

# Tree crown defoliation in forest monitoring: concepts, findings, and new perspectives for a physiological approach in the face of climate change

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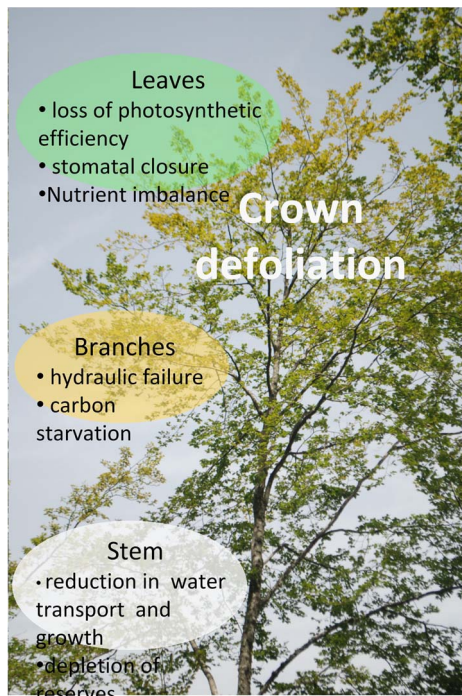
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Recurrent climate-driven disturbances impact on the health of European forests that reacted with increased tree dieback and mortality over the course of the last four decades. There is therefore large interest in predicting and understanding the fate and survival of forests under climate change. Forest conditions are monitored within the pan-European ICP Forests programme (UN-ECE International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests) since the 1980s, with tree crown defoliation being the most widely used parameter. Defoliation is not a cause-specific indicator of tree health and vitality, and there is a need to connect defoliation levels with the physiological functioning of trees. The physiological responses connected to tree crown defoliation are species-specific and concern, among others, water relations, photosynthesis and carbon metabolism, growth, and mineral nutrients of leaves. The indicators to measure physiological variables in forest monitoring programs must be easy to apply in the field with current state-of-the-art technologies, be replicable, inexpensive, time efficient and regulated by *ad hoc* protocols. The ultimate purpose is to provide data to feed process-based models to predict mortality and threats in forests due to climate change. This study reviews the problems and perspectives connected to the realization of a systematic assessment of physiological variables and proposes a set of indicators suitable for future application in forest monitoring programs.

## Graphical Abstract



Handling editor: Dr. Fabian Fassnacht

Received: January 19, 2023. Revised: December 7, 2023. Accepted: December 9, 2023.

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## Introduction

In the context of climate change, where extreme climatic events are expected to become more frequent and harsher (Spinoni et al. 2018, Hari et al. 2020, Moravec et al. 2021), the future condition and fate of forests are of growing importance. In recent years, the increased recurrence and severity of climate-driven disturbances have been impacting European forests (Forzieri et al. 2021, Romeiro et al. 2022, Patacca et al. 2023). The impact of climate on defoliation, crown dieback and tree mortality has been discussed previously (Allen et al. 2010, Anderegg et al. 2013, 2015). Taking the uncertainty related to the magnitude and character of climate change as context, several papers addressed tree vitality on country, regional and European level in recent years (Neumann et al. 2017, Gazol and Camarero 2022, George et al. 2022, Jaime et al. 2022), with many basing their analysis on the ICP Forests dataset.

The systematic assessment of the condition of European forests was launched in the 1980s within the ICP Forests programme (Sanders et al. 2016) (UN-ECE International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests, <https://unece.org/environmental-policy/air/forests>; Supplementary Information—SI1). Within this framework, several parameters are monitored. The most widely used parameter is tree crown defoliation. Defoliation is defined in the ICP Forests Manual—Part IV (Visual assessment of crown condition and damaging agents), as needle or leaf loss in the crown as compared to a reference tree (Eichhorn and Roskams 2014, Eichhorn et al. 2020). Defoliation is an unspecific indicator, integrating the intrinsic genetic constitution of trees and site effects (soil fertility, climatic features, structure, and composition of the forest stand), and can be considered indicative of the equilibrium of a tree in its own environment, representing the result of accumulated impacts of stressful environmental conditions. External fluctuating pressures, such as abiotic and biotic factors, can cause year-to-year variations of defoliation. In addition to defoliation, other parameters concerning damage symptoms on different parts of the tree (leaves, branches, trunk) are assessed. The term ‘tree condition’, therefore, refers to the overall appearance of a tree, encompassing defoliation and damage symptoms. Concurrently, the term ‘tree health’, as defined by Innes (1993), refers to the incidence of both abiotic and biotic factors affecting trees within a forest. The vitality of a tree concerns ‘the capacity to assimilate carbon, to resist stress, to adapt to changing environmental conditions and to reproduce’ (Brang 1998). The concept of ‘tree vitality’ has been reviewed by Dobbertin (2005), who concluded that physiological indicators may best reflect the reaction of trees to environmental stressors. Unfortunately, many such indicators are difficult to measure in the field.

Because of the complex interactions of external and internal factors influencing defoliation and tree vitality, evidence concerning the relationships between levels of defoliation and physiological status of trees were often considered elusive and contradictory (Innes 1988a), although recent studies (reviewed in this paper) filled this gap at least partially. In current and future scenarios of climate change, the fate of forests is strictly connected to the physiological impacts and responses (acclimatization, recovery, decline) of trees. It is, therefore, of crucial importance to connect ‘condition’ (defoliation and damage symptoms) and ‘vitality’ of trees by means of physiological indicators.

In this paper, we undertake a comprehensive review of the concepts and key findings associated with defoliation, drawing on over 30 years of monitoring activities within the ICP Forests

programme. We explore the role of main factors as determinants for defoliation and subsequently investigate the physiological aspects connected to this phenomenon. The aims of this review are: (i) to analyse the physiological implications of defoliation in the light of the currently available literature, (ii) to outline a strategy for the assessment of the physiological condition of trees in the field; (iii) to identify a set of indicators suitable for assessing the physiological condition of trees in the field. The methods for the selection of literature are reported in Supplementary Information 2 (SI2).

## Assessment of defoliation and quality assurance in the ICP Forests programme

Defoliation is assessed visually regardless of the cause of foliage loss, and it is scored in 5% steps, starting from 0% (no defoliation) up to 100% defoliation (indicating a dead tree). Defoliation has been criticized because it is assessed visually and may be affected by the subjectivity of field surveyors and serious errors can occur (Innes 1988a, 1988b, 1990, Innes et al. 1993, Ghosh et al. 1995, Ghosh and Innes 1995, Redfern and Boswell 2004). To assess and reduce the subjectivity of field crews, a lot of effort was invested within ICP Forests into the development and implementation of Quality Assurance (QA) protocols (Ferretti et al. 2009, 2021a, Ferretti and König 2013). The QA activities included the production of a field manual (latest version: Eichhorn et al. 2020), photo-guides for the most important tree species and environmental conditions (Innes 1990, Müller and Stierlin 1990, Ferretti 1994), photo-exercises and international and national training/intercalibration/intercomparison courses for the personnel involved in field assessments. Results demonstrated that the QA objectives can be reached with mean deviation of defoliation (with respect to the crown assessment ‘reference’ team) within the  $\pm 10\%$  interval for single sample trees and  $\pm 5\%$  per plot (Ferretti et al. 1999, Solberg and Strand 1999, Bussotti et al. 2009, Eickenscheidt and Wellbrock 2014, Meining et al. 2016). These achievements make defoliation data quite reliable in a time series, but differences between countries persist because of differences in the methodological approaches (Klap et al. 2000). Defoliation levels and patterns at European level are analyzed in ICP Forests Technical reports annually (<http://icp-forests.net/page/icp-forests-technical-report>), revealing a general trend of increasing defoliation over time, with species-specific patterns (Potočić et al. 2021, Timmermann et al. 2022).

## Site factors and environmental stress as the driving factors for defoliation

Analyses of ICP Forests data reveal that site factors (physical like elevation, climate, and soil conditions, and vegetational like forest structure and composition) are of fundamental importance in explaining the levels of defoliation, with defoliation being higher in higher elevation and dryer sites (Klap et al. 2000, Seidling 2001, Seidling and Mues 2005). In a study carried out in Bavarian Alps (Germany), Ewald (2005) found that defoliation is influenced by soil chemistry, increasing towards shallow calcareous soils.

## Forest age, structure, and tree species composition

Crown defoliation was found to increase with stand age in several studies (Table 1, Solberg 1999a, Eichhorn et al. 2005, Pokorný and Stojnič 2012, Eickenscheidt et al. 2019); however, exceptions have been observed (Iacopetti et al. 2019). Basal area, leaf area index,

**Table 1.** Papers dealing with the relationships of defoliation with forest age and structure, on the ICP Forests monitoring plots.

Authors	Country/Region	Species	Main findings
Solberg (1999b)	Norway (country)	<i>Picea abies</i>	Highly significant correlations were found between crown density and age on <i>P. abies</i>
Ewald (2005)	Germany (Bavarian Alps)	<i>P. abies</i>	Defoliation was controlled by soil chemistry (defoliation increased towards shallow calcareous soils) and stand age.
Eichhorn et al. (2005)	Germany (country)	<i>Fagus sylvatica</i> , <i>Quercus</i> sp.pl.	Defoliation shows clear relations with age, relative crown spacing, composition, and fruit bearing.
Pokorný and Stojnič (2012)	Czech Republic	<i>P. abies</i>	Defoliation increases with Leaf Area Index reduction in oldest forests
Vitale et al. (2014)	South Europe	<i>F. sylvatica</i> , <i>P. abies</i>	Tree crown defoliation was mainly related to age in <i>P. abies</i> and in <i>F. sylvatica</i> .
Ferretti et al. (2014a)	France (country)	Several species	Defoliation correlates with tree density and frequency of trees with reported health problems.
Pollastrini et al. (2016)	Italy (Tuscany)	Broadleaved species	The shape of the crowns and their area (LAI) affected forest defoliation.
Eickenscheidt et al. (2019)	Germany (country)	Several species	Stand age is the most relevant factor explaining defoliation in German forests.
Ugarkovic et al. (2021)	Croatia (country)	<i>Abies alba</i>	Decline of <i>A. alba</i> trees was slower in mixed stands, and tree mortality was higher in pure stands.

and tree density are also predictors for defoliation, but their relative role changes according to the species and site characteristics (Ferretti et al. 2014b, 2015, Pollastrini et al. 2016a). Basal area and leaf area index were negatively correlated to defoliation in a regional survey in Central Italy (Pollastrini et al. 2016a), with species-specific effects. Ferretti et al. (2014b), in a study on French forests, have shown that the direction of the effect of tree density may be different according to the species and the site. In a successive study, Ferretti et al. (2015) found that tree density was negatively correlated to defoliation in Central European forests. Higher tree density may increase defoliation in drought-sensitive forests (Carnicer et al. 2011, Toigo et al. 2020) because of the competition among trees for water resources in the soil. The effects of the combination of these variables may be complex, depending also on the ecological requirements of species (sun loving trees/Heliophytes vs. shade loving trees/Sciophytes; early successional vs. late successional). The role of species composition on defoliation was explored by the studies listed in Table 2. The variation in defoliation in beech was found to mostly depend on the basic tree and stand variables such as age, relative crown spacing, stand composition and fruiting (Eichhorn et al. 2005). High basal area and leaf area index in a forest stand can be achieved with few large dominant trees, which correspond to low density and low tree–tree competition, or with a greater number of small trees (with high density and high competition among trees). Ugarkovic et al. (2021) also found that the decline of *Abies alba* Mill. trees was slower in mixed stands, and that tree mortality was higher in pure stands. Tree diversity was proven to increase the resilience of forests under increasing stress conditions, as observed by Sousa-Silva et al. (2018) in Belgian forests, Bussotti et al. (2018a) and Iacopetti et al. (2019) in Italy.

### Atmospheric deposition and air pollutants

The ICP Forests monitoring programme was launched as a reaction to the concerns about the alleged impacts of air pollution on forests. In the 1980s, acidifying atmospheric depositions of sulfur (S) and nitrogen (N) were singled out as causal agent of the so-called ‘forest decline’ (Waldsterben, in the German literature) in Central Europe and North America (Schütt and Cowling 1985, Schulze 1989), although this interpretation was questioned by

Skelly and Innes (1994) and Kandler and Innes (1995). For example, atmospheric nitrogen depositions are nowadays known to both act as acidifying factor, but also as fertilizer that positively affects tree growth (Etzold et al. 2020). The latter effect is expected to alleviate defoliation (De Marco et al. 2014). Sulfur and nitrogen inputs to the ecosystems have been decreasing since the beginning of the 21st century (Waldner et al. 2014, Schmitz et al. 2019) whereas increasing attention was devoted to tropospheric ozone concentrations (O<sub>3</sub>), that is now the most widespread air pollutant impacting the forests in some parts of Europe (Gerosa et al. 2007). In a Europe wide analysis, De Vries et al. (2014) concluded that subtle effects on defoliation of long-term nitrogen inputs and high tropospheric ozone levels, can be masked by other stronger influences, such as climate and site factors. It is hence difficult to clearly discern the effects of air pollution on defoliation from other site and stress factors.

Statistical analyses of the data from the ICP Forests monitoring network tried to discern the role of pollutants as contributing factors for tree crown defoliation at national and transnational levels, with contrasting results summarized in Table 3. Of the 14 papers listed, connection between air pollution and atmospheric deposition with defoliation were found by 8 of them (Rehfuess 1991, Innes 1992, Nelleman and Frogner 1994, Hendricks et al. 1997, Augustaitis et al. 2007, Thimonier et al. 2010, Vitale et al. 2014, Ferretti et al. 2014a), whereas 6 (Andersson 1990, Innes and Whittaker 1993, Solberg and Tørseth 1997, Aamlid et al. 2000, Ferretti et al. 2015, Jakovljević et al. 2019) found contradictory results or no relationships. The results, however, depend on the statistical analysis method, the species assessed (most papers deal with conifers, especially *Picea abies* (L.) Karst. and *Pinus sylvestris* L.), the air pollution metrics and the geographical range considered.

In Table 4, 16 papers discussing the role of ozone as contributing factor to defoliation are listed. A negative impact of the environmental levels of ozone was recognized in 10 papers (Sanz et al. 2000, Ferretti et al. 2003, Ferretti et al. 2007, Augustaitis and Bytnerowicz 2008, Sicard and Dalstein-Richier 2015, Diaz-de-Quijano et al. 2016, Sicard et al. 2016, De Marco et al. 2017, Araminiene et al. 2019, Sicard et al. 2020). Only one paper deals with fluxes (Zierl 2002) and 5 papers found no effect

**Table 2.** Papers dealing with the relationships of defoliation with stand composition and tree diversity, on the ICP Forests monitoring plots.

