10.1007/s00382-004-0442-9

Modarres M, Almeida M, Viegas DX (2024) Experimental and numerical fire behaviour analysis in Eucalyptus globulus trees. Int J Wildland Fire 33:WF23131. https://doi.org/10.1071/WF23131

Monteiro AFM, Martins FB, Torres RR, Almeida VHM, Abreu MC, Mattos EV (2021) Intercomparison and uncertainty assessment of methods for estimating evapotranspiration using a high-resolution gridded weather dataset over Brazil. Theor Appl Climatol 146:583–597. https://doi.org/10.1007/s00704-021-03747-1

Mota JS, Barbosa LR, Marchioro CA (2022) Suitable areas for invasive insect pests in Brazil and the potential impacts for eucalyptus forestry. Pest Manag Sci 78:2596–2606. https://doi.org/10.1002/ps.6891

Mota JS, Barbosa LR, Marchioro CA (2023) Climate change impacts the risk of invasion of eucalypt pests in Brazil. Agric Entomol 26:101–114. https://doi.org/10.1111/afe.12599

National Forest Inventory Steering Committee (2019) Australia's state of the forests report 2018. Australia

Nazarenko LS, Tausnev N, Russell GL, Rind D, Miller RL, Schmidt GA, Bauer SE, Kelley M, Ruedy R, Ackerman AS, Aleinov I, Bauer M, Bleck R, Canuto V, Cesana G, Cheng Y, Clune TL, Cook BI, Cruz CA, Del Genio AD, Elsaesser GS, Faluvegi G, Kiang NY, Kim D, Lacis AA, Leboissetier A, LeGrande AN, Lo KK, Marshall J, Matthews EE, McDermid S, Mezuman K, Murray LT, Oinas V, Orbe C, Pérez García-Pando C, Perlwitz JP, Puma MJ, Romanou A, Shindell DT, Sun S, Tsigaridis K, Tselioudis G, Weng E, Wu J, Yao M (2022) Future climate change under SSP emission scenarios with GISS-E2.1. J Adv Model Earth Syst 14:e2021MS002871. https://doi.org/10.1029/2021MS002871

Neiva D, Fernandes L, Araújo S, Lourenço A, Gominho J, Simões R, Pereira H (2015) Chemical composition and kraft pulping potential of 12 eucalypt species. Ind Crops Prod 66:89–95. https://doi.org/10.1016/j.indcrop.2014.12.016

Nievola CC, Carvalho CP, Carvalho V, Rodrigues E (2017) Rapid responses of plants to temperature changes. Temperature 4:371–405. https://doi.org/10.1080/23328940.2017.1377812

Nomi C, Sato H, Kobayashi T (2000) Occurrence and life-history of pink disease caused by *Erythricium salmonicolor* in northern Kanto, Honshu, Japan. J Agric Sci Tokyo Univ 44

Oberschelp GPJ, Guarnaschelli AB, Teson N, Harrand L, Podestá FE, Margarit E (2020) Cold acclimation and freezing tolerance in three Eucalyptus species: A metabolomic and proteomic approach. Plant Physiol Biochem 154:316–327. https://doi.org/10.1016/j.plaphy.2020.05.026

Old KM, Dudzinski MJ, Pongpanich K, Yuan ZQ, Pham Quang T, Nguyen Tran N (2002) *Cryptosporiopsis* leaf spot and shoot blight of eucalypts. Australas Plant Pathol 31:337–344. https://doi.org/10.1071/AP02037

Palma JHN, Hakamada R, Moreira GG, Nobre S, Rodriguez LCE (2021) Using 3PG to assess climate change impacts on management plan optimization of Eucalyptus plantations: A case study in southern Brazil. Sci Rep 11:2708. https://doi.org/10.1038/s41598-021-81907-z

Pandey PK, Dabral PP, Pandey V (2016) Evaluation of reference evapotranspiration methods for the northeastern region of India. Int Soil Water Conserv Res 4:52–63. https://doi.org/10.1016/j.iswcr.2016.02.003

