Eesti Maaülikool

Stress tolerance and cultivation technologies of oilseed hemp – their effect on plant productivity and seed quality

Õlikanepi stressitaluvus ja kasvatustehnoloogiad – nende mõju taimede produktiivsusele ja seemnete kvaliteedile

Erkki Mäeorg

Doctoral Thesis in Agriculture
Doktoritöö põllumajanduses

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on three original publications (**I–III**), which are referred to throughout the text by their respective Roman numerals.

I. **Mäeorg, E.**, Lääniste, P., Nassar, H., Kännaste, A., Tedersoo, L., Niinemets, Ü., & Runno-Paurson, E. (2026). How do the nitrogen level and form and crop density influence the progression of Alternaria leaf spot disease on hemp crop in Northern Baltic region? Cogent Food & Agriculture,12(1). https://doi.org/10.1080/23311932.2026.2620864

II. **Mäeorg, E.**, Lääniste, P., Tedersoo, L., Niinemets, Ü., & Runno-Paurson, E. (2026). Nitrogen fertilization outweighs disease-associated variation in hemp seed yield under highly fluctuating northern temperate field conditions. Crop Protection, Volume(Issue), 1–10. https://doi.org/10... (Status: Major revision)

III. Runno-Paurson, E., **Mäeorg, E.**, Kurina, O., Õunap, E., Kännaste, A., Niinemets, Ü., & Lääniste, P. (2024). Widespread occurrence of European corn borer (*Ostrinia nubilalis*) and damage of industrial hemp (*Cannabis sativa*) crop in Northern Europe. Gesunde Pflanzen, 76, 437–444. https://doi.org/10.1007/s10343-023-00940-2.

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ABBREVIATIONS

AN	Ammonium nitrate fertilizer
AUDPC	Area under the disease progress curve
BLAST	Basic Local Alignment Search Tool
CBD	Cannabidiol
COI	Cytochrome c oxidase subunit I gene
C. sativa	*Cannabis sativa* L.
CV	Coefficient of variation
DNA	Deoxyribonucleic acid
ECB	European corn borer
GDD	Growing degree days
ha	Hectare
ITS	Internal transcribed spacer
N	Nitrogen
NCBI	National Center for Biotechnology Information
NH_4^+	Ammonium ion
NO_3^-	Nitrate ion
NPK	Compound mineral fertilizer containing nitrogen, phosphorus and potassium
O. nubilalis	*Ostrinia nubilalis* Hübner
PCR	Polymerase chain reaction
rAUDPC	Relative area under the disease progress curve
SD	Standard deviation
SE	Standard error
TSM	Thousand-seed mass
WRB	World Reference Base for Soil Resources

1. INTRODUCTION

Industrial hemp (*Cannabis sativa* L.) has re-emerged as an important agricultural crop worldwide during the last two decades (Michels et al., 2025). Global interest in hemp cultivation has been driven by the growing demand for renewable raw materials, plant-based proteins and oils, sustainable fibres, and bio-based industrial products. Although hemp was historically cultivated across Europe, Asia, and North America, legal restrictions during the twentieth century substantially reduced its cultivation area and limited breeding efforts (Small & Marcus, 2002). Following regulatory changes in many countries, hemp production has increased rapidly, and the crop is now cultivated on all inhabited continents. The European Union remains one of the major production regions (Amaducci et al., 2015), but significant expansion has also occurred in Canada, China, Australia, and the United States (Adesina et al., 2020). As markets for hemp-derived food, fibre, construction materials, cosmetics, and biocomposites continue to develop and demand for the raw material remains high, further increases in cultivation area are expected globally. The main hindrance in its cultivation expansion has been the lack of localized production facilities for hemp stalk treatment. Although dried seeds could be transported globally, the sufficient capacity for storage and treatment of other valuable plant parts remains challenging (Carus & Sarmento, 2016).

Despite the renewed interest, hemp remains an underused crop in modern agricultural systems. In most countries, hemp has not yet become a routine component of crop rotations, and cultivation is still concentrated among a limited number of specialized growers. Consequently, practical agronomic knowledge remains fragmented compared with major field crops such as cereals, oilseed rape, or maize. Estonia represents a notable exception within Europe, having one of the largest oilseed hemp cultivation areas with 9201 hectares (Statistics Estonia, 2026). Furthermore, Estonia has developed a rapidly growing hemp-processing sector that aims to utilize the entire plant, including seeds, fibers, shives, and biomass, thereby increasing the economic value and sustainability of hemp production beyond seed products alone.

From both biological and agronomic perspectives, hemp possesses several characteristics that make it attractive for sustainable cropping systems, especially vital for future trends in agriculture in Europe. Hemp is a fast-growing annual crop with extensive root systems, high biomass production potential, and strong competitiveness against weeds (Campiglia et al., 2017). It functions as an excellent break crop in cereal-dominated rotations, improving soil structure and contributing to crop diversification (Apazhev, 2005). Hemp cultivation generally requires no or fewer pesticide applications than many conventional crops and can often be integrated into low-input or organic production systems (Finnan & Styles, 2013; Michels et al., 2025). In addition, hemp is a promising crop for carbon sequestration, biomass

production, and the development of renewable materials (Amaducci et al., 2015; Adesina et al., 2020). Unlike many other crops, hemp offers multiple marketable outputs, increasing its versatility and resilience within agricultural systems.

Nevertheless, successful hemp cultivation requires improved understanding of crop management under northern temperate conditions. Although hemp is frequently described as a low-maintenance crop, the production of high and stable seed yields remains challenging in regions characterized by short growing seasons and long photoperiods (Runno-Paurson et al., 2019). Oilseed hemp cultivars often retain many traits associated with the species' wild ancestry, including extensive branching, strong phenotypic plasticity, and variable responses to environmental conditions (Ansari et al., 2025). These characteristics complicate the optimization of sowing density, nutrient management, and harvest timing. In addition, substantial differences in seed yield, stem yield and seed quality traits have been reported among hemp cultivars, highlighting the importance of genotype-specific adaptation and management strategies (Flajšman et al., 2026). In northern regions such as Estonia, the timely formation and maturation of seeds is often one of the most important factors determining production success.

The limited use of pesticides has been a defining characteristic of hemp cultivation. Most hemp production in Northern Europe has been conducted without routine pesticide applications, and a considerable proportion of production has been certified as organic. Previously, hemp fields in its northern cultivation area have been regarded as relatively free from economically important pests and diseases (Runno-Paurson et al., 2020; Mäeorg et al., 2026). However, as cultivation areas expand and the crop becomes increasingly integrated into agricultural landscapes, this situation may change. Higher climatic variability, increasing host availability, and the shift of pests and pathogens into northern regions can alter pest pressure and threaten the sustainability of low-input hemp production systems.

Among the emerging biotic threats, the European corn borer (*Ostrinia nubilalis* Hübner) has attracted increasing attention. This highly polyphagous insect is one of the most important pests of maize (*Zea mays*) worldwide and has previously been associated with warmer maize-growing regions of Europe (Bereś & Konefał, 2010; Kaçar et al., 2023). However, recent observations suggest a northward expansion of *O. nubilalis* populations into Northern Europe, including Estonia, where the species has increasingly been observed in maize fields since the early 2020s and has subsequently been observed infesting hemp crops. Larval feeding damages stems and reproductive structures, reduces harvestability, and may facilitate secondary pathogen infections (McPartland, 1996). As hemp cultivation expands in northern regions, the importance of *O. nubilalis* as a potential production constraint requires careful evaluation.

Similarly, fungal pathogens belonging to the genus *Alternaria* have emerged as a significant concern in hemp fields. Alternaria leaf spot disease reduces photosynthetically active leaf area, leads to premature leaf senescence, and may affect both crop productivity and product quality. Furthermore, several *Alternaria* species are capable of producing mycotoxins that pose risks to food and feed safety. While hemp has traditionally been regarded as relatively disease tolerant in Northern Europe (Visković et al., 2024), increasing observations of *Alternaria* infections suggest that pathogen pressure may intensify under changing climatic conditions and expanding cultivation areas.

In addition to understanding emerging pests and diseases, there is a need for improved agronomic knowledge regarding seed hemp production in northern temperate environments. Establishing field experiments in Estonia with oilseed hemp has been driven by strong incentive from the farmers and raw material processing industry, as well as the lack of agronomic trials in Europe (Lääniste et al., 2020). Compared with major field crops, information on hemp nutrient requirements, fertilization strategies, crop density management, and yield formation remains limited. Particular attention is needed for the interaction between agronomic practices and biotic stress factors, as management decisions may simultaneously influence crop productivity and susceptibility to pests and pathogens.

The development of new cultivars specifically adapted to northern growing conditions represents an important step toward improving seed hemp production. Achieving reliable seed yield and uniform maturation remains a major breeding challenge under the long-day conditions of Northern Europe. The recently developed oilseed hemp cultivar 'Estica' was bred specifically for Baltic conditions, and studying its agronomic performance under field conditions provides valuable information for both researchers and growers (Nordic Hemp, 2022). Thus, in this thesis the field experiments included different nitrogen fertilization rates, fertilizer types (ammonium nitrate versus complex NPK fertilizer), fertilizer application methods (application at sowing versus top dressing), and sowing rates, allowing evaluation of the impact of key management factors on crop performance, disease development, and pest occurrence.

The main aim of this thesis was to gain an insight into the occurrence and progression of Alternaria leaf spot disease in oilseed hemp and to evaluate how cultivation technologies (nitrogen addition rate, fertilizer type and application timing, and sowing rate), as well as cultivar and plant sex influence disease development, disease foliar resistance and seed yield under Northern Baltic conditions (**I**, **II**). The third study (**III**) assessed the occurrence, spread, and yield impact of the European corn borer (*O. nubilalis*) in hemp fields and evaluated how different fertilization practices influence pest damage and crop productivity.

2. REVIEW OF LITERATURE

2.1. Hemp as a re-discovered old crop

Industrial hemp is among the oldest cultivated plant species and has been utilized for fibre, food, oil, and medicinal purposes (Small & Marcus, 2003; Callaway, 2004). Despite its long cultivation history, modern hemp production differs substantially from that of major field crops such as wheat, maize, and oilseed rape, mainly by high yield variation, low harvest index and minimal reliance on plant protection measures. During much of the twentieth century, legal restrictions and declining demand for traditional hemp products led to a reduction in cultivation area throughout Europe and North America. Consequently, breeding efforts, cultivar development, and crop-specific agronomic research progressed more slowly than in most economically important arable crops (Amaducci et al., 2015).

The renewed interest in hemp cultivation during the last two decades has been driven largely by increasing demand for plant-based food products, sustainable raw materials, and renewable industrial feedstocks. However, the expansion of cultivation has occurred considerably faster than the accumulation of agronomic knowledge. While cultivation technologies for major crops have been refined through decades of intensive research, many aspects (sowing rate, fertilization rate and timing) of hemp production remain dependent on local experience and relatively limited experimental evidence (Amaducci et al., 2015; Campiglia et al., 2017; Visković et al., 2024).

The issue of limited agronomic knowledge is particularly true for oilseed hemp production. Although hemp seed has been utilized throughout the crop's cultivation history, dedicated oilseed hemp production is a comparatively recent agricultural development. Previously, European hemp cultivation was primarily directed towards fibre production, while seed served mainly as propagation material and a secondary source of food and oil. However, hemp seed oil is rich in polyunsaturated fatty acids and many biologically active compounds including phytosterols and has become highly valued in food, pharmaceutical and cosmetic industry (Montserrat-de la Paz et al., 2014). Given the increasing demand, modern seed cultivars adapted for commercial oil production have largely been developed during the last three to four decades in response to increasing demand for hemp seed oil and protein-rich food products (Callaway, 2004; Amaducci et al., 2015; Stramkale et al., 2024).

Compared with fibre cultivars, maximization of seed yield in oilseed hemp requires a different plant architecture and production strategy. Whereas fibre hemp has traditionally been grown at high plant densities to promote stem elongation and suppress branching, seed production relies on lower crop densities that favour branching and reproductive development (Brown et al., 2025). Consequently, many

agronomic recommendations developed for fibre hemp cannot be directly transferred to oilseed production systems (Campiglia et al., 2017; Stramkale et al., 2024). Furthermore, substantial variation in flowering behaviour, branching intensity, and maturation timing continues to characterize modern seed cultivars. Such variability reflects the comparatively limited breeding history of oilseed hemp and the considerable genetic diversity still present within modern cultivars (Benkirane et al., 2026). Under northern growing conditions, differences in flowering behaviour and maturation timing may result in substantial variation in seed yield among cultivars and years (Adamovics et al., 2016; Stramkale et al., 2024).

As the hemp cultivation started in Central and East Asia under warm climatic conditions (McPartland et al., 2019; Ren et al., 2021), the adaptation of oilseed hemp to northern growing conditions, in particular, to long days and limited growing season length, presents additional challenges. Successful seed production depends on the timing of flowering and seed maturation such that the whole life cycle can be accomplished during the suitable growing period. A recent study has demonstrated considerable variation in photoperiod responses among cultivars, highlighting the importance of adaptation to latitude and growing season length (Ansari et al., 2025). Compared with other major oilseed crops, for oilseed hemp, information concerning optimal crop density, nutrient management, photoperiod-related reproductive development, and yield formation remains limited under northern European conditions (Adamovics et al., 2016; Stramkale et al., 2024).

Within Europe, Estonia has become one of the leading producers of oilseed hemp, with cultivation areas currently approaching 8,000–10,000 ha (Statistics Estonia, 2026). The progress in the oilseed hemp cultivation has been supported primarily by seed production and processing, including the establishment of one of the largest hemp seed dehulling facilities in Europe. Despite these developments, oilseed hemp remains a comparatively minor crop, with crop-specific agronomic recommendations being limited. In addition, the hemp processing industry still lacks the hemp stalk treatment facilities.

In summary, despite increasing cultivation area and growing economic importance, oilseed hemp cultivation practises remain much less studied than those of major arable crops. Information concerning nutrient management, crop density, cultivar adaptation and yield formation is particularly limited under northern European conditions, where environmental constraints differ substantially from those encountered in many traditional hemp-growing regions.

2.2. Hemp as a low-input crop

One of the characteristics frequently associated with hemp cultivation is its relatively limited requirement of plant protection products: according to the

European Commission, insecticides, fungicides and herbicides can be avoided in many hemp production systems (European Commission, n.d.). Although hemp is often considered a biologically resilient crop, this characterization should be treated cautiously because pest and disease pressure varies among production systems and environments, and the mechanisms underlying its presumed resilience remain poorly understood (Sirangelo et al., 2023).

Several biological characteristics may contribute to the relatively low pest and disease pressure observed in hemp cultivation. Hemp exhibits rapid early growth, forms a tall competitive canopy and thus, outcompetes low-stature weeds, and demonstrates substantial morphological plasticity in response to variation in environmental conditions (Myers et al., 2025; Brown et al., 2025). In addition, this crop produces a diverse array of secondary metabolites, including cannabinoids, terpenoids, flavonoids and phenolic compounds, many of which have been suggested to participate in ecological interactions with herbivores and microorganisms (Andre et al., 2016; Benelli et al., 2018; Park et al., 2022).

However, the perception of hemp as a crop with limited biotic challenges has developed under circumstances that differ markedly from those of major agricultural crops. Cultivation areas have generally remained small, production systems fragmented, and scientific monitoring of hemp-associated organisms considerably less intensive than in major agricultural crops. As the hemp cultivation areas have expanded and hemp has become a more regular component of agricultural landscapes, infections by economically important insect pests and fungal pathogens have been reported in several production regions (Punja, 2021; Punja & Scott-Dupree, 2022).

Recent advances in plant microbiome research have demonstrated that crop performance is influenced not only by plant genetics and environmental conditions but also by associated microbial communities inhabiting roots, leaves, stems, reproductive structures and surrounding soil environments (Hassani et al., 2018; Ahmad et al., 2024; Compant et al., 2019). In hemp, microbial community composition varies among genotypes, plant organs and growing environments, indicating that both host genetics and environmental conditions influence microbiome assembly (Dumigan & Deyholos, 2022; Ahmad et al., 2024). Plant-associated microorganisms have been implicated in nutrient acquisition, stress tolerance, growth promotion and the regulation of secondary metabolite production, although evidence for these functions in hemp remains more limited than in major agricultural crops (Compant et al., 2019; Dumigan & Deyholos, 2022).

Increasing evidence suggests that many microorganisms do not occupy fixed ecological roles. Depending on host physiological status, environmental conditions, nutrient availability and interactions within the surrounding microbial community, the same microorganism may function as an endophyte, commensal, mutualist

or pathogen (Hassani et al., 2018; Compant et al., 2019). Consequently, disease development is increasingly viewed not solely as the result of pathogen presence but as an outcome of broader ecological interactions occurring within the crop system.

This perspective provides a useful framework for understanding the emergence of new pests and pathogens in hemp cultivation and for evaluating how agronomic practices may influence crop health. As hemp cultivation expands and production systems continue to develop, understanding these interactions may become increasingly important for maintaining its low-input character that has distinguished the crop until recently.

2.3. Agronomic management, plant health and biological interactions

Agronomic management influences crop productivity through its effects on plant growth, physiological development and resource availability. However, management practices also affect the biological environment in which crops develop. Nutrient availability, crop density, tillage, crop rotation, and plant protection strategies alter the interactions among plants, microorganisms, herbivores, and environmental factors (Morugán-Coronado et al., 2022; Heinen et al., 2024). Consequently, crop health cannot be considered independently of agronomic management, particularly in hemp, which has received limited breeding attention and whose rich secondary metabolite profile and diverse plant-associated microbiome may contribute to its resilience against several biotic stressors (Ahmed et al., 2021; Biteżnik et al., 2023; Ahmad et al., 2024).

2.3.1. Nitrogen availability and crop health

Nutrient availability is one of the major factors regulating interactions among plants, microorganisms and pathogens in agricultural systems (Morugán-Coronado et al., 2022). Traditionally, fertilization has been viewed primarily as a means of increasing crop productivity. However, accumulating evidence suggests that nutrient availability simultaneously affects soil microbial communities, plant-associated microorganisms, pathogen activity and plant defence responses (Veresoglou et al., 2013; Lekberg et al., 2021; Bai et al., 2022).

Long-term fertilization studies have demonstrated that nutrient inputs can substantially alter microbial community composition and diversity. Excessive nutrient availability frequently reduces microbial diversity and modifies the relative abundance of functional groups involved in nutrient cycling, pathogen suppression and plant growth promotion (Wang et al., 2018; Zhao et al., 2019). Similar responses to nutrient availability have been reported in both soil and plant-associated microbial communities (Cui et al., 2021; Koch & Sessitsch, 2024; Han et al., 2025),

indicating that fertilization influences not only crop nutrition but also the biological environment in which crops develop.

Changes in microbial diversity have important consequences for crop health. Diverse microbial communities are generally considered more functionally stable and may provide greater resistance against pathogens through competition for resources, niche occupation and antagonistic interactions (Hassani et al., 2018; Compant et al., 2019). Conversely, reductions in microbial diversity may weaken these regulatory mechanisms and facilitate disease development under environmental conditions favourable for pathogen development and spread (Wei et al., 2015).

Evidence from both natural and agricultural ecosystems suggests that nutrient enrichment can alter the balance between mutualistic, commensal and pathogenic microorganisms. Lekberg et al. (2021) demonstrated that fertilization increased the relative abundance of fungal pathogens while reducing the prevalence of mutualistic fungi across multiple grassland ecosystems. Similar observations have led to the hypothesis that nutrient management may influence disease expression not only through direct effects on host plants but also through changes in the structure and functioning of associated microbial communities (Trivedi et al., 2020; Koch & Sessitsch, 2024).

The relationship between nutrient availability and disease severity is therefore often indirect and context-dependent. While increased nutrient supply may enhance plant growth and improve physiological capacity to tolerate stress, it may simultaneously alter canopy structure, microbial diversity and ecological interactions that regulate pathogen activity (Mur et al., 2017; Balint-Kurti, 2019).

The evidence highlighted indicates that in hemp, fertilization research has focused primarily on biomass production, seed yield and quality, whereas interactions among nutrient availability, microbial diversity and disease expression have received comparatively little attention.

2.3.2. Fertilizer type and timing of nutrient availability

Although the total amount of nitrogen supplied to crops often receives the greatest attention, the form and timing of nutrient availability may also influence plant performance, nitrogen-use efficiency and crop health (Raun & Johnson, 1999; Mur et al., 2017). Plants possess distinct uptake and signalling pathways for nitrate (NO_3^-) and ammonium (NH_4^+), resulting in differences in metabolism, growth responses, and physiological regulation (Hachiya & Sakakibara, 2017; Kiba & Krapp, 2016). In addition, NH_4^+ is less mobile in soil compared with NO_3^-, and thus, NH_4^+ uptake more strongly depends on extensive root systems and plant-growth promoting microbia, including arbuscular mycrorrhizal fungi (AMF) (Seemakram et al., 2026).

Nitrogen form influences plant defence mechanisms through alteration of signalling, biomass allocation and modification in plant-associated microbiome (Mur et al., 2017; Wang et al., 2019). Nitrate availability is associated with signalling processes involving nitric oxide and defence-related metabolites, whereas ammonium nutrition may alter carbon allocation, amino acid composition, and interactions with associated microorganisms (Mur et al., 2017). However, impacts of different N sources are often species-specific and strongly dependent on environmental conditions (Fagard et al., 2014).

The timing of nutrient availability may be equally important. Early nutrient supply promotes rapid canopy development and biomass accumulation, whereas later applications may alter the balance between vegetative and reproductive growth (Ciampitti & Vyn, 2012; Hachiya & Sakakibara, 2017). Changes in canopy development can indirectly influence biological interactions by modifying humidity, temperature and light penetration within the crop stand (Madden et al., 2007). Consequently, nutrient timing has the potential to affect both productivity and disease development, although responses remain highly dependent on crop species, environmental conditions and pathosystems (Mur et al., 2017; Veresoglou et al., 2013).

In hemp, information of the influence of fertilizer type and timing on crop health remains extremely limited. Existing research has primarily focused on yield formation and seed quality, leaving the ecological consequences of nutrient management largely unexplored.

2.3.3. Crop density and canopy-mediated biological interactions

Crop density is among the most important agronomic factors influencing hemp growth, architecture and yield formation. More than major cereal crops, hemp exhibits substantial phenotypic plasticity and is capable of modifying branching patterns, stem diameter and biomass allocation in response to plant density and resource availability (Campiglia et al., 2017; Visković et al., 2024).

The importance of crop density differs considerably between fibre and oilseed production systems. Fibre hemp is generally established at high densities, commonly sown at approximately 45–90 kg seed ha^{-1}, with experimental and recommended densities often ranging from about 100 to 250 plants m^{-2} to produce slender, minimally branched stems suitable for fibre production (Brown et al., 2025). Oilseed hemp is commonly sown at lower densities (approximately 100–150 plants m^{-2}) than fibre hemp, but reported seeding rates and established plant densities vary widely among cultivars, environments and production systems (Campiglia et al., 2017; Stramkale et al., 2024; Bajwa et al., 2025). Lower densities generally

promote branching and reproductive development per plant, although this does not necessarily result in greater seed yield per unit area.

One consequence of this plasticity is that crop density affects not only yield but also canopy structure and the biological environment within the crop stand. Increased plant density generally reduces air movement, increases relative humidity and prolongs leaf wetness duration within the canopy, conditions that are known to favour the development of many foliar pathogens (Madden et al., 2007; Termorshuizen, 2016). Conversely, sparse stands improve airflow and reduce humidity but may alter resource availability, branching patterns and host accessibility for herbivorous insects.

The information summarized emphasizes that crop density influences several factors relevant to disease epidemiology, including canopy humidity, air movement, leaf wetness duration and light penetration (Madden et al., 2007). Despite the importance of crop density in hemp production systems, only a few studies have examined its effects on plant health. Most available research has focused on yield formation and plant architecture rather than pest or disease development (Campiglia et al., 2017; Stramkale et al., 2024). Because oilseed hemp is typically grown at substantially lower densities than fibre hemp, significant variation in canopy structure may occur among production systems, potentially altering the biological environment experienced by both microorganisms and herbivores.

The relationship between crop density and severity of insect pest infection remains poorly understood in hemp. Denser canopies may modify host accessibility, microclimatic conditions and plant morphology (Brown et al, 2025), thereby influencing herbivore performance and distribution. Conversely, sparse stands often produce larger and more heavily branched plants that may provide greater resource availability for certain herbivores. Similar relationships between host density and herbivore abundance have been described in numerous crop systems through the resource concentration hypothesis (Root, 1973). Such responses are likely to be species-specific and remain poorly studied in hemp production systems.

The strong plasticity of hemp further complicates density responses. Reduced plant density commonly promotes branching and increases the size of individual plants, whereas dense stands favour stem elongation and reduced branching (Campiglia et al., 2017). Consequently, crop density influences not only resource competition but also the canopy architecture thereby potentially altering biological interactions.

The considerable plasticity of hemp distinguishes it from many major crops and complicates the identification of universal density recommendations. Similar seed yields may be achieved through different combinations of plant density and individual plant productivity. Consequently, crop density should be viewed not

only as a determinant of yield formation but also as a regulator of the physical and biological environments within hemp production systems.

2.3.4. Dioecious nature of hemp and implications for crop performance

One of the unique characteristics of hemp is the occurrence of both monoecious and dioecious reproductive systems within cultivated germplasm. In dioecious cultivars, male and female flowers develop on separate plants, resulting in differences in flowering dynamics, senescence patterns and reproductive allocation.

Male plants typically flower earlier, complete reproduction more rapidly, and undergo senescence sooner than female plants. Female plants remain physiologically active for longer periods because seed development continues after pollination. Consequently, the relative abundance of male and female plants influences canopy structure, reproductive dynamics, and ultimately seed production.

The sex ratio of dioecious hemp populations is therefore an important agronomic trait because it directly influences the proportion of plants contributing to seed production, canopy persistence during grain filling and the overall productivity of the crop stand. In seed production systems, excessive proportions of male plants may reduce yield potential because only female plants contribute directly to seed production. Conversely, insufficient numbers of male plants may compromise pollination efficiency (Small & Marcus, 2003; Callaway, 2004). Modern oilseed cultivars differ substantially in reproductive strategy, ranging from predominantly female populations to more balanced dioecious stands, further emphasizing the importance of reproductive composition for yield formation.

Despite the obvious agronomic importance of plant sex, relatively little information is available regarding its influence on crop health, pest occurrence, or disease development in hemp. Studies in other dioecious plant species indicate that differences among male and female plants in resource allocation, physiology, and phenology may influence interactions with environmental stresses and associated organisms (Delph & Ashman, 2006; Barrett & Hough, 2013; Xia et al., 2024).

2.4. Emerging biological challenges in hemp cultivation

Industrial hemp is commonly regarded as a crop requiring very limited or no plant protection inputs compared with many major arable species. As a result, research attention has focused predominantly on crop establishment, yield formation, fibre quality, and seed production, whereas pests and diseases have received considerably less attention. During recent decades, however, increasing cultivation areas, changing climatic conditions, and improved monitoring have led to a growing number

of reports describing herbivorous insects and pathogens associated with hemp production systems (Roberts & Punja, 2022; Visković et al., 2024).