Authors	Country/Region	Species	Main findings
Eichhorn et al. (2005)	Germany (country)	<i>Fagus sylvatica</i> , <i>Quercus</i> sp.pl.	Tree diversity is an explicative variable for defoliation in <i>Fagus</i> but not in <i>Quercus</i> .
Pollastrini et al. (2016)	Italy (Tuscany)	Broadleaved species	Tree diversity reduced defoliation in <i>Castanea sativa</i> affected by <i>Dryocosmus kuriphilus</i>
Sousa-Silva et al. (2018)	Belgium (country)	<i>F. sylvatica</i> , <i>Quercus</i> sp.pl.	Higher species diversity reduces the impacts of severe drought stress.
Bussotti et al. (2018)	Italy (North)	<i>Picea abies</i>	Defoliation of <i>P. abies</i> is higher in ecotonic zones with high diversity.
Iacopetti et al. (2019)	Italy (country)	Several species	A beneficial role of diversity has been observed in <i>Quercus ilex</i> and <i>P. abies</i> after dry periods.
Ugarkovic et al. (2021)	Croatia (country)	<i>Abies alba</i>	Different effects of tree diversity are explicated with the structure of forests.

**Table 3.** Papers dealing with the relationships of defoliation with primary air pollutants (Nitrogen and Sulfur) and acidic deposition.

Authors	Country/Region	Species	Main findings
Andersson (1990)	Sweden	Conifers	The defoliation of conifers does not have a linear relationship with the pollution gradient.
Rehfuess (1991)	Germany	<i>Picea abies</i>	The significance of pollutants and acidic deposition has been identified only for the high elevation sites.
Innes (1992)	UK (country)	Several species	Surveys of tree condition have provided no indication that forest trees in the UK are being adversely affected by air pollution.
Innes and Whittaker (1993)	UK (country)	<i>P. abies</i>	Relationships with pollution variables were identified with <i>Picea sitkensis</i> and <i>P. abies</i> .
Nelleman and Frogner (1994)	Norway (country)	<i>P. abies</i>	Defoliation was connected to stand acidification
Hendricks et al. (1997)	The Netherland (country)	<i>P. abies</i>	Defoliation was connected to stand acidification
Solberg and Tørseth (1997)	Norway (country)	<i>P. abies</i>	No evident support for the hypothesized negative effect on crown condition from sulfur and nitrogen deposition.
Aamlid et al. (2000)	Norway (country)	<i>P. abies</i>	The actual effect of the air pollution is difficult to estimate but its importance is not discounted.
Augustaitis et al. (2007)	Lithuania (country)	<i>Pinus sylvestris</i>	Significant impact of SO <sub>2</sub> on <i>P. sylvestris</i> defoliation
Thimonier et al. (2010)	Switzerland (country)	Conifers	Crown defoliation tended to be negatively correlated with nitrogen concentrations in the needles.
Vitale et al. (2014)	South Europe	<i>Quercus ilex</i>	Tree crown defoliation was related to air pollution predictors in <i>Q. ilex</i> .
Ferretti et al. (2014a)	Europe	Several species	Variables related to nitrogen deposition improve defoliation models for European forests
Ferretti et al. (2014a)	Italy (country)	Several species	No impact on crown condition attributed to nitrogen depositions in permanent monitoring plots in Italy.
Jakovljević et al. (2019)	Croatia (country)	Several species	No relevant differences in mean defoliation between the plots were observed in relation to air pollutants.

(Bussotti and Ferretti 2009, Ciriani and Dalstein 2018, Gottardini et al. 2018, Paoletti et al. 2019, Jakovljević et al. 2021). Responsive tree species were *Pinus* sp.pl. and to a lesser extent, *Fagus sylvatica* L.

### Climatic factors

The main findings concerning the relationships between tree crown defoliation and climatic factors are summarized in Table 5. Baseline levels of defoliation are expected to be higher in dry and warm sites (Popa et al. 2017). Correlations between climatic factors and defoliation (positive for temperature, negative for precipitation) were found by Popa et al. (2017) in Romania, although with species-specific and site-specific effects (high altitude species favor increasing temperatures). Fluctuating seasonal drought conditions explain year-to-year changes in defoliation (de la Cruz et al. 2014, Ferretti et al. 2014b, Sánchez-Cuesta et al. 2021). Several studies indicate that defoliation can be

delayed with respect to the drought event (Solberg 2004, Zierl 2004, Seidling 2007, Ferretti et al. 2014b, Ognjenović et al. 2022). For example, Solberg (2004) specified that in the 1990s Southern Norway was repeatedly affected by summer drought inducing increased needle-fall in *P. abies*, in the autumns after dry summers.

Drought and climatic factors interact with biotic factors in determining defoliation and tree death (Anderegg et al. 2015). *P. abies* and other conifers are threatened by mass outbreaks of the bark beetle *Ips typographus* L. promoted by heat, wind throw and drought (Netherer et al. 2015, 2019, 2021). Infective diseases can also be promoted by drought stress. This is the case for oomycetes in the genus *Phytophthora*, involved in the decline of several *Quercus* species affected by drought stress in Central and Mediterranean Europe (Jung et al. 1999, 2000, Jung 2009, Colangelo et al. 2018), with similar effects recorded also in *F. sylvatica* (Jung 2009). Environmental stress factors may trigger shifts from latent to pathogenic stages in endophytes such as *Biscogniauxia*

**Table 4.** Papers dealing with the relationships of defoliation with tropospheric ozone.

Authors	Country/Region	Species	Main findings
Sanz et al. (2000)	Spain (country)	<i>Pinus halepensis</i>	In <i>P. halepensis</i> ozone injury affects needle retention and increases defoliation
Zierl (2002)	Switzerland (country)	Several species	A hydrological model connected crown conditions with stomatal ozone uptake in Swiss forests.
Ferretti et al. (2003)	Italy (country)	<i>Fagus sylvatica</i> , <i>Picea abies</i>	Defoliation increases with ozone levels in <i>F. sylvatica</i> but not in <i>P. abies</i> .
Ferretti et al. (2007)	Italy (country—selected plots)	<i>F. sylvatica</i>	Ozone levels are significant predictor for defoliation in <i>F. sylvatica</i> .
Augustaitis and Bytnerowicz (2008)	Lithuania (country)	<i>Pinus sylvestris</i>	Peak of ambient O <sub>3</sub> have a negative impact on <i>P. sylvestris</i> crown defoliation and stem growth reduction.
Bussotti and Ferretti (2009)	Italy (country—selected plots)	<i>F. sylvatica</i>	Ozone is a predictor of crown transparency in <i>F. sylvatica</i> , but the variance explained amounts to less than 10%.
Sicard and Dalstein-Richier (2015)	SE France	<i>Pinus cembra</i> , <i>P. halepensis</i>	On <i>P. cembra</i> and <i>P. halepensis</i> , ozone caused yellow spots and then the older needles dropped off, causing a defoliated canopy.
Diaz-de-Quijano et al. (2016)	Spain (Pyrenée)	<i>Pinus uncinata</i>	Ozone contributed to the crown defoliation and tree mortality in <i>P. uncinata</i> .
Sicard et al. (2016)	SE France—NW Italy	<i>Pinus</i> sp.pl. and various broadleaves	Ozone levels significantly correlated with crown discoloration and crown defoliation in conifers ( <i>Pinus</i> ) and broadleaves
De Marco et al. (2017)	Romania (country)	Several species	Ozone concentration and levels were the most important predictors of defoliation. Ozone uptake was not related to defoliation.
Ciriani and Dalstein (2018)	France (country)	Several species	No relation was found between ozone levels and defoliation.
Gottardini et al. (2018)	Italy (Trentino)	<i>P. abies</i>	Tree defoliation and growth are not in relationship with ozone exposure.
Araminiene et al. (2019)	Lithuania (country)	<i>P. sylvestris</i>	Ozone levels was correlated with crown defoliation and doses with visible foliar injury
Paoletti et al. (2019)	Italy, France, Romania	Several species	Defoliation is not related to ozone.
Sicard et al. (2020)	Italy, France, Romania	Several species	Ozone levels was correlated with crown defoliation in a transnational assessment.
Jakovljević et al. (2021)	Croatia—Mediterranean forests	<i>Quercus pubescens</i> , <i>Pinus nigra</i> , <i>Pinus halepensis</i>	Defoliation was significantly correlated with soil water content at various depths, but not with ozone

(=*Hypoxylon mediterranea* (De Not.) Kuntze, *Biscognauxia nummularia* (Bull.) Kuntze and *Sphaeropsis sapinea* (Fr.) Dyko & B. Sutton (Vannini and Valentini 1995, Desprez-Loustau et al. 2006, Capretti and Battisti 2007).

The impact of biotic stressors on tree defoliation and mortality has also been explored on data from the ICP Forests network (Table 6). Jaime et al. (2022) observed that the combined influence of drought events and bark beetle attacks can threaten the persistence of European coniferous forests. Extensive decline and mortality in alpine coniferous forests was also detected on the Italian Level I plots (Bussotti et al. 2022) as a consequence of bark beetle attacks following severe windstorms and a sequence of dry years. The increased occurrence of infectious diseases favored by climatic conditions was observed by Sánchez-Cuesta et al. (2021) in Southern Spain (*Phytophthora* sp.pl.) and Bussotti et al. (2023a, 2023b) in central Italy (*Biscognauxia* sp.pl.). Toïgo et al. (2020), in a French survey, also confirmed that year-to-year fluctuations of defoliation depend mainly on climatic factors, biotic agents and their interactions.

## Defoliation and mortality of trees under climate change

Under a sudden and severe stress event, such as a drought and heat wave, defoliation increases sharply (Fig. 1). After that, different pathways are possible: (i) the level of defoliation goes back to the optimal condition (resilience, Lloret et al. 2011); (ii) defoliation increases with respect to the pre-event levels (sub-optimal condition); (iii) successive stress events can increase decline and lead to death (rupture).

The shifting of climatic conditions, with a progressive increase in temperature across Europe (IPCC 2021), and the recurrence of drought and heat waves are the new challenges for the forests. Recently, widespread defoliation, premature leaf senescence, crown dieback and tree mortality in different European countries and bio-climatic zones (Bréda et al. 2006, Pollastrini et al. 2019, Rohner et al. 2021, Brun et al. 2020) were attributed to extreme heat and drought events that are recurring in Central and Southern Europe from the beginning of the 21st century (Rebetez et al. 2006, Rita et al. 2019, Schuldt et al. 2020).

**Table 5.** Papers dealing with the relationships of defoliation with basic climatic factors (year-to-year fluctuations of temperature and seasonal drought) on the ICP Forests monitoring plots

Authors	Country/Region	Species	Main findings
Katzensteiner et al. (1992)	Austria (Bohemian forest)	<i>Picea abies</i>	Drought periods and nutritional imbalances enhance needle loss.
Zierl (2004)	Switzerland (country)	Several species	Significant impacts of drought were detected for deciduous tree species. Weak correlations were found for conifers.
Solberg (2004)	Norway	<i>P. abies</i>	Defoliation in <i>P. abies</i> resulted from increased needle-fall in the autumn after dry summers.
Potočić et al. (2005)	Croatia (country)	<i>Abies alba</i>	The combined influence of drought and acid soils affects especially <i>A. alba</i> trees of higher defoliation.
Seidling (2007)	Germany (country)	<i>Pinus sylvestris</i> , <i>P. abies</i> , <i>Fagus sylvatica</i>	The responses of <i>P. sylvestris</i> , <i>P. abies</i> and <i>F. sylvatica</i> after 2003 hot and dry summer responded 1-year late
Ferretti et al. (2014b)	France (country)	Several species	Defoliation correlates precipitation-related variables of the current and previous years.
de la Cruz et al. (2014)	Spain (country)	Several species	Significant factors related to defoliation were the thermal-related factors and oscillation of both the current year and the previous year.
Popa et al. (2017)	Romania (country)	Several species	The influence of temperature on defoliation was lower than precipitation.
Eickenscheidt et al. (2019)	Germany (country)	Several species	Fluctuations in defoliation were related to weather conditions. South-Western Germany was the region with the highest defoliation since the drought year 2003.
Ognjenović et al. (2020)	Croatia (country)	<i>F. sylvatica</i>	High temperatures during spring and summer months of current and previous year induce the increase of defoliation.
Sánchez-Cuesta et al. (2021)	Spain (Andalusia)	<i>Quercus</i> sp.pl.	The annual defoliation and mortality were correlated with the mean annual temperature, drought and soil organic matter content.

**Table 6.** Papers dealing with the relationships of defoliation with biotic interactions on the ICP Forests monitoring plots.

Authors	Country/Region	Species	Main findings
Toigo et al. (2020)	France (country)	<i>Fagus sylvatica</i> , <i>Quercus</i> sp.pl.	Crown defoliation was generally higher in the event of insect attack and under drought.
Sánchez-Cuesta et al. (2021)	Spain (Andalusia)	<i>Quercus</i> sp.pl.	Mortality is connected to <i>Phytophthora</i> interactions.
Bussotti et al. (2021)	Italy (Alps)	<i>Picea abies</i>	High defoliation and mortality in Alpine regions connected to bark beetle attacks following a severe windstorm.
Bussotti et al. (2022)	Italy (Tuscany)	<i>Quercus</i> sp.pl., <i>F. sylvatica</i>	Death is induced by endophytes ( <i>Biscognauxia</i> sp.pl.) in declining <i>F. sylvatica</i> and <i>Quercus</i> sp.pl. tree species
Jaime et al. (2022)	Europe	Conifers	The joint influence of drought events and bark beetle disturbance will threaten the persistence of European coniferous forests.

Drought and heat events and their effects on defoliation are discussed in the papers listed in Table 7. Trends of increasing crown defoliation and tree mortality in relation to recurrent severe droughts, and defoliation peaks in dry years, have been recorded in Southern Europe (Carnicer et al. 2011), Italy (Bussotti et al. 2021, 2023a, 2023b), Switzerland (Rohner et al. 2021); Serbia (Češljar et al. 2022) and Southern Spain (Navarro et al. 2022). Recent heat and drought waves were characterized, alongside a strong water deficit in the soil, by high temperatures and increased vapor pressure deficit (VPD) and were found partially responsible for increasing tree mortality in Europe (Gazol and Camarero 2022).

## Defoliation and physiological processes

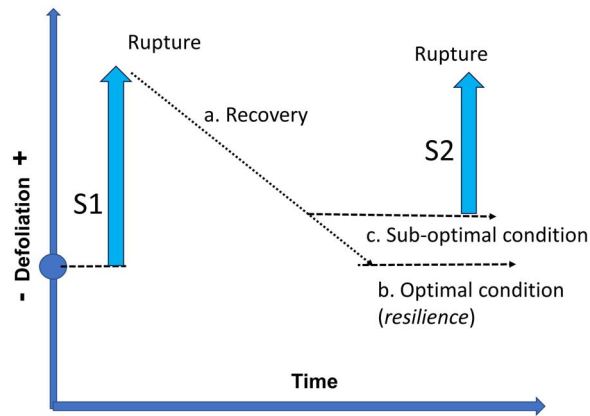
### Water relations and transport

With drought being one of the most important drivers for defoliation, water relations play a central role in the dynamic leaf loss and in the vitality of a tree. Drought stress can be induced both by low levels of water in the soil and by high VPD (Schönbeck et al. 2022). VPD regulates xylem cavitation and recovery processes (Grossiord et al. 2020).