Pegg GS, Webb RI, Carnegie AJ, Wingfield MJ, Drenth A (2009) The infection and disease development of *Quambalaria* spp. on *Corymbia* and Eucalyptus species. Plant Pathol 58:642–654. https://doi.org/10.1111/j.1365-3059.2009.02087.x

Penna AC, Torres RR, Garcia SR, Marengo JA (2021) Moisture flows in southeast Brazil: Present and future climate. Int J Climatol 41:E935–E951. https://doi.org/10.1002/joc.6738

Petro R, Madoffe SS, Iddi S, Mugasha WA (2015) Impact of *Leptocybe invasa* infestation on growth and biomass production of *Eucalyptus grandis* and *E. saligna* seedlings in Tanzania. Int J Pest Manag 61:220–227. https://doi.org/10.1080/09670874.2015.1039096

Pham NQ, Wingfield BD, Marincowitz S, Brawner JT, Hulcr J, Wingfield MJ (2025) *Cryphonectria canker* on Eucalyptus in Florida reconsidered. https://doi.org/10.1111/efp.70031. For Pathol e70031

Piveta G (2013) Morfologia, caracterização molecular e patogenicidade de *Ceratocystis fimbriata* no Rio Grande do Sul. Tese (Doutorado em Engenharia Florestal), Universidade Federal de Santa Maria, Santa Maria

Pizzi MB (2016) Perdas de produtividade de 12 clones de eucalipto submetidos a desfolhas artificiais sucessivas. Dissertação (Mestrado em Ciência Florestal). Universidade Estadual Paulista Júlio de Mesquita Filho, São Paulo

Pradhanang PM (1994) Pink disease (*Corticium salmonicolor* Berks & Broome) control in mandarin orange (*Citrus reticulata Blanco*) by application of Bordeaux mixture. Crop Prot 13:550–552. https://doi.org/10.1016/0261-2194(94)90109-0

Protasov A, La Salle J, Blumberg D, Brand D, Saphir N, Assael F, Fisher N, Mendel Z (2007) Biology, revised taxonomy and impact on host Trachymela sloanei plants of *Ophelimus maskelli*, an invasive gall inducer on *Eucalyptus* spp. in the Mediterranean area. Phytoparasitica 35:50–76. https://doi.org/10.1007/BF02981061

Puretz BO, Potrich M, Miranda FDA, Lozano ER, Freddo Á (2015) Nota científica: Distribuição da vespa da galha do eucalipto. Pesq Florest Bras 35:329–334

Purvis G, Chauzat MP, Segonds-Pichon A, Dunne R (2002) Life history and phenology of the eucalyptus psyllid, *Ctenarytaina eucalypti*, in Ireland. Ann Appl Biol 141:283–292. https://doi.org/10.1111/j.1744-7348.2002.tb00220.x

Queiroz DL, Künast TBS, Cremonese JT, Dalle Cort G, Sá LAN, Barbosa LR, Schnell BG, Burckhardt D (2020) Criação de *Blastopsylla occidentalis*. Hemiptera: Aphalaridae), psilídeo das ponteiras do eucalipto, em casa de vegetação. Comunicado Técnico 442. Embrapa, Colombo

Rao NH, Sarma PBS, Chander S (1988) A simple dated water-production function for use in irrigated agriculture. Agric Water Manag 13:25–32. https://doi.org/10.1016/0378-3774(88)90130-8

Rapley LP, Allen GR, Potts BM (2004) Oviposition by autumn gum moth (Mnesampela privata) in relation to Eucalyptus globulus defoliation, larval performance and natural enemies. Agric Entomol 6:237–243. https://doi.org/10.1111/j.1461-9555.2004.00224.x