Most reported hemp pests and pathogens currently cause only localized or moderate damage, and only a few can be considered major limitations to production (McPartland & Cubeta, 1997; Roberts & Punja, 2022). Nevertheless, the increasing frequency of observations suggests that hemp cultivation is becoming exposed to a broader range of biological interactions than previously recognized (Visković et al., 2024). Similar developments have been observed in other agricultural crops as production areas expand and the geographic range of the cultivation area increases.

Among fungal organisms associated with hemp, species belonging to the genus *Alternaria* have attracted increasing attention. Members of this genus are widely distributed in agricultural fields and may occur as saprophytes, endophytes, or plant pathogens depending on environmental conditions and host status (Thomma, 2003; Roberts & Punja, 2022). Several *Alternaria* species have been isolated from hemp tissues, including *A. alternata*, the recently described *Cannabis*-associated species *A. cannabina* and other closely related taxa (Cheng et al., 2022). *Alternaria* species have been reported both from symptomatic and asymptomatic hemp tissues, and under favourable conditions they may be associated with leaf spot diseases, reductions in photosynthetically active leaf area, and premature senescence. Environmental factors such as humidity, temperature, crop density and host nutritional and physiological status appear to play important roles in determining disease expression (Matić et al., 2020; Roberts & Punja, 2022).

In addition to fungal pathogens, several insect species have increasingly been reported from hemp cultivation systems. One of the most widely recognized examples is the European corn borer (*O. nubilalis*), a highly polyphagous species whose primary host is maize but which has also been associated with hemp cultivation. Reports from Europe have documented larval feeding in stems and reproductive structures, resulting in reduced seed formation, damage to inflorescences and weakened stalks that may complicate harvesting operations (Grigoryev, 1998; Parisi & Ranalli, 2000). Small et al. (2007) further demonstrated that damage by *O. nubilalis* may induce compensatory branching responses in hemp, illustrating the complexity of plant–herbivore interactions in this crop. Although quantitative information on economic losses remains limited compared with major agricultural crops, the broad host range, ecological adaptability and continuing northward expansion of *O. nubilalis* suggest that this insect warrants continued monitoring in regions where hemp cultivation is increasing (Bažok et al., 2020; Zhukovskaya & Frolov, 2022).

The increasing occurrence of pests and pathogens highlights the need to better understand the biological processes governing crop resilience, disease expression and yield stability in expanding hemp production systems. In particular, understanding

how agronomic management influences crop physiology and signalling may be important for maintaining the low-input character associated with hemp cultivation.

2.5. Yield stability and resilience in oilseed hemp

The economic viability of oilseed hemp production depends on achieving high seed yields but also on maintaining stable productivity under variable environmental conditions. Compared with major arable crops, oilseed hemp remains a relatively young production system, and there is often substantial variation in yield performance among cultivars, environments and years (Amaducci et al., 2015; Adamovics et al., 2016; Stramkale et al., 2024; Lääniste et al., 2016). In fact, differences in growing season length, precipitation patterns and temperature regimes may result in substantial year-to-year variation even within the same cultivar and production system (Stramkale et al., 2024). Consequently, yield stability is as important as maximum yield potential when evaluating the suitability of cultivars and management practices.

Reported seed yields of oilseed hemp commonly range between 0.5 and 3.0 t ha^{-1} depending on cultivar, climate and agronomic management, although higher yields have occasionally been achieved under favourable experimental conditions (Amaducci et al., 2015; Adamovics et al., 2016). In Northern Europe, the yield variability is often amplified by fluctuating weather conditions during flowering, pollination and seed maturation.

Several lines of evidence suggest that hemp possesses substantial compensatory capacity. Reduced plant density commonly promotes branching and increases the size and productivity of individual plants, partially compensating for lower stand densities (Campiglia et al., 2017). A compensatory capacity has been reported following biotic damage. Small et al. (2007) observed increased branching and apparent compensation in hemp plants damaged by the European corn borer (*O. nubilalis*), demonstrating that visible injury does not necessarily translate directly into yield loss (Runno-Paurson et al., 2024). Such observations highlight the importance of distinguishing between biological damage, disease severity and economic impact.

The relationship between crop health and productivity is often more complex than simple cause-and-effect relationships imply. Area of disease spread, severity of insect infestation and other indicators of biological stress may not correspond directly to reductions in seed yield. The magnitude of yield loss depends on multiple factors, including the timing of damage, crop developmental stage, environmental conditions and the capacity of the crop to compensate through physiological or morphological adjustments (Madden et al., 2007). Consequently, assessments of crop health should ideally consider both biological indicators and their implications for productivity.

Available evidence suggests that environmental variability often exerts a stronger influence on hemp yield than individual pests or diseases. In northern production regions, weather conditions during flowering and seed maturation frequently determine final yield outcomes to a greater extent than moderate levels of biological damage. This does not diminish the importance of pests and pathogens but emphasizes the need to evaluate them within the broader context of crop performance and production stability.

From a production perspective, the objective of crop management is therefore not necessarily the complete elimination of biological stress factors but the maintenance of productive and resilient cropping systems. In hemp cultivation, resilience appears to depend on a combination of cultivar adaptation, agronomic management, environmental conditions and biological interactions.

Oilseed hemp cultivation in Northern Europe represents a relatively young production system characterized by substantial, especially year-to-year, environmental variability, limited agronomic optimization and increasing biological complexity. Recent observations suggest that in addition to genotype and management crop productivity also depends on interactions among environmental conditions, pests, pathogens and associated microbial communities. Understanding how these factors influence yield stability may be particularly important for preserving the relatively low-input character that has distinguished hemp production from many major agricultural crops.

3. AIMS OF THE STUDY

Industrial hemp cultivation has expanded considerably during recent decades, particularly in oilseed production systems. Despite increasing cultivation areas and economic importance, agronomic knowledge regarding oilseed hemp remains limited compared with major arable crops, especially under Northern European conditions. At the same time, increasing observations of pests and pathogens suggest that biological interactions may become increasingly important determinants of crop performance as hemp cultivation expands. Understanding how agronomic management influences crop productivity and biological challenges is therefore important for maintaining productive and sustainable hemp production systems.

The overall aim of the present thesis was to investigate the effects of agronomic management practices on oilseed hemp productivity, disease development and pest occurrence under Northern European growing conditions.

The specific aims of the thesis were:

1. To assess the occurrence and agronomic significance of emerging biological challenges in hemp cultivation under Northern European conditions (**I-III**).
2. To assess the influence of nitrogen availability and fertilization strategy on the development of Alternaria leaf spot disease in oilseed hemp (**I, II**).
3. To evaluate the agronomic performance of the oilseed hemp cultivars under northern growing conditions (**II**).
4. To evaluate the effects of nitrogen fertilization on seed yield in oilseed hemp under Northern European growing conditions (**I, II**).
5. To determine the occurrence, damage potential and agronomic importance of the European corn borer (*O. nubilalis*) in hemp cultivation (**III**).

Hypotheses

H1. Fertilizer management, including nitrogen addition rate, fertilizer form and application strategy, influences disease development (**I, II**).
H2. Oilseed hemp cultivars differ in agronomic performance and yield stability under northern growing conditions (**II**).
H3. Increased nitrogen availability improves growth and seed yield of oilseed hemp under northern growing conditions (**I, II**).
H4. Fertilizer management, including fertilizer form and application strategy, influences hemp productivity (**I, II**).
H5. European corn borer (*O. nubilalis*) occurs in hemp cultivation under Northern European conditions and affects crop productivity (**III**).

4. MATERIALS AND METHODS

This dissertation comprises three studies (**I–III**) conducted within a long-term hemp agronomy and crop health research programme established at the Estonian University of Life Sciences. The studies were conducted in the same experimental station using similar routine crop management practices, while experimental treatments and response variables investigated differed. A concise summary of the materials and methods is provided below. Detailed descriptions are available in the original publications (**I–III**).

4.1. Experimental site and environmental conditions

Field experiments were conducted during 2019–2024 (Fig. 4.1) at the Eerika experimental station of the Estonian University of Life Sciences in Tartu County, Estonia (58°21′ N, 26°40′ E) (**I–III**).

Figure 4.1. Experimental periods according to published papers.

The experimental area is located in the northern temperate climatic zone and is characterized by substantial interannual variation in temperature and precipitation. The soil type of the experimental field was a sandy loam Stagnic Luvisol according to the World Reference Base classification system (**I, II**).

Meteorological data, including daily air temperature, precipitation and accumulated temperatures expressed as growing degree days (**I, II**), were obtained from an automated weather station (Tartu) located adjacent to the experimental fields (**I–III**). Daily air temperature and precipitation was compared with the long-term average (**I-III**).

4.2. Plant material

Two oilseed hemp cultivars were used in the studies: dioecious cultivar 'Finola' (**I** and **III**), dioecious cultivar 'Estica' (**II** and **III**). Both cultivars have been bred for short-season northern conditions.

4.3. Experimental design and agronomic treatments

The studies were conducted as replicated field experiments. Plot size was 10 m^2 and each treatment was randomly allocated and replicated three times. Throughout the study period no plant protection measures were used in the experimental field (**I–III**).

The experimental factors evaluated are listed in Table 4.1.

Table 4.1. Experimental set-up during 2 study periods (**I-III**).

Characteristic	2019–2021	2022–2024
Cultivar	Finola	Estica
Nitrogen range	0–150	0–200
Fertilizer source	AN, NPK	AN, NPK
Application timing	Sowing, top dressing	Split application
Sowing-rate treatments	Yes	No

4.4. Assessment of fungal disease development (I, II)

The occurrence and development of Alternaria leaf spot disease were monitored under natural infection conditions in Studies **I** and **II**. Disease severity was assessed under natural infection conditions at regular intervals throughout the growing season by estimating the percentage of infected leaf area (0–100%) of 10 female plants in paper **I** and in 5 female and 5 male plants in paper **II**. The area under the disease progress curve (AUDPC) was calculated according to Shaner & Finney (1977):

$$\mathrm{AUDPC} = \sum_{i=1}^{n-1} \frac{y_i + y_{i+1}}{2} \times (t_{i+1} - t_i)$$

where n is the total number of observations, y_1 is the disease severity at the i-th observation, and t is the time (date) of the i-th observation. To allow comparisons among years with different monitoring periods (**I, II**), relative AUDPC (rAUDPC) was calculated as follows:

$$r\mathrm{AUDPC} = \frac{\mathrm{AUDPC}}{t_{i-1}} \times 100$$

where t_{i-1} is the time in days between the first and the last assessment.

For pathogen identification, genomic DNA was extracted from infected hemp leaf material as well as from isolated mycelia samples grown on potato dextrose agar in Petri dishes. DNA barcoding was used (ITS5/ITS4 primers; White et al., 1990), followed by PCR amplification and sequencing (MinIon, Oxford Nanopore). Following MinION sequencing, reads were analyzed through a bioinformatic processing pipeline comprising basecalling, demultiplexing, quality filtering, and taxonomic classification (paper **I, II**). National Center for Biotechnology Information (NCBI) GenBank database (BLASTn) was used to confirm species identity using only sequence identity values above 99%. The pathogen sequences showed the highest similarity to *Alternaria* spp., including *A. alternata* and *A. brassicae* (≥99% identity with each). The sequences are available in Genbank under accession numbers PZ236438–PZ236442.

4.5. Assessment of insect damage (III)

The occurrence and damage caused by the European corn borer (*O. nubilalis*) were evaluated in Paper **III**. Pest monitoring was conducted throughout the growing season, and the number of damaged plants per plot was recorded during repeated assessments, starting when the damage became visible in the field and finished at the harvest.

For molecular confirmation, larval specimens were collected and identified using DNA barcoding techniques. DNA of the larva of *O. nubilalis* was extracted from the last abdominal segment using DNEasy Blood & Tissue Kit (Quiagen N.V., Venlo, Netherlands). A standard barcoding fraction (658 bp) of the mitochondrial COI gene was sequenced and the identity was verified using the identification engine of the Barcode of Life Data Systems (BOLD; Ratnasingham & Hebert, 2007) web portal (as detailed in the paper **III**.

4.6. Seed and biomass yield and yield loss due to insect damage

At the end of the growing seasons, the final pathogen assessment dates coincided with the maturity of the seeds and the harvest times. A customized combine harvester was used and seed yield per plot was obtained (**I, II, III**). Right before the harvest, samples (plants from 0.25 m^2 in each plot) were taken for determination of the seed yield, total above-ground biomass yield, number of female plants, and average plant height and stem diameter (**I, III**). Seed quality characteristics, including seed oil content (%) and thousand-seed mass (TSM), were determined from harvested seed samples as described in Paper **I**.

Seed and biomass yield losses associated with insect damage were estimated based on the number of damaged plants and yield measurements obtained from individual plots (**III**).

4.7. Statistical analyses

Impact of experimental treatments, and pathogen impacts were analysed using linear models, analysis of variance (ANOVA), correlation analyses and post-hoc multiple comparison procedures, depending on the experimental objectives and data structure (**I–III**) using R version 4.3.2. All statistical effects were considered significant at $p < 0.05$.

Disease progression, yield responses and pest occurrence were evaluated in relation to agronomic treatments, environmental conditions and growing season variability. Detailed descriptions of statistical procedures are provided in the original publications (**I–III**).

For the integrated analyses presented in the thesis, nitrogen addition rate was analysed both as a continuous and categorical variable depending on the research question. Disease severity and seed yield responses to nitrogen addition rate across years were evaluated using linear models including nitrogen addition rate, year and their interaction. For comparisons among years and among selected nitrogen treatments, one-way ANOVA followed by Tukey-adjusted pairwise comparisons of estimated marginal means were used.

In addition to the analyses presented in the original publications, integrated analyses were conducted using the combined dataset from 2019–2024. Interannual differences in disease severity and seed yield were evaluated using one-way ANOVA followed by Tukey-adjusted pairwise comparisons of estimated marginal means. Linear models including nitrogen addition rate, year and their interaction were used to evaluate nitrogen responses across years. Yield stability was characterized using average yield, standard deviation (SD), and coefficient of variation (CV) calculated from all plot-level seed yield observations within each cultivar-specific experimental period (‘Finola’, 2019–2021; ‘Estica’, 2022–2024).

For analyses of fertilizer source (ammonium nitrate vs. complex NPK fertilizer), models were restricted to fertilized treatments only and included nitrogen addition rate, year, and fertilizer source as fixed effects. Sex-specific responses were analyzed separately for male and female plants using the same model structure (**II**).

Pearson correlation analysis was used to examine the relationships between the levels of N fertilization, disease severity, the seed and biomass yield, and seed quality parameters (**I, III**).

An independent-samples t-test was performed to assess differences in *O. nubilalis* damage between the two growing seasons, as well as differences in average biomass and seed yield among fertilizer types and fertilization method (**III**).

5. RESULTS

This thesis investigated the occurrence, development and agronomic importance of major biotic stress factors affecting industrial hemp (*C. sativa*) production under Northern Baltic conditions across the six-year study period (2019–2024).

5.1. Occurrence and progression of Alternaria leaf spot disease in hemp

Alternaria leaf spot was the only consistently observed disease throughout the experimental period. Molecular analyses confirmed infection by *Alternaria* species, including *A. alternata* and *A. brassicae*-related taxa, demonstrating that *Alternaria* spp. were responsible for the characteristic leaf spot symptoms observed on hemp plants.

In cultivar 'Finola' (2019–2021), disease severity varied substantially among years (**I**, Fig. 3). The highest disease pressure occurred during 2019 and 2020, whereas the warm and dry growing season of 2021 markedly suppressed disease development. Maximum disease severity reached 27.8 ± 4.2%, while average disease severity at the end of the growing season was 12.7 ± 0.8%. Disease progression accelerated during mid-to-late summer, but the onset of rapid disease increase was delayed under drought conditions (**I**, Fig. 3).

Similar seasonal variation was observed in the dioecious cultivar 'Estica' during 2022–2024 (**II**, Fig. 2a). Disease pressure differed significantly among years, with the highest cumulative disease severity (AUDPC) recorded in 2022 and progressively lower severity in 2023 and 2024. Male and female plants exhibited distinct disease progression patterns. Disease severity increased more rapidly in male plants, whereas female plants showed a slower but more prolonged disease development due to their differences in phenology and duration of observation.

In addition to the publication-specific analyses, the disease development was evaluated across all six growing seasons using accumulated growing degree days (GDD), and substantial interannual differences in epidemic development were observed (Fig. 5.1; Mäeorg et al., 2026). Despite variation in epidemic onset and progression rate, Alternaria leaf spot occurred every year, indicating successful establishment of the pathogen under Northern Baltic conditions.

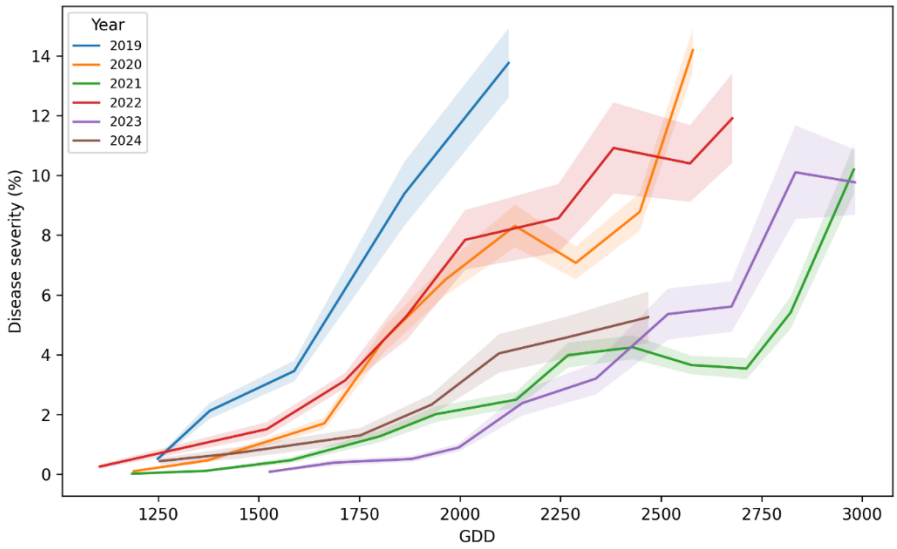

Figure 5.1. Development of Alternaria leaf spot disease severity (%) in seed hemp during six growing seasons (2019–2024) expressed as accumulated growing degree days (GDD; base temperature 5 °C). Disease severity (%) represents the mean infection level of female hemp plants across all treatments within each year. Shaded areas indicate standard errors of the means.

Relative cumulative disease severity (rAUDPC) differed significantly among years (ANOVA: $F_{5,237} = 11.91$, $p < 0.001$; Fig. 5.2). The highest rAUDPC values were recorded in 2019 and 2022, whereas the lowest values occurred in 2021 and 2024. Disease pressure in 2023 was intermediate and overlapped statistically with both lower- and higher-severity years according to Tukey-adjusted pairwise comparisons of estimated marginal means (Fig. 5.2; Mäeorg et al., 2026).

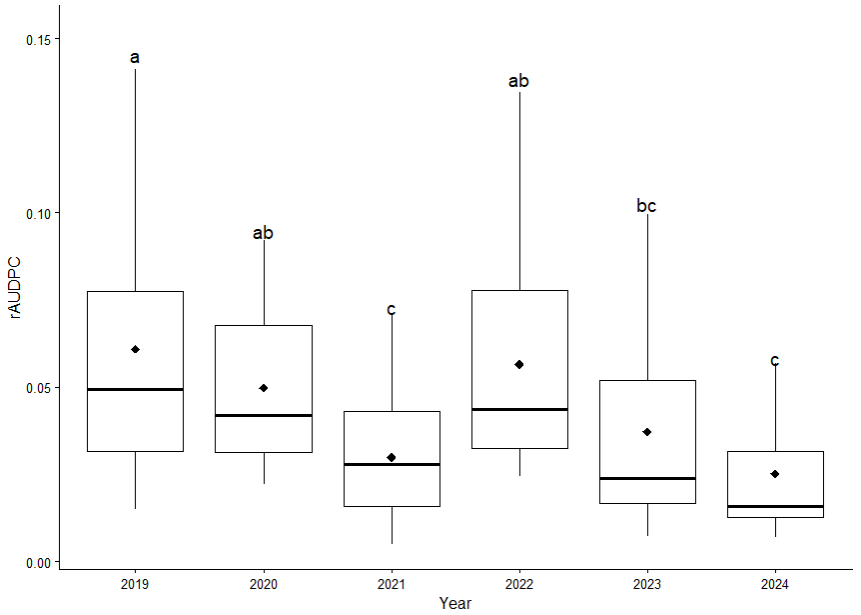

Figure 5.2. Interannual variation in relative Alternaria disease severity (rAUDPC) during six consecutive growing seasons (2019–2024). Boxplots represent the distribution of plot-level observations across all treatments within each year. The horizontal line within each box indicates the median, the black diamond indicates the mean value, boxes represent the interquartile range, and whiskers indicate the range excluding outliers. Years sharing at least one lowercase letter are not significantly different according to Tukey-adjusted pairwise comparisons of estimated marginal means ($p < 0.05$).

Overall, climatic conditions strongly regulated infection intensity. Warmer and drier seasons delayed disease progression and reduced final disease severity, whereas more humid seasons favoured disease development.

5.2. Effects of nitrogen fertilization and crop management on Alternaria disease development

Nitrogen availability was one of the strongest factors influencing disease severity. In both hemp cultivars investigated, increasing nitrogen application rates consistently reduced disease progression.

In cultivar 'Finola', cumulative disease severity (rAUDPC) decreased significantly with increasing nitrogen application rate (**I**, Fig. 4). The unfertilized control consistently exhibited the highest disease levels, whereas the highest nitrogen treatment (150 kg N ha^{-1}) reduced rAUDPC by approximately 75% relative to the control. This negative relationship between nitrogen addition rate and disease severity was observed in all years despite substantial differences in weather conditions.

The same trend was confirmed for the cultivar 'Estica'. Nitrogen application significantly reduced AUDPC values in both male and female plants (**II**, Fig. 3). Across the tested nitrogen addition range (0–200 kg N ha^{-1}), disease severity decreased markedly relative to the unfertilized control. Although the magnitude of the response varied among years, the suppressive effect of nitrogen availability remained consistent.

Across the combined six-year dataset, relative disease severity decreased significantly with increasing nitrogen addition rate (Fig. 5.3; Mäeorg et al., 2026). Mean rAUDPC declined from 0.088 in the unfertilized control to 0.021 at 200 kg N ha^{-1}, corresponding to a 76% reduction in disease severity. Nitrogen addition rate significantly affected disease development ($F_{1,204}$ = 212.72, p < 0.001). Nitrogen addition rate alone explained 41.1% of the variation in rAUDPC values (R^2 = 0.411). Disease severity also differed among years ($F_{5,204}$ = 18.39, p < 0.001), whereas the nitrogen × year interaction was not significant ($F_{5,204}$ = 1.78, p = 0.119), indicating a consistent suppressive effect of high nitrogen availability across growing seasons.

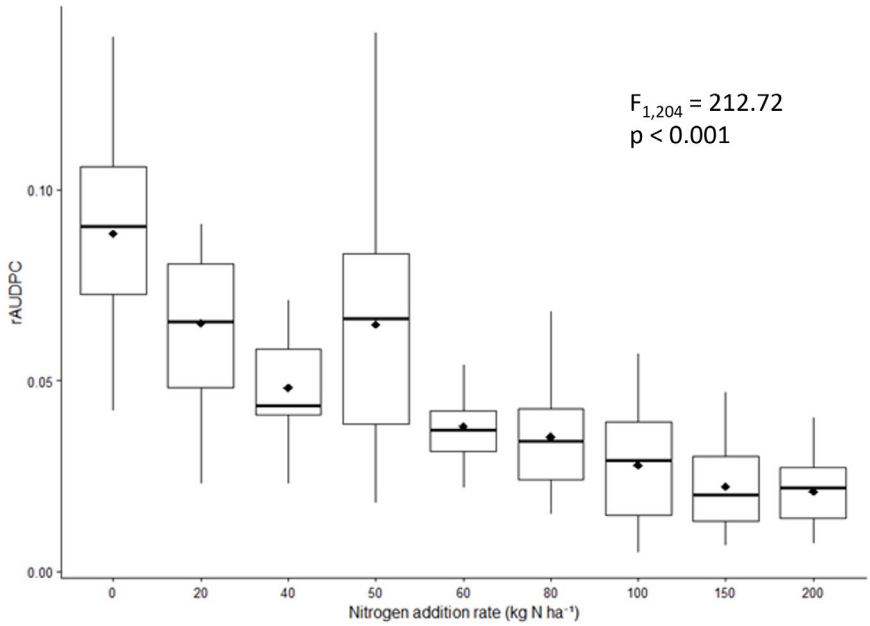

Figure 5.3. Effect of nitrogen addition rate on relative Alternaria disease severity (rAUDPC) in oilseed hemp across six growing seasons (2019–2024). Boxplots represent plot-level observations pooled across years and fertilizer treatments. The horizontal line within each box indicates the median, the black diamond indicates the mean value, boxes represent the interquartile range, and whiskers indicate the range excluding outliers.

Fertilization timing also influenced disease development. In cultivar 'Finola', fertilizer application at sowing resulted in significantly higher disease severity than top-dressing fertilization. Across years, average AUDPC values were approximately 39% higher when fertilizers were applied at sowing.

In contrast, fertilizer source had little influence on disease development. In the combined six-year analysis, fertilizer type had no significant effect on relative disease severity ($F_{1,186}$ = 1.06, p = 0.305), and no significant fertilizer type × year interaction was detected (p = 0.081).

Crop density effects were less consistent (**I**, Fig. 5). Higher sowing rates tended to increase disease severity during years with high disease pressure, but the relationship was not significant under low disease conditions.

5.3. Interannual variation in seed yield and yield stability

Seed yield varied substantially among years and management treatments. Across all treatments, seed yield ranged from approximately 0.6 to 2.7 t ha^{-1}.

Interannual differences in productivity were significant (ANOVA: $F_{5,210}$ = 8.90, p < 0.001; Fig. 5.4). Mean seed yield ranged from 1.09 t ha^{-1} in 2020 to 1.95 t ha^{-1} in 2019. According to Tukey-adjusted pairwise comparisons, 2020 was the only year that differed significantly from the remaining growing seasons, whereas no significant differences were detected among 2019 and 2021–2024 (Figure 5.4).

