LIGHT AFTER DEATH:

THE IMPORTANCE OF SPECTRAL COMPOSITION IN LITTER DECOMPOSITION PROCESSES

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DOCTORAL DISSERTATION

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CONTENTS

LIST OF PUBLICATIONS

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TABLE OF CONTRIBUTIONS

	I	II	III	IV
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ABSTRACT

This dissertation focuses on the effect of sunlight on leaf litter decomposition. Sunlight can affect litter decomposition positively or negatively through the process known as photodegradation. Photodegradation is the ensemble of direct, indirect and mediated mechanisms. Short-wavelength solar radiation, carrying high energy, has the capacity to directly break down relatively stable components of plant tissues, such as lignin and cellulose, through photochemical mineralization causing the release of volatile carbon compounds into the atmosphere. Photochemical mineralization produces more-labile molecules, which can enhance the activity of microbial decomposers through a process known as photofacilitation or photopriming. Solar radiation has also the ability to indirectly alter decomposition through negative effects (photoinhibition) on both the activity and community composition of decomposer organisms.

We examined the process of photodegradation under forest canopies in a temperate and a boreal environment. Through two field experiments, we tested the effects of photodegradation on mass loss and carbon content during leaf litter decomposition in each environment (I in France and II in Finland). We also studied these processes under controlled conditions in a filter experiment (II). In France, we performed an additional field experiment, in the same forest as the first, to analyse the effect of photodegradation on microbial assemblages colonizing the litter (III). In these experiments, we employed "photodegradation-litterbags", bespoke litterbags adapted from classical litterbags used in litter decomposition studies incorporating different types of film filter-material, allowing us to manipulate the spectral composition of sunlight. Finally, we conducted a meta-analysis (IV) to summarise the effect of photodegradation driven by different spectral regions of solar radiation at the global scale, and across different biomes, and to test whether the photodegradation rate is modulated by initial litter traits.

This dissertation highlights the importance of blue light as a major driver of photodegradation in a temperate mid-latitude forest understorey,

with the potential to enhance both litter mass loss and carbon loss. However, at a higher latitude, the full spectrum of sunlight decreased mass loss, suggesting that the effect of photodegradation is specific to each biome. Forest canopies not only modify the amount of incoming solar radiation and its spectral composition, but also shape the microclimate of the understorey, producing unique combinations of temperature, moisture and snow-pack depth. Hence, each canopy generates novel interactions of solar radiation and other environmental factors which act on leaf litter to determine the photodegradation rate. At both boreal and temperate latitudes, our spectral manipulations revealed the effect of photodegradation to be litter species-specific, with recalcitrant litter experiencing higher rates of photodegradation. In terms of microbial decomposition, we highlighted how blue light, UV-A radiation and green light, act synergistically to shape the structure of microbial decomposer communities, with bacteria tending to dominate in sunlight and fungi in dark conditions.

The results of our meta-analysis show that the direction and magnitude of photodegradation are dependent on the spectral region considered. We highlight the crucial role of blue light and UV-A radiation as drivers of photodegradation across biomes. Blue light has a positive effect in enhancing mass loss, while UV-A radiation has a negative effect. Moreover, our meta-analysis shows that the rate of photodegradation at the global level is modulated by climate and ecosystem type; whereby arid and semiarid ecosystems with low canopy cover experience the highest photodegradation rates. On the other hand, initial litter traits failed to predict the rate of photodegradation on the global scale, despite being important at the local level; suggesting that different traits could be important in different biomes.

Photodegradation is known to have a role in the carbon cycle, as the process of photochemical mineralization causes the release of volatile carbon compounds into the atmosphere. Therefore, we can expect photodegradation to reduce the amount of carbon sequestered by ecosystems. However, further research is needed to estimate the actual contribution of photodegradation to the global carbon cycle. Moreover, this contribution is likely to be affected by climate change, which modifies environmental factors such as temperature

and the amount and pattern of precipitation; these factors together with spectral irradiance determine the photodegradation rate.

Overall, our results show that the process of photodegradation has an effect on litter decomposition in the understorey of mid- and high- latitude forests, despite the low irradiance to which litter in these ecosystems is exposed. Blue light appears to be more important than other spectral regions in driving photodegradation in these habitats. However, the photodegradation rate is modulated by both climate and ecosystem type.

RÉSUMÉ

Cette thèse s'interesse à l'effet du rayonnement solaire sur la décomposition des litières. La lumière du soleil peut impacter la décomposition des litières de manière positive ou négative grâce au processus connu sous le nom de photodégradation. On définit la photodégradation comme l'ensemble des mécanismes directs et indirects par lesquels le rayonnement solaire peut impacter la décomposition des litières. Au sein du spectre solaire, les rayonnements à courtes longueurs d'ondes mais fortes énergies peuvent accélérer la décomposition au travers de la dégradation directe de la matière organique (ex: lignine, cellulose) via le processus connu sous le nom de « dégradation photochimique » provoquant ainsi la libération de composés de carbone volatils dans l'atmosphère. La dégradation photochimique peut également améliorer la décomposition microbienne grâce à la production de molécules plus labiles. Ce second processus est appelé « photofacilitation » (ou « photopriming »). Enfin, le rayonnement solaire a également la capacité d'impacter négativement la décomposition au travers de l'inhibition de l'activité des organismes décomposeurs et de la modification des communautés microbiennes (« photoinhibition »).

Nous avons étudié le processus de photodégradation sous différentes canopées forestières en milieu tempéré et boréal. Au travers deux études de terrain nous avons testé les effets de la photodégradation sur la perte en masse et la teneur en carbone lors de la décomposition de la litière dans chaque environnement (I en France et II en Finlande). Nous avons également étudié ces processus dans des conditions contrôlées dans le laboratoire (II). En France, nous avons réalisé une étude de terrain supplémentaire dans la même forêt que la première, pour analyser l'effet de la photodégradation sur les communautés microbiennes colonisant la litière (III). Nous avons utilisé des «photodegradation-litterbags» qui sont des sachets de litières permettant de filtrer différentes compositions du spectre solaire. Nous avons ensuite réalisé une méta-analyse (IV) afin de comprendre l'effet des différentes parties du spectre sur la photodegradation à l'échelle mondiale et dans différents biomes.

Dans cette étude, nous avons aussi cherché s'il existait des corrélations entre les traits initiaux des litières et leur taux de photodegradation pour prédire cette photodégradation.

Les résultats de cette thèse montrent que malgré des niveaux relativement faibles d'irradiations (sous-bois d'une forêt tempérée), la photodegradation reste importante dans le processus de décomposition de la litière. Cette thèse met également en évidence l'importance de la lumière bleue en tant que principal moteur de la photodégradation qui peut dans ces milieux tempérés de moyenne latitude, augmenter la perte de masse de litière et la perte de carbone. Cependant, à des latitudes plus élevées, le spectre complet de la lumière solaire limite la perte de masse suggérant ainsi que l'effet de la photodégradation soit dépendant du biome. De plus, l'effet des différentes régions spectrales est modulé par l'espèce constituant la canopée. En effet, des différences de canopées peuvent modifier la quantité du rayonnement solaire entrant et sa composition spectrale, mais également le microclimat du sous-étage, caractérisé par des combinaisons uniques de température, d'humidité et de hauteur de manteau neigeux. Cela suggère que l'interaction de la photodégradation avec d'autres facteurs environnementaux joue un rôle dans la détermination du taux de photodégradation. Par ailleurs, aux deux latitudes étudiées, l'effet de la photodégradation semble être spécifique à l'espèce de litière étudiée, avec un taux de photodegradation plus élevée pour les litières récalcitrantes. En termes de décomposition microbienne, nous avons mis en évidence l'effet de la lumière bleue, du rayonnement UV-A et de la lumière verte, agissant en synergie, sur la structuration des communautés microbiennes. Les bactéries ont tendance à dominer au soleil tandis que les champignons sont favorisés par l'absence de lumière bleue, verte et rayonnement UV-A.

Les résultats de notre méta-analyse montrent que le taux de photodegradation dépend de la partie du rayonnement solaire considérée. Nous soulignons le rôle très important de la lumière bleue et du rayonnement UV-A en tant que moteurs de la photodégradation dans différents biomes, bien que le rayonnement UV-B soit considéré depuis longtemps comme la principale région spectrale responsable de ce processus. La lumière bleue a un

effet positif sur la perte de masse et le rayonnement UV-A a un effet négatif. Nos résultats montrent que le taux de photodegradation à l'échelle mondiale est fonction du climat et de la typologie d'écosystème. D'autre part les traits initiaux de la litière ne semblent pas expliquer le taux de photodégradation, indiquant que différents traits pourraient être importants dans différents biomes.

La photodégradation peut jouer un rôle dans le cycle du carbone car le processus de dégradation photochimique provoque la libération de composés de carbone volatils dans l'atmosphère. Cependant, des études supplémentaires sont nécessaires pour comprendre pleinement la contribution de la photodégradation sur le cycle du carbone à l'échelle mondiale. Enfin, dans un contexte de changements climatiques, la modification des facteurs environnementaux tels que la température, la quantité et le régime des précipitations, est susceptible de modifier le taux et l'importance de la photodégradation.

TIIVISTELMÄ

Tämä väitöskirja keskittyy auringonvalon vaikutukseen karikkeen hajoamisprosessissa. Auringonvalo voi vaikuttaa karikkeen hajoamiseen positiivisesti tai negatiivisesti valon vaikutuksesta tapahtuvan hajoamisprosessin kautta (engl. photodegradation), joka koostuu suorista, epäsuorista ja välillisistä mekanismeista. Lyhytaaltoinen ja korkeaenerginen auringonsäteily voi suoraan hajottaa kasvisolukon komponentteja, kuten ligniiniä, fotokemiallisen mineralisaation avulla, aiheuttaen haihtuvien hiiliyhdisteiden vapautumista ilmakehään. Tämä prosessi tuottaa labiileja molekyylejä, jotka voivat parantaa mikrobihajottajien aktiivisuutta valoaltistuksen seurauksena. Auringonsäteily voi muuttaa karikkeen hajoamista myös epäsuorasti, vaikuttamalla negatiivisesti hajottajaorganismien aktiivisuuteen ja hajottajayhteisöjen rakenteeseen.

Tutkimme valon vaikutuksesta tapahtuvaa karikkeen hajoamisprosessia sekä kenttä- että laboratoriokokeiden avulla lauhkeassa (Ranska) ja boreaalisessa (Suomi) metsäympäristössä. Hyödynsimme klassisissa karikkeen hajoamistutkimuksissa käytettyjä karikepusseja, joihin liitettiin erityyppisiä kalvoja, joiden avulla manipuloitiin auringonvalon spektrikoostumusta. Lisäksi teimme meta-analyysin kootaksemme aurinkonvalon eri spektrialueiden vaikutukset valon aiheuttamassa karikkeen hajoamisessa globaalissa mittakaavassa ja erilaisissa biomeissa ja selvittääksemme, muuttavatko karikkeen alkuperäiset ominaisuudet hajoamisnopeutta.

Tämä väitöskirja korostaa sinisen valon merkitystä valon vaikutuksesta tapahtuvassa karikkeen hajoamisessa keskileveysasteilla sijaitsevan lauhkean vyöhykkeen metsien pohjakerroksessa, mikä voi edistää sekä karikkeen hajoamisnopeutta että hiilen kiertoa. Korkeammilla leveysasteilla kaikki auringonvalon aallonpituudet kuitenkin vähensivät karikkeen hajoamista, mikä viittaa siihen, että valon aiheuttama karikkeen hajoaminen vaihtelee biomikohtaisesti. Metsien latvustot muokkaavat pohjakerrokseen tulevan auringonsäteilyn määrään ja laatuun, mutta ne muovaavat myös

Resumé

pohjakerroksen mikroilmastoa tuottaen ainutlaatuisia lämpötilan, kosteuden ja lumipeitteen syvyyden yhdistelmiä, joilla puolestaan on merkitystä valon aiheuttamaan karikkeen hajoamiseen. Sekä boreaalisella että lauhkealla vyöhykkeellä spektrikoostumuksen manipulaatiot osoittivat että valon vaikutuksesta tapahtuva hajoaminen riippui karikkeen lajista ja oli suurempi hitaasti hajoavaan karikkeeseen. Mikrobihajotustoiminnan osalta havaittiin että sininen valo, UV-A-säteily ja vihreä valo vaikuttivat synergistisesti, muokaten mikrobiyhteisöiden rakennetta niin, että bakteerien osuus korostui auringonvalossa ja sienten valottomissa olosuhteissa.