Trees subjected to drought stress reduce the density of the crown (reduction of the number and size of leaves) to regulate the transpiration rates. Drought during the time of bud formation, on

**Table 7.** Papers dealing with the patterns of defoliation of trees under severe climate change and heat and drought waves, on the ICP Forests monitoring plots.

Authors	Country/Region	Species	Main findings
Carnicer et al. (2011)	Spain (country)	Several species	Defoliation trends are paralleled by significant increases in tree mortality rates in drier areas that are related to tree density and temperature effects.
Bussotti et al. (2021)	Italy (country)	Different species	Deciduous species suffer the loss of leaves in during the 2017 drought and heat wave. Extremely defoliated and dead trees increased over time.
Rohner et al. (2021)	Switzerland	<i>Fagus sylvatica</i>	The 2018 summer drought induced severe crown transparency, leaf browning and growth reduction in Swiss <i>F. sylvatica</i> forests.
Češljár et al. (2022)	Serbia (country)	Different species	High defoliation and mortality were observed in the dry 2014–2018 period.
Navarro et al. (2022)	Spain (Andalusia)	<i>Abies pinsapo</i>	Increasing defoliation and mortality in the 2001–2017 period.
Gazol and Camarero (2022)	Europe	Several species	Increasing mortality in the European Level I network is connected to 'composite' drought events (with high VPD)
Bussotti et al. (2023a)	Italy (Tuscany)	Broadleaved species	Severe dieback of evergreen Mediterranean vegetation and extensive foliar abscission in deciduous species happened during the severe heat and drought 2017–2022.
George et al. (2022)	Europe	Several species	An increasing trend in mortality rates was found, accompanied by decreasing soil moisture. Drought was the most important driver of mortality patterns in conifers.

**Figure 1.** Events following the impact of a severe stress event (S1) that provokes an increase of defoliation. The tree can undergo death or decline (i.e. rupture), or go toward a recovery process (a). Recovery can lead to defoliation levels of the previous optimal condition (resilience, b) or to defoliation levels of sub-optimal conditions with higher defoliation with respect to the pre-event state (c). Successive impacts can provoke the rupture of the system (S2).

the other hand, influences both the number of new leaves and leaf surface area in the following year (Bréda et al. 2006), resulting in a delayed effect on crown defoliation. Moreover, current-year level of crown defoliation and preceding-year atmospheric drought conditions were observed to influence leaf traits in beech such as leaf mass (LM) or leaf mass per area (LMA), while needle mass and length in spruce were influenced by the current year spring climate (Zhu et al. 2022). Leaf rolling is also a consequence of drought (Terzi 2007, Kadiouglua et al. 2012).

Walthert et al. (2021) evidenced that defoliation in *F. sylvatica* trees, under drought stress, is induced by cavitation in the xylem vessels (hydraulic failure), that may have consequences on tree water transport also in the following years (Braun et al. 2021). Under extreme drought, hydraulic failure is one of the most likely causes of leaf shedding, branch desiccation and death of trees (García-Fórner et al. 2019, Limousin et al. 2022). Therefore, leaf and twig abscission can be viewed as a final adaptation strategy to reduce evapotranspiration (McDowell et al. 2008).

In case of defoliation induced by insect herbivory, the alterations of the structure of the overall vascular transport (xylem and phloem) may increase tree vulnerability to drought (Foster 2017, Hillabrand et al. 2019). Hydraulic conductivity measurements showed that defoliated trees had both increased vulnerability to embolism and decreased water transport efficiency. Phloem sieve tube diameter was reduced in the stems of defoliated trees, suggesting reduced transport capability (Hillabrand et al. 2019).

During leaf shedding, the remaining leaves of affected trees increase their stomatal conductance to maintain the overall crown transpiration at the level of non-defoliated trees (Pataki et al. 1998, Hart et al. 2000, Quentin et al. 2012, Eyles et al. 2013). Highly defoliated trees are more likely impacted from subsequent drought and heat waves (Camarero et al. 2015, Guada et al. 2016). Therefore, recurrent droughts have more severe impact on tree defoliation and mortality, compared to a progressive shift of meteorological parameters (Jentsch et al. 2007). According to Salmon et al. 2015, defoliated trees tend to have lower water potentials and smaller hydraulic safety margins, while non-defoliated trees show a typical response to drought for anisohydric species. These responses put defoliated trees at higher risk of branch and stem hydraulic failure and help explain the interaction between carbon starvation and hydraulic failure in dying trees. After the defoliation event, the stabilization of all water status parameters occurs as acclimatization process (Bouzidi et al. 2019).

## Photosynthesis and carbon metabolism (growth and defense)

### Photosynthesis

Photosynthesis is a key process for tree vitality, since it is the primary source of carbohydrates, that are essential products for growth (cellulose and other structural carbohydrates) and defense (starch and soluble sugars, non-structural carbohydrates—NSCs). The intrinsic factors that affect the rates of photosynthesis at the tree level are the foliar surface, the chlorophyll content, and the efficiency of the photosynthetic apparatus. The first effect of defoliation is therefore the decrease of photosynthesis at the tree level, followed by the increase of photosynthetic rates at

the leaf level, as a compensatory mechanism since the remaining leaves have better access to the environmental resources as water, nutrients, and light (Briske 1986, Turnbull et al. 2007, Quentin et al. 2012, Eyles et al. 2013). Plants subjected to severe or moderate defoliation may display higher content of chlorophyll, RuBisCO and soluble proteins in the residual leaves than not defoliated plants (Ovaska et al. 1993). Opposite results were found by Turnbull et al. (2007), who reported that increased photosynthetic rates immediately following partial defoliation were primarily a result of increased activity, rather than amount, of the photosynthetic machinery. Partial defoliation allows a better exploitation of sunlight energy but, at the same time, induces photoinhibition processes of the photosystem II (PSII), with the reduction of the maximum quantum yield of primary photochemistry (expressed by the parameter  $F_v/F_m$ ) (Gottardini et al. 2016, 2020). A rise of the electron transport rate beyond the photosystem I (PSI) compensates for this reduction of  $F_v/F_m$ , with species-specific patterns, as shown by Pollastrini et al. (2017).

### Tree growth

Growth is considered an integrative indicator of tree vitality (Dobbertin 2005), and new research underlines the importance of long-term monitoring of defoliation and growth as main tree health indicators (Table 8). Neycken et al. (2022) and Peters et al. (2020) found that climatic events and insect outbreaks can lead to higher defoliation and narrow tree rings in the year of the impact. Negative relations between defoliation and stem growth were found on *P. abies* in Norway (Solberg 1999b, Solberg and Tveite 2000) and *Quercus robur* L. in Southern Sweden (Drobishchev et al. 2007). Ferretti et al. (2021b), analyzing tree rings of the Alpine belt conifer species in Northern Italy (*P. abies*, *Larix decidua* Mill., *A. alba*, *Pinus cembra* L., *P. sylvestris*) found that the relationship between defoliation and growth becomes stronger when data were aggregated over longer time scales, integrating different growth dynamics and delayed impacts. Ferretti et al. (2021c) used the mean periodical defoliation (averaged over 10 years) and the 10-year cumulated growth to determine possible negative effects of defoliation on tree growth, concluding that basal area increment (BAI) is consistently negatively and significantly related to mean defoliation, across functional groups and for most of the tree species considered, at a rate of 0.9% per unit increase of defoliation. The difference in BAI becomes significant at 15% (overall) and 15%–30% (individual species) defoliation levels. Tallieu et al. (2020) also observed significant effects of soil water on the growth of *F. sylvatica* when the difference of defoliation was more than 20% with respect to the previous year.

An asynchrony between defoliation and tree ring width series was registered by several authors. Seidling et al. (2012), Ferretti et al. (2014b) and Tallieu et al. (2020), analyzing annual tree growth, observed that the sprouting of new leaves and the length of branchlets depend on the climate conditions of the previous year, whereas the radial tree growth depends on the water availability in the soil in the current year (Navarro-Cerrillo et al. 2020). Finally, in terms of sensitivity of tree health indicators, Tallieu et al. (2020) found that radial growth presents a strong common signal among trees, while the response of defoliation was more distinct at the individual tree level, resulting in defoliation capturing fewer pointer years than radial growth. However, in view of the significant negative relation of radial growth to defoliation, Ferretti et al. (2021b) support the use of defoliation as a rapid indicator of forest health and vitality.

### Non-structural carbohydrates (NSCs)

Reduced production of photosynthates and higher physiological demand for protection under stress conditions provoke the depletion of NSCs as one of the main effects of the defoliation stress induced by drought or insect attacks (for review see Hartmann and Trumbore 2016, Piper and Paula 2020, Wang et al. 2021, El Omari 2022). NSCs are essential for resource transport, energy metabolism and cell osmoregulation, and allow the synthesis of defense compounds playing a crucial role in tree physiological defense systems against environmental and biotic stress and for restoring their growth and post-stress recovery (Furze et al. 2019, Piper and Paula 2020). *L. decidua* trees defoliated by outbreaks of the larch budmoth (*Zeiraphera diniana* Guenée) every 9 years, have been shown to use NSC reserves to rebuild the crown (second flush), but growth stops earlier than during normal years causing narrower tree-rings (Peters et al. 2020).

NSCs storage buffers the asynchrony of supply and demand on daily and seasonal scales and across plant organs (Hartmann and Trumbore 2016). Low levels of NSCs constitute a condition of carbon starvation, and tree mortality is likely to occur if the amount of these compounds falls below certain species-specific thresholds (Barker Plotkin et al. 2021). NSCs are also involved in the protection against hydraulic failure. Tomasella et al. (2017) suggest that, after drought stress, *P. abies* trees repair xylem embolism thanks to the NSCs stored in xylem parenchyma. This process implies dependency on sapwood NSCs reserves for survival, especially if frequent drought spells occur.

The metabolism of carbon in drought-defoliated trees affects both growth and storage of NSCs, with different dynamics. Some studies carried out on defoliated coniferous (*Pinus pinaster* Ait., Puri et al. 2015) and broadleaved (*Quercus velutina* Lam., Wiley et al. 2013) trees evidenced the reduction of growth but not of the NSCs reserves. In an experiment on *Abies balsamea* (L.) Mill., Deslauriers et al. (2015) rejected the hypothesis of a trade-off between growth and NSCs storage, since almost all the related variables decreased in defoliated trees. The reduction of NSCs happens first in the fine roots (Kosola et al. 2001), due to their prevailing action as carbon sinks (e.g. root growth for soil water exploration), as shown by Aguadé et al. (2015). Wang et al. (2021) suggest a shift in the C allocation towards shoots over roots, and in post-defoliation years growth happens at the expense of NSCs reserves that are diverted from defense to growth.

The recovery of NSCs pools after defoliation can take several years: observations in Mediterranean evergreen forests (López Bernat et al. 2009, Galiano et al. 2012) show that 10 years after a drought event, starch stocks in *Quercus ilex* L. trees have only recovered to half of their former amount. Severely defoliated trees after an extreme event can restore their NSCs reserves and full physiological functionality when defoliation periodicity varies from 15 to 60 years (Medvigy et al. 2012), depending on species, climatic regions, and environmental conditions. When the periodicity of extreme events is more frequent, substantial changes may occur in the ecosystems (Saura-Mas et al. 2015) and the co-occurrence of stresses may lead to more severe episodes of decline and tree mortality (De Grandpré et al. 2018). Recovery of carbon reserves and growth is more rapid and complete in trees growing in resource rich environments (Erbilgin et al. 2014).

### Nutritional factors

Loss of nutrients from the system, disruption of nutrient cycling and uptake, or imbalances in nutrient status can be associated with declines in forest productivity and stability



**Table 8.** Papers dealing with the relationships of defoliation with tree growth on the ICP Forests monitoring plots.

Authors	Country/Region	Species	Main findings
Solberg (1999a)	Norway	<i>Picea abies</i>	Crown condition and growth were correlated in <i>P. abies</i> , although with moderate strength.
Solberg and Tveite (2000)	Norway	<i>P. abies</i>	Approximately 1% change in crown density corresponded to 1% change in growth in <i>P. abies</i> .
Drobishev et al. (2007)	Sweden	<i>Quercus robur</i>	Differences in tree-ring increment between <i>Q. robur</i> trees with healthy crowns and trees with heavily declining crowns were pronounced.
Seidling et al. (2012)	Germany	<i>Fagus sylvatica</i> , <i>P. abies</i>	In <i>F. sylvatica</i> and <i>Pinus sylvestris</i> current year's crown defoliation was negatively correlated with stem increment.
Tallieu et al. (2020)	French (country)	<i>F. sylvatica</i>	No relationship occurs with tree-rings in cases of slight or moderate defoliation.
Navarro-Cerrillo et al. (2020)	Sothern Spain	<i>Abies pinsapo</i>	A positive association was found between stand defoliation and relative growth.
Ferretti et al. (2021c)	France (country)	Several species	Basal Area Increment resulted negatively and significantly related to defoliation, with a significant reduction detected already at slight (15%) defoliation level in conifers and a less clear trend in broadleaves.
Ferretti et al. (2021b)	North Italy (Trentino)	Conifers	Negative correlation between defoliation and annual or periodical stem diameter growth in conifers.

(Nilsson et al. 1995, Jonard et al. 2015). Katzensteiner et al. (1992) correlated poor nutrition of *P. abies* stands with excessive needle shedding. Potočić et al. (2005) found that drought caused low needle Ca concentrations in *A. alba* trees of all defoliation classes but affected especially trees in higher defoliation classes growing on acidic soils. After conducting a fertilization experiment in young *A. balsamea* stands, Ouimet and Moore (2015) observed that an increase in K concentration in needles results in a decrease in defoliation.