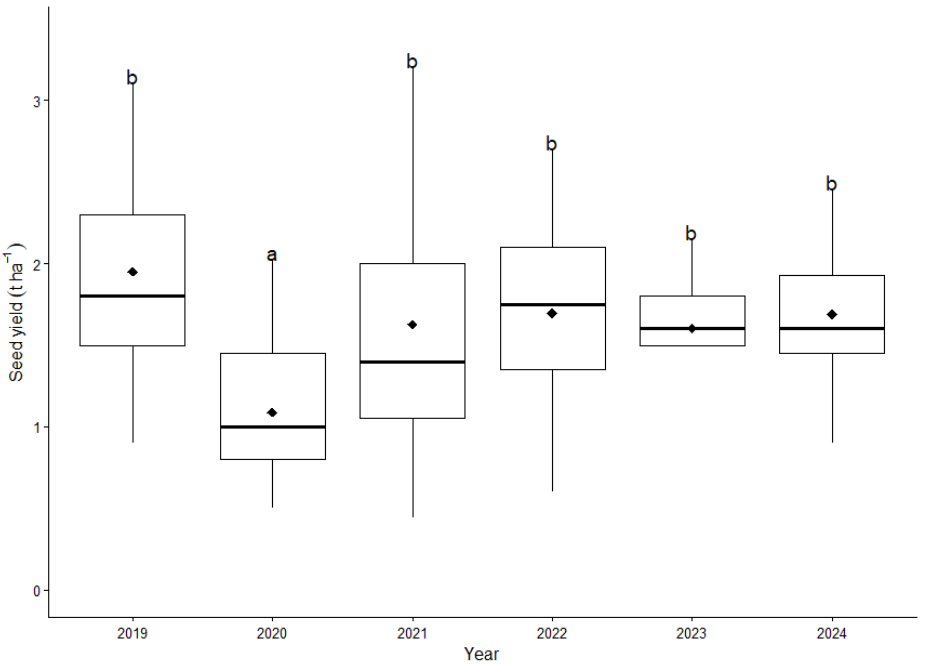

Figure 5.4. Interannual variation in hemp seed yield during six growing seasons (2019–2024). Boxplots represent plot-level observations across all treatments within each year. The horizontal line within each box indicates the median, the black diamond indicates the mean value, boxes represent the interquartile range, and whiskers indicate the range excluding outliers. Years sharing the same letter are not significantly different according to Tukey-adjusted pairwise comparisons of estimated marginal means (p < 0.05).

There was considerable variation in hemp seed and biomass productivity among years. In addition to differences in mean yield, plot-to-plot variability also differed among growing seasons, with 2023 and 2024 exhibiting relatively stable yield distributions compared with 2019 and 2021.

Table 5.1. Seed yield and yield stability characteristics of hemp production during the 2019–2021 (cv. 'Finola') and 2022–2024 (cv. 'Estica') experimental periods. Mean yield, standard deviation (SD), and coefficient of variation (CV) were calculated from plot-level observations.

Experimental period	Mean yield (t ha^{-1})	SD	CV (%)
2019–2021	1.56	0.80	51.4
2022–2024	1.66	0.45	26.8

A comparison of the two experimental periods revealed only modest differences in mean productivity but substantial differences in yield stability (Table 5.1). Mean seed yield was slightly higher during the experiment in 2022–2024 (cultivar 'Estica') than during the period 2019–2021 (cultivar 'Finola'), averaging 1.66 and 1.56 t ha^{-1}, respectively. More pronounced differences were observed in yield variability. The coefficient of variation was 51.4% during the cultivar 'Finola' period compared with 26.8% during the cultivar 'Estica' experiment, indicating substantially lower yield variability during 2022–2024.

5.4. Effects of nitrogen fertilization and fertilizer management on seed yield and quality

Nitrogen fertilization substantially increased seed yield (**I**, Fig. 5). Across the nitrogen treatments (0, 50, 100 and 150 kg N ha^{-1}), mean seed yield increased from 0.80 t ha^{-1} in the unfertilized control to 1.34, 1.59 and 1.78 t ha^{-1} at 50, 100 and 150 kg N ha^{-1}, respectively (Fig. 5.5).

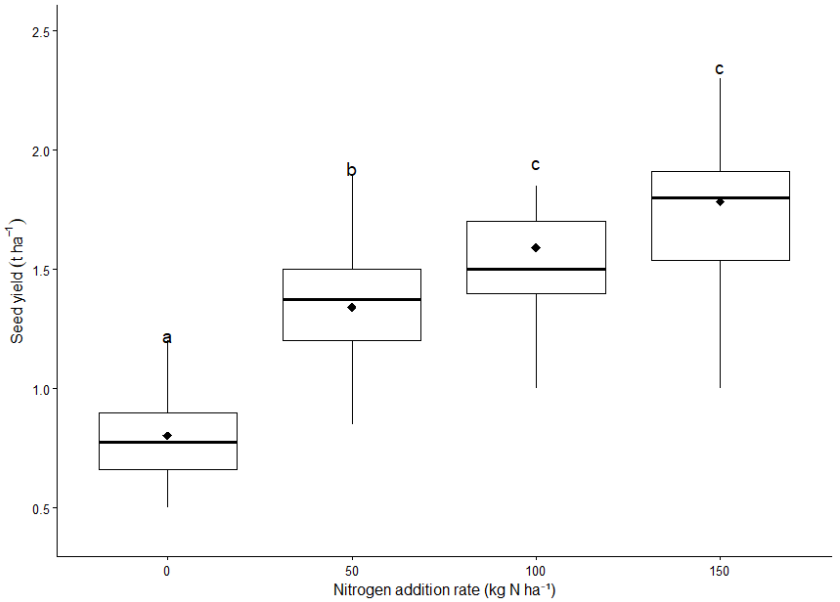

Figure 5.5. Effect of nitrogen addition rate on hemp seed yield. Boxplots represent plot-level observations from the comparable nitrogen treatments (0, 50, 100 and 150 kg N ha^{-1}). The horizontal line within each box indicates the median, the black diamond indicates the mean value, boxes represent the interquartile range, and whiskers indicate the range excluding outliers. Treatments sharing the same letter are not significantly different according to Tukey-adjusted pairwise comparisons of estimated marginal means ($p < 0.05$).

Nitrogen addition rate significantly affected seed yield (ANOVA: $F_{3,122} = 30.17$, $p < 0.001$). Tukey-adjusted pairwise comparisons showed that all fertilized treatments produced significantly higher yields than the unfertilized control. Yield at 50 kg N ha^{-1} was significantly lower than at 100 and 150 kg N ha^{-1}, whereas no significant difference was detected between the 100 and 150 kg N ha^{-1} treatments.

In the combined six-year analysis, nitrogen addition rate increased seed yield ($F_{1,204} = 65.58$, $p < 0.001$). Yield also differed among years ($F_{5,204} = 12.00$, $p < 0.001$), whereas the nitrogen × year interaction was not significant ($F_{5,204} = 1.04$, $p = 0.394$), indicating a broadly consistent yield response to nitrogen fertilization across growing seasons.

Fertilizer source did not significantly affect seed yield in the combined six-year analysis ($F_{1,186} = 0.229$, $p = 0.633$), and no fertilizer source × year interaction was detected ($p = 0.785$). However, Paper **II** reported consistently higher hemp seed yields under NPK fertilization during 2022–2024, compared to ammonium nitrate (**II**, Fig. 5). These results indicate that nitrogen availability was substantially more important for productivity than fertilizer form, although with cultivar 'Estica' significant effect of fertilizer type was observed.

Seed oil content varied between approximately 27 and 33%, whereas 1000-seed mass ranged from 10.3 to 14.7 g across years and treatments (**I**, Supplementary Tables 1-3).

Nitrogen addition rate showed a weak positive association with 1000-seed mass ($r = 0.20$, $p < 0.01$), but it was not associated with seed oil content (**I**, Supplementary Table 4). Disease severity showed weak or non-significant relationships with seed-quality characteristics.

5.5. European corn borer occurrence and impacts on hemp production

The European corn borer (*O. nubilalis*) was identified as an emerging insect pest of hemp in Estonia. Molecular analyses confirmed the identity of the collected larvae as *O. nubilalis* after the pest was first detected in hemp experimental field at low abundance in 2020 and subsequently monitored during 2021–2022.

Across study years, the pest infestation increased between years. The average number of damaged plants per plot increased from 4.45 ± 0.23 in 2021 to 11.3 ± 0.7 in 2022, indicating rapid establishment and spread of the insect under northern conditions. Within both growing seasons (**III**, Fig. 3), infestation levels increased continuously until harvest. The strongest increase occurred during 2022, when infestation rose significantly between observation dates and reached its highest levels at the end of the growing season.

Typical symptoms included stem boring, visible entry holes, larval frass, stem breakage, wilting of upper plant parts and premature senescence (**III**, Fig. 2). In severe cases, plants collapsed completely before harvest.

European corn borer infestation reduced both biomass and seed yield. Yield losses increased markedly between years, reflecting the higher infestation pressure observed in 2022. Average seed yield reduction was 12.3 ± 0.15 kg ha^{-1} in 2021 and 68.6 ± 1.07 kg ha^{-1} in 2022. Maximum losses reached approximately 120 kg ha^{-1}, corresponding to more than 7% of total seed yield (**III**, Fig. 5). Biomass yield reduction in 2021 averaged 0.92 ± 0.65 t ha^{-1}.

Nitrogen fertilization strongly increased biomass and seed yield but had only weak effects on pest infestation. In 2022, unfertilized plots experienced significantly greater yield losses than fertilized treatments. Fertilization timing also influenced damage, with fertilizer application at sowing associated with higher yield losses than top dressing. Fertilizer type did not significantly affect pest-associated yield reduction (**III**, Fig. 5; $p < 0.001$).

No significant relationships were observed between pest infestation and crop density, plant height, stem diameter or the number of female plants (**III**, Fig. 4). These findings suggest that the observed infestation levels were driven primarily by pest population dynamics rather than crop morphological characteristics.

6. DISCUSSION

6.1. Alternaria leaf spot has become an established disease of hemp under Northern Baltic conditions (I, II)

One of the most important findings of the present thesis is that Alternaria leaf spot occurred consistently throughout the entire study period, irrespective of cultivar, growing season or environmental conditions (**I, II**). Although disease severity varied substantially among years, disease symptoms were observed in every season between 2019 and 2024, indicating that *Alternaria* spp. have become well established in oilseed hemp production systems under Northern Baltic conditions. This observation contrasts with the traditional perception of hemp as a crop largely free from economically important diseases (Punja, 2021) and supports recent reports suggesting that pathogen pressure in hemp cultivation is increasing as cultivation areas expand and monitoring efforts improve (Cheng et al., 2022; Punja & Scott-Dupree, 2022).

The six-year dataset demonstrated that climatic conditions strongly influenced epidemic development. Disease progression was delayed and final disease severity reduced during warmer and drier growing seasons, whereas higher disease pressure was associated with seasons characterized by more favourable moisture conditions (**I, II**). Similar responses have been reported for Alternaria diseases in several agricultural crops, where temperature and humidity interact to determine infection efficiency, sporulation and epidemic progression (Rotem, 1994; Matić et al., 2020; Hossain et al., 2024). The observed interannual variation therefore appears consistent with the ecological requirements of *Alternaria* spp. and highlights the importance of weather conditions as a major regulator of disease development in northern production systems.

Although climatic conditions strongly influenced epidemic intensity, *Alternaria* spp. remained present throughout the study period (**I, II**). This suggests that the pathogen should be regarded as a recurring component of hemp production systems in Northern Europe rather than an occasional opportunistic infection. Consequently, long-term disease management strategies may become increasingly important as cultivation areas expand.

Molecular analyses confirmed the presence of *Alternaria* species associated with symptomatic hemp tissues. Sequences showed high similarity to *A. alternata* and closely related taxa, which agrees with recent studies identifying members of the *Alternaria* complex as important pathogens of hemp (**I**; Cheng et al., 2022). Previous reports have documented *Alternaria* infections in fibre, medical and seed hemp production systems and have associated severe epidemics with reductions in

photosynthetically active leaf area, accelerated senescence and deterioration of crop quality (Matić et al., 2020; Roberts & Punja, 2022; Cheng et al., 2022). The current results extend these observations by demonstrating sustained disease occurrence under Northern Baltic field conditions across multiple growing seasons.

The observed differences between years also emphasize the importance of evaluating disease development over sufficiently long time periods. If disease assessments had been restricted to a single season, substantially different conclusions could have been reached regarding the importance of Alternaria leaf spot in hemp production. The six-year synthesis revealed that disease severity differed by more than two-fold among years (**I, II**), highlighting the importance of long-term observations in northern temperate regions where climatic variability can strongly influence crop performance and disease development (Adamovics et al., 2016; Stramkale et al., 2024).

Although disease severity varied substantially among years (**I, II**), direct effects on seed yield were limited under the conditions of the present study (**I, II**). Nevertheless, the consistent occurrence of Alternaria leaf spot supports the conclusion that the disease has become an established component of hemp production systems under Northern Baltic conditions. Future hemp production systems will likely require continued monitoring of disease occurrence and improved understanding of the interactions among climate, crop management and pathogen development. As hemp cultivation expands and production systems intensify, the epidemiological importance of *Alternaria spp*. may increase further (Punja, 2021; Punja & Scott-Dupree, 2022), emphasizing the need for integrated disease-management approaches adapted to northern environments.

6.2. Nitrogen availability strongly influences disease development (I, II)

Nitrogen availability emerged as one of the strongest determinants of Alternaria leaf spot severity throughout the present study. Across both cultivars and all growing seasons, increasing nitrogen addition rates consistently reduced disease severity (**I, II**). This pattern was observed in the individual field experiments (**I, II**) and was further confirmed by the six-year synthesis analysis, where accumulative relative disease severity (rAUDPC) decreased by approximately 76% between the unfertilized control and the highest nitrogen treatment. The consistency of this response across contrasting environmental conditions suggests that nitrogen availability exerts a fundamental influence on the development of Alternaria leaf spot in oilseed hemp.

The relationship between nitrogen availability and disease development remains one of the most debated topics in plant pathology (Dordas, 2008). While increased nitrogen supply has frequently been associated with greater disease severity due to enhanced canopy density and prolonged leaf wetness, numerous studies have reported neutral or even suppressive effects of nitrogen depending on the host

species, pathogen biology and environmental conditions (Dordas, 2008; Veresoglou et al., 2013; Mur et al., 2017; Balint-Kurti, 2019). In many pathosystems, higher nitrogen supply promotes dense vegetative growth, increases canopy humidity and leaf wetness duration, and thereby creates conditions favourable for pathogen development. Such responses have frequently been reported for foliar diseases of cereals and other annual crops where increased nitrogen availability promotes denser canopies and more favourable microclimatic conditions for pathogen development (Madden et al., 2007; Veresoglou et al., 2013; Mur et al., 2017). However, the relationship between nitrogen and disease is highly pathosystem-specific and depends on interactions among host physiology, pathogen biology and environmental conditions (Dordas, 2008; Veresoglou et al., 2013; Mur et al., 2017). Recent reviews further emphasize that disease development is regulated by complex interactions among nutrient availability, environmental conditions and plant defence responses, making generalized predictions difficult across pathosystems (Choudhary & Senthil-Kumar, 2024; Pandey & Senthil-Kumar, 2024). The present results indicate that, in hemp, the positive effects of nitrogen on plant performance and stress tolerance outweighed any potential increase in disease favourability associated with denser canopies.

Several mechanisms may explain the observed reduction in disease severity with increasing nitrogen availability. Nitrogen plays a central role in photosynthesis, protein synthesis and the production of defence-related compounds (Dordas, 2008; Mur et al., 2017; Bai et al., 2022; Dutta et al., 2024). Adequate nutrient availability may therefore improve the capacity of hemp plants to maintain healthy foliage and respond more effectively to pathogen attack. In addition, nitrogen fertilization can influence plant architecture, canopy development and leaf longevity, potentially altering the progression of disease epidemics. The strong and consistent response observed across years suggests that physiological effects associated with improved plant nutrition were more important than any indirect effects on canopy microclimate.

The findings also support the growing recognition that disease development should be considered within a broader ecological context rather than solely as an interaction between host and pathogen (Hassani et al., 2018; Compant et al., 2019). Recent studies have demonstrated that nutrient availability can alter microbial community composition and shift the balance between mutualistic and pathogenic microorganisms, thereby influencing disease susceptibility and suppression (Lekberg et al., 2021; Bai et al., 2022). Although microbial communities were not directly assessed in the present study, the consistent relationship between nitrogen availability and disease severity raises the possibility that nutrient-mediated microbial interactions contributed to the observed patterns. Future studies examining the hemp microbiome under different fertilization regimes may provide additional insight into the mechanisms underlying disease suppression.

An important outcome of the six-year analysis was the absence of a significant nitrogen × year interaction (**I, II**). Although disease pressure differed markedly among growing seasons, the direction of the nitrogen response remained remarkably stable (**I, II**). This finding suggests that the suppressive effect of nitrogen was not restricted to particular environmental conditions but represented a robust feature of the hemp–*Alternaria* pathosystem. Such consistency is especially important from an agronomic perspective because it increases confidence that nitrogen management can be used as a practical tool for reducing disease severity under variable northern temperate conditions.

The results further indicate that nitrogen addition rate was considerably more important than fertilizer source timing of application (**I, II**). While individual experiments occasionally revealed differences between fertilizer types, these effects were not maintained in the combined six-year analysis (**I, II**). This suggests that the quantity of available nitrogen was the dominant factor regulating disease development, whereas the specific fertilizer type or application timing played a comparatively minor role (**I, II**). Consequently, disease management benefits appear to be associated primarily with achieving adequate crop nutrition rather than selecting a particular (nitrate- or ammonium-dominating) nitrogen fertilizer.

Overall, the present study demonstrates that nitrogen availability is not only a key determinant of productivity but also an important regulator of disease development in oilseed hemp (**I, II**). The strong and consistent reduction in Alternaria leaf spot severity observed across years (**I, II**) shows the potential of nutrient management as an important component of disease management strategies for hemp cultivation under Northern Baltic conditions.

6.3. Nitrogen availability is a stronger determinant of seed yield than moderate disease pressure (I, II)

The results of the present thesis indicate that nitrogen availability was a stronger determinant of seed yield than moderate levels of Alternaria leaf spot infection. Nitrogen fertilization consistently increased seed productivity across years, cultivars and experimental systems, whereas the direct relationship between disease severity and yield was comparatively weak once fertilization effects were considered (**I, II**). This finding highlights the importance of evaluating crop health and productivity within the broader context of crop nutrition and environmental conditions rather than treating disease severity as an isolated factor for yield loss.

Nitrogen addition substantially increased seed yield throughout the study period. In the six-year synthesis, yield responses to nitrogen remained remarkably consistent despite substantial variation in weather conditions and disease pressure. Seed yield increased by more than twofold between the unfertilized control and the highest

nitrogen treatments (**I, II**), demonstrating the central role of nutrient availability in determining crop productivity of oilseed hemp. These findings are consistent with previous studies reporting strong nitrogen responsiveness in oilseed hemp and confirm that adequate nitrogen supply remains one of the primary prerequisites for stable seed production in northern environments (Aubin et al., 2015; Adamovics et al., 2016; Lääniste et al., 2016; Stramkale et al., 2024).

Nitrogen simultaneously increased seed yield and reduced disease severity (**I, II**). Consequently, disease severity and yield may appear negatively associated even when both variables are responding primarily to nutrient availability rather than directly to each other. This highlights the importance of considering agronomic and environmental factors when interpreting disease–yield relationships.

This interpretation is supported by the statistical analyses performed in Paper **II**. Although simple correlations suggested a negative association between disease severity and seed yield, disease variables were no longer significant predictors of yield once nitrogen availability and year effects were included in the models (**II**). At the same time, nitrogen remained a highly significant determinant of productivity (**II**). These results indicate that the apparent disease–yield relationship was largely driven by differences in nutrient availability rather than by direct disease impacts alone. Only under low-nitrogen (Control treatments, **II**) conditions there was a clear negative relationship between disease severity and yield (**II**), suggesting that disease effects become more pronounced when plant growth is already constrained by nutrient limitation.

Several biological mechanisms may contribute to this pattern. Adequate nitrogen supply increases photosynthetic capacity, leaf area development and biomass accumulation (Masclaux-Daubresse et al., 2010; Hachiya & Sakakibara, 2017), thereby enhancing the crop ability to tolerate or compensate for moderate levels of foliar damage. Hemp is characterized by substantial phenotypic plasticity (Nicotra et al., 2010; Campiglia et al., 2017) and possesses a strong capacity for compensatory growth (Small et al., 2007). Consequently, moderate losses of photosynthetically active leaf area do not necessarily translate directly into proportional yield reductions (Gaunt, 1995; Madden et al., 2007). The ability of well-nourished plants to maintain reproductive development despite disease pressure may explain why nitrogen effects on productivity exceeded the direct effects of Alternaria infection observed in the present study.

These findings also support the broader concept that crop productivity is often influenced more strongly by environmental and agronomic factors than by moderate levels of biological stress. Previous studies have shown that the relationship between disease severity and yield loss is often non-linear and depends on the timing of infection, crop developmental stage, environmental conditions and the compensatory

capacity of the host plant (Gaunt, 1995; Madden et al., 2007; Balint-Kurti, 2019). The present results are consistent with this view and suggest that disease severity alone may provide an incomplete assessment of the agronomic importance of a pathogen.

In contrast to the strong effects observed for seed yield, nitrogen availability exerted only limited effects on seed-quality traits. Oil content remained relatively stable across treatments, whereas seed size (1000-seed mass) increased slightly with nitrogen availability (**I**, Supplementary Tables 1-4). These results suggest that nitrogen primarily influenced biomass accumulation and seed production rather than seed composition.

From a practical perspective, the findings emphasize the importance of integrated crop management approaches. Although disease management remains important, maintaining adequate crop nutrition appears to be one of the most effective strategies for sustaining productivity, particularly in oilseed hemp (Dordas, 2008; **I**; **II**), where substantial phenotypic plasticity may allow plants to partially compensate for moderate levels of biotic stress (Small et al., 2007; Amaducci et al., 2015; Campiglia et al., 2017). Fertilization not only increased seed yield directly but also reduced disease severity (**I**, **II**), thereby influencing both crop performance and crop health simultaneously. Such dual benefits highlight the potential of nutrient management as a key component of sustainable hemp production systems.

Overall, the results indicate that nitrogen availability was a more important factor for oilseed hemp productivity than moderate levels of Alternaria leaf spot infection (**I**, **II**). While disease severity contributed to variation in crop performance under specific conditions, particularly at low nitrogen availability (**II**), nutrient status had consistently greater influence on yield formation across years and production systems.

6.4. Yield stability and cultivar performance under northern conditions (I-III)

Achieving stable seed production remains one of the major challenges in oilseed hemp cultivation. Compared with many traditional field crops, hemp exhibits considerable phenotypic plasticity and responds strongly to environmental variation (Nicotra et al., 2010; Campiglia et al., 2017). Consequently, year-to-year fluctuations in temperature, precipitation and growing season length often result in significant variation in crop performance (Aubin et al., 2015). The present study demonstrated that interannual variability represented an important component of hemp productivity, with seed yields differing significantly among growing seasons and the lowest yields observed during 2020 (**I**, **II**). These results confirm that environmental conditions remain a major determinant of hemp productivity under Northern Baltic conditions.

Although mean seed yields varied among years, the comparison between experimental periods suggested notable differences in yield stability. The cultivar 'Estica' period (2022–2024) showed much lower coefficient of variation than the 'Finola' experiment (2019–2021), indicating lower yield variability among years (**I**, **II**). This finding is particularly relevant because production stability is often as important as maximum yield potential from a grower's perspective. A cultivar capable of maintaining relatively consistent yields under variable environmental conditions may provide greater practical value than a cultivar capable of producing exceptionally high yields only under favourable conditions.

The lower variability observed during the 2022–2024 period (cv. 'Estica') should be interpreted cautiously because the cultivars were not evaluated concurrently under identical environmental conditions. Consequently, the observed differences may reflect a combination of cultivar characteristics, weather conditions and management factors. Nevertheless, adaptation to northern photoperiod and growing-season constraints may have contributed to the relatively stable performance observed during the experiment with cultivar 'Estica' (**I**, **II**). Earlier studies have emphasized the importance of photoperiod adaptation and flowering behaviour in determining hemp productivity at higher latitudes, where relatively small shifts in developmental timing may strongly influence final seed yield (Lisson et al., 2000; Salentijn et al., 2019; Ansari et al., 2025).

Consequently, the present study does not come to definitive conclusions regarding cultivar suitability. Instead, the results indicate that the experimental period associated with cultivar 'Estica' cultivation was characterized by lower yield variability and slightly higher mean productivity than the period associated with cultivar 'Finola' cultivation (**I**, **II**). The observed differences nevertheless provide useful insight into the importance of cultivar suitability for northern production systems. Successful hemp cultivation at high latitudes depends on the ability of cultivars to complete reproductive development within a relatively short growing season while maintaining adequate vegetative productivity during the first part of the growing season (Lisson et al., 2000; Salentijn et al., 2019). The increasing availability of cultivars specifically developed for northern environments may therefore contribute to improving both productivity and production stability.

Another important observation is that hemp demonstrated a considerable capacity to maintain productivity despite substantial variation in disease pressure among years (**I**, **II**). Although Alternaria leaf spot severity differed markedly among growing seasons, corresponding changes in seed yield were less pronounced (**I**, **II**). This finding supports the view that hemp possesses a degree of resilience to moderate biotic stress and that environmental conditions and crop management often exert stronger influences on productivity than individual disease episodes (**I**, **II**). Such

resilience is consistent with the high phenotypic plasticity characteristic of hemp and may contribute to the crop's suitability for low-input production systems.

Overall, the results emphasize that yield stability should be considered alongside yield potential when evaluating hemp cultivars for northern temperate regions. While environmental conditions are the most important source of variation, cultivar adaptation, reproductive characteristics and agronomic management all contribute to the ability of hemp crop to maintain stable productivity under highly variable growing conditions (**I**, **II**). Future breeding efforts should therefore continue to focus not only on increasing yield potential but also on improving yield stability and adaptation to northern environments.

6.5. Fertilizer management effects (I-III)

In addition to nitrogen addition rate, the present thesis evaluated the potential influence of fertilizer source and application timing strategy on disease development and crop productivity. While nitrogen availability consistently affected both disease severity and seed yield (**I**, **II**), the effects of fertilizer management practices were generally less pronounced and appeared to depend on experimental context (**I**, **II**).

One of the objectives of the study was to determine whether fertilizer source influences crop performance beyond the effects of total nitrogen availability. In the three-year experiment with cultivar 'Estica', complex NPK fertilizer consistently produced higher seed yields than ammonium nitrate (**II**). This result suggested that the additional phosphorus and potassium supplied by the complex fertilizer may have contributed to improved crop performance under certain environmental conditions. Similar responses have occasionally been reported in hemp and other crops, where balanced nutrient availability improves reproductive development and nutrient-use efficiency (Aubin et al., 2015; Hachiya & Sakakibara, 2017; Chen et al., 2024). However, the integrated six-year analysis provided a broader perspective. When data from both experimental series were combined, fertilizer source did not significantly affect either disease severity or seed yield (**I**, **II**). Furthermore, no significant fertilizer source × year interactions were detected (**I**, **II**). These findings indicate that the apparent advantages observed in individual experiments were not sufficiently consistent across years and production systems to produce a significant overall effect. Consequently, the results suggest that nitrogen availability itself was considerably more important than fertilizer source in determining both productivity and disease development.

The comparison between individual experiments and the combined analysis illustrates the value of long-term synthesis approaches. Results obtained within a single experiment may be influenced by specific environmental conditions, whereas integrated analyses can reveal whether observed effects are robust across years and

production systems. In the present study, the six-year dataset suggests that the choice of fertilizer source is likely to be of secondary importance compared with achieving an adequate level of nitrogen nutrition.