Rapley LP, Potts BM, Battaglia M, Patel VS, Allen GR (2009) Long-term realised and projected growth impacts caused by autumn gum moth defoliation of 2-year-old Eucalyptus nitens plantation trees in Tasmania, Australia. Ecol Manag 258:1896–1903. https://doi.org/10.1016/j.foreco.2009.06.036

Reddy CS, Bird NG, Sreelakshmi S, Manikandan TM, Asra M, Krishna PH, Jha CS, Rao PVN, Diwakar PG (2019) Identification and characterization of spatio-temporal hotspots of forest fires in South Asia. Environ Monit Assess 191:791. https://doi.org/10.1007/s10661-019-7695-6

Riahi K, van Vuuren DP, Kriegler E, Edmonds J, O'Neill BC, Fujimori S, Bauer N, Calvin K, Dellink R, Fricko O, Lutz W, Popp A, Cuaresma JC, Emmerling J, Ebi K, Hasegawa T, Humpenöder F, Silva LA, Smith S, Stehfest E, Bosetti V, Eom J, Gernaat D, Masui T, Rogelj J, Strefler J, Drouet L, Krey V, Luderer G, Harmsen M, Takahashi K, Baumstark L, Doelman JC, Kainuma M, Klimont Z, Marangoni G, Lotze-Campen H, Obersteiner M, Tabeau A, Tavoni M (2017) The shared socioeconomic pathways and their energy, land use, and greenhouse gas emissions implications: An overview. Glob Environ Change 42:153–168. https://doi.org/10.1016/j.gloenvcha.2016.05.009

Rodas CA, Gryzenhout M, Myburg H, Wingfield BD, Wingfield MJ (2005) Discovery of the eucalyptus canker pathogen *Chrysoporthe cubensis* on native Miconia (Melastomataceae) in Colombia. Plant Pathol 54:460–470. https://doi.org/10.1111/j.1365-3059.2005.01223.x

Ruelland E, Zachowski A (2010) How plants sense temperature. Environ Exp Bot 69:225–232. https://doi.org/10.1016/j.envexpbot.2010.05.011

Ruv Lemes MC, Sampaio G, Garcia-Carreras L, Fisch G, Alves LM, Bassett R, Bispo PDC (2023) Impacts on South America moisture transport under Amazon deforestation and 2°C global warming. Sci Total Environ 905:167407. https://doi.org/10.1016/j.scitotenv.2023.167407

Samuel S, Dosio A, Mphale K, Faka DN, Wiston M (2023) Comparison of multi-model ensembles of global and regional climate model projections for daily characteristics of precipitation over four major river basins in southern Africa. Part II: Future changes under 1.5°C, 2.0°C and 3.0°C warming levels. Atmos Res 293:106921. https://doi.org/10.1016/j.atmosres.2023.106921

Santana DLQ, Zanol KM, Botosso PC, Mattos PP (2005) Danos causados por *Ctenarytaina spatulata* Taylor, 1977 (Hemiptera: Psyllidae) em Eucalyptus grandis. Pesq Florest Bras 50:11

Santos DR, Reichert JM (2022) Best tillage practices for eucalyptus growth and productivity: A review. Rev Bras Cienc Solo 46:e0220074

Sharma JK, Mohanan C (1991) In vitro evaluation of fungicides against *Cylindrocladium* spp. causing diseases of Eucalyptus in Kerala, India. Eur J Pathol 21:17–26

Shi C, Jiang ZH, Chen WL, Li L (2018) Changes in temperature extremes over China under 1.5°C and 2°C global warming targets. Adv Clim Change Res 9:120–129. https://doi.org/10.1016/j.accre.2017.11.003

Silva X, Asiegbu FO (2023) Eucalyptus fungal diseases. Forest microbiology. Academic, pp 313–337

Silva G, Folorunso TR, Paez AM, Lamka GF, Singh S, King J, Henderson L, Persyn M, Mwema T, Lindow T, Amiri N, Eckhardt L, Narine L, Willoughby JR (2026) Biology, Detection, and Management of Lecanosticta acicola: Emerging Challenges for the Management of Brown Spot Needle Blight in Pine Forests. Path 56(1):e70061. https://doi.org/10.1111/efp.70061