Many investigations focused on the relationship of defoliation and nutritional status of *F. sylvatica*. A study in Northern Spain recorded higher P concentrations in more defoliated *F. sylvatica* trees (Amores et al. 2006). Jonard et al. (2010) report that higher defoliation values are associated with lower Ca and Mg concentrations in a liming and P/K fertilization experiment in *F. sylvatica* stands in the Belgian Ardennes. Ferretti et al. (2015) found that the share of *F. sylvatica* trees with defoliation over 25% increase with increasing foliar N/Ca and N/K ratios, indicating that defoliation is related to imbalance in foliar nutrients. On the other hand, Ognjenović et al. (2020, 2023) were not able to establish direct relationships but found that both defoliation and foliar nutrient composition reacted to temperature variables. Ewald (2005) states heterogeneous environmental conditions as the reason for the lack of significant relationships between nutrient concentrations and *P. abies* defoliation status in Bavaria, Germany. An alteration of the chemical composition of declining *P. sylvestris* needles was found by Tzvetkova and Hadjiivanova (2006), with K deficiency and an increase of peroxidase activity. The consequences of defoliation on the chemical composition of *P. sylvestris* needles depend on the intensity and timing of defoliation, where the source–sink position of damaged needles play a relevant role (Lyytikäinen-Saarenmaa 1999). Overall, the interaction of nutrition and defoliation, as well as the relation of these two vitality indicators with climate conditions is not well understood and demands more research efforts.

## Assessing tree vitality with physiological indicators

### Towards a system for a physiological assessment of tree vitality

In a new generation of concepts and practices for forest condition monitoring, it will be desirable to combine the traditional visual system described in the current manual (Eichhorn et al. 2020) with new physiologically based indices (Niinemets 2010, Bussotti and Pollastrini 2015, Bussotti and Pollastrini 2017a, 2017b, Bussotti and Pollastrini 2021), effective to describe the vitality of trees. Such indices must be easy to apply in the field, measurable with current state-of-the-art technologies and replicable; moreover, they should be inexpensive and time efficient (Bussotti and Pollastrini 2021, Munné-Bosch and Villadangos 2023). The assessment of all the physiological indicators must be regulated with common *ad hoc* protocols elaborated and validated with direct experience in the field.

Different sets of field indicators for the assessment of the physiological condition of trees are proposed in the literature, with different levels of difficulty for sampling, measurement, and analysis. Each set of parameters is indicative of different physiological processes. The combination of different parameters with the visual assessment of tree crowns (defoliation and damage symptoms) will give a holistic picture on the impacts and processes of decline or recovery. In the following paragraphs we briefly discuss their potential and limitations.

### Physiological indicators of tree vitality

#### Tree ring analysis

Taking tree cores is simple and inexpensive. Tree ring measurement (dendrochronology) is a very informative approach for the analysis of past events (Cherubini et al. 2021). The cores, moreover, can be subjected to chemical analysis to detect stable isotopes and elements of exogenic origin (Ferretti et al. 2002), thereby

allowing a comprehensive reconstruction of the history of the tree in its environment. Tree coring also offers the possibility to analyze the xylem traits (Carrer et al. 2015, Pandey et al. 2018, Borghetti et al. 2020, Lens et al. 2022) in relation to drought stress, e.g. the relative amount of earlywood and latewood, vessel diameter, conduit area, xylem conductivity, etc. Although considered sometime a practice potentially detrimental for tree vitality, Portier et al. (2023) found no statistical evidence that tree coring reduces tree growth and mortality.

### Foliar analysis

Leaves from the top of the crowns are sampled in the Level II plots for the analysis of the mineral nutrition (Rautio et al. 2020). The collection of leaves from tall trees being an expensive operation, the costs can be optimized with the measurement of different physiological variables on the same foliar sample (Bussotti and Pollastrini 2015). The analyses proposed below don't require special permanent equipment within the plots.

Functional leaf traits, such Leaf Area (LA), Specific Leaf Area (SLA), Leaf Mass per Area (LMA), Relative Water Content (RWC) and so on, are easily assessable on detached leaves (Cornelissen et al. 2003, Pérez-Harguindeguy et al. 2013, Bussotti and Pollastrini 2017b, Zhu et al. 2022). These parameters give information about the resource acquisition strategies and acclimatization processes to persistent and fluctuating environmental stress.

Relevant information on the photosynthetic efficiency and tree vitality can be obtained by the analysis of chlorophyll fluorescence and content. These physiological variables can be assessed with optical non-destructive methods, that enable us to make a great number of measurements in a relatively short time (Strasser et al. 2000, 2004, Uchino et al. 2013). Chlorophyll fluorescence methods are currently applied to assess the vitality of trees in forests, plant nurseries, and urban green infrastructures (Pollastrini et al. 2016a, 2016b, Bussotti et al. 2020, Swoczyna et al. 2022), and can be applied directly in the field on freshly taken samples.

Biochemical status of pigments, antioxidants, and secondary metabolites (Tausz et al. 2003, Couture et al. 2016, Munné-Bosch and Villadangos 2023), as well as leaf anatomy (Vollenweider et al., 2016), can also provide a wealth of information about the relation of trees with their environment, but such analyses incorporate a number of difficulties regarding sampling time and treatment prior to the delivery to laboratory.

### Stable isotopes

Stable isotope analysis is a very powerful tool to investigate the relationship of plants with their environment (Siegwolf et al. 2022, Snyder et al. 2022), and is applicable to stored desiccated leaves and tree rings. Francey and Farquahar (1982) demonstrated that carbon isotope ( $\delta^{13}\text{C}$ ) variations are physiologically strongly controlled by gas exchange in leaves and can reflect the intrinsic water use efficiency of a plant; oxygen isotopes ( $\delta^{18}\text{O}$ ) are a time-integrated proxy for stomatal conductance (Barbour 2007) and relative humidity (Helliker and Ehleringer 2002); hydrogen isotopes ( $\delta^2\text{H}$ ) may function as a metabolic proxy helping to infer on changes in biochemistry and gas-exchange (Cormier et al. 2018, Lehmann et al. 2022), leaf nitrogen isotope ( $\delta^{15}\text{N}$ ) composition is determined by the interaction between the external N source and the physiological mechanisms of nitrogen allocation within the plant, and can be used to assess the impact of N deposition on trees (Guerrieri et al. 2009).

### Water relations

Water relations in a tree include transpiration, stomatal conductance, hydraulic conductance, water storage and capacitance (Landsberg and Waring 2017). They are of great importance when investigating the role of drought in the worsening of tree condition. The methods currently applied include the application of sap-flow sensors and point dendrometers (Vandegehuchte and Steppe 2013, Dietrich et al. 2018). These measurements require an initial investment for the instruments, that must be installed permanently on the plot (with risk of theft and vandalism), power supply and frequent visits for maintenance and data download. Therefore, this can be done only on intensively monitored plots (Level II). New technologies (Zweifel et al. 2021, 2023) allow automatic download and transmission of data, thereby reducing field work considerably.

### Non-structural carbohydrates

There is growing interest in the storage and seasonal changes of non-structural carbohydrates (starch and soluble sugars, NSCs), as key players in the process of the response of trees to extreme drought and heat (Martínez-Vilalta et al. 2016). Because of the high intra-annual dynamics of NSCs, however, it is not easy to develop a harmonized system for comparable sampling and analysis (Landhäusser et al. 2018). In addition to the aspects related to the laboratory work, the main problems concern the sampling strategy (part of the plant, timing) and variations in the ecological and vegetational characteristics of sites. At the current state-of-the-art it is unlikely that large-scale surveys on NSCs will become common soon, but NSC analyses are nevertheless a useful tool to investigate specific forest health-related events.

### Monitoring tree vitality: weaknesses and future needs

Ongoing climate change and repeated extreme climatic events pose new threats to European forests and spur a renewed interest in forest monitoring (Ferretti 2021). There is still a lack of knowledge about the distinct and combined roles of drought, VPD, and temperature (Sánchez-Salguero et al. 2017, Breshears et al. 2021), and their interactions with opportunistic insects and pathogens, as well as with past impacts on forest trees (i.e. the legacy effect of cumulative past stress events, e.g. Ruck et al. 2023). The impact of increasing temperatures and extreme weather events (droughts, storms, and temperature and precipitation extremes) on the vitality of forest trees is often difficult to separate from the impact of nitrogen deposition, tropospheric ozone, or heavy metals, as they can exhibit synergistic effects (Potočić 2023). The relative intensity and duration of each stress factor and their interactions can trigger different physiological processes with variable symptomatology even on the same tree species. Loss of leaves during a drought event, for example, may be caused by an active acclimatization process to reduced water availability, or early senescence, or, finally, a collapse of the water transport system due to embolism.

To respond to these new challenges, current field activities of forest monitoring should be combined with additional physiological measurements. Defoliation and growth patterns are considered useful proxies for the likelihood of tree mortality (Dobbertin and Brang 2001, Hülsmann et al. 2017, Cailleret et al. 2019). Ecophysiological data can improve process-based models to separate out the different mechanisms associated with mortality (Camarero 2021, Cochard et al. 2021, Petit et al. 2021) and complement regular ICP Forests damage assessments. To achieve this

goal, it is necessary to collect field data from plots representing an array of ecological conditions and tree species. In principle, the ICP Forests Level II plots are suitable for the assessment of physiological indicators, since they are more intensively surveyed, but also selected Level I plots can be upgraded when appropriate, or new *ad hoc* plots can be installed for physiological measurements.

In terms of new monitoring initiatives, *TreeNet* in Switzerland (Zweifel et al. 2021, 2023), demonstrates a perspective for an integrated monitoring network. *TreeNet* collects data from point dendrometers and air and soil sensors using an automated system. Data are collected continuously, and are being automatically transmitted, processed, and stored in a central server, to provide near real-time indicators of forest growth performance and drought stress. Valentini et al. (2019) propose the so-called 'TreeTalker©', a multi-sensor device that continuously measures and transmits various variables, including: water transport, radial growth, multispectral signature of light transmitted through the canopy, and meteorological variables in real time.

The current ICP Forests monitoring network is an invaluable infrastructure whose importance is now universally recognized in a time of increasing environmental disturbance. To enhance its informative potential, for an even better estimation of the impacts and for the prevision of the development of forest ecosystems, we hope for a closer relationship between ICP Forests and other observational activities (remote sensing, forest inventories) and *ad hoc* cause-effect experiments (Hartmann et al. 2015, 2018, Bussotti et al. 2018b, Bontemps et al. 2022, Trugman 2022). We believe that the introduction of physiological indicators in field surveys can substantially improve the understanding of cause-effect relationships of trees with their environment and contribute to models describing the future condition of forests in Europe. An *ad hoc* working group on physiological indicators has been formed under ICP Forests Expert Panel on Crown Condition and Damage Causes to explore the possibility of adapting the above proposed physiological indicators and concepts in the field.

## Acknowledgements

We are grateful to two anonymous reviewers and to the editor that with their comments allowed us to significantly improve our paper.

## Author contributions

F.B. wrote the first draft of the paper. All the authors contributed with critical reading and proposals. All the authors read and approved the final version of the paper.

## Supplementary data

Supplementary data are available at *Forestry* online.

## Conflict of interest

None declared.

## Funding

This research was funded and carried out within 'new MONitoring system to Detect the Effects of Reduced pollutants emissions resulting from NEC Directive adoption' LIFE20 GIE/IT/000091 and SNSF (Swiss National Science Foundation) grant no. 213367.

## Data availability

No data available.

## References

- Aamlid D, Tørseth K, Venn K. et al. Changes of forest health in Norwegian boreal forests during 15 years. *For Ecol Manage* 2000;**127**: 103–18. [https://doi.org/10.1016/S0378-1127\(99\)00123-1](https://doi.org/10.1016/S0378-1127(99)00123-1).
- Aguadé D, Poyatos R, Gómez M. et al. The role of defoliation and root rot pathogen infection in driving the mode of drought-related physiological decline in Scots pine (*Pinus sylvestris* L.). *Tree Physiol* 2015;**35**:229–42. <https://doi.org/10.1093/treephys/tpv005>.
- Allen CD, Macalady AK, Chenchouni H. et al. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For Ecol Manage* 2010;**259**:660–84. <https://doi.org/10.1016/j.foreco.2009.09.001>.
- Amores G, Bermejo R, Elustondo D. et al. Nutritional status of Northern Spain beech forests. *Water Air Soil Poll* 2006;**177**:227–38. <https://doi.org/10.1007/s11270-006-9157-3>.
- Anderegg WRL, Kane JM, Anderegg LDL. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat Clim Change* 2013;**3**:30–6. <https://doi.org/10.1038/nclimate1635>.
- Anderegg WRL, Hicke JA, Fisher RA. et al. Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytol* 2015;**208**:674–83. <https://doi.org/10.1111/nph.13477>.
- Andersson B. Defoliation of coniferous trees—assessments 1984–87. *Environ Monit Assess* 1990;**14**:23–43. <https://doi.org/10.1007/BF00394355>.
- Araminiene V, Sicard P, Anav A. et al. Trends and inter-relationships of ground-level ozone metrics and forest health in Lithuania. *Sci Total Environ* 2019;**658**:1265–77. <https://doi.org/10.1016/j.scitotenv.2018.12.092>.
- Augustaitis A, Bytnerowicz A. Contribution of ambient ozone to Scots pine defoliation and reduced growth in the central European forests: a Lithuanian case study. *Environ Pollut* 2008;**155**:436–45. <https://doi.org/10.1016/j.envpol.2008.01.042>.
- Augustaitis A, Augustaitiene I, Deltuvas R. Scots pine (*Pinus sylvestris* L.) crown defoliation in relation to the acidic deposition and meteorology in Lithuania. *Water Air Soil Pollut* 2007;**182**:335–48. <https://doi.org/10.1007/s11270-007-9345-9>.
- Barbour MM. Stable oxygen isotopes composition of plant tissue: a review. *Funct Plant Biol* 2007;**34**:83–94. <https://doi.org/10.1071/FP06228>.
- Barker Plotkin A, Blumstein M, Laflower D. et al. Defoliated trees die below a critical threshold of stored carbon. *Funct Ecol* 2021;**35**: 2156–67. <https://doi.org/10.1111/1365-2435.13891>.
- Borghetti M, Gentilesca T, Colangelo M. et al. Xylem functional traits as indicators of health in Mediterranean forests. *Curr Forestry Rep* 2020;**6**:220–36. <https://doi.org/10.1007/s40725-020-00124-5>.
- Bontemps JD, Bouriaud O, Vega C. et al. Offering the appetite for the monitoring of European forests a diversified diet. *Ann For Sci* 2022;**79**:19. <https://doi.org/10.1186/s13595-022-01139-7>.
- Bouzidi HA, Balducci L, Mackay J. et al. Interactive effects of defoliation and water deficit on growth, water status, and mortality of black spruce (*Picea mariana* (Mill.) B.S.P.). *Ann For Sci* 2019;**76**:21. <https://doi.org/10.1007/s13595-019-0809-z>.
- Brang P. *Sanasilva-Bericht* 1997. *Gesundheit Und Gefährdung des Schweizer Waldes—Eine Zwischenbilanz Nach 15 Jahren Waldschadenforschung*. Berichte der Eidg. Forschungsanstalt für Wald, Schnee und Landschaft: Birmensdorf, 1998.