Fertilizer application strategy appeared to influence disease development more strongly than fertilizer source. In cultivar 'Finola', fertilizer application at sowing resulted in higher disease severity than top-dressing fertilization (**I**). This response may be associated with differences in early canopy development, nutrient availability and microclimatic conditions within the crop stand. Earlier nutrient availability can stimulate rapid vegetative growth and increase canopy density, potentially creating conditions more favourable for foliar pathogen development. Similar mechanisms have been proposed in other crop systems, where fertilization timing influences both crop architecture and disease epidemiology (Madden et al., 2007; Dordas, 2008; Mur et al., 2017).

Together, these findings indicate that management decisions influencing total nitrogen availability have substantially greater impacts on crop performance than decisions regarding fertilizer source (**I**, **II**). While fertilizer type and application strategy may influence productivity or disease severity under particular conditions, their effects were generally smaller and less consistent than those associated with nitrogen addition rate (**I**, **II**).

From a practical perspective, these findings suggest that achieving an appropriate nitrogen supply should be prioritized when developing nutrient-management strategies for oilseed hemp. Optimization of fertilizer source and application timing may provide additional benefits in specific situations, but the overall productivity and health of the crop appear to depend primarily on adequate nitrogen availability (**I**, **II**). This conclusion is further supported by the observation that both disease severity and seed yield responded much more strongly to nitrogen addition rate than to fertilizer form across the six-year study period.

6.6. European corn borer as an emerging threat to hemp production (III)

The emergence of the European corn borer (*O. nubilalis*) represents one of the most important findings of the present thesis from the perspective of future hemp production in Northern Europe. Historically, hemp cultivation in the region has been characterized by relatively low pest pressure and previously insecticide applications have been very rare. Consequently, the rapid increase in European corn borer infestation observed during the study period (**III**) suggests that the biological challenges facing hemp production systems may be changing. The detection, establishment and increasing abundance of *O. nubilalis* in hemp fields (**III**) indicate that this species has the potential to become an economically important pest of oilseed hemp under northern temperate conditions.

The observed increase in infestation between 2021 and 2022 (**III**) is consistent with broader reports describing the increasing occurrence of *O. nubilalis* in European production systems (Bažok et al., 2020; Zhukovskaya & Frolov, 2022). Changing climatic conditions and increasing host availability are frequently cited as factors facilitating the establishment of insect pests outside their historical distribution ranges (Trnka et al., 2007; Kocmánková et al., 2011). The rapid increase in infestation observed in the present study suggests that hemp can serve as a suitable host for *O. nubilalis* under Northern Baltic conditions (**III**) and that local pest populations are capable of completing their life cycle successfully in this environment.

The symptoms observed in the present study were typical of European corn borer infestation and included stem boring, larval galleries, stem breakage, wilting and premature senescence (Parisi & Ranalli, 2000). Such damage directly reduces plant integrity and may interfere with the transport of water and assimilates within the stem. In seed-producing crops, damage to reproductive structures and reductions in canopy function can ultimately translate into yield losses, also through harvesting problems caused by uneven crop stands. The results demonstrated that infestation levels increased continuously throughout the growing season and that measurable reductions in both seed and biomass yield occurred under field conditions (**III**).

Although the magnitude of yield losses was lower than that commonly reported for maize (Tiwari et al., 2009; Bažok et al., 2020), the results nevertheless demonstrate that *O. nubilalis* is capable of causing economically relevant damage in oilseed hemp. Maximum seed yield losses exceeded 7% of total yield (**III**), and the average losses increased markedly between years (**III**). The current yield losses should not necessarily be interpreted as the upper limit of potential damage under northern conditions. Highly variable climatic conditions, increasing host availability and further adaptation of local populations may increase infestation pressure in the future. In particular, the establishment of additional generations per growing season could substantially increase crop damage and economic losses (Trnka et al., 2007; Kocmánková et al., 2011).

An interesting observation was that nitrogen fertilization increased crop productivity but had relatively limited effects on pest abundance (**III**). This contrasts with the strong influence of nitrogen availability on disease development observed for Alternaria leaf spot. While fertilization reduced disease severity and increased yield simultaneously, it did not substantially suppress European corn borer infestation (**III**). This suggests that the mechanisms regulating pest abundance differ fundamentally from those governing disease development and that nutrient management alone is unlikely to provide effective control of insect damage. Nevertheless, fertilized crops generally experienced lower relative yield losses (**III**), indicating that improved plant vigour may partially compensate for pest damage (Small et al., 2007).

The absence of significant relationships between infestation levels and plant morphological characteristics (**III**) further suggests that pest abundance was driven primarily by population dynamics rather than by crop architecture or density. Neither crop density, plant height, stem diameter nor the number of female plants explained variation in infestation levels (**III**). This finding differs somewhat from predictions based on the resource concentration hypothesis and indicates that factors operating at larger spatial scales, such as landscape composition, regional population dynamics and climatic conditions, may be more important determinants of infestation risk (Root, 1973).

The emergence of *O. nubilalis* in hemp fields also has implications beyond direct yield losses. Stem damage may increase lodging risk, complicate harvesting operations and potentially facilitate secondary infections by opportunistic pathogens. Consequently, the agronomic importance of European corn borer may extend beyond the direct reductions in biomass and seed production quantified in the present study (**III**). Future research should therefore examine the interactions between insect damage, crop physiology and pathogen development within integrated hemp production systems.

Overall, the findings indicate that European corn borer should be regarded as an emerging pest of hemp under Northern European conditions. The rapid increase in infestation pressure, confirmed ability to cause measurable yield losses and apparent adaptation to local environmental conditions (**III**) all suggest that continued monitoring and the development of appropriate management strategies will become increasingly important as hemp cultivation expands in the region.

Hypothesis assessment

H1. Fertilizer management, including nitrogen addition rate, fertilizer form and application strategy, influences disease development.
Partially supported. Nitrogen availability strongly influenced disease severity, and fertilizer application timing affected disease development, although fertilizer type had comparatively limited effects (**I, II**).

H2. Oilseed hemp cultivars differ in agronomic performance and yield stability under northern growing conditions.
Partially supported. Differences in productivity and yield stability were observed between experimental periods, but the non-concurrent evaluation of cultivars does not allow to contribute these differences to genotype alone (**I, II**).

H3. Increased nitrogen availability improves growth and seed yield of oilseed hemp under northern growing conditions.
Supported. Nitrogen fertilization consistently increased seed yield and biomass production across years and experimental systems (**I, II**).

H4. Fertilizer management, including fertilizer form and application strategy, influences hemp productivity.
Partially supported. Fertilizer source and application strategy influenced productivity under specific experimental conditions, but these effects were not consistently maintained in the six-year synthesis analysis (**I, II**).

H5. European corn borer (*O. nubilalis*) occurs in hemp cultivation under northern European conditions and affects crop productivity.
Supported. The pest was confirmed in hemp fields, increased in abundance during the study period and caused measurable reductions in crop productivity (**III**).

7. CONCLUSIONS

The present thesis investigated the effects of agronomic management, disease development and emerging pest pressures on oilseed hemp productivity under Northern European growing conditions. The results demonstrated that nitrogen availability was a key determinant of both crop productivity and disease development, whereas environmental variability strongly influenced disease severity, yield stability and pest occurrence. The main conclusions are summarized below.

1. Alternaria leaf spot (*Alternaria* spp.) was consistently present throughout the six-year study period in two different hemp cultivars, confirming that the disease has become an established component of oilseed hemp production systems under Northern Baltic conditions (**I, II**). Disease severity varied substantially among years and was strongly influenced by environmental conditions, particularly temperature and precipitation patterns (**I, II**).

2. Nitrogen availability was one of the strongest determinants of Alternaria leaf spot infection severity. Increasing nitrogen application rates consistently reduced disease development across years and cultivars, demonstrating that nutrient availability can substantially influence disease expression in hemp (**I, II**).

3. Nitrogen fertilization significantly increased seed yield and was a stronger factor of productivity than moderate levels of Alternaria leaf spot infection. Although disease severity was negatively associated with yield under specific conditions, nitrogen availability showed a consistently greater influence on yield formation across production systems (**I, II**).

4. Fertilizer source and application strategy had comparatively smaller effects than nitrogen addition rate (**I, II**). While individual experiments occasionally indicated advantages of specific fertilizer types, these effects were not maintained in the integrated six-year analysis, suggesting that achieving adequate nitrogen availability is more important than fertilizer form (**I, II**).

5. Significant interannual variation in seed yield was observed. The 2022–2024 experimental period (cultivar 'Estica') exhibited lower yield variability (**II**) than the 2019–2021 period (cultivar 'Finola') (**I**), indicating differences in yield stability among the experimental systems. However, the non-concurrent evaluation of cultivars does not allow definitive conclusions regarding the variation in yield stability among the cultivars (**I, II**).

6. Seed quality traits were generally less responsive to nitrogen availability than seed yield. Nitrogen application increased thousand-seed mass but had limited influence

on seed oil content, indicating that nutrient management primarily affected productivity rather than seed composition (**I, II**).

7. European corn borer (*O. nubilalis*) was confirmed as an emerging pest of hemp under Northern European conditions. Infestation levels increased rapidly during the study period and caused measurable reductions in seed and biomass yield, demonstrating the potential economic importance of this species for future hemp production (**III**).

8. Sustainable hemp production under northern conditions depends on the integration of adapted cultivars, balanced nutrient management and continued monitoring of emerging pests and diseases (**I, II, III**). Among the investigated management factors, nitrogen availability exerted the strongest and most consistent influence on both crop productivity and crop health.

Future research directions

The results of this thesis indicate that future research should extend beyond agronomic optimization and address the biological mechanisms underlying hemp adaptation and productivity. As a relatively recently reintroduced crop that retains many characteristics of its wild ancestry, hemp provides an opportunity to improve our understanding of plant–microbiome interactions and their role in crop health. Greater knowledge of the hemp microbiome may help explain natural disease suppression, stress tolerance, and nutrient acquisition, while also providing insights into how intensive breeding and over-fertilization has altered beneficial plant–microbe relationships in major agricultural crops. Such knowledge may become increasingly important for the management of fungal pathogens in low-input production systems.

The continued expansion of hemp cultivation highlights the need for long-term monitoring of emerging pests and diseases. The occurrence of the European corn borer (*O. nubilalis*) in hemp suggests that increasing hemp and maize cultivation areas may promote pest adaptation between crops with similar structural characteristics. Likewise, pathogens capable of reducing photosynthetically active leaf area or deteriorating seed yield and quality may become increasingly important in the near future.

In addition, the high phenotypic plasticity of oilseed hemp warrants further investigation of plant architecture and yield formation under northern growing conditions. Multi-year field experiments together with within-canopy measurements of environmental conditions are needed to improve understanding of compensatory responses in branching, biomass allocation, and reproductive development, and to identify management and breeding strategies that enhance seed yield stability and harvest index under short growing season conditions.

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SUMMARY IN ESTONIAN

Õlikanepi stressitaluvus ja kasvatustehnoloogiad – nende mõju taimede produktiivsusele ja seemnete kvaliteedile

Harilik kanep (*Cannabis sativa* L.) on viimastel aastakümnetel kujunenud põllumajanduskultuuriks, mille külvipind on aasta-aastalt kasvanud, kuna kasvatamise vastu tuntakse järjest suuremat huvi nii toiduainetööstuses, biomaterjalide tootmises kui ka kestliku põllumajanduse kontekstis. Põhjamaistes kasvutingimustes on õlikanepi kasvatamise peamisteks väljakutseteks suur ilmastikuline varieeruvus, piiratud kasvuperioodi pikkus ning vähene teave haiguste, kahjurite ja kasvatustehnoloogiliste võtete mõjust saagikusele. Samal ajal on kanepit traditsiooniliselt peetud suhteliselt tolerantseks mullastikutingimuste suhtes ja vähese taimekaitsevajadusega ning säästliku põllumajanduse kontseptsiooni sobituvaks kultuuriks.

Doktoritöö eesmärgiks oli hinnata kasvatustehnoloogiliste võtete mõju õlikanepi saagikusele, seemnete kvaliteedile, haiguste arengule ja kahjurite esinemisele Põhja-Euroopa tingimustes. Uuring põhines aastatel 2019–2024 Eesti Maaülikooli katsepõldudel läbi viidud välikatsetel ning kolmel teaduspublikatsioonil. Töö keskendus lämmastikväetamise, väetise vormi, väetamise ajastuse ja külvisenormi mõjule ning uuris kuivlaiksuse (*Alternaria* spp.) ja hariliku varreleediku (*Ostrinia nubilalis* Hübner) tähtsust kanepi tootmissüsteemides.

Katsetulemused näitasid, et kuivlaiksus esines õlikanepil kõigil uuritud aastatel, sortidel ning seda võib pidada piirkonna tingimustes väljakujunenud haiguseks. Haiguse tugevus sõltus oluliselt ilmastikutingimustest, kuid veelgi enam mõjutas seda lämmastiku kättesaadavus. Lämmastiku lisamine vähendas haiguse arengut järjepidevalt kõigil uuritud aastatel ning mõlema sordi puhul. Kuue aasta koondanalüüs näitas, et suhteline haiguskahjustus vähenes suurimate lämmastikunormide korral ligikaudu 76%, võrreldes väetamata kontrollvariandiga.

Tööst selgus, et lämmastikuga väetamine osutus üheks olulisemaks saagikust mõjutavaks teguriks. Seemnesaak suurenes lämmastikunormi kasvades märkimisväärselt ning see mõju oli tugevam kui mõõduka haiguskahjustuse negatiivne mõju saagikusele. Tulemused näitasid, et piisava toitainete varustatusega kanepitaimed suutsid haiguskahjustust paremini taluda. Väetise vormi ja väetamise ajastuse mõju oli oluliselt väiksem ning nende efektid ei olnud aastate lõikes järjepidevad.

Doktoritööst selgus, et seemnekvaliteedi näitajatest mõjutas lämmastik eelkõige tuhande seemne massi, samas kui seemnete õlisisaldus jäi erinevate väetustasemete

korral suhteliselt stabiilseks. See viitab sellele, et toitainete kättesaadavus mõjutab peamiselt saagikust ja vähem seemnete keemilist koostist.

Uuritud aastatel täheldati märkimisväärset aastate vahelist varieeruvust nii haiguste arengus kui ka seemnesaagikuses. Sordiga 'Estica' seotud katseperioodi (2022–2024) iseloomustas oluliselt väiksem seemnesaagikuse varieeruvus, võrreldes sordiga 'Finola' seotud perioodiga (2019–2021), mis võib viidata võimalikele erinevustele kohastumuses Põhja-Euroopa kasvutingimustega. Kuna sorte ei võrreldud samadel aastatel, ei võimalda tulemused siiski teha lõplikke järeldusi sortide paremusjärjestuse kohta.

Doktoritöö kinnitas hariliku varreleediku esinemist ja leviku suurenemist Eesti kanepipõldudel. Kahjur põhjustas seemne- ja biomassisaagikuse vähenemist ning selle arvukus suurenes uurimisperioodi jooksul kiiresti. Tulemused viitavad sellele, et varreleedikust võib tulevikus kujuneda oluline majanduslik kahjur ka põhjapoolsetes kanepikasvatuspiirkondades.

Kokkuvõttes näitas doktoritöö, et õlikanepi seemnesaaki ja haiguskindlust kujundas uuritud teguritest kõige järjekindlamalt lämmastiku kättesaadavus, samal ajal kui väetise vormi ja manustamisviisi mõju sõltus katseaastast ja kasvutingimustest. Alternaria lehelaiksuse korduv esinemine ning varreleediku arvukuse ja tekitatud saagikadude suurenemine osutavad, et biootiliste kahjustajate tähtsus võib Põhja-Euroopa kanepikasvatuses suureneda. Tulemused täpsustavad väetamise, ilmastiku, haiguste ja kahjurite omavahelisi seoseid ning loovad aluse piirkondlike kasvutingimustega arvestavate väetus- ja taimekaitsestrateegiate arendamiseks.

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I

ORIGINAL PUBLICATIONS

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How do the nitrogen level and form and crop density influence the progression of alternaria leaf spot disease on hemp crop in Northern Baltic region?

Erkki Mäeorg[a], Peeter Lääniste[a], Helina Nassar[a], Astrid Kännaste[a], Leho Tedersoo[b,c], Ülo Niinemets[a] and Eve Runno-Paurson[a]

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ABSTRACT

The cultivation of oilseed hemp (*Cannabis sativa*) has been growing in Northern Europe during the last decades, and so far, the crop has been relatively pest-free. Monitoring of *Alternaria*-like symptoms was started on the experimental field of hemp (cv 'Finola') in 2019. The aim of the research was to evaluate the resistance of hemp to Alternaria leaf spot and to assess the effect of hemp sowing rate (20–40 kg ha^{-1}), nitrogen application rate (0–150 kg ha^{-1}), fertilization method (at sowing; top dressing), and fertilizer type (complex fertilizer; ammonium nitrate) on the variation in disease progression within and among growing seasons. Across the years the maximum disease severity was 27.8 ± 4.2% (on average 12.7 ± 0.8% at the end of the growing season) with the lower degree of infection in the drier and warmer year 2021. There was a strong negative relationship with the nitrogen application rate throughout the study. The rAUDPC of the N150 treatment was on average 75% lower compared to the control. Furthermore, fertilization at the start of the growing season resulted in a higher disease occurrence throughout the study compared to the top dressing method. Higher sowing rates were related to higher disease values, but this effect was year-dependent. Although warmer and drier seasons might suppress *Alternaria* occurrence, the pathogen is progressively dispersing in the Northern climates. To avoid the increased need for pesticide use in the future, further monitoring, along with agronomic and microbiome studies is urgently needed to improve hemp cultivation in the Northern Baltic region.

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Introduction

Hemp (*Cannabis sativa* L.) cultivation in Northern Europe is still in its early stages, largely due to volatile economic and legal conditions. The development of new hemp-based products – particularly those derived from seed oil and biomass - has been the main driver of the recent expansion in cultivation area. From an agronomic perspective, hemp is an attractive choice for farmers: it serves as an excellent break crop for cereals, requires relatively low maintenance, and improves the soil physical conditions due to its extensive tap root system (Apazhev, 2005). Hemp seed oil is highly valued, mainly for its high content and good balance of omega-3, -6 and -9 fatty acids and several bioactive compounds (Callaway, 2004; Small & Marcus, 2003). Based on cultivation area, Estonia is one of the largest oilseed hemp production regions and hosts the highest capacity seed dehulling facility in Europe. Accordingly, research has been established to optimize the nutrient requirements to increase seed yield, oil and protein content under Estonian conditions (Runno-Paurson *et al*., 2019). As hemp has now been grown in Europe for several decades, its reputation as a relatively pest- and disease-free has begun to shift (Visković *et al*., 2024).

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Several emerging insect herbivores (Douglas *et al*., 2024; Runno-Paurson *et al*., 2024) and pathogens like *Fusarium* spp., *Septoria* spp., *Alternaria* spp., *Golovinomyces ambrosiae*, beet curly top virus, *Candidatus Phytoplasma trifolii* have caused significant damage to hemp crop in most cultivation areas worldwide (Schoener, 2019). The genus *Alternaria*, which includes over 300 species (Seifert *et al*., 2011) is a diverse group of fungi, mostly saprotrophic but some pathogenic species are known to be responsible for at least 20% of agricultural crop yield losses (Nowicki *et al*., 2012; Thomma, 2003). As a common foliage disease, Alternaria leaf spot (*Alternaria* spp.) infection is evident as small, dark-colored spots or lesions that may enlarge and turn brown or black, having a concentric ring pattern, as the disease progresses (Matic *et al*., 2020; Schmey *et al*., 2024). Typical pathogenic strategies of *Alternaria* within host plants include forcing immunosuppression through melanin synthesis and producing host-specific toxins (Thomma, 2003). Setting aside some variations, most *Alternaria* strains propagate via asexual spores called conidia, leaving little dark spots on the leaves in their path. These conidia are spores responsible for the reproduction of the fungus (DeMers, 2022). Sudden humidity swings can cause conidia to fall and be moved by air currents to nearby plants. Also, high humidity levels favor the infection (Balai & Ahir, 2013).

Evidence for morphological and phylogenetic variation within *Alternaria* includes the identification of a new species, *Alternaria cannabina*, and a monotypic lineage of *A. helianthiinficiens* on industrial hemp fields in Northwestern China in 2020. These species showed more aggressive pathogenicity on hemp leaves than previously described species (Cheng *et al*., 2022). In 2020, Tang *et al*. (2021) announced the first case of *A. alternata* causing leaf spot disease of industrial hemp in China.

Alternaria alternata was first reported as a pathogen of hemp in the 1970s, damaging stalks, flowers (McPartland & Cubeta, 1997), leaves (Jerushalmi *et al*., 2020), and seeds (Haney & Kutscheid, 1975; Jian *et al*., 2019). Furthermore, on numerous occasions, it has been identified from different parts of hemp plants as an endophyte (Gautam *et al*., 2013; Scott *et al*., 2018), together with other *Alternaria* spp. (Cormier *et al*., 2020; Hansen *et al*., 2020; Mersha *et al*., 2020; Wilhelm *et al*., 2018). While its pathogenicity has been suspected in some cases, it has not always been experimentally confirmed (Roberts & Punja, 2022). Besides yield loss, researchers (Jerushalmi *et al*., 2020) have also found several fungal toxins, alternariol, alternariol monomethyl ether, and others that cause human health problems. There are at least 12 host-specific toxin-producing plant pathogenic *Alternaria* species, most of which appear to be variants of *A. alternata* (Thomma, 2003).

In Northern Europe, hemp fields have generally been regarded as almost pest-free (Visković *et al*., 2024). As a result, chemical pesticides are rarely used, and many hemp growers benefit from certification as organic producers (European Commission, 2025). However, according to our earlier study (Runno-Paurson *et al*., 2024), the European corn borer (*Ostrinia nubilalis*), a pest usually related to southern areas, has been damaging hemp fields in Northern Europe during recent years. As hemp cultivation expands, increased pest pressure due to migration and host-switching could be expected. Even if regionally relevant pesticides become available in the future, a variety of agronomic practices, such as cultivar selection, crop rotation, sowing density, and fertilizer management, should always be favored. In this context, sowing rate, crop density, fertilizer application rates, and timing are among the most relevant areas of research. Also, there is a lack of scientific data on the integrated pest management options for hemp in Northern Europe.

Establishing a field experiment with oilseed hemp was based on the strong incentive from the farmers and raw material processing industry, as well as the lack of agronomic trials in Europe (Lääniste *et al*., 2020). With the cultivation area predicted to increase in the near future, the need for finding optimal sowing time, sowing rate, and nutrition requirements for oilseed hemp production in the Northern Baltic region arose (Runno-Paurson *et al*., 2019). Another key aim of these trials was to identify relevant diseases in oilseed hemp fields and to predict their behavior and damage in changing climatic conditions. Considering the above, the symptoms of *Alternaria* damage were first noticed on the experimental field of oil-type hemp in 2019 and have since been included in our regular disease monitoring program (Runno-Paurson *et al*., 2020).

More specifically, the aim of the present research was to evaluate the resistance of hemp cultivar 'Finola' plants to leaf spot-causing *Alternaria* species and to assess the effect of sowing rate, nitrogen

application rate, and fertilization method on the yearly and in-season dynamics of disease progression. The study is a part of long-term disease monitoring of hemp crops in the region.

Materials and methods

Experimental site and study design

Alternaria leaf spot damage of industrial hemp (*Cannabis sativa* L. cv. 'Finola') crop plants was evaluated during 2019–2021 in an experimental field of the Estonian University of Life Sciences, Tartu County, Estonia (58° 21′ N, 26° 40′ E). The soil type of the experimental area was a sandy loam Stagnic Luvisol (World Reference Base, 2022) with a humus layer of 20–30 cm.

The plots of 10 m^2 (3 replicates each) were sown on 22nd of April in 2019, 21st of April in 2020, and 30th of April in 2021. The field experiment included altogether 18 treatments: sowing rates (3 treatments: 20, 30, and 40 kg ha^{-1}), fertilizer types (complex fertilizer 17-4.6–10 S-Mg-B and ammonium nitrate, with 33.4% nitrogen content), fertilization application methods (fertilization at sowing and top dressing), and nitrogen addition rates (Table 1).

Each timing × N-rate combination was tested with both fertilizer types. In the control treatment no fertilizers were used.

All sowing rate treatments were fertilized with 100 kg N ha^{-1}. Systematic experimental design with fertilizer gradient within strips was used. At the end of the growing seasons, the final observation dates coincided with the maturity of the seeds and the harvest times. A customized combine harvester was used. Right before the harvest, samples (plants from 0.25 m^2 in each plot) were taken for determining the total above-ground biomass yield, number of female plants, and seed yield.

Weather data

Air temperature and daily precipitation were measured in the Eerika weather station of the Institute of Agricultural and Environmental Sciences of the Estonian University of Life Sciences (Figure 1; FieldClimate, 2024). The weather conditions in 2019 and 2020 growing seasons were similar to the long-term average, but in 2021, in June and July, the daily average air temperatures were significantly higher than in the other two growing seasons and, combined with extremely low precipitation, led to moderately severe drought conditions. The accumulated temperatures (growing degree days (GDD); base temperature of 5 °C) from the date of sowing to the last monitoring were as follows: 1081 GDD in 2019, 1269 GDD in 2020, and 1609 GDD in 2021.

Table 1. Matrix layout of fertilizers, timing of application, and nitrogen rates.

Timing of fertilization	Fertilizer	*N* rates (kg ha^{-1})
At sowing	AS/Complex	20/40/60/80
Top dressing	AS/Complex	50/100/150

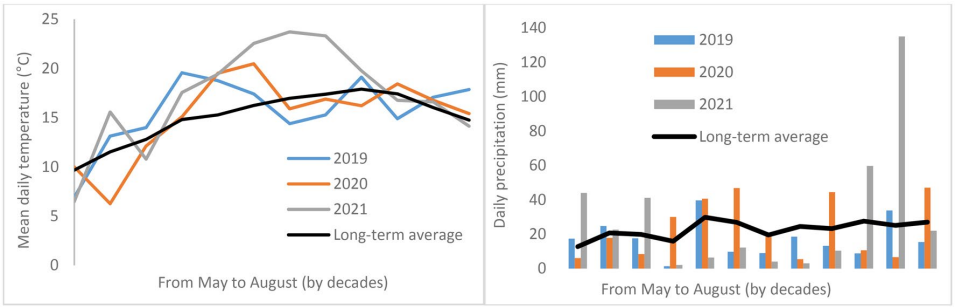

Figure 1. Average air temperature (*left*) and precipitation (*right*) in the Eerika (Central Estonia) hemp test site during 2019–2021, in comparison with long-term (1964–2022) average recordings.

Assessment of Alternaria leaf spot disease

The monitoring of the development of Alternaria leaf spot disease was started during the growing period in 2019 and continued with weekly intervals from the onset of visible symptoms on the crop until harvest for the following two years. Only Alternaria leaf spot disease (*Alternaria* spp.) occurred in each year during our study; gray mold (*Botrytis cinerea*) symptoms were noticed only on a few plants in 2021, but gray mold-dependent damage was minor and was not quantified.