Meta-analyysimme tulokset osoittavat, että valon vaikutuksesta tapahtuva hajoaminen on riippuvainen tarkasteltavasta spektrialueesta. Sinisen valon ja UV-A-säteilyn merkitys valon vaikutuksesta tapahtuvaan hajoamiseen on ratkaiseva eri biomeissa. Sinisellä valolla on positiivinen ja UV-A-säteilyllä negatiivinen vaikutus karikkeen hajoamiseen. Meta-analyysimme osoittaa, että valon vaikutuksesta tapahtuvan hajoamisen nopeuteen globaalilla tasolla vaikuttavat ilmasto ja ekosysteemityyppi; kuivissa ja semiaridisissa ekosysteemeissä, missä on vähän latvuston tarjoamaa suojaa, valon aiheuttamaa hajoamista tapahtuu nopeammin. Toisaalta alkuperäiset karikkeen ominaisuudet eivät ennustaneet tämän prosessin nopeutta globaalissa mittakaavassa, vaikka ne olivat tärkeitä paikallisella tasolla; tämä viittaa siihen, että erilaiset ominaisuudet voivat olla tärkeitä erilaisissa biomeissa.

Valon vaikutuksesta tapahtuvalla hajoamisella tiedetään olevan merkitystä hiilen kierron kannalta, koska fotokemiallisen mineralisaatioprosessin seurauksena ilmakehään vapautuu haihtuvia hiiliyhdisteitä. Siksi voidaan olettaa karikkeen valon vaikutuksesta tapahtuvan hajoamisen vähentävän ekosysteemien sitoman hiilen määrää. Tarvitaan kuitenkin lisätutkimuksia, jotta tosiasiallinen vaikutus globaaliin hiilen kiertoon voidaan arvioida.

Kaiken kaikkiaan tuloksemme osoittavat, että valon aiheuttamalla prosessilla on vaikutusta karikkeen hajoamiseen sekä keskileveysasteilla että korkeilla leveysasteilla sijaitsevien metsien pohjakerroksessa, huolimatta näiden ekosysteemien karikkeen saamasta alhaisesta säteilymäärästä. Sininen

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valo näyttää olevan valon vaikutuksesta tapahtuvan hajoamisen edistämisessä muita spektrialueita tärkeämpi näissä elinympäristöissä, mutta hajoamisnopeuteen vaikuttavat myös sekä ilmasto että ekosysteemityyppi.

ABBREVIATIONS

AFDM	Ash-Free Dry Mass
AMF	Arbuscular Mycorrhizal Fungi
B:G	Blue to green ratio
C	Carbon content
CH_4	Methane
C:N	Carbon-to-Nitrogen ratio
CO	Carbon monoxide
CO_2	Carbon dioxide
DNA	Deoxyribonucleic Acid
DOC	Dissolved Organic Carbon
F:B	Fungal-to-Bacterial biomass ratio
FAMEs	Fatty-Acid Methyl Esters
FW	Fresh Weight
DW	Dry Weight
GLI	Global Light Index
Gram-N	Gram-negative bacteria
Gram-P	Gram-positive bacteria
Gram-P:Gram-N	Gram-P bacteria to Gram-N bacteria biomass ratio
HPLC	High-Performance Liquid Chromatography
LAI	Leaf Area Index
Lig:N	Lignin-to-N ratio
N	Nitrogen content
NLFA	Neutral Lipid Fatty Acids
NMDS	Non-metric multidimensional scaling
NPP	Net Primary Production
PAR	Photosynthetically Active Radiation
PLFA	Phospholipid Fatty Acid
SLA	Specific Leaf Area
R:FR	Red to Far-red ratio
ROS	Reactive Oxygen Species
UV	Ultraviolet radiation
UV:PAR	UV to PAR ratio

1. INTRODUCTION

## 1.1. THE PROCESS OF PHOTODEGRADATION

Decomposition is a key process in forest ecosystems, as it regulates nutrients cycles (Cole 1986) and, consequently, has the potential to affect plants and belowground communities (Sylvain and Wall 2011). Several abiotic (temperature, precipitation, sunlight) and biotic (initial litter traits, decomposers assemblages) factors are involved in the process of decomposition in forest ecosystems, and interactions among them determine the litter decomposition rate (Prescott 2010). Which of these factors contribute most to the process of decomposition depends on the ecosystem and the climate considered (García-Palacios et al. 2013; García-Palacios et al. 2016; Wall et al. 2008).

Sunlight can affect litter decomposition positively or negatively through the process known as photodegradation (Bais et al. 2018). Photodegradation is an ensemble of direct, indirect and mediated mechanisms (Fig. 1). These mechanisms interact and are affected by the suite of environmental factors taking part to the decomposition process (King et al. 2012). The relative importance of these mechanisms depends on the biome and the climate (Almagro et al. 2017; Bais et al. 2018). Moreover, since these processes interact with each other in natural environments, their relative contribution is difficult to quantify.

Despite the effects of climate on litter decomposition being widely studied over several decades (Melin 1930; Olson 1963), the study of photodegradation begun only in the 1990s (Caldwell and Flint 1994; Zepp et al. 1995) and was mainly focused on the effects of UV (ultraviolet radiation, 280-400 nm) and particularly UV-B (280-315 nm) radiation, as a consequence of the Ozone Hole (Barnes et al. 2015; Song et al. 2013). At that time, in order to simulate the effect of ozone depletion, photodegradation research mainly involved litter exposure to enhanced UV or UV-B radiation, often supplemented far beyond what was present under ambient conditions and therefore producing results that were difficult to interpret in the context of

processes occurring in natural environments (Gehrke et al. 1995; Newsham et al. 1997). Only relatively recently, have the relative number of studies performed under ambient sunlight increased (reviewed by King et al. 2012 and Song et al. 2013). Consequently, attention was drawn to the potential of visible light to participate in the photodegradation process (Austin and Ballaré 2010). More specifically, the short wavelength regions of visible light, such as blue (420-490 nm) and green (500-570 nm) light, were shown to have an effect on litter decomposition, both directly and indirectly (Austin and Ballaré 2010; Austin et al. 2016).

As mentioned above, photodegradation involves several mechanisms, for the sake of simplicity, we will divide them into three categories: direct, indirect and mediated, and discuss them in the following subsections (Fig.1).
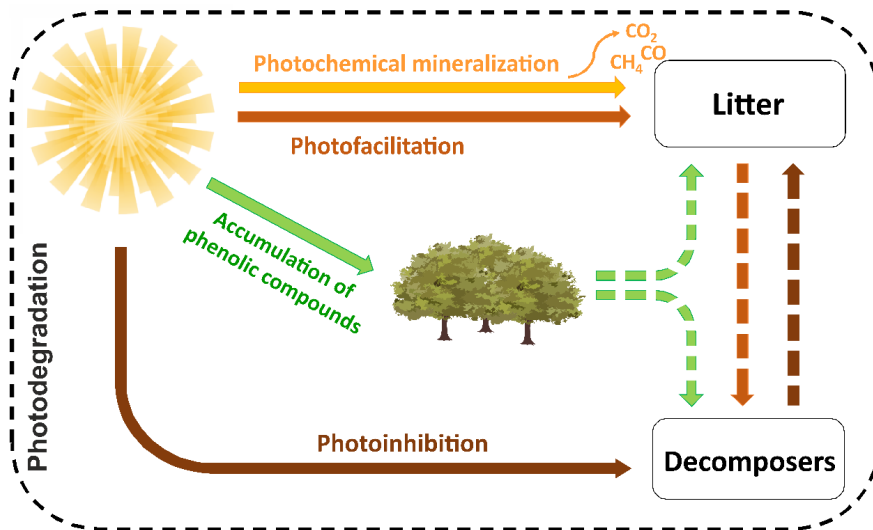
Figure 1 Schematic diagram illustrating the mechanism of photodegradation. Sunlight has three types of effects: direct (yellow arrows); indirect (brown tinted arrows) and mediated (green arrows). Direct effects involve the direct breakdown of organic matter (photochemical mineralization), described in Section 1.1.1. Indirect effects include photofacilitation (light brown) and photoinhibition (dark brown), through which sunlight enhances or inhibits the activity of decomposers (described in Section 1.1.2). Mediated effects include the accumulation of photoprotective pigments in the leaves as a consequence of exposure to sunlight (described in Section 1.1.3). Solid arrows indicate direct effects while dashed arrows indicate subsequent effects.

### 1.1.1. DIRECT EFFECTS OF SUNLIGHT ON LITTER DECOMPOSITION

Sunlight can increase the rate of litter decomposition by acting directly on litter chemistry through a process known as photochemical mineralization or photolysis (Gallo et al. 2006). This mechanism consists of the direct breakdown of organic matter due to the high energy carried by the short-wavelength part of the solar spectrum: UV radiation and blue and green light (Austin et al. 2016). Photochemical mineralization accelerates litter mass loss and carbon loss, and causes the release of volatile carbon compounds, such as methane (CH_4), carbon dioxide (CO_2) and carbon monoxide (CO), into the atmosphere (Austin et al. 2016; Brandt et al. 2009; Day et al. 2019).

The mechanism of litter photochemical mineralization is highly complex and, at present, not fully understood. Recalcitrant cell-wall polymers, particularly lignin, seem to be the target of direct photochemical mineralization (Austin and Ballaré 2010; Austin et al. 2016). This hypothesis is supported by the capability of lignin to absorb UV radiation, and blue and green light, through its chromophores and undergo the process of direct photolysis (Rahman et al. 2013). However, the formation of reactive oxygen species (ROS), caused by the photolysis of other photosensitive molecules, interacting with lignin (or vice-versa) can be another route to photochemical mineralization (indirect photolysis) (King et al. 2012). The co-existence of these two pathways could explain while several studies have found photochemical mineralization to impact different compounds from lignin.

While some studies have found a decrease in litter lignin content and failed to detect this effect on cellulose (Austin and Ballaré 2010; Austin et al. 2016), other studies have found litter cellulose content, but not in lignin content, to decrease (Baker and Allison 2015; Brandt et al. 2010; Brandt et al. 2007). Some studies have revealed the possibility that photolysis could also target hemicellulose and dissolved organic carbon (DOC) (Baker and Allison 2015; Day et al. 2015; Day et al. 2007; Wang et al. 2015). However, due to contrasting results between studies it is hard to generalize, and the target of photolysis might depend on the interaction of sunlight with other factors, such as litter quality and the pool of microbial decomposers able to utilise more or less complex biomolecules.

Box 1: The solar spectrum

The solar spectrum is an electromagnetic wave which can be divided into several spectral regions covering a discrete range of wavelengths and, consequently, carrying different amounts of energy (Aphalo et al. 2012). The quantity of energy carried by the photons decreases with increasing wavelength (Fig. 1.1). This means that, the shortest-wavelength region of the solar spectrum (UV radiation) transmitted through the atmosphere and reaching the Earth's surface, carries higher energy than visible light. Two region of UV radiation are of biological relevance: UV-B (280-315 nm) and UV-A (315-400 nm), as the wavelengths below 290nm are blocked by the stratospheric ozone layer. Despite representing only about 5% of the solar radiation reaching the Earth surface, UV radiation has a great impact on living organisms due to the large amount of energy carried by its photons (Caldwell et al. 1999). Visible light is divided into several spectral regions, identified by different colours, and includes photosynthetically active radiation (PAR = 400-700 nm) used by plants in the process of photosynthesis (Caldwell 1971). The short-wavelength parts of visible light, violet, blue and green (hereafter, we will refer to violet+blue spectral regions as "blue light"), together with UV radiation, are thought to be involved in photodegradation (Austin et al. 2016).
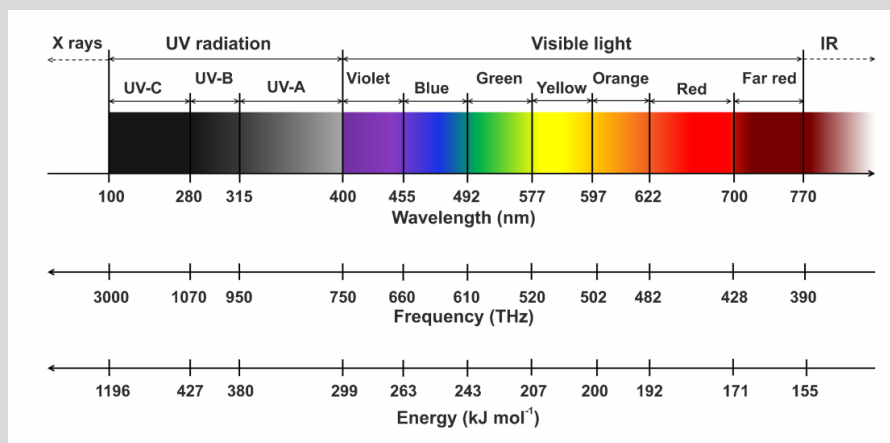
Figure 1.1: Schematic figure showing the different spectral regions that form the solar spectrum according to wavelength (nm), frequency (THz) and energy (kJ mol^{-1}) carried by their photons. Data are extracted from Aphalo et a. 2012.

