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European-wide ecosystem responses and their vulnerability to intensive drought

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Chapter 1

General introduction

Chapter 1

1.1 Increasing future drought

Overwhelming evidence has been found for rapid climate change with predicted rising global temperatures (rise by up to 4 °C by 2100) and altering precipitation (Thuiller, 2007). These deteriorating average climatic conditions are believed to also increase the frequency and magnitude of climate extremes (Easterling et al., 2000; Field et al., 2012; Meehl and Tebaldi, 2004). Indeed, climate change has led to a notable number of record-breaking climate extremes in the past decades such as heat waves, droughts, and flooding (Changnon et al., 2000; Easterling et al., 2000; Milly et al., 2002; Pokhrel et al., 2021; Zeng et al., 2023). It is important to note that these extreme events are often triggered by multiple dependent climate drivers, and occur simultaneously in different regions across the globe, causing severe and sometimes irreversible impacts on human and ecology systems (Smith, 2011).

Of all climate extremes, drought will likely bring the most complex impacts and challenges to human systems over the next century (Gregory et al., 2005; World Economic Forum, 2018). There is accumulating evidence for an increase in severe global drought events with extreme conditions (Dai, 2012). Europe is already experiencing these shifts with more frequent and severe droughts; exemplary of this is the 2018 event being the most extreme in the past 1100 years while the events in 2003, 2015 and 2022 also ranking high (Büntgen et al., 2021; Faranda et al., 2023). Other parts of the world are experiencing similar drought events such as the 2021 drought in the western United States and the 2019 drought in southern Africa (Feldman et al., 2023; Hulsman et al., 2021). In addition to the increasing frequency of various types of droughts (e.g., meteorological, agricultural, hydrological), the severity and spatial extent of droughts are also predicted to increase across many regions of the world (Field et al., 2012), especially in Europe (Christian et al., 2023; Hari et al., 2020; Lu et al., 2019; Samaniego et al., 2018).

1.2 Risks for ecosystems facing increasing drought

The increased frequency and severity of droughts in recent decades across many regions (Spinoni et al., 2019) have caused large impacts on global terrestrial ecosystems, including changes on the hydrological cycle, plant productivity and on the delivery of ecosystem services (Caldeira et al., 2015; Reichstein et al., 2013). The low soil water availability during drought can cause a series of physiological reactions of plants, such as plant stomatal adjustment or even closure, decreasing leaf transpiration and evaporative cooling, and thus carbon uptake and photosynthesis (Reichstein et al., 2013). This affects the evapotranspiration (ET) and gross

primary productivity (GPP) of the ecosystem. In particular, droughts have caused an adverse impact on forest and crop growth. For instance, accumulating evidence of crown defoliation and reductions in gross primary productivity of ecosystems under extreme droughts were reported in Europe, United States, Asia and Australia (Ciais et al., 2005; He et al., 2021; Van Mantgem et al., 2009). Given that evapotranspiration and GPP are the foundation of many ecosystem processes, the subsequent impacts of reductions in these processes affect the provisioning of ecosystem services negatively (Anderegg et al., 2013). Indeed, risks to the associated global carbon cycle balance (including carbon sequestration), climate moderation and food security have been documented (Reichstein et al., 2013).

In addition to the impacts on vegetation growth, droughts also have caused a major increase in plant mortality. Severe droughts give rise to higher gradients of vapor pressure between leaves and the atmosphere, which causes a high tension in the xylem of plants, leading to embolism and partial failure of hydraulic transportation, and ultimately resulting in plant mortality (Anderegg et al., 2012). At the same time, droughts can induce other factors that may pose additional pressure to trees such as insect attacks, changing of fungi and bacteria (McDowell et al., 2011) or fire disturbance (Brando et al., 2014). Especially, these factors can amplify the probability of tree mortality under drought (Brando et al., 2014; Hajek et al., 2022). Droughts have caused massive mortality to tropical, temperate, and boreal forests in past decades (Stovall et al., 2019). Moreover, increased tree mortality has been reported recently across globe (Allen et al., 2010; Van Mantgem et al., 2009), which could disturb ecosystem composition and structure as well as ecosystem functions, such as carbon and water cycling, surface energy balance, climate mitigation and resistance to climate extremes (Adams et al., 2012; Allen et al., 2010; Anderegg et al., 2013; Batllori et al., 2020). To mitigate these risks, it is important to identify the most vulnerable ecosystems in order to allocate water resources (e.g. through irrigation) to those ecosystems that need it most.