The damage of *Alternaria* was assessed under natural infection conditions as a percentage of total foliage based on the evaluation scale (0–100%) on female plants. In all variants in each of the replications, 10 randomly selected plants per plot were assessed for infection. The evaluations were performed weekly since the damage became visible in the field until the harvest (5 assessments in 2019, 10 assessments in 2020, and 12 assessments in 2021).

The data on disease severity (% of the infected leaf area) were compiled based on the evaluation scale values. The area under the disease progress curve (AUDPC) was calculated according to the formula (Shaner & Finney, 1976):

$$\mathrm{AUDPC} = \sum_{i=1}^{n-1} \frac{y_i + y_{i+1}}{2} \times \left(t_{i+1} - t_i\right) \tag{1}$$

where n is the total number of observations, y_1 is the disease severity at the i-th observation, and t is the time (date) of the i-th observation. As the absolute AUDPC values cannot be used to compare different seasons, a standardized measure, relative AUDPC (*r*AUDPC), was calculated as follows:

$$r\mathrm{AUDPC} = \frac{\mathrm{AUDPC}}{t_{i-1}} \times 100 \tag{2}$$

where t_{i-1} is the time in days between the first and the last evaluation

Molecular identification of the fungal species

For confirmation and molecular identification of the fungal species, genomic DNA was extracted from 13 leaf and 7 mycelia samples grown on potato dextrose agar cultured Petri dishes. DNA barcoding was used to select the ITS primers, and PCR amplification and further sequencing (MinIon, Oxford Nanopore) were performed in the Institute of Ecology and Earth Sciences (University of Tartu). The sequencing results were analyzed, and the National Center for Biotechnology Information (NCBI) GenBank database (BLASTn) was used to confirm species identity using only sequence identity values above 99%. Infection by *Alternaria* spp. was confirmed.

Data analysis

The effect of nitrogen application rates on the disease severity and rAUDPC values was assessed by one-way ANOVA followed by the Tukey *post-hoc* test. The effect of fertilizer type (complex vs. ammonium nitrate) and application method (at sowing vs. top dressing) on the disease severity and rAUDPC values was assessed by one-way ANOVA followed by the Tukey *post-hoc* test. The effect of sowing rates on disease severity was assessed by one-way ANOVA (Tukey *post-hoc* test). Normality of residuals was assessed by Q–Q plots, and no substantial deviations were seen. Homogeneity of variances was evaluated using Levene's test. A linear model was used in all cases. Pearson correlation analysis was used to examine the relationships between the levels of N fertilization, disease parameters, the yield of seed and biomass of hemp, and seed quality parameters.

Results

The hemp crop is considered relatively disease-free in Northern European fields, but in our study it showed a substantial decrease in photosynthetic leaf area due to Alternaria leaf spot disease during 2019–2021 (Figure 2).

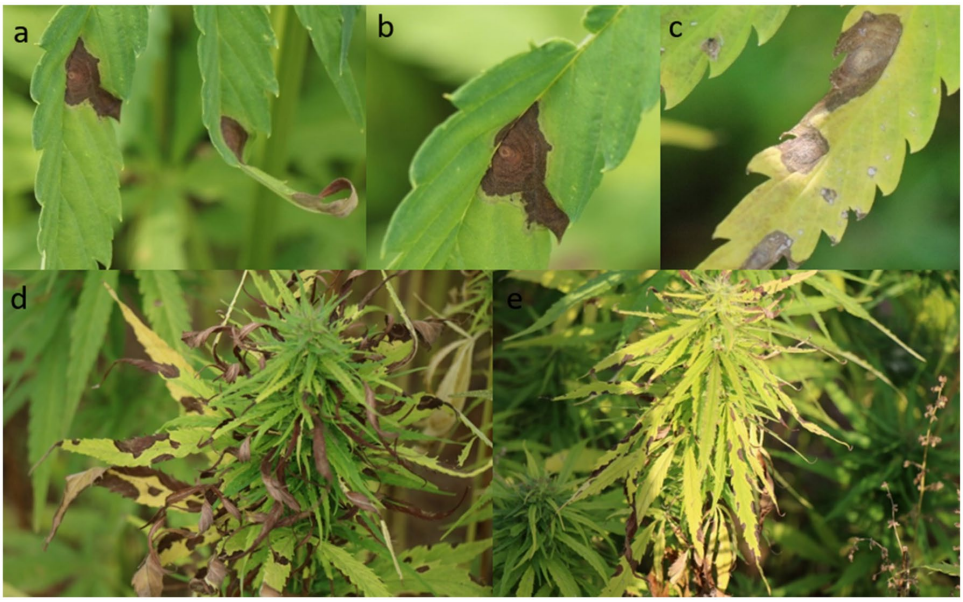

Figure 2. Typical Alternaria leaf spot (*Alternaria* spp.) infection on diseased hemp leaves (a-c) and plants (d, e).

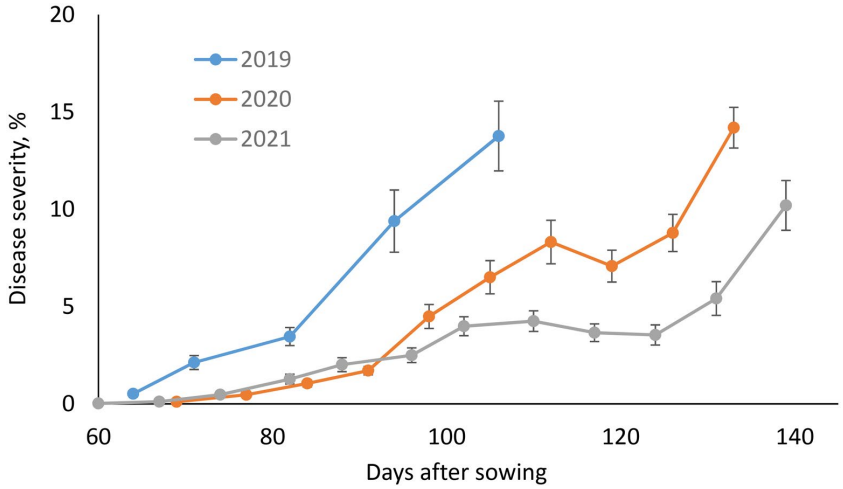

Figure 3. The average (± SE) disease severity progression of Alternaria leaf spot on hemp plants during 2019–2021. The averages are calculated across treatments. Each year $n = 54$.

In the growing seasons studied, the disease severity of Alternaria leaf spot on seed-producing plants of hemp cultivar 'Finola' was up to 37% in individual assessments, with average (± SE) maximum damage across the treatments of 27.8 ± 4.2% in 2019 (Figure 3).

In 2019, the sharp increase in infection progression began on the earliest date (80 DAS). In 2021, the potentially active period for *Alternaria* spread (July to August) was characterized by very low precipitation and unusually high temperatures. The accumulated temperatures had reached close to 1500 GDD already before the spread of Alternaria leaf spot disease started to increase at the end of August, whereas in the two previous seasons, a sharp infection increase occurred much earlier, between the first and second decades of July.

The effect of nitrogen application rates on biomass yield and disease severity

The hemp biomass yield was positively correlated with the amount of nitrogen applied ($r = 0.54$, $p < 0.01$), and the seed yield, in turn, showed a strong relationship with biomass yield ($r = 0.70$ for 2019, $r = 0.73$ for 2020, and $r = 0.81$ for 2021, $p < 0.01$ for all; see Supplementary Table S4). The impact of nutrient availability on the hemp crop was evaluated by rAUDPC values of various treatments of nutrient application across 3 years (Figure 4). The cumulative disease index rAUDPC, calculated for Alternaria leaf spot disease on hemp crop, decreased with increasing nitrogen application rate ($F_{(7,127)} = 15.214$, $p < 0.001$). The rAUDPC of the control treatment (without fertilizer addition) was the highest in each of the experimental years (Supplementary materials, Fig. S1). In 2019, average (±SE) rAUDPC values ranged from 0.120 ± 0.006 (control) to 0.029 ± 0.005 (N150). In 2020, the respective values were 0.089 ± 0.001 and 0.029 ± 0.003, and in 2021, the rAUDPC of the control treatment was 0.044 ± 0.001, and that of N150 was 0.009 ± 0.000.

An N application rate of 50 kg ha^{-1} showed the highest variability in disease severity throughout the three years.

The effect of sowing rate on the severity of Alternaria leaf spot disease

In our study, three sowing rates (20, 30, and 40 kg ha^{-1}) were used, and in all these treatments, the fertilization rate was 100 kg N ha^{-1}. The sowing rates used resulted in somewhat varying crop densities in different years (Table 2).

Here we report the impact of sowing rates on AUDPC values and rAUDPC values, which are provided in Tables S1, S2, and S3 (Supplementary materials). In 2019, with relatively high overall disease pressure on the field, the treatments with higher sowing rates also showed greater disease severity. At the last observation (106 DAS), the disease severity of the most dense hemp population (40 kg seeds ha^{-1}) was ca. 50% higher ($p < 0.05$), compared to the plots with considerably lower crop density and sowing rate of 30 and 20 kg ha^{-1} (Figure 5a).

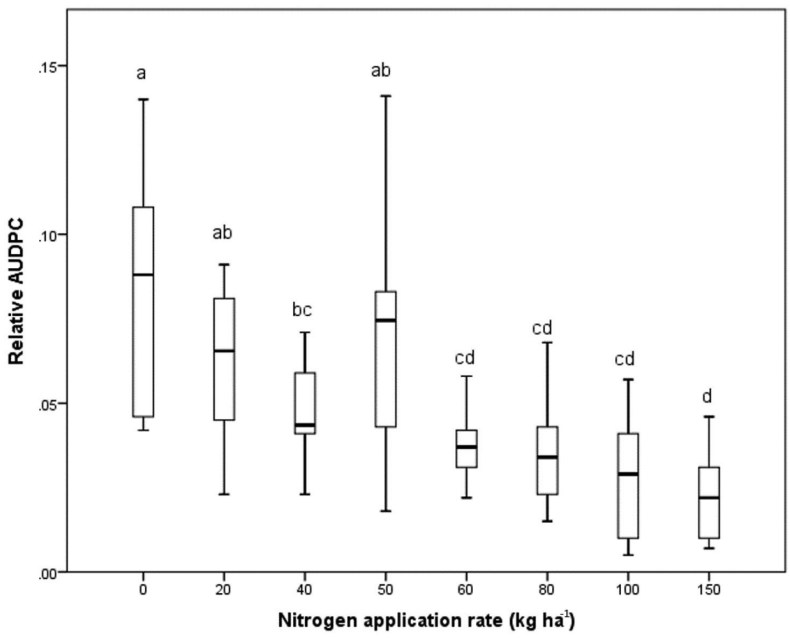

Figure 4. The effect of the nitrogen application rate on the rAUDPC values. Different letters indicate statistically significant differences between treatments ($p < 0.001$). The central line represents the median, boxes indicate the interquartile range (25th–75th percentiles), and whiskers extend to 1.5× the interquartile range.

Table 2. The average crop densities (plants per m^2) with standard error in sowing rate treatments during 2019–2021 (each case $n = 3$).

Year / treatment	2019	2020	2021
20 kg ha^{-1}	50.7 ± 2.7	40.0 ± 0.0	48.7 ± 0.0
30 kg ha^{-1}	64.0 ± 0.0	50.7 ± 2.7	74.7 ± 2.7
40 kg ha^{-1}	98.7 ± 2.7	66.7 ± 2.7	98.7 ± 2.7

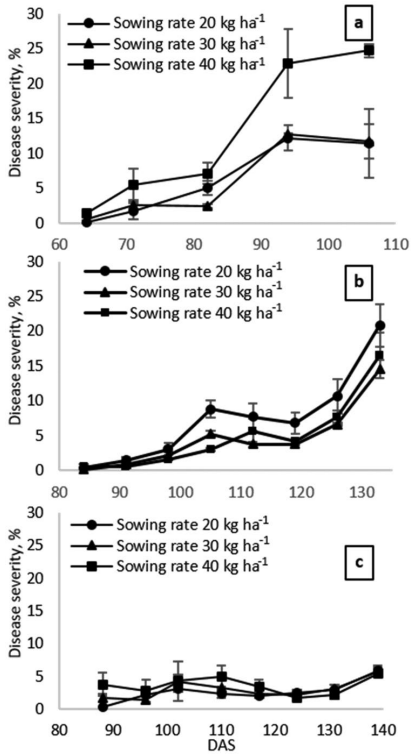

Figure 5. Time-dependent changes in disease severity of Alternaria leaf spot disease on hemp for different sowing rates during 2019 (a), 2020 (b) and 2021 (c). Standard errors of values are indicated for each observation date ($n = 3$). The values on the horizontal axis are given in days after sowing (DAS).

In 2020, due to the later onset of disease increase on the experimental field, the disease severity values did not result in significant differences ($p > 0.05$) at the end of the growing season (133 DAS), ranging from 14.5 ± 1.3% and 20.8 ± 3.0%.

In 2021, characterized by higher average temperatures and an almost two-month dry period (Figure 1), overall disease severity was low, and differences ($p > 0.05$) between sowing rates were not significant. Disease severity at the harvest time of sowing rate treatments varied between 5.4 ± 0.4% and 5.9 ± 0.6%.

The effect of fertilization method and fertilizer type on the disease severity and yield

Two fertilizer application methods were compared: application at sowing and top dressing. Across years, the above-ground biomass (1960 ± 120 g m^{-2}) as well as the seed yield (141 ± 7 g m^{-2}) of the hemp crop were significantly ($p < 0.001$) higher with top dressing method compared to fertilizer application at

sowing (1071 ± 96 g m^{-2} for biomass and 88 ± 5 g m^{-2} for seed yield). In contrast, the application of fertilizer at sowing resulted in significantly higher disease severity than with the top dressing method across the years ($F_{(1,133)}$=11.317, $p < 0.001$). The respective average (±SE) AUDPC values were 306.0 ± 15.6 for fertilizer application at sowing and 220.0 ± 20.7 for top dressing method. In 2019, the effect of fertilization application was not apparent, and the AUDPC and rAUDPC values were not significantly different between the fertilizer application methods ($p > 0.05$ for both). In 2020, the pathogen occurrence varied a lot between the plots, and the respective calculated average AUDPC values (355.0 ± 27.2 and 296.2 ± 36.6) were not statistically different. In 2021, with overall lower infection in the experimental field, the plots with springtime fertilizer application had again significantly ($p < 0.001$) higher AUDPC values (331.7 ± 20.0), compared to the top dressing method (129.1 ± 23.8).

Ammonium nitrate and complex fertilizer (NPK-S-Mg-B) were the two forms of nutrient mixtures applied. Only in 2019 the disease severity was significantly higher with complex fertilizer (AUDPC = 288 ± 32; n =) than with ammonium nitrate (169 ± 22; $p < 0.05$). Across three years, no consistent effect of fertilizer type on the disease progression was observed.

Discussion

After noticing Alternaria leaf spot disease in our oilseed hemp test site in 2018, we began systematic monitoring and incorporated it into our experiments in 2019. Throughout the study period, *Alternaria* spp. appeared as the main damaging fungal pathogen. Although weather conditions fluctuated considerably over the three-year experiment, the studied pathogen damage was relevant in each year. In 2021, with an unusually long period of high temperatures and minimal rainfall during July and August, disease spread persisted, hindering the fast vegetative growth of the crop, which resulted in overall low pathogen pressure that year.

An Important indicator of a fungal pathogen—increasing its environmental adaptability in the region and hence, its potential damage to agricultural crops in the near future—is the diversification of its reproduction patterns. With more diverse climatic conditions, i.e. lengthening of the growing seasons with highly variable precipitation, overall milder winters with fluctuating snow and frost situation, etc., *Alternaria* strains (pathotypes) capable of sexual reproduction have been identified in Europe, and their occurrence is expected to trend further north (Estiarte *et al*., 2016; Odilbekov *et al*., 2016). Besides asexual reproduction with conidia, the new pathogenic strains are characterized by much larger genetic diversity and resistance to fungicides.

Although a statistically relevant effect of Alternaria leaf spot disease on the seed yield was not found in this study and large variations in seed yield could be related to other interfering factors, the significant loss of photosynthetically active leaf area and overall biomass is alarming. Oilseed hemp is a relatively new crop in Northern Europe and has not undergone long-term breeding efforts to optimize its seed yield and hence has high plasticity in its branching ability and biomass formation. Hemp holds a lot of potential in increasing its seed yield and yield stability for farmers in Northern Europe, but as the prevalence of genetically diverse fungal pathogens increases, the potential yield gains would remain low. Moreover, the successful hemp cultivation in the region would have to rely more on pesticides, further degrading its value as an organic raw material and a sustainable option for crop rotations. Therefore, agronomic practices should be optimized to enhance the resistance of hemp crops to potential pathogens.

The effect of nitrogen fertilization rate on the Alternaria leaf spot

The results of our 3-year experiment indicate a clear negative relationship between rate of applied nitrogen and severity of Alternaria leaf spot disease. The same effect was apparent in each year, regardless of highly variable weather conditions during each growing season. It should also be pointed out that the rAUDPC value does not take into account the dynamics of disease progression during a season and is rather an accumulative parameter of the disease, although it accounts for growing seasons with varying lengths.

From the perspective of fungal disease infection, the general view among many agronomists has been that more available nutrients for a crop would result in healthier plants that could better withstand various diseases (Tripathi *et al*., 2022). Further research (Bolton & Thomma, 2008; Lekberg *et al*., 2021; Mur *et al*., 2017; Veresoglou *et al*., 2013) has shown that the amount of nutrients available for a crop could have a variable effect on the infection and damage of a fungal pathogen. There are many reports that postulate the higher nitrogen rates increase the disease severity of several common crop diseases like stem rot, leaf rust, powdery mildew, etc., while contrary results have been reported for diseases such as gray mold and leaf spot (Tripathi *et al*., 2022). The reasoning has been that, although higher input of N fertilizers improves plant defense capability, it also increases tissue growth suitable as a food source for pathogens and increases the amino acid concentration in apoplast, as well as overall larger crop canopy, which favors the growth of pathogenic spores (Solomon *et al*., 2003; Tavernier *et al*., 2007).

In a meta-analysis by Veresoglou *et al*. (2013), investigating the effect of fertilization on the fungal pathogen-related disease severity, it was found that in the vast majority of cases, the N fertilization increased disease severity. Also, the supposedly species-related negative effect of nitrogen on the disease severity should be taken into further investigation, as was the case for *Solanum* spp. Hemp crop has not been included in these studies, but according to our findings, it shows potential for making use of additional nitrogen abundance in its defense mechanisms.

Furthermore, when dealing with pathogenic microorganisms, one must soon acknowledge the importance of complex relationships with other microorganisms within the plant endophytic community and soil. Lekberg *et al*. (2021) studied the nutrient and fungal (including pathogens) relationships in 25 grasslands across 4 continents and found that fertilization promotes the relative abundance of fungal pathogens, suppresses mutualists, and also reduces the co-occurrences among fungal groups. There are many studies indicating the negative effects of excessive long-term fertilization on the benefits of having a diverse self-balancing crop and soil microbiome, including various known symbiotic relationships like arbuscular mycorrhiza (Bai *et al*., 2022; Paungfoo-Lonhienne *et al*., 2015; Ryan & Graham, 2002; Wang *et al*., 2018; Zhao *et al*., 2019). Moreover, as plant disease resistance is heavily dependent on its ability to synthesize a diversified set of secondary metabolites, these, in turn, are often mediated through endophytic organisms (Pang *et al*., 2021). Core fungal root microbiome communities related to cannabinoid biosynthesis in hemp crops, also found in the phyllosphere, enable hemp plants also to produce several other secondary metabolites related to improving plant health and growth (Ahmad *et al*., 2024; Dumigan & Deyholos, 2022). Besides the usual plant protection perspectives, questions should arise why microorganisms otherwise neutral or even beneficial turn into pathogens.

Accordingly, further comprehensive knowledge on microbiome interactions is needed in order to make better conclusions on the nutrient levels suitable for a crop for establishing more sustainable cropping systems in the future. The hemp crop besides being an object of cultivation, could also prove to be a valuable source of information and material for microbial diversity. So far the yield improvement has been the main target, and the use of pesticides has been increasing with yields. Hence, to further improve our understanding of the Alternaria leaf spot disease on oilseed hemp, the details of seasonal nutrient availability and form are also of significant value.

The effect of nitrogen form and timing of application on Alternaria leaf spot disease

Concerning the disease susceptibility, the availability of different N forms (NH_4^+ and NO_3^-) has shown contradictive effects on plant disease resistance using the assimilatory and metabolic pathways (Bolton & Thomma, 2008). The available nutrients (mainly in nitrogen form) help the crop to thrive but at the same time are a source of food for spreading pathogen. Studies performed with the fungal model organisms *Saccharomyces cerevisiae*, *Aspergillus nidulans*, and *Neurospora crassa* have shown that nitrogen sources such as ammonium, glutamine, and glutamate are preferred, but secondary sources such as nitrate, amino acids, and proteins can be utilized when these primary sources are not available (Bolton & Thomma, 2008). Furthermore, according to the study by Mur *et al*. (2017), through NO-pathway NO_3^- increases the synthesis of polyamines (spermine, spermidine), which are known defense signals in plants. Contrarily, the abundance of NH_4^+ results in decreased levels of

defense-related polyamines, lower content of nitric oxide (NO), increased levels of apoplastic sugars, amino acids, and γ-aminobutyric acid (GABA), which are all preferred nutrient sources for pathogenic fungi (Tiburcio *et al*., 2014).

Concerning the form of nutrients applied within our experiments, these two different strategies were tested. Understandably, the complex fertilizers should provide a more complete set of nutrients for the crop, but on the other hand, ammonium nitrate targets the crops ability to take advantage of the more diverse nitrogen sources, while in the case of slow-release ammonium, crops rely more on soil microbes. According to our study, significant differences were seen only in one season, showing higher leaf spot disease severity for nitrate-only treatments, contrary to what has been reported in the literature about the defense-related signaling and metabolism in case of fungal pathogens.

Common understanding and practice (according to the suggestions from the hemp breeders) with the oil-type Nordic hemp cultivar 'Finola' has been that at sowing no (or very few) nutrients should be applied, as they could accumulate in amounts that could be toxic for young seedlings. Hence, the rates in our experiment were chosen quite low for application at sowing. But as later experiments (Lääniste *et al*., 2020) have shown, from the seed yield perspective, the oil-type hemp crop benefits also from higher amounts of nutrients at the start of the growing season. We also acknowledge that conclusions based only on 'Finola' might not apply to a few other oil-type hemp cultivars used in northern regions, as hemp crops with relatively short breeding history could have large variations in biomass and harvest indexes compared to common grain species.

At the same time, with the addition of nutrients at the start of the growing period, higher vegetative mass is expected to form earlier during the season. This, in turn, provides more suitable starting conditions for potential fungal pathogens, which was also seen as higher disease severity and AUDPC values in each year within our experiment. Only in 2020, when disease severity had large variations between treatments, were the resulting seed yield values slightly higher in plots with later application of nutrients. Hence, overall higher nitrogen rates (up to 150 kg N ha^{-1}) could be justified and recommended from the seed yield perspective, but the springtime application rate should be kept low to avoid the early high biomass formation for pathogen development.

Pathogen damage related to crop density

Compared to cereal crops, the oilseed hemp does not allow for high sowing rates, as its branching ability and relatively horizontal leaf positioning are necessary for optimal light harvesting and seed yield formation. Also, due to the high seed prices, the farmers usually rely on smaller sowing rates and the crop's branching ability to further increase the seed yield. However, in order to target the uniform maturity and reduce any weed pressure, sometimes higher sowing rates have also been applied (Campiglia *et al*., 2017; Varga *et al*., 2025; Visković *et al*., 2024).

In our experiment, each year the highest biomass yield was recorded in the treatments with the highest sowing rate. Although, in 2019, accompanied also by the highest average seed yield, a significant positive effect of higher crop density (sowing rate of 40 kg ha^{-1}) on the disease severity was observed, the correlations were not found during the next two years. In 2021, the disease severity also increased with sowing rates and respective biomass yields, but due to the overall low disease pressure during that year, the effects were not statistically significant. Varying weather conditions and in-season disease progression dynamics, as well as overall disease pressure in each year, did not result in statistically significant data in order to propose conclusions on the impact of sowing rate on the disease severity.

In general, denser crops should potentially favor the spread of fungal disease through increased humidity, reduced air-flow, and lower light penetration within canopy, as well as potential stress from lower levels of available resources and intraspecies competition (Termorshuizen, 2016).

As the highest sowing rate used in our experiment is not usually applied with oilseed hemp among growers due to the extremely high seed price and plasticity of hemp crop biomass formation, the study of fungal pathogen spread in dense hemp canopies would be potentially more valued when seed prices go down with the increasing growing areas in the future.

Conclusions

Alternaria leaf spot disease is a relevant threat to hemp producers in Northern Europe and should be monitored, especially with increasing cultivation areas. A strong negative relationship with nitrogen application rate throughout the study was found. Also, the application of nutrients at the start of the growing season resulted in higher disease severity throughout the study. Higher-than-conventional seeding rates of 40 kg ha^{-1} were generally related to higher disease severity, but the effect of crop density depended on the in-season weather conditions.

Further monitoring of new pathogenic species affecting hemp fields is necessary, as well as the study of their morphology and phylogenetics. Also, the metabolomic effects of the pathogenic and endophytic organisms on the crop yield and quality should be assessed. It is exceptionally urgent because large portion of oilseed hemp is still grown organically in the region. Positive results from targeted microbiome research together with suitable agronomic measures could benefit Northern hemp production and avoid the wide use of hemp-related pesticides in the future.

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Data availability statement

The datasets generated and/or analyzed during the current study are not publicly available but are available from the corresponding author on reasonable request.

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Nitrogen fertilization outweighs disease-associated variation in hemp seed yield under highly fluctuating northern temperate field conditions

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Abstract

Nitrogen (N) availability strongly influences seed yield formation in oilseed hemp (*Cannabis sativa* L.), yet its interaction with foliar disease development under northern temperate conditions remains poorly understood. The objective of the present research was to assess how nitrogen addition rate, nitrogen source, and interannual climatic variability interact to influence seed yield formation, *Alternaria* leaf spot disease progression, and disease–yield relationships in oilseed hemp cultivation under northern temperate conditions. A three-year field experiment evaluated the effects of N addition rate (0–200 kg N ha^{-1}) and fertilizer source (complex NPK vs ammonium nitrate) on *Alternaria* leaf spot disease severity and seed yield of the dioecious cultivar 'Estica', a recently registered oilseed hemp cultivar bred for northern temperate conditions. Increased N addition rate reduced AUDPC substantially (by 260–600 %-days depending on year), while seed yield increased

by 1.0–1.7 t ha^{-1} across the tested N range. Significant N × year interactions were detected for both disease severity and yield. Complex NPK fertilizer application resulted in greater yield compared with ammonium nitrate but did not affect disease development. Across all data, seed yield was negatively associated with disease severity, but in models including N addition rate and year, disease severity had no significant impact on yield once nitrogen effects were accounted for. Under northern temperate field conditions, the positive impact of nitrogen addition can outweigh moderate foliar disease effects, highlighting the importance of evaluating nutrient–disease interactions within multi-year agronomic contexts in hemp production systems.