1.1.2.   INDIRECT EFFECTS OF SUNLIGHT ON LITTER DECOMPOSITION

Sunlight can impact litter decomposition indirectly by affecting decomposer organisms in positive or negative ways. Currently, two main opposing mechanisms are known: photofacilitation (also called photopriming) and photoinhibition.

The first process involves the facilitation of microbial decomposition following the photomineralization of complex polymers, such as lignin, otherwise difficult for microbial decomposers to exploit (Baker and Allison 2015; Lin et al. 2018; Yanni et al. 2015).

The second, concerns the inhibition of microbial decomposition, which tends to be specific to different classes of decomposer (fungi, bacteria) and, as consequence, has the potential to alter the community structure of decomposer assemblages (Barnes et al. 2015).

These two processes are often present concomitantly during the decomposition process and are likely to be waveband-dependent, in other words dependent on the spectral composition of sunlight to which litter is exposed (Lin et al. 2018). For example, Austin et al. 2016 reported photoinhibition to occur as a consequence of exposure to UV radiation but not as a consequence of exposure to blue and green light. This segregation might be explained by the higher energy carried by UV photons, which can cause DNA-damage to living organisms (Caldwell et al. 1999). On the other hand, photofacilitation was reported as a consequence of exposure to blue and green light (Austin et al. 2016) during decomposition and of exposure to enhanced UV radiation before the decomposition process (Foereid et al. 2010).

As these two processes very-often interact, it is difficult to differentiate them during photodegradation experiments. Moreover, the relative importance of photofacilitation and photoinhibition seems to depend on the duration of exposure (King et al. 2012; Lin et al. 2018).

As with photochemical mineralization, the study of photodegradation effects on microbial decomposers started as an attempt to understand the effects of ozone depletion by exposing microbes to enhanced UV and UV-B radiation, at irradiances higher than commonly found in natural conditions (Duguay and Klironomos 2000; Moody et al. 1999). These high doses

reportedly reduced spore germination and fungal hyphal length in fungi colonizing leaf litter (Moody et al. 1999; Verhoef et al. 2000), but are not necessarily interpretable in a natural context.

Only recently, have a few studies analysed photofacilitation and photoinhibition in natural conditions in arid and semiarid environments (Ball et al. 2019; Day et al. 2018). The opposite effects were found in arid and semiarid climates, suggesting that photofacilitation and photoinhibition are affected by other environmental variables as well as UV radiation. While ambient UV radiation and blue light enhanced microbial respiration in an arid environment (Day et al. 2018), microbial respiration was reduced by exposure of *Bromus diandrus* litter to UV radiation in a semiarid ecosystem (Lin et al. 2015). These contrasting effects, and the lack of studies in mesic environments and forest ecosystems, make it hard to generalize about the impact of photofacilitation and photoinhibition on the decomposition process. Moreover, it is difficult to distinguish these indirect effects from direct effects and to determine, not only their drivers, but also their relative importance over a range of different biomes.

Although in this thesis we only examined the effects of sunlight on microbial decomposers, the consequences of these effects, as well as direct photo-inhibition, may extend to larger soil fauna, which have a crucial role in the decomposition process (Coleman et al. 2004).

When considering macro and meso-fauna, evaluation of the effects of sunlight in field conditions is challenging due to their high mobility compared to microbial decomposers. Moreover, it is difficult to separate direct effects of sunlight on these groups from the indirect effects due to modification of the food chain (Klironomos and Allen 1995), as the spectral composition impacts microbial-decomposer community structure and biomass (Pancotto et al. 2003).

As an example, the abundance of microbial feeders, such as springtails and non-oribatid mites, was reported to increase under UV-B radiation in controlled conditions due to an increase in microbial biomass (Klironomos and Allen 1995). This effect persisted despite the DNA damage that was found in springtails exposed to enhanced UV-B radiation in a controlled

environment in absence of soil, where DNA repair also occurred after a recovery period in dark conditions (Hawes et al. 2012).

These kinds of studies in controlled environments are likely to overestimate the effect that would occur in natural environments where soil fauna can hide from sunlight, to avoid damaging UV-B exposure and preferentially lay their eggs in the dark (Beresford et al. 2013; Fox et al. 2007). This inconsistency can be illustrated by comparison of the negative effects of UV radiation on earthworm fertility and abundance found in a controlled environment (Hamman et al. 2003) with the lack of effects in a fen ecosystem where earthworms have a greater opportunity to escape direct UV exposure and move between the roots of plants growing under different UV treatments (Zaller et al. 2009).

In summary, the findings from realistic experiments in natural environments suggest that these groups of decomposers are more likely to be impacted indirectly by sunlight as a consequence of the altered soil food web than by direct exposure to solar UV radiation. However, further studies are needed to test this hypothesis.

1.1.3. MEDIATED EFFECTS OF SUNLIGHT ON LITTER DECOMPOSITION

The relationship of sunlight with decomposition is also mediated through plant traits. Leaf structure and biochemistry are influenced by the amount and spectral composition of sunlight received during growth. The exposure of leaves, during the vegetative season, to UV radiation and blue light causes the accumulation of photoprotective pigments, such as flavonoids, in the leaf epidermis (Brelsford et al. 2019; Caldwell et al. 1999; Coffey et al. 2017). These phenolic compounds act as a screen against UV radiation to protect the underlying mesophyll from photodamage (Day et al. 1992; Landry et al. 1995; Rousseaux et al. 1999).

After leaf senescence, these compounds remain in the leaf litter and have the potential to alter decomposition, and the contribution of photodegradation to this process, by reducing UV penetration to the mesophyll (King et al. 2012; Kotilainen et al. 2009; Pancotto et al. 2005). Moreover, they can influence

microbial and fungal succession, through differential effects on the colonisation of leaf litter during the initial stages of decomposition (Aneja et al. 2006; Conn and Dighton 2000). However, the contribution of these mediated effects to decomposition remains relatively unexplored.

Once again research has mainly focused on the effects of elevated UV-B radiation (Gehrke et al. 1995; Hoorens et al. 2004; Newsham et al. 1999; Rozema et al. 1997). Contrasting results were found in these studies, the leaves' exposure to UV-B radiation during growth reduced the subsequent decomposition rate due to an increase in lignin and tannins in litter from a sub-arctic shrubland (Gehrke et al. 1995) and a dune grassland (Rozema et al. 1997). However, in this second environment the effect disappeared in the longer term (Hoorens et al. 2004), suggesting photodegradation-mediated effects to be important only during the initial phase of decomposition or at least to be time-dependent. On the other hand, a study on *Quercus robur* litter found enhanced UV-B radiation to decrease lignin content in the litter and its colonization by basidiomycetes fungi, consequently enhancing the decomposition rate (Newsham et al. 1999). A similar result was reported in a meta-analysis by Song et al. 2013 analysing, amongst others, the effect of UV-B exposure during growth on litter decomposition. It remains to be tested whether these positive and negative effects on decomposition mediated by litter traits are also important under ambient sunlight.

1.2. PHOTODEGRADATION AS FUNCTION OF CLIMATE, ECOSYSTEM AND LITTER TRAITS

Irradiance and the spectral composition of sunlight reaching the Earth's surface change over both spatial and temporal scales (Aphalo et al. 2012; Aphalo 2018). Therefore, we can expect variation in the photodegradation rate across biomes and ecosystems, and assume it to be more relevant at lower latitudes receiving higher UV radiation (Gallo et al. 2009). The photodegradation rate is modified by all the factors that enhance litter exposure to sunlight, including latitude (Moody et al. 2001), season (Brandt et al. 2010; Rutledge et al. 2010), leaf area index (LAI) (Bravo-Oviedo et al. 2017;

Rozema et al. 1999), canopy structure and phenological stage (Rutledge et al. 2010), litter position (surface litter vs standing litter) (Almagro et al. 2015; Brandt et al. 2009) and litter layer thickness (Henry et al. 2008; Mao et al. 2018).

Photodegradation is influenced by various environmental factors during the decomposition process, such as temperature and precipitation (Song et al. 2013). The rate of photodegradation, and particularly the contribution of photochemical mineralization to this process, seems to be enhanced in drier environments where the microbial component of decomposition is low (Brandt et al. 2007). Additionally, photodegradation is also suggested to benefit from diurnal cycles of temperature, which are thought to enhance the mechanism of photofacilitation, creating the ideal conditions for micro-organisms to utilize the bioavailable products of direct photochemical mineralization (Gliksman et al. 2017).

The trade-off between positive (photochemical mineralization, with consequent photofacilitation) and negative (photoinhibition) effects of photodegradation may differ by biome (Huang et al. 2017, Almagro et al. 2017, Gliksman et al. 2017, reviewed by Bais et al. 2018). Whereby, positive effects dominate in arid climates with limited microbial activity, while the negative effects tend to dominate in mesic ecosystems were microbial decomposers play a major role (Bais et al. 2018).

The photodegradation rate has been suggested to depend on initial litter quality (King et al. 2012). For example, recalcitrant litter with high carbon-to-nitrogen ratio (C:N), whereby there is less available nitrogen for microbial decomposers, seems to benefit more from the process of photochemical mineralization (King et al. 2012). On the other hand, Pan et al. 2015 found a positive correlation between photodegradation rate and initial nitrogen (N) content.

As lignin is the supposed target of photodegradation, the magnitude of photodegradation was suggested to increase with lignin content (Austin and Ballaré 2010; Méndez et al. 2019). However, a meta-analysis by King et al. 2012 found no consistent relationship between the rate of photodegradation and initial lignin content of the litter. On the other hand, Pan et al. 2015 found

a positive correlation between photodegradation rate and specific leaf area (SLA).

It is not yet clear what initial litter traits could potentially predict photodegradation, as the classical traits used to predict decomposition rates, such as lignin to nitrogen ratio (Lig:N), or lignin content, fail in this respect (Day et al. 2018). A recent study from Day et al. 2018 analysing the relationship between initial litter traits and photodegradation, found a positive correlation between the rate of photodegradation and the initial content of hemicellulose and cellulose. The differences in results among all these studies suggest the possibility that different traits could predict photodegradation in different biomes, however, this hypothesis remains untested.

Photodegradation represents a relevant driver of litter decomposition not only in arid (Day et al. 2015; Day et al. 2007) and semiarid (Almagro et al. 2015; Austin et al. 2016) biomes at low latitudes but also at high latitudes (Jones et al. 2016; Pancotto et al. 2003; Zaller et al. 2009) and in mesic conditions (Brandt et al. 2010).

Photodegradation has been broadly studied in arid and semiarid environments, in ecosystems characterised by low or absent canopy cover, such as grasslands (Uselman et al. 2011) or open areas (Messenger et al. 2012). On the other hand, the role of photodegradation in forest ecosystems, characterised by a particular light environment that changes through the year according to canopy phenology, remains unexplored. The very few studies employing tree leaf litter, collected this litter in forests, but set up their experiments in nearby open areas (Ma et al. 2017; Messenger et al. 2012; Newsham et al. 2001), making it impossible to extrapolate the results to a forest environment. A recent study from Méndez et al. 2019 only examines the effect of shading on litter decomposition in forest understories, without taking into account the relative importance of each waveband in the process of photodegradation.