1.3 Drought responses of ecosystems

Under water stress, the vulnerability of different ecosystems varies because of their different reactions to the stress induced. At the individual scale, plants can have multiple physiological regulation strategies to adapt to drought. Classifying plants on basis of their resistance strategies (i.e., into drought avoidance, drought tolerance, and drought escape) is therefore useful for vulnerability analysis (Price et al., 2002). Drought avoidance is the ability of plants to endure moderate drought stress by maintaining high tissue water contents (Levitt, 1980). Drought

Chapter 1

avoidance can be accomplished by various adaptive responses to maintain water uptake or reduce water loss, such as developing well-developed root systems or reducing water loss and water stress through stomatal regulation and reduced leaf area (Gowda et al., 2011; Li et al., 2022). Drought tolerance is the ability of plants to endure low tissue water content through osmotic adjustment, protoplasmic tolerance or compatible solutes (Gowda et al., 2011). Drought escape is the ability of a plant to complete its life cycle before a drought, which can be related to growth adjustments according to water availability via rapid phenological development and developmental plasticity (Jones et al., 1981).

Alternatively, plants can also be classified on the regulation of the leaf water potential (an indicator of plant water stress which refers to the force with which water is held within the leaf) due to the importance of water related strategies, sorting them across the isohydric-anisohydric spectrum (Klein, 2014). Here, isohydric species are those that exert a tight regulation of their water content and maintain a constant daily leaf water potential despite the soil water status, while anisohydric species exhibit a reducing leaf water potential with the decreasing soil water potential (Tardieu and Davies, 1993; Tardieu and Simonneau, 1998). Isohydric behavior is commonly considered to have strict stomatal regulation of transpiration, which is believed to minimize the risk of damaging xylem cavitation in hydraulic system at the cost of reduced carbon assimilation (McDowell et al., 2008). In contrast, anisohydric behavior is considered to be associated with the maintenance of open stomata and carbon assimilation, which is believed under a high risk of hydraulic failure (McDowell et al., 2008). However, researchers warned that the connection between water potential regulation, stomatal behavior and the mechanisms of mortality may not be as simple as this (Garcia-Fornier et al., 2017; Nolan et al., 2017). This classification is widely used and therefore we have chosen to adopt these concepts and supplement them with specific concepts related to drought avoidance, drought tolerance, and drought escape classification.

Depending on the stress response mechanism of the plant species involved, i.e. their water-related strategies, in combination with the way a drought develops at a certain location, a mismatch between the strategy and the stress may arise. Ultimately, this leads to increased mortality probability. Several physiological responses are thought to link to the mechanisms of plant mortality such as hydraulic related adjustment; carbon regulation and stomatal control. Based on the physiological responses of plants especially the hydraulic related responses, one of the leading hypotheses of plant mortality mechanisms was built, which is the hypothesis of hydraulic failure and carbon starvation. Hydraulic failure is plant desiccation caused by

cavitation (A phenomenon in which dissolved air forms bubbles within either the vessels or the tracheids when the water tension within the xylem reaches a critical point) and subsequent conductivity loss of the xylem (McDowell et al., 2008; McDowell, 2011). Carbon starvation occurs when plants close their stomata to avoid hydraulic failure resulting in limited carbon uptake relative to carbon demand (McDowell et al., 2008). However, the mechanisms of plant mortality during drought are not fully understood based on different physiological responses, i.e., the connection of water potential regulation, carbon regulation and stomatal behavior with vegetation mortality is still unclear. For instance, the extent to which carbon starvation is directly related to tighter water and stomatal management is still controversial (Garcia-Forner et al., 2017; Martínez-Vilalta and Garcia-Forner, 2017; Mencuccini et al., 2015). Thus, it is still not clear which drought strategies or combined physiological responses of plants do effectively impact and reduce mortality.