Keywords: hemp, *Alternaria* leaf spot, dioecious, seed yield, nitrogen addition rate, ammonium nitrate

1. Introduction

Hemp (*Cannabis sativa* L.) is an emerging crop that is increasingly cultivated in Northern Europe due to the high value of seed oil such that it is profitable even with low seed yields compared to conventional oil crops (Amaducci et al., 2015; Finnan & Styles, 2013). Hemp also provides many benefits from an agronomic perspective – it is an excellent break crop for cereals, requires very low pesticide load and fertilizer inputs, and is a good option for weed suppression in crop rotations (Campiglia et al., 2017). Ecologically, hemp has high soil carbon sequestration capacity with moderate chemical inputs (Amaducci et al., 2015; Adesina et al., 2020).

In Europe, Estonia is one of the largest oilseed hemp producers (9201 ha, Statistics Estonia, 2026), corresponding to approximately one-quarter of the current hemp cultivation area in the European Union (about 40,000 ha based on recent cultivation trends; European Commission, 2026). However, average seed yields remain unstable, creating uncertainty for growers. Year-to-year differences in hemp seed yields are associated with variations in canopy leaf area index due to environmental impacts and considerable phenotypic plasticity. We have previously demonstrated the northward shift of European corn borer, leading to a major hemp canopy damage (Runno-Paurson et al., 2023). In addition, there is evidence of spread of emerging fungal pathogens that cause premature leaf senescence and decrease whole canopy leaf area (Mäeorg et al., 2026). Although several pests have been discovered recently in experimental as well as farmers' hemp fields in Estonia, hemp is still a viable option in crop rotations, also for organic production.

Alternaria leaf spot represents a relevant foliar constraint in crop production systems, particularly under humid temperate conditions (Hossain et al., 2024; Salotti et al., 2024; Matić et al., 2020). The disease development is strongly influenced by climatic conditions, particularly intra- and interannual variation in temperature and moisture, which regulate both host susceptibility and pathogen activity. (Choudhary and Senthil-Kumar, 2024; Hossain et al., 2024; Pandey and Senthil-Kumar, 2024). In annual crops, epidemics are typically polycyclic, and their progression is often summarized using integrative metrics such as the area under the disease progress curve (AUDPC), which captures both intensity and duration of infection (Madden et al., 2007). Because climatic drivers shape both host growth and pathogen activity, modest differences in seasonal humidity or temperature during flowering can shift epidemic timing and severity (Delgado-Baquerizo, 2020). Seasonal temperature variation can shift pathogen development relative to its thermal optimum, altering epidemic intensity between years. Consequently, management effects observed in one

season may not hold under contrasting weather conditions, emphasizing the need for multi-year trials.

Nitrogen availability is central in yield formation. Seed hemp production systems typically require higher N inputs than fiber hemp systems, with reported recommendations between 100 and 150 kg N ha^{-1} (Podder et al., 2024; Papastylianou et al., 2018; Aubin et al., 2015), although optimal rates depend strongly on environment and production system. Under temperate conditions in Québec, seed yield increased linearly up to 200 kg N ha^{-1} (Aubin et al., 2015). In Mediterranean environments, however, higher N application rates increased stem yield more than seed yield, suggesting environment-dependent biomass partitioning responses (Campiglia et al., 2017; Tang et al., 2017). Under northern temperate Baltic conditions, nitrogen fertilization (0-200 kg N ha^{-1}) has similarly been shown to significantly influence seed yield and quality, although optimal N application rates vary with year and cultivar (Adamovics et al., 2016; Lääniste et al., 2016). Excessive N fertilization can stimulate vegetative growth without proportional increases in seed production (Amaducci et al., 2015). As in other field crops, nitrogen responsiveness shows strong nitrogen × year interactions (Ciampitti & Vyn, 2012), reflecting climatic modulation of biomass accumulation and resource allocation.

Nitrogen application form can further influence plant performance. Plants possess distinct transport and signaling systems for nitrate and ammonium (Hachiya & Sakakibara, 2017; Kiba & Krapp, 2016). Nitrate acts not only as a nutrient but also as a systemic signal regulating gene expression, while combined nitrate and ammonium supply can enhance growth beyond single-source treatments (Britto & Kronzucker, 2002). Optimal ammonium–nitrate ratios vary among crop species and are influenced by soil pH, species-specific toxicity thresholds and nitrate/ammonium signaling interactions (Britto & Kronzucker, 2002; Chen et al., 2024; Hachiya & Sakakibara, 2017).

However, high ammonium concentrations may impair growth (Guo et al., 2007), and soil pH strongly affects ammonium–nitrate preference (Chen et al., 2024). For hemp, specific optimal ammonium–nitrate ratios have not been reported.

Nitrogen availability can further interact with disease expression. Increased N supply generally enhances vegetative growth and canopy density, potentially prolonging leaf wetness duration and favoring foliar pathogens. At the same time, N is also required for defense-related processes, including transcriptional reprogramming and early bursts of reactive oxygen species during pathogen recognition (Balint-Kurti, 2019). The net effect of N on disease severity therefore balances between enhanced susceptibility through canopy effects and strengthened physiological defense. In fact, the relationship between foliar disease severity and yield is not necessarily linear (Madden et al., 2007). Yield loss depends on timing of and progress of infection relative to reproductive development, as well as on the plant capacity to compensate for leaf area loss with increased branching. Nitrogen can simultaneously raise yield potential, modify canopy structure and susceptibility to pathogens, creating confounding effects if disease and yield are analyzed independently (Balint-Kurti, 2019). Multivariate models integrating nutrient status, epidemic progress, phenology, and environmental variables are therefore necessary to disentangle direct disease effects from indirect nutritional influences (Ciampitti & Vyn, 2012).

In addition to climatic variability and nutrient availability, crop-specific traits further shape epidemic outcomes. Hemp (*C. sativa*) is a highly variable species, with multiple subspecies (Benkirane et al., 2026; Lapierre et al., 2023). Substantial morphological diversity exists among cultivars, including differences in leaf morphology, canopy density, and inflorescence architecture as well as reproductive pattern, mono- vs. dioecious. These traits influence canopy microclimate and plant susceptibility to various pathogens. Oilseed hemp exhibits considerable phenotypic

plasticity within cultivars allowing morphological and physiological adjustment to environmental conditions. Such plasticity complicates attempts to generalize disease responses across environments. Ansari et al. (2025) proposed a novel photoperiod-based classification system for hemp varieties, offering a practical tool for aligning genotype selection (including seed producing cultivars) with specific environmental conditions, production objectives and targeted breeding programs.

In dioecious hemp, sexual dimorphism provides an additional layer of complexity. Male and female hemp plants differ in resource allocation, growth, and phenology, traits that may influence disease development and epidemic progression (Xia et al., 2024; Barrett & Hough, 2013; Delph & Ashman, 2006). Earlier senescence of male plants shortens the period available for pathogen development relative to female plants. Although evidence for sex-specific disease responses in hemp remains limited, pathogen-induced differences between sexes have been reported in other dioecious plant species (Zemp et al., 2015). Therefore, disease progression was evaluated separately in male and female plants.

In northern European production systems, oilseed hemp cultivation has largely relied on a limited number of early-maturing cultivars, most notably 'Finola', which was specifically bred for short growing season around 30 years ago (Callaway, 2004). Novel Nordic cultivar 'Estica' bred by Commercial Cooperative Nordic Hemp in cooperation with Dutch breeding company Globe Seeds B.V. and registered in 2021 has been developed for Baltic growing conditions where reliable seed maturation during a short growing season is a key constraint (Nordic Hemp, 2022). 'Estica' is characterized by large seed size, and mature seed is produced in approximately 110 days after sowing (Nordic Hemp, 2022). However, independent agronomic data of newly developed northern oilseed hemp cultivars remain scarce, particularly under multi-year field conditions. This limits the

ability to interpret disease dynamics within the broader context of yield formation and crop management. The primary objective of the present study was to determine how nitrogen addition rate, fertilizer source, and interannual climatic variability influence Alternaria leaf spot severity and seed yield in the recently registered oilseed hemp cultivar 'Estica' under northern temperate conditions. A secondary objective was to evaluate disease progression separately in male and female plants because of their contrasting phenology.

2. Materials and methods

2.1. Experimental site and design

Field experiments were conducted during 2022–2024 at the experimental station of the Estonian University of Life Sciences, Tartu County, Estonia (58°36′N, 26°66′E). The soil at the site was classified as a sandy loam stagnic luvisol (WRB, 2022) with a topsoil (humus) layer thickness of 20–30 cm. Soil sampling results from spring in 2022 were as follows: pH 5.6, organic C 1.26%, total N 0.12%, P (AL method) 94 mg kg^{-1} and K (AL method) 85 mg kg^{-1}.

The experimental design consisted of plots of 10 m^2 with three replication strips. Within each strip, the nine fertilizer treatments were arranged in the same fixed (systematic) sequence rather than being randomized. The experimental field exhibited low spatial variability, as confirmed by soil analyses from multiple sampling locations over three consecutive years. The study included 9 treatments combining five nitrogen addition levels (0, 50, 100, 150, and 200 kg N ha^{-1}) and two fertilizer types: (1) complex NPK fertilizer 6-25-34 (NPK) and (2) ammonium nitrate containing 33.4% nitrogen (AN). All treatments (except control) received 50 kg N ha^{-1} at sowing. To reach

higher nitrogen rates, additional split applications (50 kg N ha^{-1}) were made until the desired fertilization level was achieved (100-200 kg N ha^{-1}), according to the phenology and weather conditions.

2.2. Crop management and sampling

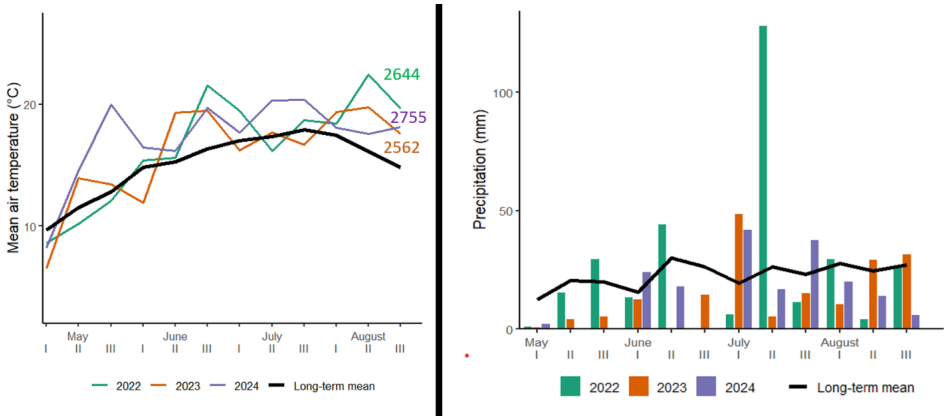
The industrial hemp (*Cannabis sativa* L. cv. 'Estica') was sown using a seeding rate of 20 kg ha^{-1}. Depending on the growing season conditions the sowing, seedling emergence and harvesting dates varied as follows:

- 2022: sown on 4 May; harvested on 5 September (growing season length 124 days)
    - Additional fertilizer applications (50 kg N ha^{-1}) were performed: 13.06, 4.07, 16.07.
- 2023: sown on 20 April; harvested on 12 September (145 days)
    - Fertilizer applications (50 kg N ha^{-1}) were performed: 7.06, 17.07, 30.07.
- 2024: sown on 8 May; harvested on 23 August (108 days)
    - Fertilizer applications (50 kg N ha^{-1}) were performed: 3.06, 12.06, 18.06.

No plant protection measures were used in the experimental field. The seeds were harvested with a customized combine harvester. Right before the harvest, samples (female plants from 0.25 m^2 in each plot) were taken for determining the seed yield.

2.3. Weather conditions

Weather data (Fig. 1) were obtained from an automated meteorological station located at the experimental site and processed using the FieldClimate data platform (Pessl Instruments GmbH, Austria).



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176 Fig. 1. Mean air temperature (°C) with standard error and (*left*) and precipitation (mm, *right*) in
177 hemp (*Cannabis sativa* cv. 'Estica') experimental field during 2022–2024, compared to long-term
178 (1964–2022) mean values. Numeric values denote the accumulated growing degree days (GDD)
179 from sowing to harvest (*left*).

180 The growing degree days (GDD) were calculated as:

181 $$\mathbf{GDD} = \sum_{i=D_s}^{i=D_h} \frac{T_{max}+T_{min}}{2} - T_{base}, \quad \text{(Eq. 1)}$$

182 where $T_{max,i}$ is the daily maximum temperature for day *i,* $T_{min,i}$ is the daily minimum temperature
183 for day *i,* T_{base} is base temperature (minimum temperature for plant growth, taken as 5 °C), D_s is
184 day of the start of the growing season (sowing date) and D_h is the day of harvesting.

185 **2.4. Assessment of *Alternaria* leaf spot disease**

Only *Alternaria* leaf spot disease (*Alternaria* spp.) occurred during the study period, and the development of the disease was monitored weekly from the appearance of visible symptoms until harvest in 2022–2024.

Disease severity was assessed under natural infection conditions by estimating the percentage of infected leaf area (0–100%). Male and female plants were assessed separately. In each monitoring event, five randomly selected male and female plants per plot were evaluated throughout the disease development period (nine assessments in 2022, ten in 2023, and seven in 2024). Final observations (for female plants) at the end of each growing season coincided with seed maturity and harvest time. The assessments of male plants was stopped after their pollen shed and rapid leaf senescence. Male and female plants were analyzed separately because of their contrasting phenology and observation periods; therefore, no formal statistical comparison between sexes was performed. Disease severity assessments were performed by the same trained evaluator throughout the study to minimize observer bias.

The area under the disease progress curve (AUDPC) was calculated using the trapezoidal method (Shaner and Finney, 1977) based on the number of days between consecutive disease assessments and are expressed as percent-days (%-days):

$$\mathrm{AUDPC} = \sum_{i=1}^{n-1} \frac{y_i + y_{i+1}}{2} \times (t_{i+1} - t_i), \qquad \text{(Eq. 2)}$$

where n is the total number of observations, y_1 is the disease severity at the i-th observation, and t is the time (date) of the i-th observation. As the absolute AUDPC values cannot be used to compare different seasons, time-standardization was used to provide an estimate of the average disease

pressure during the epidemic. A time-standardized measure, relative AUDPC (*r*AUDPC) was calculated as follows:

$$r\mathrm{AUDPC} = \frac{\mathrm{AUDPC}}{t_\mathrm{n} - t_\mathrm{i}} \times 100 \ (\%), \qquad \text{(Eq. 3)}$$

where t_n-t_1 is the time in days between the first and the last assessment.

2.5. Molecular identification of the pathogen

For molecular identification of the causal fungal species, 13 leaf samples and 7 mycelial samples cultured on potato dextrose agar. Genomic DNA was extracted from fungal mycelium and infected leaf tissue using simple lysis-based protocols (Proteinase K-based lysis buffer and Phire lysis buffer; BioDyne, Estonia; Thermo Scientific, USA). Only DNA extracted from mycelial cultures yielded reliable sequences and was used for downstream analyses. DNA barcoding was performed using the primers of ITS5/ITS4 (White et al., 1990), and PCR products were sequenced using the MinION platform (Oxford Nanopore) at the Institute of Ecology and Earth Sciences, University of Tartu. Sequences were blasted against the NCBI GenBank database (BLASTn), and only sequences with ≥99% identity were considered. Sequences showed highest similarity to *Alternaria* spp., including *A. alternata* and *A. brassicae* (≥99% identity with each). The sequences are available in Genbank under accession numbers PZ236438–PZ236442**.** Because ITS sequences do not provide sufficient resolution to distinguish among closely related *Alternaria* species, the pathogen is conservatively referred to as *Alternaria* spp. throughout this study.

2.6. Statistical analysis

All statistical analyses were performed in R (version 4.3.2). Seasonal cumulative disease severity (AUDPC) and seed yield were analyzed at the plot level using linear models. Nitrogen addition rate (continuous) and year (factor) were included as fixed effects, along with their interaction, to assess responses across the full nitrogen addition range (0–200 kg N ha^{-1}).

For analyses of fertilizer source (ammonium nitrate vs. complex NPK fertilizer), models were restricted to fertilized treatments only and included nitrogen addition rate, year, and fertilizer source as fixed effects. Sex-specific responses were analyzed separately for male and female plants using the same model structure.

The relationship between AUDPC and seed yield was assessed using linear models including nitrogen addition rate, fertilizer source, and year, based on fertilized treatments. Model assumptions were assessed by visual inspection of residual versus fitted values and normal Q-Q plots (no deviations were detected). Variance inflation factors (VIFs) were calculated to assess multicollinearity among predictors. Statistical significance was determined at $p < 0.05$.

3. Results

3.1. Disease development across years

Alternaria leaf spot disease was the only disease observed in hemp cultivar 'Estica' during 2022–2024. The disease pressure differed significantly among years ($p < 0.001$; Fig. 2). Mean female AUDPC values were 379 ± 42, 235 ± 33, and 126 ± 19 %-days in 2022, 2023, and 2024, respectively, with the highest cumulative disease severity in 2022 and the lowest in 2024.

In males, AUDPC at the end of the assessment period was lower in 2023 ($p = 0.0039$) and 2024 ($p < 0.001$) compared with 2022, and was also lower in 2024 than in 2023 ($p = 0.0018$). Disease pressure was lowest in 2024, which was reflected both in reduced AUDPC and consistently lower disease severity throughout the assessment period (Fig. 2).

In females, AUDPC was lower in both 2023 and 2024 relative to 2022 ($p < 0.001$; Fig. 2).

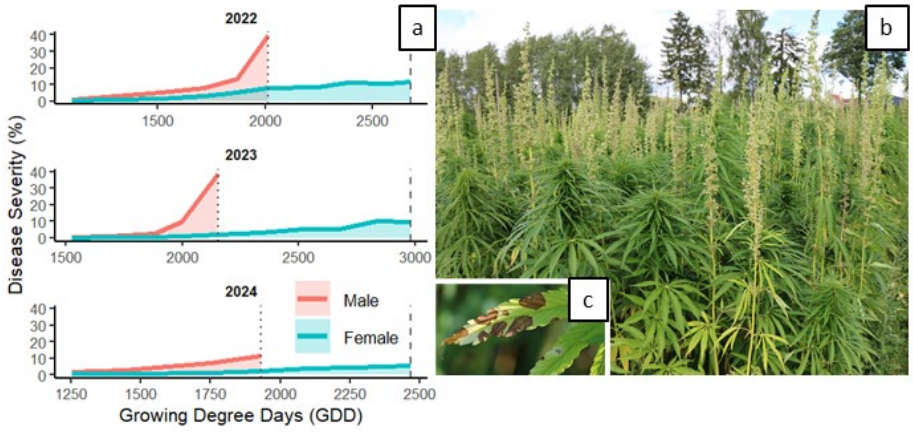


Fig. 2. (a) Disease severity progression in male and female hemp (*Cannabis sativa* cv. 'Estica') plants across growing seasons. Dotted vertical lines indicate male senescence, and dashed vertical lines indicate the final observation (at harvesting) for each year; (b) Experimental field, with male plants with fully developed panicles and female at the start of flowering; (c) *Alternaria* leaf spot symptoms. Photos by Eve Runno-Paurson.

Disease progression patterns differed between male and female plants, with males showing a more rapid increase in disease severity over a shorter observation period, whereas females exhibited a

more gradual and prolonged progression, which may reflect differences in phenology and duration of observation.

3.2. Disease severity in relation to nitrogen addition rate

For all years pooled, increasing nitrogen addition rate reduced cumulative disease severity in female plants (Fig. 3).

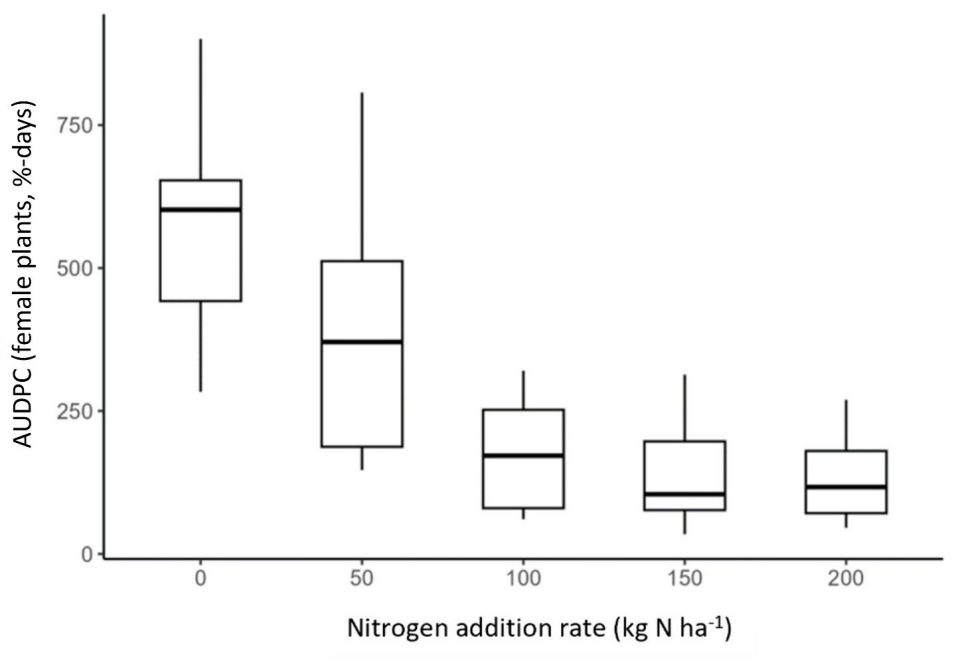
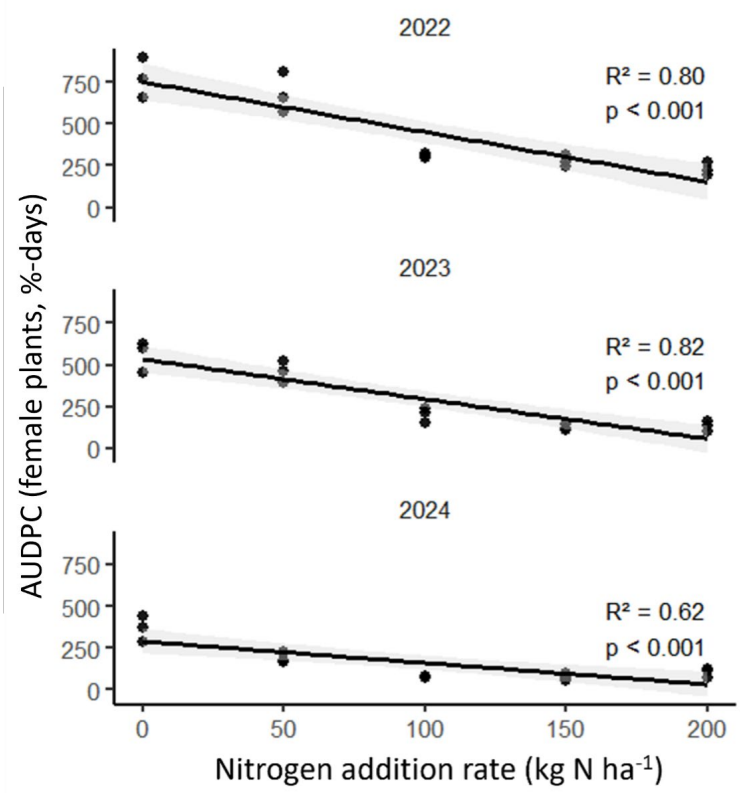


Fig. 3. Distribution of cumulative disease severity (AUDPC, %-days) at the end of the growing season in female hemp (*C. sativa* cv. 'Estica') plants across nitrogen application rates (kg N ha^{-1}) pooled over three growing seasons. Boxes represent the interquartile range, horizontal lines represent the median values, and the whiskers show 1.5× IQR.

Analysis of the full model, nitrogen addition rate, year and their interaction, revealed that the impact of nitrogen addition rate on female AUDPC was affected by both nitrogen addition rate ($F_{1,39} = 129.3$, $p < 0.001$) and year ($F_{2,39} = 36.9$, $p < 0.001$), with a significant nitrogen × year interaction ($F_{2,39} = 6.54$, $p = 0.0036$), indicating that the slope of the AUDPC vs. nitrogen addition rate relationship varied among years (Fig. 4). The estimated decrease in female AUDPC with increasing nitrogen rate was 2.98, 2.38, and 1.37 %-days per kg N ha^{-1} in 2022, 2023, and 2024, respectively.

Across the nitrogen addition range used in this experiment (0–200 kg N ha^{-1}), AUDPC was reduced by approximately 600 %-days in 2022, 480 %-days in 2023, and 260 %-days in 2024 at 200 kg N ha^{-1} compared with the control treatment.

In male plants, nitrogen addition rate also significantly reduced AUDPC ($p < 0.001$, data not shown), but the nitrogen × year interaction was not significant ($p > 0.13$), indicating a more consistent response across years. Fertilizer source (ammonium nitrate vs complex NPK fertilizer) did not significantly affect AUDPC in either sex ($p > 0.72$ for males and $p > 0.89$ for females) and was excluded from the final disease models. Analyses using relative AUDPC were qualitatively similar (data not shown).



285

286 Fig. 4. Cumulative disease severity (AUDPC, %-days) in dependence on nitrogen addition rate (kg
287 N ha^{-1}) in female hemp (*C. sativa* cv. 'Estica') plants across three growing seasons. Points represent
288 plot-level values (n = 3 per nitrogen level and year), with fertilizer treatments averaged within
289 plots. Solid lines show linear regressions fitted separately for each year; shaded areas represent
290 95% confidence intervals.

291 **3.3. Seed yield in relation to nitrogen addition rate**

Across all treatments and years, hemp seed yield ranged from 0.6 to 2.7 t ha^{-1} (Fig. 5). Across the nitrogen addition range (0–200 kg N ha^{-1}), seed yield increased by approximately 1.0–1.7 t ha^{-1} depending on year (Fig. 5). In a linear model including nitrogen rate (0–200 kg N ha^{-1}) and year, nitrogen rate had a highly significant positive effect on yield ($F_{1,75}$ = 324.65, p < 0.001). Year effects alone were not significant ($F_{2,75}$ = 1.99, p = 0.144). However, the nitrogen rate × year interaction was significant (p < 0.001), showing that the magnitude of the yield response differed among years, with the weakest response observed in 2023 (Fig. 5).

