

**Zróźnicowanie nisz ekologicznych i wzorce
rozmieszczenia inwazyjnych gatunków makrofitów
jako klucz do ich zwalczania**



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**Ecological niche differentiation and distribution
patterns of invasive macrophyte species as a key to
their control**



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Streszczenie

Do niedawna rozprzestrzenianie się obcych gatunków roślin wodnych w Europie było nierównomierne - większość inwazji miała miejsce w Europie Zachodniej i Południowej, podczas gdy kraje Europy Środkowej i Wschodniej, takie jak Polska, były stosunkowo mało narażone na ich presję. Należy podkreślić, że wiedza na temat rozmieszczenia, podstawowych uwarunkowań środowiskowych i behawioru wielu gatunków obcych w kraju pozostaje na niewystarczającym poziomie. Stąd zrozumienie biologii i ekologii obcych gatunków roślin wodnych jest kluczowe dla poznania podstawowych mechanizmów stojących za ich inwazyjnością. Celem niniejszej pracy doktorskiej była: (1) ocena składu gatunkowego obcych gatunków roślin wodnych, wzorców rozmieszczenia, zasobów i ich dynamiki z różnych typów ekosystemów wodnych; (2) wyznaczenie gradientów środowiskowych, względem których rozmieszczone są obce gatunki roślin wodnych w różnych typach ekosystemów wodnych; (3) przedstawienie najważniejszych parametrów abiotycznych (parametry klimatyczne, fizyczno-chemiczne wód) wyjaśniających zróżnicowanie występowania obcych gatunków roślin wodnych i zmian czasowych ich siedlisk; (4) wyznaczenie modeli nisz siedliskowych poszczególnych gatunków obcych gatunków roślin wodnych.

Przeprowadzone badania wykazały obecność 15 gatunków roślin obcych obecnych na ponad 300 stanowiskach rozprzestrzenionych na terenie tego kraju, a także ujawniły wzorce ich rozmieszczenia w różnych typach środowisk wodnych, uwzględniając uwarunkowania klimatyczne i środowiskowe. Ponadto, stworzone modele nisz wykazały kluczową rolę rosnących zimowych temperatur na rozprzestrzenianie się większości z analizowanych gatunków.

W celu określenia reakcji wzrostu czterech gatunków (*Cabomba caroliniana*, *Elodea nuttallii*, *Azolla filiculoides* i *Vallisneria spiralis*) na czynniki temperaturowe i świetlne przeprowadzono szereg eksperymentów laboratoryjnych i terenowych. Na tej podstawie następnie wyciągnięto wnioski na temat nie tylko uwarunkowań środowiskowych i realizowanych nisz przez badane gatunki inwazyjne, ale również oceniono wpływ wynikających ze zmian klimatycznych rosnących temperatur na dalsze losy ich inwazji. Co więcej, badane gatunki wykazały się wysoką tolerancją na zacienienie i szybkim wzrost w wodzie o podwyższonej temperaturze, co zapewne przekłada się na ich wysoką konkurencyjność.

Poznanie biologii inwazyjnych gatunków obcych pozwoliło zaplanować i przetestować metody zwalczania i kontroli, z możliwością zastosowania w warunkach wód Europy środkowej. W tym celu przeprowadzono zarówno badania terenowe, hodowlane jak i przetestowano efektywność łącznie pięciu różnych metod kontroli. Testowane metody kontroli wykazały, że chociaż tego typu zabiegi wymagają dużej precyzji w wykonaniu, to ograniczanie rozwoju populacji obcych roślin wodnych jest możliwe.

Dodatkowym efektem niniejszej pracy było stworzenie unikalnej i stale rozwijanej, bazy danych monitorującej historię rozprzestrzeniania się obcych gatunków roślin wodnych na terenie Polski.

Słowa kluczowe: gatunki inwazyjne, makrofity, rozmieszczenie, siedliska, wzorce rozmieszczenia, nisze ekologiczne, metody kontroli, badania podwodne

Abstract

Until recently, the spread of non-native aquatic plant species in Europe was uneven—most invasions occurred in Western and Southern Europe, while Central and Eastern European countries, such as Poland, were relatively less exposed to their pressure. It is important to emphasize that knowledge about the distribution, environmental conditions, and behavior of many non-native species in Poland remains insufficient. Therefore, understanding the biology and ecology of non-native aquatic plant species is crucial for uncovering the fundamental mechanisms behind their invasiveness.

The objectives of this doctoral thesis were: (1) to assess the species composition, distribution patterns, abundance, and dynamics of non-native aquatic plants across different types of aquatic ecosystems; (2) to identify environmental gradients along which non-native aquatic plants are distributed in various types of aquatic ecosystems; (3) to present the key abiotic parameters (climatic and physicochemical water parameters) that explain the variability in the occurrence of non-native aquatic plants and the temporal changes in their habitats; and (4) to determine habitat niche models for individual non-native aquatic plant species.

The research identified the presence of 15 non-native plant species across more than 300 locations throughout the country and revealed their distribution patterns in different aquatic environments, considering climatic and environmental factors. Additionally, the developed niche models demonstrated the critical role of increasing winter temperatures in the spread of most of the analyzed species.

To evaluate the growth response of four species (*Cabomba caroliniana*, *Elodea nuttallii*, *Azolla filiculoides*, and *Vallisneria spiralis*) to different temperature and light conditions, a series of laboratory and field experiments were conducted. Based on these experiments, conclusions were drawn not only about the environmental preferences and realized niches of the studied invasive species but also about the impact of rising temperatures due to climate change on their future invasions. The studied species exhibited high tolerance to shading and rapid growth in water with elevated temperatures.

Understanding the biology of invasive non-native species was then the basis for planning and testing control methods with potential applicability in the conditions of Central European waters. For this purpose, both field and cultivation studies were conducted, testing the effectiveness of five different control methods. The tested methods showed that, although such methods require great precision, limiting the growth of non-native aquatic plant populations is possible. An additional outcome of this work was the creation of a unique and continuously expanded database that monitors the history of the spread of non-native aquatic plant species in Poland.

Keywords: invasive species, macrophytes, distribution, habitats, distribution patterns, ecological niches, control methods, underwater research

List of original publications:

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- 1) **Draga M.**, Szczeńiak E., Rosadziński S., Bryl Ł., Lisek D., Gąbka M. (2024). Alien aquatic plants in Poland: temporal and spatial distribution patterns and the effects of climate change. *Global Ecology and Conservation*. <https://doi.org/10.1016/j.gecco.2024.e03247>

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- 3) **Draga, M.** & Gąbka, M. (2024). The beneficial effect of barley straw extract addition on the growth of two aquatic invasive alien species (*Elodea nuttallii* and *Cabomba caroliniana*) under laboratory conditions. *Biologia*, 79(1), 11-21. <https://doi.org/10.1007/s11756-023-01550-z>

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- 4) Gąbka M., Bryl Ł., **Draga M.**, Lisek D., Rosadziński S., Dominiak K., Ciężyńska W., Leperowski P. (2022). Opracowanie metod zwalczania dla minimum 10 inwazyjnych gatunków obcych wraz z przeprowadzeniem działań pilotażowych w terenie. Kompendium dotyczące metod zwalczania kabomby karolińskiej (*Cabomba caroliniana*). Generalna Dyrekcja Ochrony Środowiska;
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<https://www.gov.pl/web/gdos/kompendia-zwalczania-wybranych-igo>

Introduction

Invasive species are widely recognized as one of the major threats to ecosystem functioning and global biodiversity, alongside other threats such as habitat loss, over-exploitation, climate change, and pollution (Brook et al., 2008; Cafaro, 2015). While species distribution, migration, and colonization are natural processes for all living organisms, the past few centuries have seen a dramatic increase in the scale of alien species invasions (Seebens et al., 2017). This has led to the disruption or irreversible alteration of numerous ecosystems. The main cause of this situation is likely the rapid advancement of human civilization and the resulting globalization process (Amano et al., 2016). Improvements in logistics and the intensification of international trade have enabled many species to overcome natural dispersal barriers - such as mountains, oceans, and long distances - that had previously kept distinct ecosystems isolated. While some species were intentionally introduced for cultivation of ornamental purposes, a large number have accidentally been introduced to new habitats.

Although only a small portion of introduced species is able to establish itself in a new environment, and an even smaller number become invasive, there is almost no part of the Earth that remains unaffected by the pressure of alien species. (Dawson et al., 2017). While the negative impact of these species on local biodiversity and ecosystem functioning is well-documented, it should also be noted that their spread leads to enormous global socioeconomic losses (Pimentel et al., 2005; Kettunen et al., 2008; Cuthbert et al., 2021; Eschen et al., 2021). It is estimated that invasive species cost the European Union and the USA billions of euros annually, as they disrupt agriculture, fisheries, forestry, and energy sectors, and serve as vectors for parasites and diseases. It is therefore unsurprising that biological invasions are viewed as an urgent issue, not only from an environmental protection perspective but also from a national economic standpoint. The problem is particularly severe in developing countries, where many valuable ecosystems still exist, but financial resources to combat invasive species are limited (van Wilgen, 2018).

As the issue of alien invasions continues to grow in scale, new laws and projects are being implemented—in order to slow down their expansion. A good example of such legislation is the ‘Regulation (EU) No 1143/2014 of the European Parliament and of the Council of 22 October 2014 on the prevention and management of the introduction and spread of invasive alien species’ directive. This regulation requires all the EU member states to monitor, eradicate, and develop national control methods and strategies for alien species of concern. The list of species subject to control at the EU level is continuously expanding, currently including 41 plant and 47 animal species identified as a serious threats to the Union. Additionally, since EU countries often differ significantly in their climate conditions and may face threats from different types of alien species, this directive requires each member state to create its own list of alien species that pose a threat on a national level. The document also provides clear definitions for distinguishing between alien and invasive species - crucial, as these terms are frequently misused as synonyms. In invasion biology, a species is typically considered

'invasive' if it is able to spread rapidly over large distances, successfully establish itself in new habitats, and produce a significant number of offspring that disperses quickly (Pyšek et al., 2004; Pyšek et al., 2020). Under this directive, a species is classified as invasive if it is alien, exhibits a strong negative impact on local ecosystems, and causes serious socioeconomic damage, leading to its inclusion on the European list of invasive alien species. Thus, according to this directive, the term 'invasive species' refers only to those included on the European list of invasive alien species, whether at the EU or national level.

Unfortunately, despite the measures taken so far, the number of new alien species introductions continues to grow (Seebens et al., 2017; Pyšek et al., 2020), and predicting which of these species will exhibit invasive behavior remains nearly impossible. This is often because invasive species can behave very differently in their native versus introduced ranges (Hejda et al., 2015). The difference can be so profound that a species highly invasive in its introduced range, where it dominates local competitors, may play only a minor role in its native ecosystem.

While this phenomenon is not yet fully understood, several explanations have been proposed, including the absence of predators, diseases, or parasites in the new environment, novel competition mechanisms, and purging of genetic loads (Parker et al., 2013). Another factor that complicates the prediction of alien species' impact is the 'lag phase' - a dormant period in the invasion process (Dietz and Edwards, 2006). In many cases, there is a significant time gap between the initial introduction of a species and its rapid spread, which can range from a few years to several decades. During this time, the alien species may be undergoing adaptation to its new environment, such as adjusting to lower temperatures, which will lead to its later rapid spread. Given that we can never be certain whether a species will exhibit invasive characteristics or not, it is essential to closely monitor every such species. By doing so, appropriate control measures can be taken at the very early steps of the invasion.

To combat the negative effects of alien species on both the environment and the economy, a variety of control methods - some quite sophisticated - have been applied for decades. Unfortunately, experience shows that once an alien species establishes a strong population within its novel range, eradicating it or even slowing its further expansion becomes a difficult, time-consuming, and costly task. A one which in some cases is nearly impossible (Hussner et al., 2017; Simberloff, 2021). Control methods can generally be divided into one of the three categories: chemical, biological, and mechanical. In general, chemical methods of control involve the application of pesticides to eliminate or weaken the alien population within a given area, while biological methods rely on the introduction of natural predators or diseases to control the growth and reproduction of the invasive species. Among these, mechanical control methods are perhaps the most diverse, as they include such techniques as: mechanical harvesting and cutting, water level drawdowns, shading, or the application of dyes (Hussner et al., 2017). While a wide array of control methods is available, only a few have a potential to hinder the invasive population in any meaningful way. Thus a selection of a proper control method is never an

easy task, especially that these methods also differ greatly in terms of cost, time investment, and implementation difficulty.

Moreover, many methods can prove harmful to the very ecosystems they aim to protect (Zehnsdorf et al., 2015). For instance, pesticides often affect more than just the targeted species, particularly in aquatic environments. Similarly, biological methods involve introducing another alien species to combat the invader, and the consequences of such introductions are difficult to predict. As a result, selecting an appropriate control method is a complex and challenging task (Hussner et al., 2017; Simberloff, 2021). Experience has shown that the most effective methods are those that are based on a deep understanding of the biology and ecology of the target species (Hussner et al., 2017). However, our knowledge of the environmental preferences and behavior of alien species is typically limited to only a few of the most problematic invaders, leaving many invasive species in need of further study. Since well-established alien populations are notoriously difficult to eradicate, it is widely recognized that the best chance for success lies in controlling them during the early stages of invasion, when both the number of individuals and the area of infestation remain small (Hussner et al., 2017). This highlights the critical importance of environmental monitoring aimed at early detection of alien species, as early invasions are often overlooked (Larson et al., 2020). However, the shortage of specialists capable of accurately identifying alien species means that the spread of many invaders is often underestimated (Kaplan, 2010). Thus, the growing threat posed by invasive species, combined with the challenges of managing their spread, underscores the need for new monitoring and control methods based on a comprehensive understanding of species traits.

Although freshwater ecosystems cover less than 1% of the Earth's surface, they are recognized as global biodiversity hotspots. It is estimated that nearly 10% of the world's species are associated with these unique ecosystems (Dudgeon, 2019). As such, preserving them is essential to slowing the alarming trend of global species extinction and biodiversity loss. It is thus deeply concerning that freshwater ecosystems are under intense anthropogenic pressure and are degrading at a faster rate even than terrestrial ecosystems (Dudgeon et al., 2006). Alien aquatic species are widely acknowledged as one of the most significant challenges these ecosystems face (Ricciardi and Rasmussen, 1999; Dudgeon et al., 2006). Among other threats such as eutrophication, pollution, water drainage, and rising air and water temperatures, alien species invasions are unique due to their ability to alter ecosystem structures and relationships between various organisms, often leading to irreversible changes in their composition. This is particularly concerning, as aquatic species play a critical role in shaping the physicochemical properties of water bodies, and any significant disturbance to their communities is likely to disrupt the habitat itself. Among these organisms, aquatic plants are particularly prominent in their influence on ecosystem functioning. Healthy plant communities perform a range of essential functions, such as nutrient uptake, improving water oxygenation and clarity, stabilizing sediments, preventing algal blooms, and creating new habitats. For these reasons, they are often called 'ecosystem engineers'

(Emery-Butcher et al., 2020). Protecting these vital communities, especially from the threat of invasive aquatic plants, is therefore of the utmost importance.

Unfortunately, managing alien aquatic plant populations is particularly challenging. While some alien plant species may be unable to reproduce sexually in their introduced environments, aquatic plants often rely on vegetative reproduction, a process at which invasive species excel (Havel et al., 2015; Hussner et al., 2017). This means that any method causing plant fragmentation may actually accelerate their further spread, as these plant fragments can often survive and establish themselves in new areas. Moreover, managing plant populations tends to be more difficult than controlling animal populations due to the plants' general resilience to mechanical damage and their effective propagation strategies. Successful control methods for invasive plants are thus relatively rare (Van Driesche et al., 2010). The challenge of managing aquatic plant populations is further compounded by the inherent difficulty of conducting any control technique on or beneath the water. Control methods that are effective on land are often much harder to implement in aquatic environments. Consequently, managing aquatic plants is generally considered more difficult than managing terrestrial plants. Furthermore, many control techniques commonly used for alien aquatic plants - such as pesticide application, mechanical cutting, or draining - can have severe negative effects on the entirety of the freshwater ecosystem (Hussner et al., 2017). Due to the interconnected nature of aquatic environment, it is difficult to target only a specific part of the ecosystem without affecting it as a whole. The herbicides spread easily in water, while mechanical control methods often disturb sediments, leading to a drop in water clarity and the release of the significant amount of nutrients back into the water column. Given these complexities, extreme care must be taken when planning any control measures, particularly in a valuable or protected environment.

Finally, it is also important to acknowledge humans' significant role in facilitating the spread of invasive aquatic species. Many of the most invasive aquatic plants were once part of the ornamental trade, cultivated in garden ponds and aquariums (Hussner, 2012). From these controlled environments, they either escaped or, in some cases, were deliberately released into the wild. Beyond intentional introductions, humans also unintentionally contribute to the propagation of alien aquatic plants, following their initial introduction. Small plant fragments frequently attach to fishing gear and boats, which then transport these fragments to new water bodies, facilitating their further spread (Bruckerhoff et al., 2015). Additionally, human-induced disturbances to ecosystems also significantly contribute to the spread of invasive aquatic plants. Natural habitats with robust native plant communities are generally regarded as more resistant to biological invasions. However, human activities, such as shoreline modifications, eutrophication, and the construction of beaches or fishing platforms weaken these ecosystems, making them more susceptible to invasion. Invasive species typically thrive in such disturbed environments, which is why alien aquatic plants are most often found in human-made or human-altered water bodies (Hussner, 2012). Moreover, human-induced global changes—such as climate change and extreme weather events - further promote the spread of invasive species by

destabilizing natural ecosystems (Turner et al., 2020) and thus making them more vulnerable to invasion (Diez et al., 2012).