Soares TP, Ferreira MA, Mafia RG, Oliveira LS, Hodges CS, Alfenas AC (2018) Canker disease caused by Chrysoporthe doradensis and *C. cubensis* on Eucalyptus sp. and Tibouchina spp. in Brazil. Trop Plant Pathol 43:314–322. https://doi.org/10.1007/s40858-018-0238-9

Solís M, Hammerbacher A, Wingfield MJ et al (2025) Enhancing plantation forest sustainability: A review of Eucalyptus defence mechanisms to foliar fungal pathogens. Curr Rep 11:13. https://doi.org/10.1007/s40725-024-00243-3

Souza SE, Sansigolo CA, Furtado EL, Jesus Junior WC, Oliveira RR (2010) Influência do cancro basal em *Eucalyptus grandis* nas propriedades da madeira e polpação kraft. Sci For 38:547–557

Souza NM, Soliman EP, Ribeiro MF, Wilcken CF (2021) *Gonipterus platensis* e *Gonipterus pulverulentus*. In: Lemes PG, Zanuncio JC (eds) Novo manual de pragas florestais brasileiras. Instituto de Ciências Agrárias, Universidade Federal de Minas Gerais, Montes Claros, pp 840–853

Steinbauer MJ, McQuillan PB, Young CJ (2001) Life history and behavioural traits of *Mnesampela privata* that exacerbate population responses to eucalypt plantations: comparisons with Australian and outbreak species of forest geometrid from the Northern Hemisphere. Austral Ecol 26:525–534

Steinbauer MJ, Kriticos DJ, Lukacs Z, Clarke AR (2004) Modelling a forest lepidopteran: phenological plasticity determines voltinism which influences population dynamics. Ecol Manag 198:117–131. https://doi.org/10.1016/j.foreco.2004.03.041

Szyniszewska AM, Akrivou A, Björklund N, Boberg J, Bradshaw C, Damus M, Gardi C, Hanea A, Kriticos J, Maggini R, Musolin DL, MacLeod A (2024) Beyond the present: How climate change is relevant to pest risk analysis. EPPO Bull 54:20–37. https://doi.org/10.1111/epp.12986

Tambarussi EV, Silva ED, Costa RM, Santos JFF, Jatzek VA, Resende RT (2023) Growth and survival of *Eucalyptus viminalis* in a frost-prone site in southern Brazil, and implications for genetic management. N Z J Sci 53:e236. https://doi.org/10.33494/nzjfs532023x236x

Teulières C, Bossinger G, Moran G, Marque C (2007) Stress studies in Eucalyptus. Global Science Books

Thornthwaite CW, Mather JR (1955) The water balance. Drexel Institute of Technology, Laboratory of Climatology

Thornthwaite CW, Mather JR (1957) Instructions and tables for computing potential evapotranspiration and the water balance. Drexel Institute of Technology, Laboratory of Climatology

Thrasher B, Wang W, Michaelis A, Melton F, Lee T, Nemani R (2022) NASA global daily downscaled projections, CMIP6. Sci Data 9:262. https://doi.org/10.1038/s41597-022-01393-4

Tomé M, Almeida MH, Barreiro S, Branco MR, Deus E, Pinto G, Silva JS, Soares P, Rodríguez-Soalleiro R (2021) Opportunities and challenges of Eucalyptus plantations in Europe: the Iberian Peninsula experience. Eur J Res 140:489–510. https://doi.org/10.1007/s10342-021-01358-z

Torres RR, Benassi RB, Martins FB, Lapola DM (2021) Projected impacts of 1.5°C and 2°C global warming on temperature and precipitation patterns in South America. Int J Climatol 42:1597–1611. https://doi.org/10.1002/joc.7322