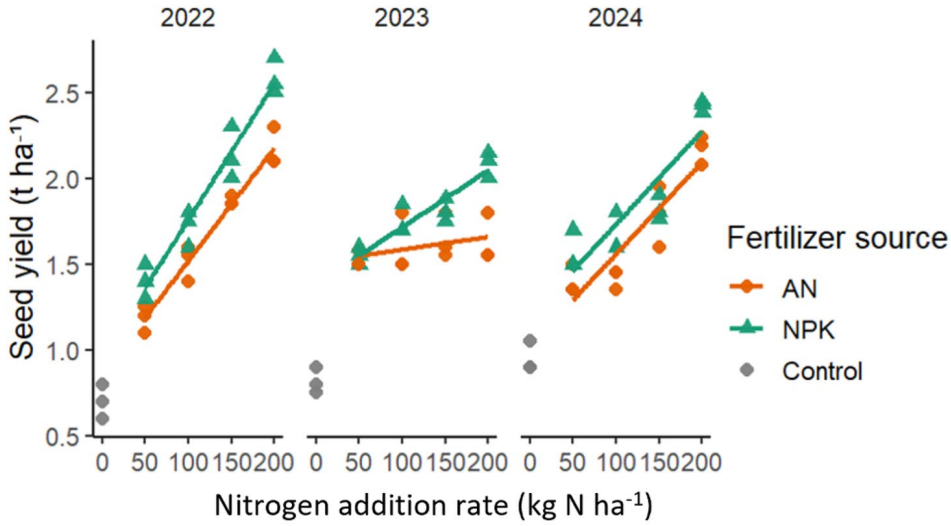


Fig. 5. Hemp (*C. sativa* cv. 'Estica') seed yield (t ha^{-1}) as a function of nitrogen application rate (kg N ha^{-1}) in 2022–2024. Points represent individual plots (n = 3 per nitrogen level and fertilizer source). Solid lines indicate linear regressions fitted to the data for each fertilizer source within year. AN - fertilization with ammonium nitrate, NPK - fertilization with a complex fertilizer.

When considering fertilized treatments only, fertilizer source had a significant effect on seed yield, with complex NPK resulting in consistently higher yields than ammonium nitrate (Fig. 5; $F_{1,65}$ = 50.27, $p < 0.001$). In this model, both nitrogen rate and the nitrogen rate × year interaction were also significant ($p < 0.001$), indicating that yield responses to nitrogen differed among years.

3.4. Relationship between disease severity and seed yield

Across all treatments and years, seed yield was negatively associated with female AUDPC in simple bivariate analyses. However, when nitrogen rate, fertilizer source, and year were included in the model, the effect of female AUDPC on yield was not significant ($F_{1,64}$ = 0.72, p = 0.40). Within the range of disease severity observed in this study, nitrogen addition rate had seemingly opposing effects on the two variables, increasing yield while reducing disease severity, thereby confounding the apparent relationship between AUDPC and yield. Accordingly, the estimated direct effect of female AUDPC on yield was small and not significant.

In control treatments, seed yield was negatively associated with female AUDPC (p = 0.009), suggesting a direct negative relationship between disease severity and yield under low nitrogen conditions.

Male AUDPC was likewise not significantly associated with yield after accounting for nitrogen rate, fertilizer source, and year ($F_{1,64}$ = 3.13, p = 0.082). Inclusion of either female or male AUDPC did not alter the effects of nitrogen rate or fertilizer source on yield. This is consistent with the fact that seed yield is determined by female plants, and disease severity in male plants may have limited direct influence on yield.

Together, these results show that nitrogen rate explained more variation in seed yield, whereas disease severity did not independently contribute to yield differences once fertilization effects were accounted for, except under low nitrogen conditions where a negative relationship was observed.

4. Discussion

4.1. Yield performance and nitrogen responsiveness

The present experiment provides the first independent multi-year agronomic evaluation of the recently registered cultivar 'Estica' under northern temperate field conditions. Across all treatments and years, seed yield ranged from 0.6 to 2.7 t ha^{-1} (mean ± SD = 1.66 ± 0.44 t ha^{-1}), reflecting substantial variability typical of northern production systems. This range is consistent with northern European cultivar trials, where seed yields typically vary between approximately 1 and 3 t ha^{-1} depending on genotype and season (Stramkale et al., 2024; Adamovics et al., 2016). High-yielding cultivars such as 'Henola' may exceed 3 t ha^{-1} under favorable conditions, whereas earlier-maturing cultivars such as 'Finola' generally show lower but more stable yields across variable seasons (Stramkale et al., 2024). In this context, the observed yield performance places 'Estica' within a moderate yield class, reflecting the well-documented trade-off between earliness and yield potential in hemp. Cultivars adapted to shorter growing seasons ensure reproductive completion but often accumulate lower biomass, hence face yield ceilings. Given the current lack of independent agronomic data for newly registered northern hemp cultivars, these results provide important baseline information on yield potential, variability, and nitrogen responsiveness under practical field conditions. This wide yield range reflects strong environmental and management-driven variability in seed production under northern temperate conditions.

Seed yield increased with nitrogen rate and showed significant nitrogen × year interactions (Fig. 5), indicating environment-dependent nitrogen responsiveness. Such variability in nitrogen response has been widely reported in other hemp cropping systems (Aubin et al., 2015; Campiglia et al., 2017; Tang et al., 2017; Adamovics et al., 2016; Lääniste et al., 2016). Fertilizer source significantly affected yield, with NPK resulting in consistently higher yields than ammonium nitrate, but did not influence disease severity. Although nitrogen form influences plant signaling, metabolism and microbiota formation (Hachiya & Sakakibara, 2017; Britto & Kronzucker, 2002; Chen et al., 2024), our results indicate that nitrogen form influenced productivity primarily through growth responses rather than through changes in disease development.

4.2. Disease dynamics and nitrogen effects

Interannual variability was the dominant factor influencing *Alternaria* epidemic intensity. Cumulative disease severity differed markedly among years (Fig. 2), consistent with the established role of climatic drivers in regulating foliar disease development (Hossain et al., 2024; Madden et al., 2007). Even moderate seasonal differences during flowering can substantially alter epidemic timing and progression, emphasizing the importance of multi-year evaluation when interpreting nutrient–disease interactions in field systems.

Nitrogen addition was consistently associated with reduced cumulative disease severity in our study, contrary to the general expectation that increased nitrogen promotes foliar disease through denser canopies and prolonged leaf wetness. The observed nitrogen × year interaction further indicates that the extent of this response depended on seasonal conditions. Although weather conditions differed among years (Fig. 1), the contribution of individual weather variables to disease severity was not formally evaluated. Although, nitrogen can support plant physiological and

defense-related processes, its effects on plant–pathogen interactions are complex and species dependent (Snoeijers et al., 2000; Sun et al., 2020). Accordingly, the lower *Alternaria* leaf spot severity under higher nitrogen supply may partly reflect greater plant growth, whereby increased leaf production could have resulted in a dilution effect, reduced the proportion of symptomatic tissue and altered symptom expression rather than directly suppressing pathogen infection. These observations may indicate that improved plant vigor outweighed any increased disease risk associated with greater canopy development, although the underlying mechanisms were not directly measured in the present study.

Disease progression also differed between male and female plants, primarily reflecting differences in phenology and canopy persistence. Earlier senescence of male plants shortened the period available for disease development, whereas female plants remained susceptible for longer. These observations highlight the importance of considering plant sex when assessing disease progression in dioecious hemp.

4.3. Disease–yield relationships

Disease–yield relationships are often nonlinear and context-dependent (Madden et al., 2007). Although seed yield was negatively associated with disease severity in simple analyses, this relationship disappeared after accounting for nitrogen rate, fertilizer source, and year. This indicates that the apparent disease–yield relationship was largely driven by confounding effects of nitrogen, which may have simultaneously increased yield and reduced disease severity, rather than direct yield limitation by *Alternaria* leaf spot.

However, under control (low nitrogen) conditions, seed yield was negatively associated with disease severity, suggesting that Alternaria leaf spot may reduce yield when nitrogen availability

is limited. In contrast, no independent relationship between disease severity and yield was detected under fertilized conditions, indicating that adequate nitrogen supply may mitigate disease-associated yield losses under the epidemic intensities observed in the present study. This observation is consistent with evidence that nitrogen nutrition influences both plant productivity and disease outcomes (Sun et al., 2020). Moreover, yield loss depends not only on disease severity but also on the crop's capacity to maintain growth during epidemic development (Madden et al., 2007).

In contrast, male disease severity was not associated with yield after accounting for nitrogen rate, fertilizer source, and year. This may reflect the dominant role of nitrogen-driven resource availability in seed production and the timing of disease development relative to reproductive development, as major disease development occurred when seeds were already approaching maturity (Madden et al., 2007; Ciampitti & Vyn, 2012). Together, these findings suggest that, under the epidemic intensities observed here, nitrogen availability explained more variation in seed yield than disease severity.

4.4. Agronomic implications and limitations

These findings have important implications for hemp production in northern regions. Nitrogen management represents a primary lever for optimizing and stabilizing seed yield, whereas moderate levels of foliar disease may not significantly constrain productivity under fertilized conditions. However, under low-input systems, disease effects may become more relevant. As climatic conditions continue to change and pathogen pressure potentially increases, the balance between nitrogen-driven yield gains and disease-related losses may shift.

A limitation of the present study is the absence of pathogenicity testing and re-isolation procedures required for fulfillment of Koch's postulates. Consequently, the causal role of the detected *Alternaria* taxa should be interpreted with caution. Also, the present study was conducted under natural infection conditions, limiting inference on pathogen thresholds and resistance mechanisms. Similarly, the influence of weather on disease development remains inferential because no formal analyses relating weather variables to disease severity were performed. Future studies integrating controlled experiments with environmental and physiological measurements would help to further clarify nitrogen–disease interactions in hemp production systems. The present findings are based on the first multi-year agronomic evaluation of the recently registered cultivar ‘Estica’, and additional studies will be needed to evaluate the consistency of these responses across other oilseed hemp cultivars. Although, disease progression was assessed separately for male and female plants, the present study did not investigate the physiological mechanisms underlying these differences. Future studies integrating disease assessments with physiological and molecular measurements would help clarify sex-specific responses to pathogen infection in hemp. As oilseed hemp cultivation expands into new regions and climatic conditions continue to change, the importance of Alternaria leaf spot may increase, highlighting the need for continued research on disease epidemiology, yield loss relationships, and effective management strategies in hemp.

5. Conclusions

Alternaria leaf spot severity in seed hemp varied strongly among years, highlighting the dominant role of interannual climatic conditions in epidemic development under northern temperate field

conditions. Disease progression differed between male and female plants, primarily reflecting differences in phenology and canopy persistence.

Nitrogen addition rate significantly influenced both *Alternaria* leaf spot severity and seed yield, although responses varied among growing seasons. Increasing nitrogen supply reduced cumulative disease severity and enhanced seed yield; however, disease severity did not independently explain yield variation once nitrogen and environmental effects were accounted for.

Together, these results highlight the importance of climate and nitrogen management for hemp production and show that disease progression differs between male and female plants. These findings emphasize the importance of multi-year evaluation and nitrogen management in developing agronomic recommendations for dioecious hemp under northern European conditions. As disease pressure may increase under changing climatic conditions, continued monitoring of *Alternaria* leaf spot and its relationship with yield will be important for sustainable hemp production.

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Declaration of Competing Interests

No potential conflict of interest was reported by the author(s).

CRediT authorship contribution statement

Erkki Mäeorg: Writing – original draft, Data curation, Formal analysis. **Peeter Lääniste**: Methodology, Investigation, Writing – review and editing. **Leho Tedersoo**: Formal analysis, Writing – review and editing, **Ülo Niinemets**: Writing – review and editing, Supervision. **Eve Runno-Paurson**: Conceptualization, Data curation, Writing – review and editing, Supervision.

Data availability

Data will be made available on request.

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III

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ORIGINAL ARTICLE / ORIGINALBEITRAG

Widespread Occurrence of European Corn Borer (*Ostrinia nubilalis*) and Damage of Industrial Hemp (*Cannabis sativa*) Crop in Northern Europe

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Abstract
Industrial hemp cultivation restarted in Estonia in mid 2000s and the hemp cultivation area has increased very fast in recent years, but it is unknown to what extent hemp productivity can be curbed by widespread crop pests. Thus, the main aim of this study was to evaluate the presence and damage of hemp pests in northern field conditions. A field trial with the hemp cultivars 'Finola' (2021) and 'Estica' (2022) was established in Central Estonia (58° N, 26° E), and the plants were grown with different fertilizer types (complex fertilizer, ammonium nitrate), fertilization methods (at sowing/top dressing) and nitrogen rates (0–200 kg ha^{-1}) and their effect on the European corn borer (ECB, *Ostrinia nubilalis*) damage was assessed. The *O. nubilalis* infestation increased with every observation date throughout the seasons until the harvest. The *O. nubilalis* damage was overall greater in 2022 than in 2021, and the seed yield reduction reached to 120 kg ha^{-1} in 2022, indicating progressive increase in *O. nubilalis* damage. Fertilization rate strongly increased biomass and seed yields, but weakly reduced *O. nubilalis* infection. Estonia is one of the most important hemp-cultivation areas in Europe, and in northern conditions, the crop was previously considered to be relatively pest-free. The northward movement of crop infection by *O. nubilalis* implies that future hemp cultivation might need integrated *O. nubilalis* control practices adapted to site-specific agro-climatic conditions.

Keywords European corn borer · Hemp · Fertilization method · Fertilization rate · Northern climate · Yield reduction

Introduction

European corn borer (ECB), *Ostrinia nubilalis* Hübner (*Lepidoptera*: *Crambidae*) has become one of the major pests in Europe, Asia and in Americas, damaging mainly maize (*Zea mays*). It is native to Europe and it has been suggested that wild hop (*Humulus lupulus*) and wild hemp (*Cannabis sativa* var. *spontanea*) were the original host plants (Nagy 1976). It became a major maize pest in the beginning of the 20th century (Calvin et al. 1991; Got et al. 1996; Bereś and Konefał 2010), and currently the overall yield losses because of *O. nubilalis* are estimated at US$ 1 billion per year (Bažok et al. 2020).

European corn borer is an extremely polyphagous insect and besides maize its host range has more than 200 different plant species belonging to 40 different botanical families, including sorghum (*S. bicolor*), pepper (*Piperaceae*), hemp (*C. sativa*), millet (*P. miliaceum*), mugwort (*A. vulgaris*), chrysanthemums (*Chrysanthemum*) etc. (Gaspers and Schuphan 2010; Leppik 2011; Bažok et al. 2020). It is considered to attack any herbaceous plants with stems large enough for the larva to enter (Bourguet et al. 2000; Leppik 2011). It has been assumed that the *O. nubilalis* spreads 3–5 km a year (Lisowicz 1995), while in the US the spread has reached 32–42 km yearly (Schurr and Holdaway 1965, as cited in Bereś and Konefał 2010). The spreading speed is determined mostly by the availability of host plants and natural predators and parasites (Trnka et al. 2007). To have time to complete its development in colder climates, *O. nubilalis* individuals start feeding largely on the whorl leaves, which requires development of certain physiological and behavioural adaptations and is associated with

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polyphagousness as well as segregation from populations retaining initial trophic connections with dicotyledonous host plants (Zhukovskaya and Frolov 2022). Previous observations suggest that the *O. nubilalis* prefers larger plants (Small et al. 2007). European corn borers may prefer to bore into larger stems simply because smaller stems are too narrow to accommodate full-grown caterpillars as they begin pupation. Larvae have been found to move up and down the stalk to find more suitable temperature and buffer from outside conditions (Keszthelyi et al. 2021).

Apart from damage to maize, *O. nubilalis* is one of the most destructive pests of hemp (*Cannabis sativa* L.) in North America, and in Europe, and it can cause appreciable hemp crop losses (Grigoryev 1998; Benelli et al. 2018; Park et al. 2019). A heavy infestation on hemp was already reported in 1945–55 in Hungary (Nagy and Csehi 1955, as cited in Nagy 1976) that drew attention to the problem of geographical strains.

Hemp is exceptionally resistant to lodging and usually not affected by ordinary storms, but *O. nubilalis* tunnels into larger stems and stalks of hemp and has the potential to weaken plants to the extent that they are prone to breakage. Grigoryev (1998) found that under low air humidity conditions the major part of the *O. nubilalis* damage is to the inflorescences of hemp. Young ovules and immature seeds are gnawed first by the caterpillars. The next instar larvae causes dryness of the inflorescence and stalk through the action of young larvae gnawing out the inside tissues of plant stems. This leads to inflorescence damage and a breaking of hemp stalks in the field with consequent entanglement of plantings, which greatly hampers mechanized harvesting. Adult larvae of this pest survive winter as pupae inside the stalks of hemp plants, in harvested maize stalk residues or in weed stems. Damaged plants are also susceptible to various fungal pathogens (Grigoryev 1998). *O. nubilalis* causes stalk cankers and break; larvae boring into smaller branches cause wilting of distal plant parts. Under substantial damage entire plants collapse. The damage is more severe in fibre crops, which are grown in tight proximity (Parisi and Ranalli 2000). On the other hand, Grigoryev (1998) studied the relationships of resistant hemp accessions to *O. nubilalis* and the density of plantings in the field and found the most severe incidences of damage in sparse hemp plantings at 500,000 plants per hectare with a row spacing of 45 cm. In addition, Small et al. (2007) found that within the plots of most hemp cultivar accessions, *O. nubilalis*-affected plants branched extraordinarily and even appeared to produce more biomass and seeds than normal plants.

Compared to other field crops, hemp is considered relatively pest-tolerant plant because of the potential pest-repellent properties of its cannabinoids and terpenoids (Dambolena et al. 2016). Recent studies have demonstrated that cannabinoid-enriched extracts show pesticidal activity to defend the plants from insect herbivore attacks (Benelli et al. 2018; Park et al. 2019, 2022). However, one of the main cannabinoids—tetrahydrocannabinol (THC) did not have any effect on the infestation and damage by *O. nubilalis* (Park et al. 2019).

The pheromone polymorphism of the *O. nubilalis* is the basis for a successful reproductive isolation. Males might use a blend of host volatiles and sex pheromones for mating and females are expected to use host volatiles for finding the host before or after mating (Bengtsson et al. 2006; Sole et al. 2010). Monocots are attacked mainly by Z pherotype and dicots by E pherotype (Ponsard et al. 2004; Leppik 2011). In the case of maize, there are no specific plant volatile compounds that are responsible for attracting *O. nubilalis*, but probably blends of many volatiles in specific ratios are behaviourally effective (Leppik and Frérot 2012).

The most important environmental factors affecting *O. nubilalis* spread and their uni-, bi- and multivoltine nature include ambient temperature, moisture and food resources (Frolov 1998; Zhukovskaya and Frolov 2022). Daily temperatures and precipitation are very important factors for the *O. nubilalis* population dynamics (Bažok et al. 2020). The increase in the population size and harm caused by this pest is mainly facilitated by simplified crop production methods, monoculture, crop residues left on the field, late ploughing before winter, global warming and especially by the growing area of maize cultivation (Lisowicz 1995; Kocmankova et al. 2011; Kozak et al. 2019; Enos and Kozak 2021). Camerini et al. (2018) studied the potential parasitoid species for *O. nubilalis* and found that in USA the number of parasitoids decreased from 18 species in 1930s to only 9 species in more recent studies, due to the loss of biodiversity. The possible reasons of such a biodiversity decline include monocultural patterns and overall landscape structure simplification.

In Estonia, *O. nubilalis* has been registered as a component of natural insect fauna, and it has not been considered as a pest on the crop fields until recently. According to farmers' reports, in Estonian maize fields, *O. nubilalis* has been reported only in the last two years. Despite that oil hemp is a widely-grown crop in Estonia, there have been no reports of *O. nubilalis* damage until a few *O. nubilalis*-injured hemp plants were observed at the experimental field of Estonian University of Life Sciences in autumn of 2020. Furthermore, previous knowledge of the *O. nubilalis* damage on the fields of oil hemp in Northern Europe was missing. Motivated by the observation that *O. nubilalis* could be a significant hemp pest in northern conditions, we started detailed monitoring of the occurrence and damage of *O. nubilalis* in hemp fields for two subsequent years to assess the spread of the insect and potential damage for hemp cultivation. As it has been shown, the spread of pests can be strongly affected by management practices, particularly the

choice of crops in the rotation, the objective of the experiment was to assess the effect of cultivation technologies (fertilizer type, fertilization rate, fertilization method) on the occurrence of *O. nubilalis* and estimate the possible seed yield losses.

Materials and Methods

Experimental Site and Design

European corn borer (*Ostrinia nubilalis*) infection was evaluated in 2021 and 2022 on industrial hemp (*Cannabis sativa* L.) crop plants in an experimental field of the Estonian University of Life Sciences, Tartu County, Estonia (58° 36′ N, 26° 66′ E). The two growing seasons were mostly characterized by usual temperature patterns, compared to the long-term average (Fig. 1). However, in June and July of 2021, the daily average air temperatures were significantly higher and combined with extremely low precipitation values led to moderately severe drought conditions. In August of 2022, the average temperatures were also above the long-term average, reaching over 22 °C in the second decade (Fig. 1). The precipitation was significantly lower in both seasons, compared to long-term average value and was also characterized by high variability (Fig. 1). The precipitation exceeded the long-term average values only in the second decade of August in 2021 and the second decade of July in 2022 (Fig. 1).

The field experiment included various seeding rates (20–40 kg ha^{-1}), fertilizer types (Type 1: complex fertilizer 17-4.6-10 S-Mg-B; Type 2: ammonium nitrate), fertilization methods (at sowing/top dressing) and nitrogen addition rates (0–200 kg ha^{-1}). Oil-type hemp cultivars

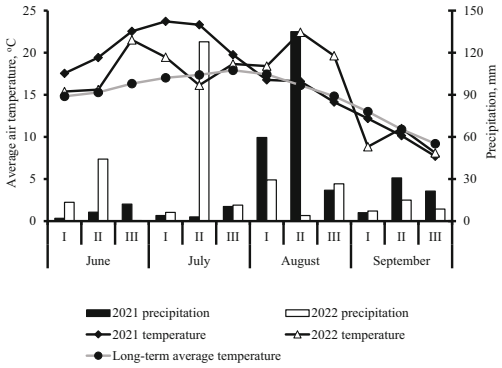

Fig. 1 Average air temperature and precipitation on the Eerika (Central Estonia) *Cannabis sativa* test site in 2021 and 2022 and comparison with long-term (1964–2022) average temperature

'Finola' (2021) and 'Estica' (2022) were used. Plots were sown on 22 April in 2021 and 4 May in 2022. Size of a test plot was 10 m^2 and three replications were used for each treatment. The seeds were harvested on 28 September in 2021 and 25 September in 2022. Total above-ground biomass yield (2021) and seed yield (2021, 2022) were measured for the entire plot, and a random sample of plants from 0.25 m^2 were used to measure plant height and stalk diameter (2021).

The damage of European corn borer was assessed based on the number of plants damaged per plot. The evaluations were performed weekly when the damage became visible in the field until the harvest (2 assessments in 2021, 4 assessments in 2022). The weather data were obtained from the local weather station next to the sample plots in Eerika, Tartu.

Molecular Identification of the Pest and Pest Damage Assessment

For molecular confirmation of the identification of the pest, genomic DNA of the larva of *Ostrinia nubilalis* was extracted from the last abdominal segment using DNEasy Blood & Tissue Kit (Quiagen N.V., Venlo, Netherlands) following the manufacturer's instructions. A standard barcoding fraction (658 bp) of the mitochondrial COI gene (Hebert et al. 2004) was sequenced, following the protocol described in Õunap et al. (2021). The identity of the larva was verified using the identification engine of the Barcode of Life Data Systems web portal (http://www.boldsystems.org/index.php).

Data Analysis

Independent samples *t*-test was conducted to explore the differences between the *O. nubilalis* damage in two seasons. The differences in the number of *O. nubilalis*-damaged plants between the observation dates within the given year were assessed by one-way ANOVA followed by Tukey *post-hoc* test and the effect size η_p^2 is presented. Pearson correlation analysis was used to examine the relationships between the levels of N fertilization and seed yield of hemp. Independent samples *t*-test was used to explore differences between fertilization method and fertilizer type and average biomass and seed yields.

The reductions of seed and biomass yields due to *O. nubilalis* were calculated based on the total seed and biomass yield of the plot, the number of plants per plot, the number of female individuals and the number of *O. nubilalis* damaged plants. The effect of harvest dates, fertilizer type and fertilization method on the seed yield reduction due to *O. nubilalis* was analysed with independent samples *t*-tests.

Fig. 2 A typical hemp (*Cannabis sativa*) plant infested by European corn borer (*Ostrinia nubilalis*) in hemp field in Estonia in 2021 (**a**); hole in stem of hemp plant (*arrow*) caused by *O. nubilalis* (**b**). (Photos E. Runno-Paurson)

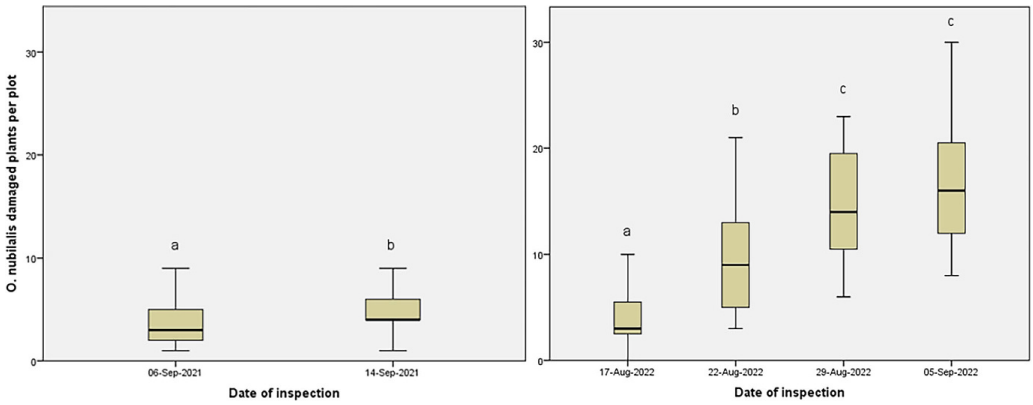

Fig. 3 Number of *O. nubilalis* damaged plants per plot of cultivar 'Finola' in 2021 (*left*) and 'Estica' 2022 (*right*). Different letters (*a*, *b*, *c*) indicate significant differences between the groups each year ($p < 0.001$)

Results

Variation in *O. nubilalis* Damage Among the Two Growing Seasons

The European corn borer larvae were first noticed in industrial hemp trials of Estonian University of Life Sciences (EMU) in 2020, However, the larva were present in low numbers and the visual symptoms of *O. nubilalis*-infection were rare (less than 0.1% of plants showing visual symptoms of damage) and appeared mostly on fertilized plots. The upper portion of damaged plants looked necrotic and brown (Fig. 2). In addition, the stems became soft, visible borer entrance holes were detected and in some cases the stems broke off, showing larval frass (feces). In previous seasons, no damage on the EMU trial fields was observed nor has there been any report on *O. nubilalis* occurrence on the commercial fields in Estonia. After first noticing the European corn borer damage in 2020, the potentially harmful pest dispersal was studied in 2021 and 2022. The level of *O. nubilalis* damage increased from 2021 (average ± SE = 4.45 ± 0.23 number of damaged plants per plot, 10 m^2, $n = 108$ observations) to 2022 (11.3 ± 0.7 per plot, $t_{(131,028)} = -9.93$, $p < 0.001$, independent samples *t*-test for sample populations with unequal variance).

The Dynamics of *O. nubilalis* Damage During Growing Seasons

In 2021, *O. nubilalis* damage was assessed twice, and in 2022 four times. In 2021, the number of damaged plants per plot (10 m^2) was lower in the beginning of September than in the middle of September just before harvest (Fig. 3; for ANOVA, $F_{(1,106)} = 12.80$, $p < 0.001$ $\eta_p^2 = 0.11$). The average number of *O. nubilalis* damaged plants during the first and the last evaluation were 3.7 ± 0.28 and 5.24 ± 0.34, respectively.