At present, little is understood about the role played by photodegradation in litter decomposition in the understorey, under unique characteristics of irradiance and spectral composition changing throughout the year.

## 1.3. THE FOREST FLOOR: A DYNAMIC LIGHT ENVIRONMENT

Forest ecosystems are spatially complex communities characterized by a composite vertical structure formed by an upper canopy and an understorey layer of shade-loving plants (Oliver and Larson 1996). This multi-layered structure heavily modifies the irradiance and spectral composition of sunlight reaching the forest floor by processes such as transmittance, reflectance and absorption (Aphalo et al. 2012).

The forest canopy modifies the understorey light environment not only spatially but also temporally, through the seasons, according to the combination of several factors such as canopy phenology and solar path length, elevation, latitude and weather conditions (Aphalo et al. 2012). The interaction of these biotic and abiotic processes creates light conditions specific to each geographical location and forest type (Chazdon and Pearcy 1991). As a consequence, the forest floor is subject to a dynamic and ever-changing light environment, constituted by the formation of micro-sites with different light conditions, defined as sunflecks (a sun-patch of direct light reaching the forest floor, Fig.2b) and shades areas (Fig.2c) (Smith and Berry 2013; Way and Pearcy 2012).

The irradiance on the forest floor is lower than in areas without canopy cover and its spectral composition differs greatly from the irradiance characteristic of open areas for the large part of the year. In deciduous forests, understorey irradiance greatly decreases during the period of spring canopy flush and increases again during leaf fall, therefore presenting the opposite annual trend to those of solar UV-B radiation and PAR (400-700 nm) (Ross et al. 1986). Following canopy closure, the light environment on the forest floor is characterized by higher UV to PAR ratios (UV:PAR) compared to open areas, probably largely due to differences in the spectral composition of diffuse radiation compared to direct radiation.

Diffuse radiation in the understorey consists of radiation scattered by the atmosphere and reflected in the canopy: short wavelengths are scattered more than long wavelengths, so are enriched in diffuse radiation (Aphalo et al. 2012; Brown et al. 1994) (Fig.2c). Moreover, the solar radiation reaching the forest

floor is depleted in blue and red (622-700 nm) light, due to the high absorption of these spectral regions used in photosynthesis, and has a lower blue to green ratio (B:G) and red to far-red (700-780 nm) ratio (R:FR) than that found in open areas (Ross et al. 1986) (Fig.2c). These unique characteristics, in terms of spectral irradiance, are likely to impact the contribution of photodegradation to the decomposition process under canopies compared to open areas. For this reason, there are likely to be differences in the contribution of different spectral regions to photodegradation in forested ecosystems compared to open areas, and in the relative contribution of the three different mechanisms constituting photodegradation (described in section 1.1).
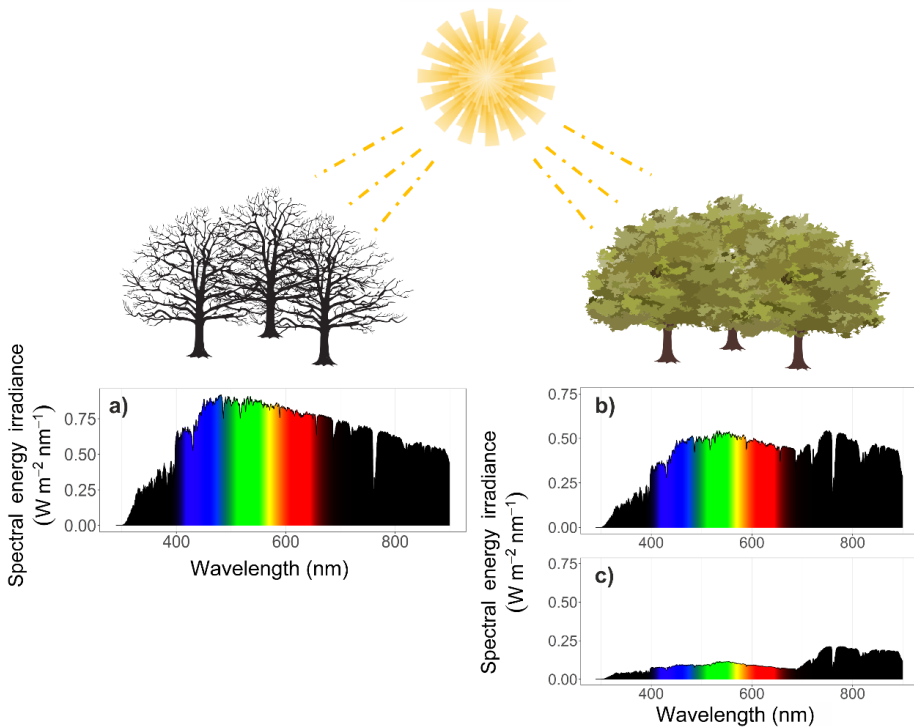
Figure 2 Schematic figure showing the spectral irradiance reaching the forest floor in a deciduous forest a) during dormancy in autumn and winter compared with b) and c) during the vegetative season. During this period, we observe the formation of b) sunflecks and c) shaded areas with different spectral composition and irradiance. Sunflecks (b) are events of very short duration that can last for just a few seconds (Smith and Berry 2013).

Sunlight in a forest understorey, as well as affecting the decomposition process through irradiance, concomitantly impacts the temperature of leaf litter and soil (Smith and Berry 2013). This increase in temperature is likely to increase evaporation of surface moisture and change the microclimate at the soil-litter interface. All of these environmental effects of sunlight interact and are likely to cause a complex final shift on litter decomposition rate.

Forests cover up to 31% of the Earth surface, these ecosystems are responsible for the absorption of about 2 billion tonnes of CO_2 per year (FAO 2018). In 2017, forests absorbed about 38% of carbon emissions from industries and fossil fuels (Brack 2019). Therefore, considering the release of carbon compounds into the atmosphere due to photodegradation in these ecosystems is fundamental to understanding the impact of photodegradation on the global carbon sink.

2. AIMS

The first aim of this thesis is to investigate the role of photodegradation in temperate and boreal forest ecosystems. First, by assessing if this process is relevant in litter decomposition in the forest, under low irradiance, and thereafter by determining which spectral regions of sunlight have the most impact on litter decomposition under forest canopies.

In order to do this, we set up several experiments that allowed us to answer to the following questions:

- Does photodegradation have an effect on litter decomposition in the understorey of temperate forests at mid-to-high latitudes where the irradiance is low? And which spectral regions are responsible for photodegradation in forest ecosystems? I-II-III (Assessed in section 4.1)

 Prediction: We expect UV radiation and blue light to enhance litter mass loss, and consequently carbon loss, as a result of both photochemical mineralization and photofacilitation. Moreover, we expect blue light to have a greater effect than UV radiation due to the low UV irradiance at mid-to-high latitudes.

- Does photodegradation impact microbial biomass and community structure, and what spectral regions are the most important in this process? III (Assessed in section 4.2)

 Prediction: We expect treatments excluding UV radiation to have higher fungal and bacterial biomass due to removal of the inhibitory effect of UV-B radiation. We expect the exclusion of UV radiation and blue light to favour fungal decomposers as they tend to prefer darker environments, but to penalise bacterial decomposers which would benefit more from photofacilitation, as they are unable to exploit complex carbon compounds.

Our second aim is to investigate how photodegradation changes across biomes and how the contribution of different environmental factors determines the photodegradation rate across the globe. Additionally, we aim to identify which initial litter traits can predict the rate of photodegradation. In order to do this, we performed a meta-analysis to answer to the following questions:

- What determines the magnitude of photodegradation operated by different spectral regions across the globe? Is it principally dependent on the climate, ecosystem type, decay period, or litter type? IV (Assessed in section 4.3)

  Prediction: Overall, we expect photodegradation to enhance litter decomposition when driven by blue light, due to the capability of this spectral region to achieve photochemical mineralization while having a minimal photoinhibitory effect. On the other hand, we expect a smaller effect of UV radiation, and little-or-no measurable effect of its constituent UV-B radiation, as the capacity of UV radiation for direct photolysis may be counter-balanced by its high photo-inhibition capacity. Furthermore, we expect the rate of photodegradation to contribute more to decomposition in arid than mesic climates, as well as in ecosystems with lower canopy cover, and to change according to the decay period. Moreover, we expect different spectral regions to be of different importance according to climate, ecosystem type and decay phase under consideration.

- What initial litter traits predict the magnitude of photodegradation? IV (Assessed in section 4.4)

  Prediction: We expect the C:N ratio and lignin content to be positively correlated with photodegradation rate, as lignin represents the main target of this process and recalcitrant litter, with lower N availability, benefits the most from the process of photochemical mineralization and consequent photofacilitation. Moreover, we expect photodegradation to have a greater impact on litter with a high surface:volume ratio due to its greater exposure to sunlight.

3. MATERIALS AND METHODS

This dissertation presents the results of three different field experiments (I, II and III), a controlled-environment study (III), and one meta-analysis (IV). The field manipulation in chapter I follows decomposition through its natural time course, in an open canopy from leaf fall through winter, to spring when received irradiance is at its highest, and summer when only occasional sunflecks provide most of the irradiance received in the understorey. Chapter II consists of two parallel experiments, one conducted in the field, concentrating on the open-canopy period from autumn to spring, and one in a controlled environment to explore the mechanisms of photodegradation more precisely. The order of the chapters was chosen because it allows a logical progression through the discussion of the results in that: chapter I and II focus on the impact of photodegradation on litter mass loss and carbon content, while chapter III extends this work to consider the impact of photodegradation on microbial assemblages colonizing the litter. Later, the capacity for these local results to be scaled up to the global level is discussed, accounting for variation in photodegradation rate across biomes (IV).

3.1. STUDY SITES

We conducted the photodegradation experiments in chapters I and III in a mature beech forest (*Fagus sylvatica* L.) in Normandy (France, 49°31'12.6"N 1°07'00.7"E). We chose this location as beech forests form a dense canopy with a large contrast in light environment in the understorey between the growing season and winter season. The study site had the advantage of flat topography and the almost total absence of understorey vegetation meaning the leaf litter is not overgrown and allowing the deployment of many litterbags over large contiguous plots.

In the experiment described in chapter I, we deployed the litterbags on 20th Dec 2016 and collected five replicate litterbags from each treatment

combination after about 3 (4th Apr 2017), 5 (6th June 2017) and 7 (27th July 2017) months for the fast-decomposing ash litter, and 3 (4th Apr 2017), 6 (27th June 2017) and 10 (10th Oct 2017) months for oak and beech litter, which is slower to decompose.

In chapter III we deployed the litterbags on 5th Dec 2017 and collected five replicate litterbags after about 1 (9th Jan 2018), 3 (07th Mar 2018), 6 (7th June 2017) months to measure mass loss and C and N contents. We also collected six replicate litterbags after about 1 (9th Jan 2018), 2 (7th Feb 2018), 3 (07th Mar 2018), 6 (7th June 2017) months to characterized microbial biomass.

To set up the outdoor experiment in chapter II we choose four forest stands in Viikki, Helsinki (II, 60°13'39.7'N, 25°01'09.5'E) characterized by different canopy species: silver birch (*Betula pendula* Roth.); Norway maple (*Acer platanoides* L.); European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) H. Karst). The presence of different dominant species allowed us to test the effect of the canopy species on the photodegradation rate. We deployed the litterbags on 7th Oct 2016 (silver birch leaves) and 19th Oct 2016 (European beech leaves) and collected them after 6 months (11th Apr 2017) with six replicates for each treatment combination.

We conducted the controlled-environment photodegradation experiment (II) in a fully temperature-controlled growth room at the Viikki Campus of the University of Helsinki, Finland. Lighting in the growth room aimed to capture the key aspects of the light environment outdoors through a combination of broad-spectrum LED lamps installed specifically for the experiments and purpose-built UV-A LED lights. Details on the spectral composition and irradiance in the growth room are given in II. We exposed the litterbags to the light treatments for 6 and 10 weeks and then collected them for the analysis with 16 replicates per each treatment combination.