- Braun S, Hopf SE, Tresch S. et al. 37 years of Forest monitoring in Switzerland: drought effects on *Fagus sylvatica*. *Front For Glob Change* 2021;**4**:765782. <https://doi.org/10.3389/ffgc.2021.765782>.
- Bréda N, Huc R, Granier A. et al. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Ann For Sci* 2006;**63**:625–44. <https://doi.org/10.1051/forest:2006042>.
- Breshears DD, Fontaine JB, Ruthrof KX. et al. Underappreciated plant vulnerabilities to heat waves. *New Phytol* 2021;**231**:32–9. <https://doi.org/10.1111/nph.17348>.
- Briske DD. Plant response to defoliation: morphological considerations and allocation priorities. In: Joss PJ, Lynch PW, Williams OB, eds. *Rangelands: A Resource Under Siege*. Cambridge, UK: Cambridge University Press, 1986; 425–7.
- Brun P, Psomas A, Ginzler C. et al. Large-scale early-wilting response of central European forests to the 2018 extreme drought. *Glob Chang Biol* 2020;**26**:7021–35. <https://doi.org/10.1111/gcb.15360>.
- Bussotti F, Ferretti M. Visible injury, crown condition, and growth responses of selected Italian forests in relation to ozone exposure. *Environ Pollut* 2009;**157**:1427–37. <https://doi.org/10.1016/j.envpol.2008.09.034>.
- Bussotti F, Pollastrini M. Evaluation of leaf features in forest trees: methods, techniques, obtainable information and limits. *Ecol Indic* 2015;**52**:219–30. [doi.org/10.1016/j.ecolind.2014.12.010](https://doi.org/10.1016/j.ecolind.2014.12.010).
- Bussotti F, Pollastrini M. Observing climate change impacts on European forests: what works and what does not in ongoing long-term monitoring networks. *Front Plant Sci* 2017a;**8**:629. <https://doi.org/10.3389/fpls.2017.00629>.
- Bussotti F, Pollastrini M. Traditional and novel indicators of climate change impacts on European forest trees. *Forests* 2017b;**8**:137. <https://doi.org/10.3390/f8040137>.
- Bussotti F, Pollastrini M. Revisiting the concept of stress in forest trees at the time of global change and issues for stress monitoring. *Plant Stress* 2021;**2**:100013. <https://doi.org/10.1016/j.stress.2021.100013>.
- Bussotti F, Cozzi A, Cenni E. et al. Measurement errors in monitoring tree crown conditions. *J Environ Monit* 2009;**11**:769–73. <https://doi.org/10.1039/b818166g>.
- Bussotti F, Feducci M, Iacopetti G. et al. Linking forest diversity and tree health: preliminary insights from a large-scale survey in Italy. *For Ecosys* 2018a;**5**:12. <https://doi.org/10.1186/s40663-018-0130-6>.
- Bussotti F, Pollastrini M, Gessler A. et al. Experiments with trees: from seedlings to ecosystems. *Environ Exp Bot* 2018b;**152**:1–6. <https://doi.org/10.1016/j.envexpbot.2018.04.012>.
- Bussotti F, Gerosa G, Digrado A. et al. Selection of chlorophyll fluorescence parameters as indicators of photosynthetic efficiency in large scale plant ecological studies. *Ecol Ind* 2020;**108**:105686. <https://doi.org/10.1016/j.ecolind.2019.105686>.
- Bussotti F, Papitto G, Di Martino D. et al. Defoliation, recovery and increasing mortality in Italian forests: levels, patterns and possible consequences for forest multifunctionality. *Forests* 2021;**12**:1476. <https://doi.org/10.3390/f12111476>.
- Bussotti F, Papitto G, Di Martino D. et al. Are the conditions of the Italian forests worsening due to extreme climatic events? Evidence from the national monitoring networks ICP forests—CON. *ECOFOR Forest@* 2022;**19**:74–81. <https://doi.org/10.3832/efor4134-019>.
- Bussotti F, Bettini D, Carrari E. et al. Climate change in progress: observations on the impacts of drought events on Tuscan forests. *Forest@* 2023a;**20**:1–9. <https://doi.org/10.3832/efor4224-019>.
- Bussotti F, Bettini D, Carrari E. et al. Health condition of forests in Central Italy (Tuscany) after recurrent droughts and heat events. *Ecol Medit* 2023b;**49**:37–47.
- Cailleret M, Dakos V, Jansen S. et al. Early-warning signals of individual tree mortality based on annual radial growth. *Front Plant Sci* 2019;**9**:1964. <https://doi.org/10.3389/fpls.2018.01964>.
- Camarero JJ. The drought–dieback–death conundrum in trees and forests. *Plant Ecol Div* 2021;**14**:1–12. <https://doi.org/10.1080/17550874.2021.1961172>.
- Camarero JJ, Franquesa M, Sangüesa-Barreda G. Timing of drought triggers distinct growth responses in holm oak: implications to predict warming-induced forest defoliation and growth decline. *Forests* 2015;**6**:1576–97. <https://doi.org/10.3390/f6051576>.
- Capretti P, Battisti A. Water stress and insect defoliation promote the colonization of *Quercus cerris* by the fungus *Biscogniauxia mediterranea*. *For Pathol* 2007;**37**:129–35. <https://doi.org/10.1111/j.1439-0329.2007.00489.x>.
- Carnicer J, Coll M, Ninyerola M. et al. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proc Natl Acad Sci U S A* 2011;**108**:1474–8. <https://doi.org/10.1073/pnas.1010070108>.
- Carrer M, von Arx G, Castagneri D. et al. Distilling allometric and environmental information from time series of conduit size: the standardization issue and its relationship to tree hydraulic architecture. *Tree Physiol* 2015;**35**:27–33. <https://doi.org/10.1093/treephys/tpu108>.
- Češljarić G, Jovanović F, Brašanac-Bosanac L. et al. Impact of an extremely dry period on tree defoliation and tree mortality in Serbia. *Plan Theory* 2022;**11**:1286. <https://doi.org/10.3390/plants11101286>.
- Cherubini P, Battipaglia G, Innes JL. Tree vitality and forest health: can tree-ring stable isotopes be used as indicators? *Curr Forestry Rep* 2021;**7**:69–80. <https://doi.org/10.1007/s40725-021-00137-8>.
- Ciriani ML, Dalstein L. Forest health monitoring highlights progress in forest deterioration in France. *Water Air Soil Pollut* 2018;**229**:311. <https://doi.org/10.1007/s11270-018-3922-y>.
- Cochard H, Pimont F, Ruffault J. et al. SurEau: a mechanistic model of plant water relations under extreme drought. *Ann For Sci* 2021;**78**:55. <https://doi.org/10.1007/s13595-021-01067-y>.
- Colangelo M, Camarero JJ, Borghetti M. et al. Drought and *Phytophthora* are associated with the decline of oak species in southern Italy. *Front Plant Sci* 2018;**9**:1595. <https://doi.org/10.3389/fpls.2018.01595>.
- Cormier M-A, Werner RA, Sauer PE. et al. <sup>2</sup>H-fractionations during the biosynthesis of carbohydrates and lipids imprint a metabolic signal on the  $\delta^2\text{H}$  values of plant organic compounds. *New Phytol* 2018;**218**:479–91. <https://doi.org/10.1111/nph.15016>.
- Cornelissen JHC, Lavore LS, Garnier E. et al. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Austr J Bot* 2003;**51**:335–80. <https://doi.org/10.1071/BT02124>.
- Couture JJ, Singh A, Rubert-Nason KF. et al. Spectroscopic determination of ecologically relevant plant secondary metabolites. *Methods Ecol Evol* 2016;**7**:1402–12. <https://doi.org/10.1111/2041-210X.12596>.
- De Grandpré L, Kneeshaw DD, Perigon S. et al. Adverse climatic periods precede and amplify defoliator-induced tree mortality in eastern boreal North America. *J Ecol* 2018;**107**:452–67. <https://doi.org/10.1111/1365-2745.13012>.
- de la Cruz AC, Gil PM, Fernandez-Cancio A. et al. Defoliation triggered by climate induced effects in Spanish ICP Forests monitoring plots. *For Ecol Manage* 2014;**331**:245–55. <https://doi.org/10.1016/j.foreco.2014.08.010>.
- De Marco A, Proietti C, Cionni I. et al. Future impacts of nitrogen deposition and climate change scenarios on forest crown defoliation. *Environ Pollut* 2014;**194**:171–80. <https://doi.org/10.1016/j.envpol.2014.07.027>.

- De Marco A, Vitale M, Popa I. et al. Ozone exposure affects tree defoliation in a continental climate. *Sci Total Environ* 2017;**596–597**: 396–404. <https://doi.org/10.1016/j.scitotenv.2017.03.135>.
- de Vries W, Dobbertin M, Solberg HS. et al. Impacts of acid deposition, ozone exposure and weather conditions on forest ecosystems in Europe: an overview. *Plant and Soil* 2014;**380**:1–45. <https://doi.org/10.1007/s11104-014-2056-2>.
- Deslauriers A, Caron L, Rossi S. Carbon allocation during defoliation: testing a defense-growth trade-off in balsam fir. *Front Plant Sci* 2015;**6**:338. <https://doi.org/10.3389/fpls.2015.00338>.
- Desprez-Loustau ML, Marçais B, Nageleisen LM. et al. Interactive effects of drought and pathogens in forest trees. *Ann For Sci* 2006;**63**:597–612. <https://doi.org/10.1051/forest:2006040>.
- Diaz-de-Quijano M, Kefauver S, Ogaya R. et al. Visible ozone-like injury, defoliation, and mortality in two *Pinus uncinata* stands in the Catalan Pyrenees (NE Spain). *Eur J For Res* 2016;**135**:687–96. <https://doi.org/10.1007/s10342-016-0964-9>.
- Dietrich L, Zweifel R, Kahmen A. Daily stem diameter variations can predict the canopy water status of mature temperate trees. *Tree Physiol* 2018;**38**:941–52. <https://doi.org/10.1093/treephys/tpy023>.
- Dobbertin M. Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review. *Eur J Forest Res* 2005;**124**: 319–33. <https://doi.org/10.1007/s10342-005-0085-3>.
- Dobbertin M, Brang P. Crown defoliation improves tree mortality models. *For Ecol Manage* 2001;**141**:271–84. [https://doi.org/10.1016/S0378-1127\(00\)00335-2](https://doi.org/10.1016/S0378-1127(00)00335-2).
- Drobishev I, Linderson H, Sonesson K. Relationship between crown condition and tree diameter growth in southern Swedish oaks. *Environ Monit Assess* 2007;**128**:61–73. <https://doi.org/10.1007/s10661-006-9415-2>.
- Eichhorn J, Roskams P. Assessment of tree condition. In: Ferretti M, Fischer R (eds) *Forest Monitoring. Methods for Terrestrial Investigations in Europe with an Overview of North America and Asia*, Developments in Environmental Science, Vol. 12, Amsterdam: Elsevier, 2014, 139–67. <https://doi.org/10.1016/B978-0-08-098222-9.00008-X>.
- Eichhorn J, Icke R, Isenberg A. et al. Temporal development of crown condition of beech and oak as a response variable for integrated evaluations. *Eur J For Res* 2005;**124**:335–47. <https://doi.org/10.1007/s10342-005-0097-z>.
- Eichhorn J, Roskams P, Potočić N. et al. 2020 Part IV: visual assessment of crown condition and damaging agents. Version 2020-3. In: UNECE ICP Forests Programme co-Ordinating Centre (ed.) *Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests*. Eberswalde, Germany: Thünen Institute of Forest Ecosystems, 49p + Annex. <https://www.icp-forests.org/manual.html> ISBN: 978-3-86576-162-0
- Eickenscheidt N, Wellbrock N. Consistency of defoliation data of the national training courses for the forest condition survey in Germany from 1992 to 2012. *Environ Monit Assess* 2014;**186**: 257–75. <https://doi.org/10.1007/s10661-013-3372-3>.
- Eickenscheidt N, Augustin NH, Wellbrock N. Spatio-temporal modelling of forest monitoring data: modelling German tree defoliation data collected between 1989 and 2015 for trend estimation and survey grid examination using GAMMs. *IForest* 2019;**12**: 338–48. <https://doi.org/10.3832/ifor2932-012>.
- El Omari B. Accumulation versus storage of total nonstructural carbohydrates in woody plants. *Trees* 2022;**36**:869–81. <https://doi.org/10.1007/s00468-021-02240-6>.
- Erbilgin N, Galvez DA, Zhang B. et al. Resource availability and repeated defoliation mediate compensatory growth in trembling aspen (*Populus tremuloides*) seedlings. *PeerJ* 2014;**2**:e491. <https://doi.org/10.7717/peerj.491>.
- Etzold S, Ferretti M, Reinds GJ. et al. Nitrogen deposition is the most important environmental driver of growth of pure, even-aged and managed European forests. *For Ecol Manage* 2020;**458**:117762. <https://doi.org/10.1016/j.foreco.2019.117762>.
- Ewald J. Ecological background of crown condition, growth and nutritional status of *Picea abies* (L.) Karst. in the Bavarian Alps. *Eur J For Res* 2005;**124**:9–18. <https://doi.org/10.1007/s10342-004-0051-5>.
- Eyles A, Pinkard EA, Davies NW. et al. Whole-plant versus leaf-level regulation of photosynthetic responses after partial defoliation in *Eucalyptus globulus* saplings. *J Exp Bot* 2013, 2013;**64**:1625–36. <https://doi.org/10.1093/jxb/ert017>.
- Ferretti M. *Mediterranean Forest Trees. A Guide for Crown Assessment* CEC-UNECE. Brussels, Geneva, 1994.
- Ferretti M. New appetite for the monitoring of European forests. *Ann For Sci* 2021;**78**:94. <https://doi.org/10.1007/s13595-021-01112-w>.
- Ferretti M, König N. Methods to ensure monitoring quality. In: Ferretti M, Fischer R (eds), *Forest Monitoring. Methods for Terrestrial Investigations in Europe with an Overview of North America and Asia*, Developments in Environmental Science, Vol. 12. Elsevier, Amsterdam, 2013; 387–96.
- Ferretti M, Bussotti F, Cenni E. et al. Implementation of quality assurance procedures in the Italian programs of forest condition monitoring. *Water Air Soil Pollut* 1999;**116**:371–6. <https://doi.org/10.1023/A:1005240000294>.
- Ferretti M, Innes JL, Jalkanen R. et al. Air pollution and environmental chemistry—what role for tree-ring studies? *Dendrochronologia* 2002;**20**:159–74. <https://doi.org/10.1078/1125-7865-00014>.
- Ferretti M, Gerosa G, Bussotti F. et al. Ozone exposure, crown transparency and basal area increment at the permanent monitoring plots of the CONECOFOR programme in Italy. *Ann Ist Sper Selv* 2003;**30**:107–20.
- Ferretti M, Calderisi M, Bussotti F. Ozone exposure, defoliation of beech (*Fagus sylvatica* L.) and visible foliar symptoms on native plants in selected plots of South-Western Europe. *Environ Pollut* 2007;**145**:644–51. <https://doi.org/10.1016/j.envpol.2006.02.028>. <http://hdl.handle.net/2158/250787>.
- Ferretti M, Koenig N, Rautio P. et al. Quality assurance (QA) in international forest monitoring programmes: activity, problems and perspectives from East Asia and Europe. *Ann For Sci* 2009;**66**:403. <https://doi.org/10.1051/forest/2009025>.
- Ferretti M, Marchetto A, Arisci S. et al. On the tracks of nitrogen deposition effects on temperate forests at their southern European range—an observational study from Italy. *Glob Chang Biol* 2014a;**20**:3423–38. <https://doi.org/10.1111/gcb.12552>.
- Ferretti M, Nicolas M, Bacaro G. et al. Plot-scale modeling to detect size, extent, and correlates of changes in tree defoliation in French high forests. *For Ecol Manage* 2014b;**311**:56–69. <https://doi.org/10.1016/j.foreco.2013.05.009>.
- Ferretti M, Calderisi M, Marchetto A. et al. Variables related to nitrogen deposition improve defoliation models for European forests. *Ann For Sci* 2015;**72**:897–906. <https://doi.org/10.1007/s13595-014-0445-6>.
- Ferretti M, Koenig N, Granke O, Nicolas M. 2021a Part III: quality assurance within the ICP Forests monitoring programme. Version 2021-1. In: UNECE ICP Forests Programme co-Ordinating Centre (ed.) *Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests*. Eberswalde, Germany: Thünen Institute of Forest Ecosystems, (14p + Annex). <https://www.icp-forests.org/Manual.htm>.