1.4 Remote sensing application in evaluation of ecosystem response to drought

1.4.1 Advantage of remote sensing in large-scale drought and drought impacts monitoring

As traditional in situ measurements are time-consuming and labor-intensive, they are difficult to provide continuous and large-scale monitoring (Bhaga et al., 2020). As a result, the available observations are sometimes insufficient to capture the spatiotemporal variability of drought and ecosystem responses on a large scale. Furthermore, observations from different regions can have inconsistent data quality and time period, making consistent large-scale drought and drought impact analysis challenging (AghaKouchak et al., 2015). In addition, because of the interactions between different species within ecosystems, it is difficult to scale up observations at individual levels via in situ measurements to an ecosystem level (Martínez-Vilalta and Garcia-Forner, 2017; Skelton et al., 2015). Remote sensing, with its real-time and large-scale long term monitoring, provides opportunities to overcome the above difficulties (West et al., 2019). Remote sensing has been widely used for drought monitoring and subsequent drought ecosystem impacts in the past decades (AghaKouchak et al., 2015; Asner and Alencar, 2010; Fang et al., 2019), which provides timely detection of spatial-temporal dynamics for drought and its impacts over large scales across the globe.

1.4.2 The potential application of remote sensing in ecosystems facing increasing drought

The application of remote sensing enables the monitoring and analysis of long-term changes in vegetation over climate conditions (West et al., 2019). So far, remote sensing has achieved success in monitoring vegetation vulnerability via analyzing the correlation between vegetation growth and drought as indicated by indexes based on remote sensing (Gouveia et al., 2017; Xu et al., 2018; Zhang et al., 2017). For a long period of time, indices like the Normalized Difference Vegetation Index (NDVI) or Enhanced Vegetation Index (EVI) (Huete et al., 2002) have been used as indicators for vegetation growth during drought, and the Standardized Precipitation Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010), Standardized Precipitation Index (SPI) (McKee, 1993) or Palmer Drought Severity Index (PDSI) (Palmer, 1965) have been used as drought indicators. However, such analyses only focus on responses into drought through long-term correlations, while lacking an accurate coupling of drought events and vegetation anomaly events. Thus, it is difficult to predict drought impacts on ecosystems in future climate scenarios by these correlation analyses. Facing the increasingly frequent and severe droughts (Field et al., 2012), a major question is whether the damage to ecosystems will also increase proportionally with drought, and which ecosystems will collapse more quickly than others. The answer to this question can provide us with critical information for reasonable and effective water allocation strategies among different types of ecosystems under drought. High resolution remote sensing provides a potential opportunity to solve this challenge: By using high-resolution drought and vegetation growth data from remote sensing, a more accurate analysis of the linkage between drought events and vegetation anomaly events can be achieved at ecosystem level.

To build accurate prediction models of drought impacts in the future, not only the linkage between biomass damage and drought should be investigated, but ecosystem adaptation strategies should also be analyzed. Especially, large-scale and real-time analyses of ecosystem strategies to drought are needed for building global prediction models of drought impacts and making timely ecosystem management measures under drought. However, current research on the physiological response or regulation strategies of vegetation to drought is mainly limited to local field measurements. While, these field measurements effectively revealed the physiological changes of plants under water stress from an individual perspective, they also elicited the diversity of plant strategies with multiple physiological adjustments and responses to drought. Given the discontinuity in time and space of these field measurement data, it

becomes very difficult to investigate ecosystem strategies at a large scale (Martínez-Vilalta and Garcia-Forner, 2017) and to evaluate general patterns of responses. Moreover, because different strategies among different species may compensate each other within an ecosystem (Mayoral et al., 2015; Pardos et al., 2021), strategies measured over individual plants can hardly effectively represent the strategies on the entire ecosystem hierarchy (Skelton et al., 2015). High resolution remote sensing observations allow evaluating physiological responses to drought at the ecological level and provide the opportunity to overcome these challenges. Actually, remote sensing has already achieved monitoring of crucial physiological changes of vegetation related to water and carbon regulation in the past decades, such as monitoring canopy water content using vegetation optical depth (VOD) (Lyons et al., 2021; Tian et al., 2018; Togliatti et al., 2019) or normalized difference infrared index (NDII) (Hunt and Rock, 1989; Liu et al., 2021), monitoring ecosystem evapotranspiration using evapotranspiration (ET) products (Ahmed et al., 2021; Zhang et al., 2016) and monitoring biomass or structure of vegetation using leaf area index (LAI) (CHEN and BLACK, 1992; Clark et al., 2008; Zheng and Moskal, 2009). Unfortunately, remote sensing has currently not been applied in the analysis of vegetation response strategies consisting of various physiological responses facing drought. Only by observing multiple plant physiological traits simultaneously, we can classify and understand ecosystem wide responses.