3.2. LITTER MATERIAL

In each of our experiments, we selected leaf-litter material from several different tree species. This enabled us to compare leaf litter characterized by

different initial traits, such as C content, N content, C:N. Species at different successional stages with leaves known to decompose at different rates were chosen.

In chapter I, we selected leaf litter from three species growing locally in forest stands close to Rouen: pedunculate oak (*Quercus robur* L.); European beech (*Fagus sylvatica* L.) and European ash (*Fraxinus excelsior* L.). We collected fully senescent leaves at the point of abscission directly from trees and we oven dried them at 35°C for a week before deploying them in the field.

In chapter II we selected two contrasting species: silver birch (*Betula pendula* Roth) and European beech (*Fagus sylvatica* L.). We harvested both green leaves and fully senescent leaves of the two species to evaluate the effects of senescence stage on the photodegradation rate. We oven dried the leaves at 37°C until they achieved a constant weight before deploying them in the field. We used fresh litter material of the same origin in the controlled experiment. In this case, half of the leaves were deployed with the adaxial (upper) epidermis facing upwards and half with the abaxial (lower) epidermis facing upwards. This was used as a proxy for the amount of radiation penetrating the leaf to the mesophyll. Typically, the adaxial epidermis in these species has a higher concentration of UV-screening compounds than the abaxial epidermis, and these compounds absorb solar radiation in the shortwave region of the spectrum.

In chapter III we employed fully senescent leaves of European beech (*Fagus sylvatica* L.) collected at the point of abscission and we oven dried them at 35°C for a week before deploying them in the field.
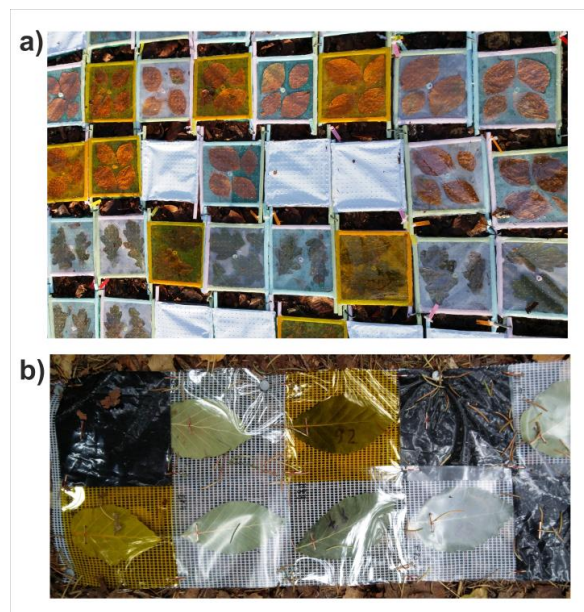
3.3. PHOTODEGRADATION-LITTERBAGS

We employed two types of bespoke litterbags, from hereafter referred as "photodegradation-litterbags", adapted from classical litterbags used in litter decomposition studies.

The first prototype of photodegradation-litterbags used in II (Fig. 3a), consisted of 8-x-8-cm squares of plastic-film filter material stapled to equal sizes mesh material made from Teflon mosquito netting. Later on, we

developed a second prototype with the addition of plastic straws between the filter and the mesh sheet to prevent the contact between the litter and the filter sheet and reduce the build-up of condensation (Fig. 3b). For technical details concerning photodegradation-litterbags refer to I, II & III.

Photodegradation-litterbags have the advantage of incorporating the attenuating filter directly into the "bag", avoiding additional shade otherwise produced by the mesh material used for the construction of traditional litterbags. This adaptation to avoid an overall reduction in the received irradiance is particularly important in temperate and boreal forests where the incident irradiance is already low. Moreover, the typical Teflon material used for decomposition litterbags can alter the spectral composition of the light treatments by selectively absorbing different wavelengths. Another advantage of our photodegradation litterbags is their ability to hold a single layer of litter, avoiding shading caused by the overlapping of leaves and potential confounding effects that occur when not all the litter material is directly exposed to the radiation treatments.

Figure 3 Photographs showing the first (a) and the second (b) prototype of the photodegradation-litterbags.

We used six different plastic-film filters that selectively attenuate solar radiation to create six spectral treatments (Fig.4) in order to analyse the effect of several spectral regions:

- "**Full-spectrum**" treatment (full-spectrum at near-ambient sunlight) of polyethene film (0.05 mm thick, 04 PE-LD; Etola, Jyväskylä, Finland) transmitting > 95% of incident PAR and UV radiation;

- "**No-UV-B**" treatment (attenuating UV-B radiation < 320 nm) using polyester (0.125 mm thick, Autostat CT5; Thermoplast, Helsinki, Finland);

- "**No-UV**" treatment using Rosco #226 (0.2 mm thick, Westlighting, Helsinki, Finland) attenuating UV radiation < 380 nm;

- "**No-UV/Blue**" treatment using Rosco #312 Canary yellow (0.2 mm thick, Westlighting, Helsinki, Finland) attenuating UV radiation and blue light < 480 nm;

- "**No-UV/Blue/Green**" treatment using Rosco #135 deep golden amber (0.2 mm thick, Westlighting, Helsinki, Finland) attenuating UV radiation and blue and green light < 580 nm (this treatment was used only in III);

- "**Dark**" treatment using solid polyethene film, white on the upper-side and solid black on the lower-side (0.15 mm thick, Casado sarl, France and 0.07mm thick, Siemenliike Siren, Helsinki, Finland), attenuating > 95% of PAR and UV radiation.
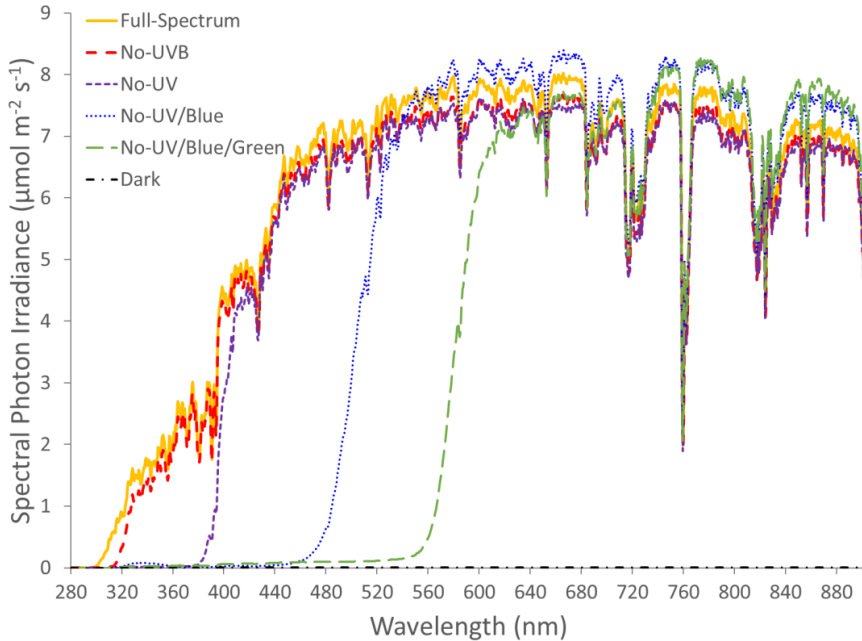
Figure 4 Spectral irradiance measured outdoors under the six filter treatments.

3.4. SPECTRAL IRRADIANCE MEASUREMENTS

Punctual measurements of spectral irradiance were done both outdoors (in the forest site and in a nearby open area) and in the growth room using an array spectroradiometer (Maya2000 Pro Ocean Optics, Dunedin, FL, USA; D7-H-SMA cosine diffuser, Bentham Instruments Ltd, Reading, UK, see I, II & III for details about measurements and calibration).

Canopy flush and light regime in the forest understorey were monitored through hemispherical photographs taken regularly during the experiments and used to calculate the global light index (GLI) with the software Hemisfer (Schleppi et al. 2007; Thimonier et al. 2010) following the protocol of Hartikainen et al. 2018 (see I, II & III for further details). Punctual measurements of the outdoor spectral irradiance and GLI obtained from hemispherical photos were used to model the spectral irradiance in the understorey over the experimental periods and to calculate light doses

received by the litter under each filter treatment (see I, II & III for details about irradiance doses estimation).

3.5. LITTER MASS LOSS AND CARBON AND NITROGEN CONTENT

Litter mass loss was determined as a percentage of initial mass, ash content was calculated to exclude errors due to litter contamination from inorganic material by combustion of a subsample of each replicate in a muffle oven at 550 °C for 12 h. Carbon (C) and nitrogen (N) contents and the carbon-to-nitrogen ratio (C:N) were determined using a CN Soil Analyzer Flash 2000 (Thermo Scientific, Waltham, USA) in I and III and a Vario Micro Cube (Elemental Analysis Systems GmbH, Hanau, Germany) in II.

3.6. MICROBIAL BIOMASS AND COMMUNITY STRUCTURE

We determined microbial biomass and the structure of microbial communities (bacteria and fungi) colonizing leaf litter through PLFA (Phospholipid Fatty Acid) and NLFA (Neutral Lipid Fatty Acid) analyses as in III, using a subsample of 0.15 g of freeze-dried litter from each litterbag. Lipid extraction was performed according to (Frostegård et al. 1991) and the resulting fatty acids were identified by comparing their mass spectra with the standard mass spectra in the NIST MS library.

We determined the amounts of the NLFA 16:1ω5 and the PLFA 16:1ω5 in the litter and used the ratio as indicator of the AMF (Arbuscular Mycorrhizal Fungi) biomass. As an indicator of saprotrophic fungi biomass we used the PLFA c18:2ω6,9 (Frostegård et al. 1991).

We estimated the biomass of Gram-positive bacteria (Gram-P) by the quantification of the PLFA: i15:0, a15:0, i16:0, i17:0, a17:0 and Gram-negative bacteria (Gram-N) by the quantification of the PLFA: cy17:0, c18:1ω7 and cy19:0 in the litter (Frostegård et al. 2011). As an indicator of total microbial biomass in the sample, we used the total amount of PLFA. We chose PLFA and

NLFA analysis over metabarcoding because we were mainly interested on the biomass and on the relations between fungal and bacterial biomass in the litter.

3.7. STATISTICAL ANALYSES

All statistical analyses where performed in R for Windows (ver. 3.6.1., R_Core_Team 2013). Multi-factor ANOVA were used to analyse the difference between filter treatments on mass loss and C and N contents (I, II & III). A multivariate analysis (NMDS) was used to explore the differences in microbial community structures due to our filter treatments (III).

A multi-level meta-analysis was done to evaluate the effects of photodegradation driven by the different spectral region across ecosystems and climates (IV).

Furthermore, we evaluated the potential correlation between photodegradation driven by each spectral region and initial litter traits, through a mixed-effect model (IV), in order to identify traits that could act as predictors of the photodegradation rate. We considered the following traits in our analysis: carbon content (C); nitrogen content (N); carbon to nitrogen ratio (C:N); lignin content; lignin to nitrogen ratio (Lig:N) and specific leaf area (SLA).

Litter type	I	II	III	IV
European beech (*Fagus sylvatica* L.)	x	x	x	
European ash (*Fraxinus excelsior* L.)	x			
Pedunculate oak (*Quercus robur* L.)	x			
Silver birch (*Betula pendula* Roth)		x		
Canopy species				
European beech (*Fagus sylvatica* L.)	x	x	x	
Silver birch (*Betula pendula* Roth)		x		
Norway maple (*Acer platanoides* L.)		x		
Norway spruce (*Picea abies* (L.) H. Karst)		x		
Litterbags				
Prototype 1		x		
Prototype 2	x		x	
Measured/collected variables				
Mass loss	x	x	x	x
AFDM	x		x	
C content	x	x	x	
N content	x	x	x	
C:N	x	x	x	
PLFA			x	
NLFA			x	
HPLC		x		
Initial C	x	x	x	x
Initial N	x	x	x	x
Initial C:N	x	x	x	x
Initial SLA	x	x	x	x
Initial Lignin				x
Initial Lig:N				x
Initial Anthocyanin	x	x	x	
Initial Chlorophyll	x	x	x	
Initial Flavonoids	x	x	x	

Table 1: Overview of methods applied and data collected in the four chapters.