- Ferretti M, Ghosh S, Gottardini E. Stem radial growth is negatively related to tree defoliation and damage in conifers, Northern Italy. *Front For Glob Change* 2021b;**4**:775600. <https://doi.org/10.3389/ffgc.2021.775600>.
- Ferretti M, Bacaro G, Brunialti G. et al. Tree canopy defoliation can reveal growth decline in mid-latitude temperate forests. *Ecol Indic* 2021c;**127**:107749. <https://doi.org/10.1016/j.ecolind.2021.107749>.
- Forzieri G, Girardello M, Ceccherini G. et al. Emergent vulnerability to climate-driven disturbances in European forests. *Nat Commun* 2021;**12**:1081. <https://doi.org/10.1038/s41467-021-21399-7>.
- Foster JR. Xylem traits, leaf longevity and growth phenology predict growth and mortality response to defoliation in northern temperate forests. *Tree Physiol* 2017;**37**:1151–65. <https://doi.org/10.1093/treephys/tpx043>.
- Francey JR, Farquhar GD. An explanation of  $^{13}\text{C}/^{12}\text{C}$  in tree rings. *Nature* 1982;**297**:28–31. <https://doi.org/10.1038/297028a0>.
- Furze ME, Huggett BA, Aubrecht DM. et al. Whole-tree nonstructural carbohydrate storage and seasonal dynamics in five temperate species. *New Phytol* 2019;**221**:1466–77. <https://doi.org/10.1111/nph.15462>.
- Galiano L, Martinez-Vilalta J, Sabaté S. et al. Determinants of drought induced effects on crown condition and their relationship with depletion of carbon reserve in a Mediterranean holm oak forest. *Tree Physiol* 2012;**32**:478–89. <https://doi.org/10.1093/treephys/tps025>.
- García-Fórner N, Biel C, Savé R. et al. Isohydric species are not necessarily more carbon limited than anisohydric species during drought. *Tree Physiol* 2019;**37**:441–55. <https://doi.org/10.1093/treephys/tpw109>.
- Gazol A, Camarero J. Compound climate events increase tree drought mortality across European forests. *Sci Tot Environ* 2022;**816**:151604. <https://doi.org/10.1016/j.scitotenv.2021.151604>.
- George J-P, Bürkner P-C, Sanders TGM. et al. Long-term forest monitoring reveals constant mortality rise in European forests. *Plant Biol* 2022;**24**:1108–19. <https://doi.org/10.1111/plb.13469>.
- Gerosa G, Ferretti M, Bussotti F. et al. Estimates of ozone AOT40 from passive sampling in forest sites in South-Western Europe. *Environ Pollut* 2007;**145**:629–35. <https://doi.org/10.1016/j.envpol.2006.02.030>.
- Ghosh S, Innes JL. Combining field and control team assessments to obtain error estimates for surveys of crown condition. *Scand J For Res* 1995;**10**:264–70. <https://doi.org/10.1080/02827589509382892>.
- Ghosh S, Innes JL, Hoffmann C. Observer variation as a source of error in assessments of crown condition through time. *For Sci* 1995;**41**:235–54. <https://doi.org/10.1093/forestscience/41.2.235>.
- Gottardini E, Cristofolini F, Cristofori A. et al. Consistent response of crown transparency shoot growth and leaf traits on Norway spruce (*Picea abies* (L.) H. Karst.) trees along an elevation gradient in Northern Italy. *Ecol Indic* 2016;**60**:1041–4. <https://doi.org/10.1016/j.ecolind.2015.09.006>.
- Gottardini E, Cristofolini F, Cristofori A. et al. In search for evidence: combining ad hoc survey, monitoring, and modeling to estimate the potential and actual impact of ground level ozone on forests in Trentino (Northern Italy). *Environ Sci Pollut Res* 2018;**25**:8206–16. <https://doi.org/10.1007/s11356-017-9998-x>.
- Gottardini E, Cristofolini F, Cristofori A. et al. A multi-proxy approach reveals common and species-specific features associated with tree defoliation in broadleaved species. *For Ecol Manage* 2020;**467**:118151. <https://doi.org/10.1016/j.foreco.2020.118151>.
- Grossiord C, Buckley TN, Cernusak LA. et al. Plant responses to rising vapor pressure deficit. *New Phytol* 2020;**226**:1550–66. <https://doi.org/10.1111/nph.16485>.
- Guada G, Camarero JJ, Sánchez-Salguero R. et al. Limited growth recovery after drought-induced Forest dieback in very defoliated trees of two pine species. *Front Plant Sci* 2016;**7**:418. <https://doi.org/10.3389/fpls.2016.00418>.
- Guerrieri MR, Siegwolf RTW, Surer M. et al. Impact of different nitrogen emission sources on tree physiology as assessed by a triple stable isotope approach. *Atmos Environ* 2009;**43**:410–8. <https://doi.org/10.1016/j.atmosenv.2008.08.042>.
- Hari V, Rakovec O, Markonis Y. et al. Increased future occurrences of the exceptional 2018–2019 Central European drought under global warming. *Sci Rep* 2020;**10**:12207. <https://doi.org/10.1038/s41598-020-68872-9>.
- Hart M, Hogg EH, Lieffers VJ. Enhanced water relations of residual foliage following defoliation in *Populus tremuloides*. *Can J Bot* 2000;**78**:583–90. <https://doi.org/10.1139/b00-032>.
- Hartmann H, Trumbore S. Understanding the roles of nonstructural carbohydrates in forest trees—from what we can measure to what we want to know. *New Phytol* 2016;**211**:386–403. <https://doi.org/10.1111/nph.13955>.
- Hartmann H, Adams HD, Anderegg WRL. et al. Research frontiers in drought-induced tree mortality: crossing scales and disciplines. *New Phytol* 2015;**205**:965–9. <https://doi.org/10.1111/nph.13246>.
- Hartmann H, Moura CF, Anderegg WRL. et al. Research frontiers for improving our understanding of drought-induced tree and forest mortality. *New Phytol* 2018;**218**:15–28. <https://doi.org/10.1111/nph.15048>.
- Helliker BR, Ehleringer JR. Grass blades as tree rings: environmentally induced changes in the oxygen isotope ratio of cellulose along the length of grass blades. *New Phytol* 2002;**155**:417–24. <https://doi.org/10.1046/j.1469-8137.2002.00480.x>.
- Hendricks CMA, Van den Burg J, Oude Voshaar JH. et al. *Relationships Between Forest Condition and Stress Factors in the Netherlands* in 1995. Wageningen, Netherlands: DLO Winand Staring Centre, 1997; Report 148.
- Hillbrand RM, Hacke UG, Lieffers VJ. Defoliation constrains xylem and phloem functionality. *Tree Physiol* 2019;**39**:1099–108. <https://doi.org/10.1093/treephys/tpz029>.
- Hülsmann L, Bugmann H, Brang P. How to predict tree death from inventory data—lessons from a systematic assessment of European tree mortality models. *Can J For Res* 2017;**47**:890–900. <https://doi.org/10.1139/cjfr-2016-0224>.
- Iacopetti G, Bussotti F, Selvi F. et al. Forest ecological heterogeneity determines contrasting relationships between crown defoliation and tree diversity. *For Ecol Manage* 2019;**448**:321–9. <https://doi.org/10.1016/j.foreco.2019.06.017>.
- Innes JL. Forest health surveys: a critique. *Environ Pollut* 1988a;**54**:1–15. [https://doi.org/10.1016/0269-7491\(88\)90171-6](https://doi.org/10.1016/0269-7491(88)90171-6).
- Innes JL. Forest health surveys: problems in assessing observer objectivity. *Can J For Res* 1988b;**18**:560–5. <https://doi.org/10.1139/x88-081>.
- Innes JL. *Assessment of Tree Condition*. Field Book 12. Forestry Commission. London, 1990; 96.
- Innes JL. Forest condition and air pollution in the United Kingdom. *For Ecol Manage* 1992;**51**:17–27. [https://doi.org/10.1016/0378-1127\(92\)90468-O](https://doi.org/10.1016/0378-1127(92)90468-O).
- Innes JL. Methods to estimate forest health. *Silva Fennica* 1993;**27**:145–57. <https://doi.org/10.14214/sf.a15668>.

- Innes JL, Whittaker RJ. Relationships between the crown condition of Sitka and Norway spruce and the environment in great Britain: an exploratory analysis. *J Appl Ecol* 1993;**30**:341–60. <https://doi.org/10.2307/2404636>.
- Innes JL, Landmann G, Mettendorf B. Consistency of observations of forest tree defoliation in three European countries. *Environ Monit Assess* 1993;**25**:29–40. <https://doi.org/10.1007/BF00549790>.
- IPCC. In: Masson-Delmotte V, Zhai P, Pirani A., et al. (eds), *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge, UK and New York, NY, USA: Cambridge University Press, 2021, 2391 pp. <https://doi.org/10.1017/9781009157896>.
- Jaime L, Battlori E, Ferretti M. et al. Climatic and stand drivers of forest resistance to recent bark beetle disturbance in European coniferous forests. *Glob Chang Biol* 2022;**28**:2830–41. <https://doi.org/10.1111/gcb.16106>.
- Jakovljević T, Marchetto A, Lovreškov L. et al. Assessment of atmospheric deposition and vitality indicators in Mediterranean forest ecosystems. *Sustainability* 2019;**11**:6805. <https://doi.org/10.3390/su11236805>.
- Jakovljević T, Lovreškov L, Jelić G. et al. Impact of ground-level ozone on Mediterranean forest ecosystems health. *Sci Tot Environ* 2021;**783**:147063. <https://doi.org/10.1016/j.scitotenv.2021.147063>.
- Jentsch A, Kreyling J, Beierkuhnlein C. A new generation of climate change experiments: events, not trends. *Front Ecol Environ* 2007;**5**:315–24. [https://doi.org/10.1890/1540-9295\(2007\)5\[365:ANGOCE\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2007)5[365:ANGOCE]2.0.CO;2).
- Jonard M, André F, Giot P. et al. Thirteen-year monitoring of liming and PK fertilization effects on tree vitality in Norway spruce and European beech stands. *Eur J For Res* 2010;**129**:1203–11. <https://doi.org/10.1007/s10342-010-0410-3>.
- Jonard M, Fürst A, Verstraeten A. et al. Tree mineral nutrition is deteriorating in Europe. *Glob Chang Biol* 2015;**21**:418–30. <https://doi.org/10.1111/gcb.12657>.
- Jung T. Beech decline in Central Europe driven by the interaction between *Phytophthora* infections and climatic extremes. *For Pathol* 2009;**39**:73–94. <https://doi.org/10.1111/j.1439-0329.2008.00566.x>.
- Jung T, Blaschke H, Oßwald W. Involvement of soilborne *Phytophthora* species in central European oak decline and the effect of site factors on the disease. *Plant Pathol* 2000;**49**:706–18. <https://doi.org/10.1046/j.1365-3059.2000.00521.x>.
- Jung T, Cooke DEL, Blaschke H. et al. *Phytophthora quercina* sp. nov., causing root rot of European oaks. *Mycol Res* 1999;**103**:785–98. <https://doi.org/10.1017/S0953756298007734>.
- Kadiouglua A, Rabiye T, Neslihan S. et al. Current advances in the investigation of leaf rolling caused by biotic and abiotic stress factors. *Plant Sci* 2012;**182**:42–8. <https://doi.org/10.1016/j.plantsci.2011.01.013>.
- Kandler O, Innes JL. Air pollution and forest decline in Central Europe. *Environ Pollut* 1995;**90**:171–80. [https://doi.org/10.1016/0269-7491\(95\)00006-D](https://doi.org/10.1016/0269-7491(95)00006-D).
- Katzensteiner K, Glatzel G, Kazda M. Nitrogen-induced nutritional imbalances—a contributing factor to Norway spruce decline in the Bohemian Forest (Austria). *For Ecol Manage* 1992;**51**:29–42. [https://doi.org/10.1016/0378-1127\(92\)90469-P](https://doi.org/10.1016/0378-1127(92)90469-P).
- Klap JM, Oude Voshaar JH, De Vries W. et al. Effects of environmental stress on forest crown condition in Europe. Part IV: statistical analysis of relationships. *Wat Air Soil Pollut* 2000;**119**:387–420. <https://doi.org/10.1023/A:1005157208701>.
- Kosola KR, Dickmann DI, Paul EA. et al. Repeated insect defoliation effects on growth, nitrogen acquisition, carbohydrates, and root demography of poplars. *Oecologia* 2001;**129**:65–74. <https://doi.org/10.1007/s004420100694>.
- Landhäusser SML, Chow PS, Dickman LT. et al. Standardized protocols and procedures can precisely and accurately quantify non-structural carbohydrates. *Tree Physiol* 2018;**38**:1764–78. <https://doi.org/10.1093/treephys/tpy118>.
- Landsberg J, Waring R. Water relations in tree physiology: where to from here? *Tree Physiol* 2017;**37**:18–32. <https://doi.org/10.1093/treephys/tpw102>.
- Lehmann MM, Schuler P, Cormier MA. et al. (2022). The stable hydrogen isotopic signature: from source water to tree rings. In: Siegwolf RTW, Brooks JR, Roden J, Saurer M (eds), *Stable Isotopes in Tree Rings. Tree Physiology*, Vol. 8. Cham: Springer, [https://doi.org/10.1007/978-3-030-92698-4\\_11](https://doi.org/10.1007/978-3-030-92698-4_11)
- Lens F, Gleason SM, Bortolami G. et al. Functional xylem characteristics associated with drought-induced embolism in angiosperms. *New Phytol* 2022;**236**:2019–36. <https://doi.org/10.1111/nph.18447>.
- Limousin J-M, Roussel A, Rodríguez-Calcerrada J. et al. Drought acclimation of *Quercus ilex* leaves improves tolerance to moderate drought but not resistance to severe water stress. *Plant Cell Environ* 2022;**45**:1967–84. <https://doi.org/10.1111/pce.14326>.
- Lloret F, Keeling EG, Sala A. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. *Oikos* 2011;**120**:1909–20. <https://doi.org/doi:10.1111/j.1600-0706.2011.19372.x>.
- López Bernat C, Gracia CA, Sabaté S. et al. Assessing the resilience of Mediterranean holm oaks to disturbances using selective thinning. *Acta Oecol* 2009;**35**:849–54. <https://doi.org/10.1016/j.actao.2009.09.001>.
- Lyytikäinen-Saarenmaa P. The response of Scots pine, *Pinus sylvestris*, to natural and artificial defoliation stress. *Ecol App* 1999;**9**:469–74. [https://doi.org/10.1890/1051-0761\(1999\)009\[0469:TROSPJ\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1999)009[0469:TROSPJ]2.0.CO;2).
- Martínez-Vilalta J, Sala A, Asensio D. et al. Dynamics of non-structural carbohydrates in terrestrial plants: a global synthesis. *Ecol Monogr* 2016;**86**:495–516. <https://doi.org/10.1002/ecm.1231>.
- McDowell N, Pockman WT, Allen CD. et al. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol* 2008;**178**:719–39. <https://doi.org/10.1111/j.1469-8137.2008.02436.x>.
- Medvigy D, Clark KL, Skowronski NS. et al. Simulated impacts of insect defoliation on forest carbon dynamics. *Environ Res Lett* 2012;**7**:045703. <https://doi.org/10.1088/1748-9326/7/4/045703>.
- Meining S, Morgenstern Y, Wellbrock N. et al. *Results of the European Photo International Cross Comparison Course as Part of the Quality Assurance of the Crown Condition Assessment 2015 (Photo ICC 2015)*, 2016, Thünen Institut, Eberswalde, Germany. Working Paper 61; 57.
- Moravec V, Markoni SY, Rakovec O. et al. Europe under multi-year droughts: how severe was the 2014–2018 drought period? *Environ Res Lett* 2021;**16**:034062. <https://doi.org/10.1088/1748-9326/abe828>.
- Müller E, Stierlin HR. *Tree Crown Photos. Sanasilva*. Birmensdorf, Switzerland: Swiss Federal Institute for Forest Snow and Landscape Research, 1990.
- Munné-Bosch S, Villadangos S. Cheap, cost-effective, and quick stress biomarkers for drought stress detection and monitoring in plants. *Trends Plant Sci* 2023;**28**:527–36. <https://doi.org/10.1016/j.tplants.2023.01.004>.
- Navarro-Cerrillo RM, Gazol A, Rodríguez-Vallejo C. et al. Linkages between climate, radial growth and defoliation in *Abies pinsapo*