Until relatively recently, the spread of alien aquatic species in Europe was uneven, with the majority of invasions occurring in southern and Western Europe, while Central and Eastern European countries, such as Poland, experienced relatively low pressure from alien aquatic plant species (Hussner, 2012). Recent trends, however, indicate a rapid increase in the number of invasive species in these regions, highlighting the growing severity of yet another threat to central European freshwater ecosystems. Therefore, this work aims to improve our understanding of the biology and ecology of invasive aquatic plant species and to explore effective methods for their control in response to this escalating threat.

Research questions

The aim of this work is to deepen our understanding of the biology and ecology of alien aquatic plant species in Central Europe, as well as to identify effective methods for controlling their spread. To achieve this, the following research questions were formulated:

- 1) What are the preferred environmental conditions for alien aquatic plant species, and how do their behavior, distribution patterns, and resource allocation influence their growth and reproduction in the temperate climate of Central Europe?
- 2) Which environmental factors are key to determining the distribution of alien aquatic plant species across various aquatic ecosystems?
- 3) How do different light and water temperature levels affect the growth and reproduction of alien aquatic plant species, and what are the mechanisms behind their spatial colonization and growth potential?
- 4) What are effective strategies for controlling or limiting the spread of alien aquatic plant species in Central Europe's temperate climate?

This study seeks to address these questions by focusing primarily on four alien aquatic plant species: *Cabomba caroliniana*, *Elodea nuttallii*, *Azolla filiculoides* and *Vallisneria spiralis*. However, the distribution and environmental preferences of other alien aquatic plant species observed in Poland was also analyzed to an extent. The importance of the selected species is underscored by the fact that *C. caroliniana* and *E. nuttallii* are listed as ‘Invasive Alien Species of Union Concern’ while *A. filiculoides* appears on Poland's list of ‘Invasive Alien Species of Member State Concern’ for Poland. Both lists are grounded in the ‘Regulation (EU) No 1143/2014 of the European Parliament and of the Council of 22 October 2014 on the prevention and management of the introduction and spread of invasive alien species’. This directive identifies the most dangerous invasive species that pose a serious

and imminent threat to the natural environment and the socioeconomic stability of the European Union, requiring member states to monitor and eradicate them.

Research tasks

To better present the efforts made to address the research questions, the tasks performed in this study have been divided into the following three categories. However, it should be noted that in practice, many tasks are difficult to assign to a single category, and thus their functions may overlap.

I. Understanding the biological niches, environmental gradients, behavior, distribution patterns, and interactions of invasive macrophytes (field study)

A proper understanding of the relationships between a species and its environment - involving its niche, behavior, and the strategies that enable its rapid expansion - is only achievable through field studies. Therefore, as part of this research, environmental observations of domestic populations of the selected macrophytes were conducted. Firstly, a large-scale survey was conducted to locate sites of various alien aquatic plant species all across Poland. Following these surveys, a subset of sites (10 sites in total with present specimens of *E. nuttallii* or *C. caroliniana*) were selected for more detailed ecological monitoring. At a later stage, these same sites were also used for the testing of alien aquatic plants control methods. As part of this ecological monitoring, the state of the populations, their distribution patterns, depth of occurrence, presence of accompanying native species, and basic physicochemical parameters of the water bodies, such as pH, water transparency, and the levels of various forms of nitrogen, phosphorus, and other key elements were assessed. In two of the water bodies, water temperature changes throughout the year were also measured using waterproof diver-type loggers. Based on this data, niche models were developed for the selected alien species, and their distribution patterns, along with their interactions with native aquatic plants, were determined. Field observations and morphological measurements of the collected individuals conducted during this phase were later used in the chapters 'Charakterystyka kabomby karolińskiej' and 'Charakterystyka moczarki delikatnej' in both handbooks (**Orig. Pub. No. 4** and **5** respectively).

Additionally, the data collected during ecological monitoring on the distribution of *C. caroliniana*, *E. nuttallii*, *A. filiculoides*, and *V. spiralis*, and other alien aquatic plant species, was later supplemented with comprehensive literature study and unpublished observations from other experts on alien aquatic plants in Poland. This effort led to the creation of a unique relational database, developed by the author in the MySQL program, which compiles all currently known records of alien aquatic plant species in Poland. The database includes not only basic information such as species names and locations, but also details on the timing of observations, population sizes, associated native plant species, types of water bodies, and physicochemical data (when available). It is important to note that

no such database documenting the history of aquatic plant invasions in Poland has ever been created before, and it continues to be expanded with new field observations. The current distribution of alien aquatic plants in Poland, the impact of environmental gradients, and their distribution patterns were subjects of analyses described in the paper 'Alien aquatic plants in Poland: temporal and spatial distribution patterns and effects of climate changes' (**Orig. Pub. No. 1**) which were based on the records from this database.

II. Investigating the impact of abiotic factors on the growth of invasive macrophytes (experimental study)

Understanding the influence of key abiotic factors is crucial for comprehending the relationship between an alien plant species and its environment, as well as its competitiveness and its spread potential. Since some of the selected alien macrophytes have only recently started spreading in Poland, it is possible that their current distribution is driven by rising average air and water temperatures associated with global warming. Furthermore, as many of alien aquatic plant species originate from warmer regions of the world, it may be assumed that it is their low tolerance to low winter temperatures that so far limited their presence in Central Europe. Another key factor that could explain the invasive character presented by some of the alien plant species is their tolerance to low light conditions, as light competition is typically intense in the freshwater ecosystems. Therefore, in order to better understand the mechanisms driving the growth and invasiveness of selected alien plant species, laboratory studies were performed with particular focus on the species response of low to medium temperature and light conditions. The results of this study were presented in the paper titled: 'Can invasive aquatic plants thrive in cold water and low light conditions? Implications for control – an experimental study' (**Orig. Pub. No. 2**).

Additionally, the already described database on the distribution of alien aquatic plant species in Poland, also served as the basis for another analysis of the influence of abiotic factors such as air temperature, sunlight, and the number of rainy or snowy days on the development of alien aquatic plant species. For this purpose, data on the locations of alien species were combined with climate data from nearby meteorological stations. The resulting dataset was then used to conduct an RDA analysis of the impact of these factors on alien aquatic plants as well as to create GLM models describing the relationship between the occurrence of these species and the average monthly minimum air temperature. The entire process, along with the results, was described in the paper 'Alien aquatic plants in Poland: temporal and spatial distribution patterns and effects of climate changes' (**Orig. Pub. No. 1**).

III. Evaluating the effects and the response of invasive aquatic plants to the selected control methods under Central and Eastern European conditions

The search for effective control methods for alien aquatic plant species must be based on a thorough understanding of their biology and ecology. Therefore, based on field observations and literature studies, several control methods with a high likelihood of success were selected for each of the three following species: *C. caroliniana*, *E. nuttallii*, and *A. filiculoides*. A total of six methods were designated for testing across 13 of the 22 initially selected sites. A key criterion for their selection was their minimal environmental impact, ensuring they could be implemented even in legally protected, valuable natural habitats. Unfortunately, due to the disappearance of *A. filiculoides* from its only known locations on the Oder River, the project funding the selected control methods was limited to testing methods for only two species: *C. caroliniana* and *E. nuttallii*. As a result, the planned methods for controlling *A. filiculoides* (removal with suction pumps, barley straw barriers, and manual removal from the surface) were not tested.

Ultimately, four different control methods were tested across 16 sites located within 10 different water bodies. Each method was preceded by a detailed environmental monitoring, during which three permanent transects were established at each site in order to assess the population status and characteristics of the invasive species, as well as their reaction to the tested method. Simultaneously, basic data on the physicochemical conditions of the water bodies were collected. Additionally, 45 individuals were sampled from each site for morphological analysis. Three subsequent monitoring were performed at each site in an identical manner, after the initial application of each of the tested methods. Each time, new specimens were collected for further morphological analysis and to evaluate their response to the treatments, if they were present. In total, over the course of study, a total of 1,570 specimens were analyzed in terms of total length, main shoot length, number of offshoots, offshoots length, and dry mass. In many cases, monitoring was carried out using diving techniques. A comprehensive description of the work, environmental impact, as well as the advantages and disadvantages of each method, is provided for each species in their respective compendiums (**Orig. Pub. No. 4 and 5**).

Additionally, an alternative control method for alien aquatic plant species was tested in another experimental study. The effects of barley straw extracts, widely used to limit undesirable phytoplankton blooms due to their effectiveness, low environmental risk, and cost-efficiency, on the growth of two invasive plant species (*C. caroliniana* and *E. nuttallii*) were also evaluated. However, the experiment did not demonstrate any negative effect on the studied aquatic plant species. On the contrary, in some cases, the extract seemed to promote the growth of selected invasive species. A detailed description of the experiment and its findings is presented in the publication titled 'The Beneficial Effect of Barley Straw Extract Addition on the Growth of Two Aquatic Invasive Alien Species' (**Orig. Pub. No. 3**).

Effective monitoring is crucial for detecting and controlling invasive species, as methods applied during the early stages of invasion are known to have the highest chances of success. Monitoring efforts typically require considerable time, resources, and expertise in species identification. However, ongoing advancements in machine learning are offering innovative tools that are proving increasingly effective in addressing a range of ecological issues. In order to improve monitoring efforts, a novel approach was tested for the *A. filiculoides* detection, which relies on semantic pixel segmentation of multispectral images with the help of machine learning techniques. This method leveraged the distinctive coloration of the fern, for the effective training of a machine learning algorithm. Once trained, the algorithm could accurately detect pixels with *A. filiculoides* on the presented images. The method was then tested on a section of the Tagus River in Spain, which in recent years has experienced an unprecedented invasion by *A. filiculoides*. The pre-trained model was applied to satellite images of selected sections of the river over two years to track monthly changes in the species' population. The project demonstrated that remote monitoring of such species is possible if images of sufficient resolution are provided. Additionally, it revealed interesting seasonal fluctuations in the species' density, likely reflecting the influence of basic climatic factors. The project culminated in the successful defense of a master's thesis titled 'Random Forest Detection of the Invasive Species *Azolla filiculoides* from Multispectral Data,' completed as part of the author's Data Science master studies at the Faculty of Mathematics and Computer Science, Adam Mickiewicz University in Poznań.

Chapter 1

Alien aquatic plants in Poland: temporal and spatial distribution patterns and the effects of climate change

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Oświadczenie współautora pracy


Ja, Mateusz Draga, oświadczam, że jestem współautorem pracy pt. „**Alien aquatic plants in Poland: temporal and spatial distribution patterns and the effects of climate change**” autorstwa: Mateusza Dragi*, Ewy Szczęśniak, Stanisława Rosadzińskiego, Łukasza Bryła, Daniela Liska oraz Macieja Gąbki, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Mój udział polegał na: konceptualizacji pracy, zbiorze danych dotyczących rozmieszczenia obcych gatunków roślin wodnych, stworzeniu relacyjnej bazy danych zawierającej wszystkie znane stanowiska obcych roślin wodnych na terenie Polski, selekcji i opracowaniu danych klimatycznych, wykonaniu analiz statystycznych, tabel oraz rycin, jak i na stworzeniu oraz edycji manuskryptu, zgłoszenia go do czasopisma oraz korespondencji z edytorem i naniesieniu poprawek zgodnie z uwagami recenzentów.

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Podpis współautora



Podpis promotora

Poznań 16.09.2024

Oświadczenie współautora pracy

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Mój udział polegał na: przeglądzie danych zielnikowych, zbiorze i udostępnieniu danych dotyczących rozmieszczenia obcych gatunków roślin wodnych, edycji tekstu manuskryptu oraz naniesieniu poprawek zgodnie z wytycznymi recenzentów.

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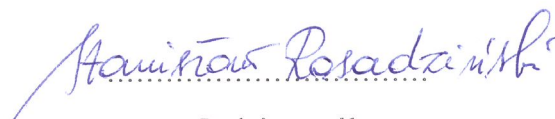
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Podpis współautora

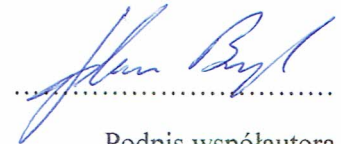
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Mój udział polegał na zbiorze i udostępnieniu danych dotyczących rozmieszczenia obcych gatunków roślin wodnych.

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Mój udział polegał na: zbiorze i udostępnieniu danych dotyczących rozmieszczenia obcych gatunków roślin wodnych oraz wygenerowaniu map z rozmieszczeniem obcych roślin wodnych na terenie Polski.

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Podpis współautora

Poznań 16.09.2024

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Mój udział polegał na: pomocy w konceptualizacji pracy, przeglądzie danych zielnikowych, zbiorze i udostępnieniu danych dotyczących rozmieszczenia obcych gatunków roślin wodnych.

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A handwritten signature in blue ink, appearing to read 'M. Gąbka', is written over a horizontal dotted line.

Podpis współautora

Chapter 2

Can invasive aquatic plants thrive in cold water and low light conditions?

Implications for control – an experimental study

Can invasive aquatic plants thrive in cold water and low light conditions?

Implications for control – an experimental study

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Abstract

Light and temperature are critical factors for the growth of all plants, including invasive aquatic macrophytes. The high invasiveness of these problematic species is often linked to their ability to outcompete native plants through greater shade tolerance and rapid growth in elevated temperatures. Moreover, since many invasive aquatic plants are considered thermophilic, it is believed that their spread in Europe may currently be restricted by the low water temperatures prevalent during winter, especially in the eastern and northern regions of the continent. In our experimental study we decided to test two hypotheses: [1] the high competitiveness of invasive alien species is the result of their strong tolerance for shading and [2] although thermophilic invasive aquatic plant species thrive in warm water, they are still capable of surviving in colder conditions. In order to do so, three invasive aquatic plant species - *Elodea nuttallii*, *Cabomba caroliniana*, and *Vallisneria spiralis* - were cultivated under low to moderate light and temperature conditions for seven weeks. After this period, key morphological traits, including shoot length, number of offshoots, dry mass, and chlorophyll *a* content, were measured for each species. Our results indicate that while all species showed the highest growth in the warmest water conditions, they were all capable of surviving in water as cold as 7°C, though in some cases growth was significantly inhibited. Moreover, *V. spiralis* and the typically described as light-dependent *C. caroliniana* displayed broad tolerance to varying light levels, whereas *E. nuttallii* thrived under low light conditions but showed reduced growth at higher light intensities. Additionally, low temperature and light levels were found to inhibit daughter ramet production in *V. spiralis*, while extremely low light conditions induced partial necrosis in the lower parts of *E. nuttallii* shoots, possibly as a strategy to escape unfavorable light conditions. Overall, our research underscores the critical role of temperature in the development of invasive aquatic plants and confirms their high shade tolerance, a key factor in their competitiveness. It is therefore expected that ongoing global warming, combined with reduced water clarity due to increasing eutrophication of water bodies, will likely support the further expansion of invasive aquatic plants, amplifying their already substantial ecological impact.

Keywords

***Elodea nuttallii*, *Cabomba caroliniana*, *Vallisneria spiralis*, invasive aquatic plant species, light, temperature, control methods**

1. Introduction

Despite the growing impact of climate change on the environment, the spread of invasive species continues to be a leading threat to ecosystems worldwide (Brook et al., 2008; Cafaro, 2015). In many cases, these environmental changes actually accelerate the spread of alien species (Lodge, 1993; Sage, 2020). Rising temperatures and increasingly frequent catastrophic events disrupt natural ecosystems, making them more susceptible to invasion by thermophilic and highly competitive species (Rahel and Olden, 2008; Robinson et al., 2020). Unfortunately, freshwater ecosystems, which are recognised as distinctive biodiversity hotspots (Dudgeon, 2019), remain particularly vulnerable to invasion by alien aquatic species (Ricciardi and Rasmussen, 1999; Dudgeon et al., 2006). Aquatic invasive plants (IAP) are particularly problematic within this group of species due to their ability to alter the physico-chemical water conditions of a water body, once their biomass reaches a certain threshold. While the presence of a strong plant community within a water body usually tends to have a strong beneficial effect on the state of the ecosystem, massive development of IAP can also have a detrimental effect on the water quality (Nino et al., 2005; Stiers et al., 2011; Ribaudó et al., 2018; Pinero-Rodríguez et al., 2021). Consequently, their rapid spread has the potential to endanger the structure of entire habitats, usually leading to a severe damage to local biodiversity (Tasker et al., 2022). Unfortunately, halting the expansion of alien aquatic plants despite decades of experience remains an extremely difficult and expensive task (Hussner et al., 2017). Moreover, field experience has shown that in many cases, once well established, a population of alien aquatic plants is almost impossible to remove without also inflicting significant damage to the environment itself (Zehnsdorf et al., 2015; Simberloff, 2021). For this reason, it is preferable to act while the invasion is still in its early stages, while the plant is still adapting to the local environment and covers only a small area of the water body. There is a general consensus that a thorough understanding of the biology and ecology of invasive species is crucial for any serious attempt to stop their expansion (Hussner et al., 2017). Such specialized knowledge is also essential for an early identification of aquatic ecosystems most susceptible to biological invasions and for accurate selection and application of the most suitable control methods.