4. MAIN RESULTS AND DISCUSSION

4.1. EFFECTS OF PHOTODEGRADATION ON LITTER MASS LOSS AND CARBON CONTENT

We monitored dry mass and carbon content of leaf litter of three tree species: European ash (*Fraxinus excelsior* L.), pedunculate oak (*Quercus robur* L.) and European beech (*Fagus sylvatica* L.) in a mature beech forest in Normandy (France, I).

By the end of the experiment, after 10 months, oak and beech litter exposed to ambient sunlight (full-spectrum) had lost 20% and 30% respectively more mass than when decomposing in dark conditions (pairwise full-spectrum-dark: $p < 0.001$ for both species, I). This result is in agreement with recent findings from a semiarid forest in Argentina, where the full spectrum of sunlight enhanced litter mass loss by 15% after 6 months (of winter) and 57% after 1 year of exposure compared with a treatment excluding wavelengths of 280-580 nm (Méndez et al. 2019). Similar results have been obtained from experiments in other biomes, such as subtropical forests (Ma et al. 2017) and arid shrublands (Pan et al. 2015), as a consequence of artificial shading. Contrarily, our ash litter decomposing in dark conditions over 7 months, had lost a similar proportion of its mass to litter exposed to sunlight (pairwise full-spectrum-dark: $p = 0.462$, I).

The species-specific difference between our results suggests that photodegradation is dependent on initial litter traits. It is likely that recalcitrant litter, with a low content of easily-broken-down simple carbon compounds available to microbial decomposers (Hodge et al. 2000), could benefit most from photofacilitation. This is in agreement with findings in arid (Day et al. 2015) and semiarid (Gaxiola and Armesto 2015) ecosystems, where the photodegradation rate depended on the litter species. However, this effect is thought to be more relevant in mesic ecosystems (Bais et al. 2018), where microbial decomposers are crucial in determining the decomposition rates (Asplund et al. 2018).

In our experiment (I), blue light was the spectral region that most affected litter decomposition by enhancing litter mass loss by 6 to 9%, according to litter-species, over 10 months (pairwise No-UV - No-UV/Blue: p = 0.020 and 0.050 for oak and beech respectively, I). Exposure to blue light also led to a greater carbon loss by the end of the experiment (+6-9%; pairwise No-UV - No-UV/Blue: p = 0.016 and 0.023 for oak and beech respectively, I). This result confirms our hypothesis that blue light is the main driver of photodegradation in a temperate mid-latitude forests and highlight the potential of this spectral region to operate photochemical mineralization. Various studies have suggested that short-wavelength visible light is important in the process of photodegradation (reviewed by King et al. 2012). Austin et al. 2016 reported a 30% increase in mass loss from 23 species' litter in an open semiarid environment after exposure to blue and green light. A similar result was reported by Day et al. 2018 in a study analysing photodegradation of 12 different species' litter under arid conditions. However, in that study in the Sonoran Desert the photodegradation rate depended on the litter type, suggesting once more a role of initial litter trait in determining the rate of photodegradation.

In our experiment (I), UV radiation had no significant effect on mass loss (pairwise full-spectrum – No-UV p = 1.000 ash, p = 0.154 oak and p = 0.377 beech, I), this confutes our hypothesis that UV radiation would enhance litter mass loss in a temperate forest. Moreover, within the UV-region, UV-B radiation had no significant effect on mass loss (p = 1.000 ash, p = 0.057 oak and p = 0.438 beech, I), while UV-A radiation enhanced mass loss by 9% in beech litter (pairwise No-UV – No-UV-B p = 0.031, I). This result could be due to the higher irradiances of UV-A radiation and blue light, compared to UV-B radiation reaching the litter in the understorey; particularly at mid and high latitudes (Aphalo et al. 2012; Hartikainen et al. 2018).

Another possible explanation for the lack of a UV-effect could be a trade-off between the positive and negative effects of UV-driven photodegradation, as UV radiation and particularly UV-B radiation are often reported to inhibit microbial decomposition (Duguay and Klironomos 2000; Moody et al. 1999).

However, it is not possible to disentangle the two opposing mechanisms of photochemical mineralization and photoinhibition under field conditions.

Past studies in arid (Gallo et al. 2009; Gallo et al. 2006) and semiarid (Almagro et al. 2015; Austin and Ballaré 2010) ecosystems reported UV and UV-B radiation to enhance litter decomposition. However, this effect was reversed at high latitudes (Pancotto et al. 2003; Pancotto et al. 2005), suggesting that the impact of photodegradation is dependent on the biome. As an example, in our second experiment, monitoring litter mass loss of leaf litter of two tree species, silver birch (*Betula pendula*) and European beech (*Fagus sylvatica*), in southern Finland in four forest stands results were very different (60°N, II) from those obtained at mid-latitude in northern France (49°N, I). Spectral treatments impacted only litter mass loss of beech litter ($p < 0.001$, while $p = 0.807$ for birch, II), the more recalcitrant of the two species, once again confirming the importance of litter quality in determining the photodegradation rate.

The effects of spectral treatments on beech litter changed according to the stand ($p < 0.001$, II). At this higher latitude, blue light did not have a significant effect on mass loss of beech litter in any of the stands (pairwise No-UV - No-UV/Blue: $p > 0.100$ for all the stands, II). While the full-spectrum of sunlight decreased mass loss by 2.5% over 6 months in the beech stand (pairwise full-spectrum-dark: $p = 0.018$, II), UV radiation increased mass loss by 2.4% in the spruce and by 2.1% in the birch stand (pairwise full-spectrum – No-UV $p = 0.025$ and $p = 0.041$ respectively, II).

This difference among stands can be explained by the capacity of different tree canopies to modify the amount of incoming solar radiation and its spectral composition reaching the forest floor (Hartikainen et al. 2018), and create different microclimates characterised by unique combinations of temperature, moisture, snow pack depth (Augusto et al. 2015; Joly et al. 2017; Kovács et al. 2017; Zellweger et al. 2019). In fact, closed canopies not only intercept and filter more light, but they also intercept more snow and consequently reduce the snow cover on the forest floor exposing the litter to freeze-thaw cycles (Davis et al. 1997; Mellander et al. 2005; Pomeroy and Goodison 1997).

4.2. EFFECTS OF PHOTODEGRADATION ON MICROBIAL ASSEMBLAGES AND ASSOCIATED LITTER DECOMPOSITION PROCESS

We monitored biomass and community structure of microbial decomposers colonizing beech leaf litter during the first 6 months of decomposition in a mature beech forest in Normandy (France, III).

Manipulation of the spectral composition of sunlight had a significant effect on the total microbial biomass (p = 0.022, III) and on both bacterial (p = 0.001, III) and fungal biomass (p = 0.021, III) therein. However, biomass of fungi and bacteria were not significantly affected by individual spectral regions but rather by a combination of them; suggesting multiple spectral regions to act synergistically in determining the effect of sunlight on microbial biomass. A plausible reason why we did not detect a clear overarching effect of each spectral region is that the effects, positive or negative, of different spectral regions on decomposers differ among decomposer species (Kumagai 1988; Pancotto et al. 2005; Paul and Gwynn-Jones 2003).

UV-A radiation and blue and green light, when present altogether, significantly reduced the total microbial biomass (-34%, pairwise No-UV/Blue/Green − No-UVB: p = 0.006, III). This was mainly due to a reduced fungal biomass (-37%, pairwise No-UV/Blue/Green − No-UVB: p = 0.006, III). Even though UV-B radiation tended to increase fungal biomass, its effect was not significant (+19%, pairwise No-UVB − Full-Spectrum: p = 0.279, III). A positive effect of UV-B radiation is not uncommon, as this spectral region was previously documented to favour some fungal decomposers (Pancotto et al. 2005; Robson et al. 2004) by stimulating sexual and asexual morphogenesis (Ensminger 1993). On the other hand, bacterial biomass was significantly increased by the full-spectrum of sunlight (+23%, pairwise Dark − Full-Spectrum: p = 0.024, III).

Our results indicate that different combinations of spectral regions had diametrically opposing effects on fungal and bacterial decomposers. Fungi were reduced by the short-wavelength visible light (blue and green light) and UV-A radiation, whereas bacteria were promoted.

Exposure to green and blue light decreased the biomass and reduced hyphal length of several fungal species under controlled conditions on a synthetic growing medium (Velmurugan et al. 2010). UV-A radiation is known to enhance sporulation in some fungal phytopathogens (Paul and Gwynn-Jones 2003). This effect depends on the dose of UV-A radiation, the length of the exposure, the interaction with UV-B radiation (Fourtouni et al. 1998; Kumagai 1988; Osman et al. 1989) and, most importantly, on the fungal species (Paul and Gwynn-Jones 2003).

In several saprophytic fungi, UV-A radiation can inhibit sporulation and delay germination of conidia (García-Cela et al. 2015; Osman et al. 1989), this finding also supports our results. Bacterial decomposers, on the other hand, were more abundant under the full spectrum of sunlight, suggesting that they prefer light environments. A possible explanation for this result could be the increase of nutrients available to bacterial decomposers as a consequence of photochemical mineralization under the full spectrum of sunlight, the so called photofacilitation effect.

Exposure to both UV radiation and visible light have been proven to stimulate subsequent microbial decomposition in several arid and semiarid environments (Austin et al. 2016; Baker and Allison 2015; Lin et al. 2018). In our results, the existence of a negative correlation between litter carbon content and bacterial biomass would support this assertion ($R^2 = 0.4$, $p < 0.001$, III). However, we did not find that bacterial biomass was impacted by specific spectral regions, this might be due to the fact that photosensitivity of bacteria depends on the species and on traits such as pigmentation (Paul and Gwynn-Jones 2003), thus species-specific differences even out across the entire bacterial community.

The opposing effects of sunlight on bacterial and fungal decomposers could modify the community structure of microbial assemblages even at higher latitudes, with bacteria tending to dominate in sunlight and fungi in dark conditions. Additionally, the competitive relationship between bacteria and fungi, previously observed in microbes colonizing beech litter (Møller et al. 1999), could represent a factor responsible for the segregation of light and dark microbial assemblages.

In our experiment, only a small part of the variation in community structure (10.9%, III), analysed through PLFA biomarkers, was explained by spectral composition; while time, in terms of length of the decomposition period, accounted for 31.9% of the variation (III). This ability of spectral composition to shape microbial communities was previously suggested for litter decomposing under UV-B radiation in a heath ecosystem in Tierra del Fuego (Pancotto et al. 2005). Our results support this conjecture for other spectral regions such as blue light and UV-A radiation.
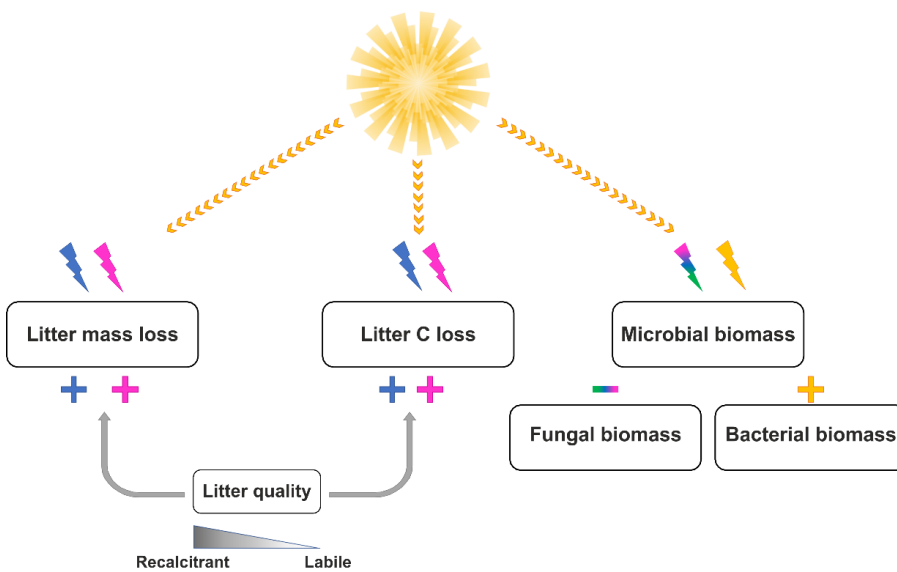
Figure 5: Schematic figure showing the process of photodegradation in a temperate beech forest. The lightening symbols represent the regions of the solar spectrum impacting litter mass loss, C loss and microbial biomass. Blue light (blue lightening) and UV-A radiation (pink lightening) enhance mass and carbon loss in litter. This effect is modulated by litter quality, with a greater effect on recalcitrant litter (section 4.1). The full-spectrum of sunlight (yellow lightening) increases bacterial biomass colonizing the litter, while the synergistic action of UV-A radiation, blue and green light (multicoloured lightening) reduces fungal biomass (section 4.2).