- forests from Southern Spain. *Forests* 2020;**11**:1002. <https://doi.org/10.3390/f11091002>.
- Navarro-Cerrillo RM, González-Moreno P, Ruiz-Gómez FJ. et al. Drought stress and pests increase defoliation and mortality rates in vulnerable *Abies pinsapo* forests. *For Ecol Manage* 2022;**504**:119824. <https://doi.org/10.1016/j.foreco.2021.119824>.
- Nelleman C, Frogner T. Spatial patterns of spruce defoliation seen in relation to acid deposition, critical loads and natural growth condition in Norway. *Ambio* 1994;**23**:255.
- Netherer S, Matthews B, Katzensteiner K. et al. Do water-limiting conditions predispose Norway spruce to bark beetle attack? *New Phytol* 2015;**205**:1128–41. <https://doi.org/10.1111/nph.13166>.
- Netherer S, Panassiti B, Pennerstorfer J. et al. Acute drought is an important driver of bark beetle infestation in Austrian Norway spruce stands. *Front For Glob Chang* 2019;**2**:39. <https://doi.org/10.3389/ffgc.2019.00039>.
- Netherer S, Kandasamy D, Jirosová A. et al. Interactions among Norway spruce, the bark beetle *Ips typographus* and its fungal symbionts in times of drought. *Journal of Pest Science* 2021;**94**:591–614. <https://doi.org/10.1007/s10340-021-01341-y>.
- Neumann M, Mues V, Moreno A. et al. Climate variability drives recent tree mortality in Europe. *Glob Chang Biol* 2017;**23**:4788–97. <https://doi.org/10.1111/gcb.13724>.
- Neycken A, Scheggia M, Bigler C. et al. Long-term growth decline precedes sudden crown dieback of European beech. *Agric For Meteor* 2022;**324**:109103. <https://doi.org/10.1016/j.agrformet.2022.109103>.
- Niinemets Ü. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. *Forest Ecol Manag* 2010;**260**:1623–39. <https://doi.org/10.1016/j.foreco.2010.07.054>.
- Nilsson LO, Huettl RF, Johansson UT. et al. Nutrient uptake and cycling in forest ecosystems—present status and future research directions. *Plant and Soil* 1995;**168-169**:5–13. [https://doi.org/10.1007/978-94-011-0455-5\\_1](https://doi.org/10.1007/978-94-011-0455-5_1).
- Ognjenović M, Levanić T, Potočić N. et al. Interrelations of various tree vitality indicators and their reaction to climatic conditions on a European beech (*Fagus sylvatica* L.) plot. *Šumarski list* 2020;**144**:351–65. <https://doi.org/10.31298/sl.144.7-8.2>.
- Ognjenović M, Seletković I, Potočić N. et al. Defoliation change of European beech (*Fagus sylvatica* L.). *Depends on Previous Year Drought Plants* 2022;**11**:730. <https://doi.org/10.3390/plants11060730>.
- Ognjenović M, Seletković I, Marušić M. et al. The effect of environmental factors on the nutrition of European beech (*Fagus sylvatica* L.) varies with defoliation. *Plan Theory* 2023;**12**:168. <https://doi.org/10.3390/plants12010168>.
- Quimet R, Moore J-D. Effects of fertilization and liming on tree growth, vitality and nutrient status in boreal balsam fir stands. *For Ecol Manage* 2015;**345**:39–49. <https://doi.org/10.1016/j.foreco.2015.02.032>.
- Ovaska J, Ruuska S, Rintamäki E. et al. Combined effects of partial defoliation and nutrient availability on cloned *Betula pendula* saplings II. Changes in net photosynthesis and related biochemical properties. *J Exp Bot* 1993;**64**:1625–36. <https://doi.org/10.1093/jxb/ert017>.
- Pandey S, Carrer M, Castagneri D. et al. Xylem anatomical responses to climate variability in Himalayan birch trees at one of the world's highest forest limit. *Persp Pl Ecol Evol Syst* 2018;**33**:34–41. <https://doi.org/10.1016/j.ppees.2018.05.004>.
- Paoletti E, Alivernini A, Anav A. et al. Toward stomatal-flux based forest protection against ozone: the MOTTLES approach. *Sci Tot Environ* 2019;**691**:516–27. <https://doi.org/10.1016/j.scitotenv.2019.06.525>.
- Patacca M, Lindner M, Lucas-Borja ME. et al. Significant increase in natural disturbance impacts on European forests since 1950. *Glob Ch Biol* 2023;**29**:1359–76. <https://doi.org/10.1111/gcb.16531>.
- Pataki DE, Oren R, Phillips N. Responses of sap flux and stomatal conductance of *Pinus taeda* L. trees to stepwise reductions in leaf area. *J Exp Bot* 1998;**49**:871–8. <https://doi.org/10.1093/jxb/49.322.871>.
- Peters RL, Miranda JC, Schönbeck L. et al. Tree physiological monitoring of the 2018 larch budmoth outbreak: preference for leaf recovery and carbon storage over stem wood formation in *Larix decidua*. *Tree Physiol* 2020;**40**:1697–711. <https://doi.org/10.1093/treephys/tpaa087>.
- Pérez-Harguindeguy N, Díaz S, Garnier E. et al. New handbook for standardised measurement of plant functional traits worldwide. *Austr J Bot* 2013;**61**:167–234. <https://doi.org/10.1071/BT12225>.
- Petit-Cailleux C, Davi H, Lefèvre F. et al. Comparing statistical and mechanistic models to identify the drivers of mortality within a rear-edge beech population. *Peer Comm J* 2021;**e55**:1–21. <https://doi.org/10.24072/pci.ecology.100070>.
- Piper FI, Paula S. The role of nonstructural carbohydrates storage in forest resilience under climate change. *Curr For Rep* 2020;**6**:1–13. <https://doi.org/10.1007/s40725-019-00109-z>.
- Pokorný R, Stojnič S. Leaf area index of Norway spruce stand in relation to its age and defoliation. *Beskydy* 2012;**5**:173–80. <https://doi.org/10.11118/beskyd201205020173>.
- Pollastrini M, Feducci M, Bonal D. et al. Physiological significance of forest tree defoliation: results from a survey in a mixed forest in Tuscany (Central Italy). *For Ecol Manage* 2016a;**361**:170–8. <https://doi.org/10.1016/j.foreco.2015.11.018>.
- Pollastrini M, Holland V, Brüggemann W. et al. Chlorophyll a fluorescence analysis in forests. *Ann Bot (Roma)* 2016b;**6**:23–37. <https://doi.org/10.4462/annbotrm-13257>.
- Pollastrini M, Garcia Nogales A, Benavides R. et al. Tree diversity affects chlorophyll a fluorescence and other leaf traits of tree species in a boreal forest. *Tree Physiol* 2017;**37**:199–208. <https://doi.org/10.1093/treephys/tpw132>.
- Pollastrini M, Puletti N, Selv, i F, Iacopetti, G. and Bussotti, F. Widespread crown defoliation after a drought and heat wave in the forests of Tuscany (Central Italy) and their recovery—a case study from summer 2017. *Front For Glob Chang* 2019;**2**:74. <https://doi.org/10.3389/ffgc.2019.00074>.
- Popa I, Badea O, Silaghi D. Influence of climate on tree health evaluated by defoliation in the ICP level I network (Romania). *iForest* 2017;**10**:554–60. <https://doi.org/10.3832/ifer2202-009>.
- Portier J, Shackleton RT, Klesse S. et al. No evidence that coring affects tree growth or mortality in three common European temperate forest tree species. *Eur J Forest Res* 2023;**1-11**. <https://doi.org/10.1007/s10342-023-01612-6>.
- Potočić N. Advances in Forest ecophysiology: stress response and ecophysiological indicators of tree vitality. *Plan Theory* 2023;**12**:1063. <https://doi.org/10.3390/plants12051063>.
- Potočić N, Ćosić T, Pilaš I. The influence of climate and soil properties on calcium nutrition and vitality of silver fir (*Abies alba* mill). *Environ Pollut* 2005;**137**:596–602. <https://doi.org/10.1016/j.envpol.2005.01.045>.
- Potočić N, Timmermann V, Ognjenović M. et al. Tree health is deteriorating in the European forests. In: *ICP Forests. Brief no. 5*.