Among the most important species traits that are in the need of study, if we want to have a glimpse into an invasive plant's biology and ecology, are their thermal and light preferences (Bornette and Puijalon, 2011). While the issue of light limitation is crucial for all plants, the ability to cope with low light levels is especially valuable underwater, where light availability decreases dramatically with water depth (Best et al., 2001). Furthermore, the intensity of light reaching the bottom of the freshwater ecosystem may be subject to a rapid and possibly long-term decline due to phytoplankton blooms events (Sharma et al., 2010) - a harmful phenomenon increasingly observed in aquatic ecosystems worldwide - that usually have a strong negative impact for highly light dependent submerged macrophytes. It is thus unsurprising that in such environments, competition for light is usually fierce, and the high tolerance to low light levels displayed by an alien competitor may be what determines its total domination over native macrophytes (Szabó et al., 2019; Koleszár et al., 2022).

Tolerance to a wide range of temperatures is another factor that is extremely important for the evaluation of competitiveness of invasive aquatic plants and the range of habitats that they may inhabit (Kelley, 2014). While there is a great variety of invasive aquatic plant species, many of the most problematic originate from tropical regions of the world (Hussner, 2012). Although these species usually excel at vegetative reproduction, growth rate and/or biomass accumulation (Havel et al., 2015), because of their place of origin they typically lack overwintering strategies and are typically susceptible to low temperatures (Hussner et al., 2017). Thus, these species usually lose their invasive character or are outright absent in countries that experience freezing temperatures throughout the winter. The importance of temperature as a key factor in aquatic invasions is likely reflected by the uneven distribution of alien aquatic plants in Europe, which are predominantly widespread in the warmer southwestern regions or in countries with a high number of thermally altered water bodies (Hussner, 2012; Lukács et al., 2016). However, steadily rising mean air and water temperatures (O'Reilly et al., 2015), resulting from ongoing global warming events, may soon alter the current situation and likely promote their further spread into previously unsuitable regions of the world. Thus, determining the range of thermal optima for different invasive aquatic species - especially the low-temperature threshold for their growth - is crucial for both understanding range limits of these invaders and for predicting their further spread.

While some information usually exists about the environmental preferences of alien species, it often refers to their preferences within their natural range. Unfortunately, a number of studies show that in a great number of cases the behavior of invasive species differ greatly between its original and introduced range (Grigulis et al., 2001; Jakobs et al., 2004; Hejda et al., 2015; Hejda et al., 2019). While the mechanism behind this phenomenon is probably complex in its nature (Mitchell and Power, 2003; Parker et al., 2013), its role should not be underestimated, and thus researchers interested in the ecology and biology of invasive species should study the behavior of local, and already established introduced populations. This is particularly important since many invasive aquatic plant species reproduce exclusively through vegetative means in their introduced range (Hussner et al., 2017). As a result, the individuals found in the field are often genetic clones of one or a few original plants (Ren and Zhang, 2007; Zhang et al., 2010; McCracken et al., 2013) that, after a period of acclimatization, successfully established themselves in the new environment (Mounger et al., 2021). It should be expected that such populations may differ greatly in their abilities and environmental preferences from the native and more genetically diverse populations of the same species. Although a number of papers have investigated in laboratory conditions the behavior of invasive aquatic plants, it is important to note that only the most widespread species have been so far thoroughly studied. Additionally, a portion of studies addressing the topic of environmental preferences of invasive aquatic plants focus typically on rather elevated light and temperature values (Zhao et al., 2013; Mounger et al., 2021; Koleszár et al., 2022). While the tolerance of invasive species to high insolation and overheating is undoubtedly important - in temperate climates, it is their tolerance to low light levels and/or cold water that likely contributes the most to their success and competitiveness (Draga et al., in print). As in the foreseeable future, global warming and

eutrophication will only result in warmer winters (Wallace et al., 2014) and higher occurrence of algae blooms (Hou et al., 2022), the importance of these attributes may only increase.

Taking all of this into account, in our work we decided to closely investigate the thermal and light optima of three problematic invasive species found in Central Europe, with a particular focus on lower light and temperature conditions. In order to do so two hypotheses were tested: [1] the high competitiveness of invasive alien species is the result of their strong tolerance for shading, [2] although thermophilic invasive aquatic plant species thrive in warm water, they are still capable of surviving in colder conditions.

2. Material and methods

2.1 Species description

For this research three species of perennial submerged and invasive aquatic plants that pose a threat to Central Europe were selected to determine their light and thermal optima: *Cabomba caroliniana* A. Gray (carolina fanwort), *Elodea nuttallii* (Planch.) H. St. John (Nuttall's waterweed), and *Vallisneria spiralis* L. (eelweed). *E. nuttallii* is native to North America, while natural populations of *C. caroliniana* can be found in both North and South America. *V. spiralis* originates from the Mediterranean region, with natural habitats in Northern Africa, Western Asia, and Southern Europe. Among these three species, *C. caroliniana* and *V. spiralis* are widely considered thermophilic, while *E. nuttallii* is well-adapted to temperate climates. Since their introduction to Europe, as well as parts of Asia, these species have demonstrated exceptional vitality and a high rate of vegetative reproduction. These facts, combined with their strong competitiveness, difficulty of eradication and ability to form dense, monospecific stands, has led to their classification not only as alien but also as invasive aquatic plant species. Due to the threat they pose to local ecosystems and human activities, both *C. caroliniana* and *E. nuttallii* have been included on the EU's 'List of invasive alien species of Union concern EU (Commission implementing Regulation (EU) 2016/1141)' which lists species that member states are obliged to eradicate. *C. caroliniana* and *E. nuttallii* are commonly found in both natural and heavily human-altered water bodies, often those with high nutrient levels (Greulich and Trémolières, 2006; Matthews et al., 2013). In contrast, *V. spiralis* is known to proliferate in thermally altered water bodies, which are frequently created by mining or power plant activities (Gabka, 2002; Hussner and Lösch, 2005).

2.2 Experimental design

Firstly, several hundred individuals of each species, including top shoots or whole ramets in the case of *V. spiralis*, were collected from the sites and transported to Adam Mickiewicz University in Poznań. *E. nuttallii* specimens were collected from the lake Skoki (Kujawsko-Pomorskie voivodeship, Poland; N 52°36'18", E 19°23'32"), while *C. caroliniana* shoots were gathered from a small fish pond in the village Krążek (Małopolska voivodeship, Poland; N 50°17'25", E 19°27'08") and ramets of *V. spiralis* were collected from a thermally altered water canal that is used by the local power plant to discharge its heated water to a nearby lake Licheńskie (Greater Poland voivodeship, Poland; N 52°18'31", E 18°20'31"), that is part of the complex of thermally polluted Konin lakes. Individuals of all species were collected from different water bodies in Poland, as these species do not co-occur within the country. Although no genetic studies have been conducted, it is likely that all the collected specimens are clones of each other (respectively to each of their species). This assumption is supported by the fact that neither species has been reported to produce viable seeds in Poland, and alien aquatic

plant species inhabiting the same water body typically originate from a single clonal population (McCracken et al., 2013).

The laboratory cultivations of the three selected species were conducted on two separate dates. For the specimens of *E. nuttallii* and *C. caroliniana*, the collection and experiment were conducted during the summer of 2023, while for *V. spiralis*, they took place in the spring of 2024. Despite the two different dates, the experiment was conducted in exactly the same manner and under identical conditions in each case. However, due to significant structural differences between *E. nuttallii* and *C. caroliniana* compared to *V. spiralis*, both the preparation of specimens for the experiment and the morphometric measurements varied between the two groups. After the harvest, specimens of *E. nuttallii* and *C. caroliniana* were cut in such a manner so that all plants of each species had the same starting length, and included a top shoot. The starting length for the main shoot was 11 cm for *E. nuttallii* and 13 cm for *C. caroliniana*. In the case of *V. spiralis*, the selected specimens had their leaves trimmed, so that the length from the base of the shoot to the tips of the longest leaves equaled 15 cm. During this step, only healthy, similar-looking plant shoots and those without extensive branching were selected from the initially gathered specimens. Prepared individuals were then acclimated over the course of one week. After that time, 190 healthy and similar individuals were selected for each of the species. Of this group, 80 individuals were allocated to experiment testing the species' response to different light levels, 80 to experiment testing the response to varying water temperatures, and 30 were assigned to the control group. Individuals were allocated to each group randomly. After that, the morphometry of each plant was measured. In case of *E. nuttallii* and *C. caroliniana*, number of internodes, number of offshoots, offshoot's internode number, length of the main shoot and individual offshoots was measured. For *V. spiralis*, length of each leaf, leaf width, number of leaves were measured. To determine the average starting mass, plants from the control group were dried, and their dry weight was measured. Individuals outside of the control group, intended for testing the plants' response to light or water temperature, were then randomly divided into one of ten groups - five for each experiment type. In the thermal experiment, the plants were placed in aquaria exposed to the same light intensity of $46 \text{ light } \mu\text{mol m}^{-2}\text{s}^{-1}$, with one of five different water temperatures: 7, 10, 14, 17, and 21°C . In the light experiment all plants were placed in aquaria with constant temperature of 21°C and where exposed to one of five different light levels: 3, 10, 25, 50 and 100% of a maximum light value (which equaled to 2.9, 9.7, 22.0, 46.4 and $91.1 \text{ light } \mu\text{mol m}^{-2}\text{s}^{-1}$). Additionally, a 12-hour day-night cycle was provided for each treatment. In total, each group consisted of 16 specimens that were divided among four 2-liter tanks (glass cylinders, height of water column 19 cm). Tanks were filled with filtered water collected from the same location as the plants placed inside. For the water filtration GF/C fiber glass filters ($0.45 \mu\text{m}$ pore size) were used. Plants within each tank were placed in small plastic pots filled with neutral sediment. In addition, since *V. spiralis* individuals differed from each other to a greater extent than *E. nuttallii* or *C. caroliniana* specimens, each pot containing this species was assigned with a unique number to facilitate tracking the fate and changes of specific individuals. Four water tanks, filled with plants from the same study group, were then placed within a water bath made out of a 32 L aquarium that was filled up with a

distilled water. The aquarium was then placed inside a 2 cm thick polystyrene container with a lid, which isolated the plants inside from external temperature fluctuations and light sources. The light within each container was provided by a group of LED lights installed on the bottom part of containers' lids. The light intensity of LED lights could be controlled and ranged from 1.7 to 91.1 light $\mu\text{mol m}^{-2}\text{s}^{-1}$). The exact light values (photosynthetically active radiation - PAR) within each of the boxes were measured by LI-1400 light meter (LI-COR Corporation, Lincoln, Nebraska, USA) equipped with a spherical sensor (LI-193SA). The temperature in the water bath was maintained by aquarium heaters equipped with thermostats that heated the water up to desired temperature. Additionally, water temperature was monitored by submersible DIVER-type data loggers. In total, 10 containers were used for each species, one for each testing group. Containers with plants grown at a water temperature of 21°C were kept in a cultivation room with a constant temperature of 20°C, while those with plants exposed to the colder water were stored in a separate cultivation room, where the temperature was consistently maintained at 5°C. Plants of each species were kept under such conditions over the course of seven weeks. After this time period, the plants were collected and measured again. This time, however, their chlorophyll *a* content was also measured using the CCM-300 Chlorophyll Content Meter. Since in some treatments *V. spiralis* individuals produced several daughter ramets, their morphology was also measured following the same procedures as for the mother ramets. After all measurements were taken, the specimens were dried, and their dry weight was determined.

2.3 Statistics

Most of the statistical analyses were performed using the R program (R Core Team, 2023) within the RStudio environment (Posit team, 2023). To test the significance of differences in species' reactions to various treatments, a one-way analysis of variance (ANOVA) was performed, followed by Tukey's post hoc test. Before conducting the ANOVA, normality of residuals was assessed using the Shapiro-Wilk test, and homogeneity of variances was checked with Levene's test. If the assumption of the homogeneity of variances was not met, Welch's one way test was used instead of the standard one-way analysis of variance. In rare cases in which assumption of normality of residuals was strongly violated, Kruskal-Wallis test was performed. Species response curves to temperature and light gradients were modeled using GAM models (Generalized Additive Model) (Hastie and Trevor, 1990). The Poisson distribution and the complexity of the smoothing term were determined based on the Akaike Information Criterion (AIC) (Lepš and Šmilauer, 2003). For all the plots, the ggplot2 package (Wickham, 2016) was used, while the dplyr package (Hadley et al., 2023) was utilized for the data cleaning and preparation.

3. Results

3.1 Species-specific responses to different water temperatures

Tested temperature levels statistically significantly influenced elongation (total length of the main shoot and offshoots, main shoot length) and mean chlorophyll *a* content of *Cabomba caroliniana* (Fig. 1), elongation (total length of the main shoot and offshoots, main shoot length) of *Elodea nuttallii* (Fig. 2) and all the tested attributes for *Vallisneria spiralis* (Fig. 3) (change in the total length of leaves, change in mean length of the three longest leaves, change in the total number of leaves, dry mass, number of daughter ramets; mean chlorophyll *a* content) (Table 1). The parameters of *C. caroliniana* increased with the rising temperature gradient, with the longest and heaviest specimens observed in the treatments with the highest water temperature. Almost no elongation was observed for the plants kept in the temperature of 14°C or colder ($p < 0.0001$ for both total and main shoot length). While the dry mass did not differ significantly between treatments ($p = 0.0737$), its growth was observed only in treatments with water temperature equal to or above 14°C. No offshoots were present in the treatments with water temperature of 14°C or colder ($p = 0.0601$). Chlorophyll *a* content was highest in the individuals kept in 21°C ($p = 0.0002$). The elongation of *E. nuttallii* increased alongside the temperature gradient with the longest specimens found in the water temperature of 17 and 21°C ($p < 0.0001$ for both total and main shoot length). Dry mass growth was observed in every group, however the results did not differ between treatments ($p = 0.184$). Offshoots were observed in all treatments, although their numbers did not differ significantly ($p = 0.118$). In general, all the parameters of *V. spiralis* increased alongside with the rise in the temperature gradient, including total leaf length and the mean length of the three longest leaves ($p < 0.0001$ for both parameters). Leaf elongation of the plants kept at 7 or 10°C was minimal. Dry mass growth was observed across all treatments, with the highest values recorded in plants grown at temperatures of 14°C or higher ($p = 0.0026$). Plants cultivated at the temperature of 7 or 10°C on average produced close to non leaves ($p < 0.0001$), had the lowest chlorophyll *a* content ($p < 0.0001$) and did not produce any daughter ramets ($p = 0.0001$).

Table 1 Results of one-way ANOVA on the morphological parameters of *Cabomba caroliniana*, *Elodea nuttallii* and *Vallisneria spiralis* cultivated under different water temperatures. Bold text indicates parameters with statistically significant difference at $p < 0.05$. If the assumptions of ANOVA were not met, appropriate alternative test was performed: A – one-way ANOVA, W – Welch’s one way test, KW - Kruskal-Wallis test.

Variable	Temperature variant		Type of test
	F	P	
<i>Cabomba caroliniana</i>			
Total length of the main shoot and offshoots [cm]	58.62	< 0.0001	A
Main shoot length [cm]	58.72	< 0.0001	A
Dry mass [g]	2.30	0.0737	A
Mean chlorophyll a content [mg/m ²]	6.97	0.0002	A
Number of offshoots	-	0.0601	KW
<i>Elodea nuttallii</i>			
Total length of the main shoot and offshoots [cm]	25.97	< 0.0001	W
Main shoot length [cm]	6.50	0.0007	W
Dry mass [g]	1.60	0.184	A
Mean chlorophyll a content [mg/m ²]	0.81	0.5263	W
Number of offshoots	1.91	0.118	A
<i>Vallisneria spiralis</i>			
Change in the total length of leaves [cm]	26.40	< 0.0001	A
Change in mean length of the three longest leaves [cm]	15.44	< 0.0001	W
Change in the total number of leaves	21.67	< 0.0001	W
Dry mass [g]	4.49	0.0026	A
Mean chlorophyll a content [mg/m ²]	53.97	< 0.0001	A
Number of daughter ramets	-	0.0001	KW

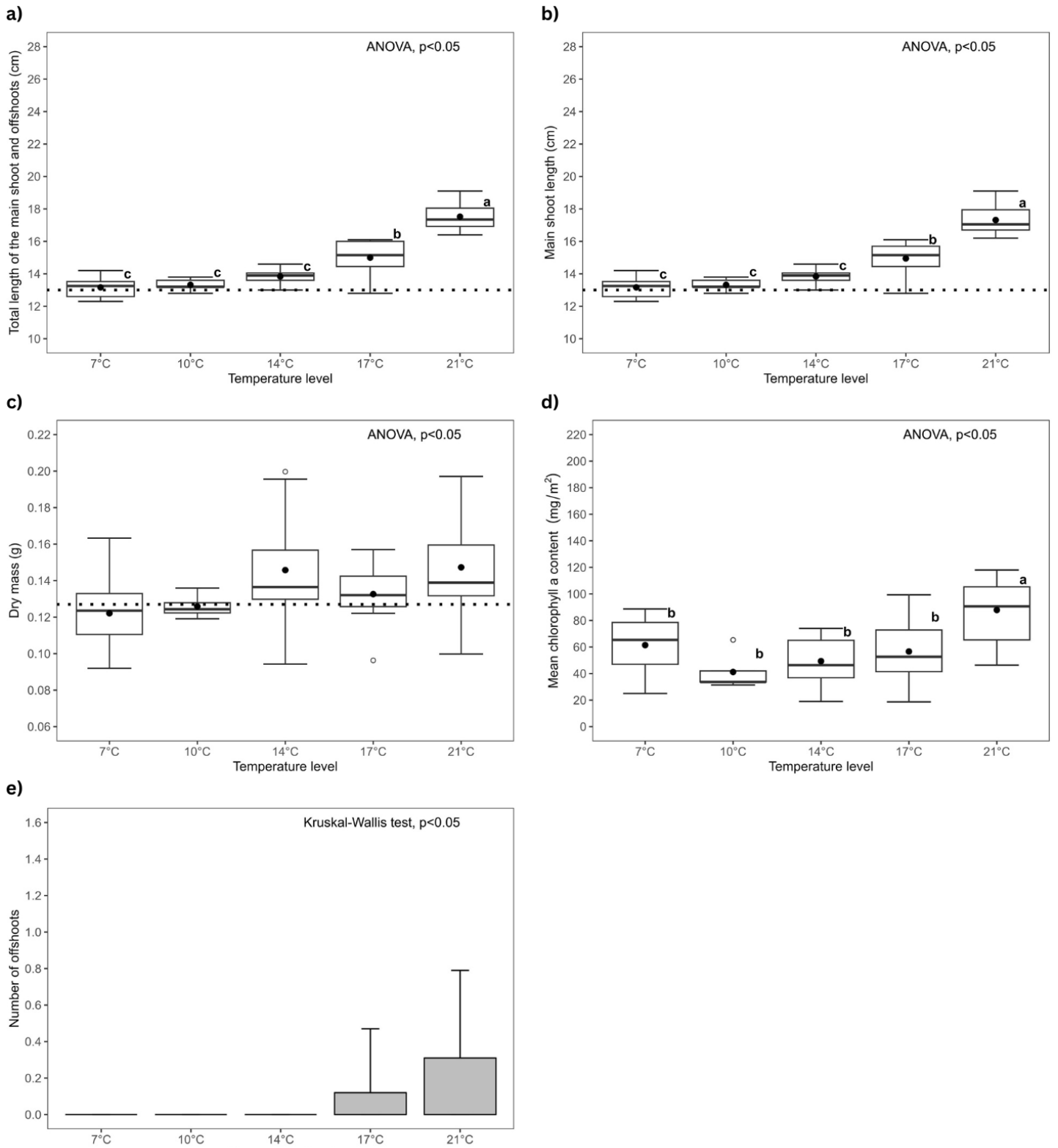


Fig. 1 Trait comparison of *Cabomba caroliniana* cultivated under different water temperatures, including the results of statistical tests. Black dots on the boxplots represent mean values, while dashed lines indicate the initial parameter values from the control group.