4.3. PHOTODEGRADATION ACROSS ECOSYSTEMS AND CLIMATES

We conducted a meta-analysis of published and unpublished studies analysing the effect of spectral composition on litter mass loss under ambient sunlight conditions.

Across all the studies considered, the full-spectrum of sunlight increased mass loss by 14% (p = 0.040, IV). This confirms the important role of photodegradation in the process of litter decomposition (King et al. 2012).

Different spectral regions had contrasting effects on litter mass loss. Blue light was the spectral region with the biggest impact on mass loss, causing it to increase by 12% over all studies (p = 0.037, IV). On the other hand, UV-A radiation had a negative effect and decreased litter mass loss by 5% (p = 0.019, IV), while UV-B radiation had no significant effect on mass loss overall (p = 0.872, IV). This confirms our hypotheses that blue light would have a positive impact on mass loss while no effect would be detected for UV-B radiation.

The absence of an effect of UV-B radiation is in agreement with results from a previous meta-analysis examining direct and indirect effects of UV-B radiation on mass loss (Song et al. 2013). Interactions among the multiple mechanisms of photodegradation could act to mask the impact of this spectral region. For example, photochemical mineralization and consequent photofacilitation may offset photoinhibition producing no net change in mass loss due to UV-B radiation (Bais et al. 2018).

Several interacting mechanisms may also counter-balance each other over other spectral regions involved in the process of photodegradation. While blue light has proved able to enhance litter decomposition through photochemical mineralization, it has not been shown to produce a photoinhibition effect (Austin et al. 2016). The opposite mechanisms are likely to operate under UV-A radiation, meaning its capability to cause photoinhibition (García-Cela et al. 2015; Osman et al. 1989) outweighs the benefits of photochemical mineralization for microbes.

When considering UV-B, UV-A and blue light, we must remember that these last two spectral regions are present at higher irradiances than UV-B radiation in natural environments, therefore their impact on decomposition

could be enhanced (Aphalo et al. 2012). Solar radiation is enriched in UV-B radiation at low latitudes, and in our meta-analysis we found a significant negative correlation between absolute latitude and UV-B photodegradation rates (slope = -0.003, R^2 = 0.24, p = 0.027, IV). This supports the assertion that UV-B radiation is more important in photodegradation a low latitudes in accordance with its higher proportional contribution to solar radiation (Aphalo et al. 2012).

Finally, the absence of a significant effect of UV radiation on litter mass loss (p = 0.255, IV) could be due to the confounding effects of UV-A and UV-B radiation, which on balance act differently when driving the direct and indirect mechanisms of photodegradation.

Climate modulated the effect of photodegradation driven by the full-spectrum of sunlight (p = 0.001, IV), blue light (p = 0.003, IV) and UV-B radiation (p < 0.001, IV), while it had no significant effect on UV-A-driven photodegradation (p = 0.529, IV). Overall, drier climates experienced higher photodegradation rates than temperate and continental climates. This result confirms our hypothesis and agrees with previous findings suggesting the process of photodegradation to be most relevant in arid environments (Bais et al. 2018; Gallo et al. 2009) under drier conditions (Brandt et al. 2007) where microbial decomposition is reduced (King et al. 2012).

However, when analysing the correlation between the photodegradation rate and the mean annual precipitation (MAP) in our meta-analysis, we only found a significant, but very weak, correlation (slope = 0.001, R^2 = 0.29, p = 0.009, IV) with full-spectrum photodegradation. This is likely due to MAP not being a biologically meaningful predictor. For example, the seasonality of rainfall might prove to be a better predictor as it captures potentially important seasonal fluctuations in precipitation. Additionally, it was suggested that photodegradation would not be reduced under mesic conditions, but simply harder to detect than in drier conditions, simply dwarfed in comparison to the effects of the predominant microbial decomposition (King et al. 2012). For the same reason, it is likely that UV and UV-B and UV-A radiation could have a negative impact on litter
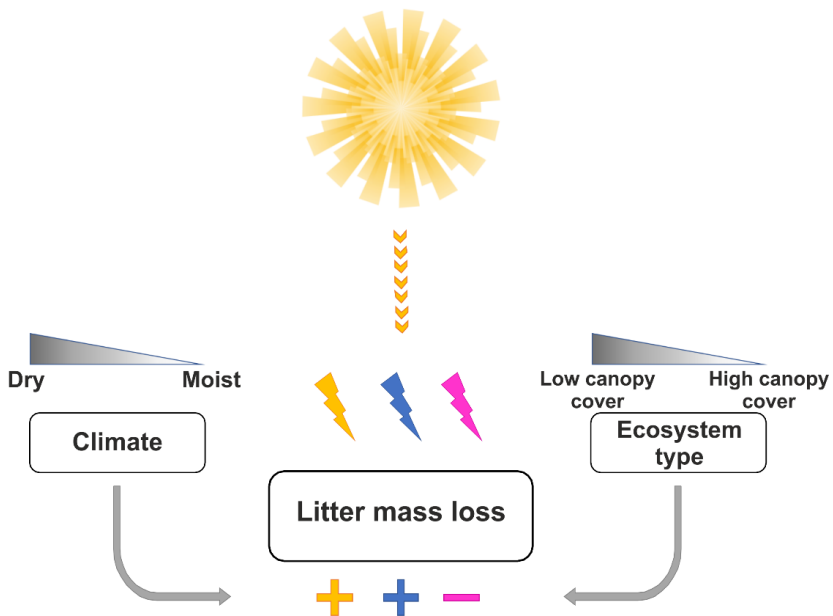
Figure 6: Schematic figure showing the photodegradation across biomes. The lightening symbols represent the regions of the solar spectrum impacting litter mass loss. The full-spectrum of sunlight (yellow lightening) and blue light (blue lightening) enhance litter mass loss, while UV-A radiation (pink lightening) reduces litter mass loss. This effect is modulated by climate and ecosystem type, with drier climates and ecosystems with low canopy cover (such as grasslands and open areas) experiencing higher rates of photodegradation.

decomposition by inhibiting microbial decomposition, which is the main driver of this process (Brandt et al. 2007; Smith et al. 2010).

The importance of the relationship between the photodegradation rate and precipitation it also likely to be dependent on the biome considered. In our field site in France, where we repeated a photodegradation experiment over two consecutive years (I & III), we obtained much lower photodegradation rates the second year. In comparing the two years, we found the second year to have double the precipitation of the first year, potentially explaining the difference in photodegradation rates (III).

Ecosystem type is also able to modulate the rate of photodegradation driven by blue light ($p < 0.001$, IV) and the full spectrum of sunlight ($p < 0.001$, IV). Ecosystem types with lower canopy cover had higher photodegradation rates: this is likely due the higher irradiance to which the litter is exposed in the open, compared for example with woodlands (Rozema

et al. 1999; Rutledge et al. 2010). In our meta-analysis we did not find a significant effect of photodegradation on litter mass loss in woodlands (IV). However, we must keep in mind that the studies were carried out in woodlands located at high latitudes in environments that are characterised by low irradiance and high precipitation.

4.4. PHOTODEGRADATION AND INITIAL LITTER TRAITS

We explored potential correlations between the photodegradation rate and those initial litter traits (IV) traditionally employed to predict decomposition rates such as carbon content (C); nitrogen content (N); carbon to nitrogen ratio (C:N); lignin content; lignin to nitrogen ratio (Lig:N) and specific leaf area (SLA). Unfortunately, due to the small amount of data available, we could not test potential correlations between photodegradation rates and initial content of hemicellulose and cellulose.

Even though the results of two of our experiments (I & II) suggested the importance of C:N in determining the rate of photodegradation in forest ecosystems, these results were not supported by the meta-analysis. In this case, none of the traits considered could predict photodegradation driven by blue light, UV-A radiation or the full spectrum of sunlight, while photodegradation due to UV and UV-B radiation was weakly negatively correlated with initial C content (slope = -0.015, R^2 = 0.08, p = 0.025 for UV and slope = -0.013, R^2 = 0.17, p = 0.043 for UV-B, IV). These results confound our expectations that SLA and lignin content would predict the photodegradation rate.

In the controlled environment experiment (II), where we deployed leaves with different orientation (abaxial or adaxial epidermis facing upwards), we found a significant difference in the photodegradation rate only in one of the two species (*Betula pendula*, p = 0.002, II). Leaves oriented with their abaxial epidermis facing the light source lost mass faster (0.05–0.10% higher daily mass loss depending on the filter treatment) than leaves with their adaxial epidermis facing the light source. This may indicate that the initial content of UV-screening compounds in the litter could affect subsequent decomposition

and photodegradation, as previously found in grey alder (*Alnus incana* (L.) Moench) litter (Kotilainen et al. 2009).

Past studies found photodegradation to be correlated with different litter traits such as initial N content (Pan et al. 2015); C:N (King et al. 2012); SLA (King et al. 2012; Pan et al. 2015); lignin content (Austin and Ballaré 2010; Méndez et al. 2019); hemicellulose and cellulose content (Day et al. 2018). The discrepancies among these results and the lack of correlations in our meta-analysis, suggest that if initial traits are important modifiers of photodegradation then their effects are likely to be specific to different biomes. Therefore, litter quality could be a good predictor at the local level but not at the global scale. However, due to the low number of studies measuring initial litter traits in each biome, we could not test this hypothesis in our meta-analysis (IV).

We must remember, however, that initial litter traits are very often determined by the climatic conditions to which the plants producing the litter are exposed (Fortunel et al. 2009; Oyarzabal et al. 2008), resulting in a correlation between climate (or type of biome) and litter quality, making it difficult to disentangle these two factors. Another issue to bear in mind is how difficult it is to separate the contribution of the various mechanisms of photodegradation, as they interact with each other, and with the microbial pool. It follows that we would be more likely to find litter traits that predict the rate of direct photochemical mineralization in a sterile environment in the absence of microbial decomposition. Additionally, the lack of correlations between photodegradation rates and initial litter traits confirms that we do not completely understand the mechanistic processes behind photodegradation.

5. PERSPECTIVE

5.1. PHOTODEGRADATION IN THE CONTEXT OF CLIMATE CHANGE

Photodegradation has a role in the carbon cycle as the process of photochemical mineralization causes the release of volatile carbon compounds into the atmosphere (Day et al. 2019; Gallo et al. 2009). Those studies that have tried to estimate the amount of CO_2, CO and CH_4 released during photodegradation under both enhanced and ambient solar radiation have obtained a wide range of results, as reviewed by King et al. 2012.

In ambient sunlight, the emission of CO_2 attributable to photodegradation was estimated to range 0.016 and 0.983 g C m^{-2} day^{-1} in grasslands and about 0.093-0.180 g C m^{-2} day^{-1} in peatlands (Brandt et al. 2009; Rutledge et al. 2010). CO emissions from photodegrading litter in studies in ambient sunlight have been estimated to be 2.0–5.5 mg C m^{-2} day^{-1} in a Brazilian shrubland and a savanna ecosystem (Kisselle et al. 2002). Whereas, under controlled conditions in a solar simulator the CH_4 emission from decomposing grass litter was the equivalent of 1.3-4.4 ng C g dw^{-1} h^{-1} (Lee et al. 2012).