Remote sensing can also aid in further resolving the various physiological adjustments and responses to drought, including those that ultimately lead to mortality (see section 1.3). Due to the lack of large-scale survey data, the understanding of the multiple types of physiological responses is limited and the spatial and temporal variation in those responses is poorly understood. This lack of understanding also constrains our current analysis of how the combination of these regulatory strategies of trees affects the overall response of ecosystems to drought, including the mortality probability of ecosystems. Remote sensing has the potential to provide multiple simultaneous physiological data and mortality data at large scale. Indeed, remote sensing has been applied in providing early warning signals of tree mortality, such as analysing abnormal changes in tree greenness (Liu et al., 2019) or water content (Brodrick and Asner, 2017) during drought to capture health abnormal signals that can indicate tree mortality. However, these studies are limited to one particular aspect of tree physiological responses to drought. The application of remote sensing to analyse the relationship between comprehensive strategies and plant responses in different ecosystems is still lacking. Given the potential application of remote sensing in vegetation strategy monitoring, it also has significant potential application value in explaining mortality mechanisms of trees threatened by drought.

Chapter 1

1.5 Research aims and questions

In light of the identified knowledge challenges, the aim of this thesis is to enhance our understanding of ecosystem responses to drought and based on these responses analysing the risks that ecosystems face under increasing droughts. To achieve this aim, the following questions were proposed:

1. How does vulnerability (i.e., the change in vegetation damage with increasing drought) vary between ecosystems across the Netherlands and Belgium during drought?
2. How does vulnerability to drought vary between and within ecosystems with increasing drought conditions in Europe?
3. What are strategies of different ecosystems to respond to drought in Europe?
4. How do different strategies of ecosystem types impact their mortality in European forests?

To answer these questions, utilizing the unprecedented 2018 European drought, a high-resolution European drought dataset was calculated, and multiple physiological responses of European ecosystems to this drought were monitored using remote sensing indicators. Based on the drought index SPEI and the vegetation canopy leaf area index LAI, a new framework for coupling drought events to anomalies in vegetation responses has been established. Based on this framework, I analyzed the vulnerability risks of different ecosystems. Furthermore, based on LAI, the vegetation water content index NDII and the vegetation evapotranspiration index ET, the main responses of ecosystems to drought have been analyzed in Europe in relation to their strategies to deal with drought. Finally, the relationship between these drought strategies of the ecosystem and drought-induced mortality was analyzed in European forests.

1.6 Thesis outline

The conceptual outline of this thesis is shown in Figure 1.1.