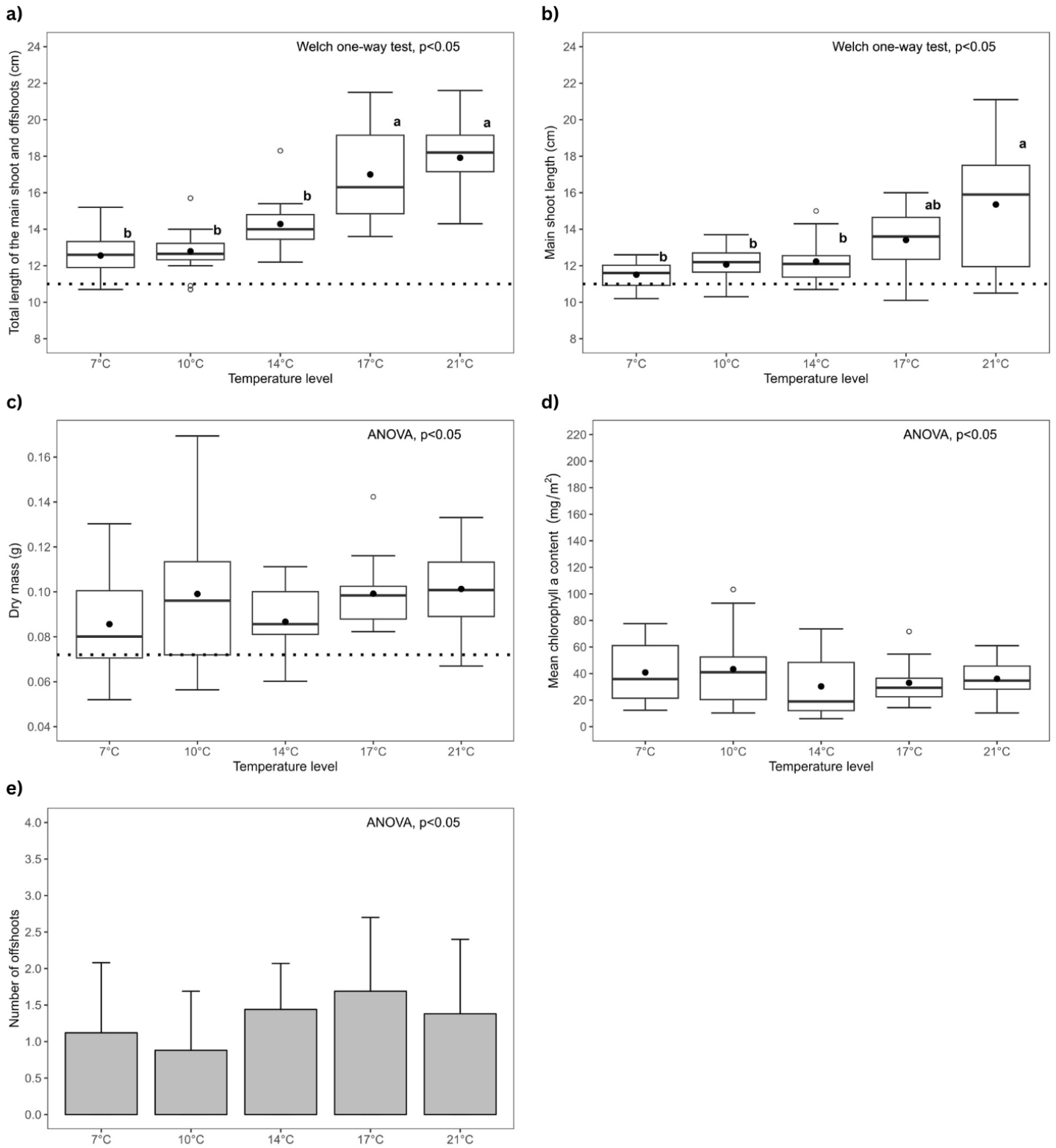


Fig. 2 Trait comparison of *Elodea nuttallii* cultivated under different water temperatures, including the results of statistical tests. Black dots on the boxplots represent mean values, while dashed lines indicate the initial parameter values from the control group.

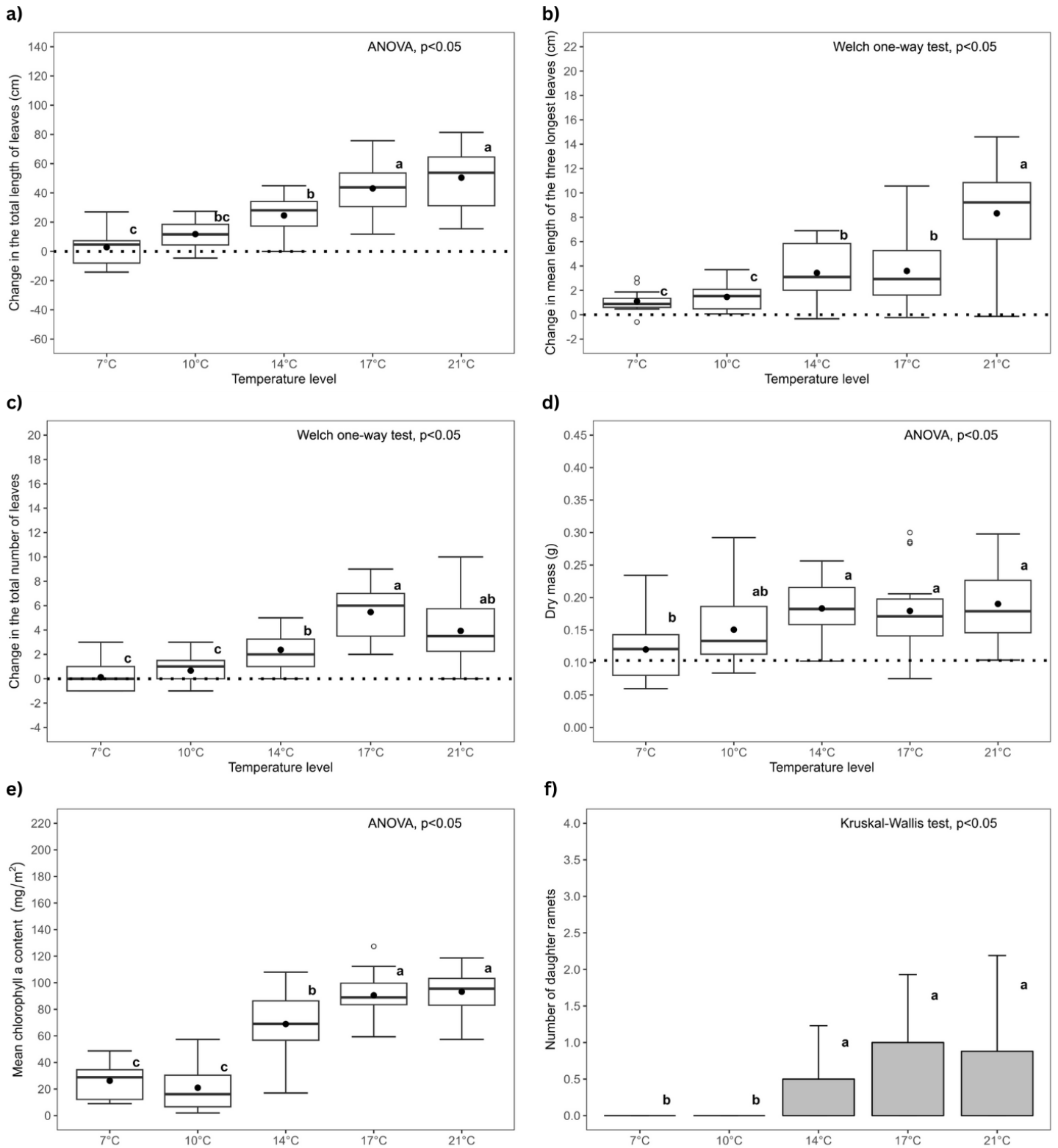


Fig. 3 Trait comparison of *Vallisneria spiralis* cultivated under different water temperatures, including the results of statistical tests. Black dots on the boxplots represent mean values, while dashed lines indicate the initial parameter values from the control group.

3.2 Species-specific responses to different light intensities

Significant differences between treatments exposed to different light intensities were observed across all species. Elongation (total length of the main shoot and offshoots, main shoot length) and mean chlorophyll *a* content differed between groups of *C. caroliniana* (Fig. 4), while in case of *E. nuttallii* (Fig. 5) and *V. spiralis* (Fig. 6), all of the tested parameters differed significantly between treatments (total length of the main shoot and offshoots, main shoot length, dry mass, number of offshoots, mean chlorophyll *a* content for *E. nuttallii* and change in the total length of leaves; change in mean length of the three longest leaves; change in the total number of leaves; dry mass; number of daughter ramets; mean chlorophyll *a* content for *V. spiralis*) (Table 2). Longest *C. caroliniana* specimens were observed at the highest water temperature ($p < 0.0001$ for both total and main shoot length), although the dry mass did not differ significantly between treatments ($p = 0.492$). Dry mass loss was observed for the plants grown at the lowest light level. New offshoots were present in every treatment and did not differ in number ($p = 0.0701$). The highest chlorophyll *a* concentration was observed for the light intensity of 25% of maximal value ($p = 0.0112$), while lower values were recorded for both sides of the spectrum. Highest values of the most parameters of *E. nuttallii* were observed in plants cultivated at 25% and 50% light intensity. Individuals grown at these light levels were both the longest ($p < 0.0001$ for both total and main shoot length) and had the highest dry mass ($p < 0.0001$). No elongation and even drop in dry mass was observed for the plants grown at the lowest light intensity. Additionally, in the case of the 7 specimens from the 3% light treatment, up to 1.5 cm of the basal part of the shoot (0.86 cm on average) was affected by necrosis. During the measurement, these parts were cut off and only green parts of the plants were analyzed. New offshoots were observed in every treatment, but their number decreased in the lowest light condition ($p = 0.0138$). The chlorophyll *a* content was similar between the 3% and 10% treatments, as well as between the 25%, 50%, and 100% treatments, but significantly different between these two groups ($p < 0.0001$). The growth parameters of *V. spiralis* increased with rising light intensity. Plants grown under the highest light levels showed the greatest dry mass ($p < 0.0001$), as well as the highest increase in leaf number ($p < 0.0001$) and the number of daughter ramets ($p < 0.0001$). Daughter ramets were present only in 25%, 50%, and 100% light level treatments. Additionally, although the total leaf length and the length of the three longest leaves did not differ significantly between treatments with 10%, 25%, 50%, and 100% light intensity, plants cultivated at 3% showed a significant reduction in these parameters ($p < 0.0001$ and $p < 0.0001$ respectively). Furthermore, individuals exposed to the lowest light level showed loss in the dry mass as well on average lost some of their leaves. In general, mean chlorophyll *a* content decreased as light intensity increased ($p < 0.0001$). However, its amount in plants grown at 3% of the maximum light value was significantly lower than in those grown at 10% or 25%.

Table 2 Results of one-way ANOVA on the morphological parameters of *Cabomba caroliniana*, *Elodea nuttallii* and *Vallisneria spiralis* cultivated under different light intensities. Bold text indicates parameters with statistically significant difference at $p < 0.05$. If the assumptions of ANOVA were not met, appropriate alternative test was performed: A – one-way ANOVA, W – Welch’s one way test, KW - Kruskal-Wallis test.

Light variant			
Variable	F	P	Type of test
<i>Cabomba caroliniana</i>			
Total length of the main shoot and offshoots [cm]	8.84	0.0002	W
Main shoot length [cm]	11.13	< 0.0001	A
Dry mass [g]	0.86	0.4920	A
Mean chlorophyll a content [mg/m ²]	3.63	0.0112	A
Number of offshoots	-	0.0676	KW
<i>Elodea nuttallii</i>			
Total length of the main shoot and offshoots [cm]	29.16	< 0.0001	A
Main shoot length [cm]	7.70	< 0.0001	A
Dry mass [g]	21.41	< 0.0001	A
Mean chlorophyll a content [mg/m ²]	11.66	< 0.0001	W
Number of offshoots	7.88	0.0003	W
<i>Vallisneria spiralis</i>			
Change in the total length of leaves [cm]	17.28	< 0.0001	A
Change in mean length of the three longest leaves [cm]	8.72	< 0.0001	W
Change in the total number of leaves	-	0.0001	KW
Dry mass [g]	28.11	< 0.0001	W
Mean chlorophyll a content [mg/m ²]	21.28	< 0.0001	A
Number of daughter ramets	-	< 0.0001	KW

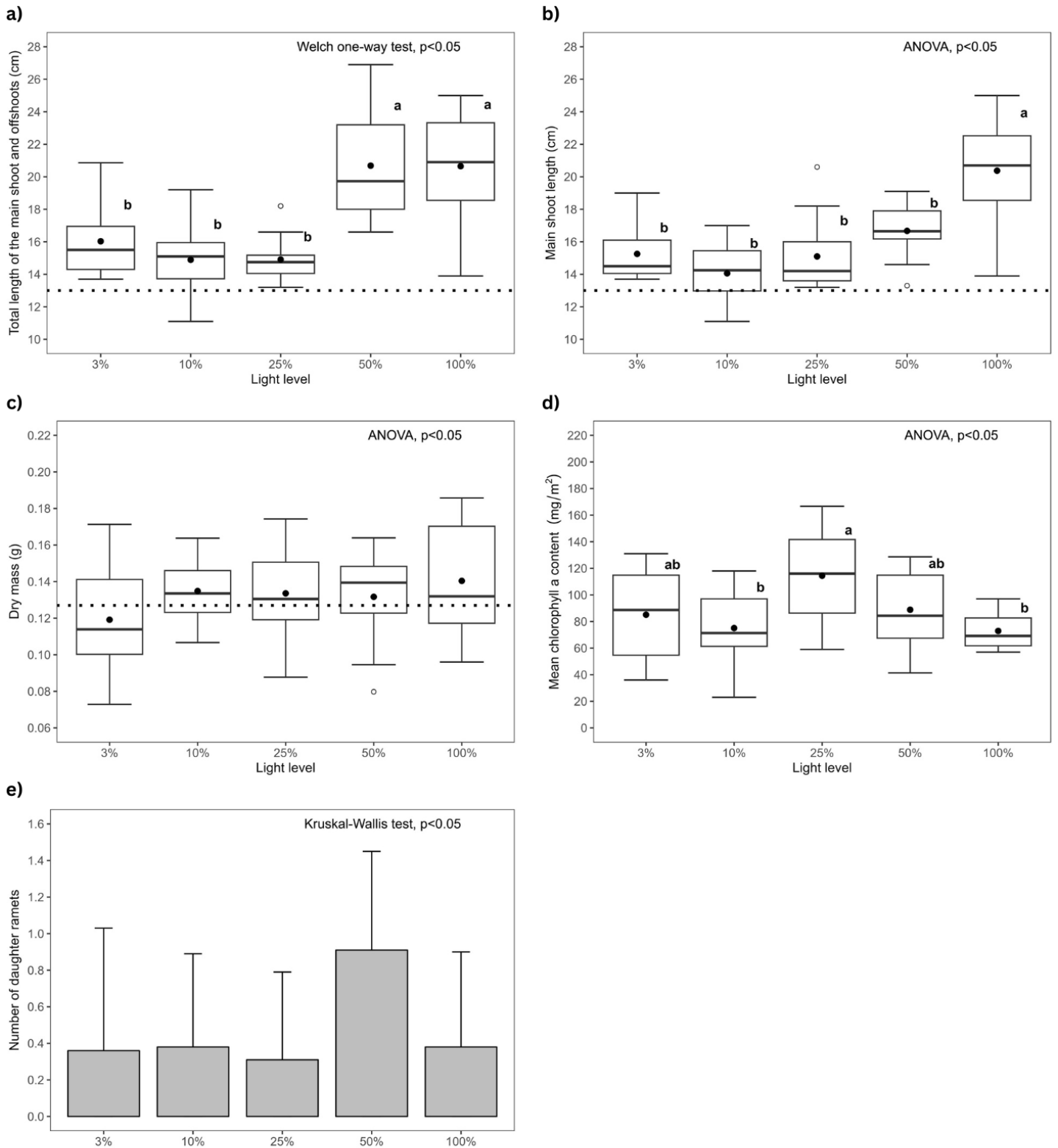


Fig. 4 Trait comparison of *Cabomba caroliniana* cultivated under different light intensities, including the results of statistical tests. Black dots on the boxplots represent mean values, while dashed lines indicate the initial parameter values from the control group.