Trajkovic S, Kolakovic S (2009) Evaluation of reference evapotranspiration equations under humid conditions. Water Resour Manag 23:3057–3067. https://doi.org/10.1007/s11269-009-9423-4

Turc L (1961) Estimation of irrigation water requirements, potential evapotranspiration: a simple climatic formula evolved up to date. Ann Agron 12:13–49

UNFCCC (2015) Adoption of the Paris Agreement. United Nations Framework Convention on Climate Change, Paris

van Groeningen T, Mngomezulu LB, Meincken M (2019) Thermal degradation of *Eucalyptus dunnii* and *Eucalyptus macarthurii* trees exposed to fire. Eur J Wood Wood Prod 77:1151–1160. https://doi.org/10.1007/s00107-019-01451-6

Vitasse Y, Spafford L, Reim J, Baumgarten F, Martínez-Sancho E (2025) Emerging trend of increasing spring frost damage for beech at higher elevations in the Jura Mountains: evidence from tree-ring data. New Phytol 248:600–614. https://doi.org/10.1111/nph.70471

Walker PW, Allen GR (2011) Delayed mating and reproduction in the autumn gum moth *Mnesampela privata*. Agric Entomol 13:149–156. https://doi.org/10.1111/j.1461-9563.2011.00524.x

Walsh M, Backlund P, Buja L, DeGaetano A, Melnick R, Prokopy L, Ziska L (2020) Climate indicators for agriculture. USDA Tech Bull 1953:1–75. https://doi.org/10.22004/ag.econ.320800

Warburton ML, Schulze RE (2008) Potential impacts of climate change on the climatically suitable growth areas of Pinus and Eucalyptus: results from a sensitivity study in South Africa. South For 70:27–36. https://doi.org/10.2989/SOUTH.FOR.2008.70.1.5.515

Xavier RG, Martins FB, Dias CG (2026) Integrated climate, pest, and disease risk indicators for Pinus plantations under current and future climates. Earth Syst Environ, pp 1–26. https://doi.org/10.1007/s41748-026-01195-3

Xu J, Peng S, Ding J, Wei Q, Yu Y (2012) Evaluation and calibration of simple methods for daily reference evapotranspiration estimation in humid East China. Int J Biometeorol 56:845–858. https://doi.org/10.1007/s00484-011-0481-5

Xu J, Xie S, Han A, Rao R, Huang G, Chen X, Jue H, Qian L, Xueyun Y, Zhang L (2019) Forest resources in China: the 9th national forest inventory. National Forestry and Grassland Administration, Beijing

Yaduvanshi A, Zaroug M, Bendapudi R, New M (2019) Impacts of 1.5°C and 2°C global warming on regional rainfall and temperature change across India. Environ Res Commun 1:125002. https://doi.org/10.1088/2515-7620/ab4ee2

Yang L, Kong J, Gao Y, Chen Z, Lin Y, Zeng S, Su Y, Li J, He Q, Qiu Q (2023) A simulated drier climate reduces growth and alters functional traits of Eucalyptus trees: a three-year experiment in South China. Ecol Manag 549:121435. https://doi.org/10.1016/j.foreco.2023.121435

Yousuf M, Singh S, Ikram M, Khan S (2020) Biological control of eucalyptus gall wasp, *Leptocybe invasa* Fisher & La Salle (Hymenoptera: Eulophidae) in Punjab, India. J Appl Nat Sci 5

Zhang G, Zeng G, Yang X, Jiang Z (2021) Future changes in extreme high temperature over China at 1.5°C–5°C global warming based on CMIP6 simulations. Adv Atmos Sci 38:253–267. https://doi.org/10.1007/s00376-020-0182-8

Fagundes FFA, Martins FB, Reis YFS, Costa HF (2024) Predicting temperature ranges for the initial development of two native Brazilian tree species using multiple sowing dates. Ecol Manag 562:121912. https://doi.org/10.1016/j.foreco.2024.121912

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

suzano

FuturaGene®

Yielding the Future