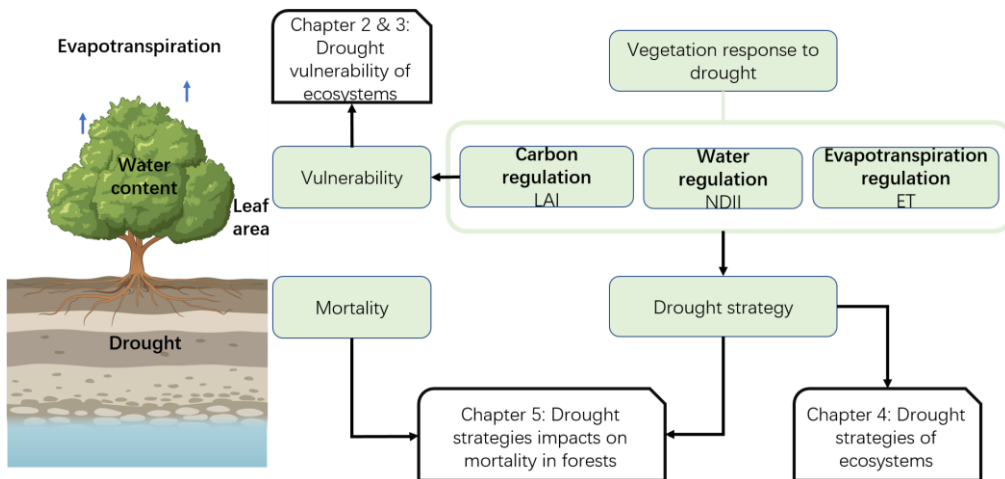


Fig. 1.1. The conceptual outline of this thesis (Tree figure created with BioRender.com).

Chapter 1: General introduction

This chapter provides a general introduction about the increasing drought and the subsequent ecosystem risks, strategies of ecosystems to deal with these droughts and the potential application of remote sensing in this field. The main research questions are listed in this chapter.

Chapter 2: A multi-metric assessment of drought vulnerability across different vegetation types using high resolution remote sensing

This chapter presents a new framework to analyze drought events and the subsequent damage in vegetation, aiming to achieve a better understanding of the multiple perspectives of drought impacts. Drought events and damage were characterized from multiple perspectives including the onset, duration and severity of these events. Then, the relationships between these drought characteristics and vegetation damage characteristics were investigated. Finally, the vulnerability of different ecosystems to drought was evaluated across the Netherlands and Belgium in 2018. This framework can be widely applied in the analysis of future drought impacts on ecosystems to obtain more comprehensive insights.

Chapter 3: Ecosystems threatened by intensified drought with divergent vulnerability

This chapter quantitatively evaluates the vulnerability to drought of the main ecosystem types

Chapter 1

across Europe by further quantifying the relationships between drought characteristics and vegetation damage characteristics based on the drought analysis framework built previously. This chapter reveals that as drought conditions increase, the vulnerability (i.e., sensitivity of damage) in each ecosystem varies. Among all ecosystems, irrigated crops are particularly vulnerable, while mixed forests show a low vulnerability facing intensified drought. Furthermore, this chapter reveals the disproportionate increase of ecosystem sensitivity with increasing drought severity, which represents that ecosystems will become more vulnerable in the 21st century in response to the projected intensified droughts.

Chapter 4: Variations in ecosystem-scale vegetation drought strategies across Europe

This chapter explores vegetation drought strategies in different ecosystem types across Europe via remote sensing. Three key ecosystem physiological responses were identified to represent drought strategies associated with plant carbon and water regulation processes, including canopy carbon regulation indicated by the variation of LAI, canopy water content regulation indicated by the variation of NDII and evapotranspiration regulation indicated by the variation of ET. Ecosystems show different responses in these regulation processes, which represents their different priorities in water and carbon management during drought. In addition, ecosystems generally keep a stable strategy as the drought gradient increases, while some vulnerable types such as irrigated croplands start to dysfunction at some point and fail to adapt to drought. Drought strategies detected from remote sensing provide real-time methods for analyzing drought impacts on a large scale.

Chapter 5: A combination of vegetation responses identifies drought mortality across European forests

Based on three key ecosystem physiological responses (water regulation, carbon regulation, and stomatal regulation) detected from remote sensing, this chapter further looks into how these combined physiological responses impact ecosystem mortality during drought. An early reduction in canopy water content and leaf area normally indicates a high mortality probability of forests, and large reduction in these two indexes indicates an extremely high mortality probability. In this case, the adoption of these two indexes can provide early warning signals of drought-related mortality. In addition, during the 2018 drought across Europe, hydraulic failure might have had a larger impact on forest mortality probabilities than solely carbon starvation. This analysis addresses the potential of remote sensing in explaining forest mortality upon

vegetation responses and developing mortality prediction models.

Chapter 6: General discussion

This chapter presents the principal findings and implications of this research project. First, the increasing risks of ecosystems facing intensified droughts are discussed. Then, the benefits of detecting drought strategies through remote sensing for evaluating drought impacts and finding early warning signals for vegetation mortality are emphasized. Finally, based on the results from previous chapters, the implications for future ecosystem management facing drought are discussed.

Chapter 1

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Chapter 1

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