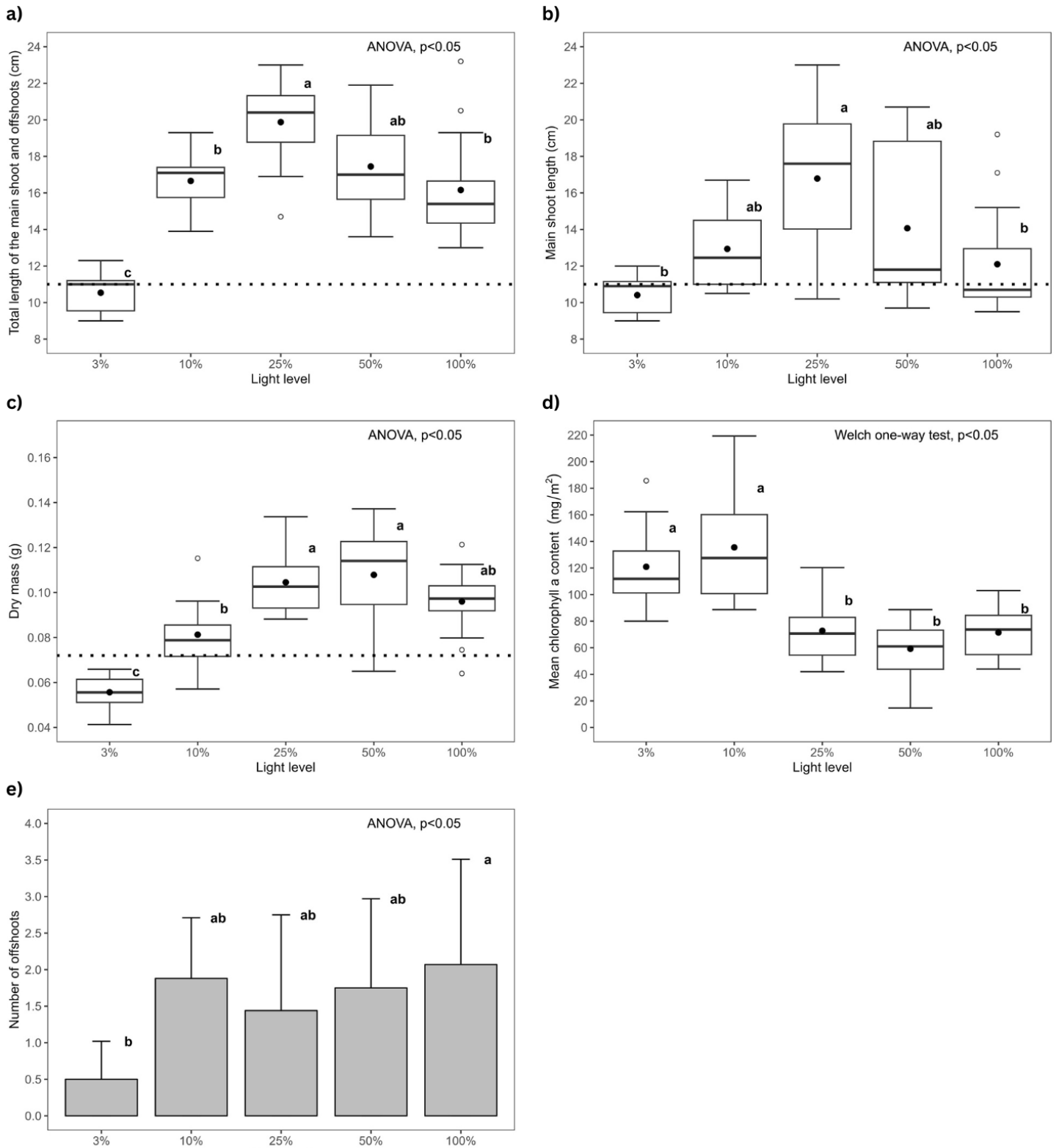


Fig. 5 Trait comparison of *Elodea nuttallii* cultivated under different light intensities, including the results of statistical tests. Black dots on the boxplots represent mean values, while dashed lines indicate the initial parameter values from the control group.

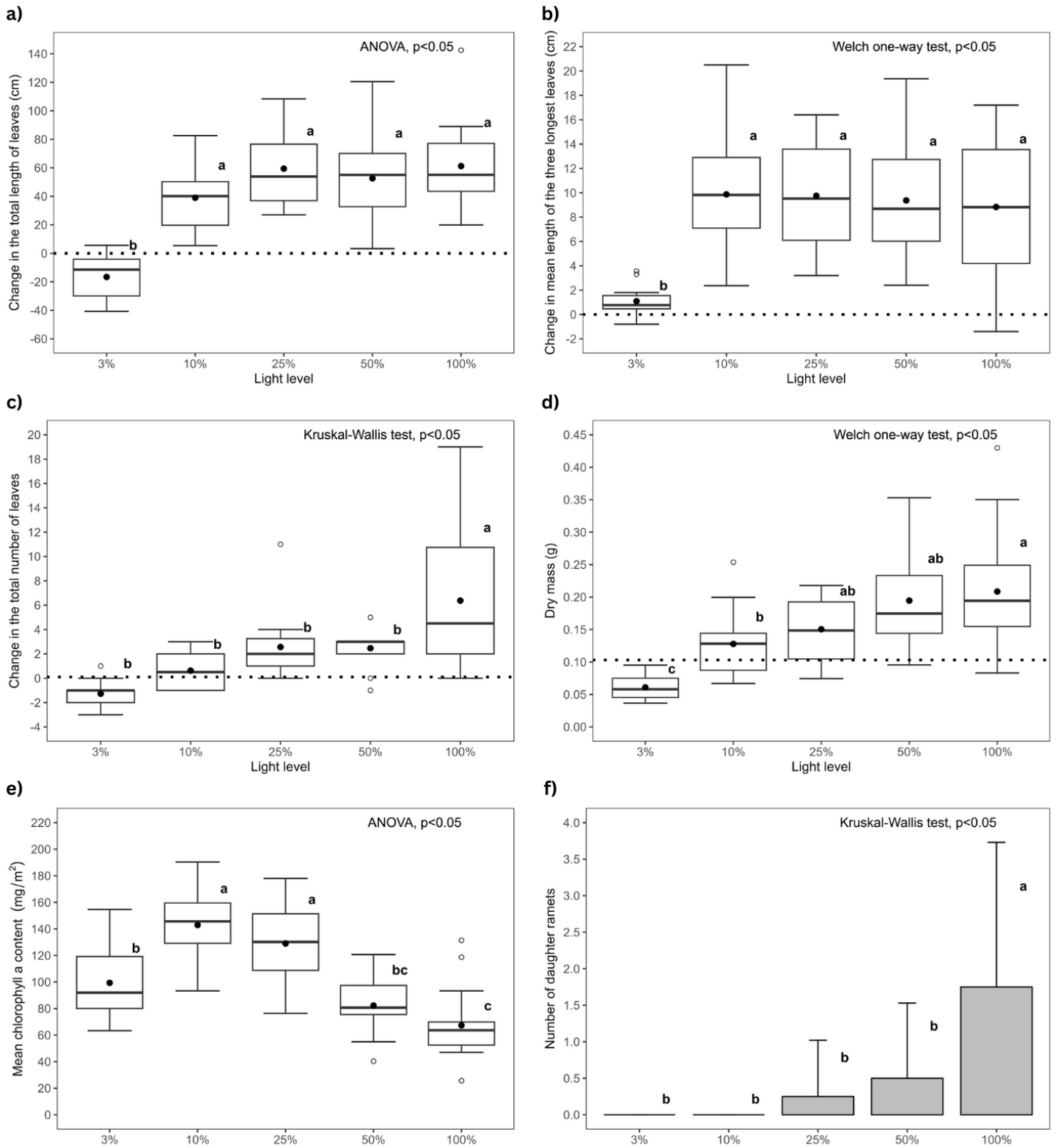


Fig. 6 Trait comparison of *Vallisneria spiralis* cultivated under different light intensities, including the results of statistical tests. Black dots on the boxplots represent mean values, while dashed lines indicate the initial parameter values from the control group.

3.3 Response curves (GAMs)

Our findings shows that the three of the studied species exhibit unique responses to thermal and light conditions, occupying distinct ecological niches. Using Generalized Additive Models (GAM), we analyzed the response of key morphological traits to PAR and temperature. The results demonstrated significant differences in how each species reacted to these factors, with each showing distinct quantitative response patterns (a monotonically decreasing curve, a unimodal curve with an optimum near the center, and a monotonically increasing curve, Figs 7–12). All species exhibited positive growth responses to increasing water temperatures, following a monotonically increasing trend (Figs. 7–9). However, growth in *C. caroliniana* notably accelerated once the water temperature exceeded 15°C. Strong positive growth reaction to the high light intensities was observed for *C. caroliniana* and *V. spiralis*. Notably, this included increases in total length of the main shoot and the offshoots, main shoot length for *C. caroliniana* and increase in the total length of the leaves, dry mass, change in the total number of leaves for *V. spiralis* (monotonically increasing curve, Figs. 10 and 12). At the same time, as light intensity increased, the mean chlorophyll *a* concentration decreased in both species. In contrast, *E. nuttallii* exhibited a distinctly different response to rising PAR levels, following a mostly unimodal pattern with an optimum around 50-55 light $\mu\text{mol m}^{-2}\text{s}^{-1}$ (Fig. 11). Peak growth occurred at these light intensities, with a significant decline at higher values. However, an increase in the number of offshoots was observed as light intensity continued to rise.

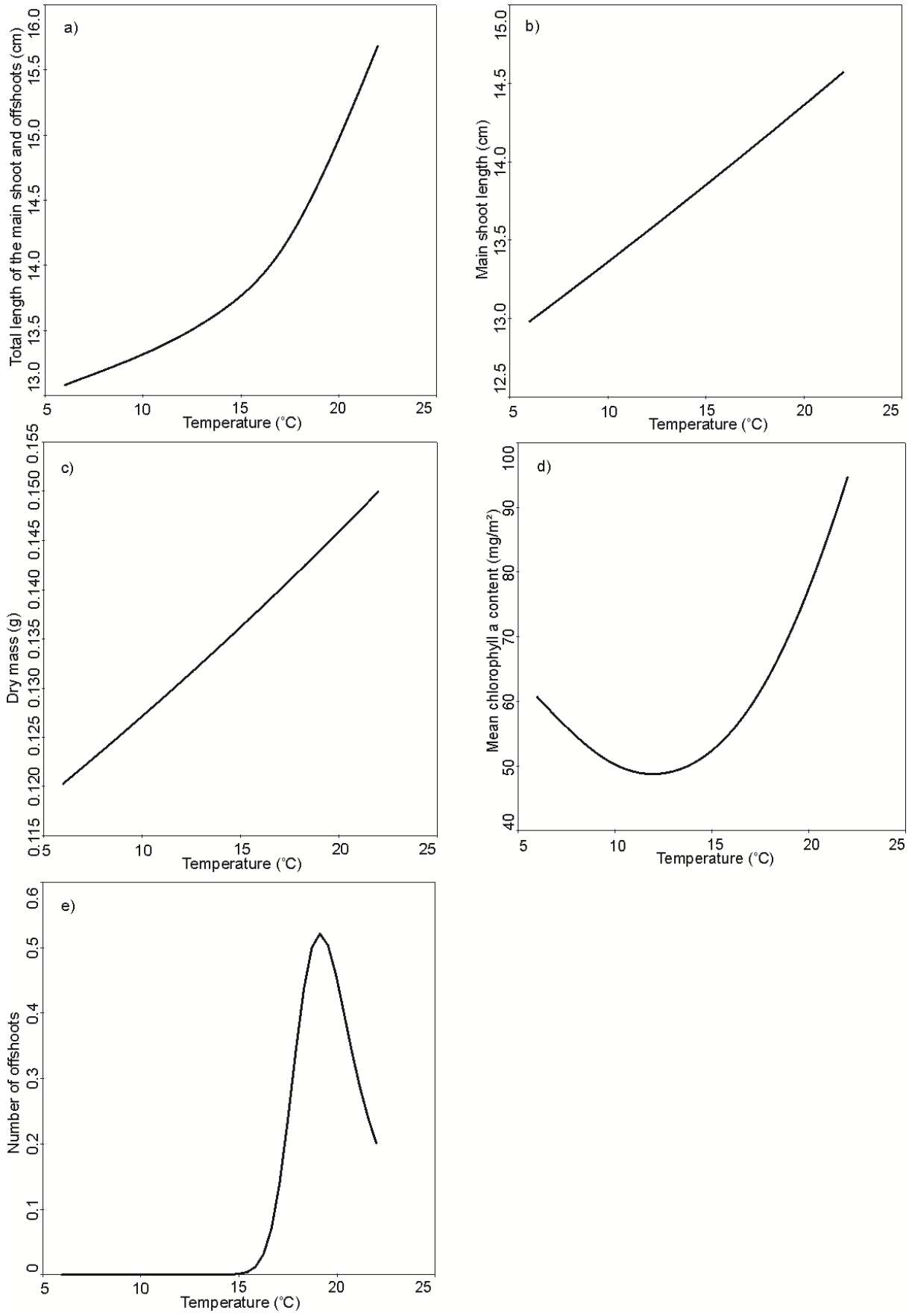


Fig. 7 Generalized Additive Model (GAM) showing the response of statistically significant growth traits of *Cabomba caroliniana* grown under different water temperatures.

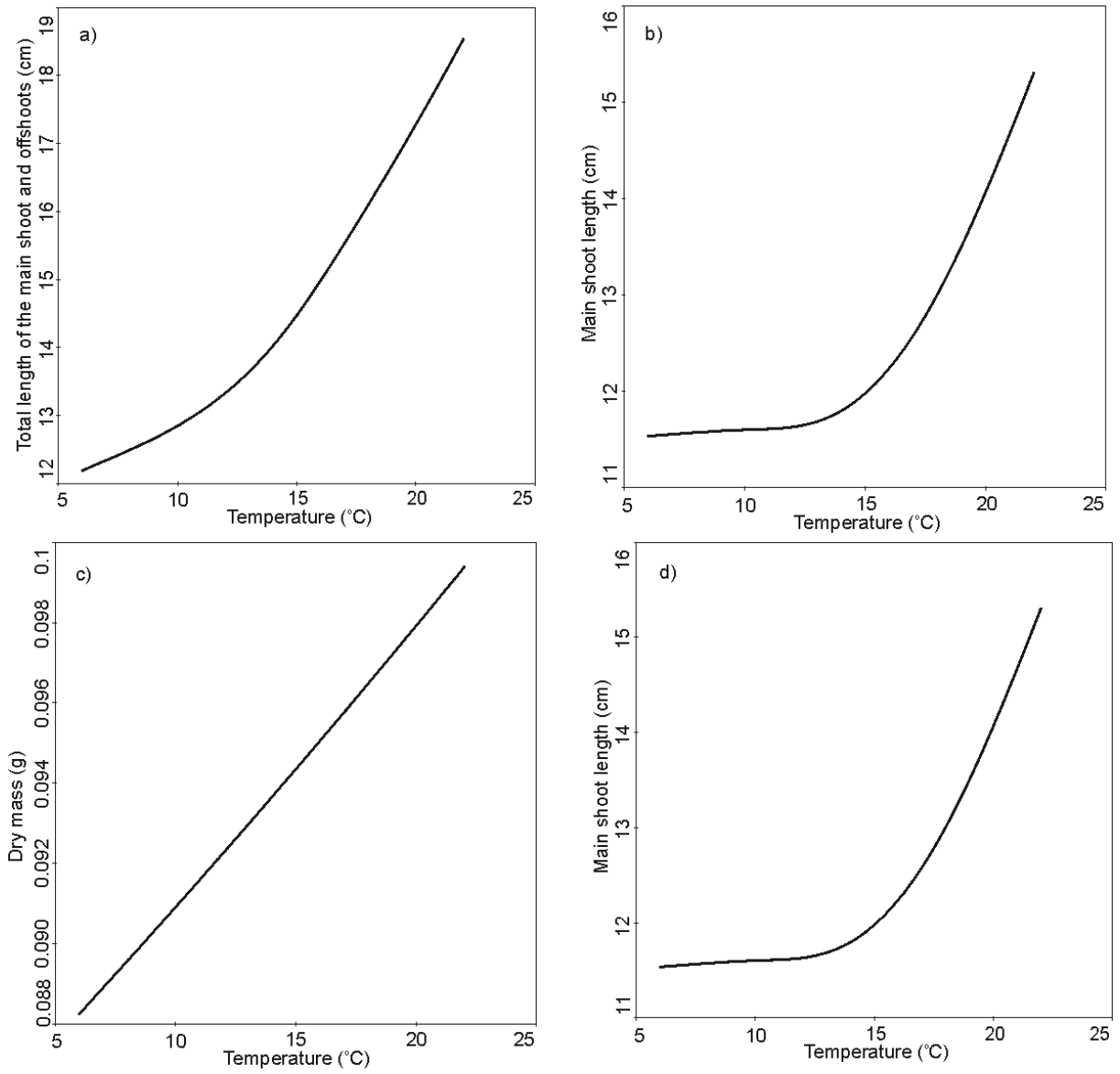


Fig. 8 Generalized Additive Model (GAM) showing the response of statistically significant growth traits of *Elodea nuttallii* grown under different water temperatures.