- Programme Co-ordinating Centre of ICP Forests, Thünen Institute of Forest Ecosystems, Eberswalde, Germany. 2021; 6. <https://doi.org/10.3220/ICP1638780772000>.
- Puri E, Hoch G, Korner C. Defoliation reduces growth but not carbon reserves in Mediterranean *Pinus pinaster* trees. *Trees* 2015;**29**: 1187–96. <https://doi.org/10.1007/s00468-015-1199-y>.
- Quentin AG, O'Grady AP, Beadle CL. et al. Interactive effects of water supply and defoliation on photosynthesis, plant water status and growth of *Eucalyptus globulus* Labill. *Tree Physiol* 2012;**32**:958–67. <https://doi.org/10.1093/treephys/tps066>.
- Rautio P, Fürst A, Stefan K. et al.. Part XII: sampling and analysis of needles and leaves. Version 2020-3. In: UNECE ICP Forests Programme Co-ordinating Centre (ed.): *Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests*. Germany: Thünen Institute of Forest Ecosystems, Eberswalde, 2020, 16 Annex, <http://www.icp-forests.org/Manual.htm>.
- Rebetez M, Mayer H, Dupont O. et al. Heat and drought 2003 in Europe: a climate synthesis. *Ann For Sci* 2006;**63**:569–77. <https://doi.org/10.1051/forest:2006043>.
- Redfern DB, Boswell RC. Assessment of crown condition in forest trees: comparison of methods, sources of variation and observer bias. *For Ecol Manage* 2004;**188**:149–60. <https://doi.org/10.1016/j.foreco.2003.07.011>.
- Rehfuess KE. Review of forest decline research activities and results in the Federal Republic of Germany. *J Environ Sci Health A Environ Sci Eng Tox* 1991;**26**:415–45. <https://doi.org/10.1080/10934529109375643>.
- Rita A, Camarero JJ, Nolé A. et al. The impact of drought spells on forests depends on site conditions: the case of 2017 summer heat wave in southern Europe. *Glob Chang Biol* 2019;**26**:851–63. <https://doi.org/10.1111/gcb.14825>.
- Rohner B, Kumar S, Liechti K. et al. Tree vitality indicators revealed a rapid response of beech forests to the 2018 drought. *Ecol Indic* 2021;**120**:106903. <https://doi.org/10.1016/j.ecolind.2020.106903>.
- Romeiro JMN, Eid T, Antón-Fernández C. et al. Natural disturbances risks in European boreal and temperate forests and their links to climate change—a review of modelling approaches. *For Ecol Manage* 2022;**509**:120071. <https://doi.org/10.1016/j.foreco.2022.120071>.
- Ruck S, Sanders TGM, Krüger I. et al. Distinct responses of European beech (*Fagus sylvatica* L.) to drought intensity and length—a review of the impacts of the 2003 and 2018–2019 drought events in Central Europe. *Forests* 2023;**14**:248. <https://doi.org/10.3390/f14020248>.
- Salmon Y, Torres-Ruiz JM, Poyatos R. et al. Balancing the risks of hydraulic failure and carbon starvation: a twig scale analysis in declining Scots pine. *Plant Cell Environ* 2015;**38**:2575–88. <https://doi.org/10.1111/pce.12572>.
- Sánchez-Cuesta R, Ruiz-Gómez FJ, Duque-Lazo J. et al. The environmental drivers influencing spatio-temporal dynamics of oak defoliation and mortality in dehesas of southern Spain. *For Ecol Manage* 2021;**485**:118946. <https://doi.org/10.1016/j.foreco.2021.118946>.
- Sánchez-Salguero R, Camarero JJ, Grau JM. et al. Analysing atmospheric processes and climatic drivers of tree defoliation to determine forest vulnerability to climate warming. *Forests* 2017;**8**:13. <https://doi.org/10.3390/f8010013>.
- Sanz MJ, Calataud V, Calvo E. Spatial pattern of ozone injury in Aleppo pine related to air pollution dynamics in a coastal-mountain region of eastern Spain. *Environ Pollut* 2000;**108**:239–47. [https://doi.org/10.1016/S0269-7491\(99\)00182-7](https://doi.org/10.1016/S0269-7491(99)00182-7).
- Saura-Mas S, Bonas A, Lloret F. Plant community response to drought-induced canopy defoliation in a Mediterranean *Quercus ilex* forest. *Eur J For Res* 2015;**134**:261–72. <https://doi.org/10.1007/s10342-014-0848-9>.
- Schmitz A, Sanders TGM, Bolte A. et al. Responses of forest ecosystems in Europe to decreasing nitrogen deposition. *Environ Pollut* 2019;**244**:980–94. <https://doi.org/10.1016/j.envpol.2018.09.101>.
- Schönbeck LC, Schuler P, Lehmann MM. et al. Increasing temperature and vapour pressure deficit lead to hydraulic damages in the absence of soil drought. *Plant Cell Environ* 2022;**45**:3275–89. <https://doi.org/10.1111/pce.14425>.
- Schuldts B, Buras A, Arend M. et al. A first assessment of the impact of the extreme 2018 summer drought on central European forests. *Bas Appl Ecol* 2020;**45**:86–103. <https://doi.org/10.1016/j.baee.2020.04.003>.
- Schulze ED. Air pollution and Forest decline in a spruce (*Picea abies*) Forest. *Science* 1989;**244**:776–83. <https://doi.org/10.1126/science.244.4906.776>.
- Schütt P, Cowling EB. Waldsterben, a general decline of forests in Central Europe: symptoms, development, and possible causes. *Plant Dis* 1985;**69**:548–58.
- Seidling W. *Integrative Studies on Forest Ecosystem Conditions. Multivariate Evaluations on Tree Crown Condition for Two Areas with Distinct Deposition Gradients*. Programme co-Ordinating Centre of ICP Forests, Federal Research Centre for Forestry and Forest Products (BFH) and Forest Soil co-Ordinating Centre (FSCC). EC, Flemish Community: Ghent University, UN-ECE, 2001: 91.
- Seidling W. Signals of summer drought in crown condition data from the German level I network. *Eur J For Res* 2007;**126**:529–44. <https://doi.org/10.1007/s10342-007-0174-6>.
- Seidling W, Mues V. Statistical and geostatistical modelling of preliminarily adjusted defoliation on an European scale. *Environ Monit Assess* 2005;**101**:233–47. <https://doi.org/10.1007/s10661-005-9304-0>.
- Seidling W, Ziche D, Beck W. Climate responses and interrelations of stem increment and crown transparency in Norway spruce, Scots pine, and common beech. *For Ecol Manage* 2012;**284**:196–204. <https://doi.org/10.1016/j.foreco.2012.07.015>.
- Sicard P, Dalstein-Richier L. Health and vitality assessment of two common pine species in the context of climate change in southern Europe. *Environ Res* 2015;**137**:235–45. <https://doi.org/10.1016/j.envres.2014.12.025>.
- Sanders T, Michel A, Ferretti M. 30 years of monitoring of long range transboundary air pollution on forests in Europe and beyond. 2016. UNECE Rep. Int. ICP Forests, Eberswalde, Germany. Available on: <http://icp-forests.net/>.
- Sicard P, De Marco A, Dalstein-Richter L. et al. An epidemiological assessment of stomatal ozone flux-based critical levels for ozone injury in southern European forests. *Sci Tot Environ* 2016;**541**: 729–41. <https://doi.org/10.1016/j.scitotenv.2015.09.113>.
- Sicard P, De Marco A, Carrari E. et al. Epidemiological derivation of flux-based critical levels for visible ozone injury in European forests. *J For Res* 2020;**31**:1509–19. <https://doi.org/10.1007/s11676-020-01191-x>.
- Siegwolf RTW, Brooks JR, Roden J. et al. Stable isotopes in tree rings. Inferring physiological, climatic and environmental responses. *Tree Physiol* 2022;**8**. Series Editors: F.C. Meinzer, Ü. Niinemets. Springer Link; 1–775. <https://doi.org/https://link.springer.com/book/10.1007/978-3-030-92698-4>.
- Skelly JM, Innes JL. Waldsterben in the forests of Central Europe and eastern North America: fantasy or reality? *Plant Disease* 1994;**78**: 1021–32. <https://doi.org/10.1094/PD-78-1021>.

- Snyder KA, Robinson SA, Schmidt S. et al. Stable isotope approaches and opportunities for improving plant conservation. *Cons Physiol* 2022;**10**:coac056. <https://doi.org/10.1093/conphys/coac056>.
- Solberg S. Crown density changes of Norway spruce and the influence from increased age on permanent monitoring plots in Norway during 1988–1997. *Eur J For Pathol* 1999a;**29**:219–30. <https://doi.org/10.1046/j.1439-0329.1999.00150.x>.
- Solberg S. Crown condition and growth relationships within stands of *Picea abies*. *Scand J For Res* 1999b;**14**:320–7. <https://doi.org/10.1080/02827589950152638>.
- Solberg S. Summer drought: a driver for crown condition and mortality of Norway spruce in Norway. *For Pathol* 2004;**34**:93–104. <https://doi.org/10.1111/j.1439-0329.2004.00351.x>.
- Solberg S, Tørseth K. Crown condition of Norway spruce in relation to sulfur and nitrogen deposition and soil properties in South-east Norway. *Environ Pollut* 1997;**96**:19–27. [https://doi.org/10.1016/S0269-7491\(97\)00010-9](https://doi.org/10.1016/S0269-7491(97)00010-9).
- Solberg S, Strand L. Crown density assessments, control surveys and reproducibility. *Environ Monit Assess* 1999;**56**:75–86. <https://doi.org/10.1023/A:1005980326079>.
- Solberg S, Tveite B. Crown density and growth relationships between stands of *Picea abies* in Norway. *Scand J For Res* 2000;**15**:87–96. <https://doi.org/10.1080/02827580050160510>.
- Sousa-Silva R, Verheyen K, Ponette Q. et al. Tree diversity mitigates defoliation after a drought induced tipping point. *Glob Chang Biol* 2018;**24**:4304–15. <https://doi.org/10.1111/gcb.14326>.
- Spinoni J, Vogt JV, Naumann G. et al. Will drought events become more frequent and severe in Europe? *Int J Climatol* 2018;**38**:1718–36. <https://doi.org/10.1002/joc.5291>.
- Strasser RJ, Srivastava A, Tsimilli-Michael M. The fluorescence transient as a tool to characterize and screen photosynthetic samples. In: Yunus M, Pathre U, Mohanty P, eds. *Probing Photosynthesis: Mechanisms, Regulation and Adaptation*. London, UK: Taylor & Francis, 2000; 445–83.
- Strasser RJ, Tsimilli-Michael M, Srivastava A. Analysis of the fluorescence transient. In: Papageorgiou G, Govindjee G (eds), *Chlorophyll Fluorescence: A Signature of Photosynthesis*, Advances in Photosynthesis and Respiration Series. The Netherlands: Springer Dordrecht, 2004; 321–62.
- Swoczyńska T, Kalaji HM, Bussotti F. et al. Environmental stress—what can we learn from chlorophyll a fluorescence analysis in woody plants? A review *Front Plant Sci* 2022;**13**:1048582. <https://doi.org/10.3389/fpls.2022.1048582>.
- Tallieu C, Badeau V, Allard D. et al. Year-to-year crown condition poorly contributes to ring width variations of beech trees in French ICP level I network. *For Ecol Manage* 2020;**465**:118071. <https://doi.org/10.1016/j.foreco.2020.118071>.
- Tausz M, Wonisch A, Grill D. et al. Measuring antioxidants in tree species in the natural environment: from sampling to data evaluation. *J Exp Bot* 2003;**54**:1505–10. <https://doi.org/10.1093/jxb/erg175>.
- Terzi R. Dehydration avoidance mechanism: leaf rolling. *Bot Rev* 2007;**73**:290–302.
- Thimonier A, Graf Pannatier E, Schmitt M. et al. Does exceeding the critical loads for nitrogen alter nitrate leaching, the nutrient status of trees and their crown condition at Swiss long-term forest ecosystem research (LWF) sites. *Eur J For Res* 2010;**129**:443–61. <https://doi.org/10.1007/s10342-009-0328-9>.
- Timmermann V, Potočić N, Ognjenović M, Kirchner T 2022 Tree crown condition in 2021. In: Michel A, Kirchner T, Prescher AK, Schwärzel K (eds), *Forest Condition in Europe: The 2021 Assessment*, ICP Forests Technical Report under the UNECE Convention on Long-range Transboundary Air Pollution (Air Convention) Eberswalde: Thünen Institute. <https://doi.org/10.3220/ICPTR1656330928000>.
- Toigo M, Nicolas M, Jonard M. et al. Temporal trends in tree defoliation and response to multiple biotic and abiotic stresses. *For Ecol Manage* 2020;**477**:118476. <https://doi.org/10.1016/j.foreco.2020.118476>.
- Tomasella M, Häberle KH, Nardini A. et al. Post-drought hydraulic recovery is accompanied by non-structural carbohydrate depletion in the stem wood of Norway spruce saplings. *Sci Rep* 2017;**7**:14308. <https://doi.org/10.1038/s41598-017-14645-w>.
- Trugman AT. Integrating plant physiology and community ecology across scales through trait-based models to predict drought mortality. *New Phytol* 2022;**234**:21–7. <https://doi.org/10.1111/nph.17821>.
- Turnbull TL, Adams MA, Warren CR. Increased photosynthesis following partial defoliation of field-grown *Eucalyptus globulus* seedlings is not caused by increased leaf nitrogen. *Tree Physiol* 2007;**27**:1481–92. <https://doi.org/10.1093/treephys/27.10.1481>.
- Tzvetkova N, Hadjiivanova C. Chemical composition and biochemical changes in needles of Scots pine (*Pinus sylvestris* L.) stands at different stages of decline in Bulgaria. *Trees* 2006;**20**:405–9. <https://doi.org/10.1007/s00468-006-0052-8>.
- Uchino H, Watanabe T, Ramu K. et al. Calibrating chlorophyll meter (SPAD-502) reading by specific leaf area for estimating leaf nitrogen concentration in sweet sorghum. *J Plant Nutr* 2013;**36**:1640–6. <https://doi.org/10.1080/01904167.2013.799190>.
- Ugarkovic D, Jazbec A, Seletkovic I. et al. Silver fir decline in pure and mixed stands at western edge of spread in Croatian Dinarides depends on some stand structure and climate factors. *Sustainability* 2021;**13**:6060. <https://doi.org/10.3390/su13116060>.
- Valentini R, Beileli Marchesini L, Gianelle D. et al. New tree monitoring systems: from industry 4.0 to nature 4.0. *Ann Silv Res* 2019;**43**:84–8. <https://doi.org/10.12899/asr-1847>.
- Vandegehuchte WM, Steppe K. Sap-flux density measurement methods: working principles and applicability. *Funct Plant Biol* 2013;**40**:213–23. <https://doi.org/10.1071/FP12233>.
- Vannini A, Valentini R. Influence of water relations on *Quercus cerris*–*Hypoxylon mediterraneum* interaction: a model of drought-induced susceptibility to a weakness parasite. *Tree Physiol* 1995;**14**:129–39. <https://doi.org/10.1093/treephys/14.2.129>.
- Vitale M, Proietti C, Cionni I. et al. Random forests analysis: a useful tool for defining the relative importance of environmental conditions on crown defoliation. *Water Air Soil Pollut* 2014;**225**:1992. <https://doi.org/10.1007/s11270-014-1992-z>.
- Vollenweider P, Menard T, Arend M, Guenthardt-Goerg MS. Structural changes associated with drought stress symptoms in foliage of Central European oaks. *Trees: Structure and Function*, 2016;**30**:883–900.
- Waldner P, Marchetto A, Thimonier A. et al. Detection of temporal trends in atmospheric deposition of inorganic nitrogen and sulphate to forests in Europe. *Atmos Environ* 2014;**95**:363–74. <https://doi.org/10.1016/j.atmosenv.2014.06.054>.
- Walthert L, Ganthaler A, Mayr S. et al. From the comfort zone to crown dieback: sequence of physiological stress thresholds in mature European beech trees across progressive drought. *Sci Tot Environ* 2021;**753**:141792. <https://doi.org/10.1016/j.scitotenv.2020.141792>.

- Wang Z, Zhou Z, Wang C. Defoliation-induced tree growth declines are jointly limited by carbon source and sink activities. *Sci Tot Environ* 2021;**762**:143077. <https://doi.org/10.1016/j.scitotenv.2020.143077>.
- Wiley E, Huepenbecker S, Casper BB. et al. The effects of defoliation on carbon allocation: can carbon limitation reduce growth in favour of storage? *Tree Physiol* 2013;**33**:1216–28. <https://doi.org/10.1093/treephys/tpt093>.
- Zierl B. Relations between crown condition and ozone and its dependence on environmental factors. *Environ Pollut* 2002;**119**:55–68. [https://doi.org/10.1016/S0269-7491\(01\)00323-2](https://doi.org/10.1016/S0269-7491(01)00323-2).
- Zierl B. A simulation study to analyse the relations between crown condition and drought in Switzerland. *For Ecol Manage* 2004;**188**:25–38. <https://doi.org/10.1016/j.foreco.2003.07.019>.
- Zhu J, Thimonier A, Etzold S. et al. Variation in leaf morphological traits of European beech and Norway spruce over two decades in Switzerland. *Front For Glob Change* 2022;**4**:778351. <https://doi.org/10.3389/ffgc.2021.778351>.
- Zweifel R, Etzold S, Basler D. et al. TreeNet—the biological drought and growth indicator network. *Front Plant Sci* 2021;**4**:1–14. <https://doi.org/10.3389/ffgc.2021.776905>.
- Zweifel R, Pappas C, Peters RL. et al. Networking the forest infrastructure towards near real-time monitoring—a white paper. *Sci Tot Environ* 2023;**872**:162167. <https://doi.org/10.1016/j.scitotenv.2023.162167>.