The high variability associated with the above-mentioned results underlines how much the emission of volatile carbon compounds through photodegradation, like the rate of photodegradation itself, varies according to the biome. At present, more studies are required to better understand the extent to which photodegradation impacts the global carbon stocks when accounting for differences between biomes. Foereid et al. 2011 attempted to estimate the proportion of that carbon fixed by net primary production (NPP) that is lost through photodegradation at the global scale. According to this model about 0.5-1.6% of the carbon captured as NPP is photodegraded.

Although a low proportion of NPP is degraded at the global scale, Foereid et al. 2011 estimate that the relative contribution of photodegradation is much higher in dry ecosystems, reaching up to 14% of NPP. This suggests that photodegradation is more important at the local level than the global

level. However, the model from Foereid et al. 2011 considers the contribution of photodegradation to be equal for all spectral regions, and simply adjusted for total received irradiance. Additionally, this model fails to account for variation in spectral composition, such as the relative contribution of UV-B radiation, according to geographical location, through elevation, latitude, time of the year, and changing atmospheric factors such as patterns of cloud cover and aerosols. Moreover, data for photodegradation rates at high latitudes are lacking in the model, as well as data for ecosystems with high canopy cover, such as forests; ignoring the role of photodegradation in these kind of ecosystems (I, II & III).

Further studies are required to incorporate photodegradation into models of the global carbon cycle as this will then allow us to assess how the importance of its contribution is likely to vary over the projected global change scenarios (Field and Raupach 2004).

Global changes have the potential to impact photodegradation rates directly and indirectly through changes in the suite of abiotic and biotic factors to which litter is exposed. As an example, ongoing land aridification at low-to-mid latitudes (Kertész and Mika 1999) is likely to enhance the effect of direct photochemical mineralization (Almagro et al. 2015), as we know that this process is promoted by arid conditions (Brandt et al. 2007), resulting in a faster carbon turnover (Chen et al. 2016). Moreover, alteration in rainfall patterns and consequent moisture availability (Fay et al. 2003; Knapp et al. 2002; Miranda et al. 2011), fundamental drivers of the photofacilitation process (Gliksman et al. 2017; Wang et al. 2017), are likely to impact the net contribution of photodegradation to the carbon cycle.

Another aspect of climate change is variation in UV radiation reaching the Earth's surface due to altered clouds patterns and aerosols concentrations in the atmosphere (Zepp et al. 2007; 2011). As we previously mentioned, exposure of leaves to UV radiation determines the accumulation of photoprotective pigments in the leaf upper epidermis (Caldwell et al. 1999; Coffey et al. 2017). This can alter the photodegradation rate of leaf litter (mediated effects of sunlight, see Section 1.1.3) by reducing the penetration of sunlight to the mesophyll (Kotilainen et al. 2009; Pancotto et al. 2005). For

example, in our experiment in controlled-environmental conditions (II), we found a significant effect of leaf orientation, as proxy for phenolic content, on the photodegradation rate. Hence, a change in the amount of UV radiation to which living plants are exposed is likely to cause variation in the photodegradation rate.

But, what about forest ecosystems? Climate change reportedly impacts forest ecosystems in several ways, such as altered: timing of phenology, forest structure and species composition, species distribution; disturbances like fires, drought and insect outbreaks (Best et al. 2007; Dale et al. 2000; Dale et al. 2001; Noce et al. 2017; Seidl et al. 2017). The interactions among these factors make it hard to predict how the rate of photodegradation could potentially change, however, we can speculate on possible consequences. Taking climate change as an example, global warming can cause changes in species distribution, and therefore to the species composition and structure of forest plant communities (Best et al. 2007; Dainese et al. 2017; Nogués-Bravo et al. 2007).

Changes in plant community composition alter litter quality through the suite of traits that potentially determine the photodegradation rate at the local scale and the consequent microbial decomposition (Araujo and Austin 2015; Bosco et al. 2016). Moreover, changes in the forest structure will alter the amount and spectral composition of the irradiance reaching the forest floor due to modification of the multi-layered canopy, as different canopies filter sunlight differently (Hartikainen et al. 2018).

On the other hand, global warming can cause phenological shifts in the timing of bud burst and leaf fall, often leading to an increase in growing season length (Buitenwerf et al. 2015; Gallinat et al. 2015; Piao et al. 2019). This results in a reduction of the period of canopy opening, and as a consequence decreases the potential for photodegradation by reducing the amount of radiation directly reaching the forest floor. Moreover, this change in the light environment in forest understoreys will be accompanied by a modification of the microclimate, exposing litter to a different combination of moisture, temperature, spectral composition and snow-pack depth (Augusto et al. 2015;

Davis et al. 1997; Kovács et al. 2017; Mellander et al. 2005; Pomeroy and Goodison 1997; Zellweger et al. 2019).

Further studies are required to improve our understanding of the impact of climate changes on photodegradation in forests and its consequences on the carbon sink capacity of these ecosystems.

5.2. FUTURE OF PHOTODEGRADATION RESEARCH

There are several questions that remain unresolved in photodegradation research, especially in forest ecosystems. In this thesis we found photodegradation to have a role in the process of litter decomposition even under the low irradiances to which litter is exposed in forest understoreys. However, we only examined photodegradation of surface litter, as that is the layer directly exposed to sunlight.

When considering litter decomposition in forests we must bear in mind that thickness of the litter layer varies according to the forest type (Bens et al. 2006). The surface layer of litter filters shortwave solar radiation (Vazquez-Yanes et al. 1990) responsible for photodegradation, meaning the underlying litter layers avoid exposure to this part of the spectrum. Consequently, we can expect photodegradation to act only on the surface litter, therefore we could argue that the effect of photodegradation is often overestimated, as it affects only a small percentage of the litter on the forest floor. In fact, the photodegradation rate has been shown to decrease with increasing litter layer thickness (Henry et al. 2008; Mao et al. 2018). However, while direct photochemical mineralization is likely to decrease with increasing litter-layer thickness, these studies do not account for the potential for a priming effect to be carried over through the litter profile. In fact, we can expect the priming effect of photofacilitation (section 1.1.2) of surface layer to persist after this litter has mixed or been covered by more litter layers and in doing so initiate to a persistent carry-over effect of photodegradation on decomposition.

The role of the canopy species affecting photodegradation in forest environments proved important in our research (II). Trees of different species, age, and density, filter the sunlight differently in terms of the irradiance and

its spectral composition reaching the understorey (Hartikainen et al. 2018). Photodegradation generally increases with factors that enhance litter exposure to sunlight (King et al. 2012), and these can be mediated through canopy structure (Rutledge et al. 2010). Hence, when canopy density increases, increasing shade decreases the photodegradation rate (Ma et al. 2017; Pan et al. 2015). So, we could expect the rate of photodegradation to change according to LAI and the canopy species composition, while interacting with other environmental factors.

Understanding the relationship, between LAI and photodegradation rate, could be the first step to empirically estimating the photodegradation rate globally and calculating its effect on forest NPP worldwide and on the fertility of forest soils. This kind of approach was previously used to model photodegradation by Foereid et al. 2011, however at that time data on photodegradation rates in forest ecosystem were not yet available.

An important limitation on the estimation of photodegradation at the global scale is the absence of a standard method for doing photodegradation experiments. The highly diverse methods employed, such as litterbags placed under filter screens (Pancotto et al. 2003; Pancotto et al. 2005), litter boxes (Austin and Vivanco 2006), photodegradation-litterbags (Day et al. 2007), shade cloths (Ma et al. 2017), filter tunnels (Messenger et al. 2012), or louvered designs (Brandt et al. 2010), can create very different microclimates and therefore make studies to be difficult to compare. A standard method for the study of photodegradation across biomes is needed to reduce confounding results caused by methodological differences.

As a step towards standardisation of dose-response, a spectral weighting function for photochemical mineralisation was recently published (Day et al. 2019). The spectral sensitivity to UV radiation of biological or biophysical responses vary according to the process of interest. To allow comparison of a response under different conditions the effective irradiance can be calculated by weighting measured irradiance according to the effectiveness of each wavelength in producing this response (Aphalo et al. 2012). After quantifying the response produced by each wavelength, it is

multiplied by a radiation amplification factor (RAF) to obtain the effective dose of radiation over the spectrum of interest.

Formulation of a weighting function for photodegradation is complicated, as several responses should be considered to account for the multiple mechanisms involved (direct, indirect and mediated effect of sunlight) (Barnes et al. 2015). Consequently, most photodegradation studies present unweighted doses of UV radiation, which can create difficulties when comparing the results of these studies (Caldwell et al. 1986; Caldwell and Flint 1997).

The recent development of a BSWF for the component mechanism of photochemical mineralisation by Day et al. 2019, excluding indirect and mediated photodegradation, opens new possibilities in the field of photodegradation research, allowing for better comparison and providing a standard way to present UV doses across studies. This polychromatic spectral weighting function was made by comparing the effects of different regions of the sunlight (280 nm – 650 nm) on several types of litter. Photochemical mineralisation declined exponentially with increasing wavelength but even at the upper limit of this range still had some activity. Applying this weighting function, the relative effectiveness at our field sites (spectra in Figure 2) were compared; for the winter canopy (Fig. 2a): 9% UV-B radiation, 64% UV-A radiation, and 24% blue light; for canopy shade (Fig. 2b) 7% UV-B radiation, 61% UV-A radiation and 27% blue light; and for canopy sunflecks (Fig. 2c) 8% UV-B radiation, 59% UV-A radiation, and 29% blue light. Although the relative differences are small, they are congruent with the heightened importance of blue light in the understorey. According to these calculations, photochemical mineralisation contributes five-times more to photodegradation in the open canopy than in a closed-canopy sunfleck, and a further ten-times more in the sunfleck than in the shade.

6. CONCLUSIONS

The first aim of this thesis was to investigate the role of photodegradation in temperate and boreal forest ecosystems. Our results show that the process of photodegradation is relevant to litter decomposition in the understorey of temperate and boreal forests, even though this litter is exposed to relatively low irradiance.

Moreover, this thesis highlights the importance of blue light as a major driver of photodegradation in temperate forest understoreys, with the potential to both accelerate litter mass loss and carbon loss. At these latitudes, blue light and UV-A radiation proved to contribute more than UV-B radiation as drivers of photodegradation, which runs contrary to their importance in arid and semiarid ecosystems at low latitudes. The direction and magnitude of the effect of photodegradation depend on the litter species and the type of forest canopy, since canopies not only filter sunlight differently, but also create different combinations of temperature, moisture and snow-pack depth.

While mass loss from litter was impacted by specific spectral regions in different ways, litter microbial biomass depended on the interaction of multiple spectral regions. In temperate forests, blue light, acting synergistically with UV-A radiation and green light, was able to impact microbial decomposition. In fact, sunlight had an opposing effect on bacterial and fungal decomposers, modifying the community structure of microbial assemblages, with bacteria tending to dominate in sunlight and fungi in dark conditions.

A second aim of the thesis was to investigate how photodegradation changes across biomes and which initial litter traits could be used to predict the rate of photodegradation. We found that at a global scale the direction and magnitude of photodegradation differ according to the spectral region considered. We highlight the crucial role of blue light and UV-A radiation as drivers of photodegradation across biomes, eclipsing that of UV-B radiation, despite UV-B radiation being regarded for decades as the main spectral region

responsible for this process. While blue light enhances mass loss, when considering several biomes, UV-A radiation decreases mass loss.

UV-A radiation has potentially very interesting effects on decomposition, as it represents a larger fraction of solar spectral irradiance than UV-B radiation and is enriched in canopy shade compared with blue light. Moreover, this spectral region combines the potential for photochemical mineralization, with a strong impact on fungal decomposers, which can be positive or negative according to species, therefore it would deserve more attention in future photodegradation research.

At a global level, our meta-analysis found that the photodegradation rate is modulated by climate and ecosystem type, with dry environments characterised by low canopy cover experiencing the highest photodegradation rates.

Finally, according to our meta-analysis results, classical litter traits such as lignin content, C:N, lig:N, are not good predictors of the rate of photodegradation at the global scale. This does not exclude the possibility that different traits could be important in different biomes, as for example results of our experiments suggested C:N to be important in determining the rate of photodegradation. These discrepancies emphasize how much there remains to discover about the mechanisms underlying the photodegradation process and its relationship with other environmental factors.

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