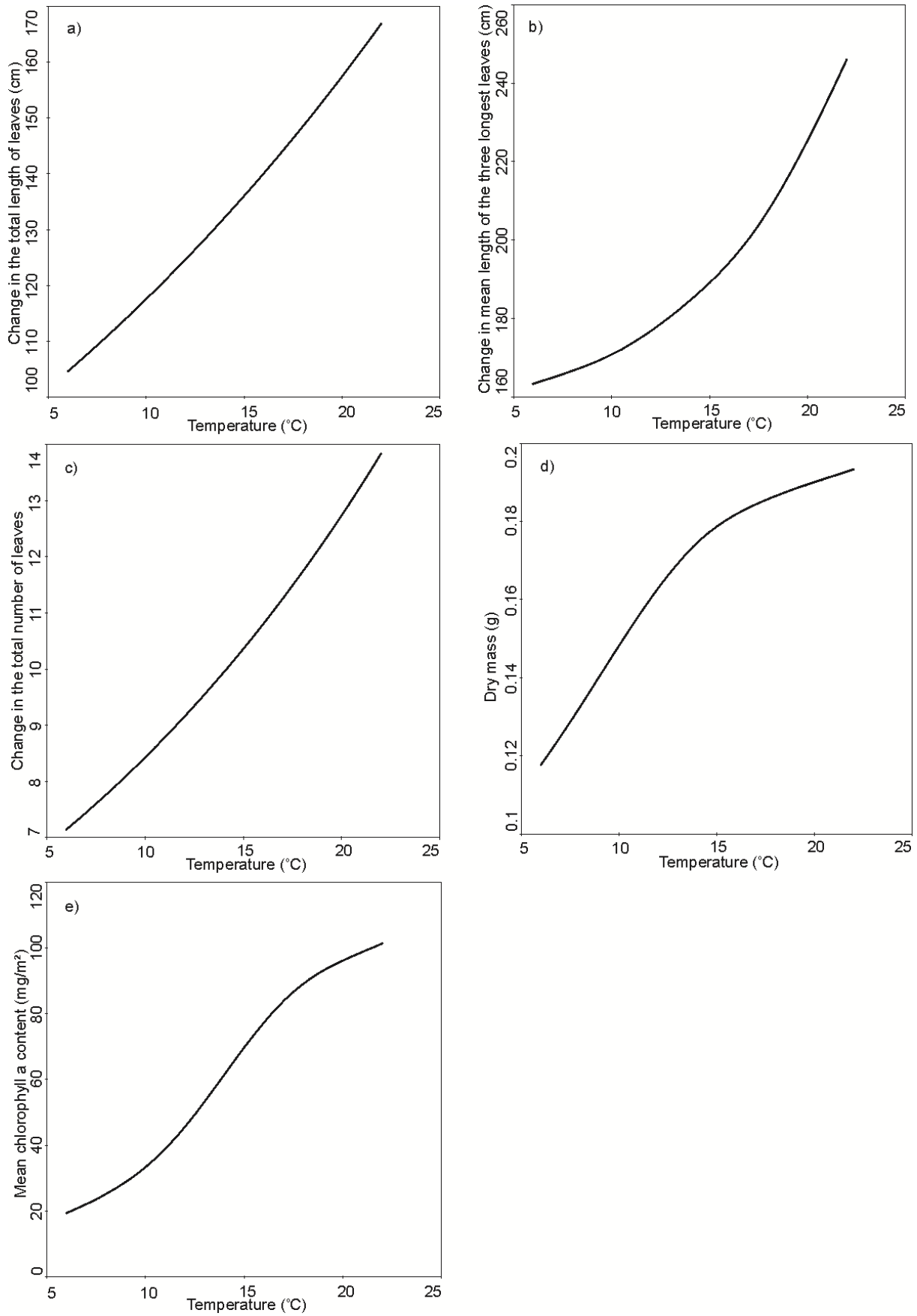


Fig. 9 Generalized Additive Model (GAM) showing the response of statistically significant growth traits of *Vallisneria spiralis* grown under different water temperatures.

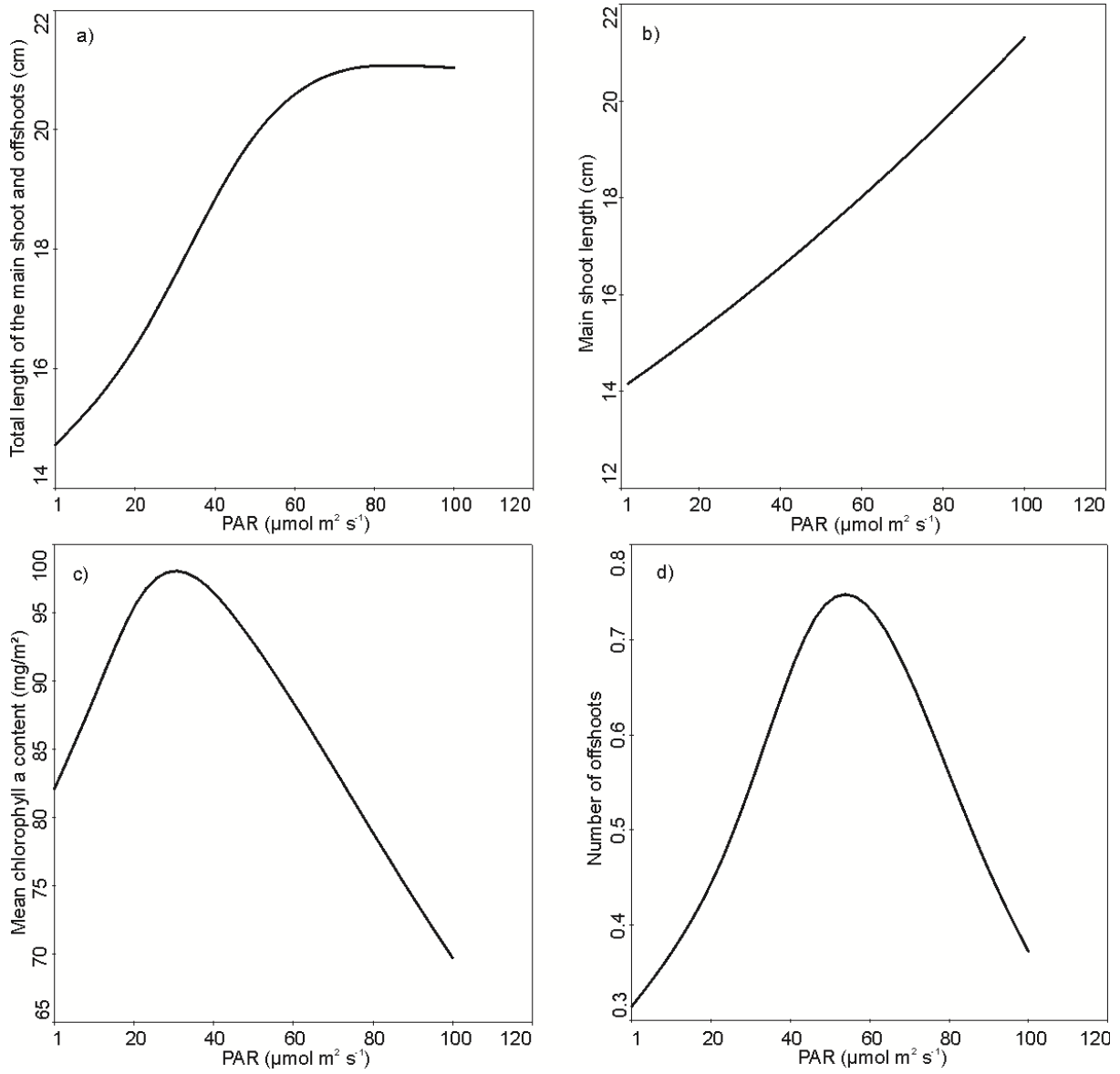


Fig. 10 Generalized Additive Model (GAM) showing the response of statistically significant growth traits of *Cabomba caroliniana* grown under different light intensities.

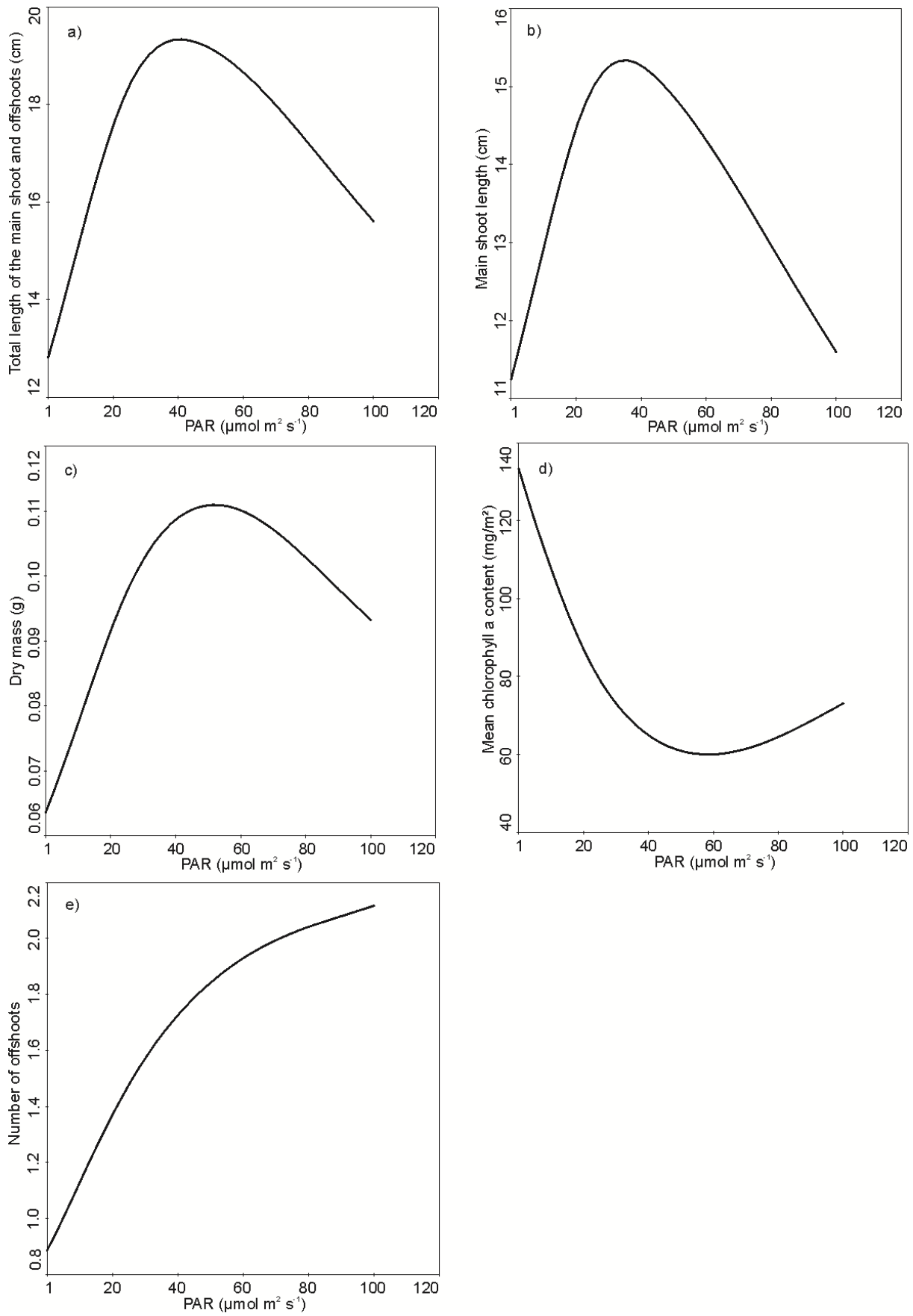


Fig. 11 Generalized Additive Model (GAM) showing the response of statistically significant growth traits of *Elodea nuttallii* grown under different light intensities.

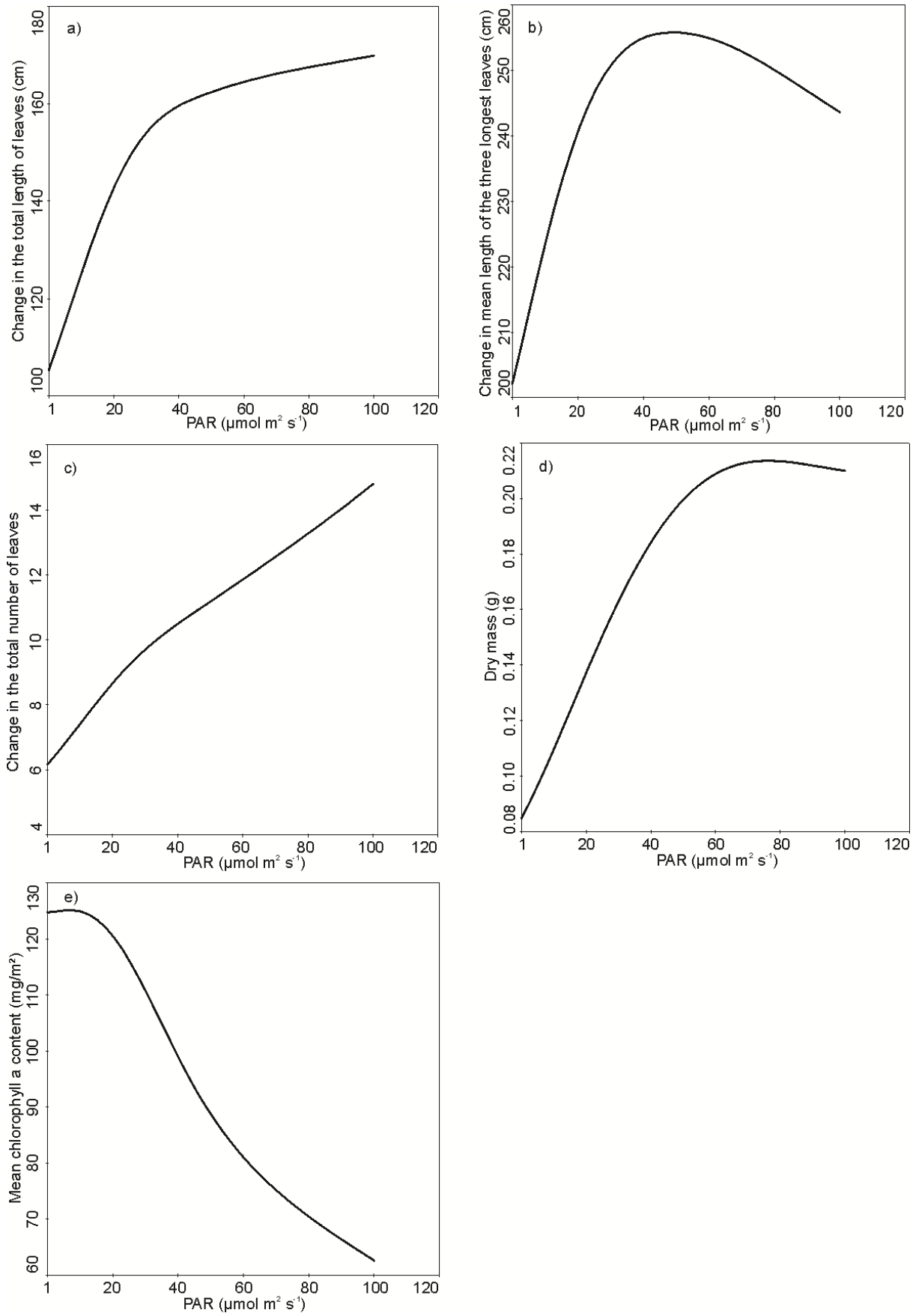


Fig. 12 Generalized Additive Model (GAM) showing the response of statistically significant growth traits of *Vallisneria spiralis* grown under different light intensities.

4. Discussion

4.1 Overall conclusions on the impact of low light and temperature conditions on the growth of the tested invasive species

All tested species showed an ability to survive or even thrive in the dim light conditions, although they differed in their response. While *Cabomba caroliniana* and *Vallisneria spiralis* could tolerate low light intensities, they were generally found to prefer higher levels of insolation (50% and 100% of maximal light level), probably even higher than those tested in this study. On the contrary, *Eloдея nuttallii* was found to thrive in low light conditions (25 and 50% of maximal light level), and higher insolation only negatively impacted the growth of this species. This result shows that while these invasive aquatic species differ in their light preferences, all of them at least tolerate dim light conditions. This ability most likely has a strong positive impact on the competitiveness of these species, particularly at the start of the growing season, when shade tolerance is crucial for interspecies competition.