In 2022, there was a progressive increase in infestation during the observation period (Fig. 3; for ANOVA, $F_{(3,102)} = 37.93$, $p < 0.001$, $\eta_p^2 = 0.53$). In this year, the level of infestation did not differ only among the last two sampling dates (29th of August and 5th of September, Fig. 3,

		1	2	3	4	5	6
1	**No of *O. nubilalis* infections (m^{-2})**						
2	**Fertilization rate (kg N ha^{-1})**	-0.23*					
3	**Plant height (cm)**	0.02	-0.23*				
4	**Stalk diameter (mm)**	0.04	-0.09	0.88**			
5	**Female plant number (m^{-2})**	0.17	-0.20*	-0.17	-0.14		
6	**Seed yield (t ha^{-1})**	-0.12	0.13	0.70**	0.58**	0.07	
7	**Biomass yield (t ha^{-1})**	-0.20*	0.51**	0.61**	0.54**	0.11	0.81**

$n = 108$, *$p < 0.05$; ** $p < 0.01$

Fig. 4 The relationships (Pearson correlations) between European corn borer (*Ostrinia nubilalis*) damage of industrial hemp (*Cannabis sativa* cv. 'Finola') plants and fertilization rate and plant characteristics in study year 2021

Tukey's *post-hoc* test). The average number of *O. nubilalis* damaged plants during the four evaluations were 4.2 ± 0.51, 9.6 ± 1.05, 14.9 ± 0.97 and 16.52 ± 1.02, respectively.

Pest-dependent Yield Reductions

Based on our two-year experiment, the seed yield of oilseed hemp varied from 0.4 to 4.4 t ha^{-1} in 2021 and from 0.6 to 2.7 t ha^{-1} in 2022. For data of both cultivars pooled, the seed yield was strongly correlated with N fertilization rate ($r_P = 0.59$, $n = 216$, $p < 0.001$). Fertilization at sowing (average ± SE = 1.71 ± 0.11 t ha^{-1}) increased the hemp seed yield, compared to the top dressing method (average ± SE = 1.28 ± 0.04; $t_{(93,368)} = 3.76$, $p < 0.0001$). In addition, the complex fertilizer (average ± SE = 1.96 ± 0.06 t ha^{-1}) improved the seed yield, compared to ammonium nitrate fertilizer in 2022 (average ± SE = 1.68 ± 0.06 t ha^{-1}; $t_{(94)} = 3.19$, $p < 0.05$).

O. nubilalis damage was negatively correlated with nitrogen fertilization rate and biomass yield, but the relationships were weak (Fig. 4). No correlation was found between the sowing rate (20, 30, 40 kg seeds ha^{-1}), plant size (height and stalk diameter), number of female plants per plot and *O. nubilalis* damage (Fig. 4). The seed yield reduction remained relatively low, on average (± SE) 12.3 ± 0.15 kg ha^{-1} (0.77 ± 0.05% of total yield) in 2021 and 68.6 ± 1.07 kg ha^{-1} (4.1 ± 0.2% of total yield) in 2022 (averages are significantly different at $p < 0.001$, ANOVA, $F_{(5,215)} = 74.5$). The highest seed yield reduction reached up to 120 kg ha^{-1} (7.1 ± 0.4% of total yield; Fig. 5). In 2021, also the biomass yield reduction was calculated (0.92 ± 0.65 t ha^{-1}).

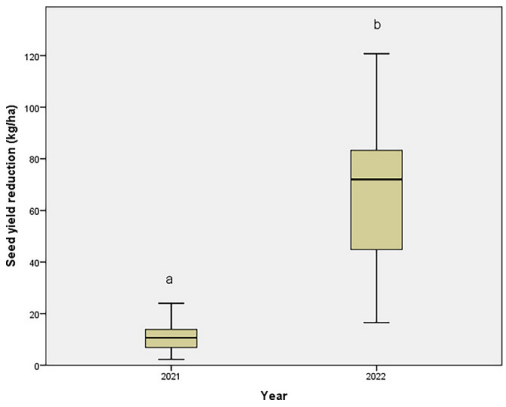

Fig. 5 Seed yield reduction (kg ha^{-1}) based on the number of *O. nubilalis* cases observed in 2021 and 2022. Different letters (*a*, *b*) indicate significant differences between observation dates ($p < 0.001$)

Fertilization rate affected the seed yield reduction in both seasons (in 2021: $F_{(7,100)} = 7.234$, $p < 0.001$; in 2022: $F_{(4,103)} = 3.565$, $p < 0.01$). In 2021, a few statistically significant effects of N fertilization rates were seen, but there was no linear correlation between fertilization rate, plant biomass and seed yield and yield loss due to *O. nubilalis* damage. In 2022, the yield loss was greater in non-fertilized treatment (N0) compared to all other nitrogen fertilization rates (N50-200). The plots with fertilization at sowing were more prone to *O. nubilalis* damage in 2021, compared to top dressing method, 13.6 ± 1.24 and 7.5 ± 0.52 kg ha^{-1} ($t_{(71.13)} = 4.55$, $p < 0.001$). The fertilizer type (complex fertilizer vs. ammonium nitrate) did not affect the seed yield reduction ($p > 0.05$).

Discussion

European Corn Borer as a Pest in Northern Conditions: General Observations

The hugely polyphagous insect European corn borer (*O. nubilalis*) is a major pest in maize and hemp cultivation areas, but in Estonia it has been considered as a component of natural flora with no significant impact on crops. After first noticing the pest in our experimental field in 2020, we started monitoring the occurrence dynamics of *O. nubilalis* on the oil hemp fields in local climatic and weather conditions. Our study demonstrates that the *O. nubilalis* damage increased through the growing season, and the degree of damage was greater in 2022 than in 2021, suggesting en-

hanced spread of the insect. Also, in 2022 the average daily temperature was much higher at the end of August and the *O. nubilalis* damage occurred much earlier, compared to 2021 season. The visual evaluation of the *O. nubilalis* damage seemed much more harmful as many plants were totally perished and dark-coloured, compared to the number of damaged plants per plot. Based on our investigation it can be stated that the European corn borer could overwinter in the area (in the soil or plant residues) and it found the host hemp plants suitable for oviposition and as a food source.

With both cultivars investigated the seed yield was strongly correlated with N fertilization rate. In case of pest damage it is also important to evaluate the seed yield reduction. For the evaluation of seed yield reduction the combined effect of seed yield, *O. nubilalis* damage and the number of female plants is considered. Nevertheless, given the diffuse and variable dispersal of the insect (1–30 per plot) the effect of *O. nubilalis* on the hemp seed yield was relatively low, on average 12.3 kg ha^{-1} in 2021 and 68.6 kg ha^{-1} in 2022, i.e. an increase of 5.5 times from 2021 to 2022.

Based on the crop density, size of the plants, stalk diameter etc., hypotheses can be formed about the preference and prevalence of the *O. nubilalis* to oviposit or the ability of the developing larvae to feed on the plant. Sarajlić et al. (2020) carried out experiments with maize and found the highest *O. nubilalis* damage on crops with greatest nitrogen fertilization rates. According to our results, although the fertilization rate had an impact on the seed yield reduction in both seasons, the *post-hoc* test revealed that only the effect of N0 in 2022 was significantly different from all other nitrogen fertilization rates (N50-200). It showed that in a relatively low infestation rate the preference to larger or denser crops was not evident. Hence, the conclusions on the effect of the fertilizer type or application method on the *O. nubilalis* damage cannot be made. Moreover, Phelan et al. (1995) studied the preference of *O. nubilalis* moth egg-laying patterns in conventionally and organically managed soils and concluded that in organic soils the egg-laying was uniformly low in all treatments. In addition, the ovipositional preference did not correlate with plant biomass, suggesting that buffering effect of soil biodiversity through soil management practices can significantly affect the susceptibility of crops without compromising the plant productivity (Phelan et al. 1995).

Previous studies have suggested that *O. nubilalis* prefers larger plants with larger stalk diameter (Small et al. 2007). This can lead to inflorescence damage and breakage of hemp stalks in the field with consequent entanglement of plantings, greatly hampering mechanized harvesting. The stalk diameter of hemp plants had been measured only in 2021 in our experiment, but in case of increasing *O. nubilalis* damage during upcoming years, it could be considered a relevant parameter for considering the sowing rates and nutrient application. In the case of maize, in addition to stalk diameter, the cell wall thickness, as well as cell wall concentrations of xylose and diferulate esters have shown to be possible crop-based defence mechanisms against the *O. nubilalis* damage (Barros-Rios et al. 2011).

On its main host—maize—*O. nubilalis* has shown to reduce the seed yield up to approximately 25% (Tiwari et al. 2009). The magnitude of damage is mainly dependent on the number of *O. nubilalis* larvae per plant and in case of maize, it is common to assess the 3–5% seed yield reduction per larva per plant. *O. nubilalis* can also significantly damage the yields of maize cultivated for silage. In our experiment, the overall reduction of biomass and seed yield due to the damage caused by European corn borer has been relatively low so far, but the increasing trend of infestation (by 154% between the years studied) is alarming and demands more attention to integrated pest control measures. The hemp plants seem to be attractive hosts for oviposition of adult females and food source for developing larvae. Moreover, lodging and breakage of damaged stalks during mechanical harvesting would probably add to the losses in seed yield in real cultivation systems.

European Corn Borer as a Range-spreading Pest

A previous study modelling the potential northern shift of *O. nubilalis* concluded that the northern limit of expansion of *O. nubilalis* can be attributed to latitude 58°N in Europe (Keszthelyi and Somfalvi-Toth 2020). It is located right on the southern part of Estonia. Although in entomological monitoring the *O. nubilalis* moths have been noticed in natural landscapes up to latitude 63°N (GBIF.org 2023), no damage of agronomical importance has not been registered.

It is known that for full completion of the life cycle (larva, pupa, moth), 711 degree-days of effective temperatures are required in Russia (Grigoryev 1998). Besides, both uni-, bi- and multivoltine ecotypes of the species have been stably represented in Europe, from which univoltine is the most widely distributed. In the USA, the ecotype change triggered by climatic fluctuation is mostly specific for the southern and middle part of the country. In summary, the northward expansion of the more generations of ecotypes of this serious pest may clearly cause increasing damage in maize and hemp cultivation areas globally (Keszthelyi and Somfalvi-Toth 2020). In our climatic region so far only univoltine ecotypes are considered potentially relevant pests, although no studies on this have been performed.

The fact that the range of *O. nubilalis* population could expand up to 40 km in a year, the increasing areas of maize cultivated mainly for animal feed and hemp cultivated for seed oil and higher winter temperatures in the northern

Baltic region provide a solid basis for the spreading of *O. nubilalis* further north, although no damage of significant agronomic importance to hemp crop has not been reported by the farmers yet The northern shift of the pest might usually initiate their polyphagous nature and as Estonia has one of the highest hemp cultivation areas in Europe, the crop previously thought as relatively pest-free might need thorough yearly pest status investigation and integrated *O. nubilalis* control practices adapted to site-specific agro-climatic conditions.

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Conflict of interest E. Runno-Paurson, E. Mäeorg, O. Kurina, E. Õunap, A. Kännaste, Ü. Niinemets and P. Lääniste declare that they have no competing interests.

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2020–2021	The use of biobased coating and binding materials in wooden sinks (L200053PKTT)
2016–2020	Kõrgkooliõpik "Taimekasvatus" (27-5/72/2016/)
2017–2017	Study on the bioactive compounds in nettle (Urtica L.) (L170072PKTM)
2017–2017	Study on the massage candles (L170141PKTM)
2010–2014	Finding alternative solutions to pre-sprouting, through longer thermal shock treatment and use of humic extract, explaining their effect on the formation of yield structure elements of potato (ETF8495)
2008–2013	Diversity, integrity and sustainability of agroecosystems (SF0170052s08)
2007–2007	Rohtsed energiakultuurid Eestis (8-2/T7059PKPK)
2003–2007	Investigation of different systems of plant and land cultivation (incl. environment friendly methods) as well as of the theoretical basis of their elements for finding optimal practical solutions (SF0172616s03)

ELULOOKIRJELDUS

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Perekonnanimi Mäeorg
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Haridustee

2022–	Doktoriõpe, Põllumajandus, Eesti Maaülikool
2002–2004	Eesti Põllumajandusülikool, magistrant (taimekasvatuse eriala)
2001-2002	Eesti Põllumajandusülikool, õpetajakoolituse program (loodusteadused gümnaasiumi tasemel)
1996–2001	Eesti Põllumajandusülikool, bakalaureuseõpe (põllumajandussaaduste tootmine ja turustamine)

Teenistuskäik

2022–	nooremteadur, Eesti Maaülikool, Põllumajandus- ja keskkonnainstituut, taimebioloogia ja maaviljeluse/taimekasvatuse ja taimebioloogia õppetool
2014–2022	lektor, Eesti Maaülikool, Põllumajandus- ja keskkonnainstituut, taimekasvatuse ja rohumaaviljeluse osakond/taimekasvatuse ja taimebioloogia õppetool
2009–2014	nimetatud lektor (0,5)/projekti koordinaator (0,5) Eesti Maaülikool
2005–2011	tõlkija, Interlex OÜ
2003–2009	agronoom, Eesti Maaülikool, Põllumajandus- ja keskonna Instituut
2003	Põllumajanduse Registrite ja Informatsiooni Amet, Toetuste kontrolli osakonna riiklike toetuste kontrolli büroo peainspektor
1998–2001	tõlkija, Patendibüroo AS Käosaar & CO

Teaduskraadid

Magistrikraad, 2004, (juh) Juhan Jõudu; Peeter Lääniste, Mõnede Eestis kasvatatavate rapsisortide õli steroolne koostis, Eesti Põllumajandusülikool

Teadustöö põhisuunad

Taimekasvatus, põllukultuuride kasvatamine, taimehaigused

Teadusorganisatsiooniline ja -administratiivne tegevus

2012–2016	Eesti Maaülikooli Agrobiotehnoloogia arenduskeskuse nõukogu liige

2012–2015 Eesti Maaülikooli Põllumajandus ja keskkonnainstituudi magistriõppekava "Taimesaaduste tootmistehnoloogiad ja tootearendus" õppekava juht

2009–2014 SA Arhimedese Kõrgkoolide koostöö ja innovatsiooni arendamine alameetme projekti "Põllumajandus- ja tehnikavaldkonna õppekavade integreerimine – biotehnilised süsteemid ning toote- ja tehnoloogiaarendus" projekti koordinaator

Osalemine uurimisprojektides

2024–2030 Agroökoloogia ja uued kultuurid tulevikukliimas (TK200U1)

2025–2029 Strateegiad vähendamaks patogeenidest tingitud kartuli haavatavust Põhja-Euroopa muutuvas kliimas (PRG2503)

2025–2029 Taimebioloogia ja taimede väärindamise teadustaristu – PKTT (TARISTU24-TK28)

2021–2023 Teravilja ja õlikultuuride väärindamine (RESTA28)

2021–2022 Biomaterjalist istutuspottide mehaaniliste omaduste parandamise uuringud (L210057PKTT)

2020–2022 Seleeni ja räniga rikastatud ja klimaatiliste tingimustega kohanenud toidu ja sööda tootmine vähemväärtuslikul mullal (ERA-Net Cofund FACCE SURPLUS rahastamistaotlus nr 45)

2020–2021 Biopõhiste katte- ja sideainete kasutamine puitvalamute valmistamisel (L200053PKTT)

2016–2020 Kõrgkooliõpik "Taimekasvatus" (27-5/72/2016/)

2017–2017 Nõgeses (Urtica L.) sisalduvate bioaktiivsete ainete uuringud (L170072PKTM)

2017–2017 Massaažiküünalde valmistamise uuringud (L170141PKTM)

2010–2014 Eelidandamisele alternatiivsete lahenduste leidmine läbi pikemaajalise termošoki ja humiinpreparaadi kasutamise, selgitades nende mõju kartuli saagistruktuuri elementide kujunemisele (ETF8495)

2008–2013 Agroökosüsteemide mitmekesisus, terviklikkus ja jätkusuutlikkus (SF0170052s08)

2007–2007 Rohtsed energiakultuurid Eestis (8-2/T7059PKPK)

2003–2007 Erinevate taimekasvatus- ja maaviljelussüsteemide (s. h. loodussäästlike viljelusviiside) ning nende elementide teoreetiliste aluste uurimine optimaalsete praktiliste lahendite leidmiseks (SF0172616s03)

LIST OF PUBLICATIONS

1.1. Scholarly articles indexed by Web of Science

Mäeorg, E.; Lääniste, P.; Nassar, H.; Kännaste, A.; Tedersoo, L.; Niinemets, Ü.; Runno-Paurson, E. (2026). How do the nitrogen level and form and crop density influence the progression of alternaria leaf spot disease on hemp crop in Northern Baltic region? Cogent Food & Agriculture,12(1).

Zekker, I.; Kännaste, A.; Eremeev, V.; Kask, K.; Meinson, P.; Nassar, H.; **Mäeorg, E.**; Runno-Paurson, E.; Niinemets, Ü. (2025). Impacts of nitrogen fertilization and planting date on the physiology and yield of purple sweet potato at the extreme Northern edge of cultivation. PLoS ONE, 20 (3), e0318531.

Eremeev, V.; Kuht, J.; Margus, K.; **Mäeorg, E.**; Loit-Harro, E.; Luik, A.; Talgre, L. (2025). Effects of potato cultivation on soil pHKCl and exchangeable calcium under organic and conventional management. Acta Agriculturae Scandinavica Section B - Soil & Plant Science, 75 (1), Art No 2577425.

Runno-Paurson, E.; **Mäeorg, E.**; Kurina, O.; Őunap, E.; Kännaste, A.; Niinemets, Ü.; Lääniste, P. (2024). Widespread Occurrence of European Corn Borer (*Ostrinia nubilalis*) and Damage of Industrial Hemp (*Cannabis sativa*) Crop in Northern Europe. Gesunde Pflanzen, 76 (2), 434–444.

Talgre, L.; Eremeev, V.; **Mäeorg, E.**; Luik, A. (2023). Diversified cropping systems for promoting the beneficial insects-ground beetles (Coleoptera: Carabidae). Agronomy Research, 21(SI2), 592–597.

Madsen, H.; Luik, A.; Eremeev, V.; **Mäeorg, E.**; Talgre, L. (2023). Changes in weed biomass, density and diversity in long-term crop rotation experiment during second rotation. Agraarteadus, 34(1), 18–30.

Kuht, J.; Eremeev, V.; Loit, E.; Alaru, M.; **Mäeorg, E.**; Talgre, L.; Luik, A. (2023). Changes in the content of soil organic carbon and total nitrogen in the organic and conventional cropping systems. Agronomy Research, 21(2), 814–823.

Kuht, J.; Eremeev, V.; Talgre, L.; Loit, E.; **Mäeorg, E.**; Margus, K.; Runno-Paurson, E.; Madsen, H.; Luik, A. (2022). Soil microbial activity in different cropping systems under long-term crop rotation. Agriculture, 12(4), 532.

Margus, K.; Eremeev, V.; Loit, E.; Runno-Paurson, E.; **Mäeorg, E.**; Luik, A.; Talgre, L. (2022). Impact of farming system on potato yield and tuber quality in Northern Baltic sea climate conditions. Agriculture, 12(4), 568.

Eremeev, V.; Talgre, L.; Kuht, J.; **Mäeorg, E.**; Esmaeilzadeh-Salestani, K.; Alaru, M.; Loit, E.; Runno-Paurson, E.; Luik, A. et al. (2020). The soil microbial hydrolytic activity, content of nitrogen and organic carbon were enhanced by organic

farming management using cover crops and composts in potato cultivation. Acta Agriculturae Scandinavica Section B - Soil & Plant Science, 70(1), 87–94.

Kuht, J.: Eremeev, V.; Talgre, L.; Alaru, M.; Loit, E.; **Mäeorg, E.**; Esmaeilzadeh-Salestani, K.; Luik, A. (2019). Changes in the soil microbial hydrolytic activity and the content of organic carbon and total nitrogen by growing spring barley undersown with red clover in different farming systems. Agriculture, 9(7), 146.

Kuht, J.; Eremeev, V.; Talgre, L.; Madsen, H.; Toom, M.; **Mäeorg, E.**; Loit, E.; Luik, A. (2017). The content of weed seeds in the soil based on the management system. Agronomy Research, 15(5), 1934–1943.

Talgre, L.; Roostalu, H.; **Mäeorg, E.**; Lauringson, E. (2017). Nitrogen and carbon release during decomposition of roots and shoots of leguminous green manure crops. Agronomy Research, 15(2), 594–601.

Lääniste, P.; Eremeev, V.; **Mäeorg, E.**; Jõudu, J. (2016). Effect of sowing date on oil, protein and glucosinolate content of winter oilseed rape. Agronomy Research, 14, 1384–1395.

Kuht, J.; Eremeev, V.; Talgre, L.; Madsen, H.; Toom, M.; **Mäeorg, E.**; Luik, A. (2016). Soil weed seed bank and factors influencing the number of weeds at the end of conversion period to organic production. Agronomy Research, 14(4), 1372–1379.

Eremeev, V.; Tein, B.; Lääniste, P.; **Mäeorg, E.**; Kuht, J. (2015). The effect of pre-planting thermal treatment of seed tubers on the yield and quality of potato. Agronomy Research, 13(5), 1193–1201.

Lääniste, P.; Jõudu, J.; Eremeev, V.; **Mäeorg, E.** (2008). Effect of sowing date and increasing sowing rates on plant density and yield of winter oilseed rape. Acta Agriculturae Scandinavica Section B, 58(4), 330–335.

Eremeev, V.; Jõudu, J.; Lääniste, P.; **Mäeorg, E.** (2008). Consequences of pre-planting treatments of potato seed tubers on leaf area index formation. Acta Agriculturae Scandinavica Section B, 58(3), 236–244.

Lääniste, P.; Jõudu, J.; Eremeev, V.; **Mäeorg, E.** (2007). Sowing date influence on winter oilseed rape overwintering in Estonia. Acta Agriculturae Scandinavica Section B, 57(4), 342–348.

1.2. Peer-reviewed articles in other international research journals

Madsen, H.; Talgre, L.; Kuht, J.; Alaru, M.; Eremeev, V.; **Mäeorg, E.**; Loit, E.; Luik, A. (2020). Organic Cropping Systems do not Increase Weed Seed Numbers but do Increase Weed Diversity. Agricultural Research & Technology Open Access Journal, 23(4).

Margus, K.; Eremeev, V.; Lääniste, P.; **Mäeorg, E.**; Tein, B.; Laes, R.; Jõudu, J. (2014). Humiinainete mõju kartuli saagikusele ja mugula mõningatele kvaliteedi näitajatele. Agraarteadus, XXV(2), 82–88.

Eremeev, V.; Tein, B.; Lääniste, P.; **Mäeorg, E.**; Laes, R.; Margus, K.; Jõudu, J. (2014). Soojalöögi ja eelidandamise mõju kartuli saagikusele ning selle kvaliteedile. Agraarteadus, XXV(2), 64–69.

Eremeev, V.; Lääniste, P.; **Mäeorg, E.**; Jõudu, J. (2008). Mugulate arvu kujunemise dünaamika sõltuvalt seemnekartuli termilisest töötlemisest. Agraarteadus, XIX(2), 3–9.

Mäeorg, E.; Lääniste, P.; Jõudu, J.; Mäeorg, U. (2007). Some important aspects of sterol analysis of vegetable oils. Proceedings of the Estonian Academy of Sciences. Chemistry, 56(2), 59–66.

1.3. Scholarly articles in Estonian and other peer-reviewed research journals with a local editorial board

Mäeorg, E.; Lääniste, P.; Jõudu, J.; Mäeorg, U. (2005). The oil content and sterol composition of spring oilseed rape seeds. Latvian Journal of Agronomy, 8, 133–136.

3.4. Articles/presentations published in conference proceedings not listed in Section 3.1

Madsen, H.; Talgre, L.; Eremeev, V.; Alaru, M.; **Mäeorg, E.**; Luik, A. (2017). Winter cover crops decrease weediness in organic cropping systems. Proceedings of NJF Seminar 495.

3.5. Articles/presentations published in local conference proceedings

Mäeorg, E.; Lääniste, P.; Nassar, H.; Kännaste, A.; Tedersoo, L.; Niinemets, Ü.; Runno-Paurson, E. (2026). Kuivlaiksuse esinemine õlikanepil erinevate väetustasemete juures. Agronoomia 2026, 164–174.

Mäeorg, E.; Lääniste, P.; Kurina, O.; Õunap, E.; Kännaste, A.; Niinemets, Ü.; Runno-Paurson, E. (2024). Hariliku varreleediku (*Ostrinia nubilalis*) esinemine ja kahjustused õlikanepil. Agronoomia 2024, 139–147.

Eremeev, V.; Kuht, J.; Tein, B.; Talgre, L.; Alaru, M.; Runno-Paurson, E.; **Mäeorg, E.**; Loit, E.; Luik, A. (2019). Kartuli kasvatamise mõju mulla mikrobioloogilisele aktiivsusele. Agronoomia 2019, 29–36.

Eremeev, V.; Lääniste, P.; Tein, B.; **Mäeorg, E.**; Kuht, J. (2015). Seemnemugulate termilise töötlemise ja humiinainete kasutamise mõju kartuli saagikusele. Agronoomia 2015, 62–69.

Eremeev, V.; Lääniste, P.; Tein, B.; **Mäeorg, E.**; Kuht, J. (2015). Humiinpreparaadi kasutamise mõju kartulile. Agronoomia 2015, 56–61.

5.2. Conference abstracts that do not belong to Thomson Reuters Web of Science

Kuht, J.; Eremeev, V.; Talgre, L.; Madsen, H.; Toom, M.; **Mäeorg, E.**; Loit, E.; Luik, A. (2017). The content of weed seeds in the soil based on the management system. 8th International Conference on Biosystems Engineering 2017 Book of Abstracts.

Kuht, J.; Eremeev, V.; Talgre, L.; Madsen, H.; Toom, M.; **Mäeorg, E.**; Luik, A. (2016). Soil weed seed bank and factors influencing the number and species of weeds at the end of conversion period to organic production. Biosystems Engineering 2016 Book of Abstracts.

Lääniste, P.; Eremeev, V.; **Mäeorg, E.**; Jõudu, J. (2016). Effect of sowing date on oil, protein and glucosinolate content of winter oilseed rape. Biosystems Engineering 2016 Book of Abstracts.

Madsen, H.; Eremeev, V.; Talgre, L.; Luik, A.; **Mäeorg, E.** (2015). In organic crop rotation winter cover crops improve soil, weed suppression and crop yields. Proceedings of the 25th NJF Congress: Nordic View to Sustainable Rural Development, Latvia, Riga , June 16-18 2015. Ed. Sandija Zeverte-Rivza. Latvia, Riga: NJF Latvia, 2015, 91–96.

Eremeev, V.; Lääniste, P; **Mäeorg, E.**; Jõudu, J. (2008). The influence of thermal shock and pre-sprouting on formation of yield structure elements in early potato varieties. EAPR Conference Proceedings.

PÕLLUMAJANDUSE ÕPPEKAVA VIIMASEID KAITSMISI

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27.märts 2026

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