Although all of the species showed a clear preference for higher water temperatures, they were still able to survive in the coldest water conditions for several weeks, even if they differed in their response and final condition. Among all the tested species, *E. nuttallii* was the best adapted to cold water, showing the ability to increase in dry mass, length, and offshoot number even in the coldest conditions. On the other hand, while *V. spiralis* also demonstrated growth even in the lowest temperature, its vegetative reproduction was stopped until the temperature was several degrees higher (14°C or more). Of all the species, it is the development of the *C. caroliniana* that has proved to be perhaps the most limited by low water temperatures. Individuals cultivated in the coldest treatments (7 and 10°C) were not only hindered in their growth but also showed a loss in their biomass and did not produce any new offshoots. Summarizing, our results indicate that the tested invasive species can survive in cold water for a limited time. That said, given that individuals cultivated in the warmest water showed a significantly greater growth, it is clear that water temperature remains a critical factor limiting further spread of the selected invasive plants.

4.2 Thermal and light optima of *Cabomba caroliniana*

In our study, *Cabomba caroliniana* showed highest growth under the highest light intensities and warmest water conditions which corresponds well with the fact that this species is considered to be a fairly thermophilic species that requires good light exposure. However, in nature, *C. caroliniana* is reported to occupy a wide range of habitats. While it is commonly found in areas with annual temperatures between 15 - 18°C, it has also been reported to occasionally tolerate freezing conditions (Ørgaard, 1991). These observations correlates well with the fact that in our study, *C. caroliniana* was able to survive the exposure to all tested temperatures, including those of 7°C or 10°C. However, specimens in these treatments showed strong signs of inhibited growth. The threshold temperature for *C. caroliniana* growth appears to be around 14°C, as plants cultivated at this temperature showed both

an increase in biomass and length, similar to those grown at higher temperatures (17°C and 21°C). However, despite the dry mass increase at 14°C, *C. caroliniana* individuals did not produce any offshoots until they were grown at temperatures of 17°C or higher, indicating that the vegetative reproduction of the species was significantly impaired until the water temperature reached nearly 20°C. *C. caroliniana*'s preference for higher water temperatures is not surprising, as several studies (Ørsgaard, 1991; Mackey and Swarbrick, 1997) have already classified it as a thermophilic species, suggesting its thermal optimum to be around average daily temperatures between 11.6°C and 25.4°C (Leslie, 1986;). Although these conclusions are based solely on field observations, they align with the experiences of hobbyist aquarists (Hiscock, 2003), who report that this species thrives best in warmer water (22-28°C). Unfortunately, there is a lack of experimental studies specifically investigating the thermal optimum of *C. caroliniana* under laboratory conditions. The few that do exist consistently show its preference for higher water temperatures. For instance, a 1970 study by Saitoh et al. found the optimal temperature for its photosynthesis to be 30°C. A more recent study (Koleszár et al., 2022), which tested the shade tolerance of *C. caroliniana* at two water temperatures (21.5°C and 27.5°C), found that while the species grew well under both conditions, its relative growth rate was highest in lower of the tested light levels and at the higher temperature. However, both studies were conducted over very short time periods (a few hours after collection and 8 days, respectively). Nevertheless, both the available literature and our research suggest that *C. caroliniana* possesses an exceptionally broad thermal tolerance. Although it thrives in very warm waters, it can also survive for extended periods in water with temperatures barely above a few degrees Celsius. This combination is concerning, as it suggests that this species can tolerate the thermal conditions of temperate regions like Central Europe. Moreover, ongoing climate change, which is raising the water temperatures, is likely to further enhance its invasiveness.

C. caroliniana is commonly described as a species with a high light dependency (Ørsgaard, 1991; Hiscock, 2003) and studies conducted by Koleszár et al. (2022) or Huang et al. (2023;) have shown that *C. caroliniana* can thrive at light levels of 300 light $\mu\text{mol m}^{-2}\text{s}^{-1}$ or higher. However, in our research, where individuals were exposed to relatively low to medium light conditions, with a maximum intensity of 91.1 light $\mu\text{mol m}^{-2}\text{s}^{-1}$, the plants were found to grow in both length and mass in almost every treatment, with the exception of those grown at the very low light level of 3%. These findings suggest that *C. caroliniana* may tolerate a significantly broader range of light intensities than it is commonly thought. Koleszár et al. (2022) and Huang et al. (2023) based on their experimental comparisons of *C. caroliniana*'s growth traits and competitiveness against few other aquatic plant species also reached the conclusion that the species can tolerate shade better than it is generally acknowledged. They found that while species like *Myriophyllum spicatum* and *Hydrilla verticillata* exhibited higher relative growth rates and could even outcompete *C. caroliniana* under high light conditions, *C. caroliniana* performed significantly better than the other tested species when exposed to light intensities of 150 light $\mu\text{mol m}^{-2}\text{s}^{-1}$ or lower. This adaptability, combined with its ability to grow and reproduce rapidly in warm water, likely contributes to its exceptional success and high invasiveness.

In summary, *C. caroliniana* demonstrates an exceptional tolerance to a wide range of light and temperature conditions. While it thrives in warm water, it can also endure periods of very cool temperatures. Similarly, although it grows best under high light conditions, it is also capable of thriving in low-light environments. This adaptability gives it a significant advantage when competing for underwater light with other aquatic plants and makes the species extremely dangerous to the local flora.

4.3 Thermal and light optima of *Elodea nuttallii*

Our results indicate that *Elodea nuttallii* exhibits a broad tolerance to temperature but has relatively specific light requirements. In the thermal variant of the experiment, while the species displayed certain growth in all treatments, higher water temperatures had a clear positive effect on the species elongation, indicating species preferences for high water temperatures. This finding aligns well with the observations of Hoffmann et al. (2015), who found in their laboratory experiment that *E. nuttallii* fragments exposed to water temperatures of either 15 or 20°C had a higher survival rate and greater growth at 20°C. Another study (Ma JianMin et al., 2009) that investigated *E. nuttallii*'s response to thermal stress, showed that individuals cultivated at 25°C, the lowest temperature tested, exhibited the highest growth rate during the experiment. Additionally, it was found that *E. nuttallii* can survive temperatures as high as 39°C, although for a limited time only. While in our study the species growth benefited from the elevated water temperature, individuals cultivated at the low water temperatures were also found to be in good condition. This is consistent with Kunii's 1981, Kunii's 1981 research, which focused on the winter growth of this species and demonstrated that *E. nuttallii* is well adapted to low water temperatures, surviving and even growing in water as cold as 4°C. These findings suggest that *E. nuttallii* tolerates an exceptionally wide temperature range, with optimal growth occurring at water temperatures slightly above 20°C. The importance of temperature in the spread of *E. nuttallii* was further highlighted by a field study conducted by Grudnik et al. (2014) in a Slovakian river, where it was observed that warmer winter and spring water temperatures, exceeding 10°C, led to higher densities of this species throughout the year. Our results also point out that the growth of total length of *E. nuttallii*'s individuals cultivated in the water temperature above 14°C accelerates significantly. This ability of *E. nuttallii* to survive in cold water, combined with its accelerated growth in warmer conditions, makes it particularly challenging from the perspective of invasive species management. It should be considered that the current water temperatures in Europe already favor this species, and the expected rise in temperatures resulting from global warming is likely to even enhance its invasiveness in this region of the world.

On the contrary, when compared to the species thermal tolerance, light tolerance of *E. nuttallii* seems to be quite narrow. Results of the experiment show that, the most optimal light conditions for the plants growth were that of 22.0 and 46.4 of light $\mu\text{mol m}^{-2}\text{s}^{-1}$ (25 and 50% of maximal light level respectively) since, individuals cultivated in those treatments exhibited both highest mass and length growth. The lowest light level - that of 2.9 light $\mu\text{mol m}^{-2}\text{s}^{-1}$ (3% light level) seemed insufficient for *E.*

nuttallii since individuals from this treatment were the only ones for which, when compared to the plants from the start control group, loss in the both mass and shoots' length was observed. Interestingly, the small necrosis observed in the lower parts of the shoots in nearly half of the cultivated specimens may be part of the plant's light adaptation strategy. In the natural environment, *E. nuttallii* is known to detach from the substrate in autumn and form dense floating mats (Zehnsdorf et al., 2015), which can significantly disrupt the aquatic environment and facilitate the colonization of new areas. In a controlled outdoor experiment conducted by Kunii (1984), it was observed that plants exposed to poor light conditions, at 4.5% of full sunlight or less, detached from the bottom of the tanks and began floating, due to the decay of their lower portions. Kunii theorized that the decay of the lower part of the plant under unfavorable light conditions might not be accidental but rather an adaptation of *E. nuttallii* that allows it to escape unfavorable photosynthetic conditions and float to areas with better sunlight exposure. Thus, perhaps the observed partial necrosis in almost half of the *E. nuttallii* individuals that were cultivated in 2.9 light $\mu\text{mol m}^{-2}\text{s}^{-1}$ may be attributed to this adaptation. Our results, indicating good tolerance of this species to low light values, also aligns well with field observations, since this species has been found to thrive in lakes experiencing algae blooms, in deeper waters, or even beneath ice cover (Angelstein and Schubert, 2009). The light optimum found during this research to be around 22.0 and 46.4 of light $\mu\text{mol m}^{-2}\text{s}^{-1}$ is similar in value yet a little lower than that found in few different studies which tested *E. nuttallii* response to different light levels: 40 - 48 (Barrat-Segretain, 2004), 28 - 80 (Szabó et al., 2019), 51 - 94 (Angelstein and Schubert, 2009) or even in case of just 12 days long experiment 80 - 200 light $\mu\text{mol m}^{-2}\text{s}^{-1}$ (Szabó et al., 2020). However, comparing these results with those of our experiment is challenging, as factors such as the duration of the studies, the range and intensity of tested light conditions, water temperature, nutrient levels, and methods of plant measurement often varied significantly. Despite these differences, the overall findings consistently portray *E. nuttallii* as a species that thrive in low light conditions, simultaneously being intolerant to higher light intensity. This narrow tolerance to the different light values may be connected with the low chlorophyll *a* content plasticity that its individuals exhibited in our study. Nevertheless the ability of this plant to withstand low light conditions is likely crucial to the plant's success in its introduced range, as it enables it to outcompete native species for light and colonize deeper areas of water bodies that are less suitable for more light-dependent species. Additionally, its ability to thrive in cold water enables it to survive the winter without relying on seeds for overwintering. As a result, *E. nuttallii* populations can begin expanding in early spring, even under low light conditions. The rising water temperatures in the following months, coupled with the plant's ability of rapid growth in warmer waters, may further enhance its advantage over local species.

4.4 Thermal and light optima of *Vallisneria spiralis*

Currently, there is a lack of detailed studies describing the light and thermal preferences of *Vallisneria spiralis*. However, the observed species distribution and experimental studies suggest that

it is associated with warm waters and tolerates a wide range of light intensities, from at least 90 to up to 500 light $\mu\text{mol m}^{-2}\text{s}^{-1}$ (Zhao et al., 2013), with the highest growth observed for the highest light values. Our research shows that the species can grow and produce new biomass even under dim light conditions as low as 9.7 light $\mu\text{mol m}^{-2}\text{s}^{-1}$. However, the production of daughter ramets, and thus vegetative reproduction, was completely inhibited until the light intensity reached 22.0 light $\mu\text{mol m}^{-2}\text{s}^{-1}$ or higher. This broad tolerance to different light conditions suggests that, for *V. spiralis*, water temperature is a more limiting factor than light intensity. This hypothesis is supported by the fact that, in its distribution across northern Europe, it is now almost exclusively associated with waters that are naturally (Wasowicz et al., 2014) or artificially heated (Hussner and Lösch, 2005; Hutorowicz, 2006), where temperatures remain above 10°C even in winter.

Our research indicates that although the individuals can survive for extended periods of time at temperatures around 10°C or slightly below, a significant change in its response occurs when exposed to temperatures of 14°C or higher. Above this value, a notable increase in growth is observed, and new ramets begin to form. The importance of this temperature threshold is also observable in the plants' chlorophyll *a* content. Individuals exposed to lower water temperatures of 7 or 10°C had significantly lower chlorophyll *a* content when compared with the individuals from the remaining treatments, which likely reflects the reduced physiological activity of those individuals. Although the plants appear capable of growing reasonably well at temperatures slightly below 20°C, *V. spiralis* seems to thrive best at temperatures above 20°C. This observation can be made based on results of this study, where *V. spiralis* showed optimal growth at the highest temperatures, as well as on the results presented by Zhao et al., (2013) who in their experimental work achieved good development of this species in an average water temperature of 24°C. Furthermore, Hutorowicz (2006) in his field studies in which he studied the development of *V. spiralis* over a single vegetative season in the context of annual water temperature changes, found out that it started to dominate the study sites when the water temperature was a few degrees warmer than 20°C. He also noted that the population decline started when water temperatures dropped below 15°C in the autumn. This observation aligns with our findings, as our experiment showed that plants grown in water temperatures below 14°C exhibited significantly poorer growth compared to that of the other treatments.

In conclusion, both our results and the literature data suggest that despite species broad tolerance to varying light conditions, the distribution of *V. spiralis* is significantly limited by its intolerance to the low water temperatures. Such temperatures hinder its development and, when close to freezing, likely lead to the death of individuals. An intriguing question remains, whether the populations currently inhabiting artificially heated water bodies will eventually adapt to the gradually increasing, but still low winter temperatures found in aquatic ecosystems of Central Europe. The emergence of frost-resistant individuals could pose a serious threat to local ecosystems. It is why we believe that the further monitoring of the *V. spiralis* population located in the Konin lakes could be both important and intriguing. Just in a few years, the coal power plant responsible for heating these lakes is scheduled to be decommissioned, and the water temperature in this area is expected to return to the

normal level. Thus, if the species continues to persist in this area in the coming years, it would indicate the development of a frost-resistant population of *V. spiralis*, potentially capable of threatening nearby aquatic ecosystems.

4.5 Implication for control

It is widely acknowledged that the most effective control methods rely on a deep understanding of a species' ecology and behavior (Hussner 2017), and this is equally true for managing invasive aquatic plants. Moreover, since most of these plants in their introduced range, such as *Cabomba caroliniana*, *Elodea nuttallii*, and *Vallisneria spiralis*, do not produce viable seeds, and instead rely solely on their highly efficient vegetative reproduction, special attention should be given to their elongation and their propagule production. Our studies show a strong relationship between water temperature and the production of offshoots and ramets in species such as *C. caroliniana* and *V. spiralis*. Therefore, for these species, it is recommended to apply control methods in early spring, before water temperatures rise to levels that allow these plants to produce new offshoots or ramets. Simultaneously, high shade tolerance of tested plants means that they may easily dominate local plant populations at the beginning of the growing season, when both the length of the day and the zenith angle of the sun limits the water insolation. Reducing the populations of these invasive species during this time of the year, would undoubtedly allow native, light-sensitive plants to develop undisturbed. Additionally, since apparently species like *C. caroliniana* and *E. nuttallii* can survive in cold water for extended periods, a second control treatment in autumn would prevent them from surviving until spring in dense patches. Such patches likely increase chances of their survival through the winter as well as speeds up the colonization process (Hoffmann et al., 2015). Furthermore, our studies show that although all the tested species could be considered shade-tolerant, light levels as low as 2.9 light $\mu\text{mol m}^{-2}\text{s}^{-1}$ significantly hindered their growth, causing their biomass to drop below the initial levels observed for the control group at the start of the experiment. This biomass drop was especially profound in the case of *E. nuttallii* and *V. spiralis* suggesting that the impact of control methods that base on complete shading of invasive aquatic plants, can be especially effective in the case of these species. Interestingly, while under the lowest light conditions *C. caroliniana* and *E. nuttallii* still managed to produce some offshoots - albeit reduced in number, *V. spiralis* failed to produce any daughter ramets when cultivated in light levels of 9.7 light $\mu\text{mol m}^{-2}\text{s}^{-1}$ or lower. If such inhibition of propagule production due to shading could also be repeated in the field, it would indicate the extremely high effectiveness of shading as a control method for this species.

In conclusion, both the high shade tolerance of the tested species as well as their significantly accelerated growth when exposed to the higher water temperatures suggests that the threat posed by these species will likely only increase in future. It is estimated that in future eutrophication levels of freshwater ecosystems are likely to rise (Jeppesen et al., 2009), leading surely to the further drop in water transparency and thus limiting the light available for aquatic submerged plants. Such a decrease

in water transparency combined with expected rise of the water temperature will most likely benefit such a shade tolerant and thermophilic species as these tested invasive aquatic plants. Thus in future, their invasiveness and range of occurrence can only be expected to increase.

Data statement

Data will be made available on request

Appendix A. Supplementary data

Appendix A contains a table presenting the basic statistics (mean, median, standard deviation, minimum, maximum) of the results obtained during this research.

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Appendix A. Supplementary data

Appendix A contains a table presenting the basic statistics (mean, median, standard deviation, minimum, maximum) of the results obtained during this research.

Elodea_Temp	7°C			10°C			14°C			17°C			21°C		
	Mean ± SD	Median	Range	Mean ± SD	Median	Range	Mean ± SD	Median	Range	Mean ± SD	Median	Range	Mean ± SD	Median	Range
Total main shoot and offshoots length, cm	12.56 ± 1.17	12,6	10.7 - 15.2	12.79 ± 1.18	12,6	10.7 - 15.7	14.28 ± 1.57	14	12.2 - 18.3	17.00 ± 2.92	16,3	13.6 - 21.5	17.91 ± 1.95	18,2	14.3 - 21.6
Main shoot length, cm	11.51 ± 0.75	11,6	10.2 - 12.6	12.06 ± 0.94	12,2	10.3 - 13.7	12.23 ± 1.31	12,1	10.7 - 15.0	13.41 ± 1.94	13,6	10.1 - 16.0	15.35 ± 3.37	15,9	10.5 - 21.1
Dry mass, g	0.02 ± 0.09	0,08	0.05 - 0.13	0.03 ± 0.10	0,1	0.17 - 0.06	0.02 ± 0.09	0,09	0.11 - 0.06	0.02 ± 0.10	0,1	0.14 - 0.08	0.02 ± 0.10	0,1	0.13 - 0.07
Number of offshoots	0.96 ± 40.85	1	0.0 - 3.0	0.81 ± 43.31	1	0.0 - 2.0	0.63 ± 30.33	1	1.0 - 3.0	1.01 ± 33.00	2	0.0 - 3.0	1.02 ± 36.06	1,5	0.0 - 3.0
Mean chlorophyll content, mg/m2	22.37 ± 35,8	3	12.33 - 77.67	27.57 ± 43.31	41	103.33	23.54 ± 30.33	19	73.67	15.14 ± 33.00	3	71.67	14.91 ± 36.06	7	61.00

Elodea_Light	0,03			0,1			0,25			0,5			1		
	Mean ± SD	Median	Range	Mean ± SD	Median	Range	Mean ± SD	Median	Range	Mean ± SD	Median	Range	Mean ± SD	Median	Range
Total main shoot and offshoots length, cm	10.54 ± 1.12	11,0	9.0 - 12.3	16.66 ± 1.73	17,1	13.9 - 19.3	19.88 ± 2.14	20,4	14.7 - 23.0	17.45 ± 2.52	17,0	13.6 - 21.9	16.16 ± 2.84	15,4	13.0 - 23.2
Main shoot length, cm	10.41 ± 1.07	10,9	9.0 - 12.0	12.94 ± 2.32	12,4	10.5 - 16.7	16.79 ± 3.90	17,6	10.2 - 23.0	14.07 ± 4.09	11,8	9.7 - 20.7	12.10 ± 2.92	10,7	9.5 - 19.2
Dry mass, g	0.06 ± 0.01	0,06	0.04 - 0.07	0.08 ± 0.02	0,08	0.12	0.10 ± 0.01	0,10	0.13	0.11 ± 0.02	0,11	0.14	0.10 ± 0.01	0,10	0.12
Number of offshoots	0.50 ± 120.89	0,5	0.0 - 1.0	1.88 ± 135.50	50	219.33	1.44 ± 72.75	7	120.33	1.75 ± 59.19	7	120.33	2.07 ± 71.47	7	103.00
Mean chlorophyll content, mg/m2	29.60 ± 111,	83	80.00 - 185.67	44.99 ± 127,	50	219.33	23.05 ± 72.75	7	120.33	21.04 ± 59.19	0	88.67	18.16 ± 71.47	7	103.00

Cab_Temp	7°C			10°C			14°C			17°C			21°C		
	Mean ± SD	Median	Range	Mean ± SD	Median	Range	Mean ± SD	Median	Range	Mean ± SD	Median	Range	Mean ± SD	Median	Range
Total main shoot and offshoots length, cm	13.17 ± 0.59	13,2	12.3 - 14.2	13.32 ± 0.39	13,2	12.8 - 13.8	13.84 ± 0.47	13,9	13.0 - 14.6	15.00 ± 1.13	15,1	12.8 - 16.1	17.52 ± 0.85	17,3	16.4 - 19.1
Main shoot length, cm	13.17 ± 0.12	13,2	12.3 - 14.2	13.32 ± 0.13	13,2	12.8 - 0.12	13.84 ± 0.15	13,9	13.0 - 0.09	14.95 ± 0.13	15,1	12.8 - 0.10	17.32 ± 0.15	17,0	16.2 - 0.10
Dry mass, g	0.02 ± 0.02	0,12	0.09 - 0.16	0.01 ± 0.01	0,12	0.14	0.03 ± 0.03	0,14	0.20	0.02 ± 0.12	0,13	0.16	0.03 ± 0.31	0,14	0.20
Number of offshoots	0 ± 0	0	0 - 0	0 ± 0	0	0 - 0	0 ± 0	0	0 - 0	0.35 ± 0.35	0	0 - 1	0.48 ± 0.48	0	0 - 1
Mean chlorophyll content, mg/m2	61.44 ± 20.91	65,3	25.00 - 88.67	41.20 ± 14.09	33,6	31.33 - 65.33	49.36 ± 18.42	46,3	19.00 - 74.00	56.63 ± 26.22	52,6	18.67 - 99.33	87.90 ± 23.19	90,6	46.33 - 118.00

Cab_Light	0,03			0,1			0,25			0,5			1		
	Mean ± SD	Median	Range	Mean ± SD	Median	Range	Mean ± SD	Median	Range	Mean ± SD	Median	Range	Mean ± SD	Median	Range
Total main shoot and offshoots length, cm	16.03 ± 2.27	15,5	13.7 - 20.86	14.89 ± 2.20	15,1	11.1 - 19.20	14.91 ± 1.42	5	18.20	20.68 ± 3.73	19,7	16.6 - 26.90	20.65 ± 3.82	20,9	13.9 - 25.00
Main shoot length, cm	15.25 ± 1.64	14,5	13.7 - 19.0	14.06 ± 1.87	14,2	11.1 - 17.0	14.64 ± 1.55	5	18.2	16.67 ± 1.74	16,6	13.3 - 19.1	20.38 ± 3.58	20,7	13.9 - 25.0
Dry mass, g	0.12 ± 0.03	0,11	0.07 - 0.17	0.13 ± 0.02	0,13	0.11 - 0.16	0.13 ± 0.03	0,13	0.17	0.13 ± 0.03	0,14	0.08 - 0.16	0.14 ± 0.03	0,13	0.10 - 0.19
Number of offshoots	0.67 ± 0.36	0	0.0 - 2.0	0.51 ± 0.38	0	0.0 - 1.0	0.48 ± 0.31	0	0.0 - 1.0	0.54 ± 0.91	1	0.0 - 2.0	0.52 ± 0.38	0	0.0 - 1.0
Mean chlorophyll content, mg/m2	85.12 ± 33.13	88,6	36.00 - 131.00	75.05 ± 27.77	71,3	23.00 - 118.00	114.44 ± 34.63	116,00	59.00 - 166.67	88.85 ± 31.68	84,3	41.33 - 128.67	72.92 ± 15.12	69,1	57.00 - 97.00

Val_Temp	7°C			10°C			14°C			17°C			21°C						
	Mean ± SD	Median Range	Mean ± SD	Median Range	Mean ± SD	Median Range	Mean ± SD	Median Range	Mean ± SD	Median Range	Mean ± SD	Median Range	Mean ± SD	Median Range					
Change in the total length of leaves	2.82 ± 12.54	4.65	-14.2 - 27 (-14.2 do 27)	11.80 ± 9.76	11.6	5	-4.6 - 27.4	24.56 ± 13.19	28.1	0	-0.1 - 44.9	43.09 ± 17.07	43.8	0	11.8 - 75.7	50.42 ± 21.22	53.8	0	15.5 - 81.4
Dry mass, g	0.12 ± 0.05	0.12	0.06 - 0.23	0.15 ± 0.06	0.13	0.29	0.08 - 0.04	0.18 ± 0.04	0.18	0.26	0.10 - 0.07	0.18 ± 0.17	0.30	0.30	0.08 - 0.06	0.19 ± 0.06	0.18	0.30	0.10 - 0.30
Change in the total number of leaves	0.12 ± 1.20	0.0	-1 - 3	0.67 ± 1.23	1.0	-1 - 3	2.38 ± 1.59	2	0 - 5	5.47 ± 2.23	6.0	2 - 9	3.93 ± 2.64	3.5	0 - 10	3.93 ± 2.64	3.5	0 - 10	0.10 - 0.10
Change in mean length of the three longest leaves	1.10 ± 0.87	0.88	-0.60 - 3.00	1.46 ± 1.07	1.53	3.70	0.07 - 2.35	3.43 ± 2.35	3.10	6.90	-0.33 - 2.92	3.59 ± 2.93	10.57	4.08	-0.23 - 9.22	8.32 ± 9.22	9.22	14.60	-0.13 - 14.60
Mean chlorophyll content, mg/m2	26.25 ± 12.46	28.8	3	20.96 ± 16.07	16.1	7	2.00 - 57.33	68.92 ± 25.70	69.0	17.00 - 108.00	90.53 ± 18.65	89.0	59.33 - 127.33	93.25 ± 18.11	95.5	57.33 - 118.67	95.5	57.33 - 118.67	0 - 118.67
Number of stolons	0 ± 0	0	0 - 0	0 ± 0	0	0 - 0	0.73	0	0 - 2	0.93	1	0 - 3	1.31	0	0 - 4	1.31	0	0 - 4	0 - 4

Val_Light	0,03			0,1			0,25			0,5			1						
	Mean ± SD	Median Range	Mean ± SD	Median Range	Mean ± SD	Median Range	Mean ± SD	Median Range	Mean ± SD	Median Range	Mean ± SD	Median Range	Mean ± SD	Median Range					
Change in the total length of leaves	-16.5 ± 16.49	11.4	0	39.01 ± 23.15	40.1	5	5.4 - 82.6	59.44 ± 26.66	53.9	27.0 - 108.4	52.62 ± 31.99	55.0	5	61.23 ± 30.87	55.1	0	19.9 - 142.5	19.9 - 142.5	
Dry mass, g	0.06 ± 0.02	0.06	0.04 - 0.10	0.13 ± 0.05	0.13	0.25	0.07 - 0.05	0.15 ± 0.05	0.15	0.22	0.07 - 0.17	0.17	0.35	0.09	0.19	0.43	0.19	0.43	0.08 - 0.43
Change in the total number of leaves	-1.27 ± 1.10	-1.0	-3 - 1	0.62 ± 1.45	0.5	-1 - 3	2.56 ± 2.66	2.56 ± 2.66	2.0	0 - 11	2.47 ± 1.55	3.0	-1 - 5	6.38 ± 6.03	4.5	0 - 19	6.38 ± 6.03	4.5	0 - 19
Change in mean length of the three longest leaves	1.09 ± 1.31	0.77	-0.80 - 3.57	9.87 ± 4.86	9.82	20.50	2.37 - 4.11	9.75 ± 4.11	9.52	16.40	9.37 ± 4.90	8.68	19.37	8.83 ± 5.62	8.82	17.20	8.82	17.20	-1.40 - 17.20
Mean chlorophyll content, mg/m2	99.36 ± 26.40	92.0	0	142.94 ± 27.73	145.	67	93.33 - 190.33	33.44 ± 178.00	130.	76.33 - 178.00	82.25 ± 20.37	80.6	40.33 - 120.67	67.35 ± 26.86	63.6	7	67.35 ± 26.86	63.6	25.67 - 131.33
Number of stolons	0 ± 0	0	0 - 0	0 ± 0	0	0 - 0	0.77	0	0 - 3	1.03	0	0 - 4	1.98	1	0 - 6	1.98	1	0 - 6	0 - 6

Poznań 16.09.2024

Oświadczenie współautora pracy

Ja, Mateusz Draga, oświadczam, że jestem współautorem pracy pt. „**Can invasive aquatic plants thrive in cold water and low light conditions? Implications for control – an experimental study**” autorstwa: Mateusza Dragi* oraz Macieja Gąbki, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Mój udział polegał na: konceptualizacji pracy, przeglądzie literaturowym, zebraniu osobników i ich pomiarze przed i po eksperymencie, przygotowaniu hodowli i specjalnych komór hodowlanych, przeprowadzeniu eksperymentów, wykonaniu analiz statystycznych, tabel oraz rycin, jak i na napisaniu oraz edycji manuskryptu jak i zgłoszenia go do czasopisma oraz korespondencji z edytorem.

*Autor korespondencyjny



Podpis współautora



Podpis promotora

Poznań 16.09.2024

Oświadczenie współautora pracy

Ja, Maciej Gąbka, oświadczam, że jestem współautorem pracy pt. „**Can invasive aquatic plants thrive in cold water and low light conditions? Implications for control – an experimental study**” autorstwa: Mateusza Dragi* oraz Macieja Gąbki, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Mój udział polegał na: pomocy w konceptualizacji pracy, zebraniu niezbędnych osobników oraz korekty stworzonego manuskryptu.

*Autor korespondencyjny



Podpis współautora

Chapter 3

The beneficial effect of barley straw extract addition on the growth of two aquatic invasive alien species

<https://doi.org/10.1007/s11756-023-01550-z>

Poznań 16.09.2024

Oświadczenie współautora pracy

Ja, Mateusz Draga, oświadczam, że jestem współautorem pracy pt. „**The beneficial effect of barley straw extract addition on the growth of two aquatic invasive alien species (*Elodea nuttallii* and *Cabomba caroliniana*) under laboratory conditions**” autorstwa: Mateusza Dragi* oraz Macieja Gąbki, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Mój udział polegał na: konceptualizacji pracy, pozyskaniu środków z projektu pt. „Wsparcie procesu aplikacji grantowych: merytoryczne, techniczne i językowe - Minigranty dla doktorantów szkół doktorskich”, przeglądzie literaturowym, zebraniu osobników i ich pomiarze przed i po eksperymencie, przygotowaniu hodowli, określeniu i przygotowaniu właściwych stężeń ekstraktu, przeprowadzeniu eksperymentów, wykonaniu analiz statystycznych, tabel oraz rycin, jak i na napisaniu oraz edycji manuskryptu, zgłoszenia go do czasopisma oraz korespondencji z edytorem i naniesieniu poprawek zgodnie z uwagami recenzentów.

*Autor korespondencyjny



Podpis współautora



Podpis promotora

Poznań 16.09.2024

Oświadczenie współautora pracy

Ja, Maciej Gąbka, oświadczam, że jestem współautorem pracy pt. „**The beneficial effect of barley straw extract addition on the growth of two aquatic invasive alien species (*Elodea nuttallii* and *Cabomba caroliniana*) under laboratory conditions**” autorstwa: Mateusza Dragi* oraz Macieja Gąbki, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Mój udział polegał na: pomocy w konceptualizacji pracy, korekty stworzonego manuskryptu, pomocy przy nanoszeniu poprawek zgodnie z uwagami recenzentów.

*Autor korespondencyjny



Podpis współautora

Chapter 4

Opracowanie metod zwalczania dla minimum 10 inwazyjnych gatunków obcych wraz z przeprowadzeniem działań pilotażowych w terenie. Kompendium dotyczące metod zwalczania kabomby karolińskiej (*Cabomba caroliniana*)

<https://www.gov.pl/web/gdos/kompendia-zwalczania-wybranych-igo>

Poznań 16.09.2024

Oświadczenie współautora pracy

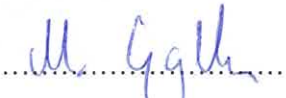
Ja, Mateusz Draga, oświadczam, że jestem współautorem pracy pt. „**Opracowanie metod zwalczania dla minimum 10 inwazyjnych gatunków obcych wraz z przeprowadzeniem działań pilotażowych w terenie. Kompendium - dotyczące metod zwalczania kabomby karolińskiej (*Cabomba caroliniana*)**” autorstwa: Macieja Gąbki, Łukasza Bryła, Mateusza Dragi, Daniela Liska, Stanisława Rosadzińskiego, Krzysztofa Dominiaka, Weroniki Ciężyńskiej oraz Piotra Leperowskiego, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Mój udział polegał na: konceptualizacji pracy, przeglądzie literatury, selekcji i wytypowaniu metod kontroli obcych gatunków roślin wodnych, wytypowaniu zbiorników nadających się do przetestowania pilotażowych metod kontroli, udziale w pracach terenowych polegających na przeprowadzeniu pilotażowych metod kontroli inwazyjnych gatunków obcych, przeprowadzeniu monitoringów przyrodniczych przed, w trakcie i po zabiegach wraz ze zebraniem i pomiarem podstawowych danych morfometrycznych osobników *Elodea nuttallii* oraz oceną efektywności podjętych działań, przeprowadzeniu dokumentacji zdjęciowej, przygotowanie manuskryptu kompendium (w szczególności rozdziałów „3. Metody zapobiegania rozprzestrzenianiu się i zwalczania moczarki delikatnej” oraz „4. Zalecenia dotyczące sposobu prowadzenia monitoringu”), wykonanie i edycji i poprawek tekstu zgodnie z zaleceniami zamawiającego.



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Podpis współautora



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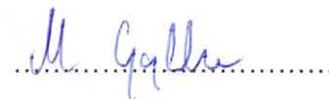
Podpis promotora

Poznań 16.09.2024

Oświadczenie współautora pracy

Ja, Maciej Gąbka, oświadczam, że jestem współautorem pracy pt. „**Opracowanie metod zwalczania dla minimum 10 inwazyjnych gatunków obcych wraz z przeprowadzeniem działań pilotażowych w terenie. Kompedium - dotyczące metod zwalczania kabomby karolińskiej (*Cabomba caroliniana*)**” autorstwa: Macieja Gąbki, Łukasza Bryła, Mateusza Dragi, Daniela Liska, Stanisława Rosadzińskiego, Krzysztofa Dominiaka, Weroniki Ciężyńskiej oraz Piotra Leperowskiego, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Mój udział polegał na: konceptualizacji pracy, komunikacji z zamawiającym, przeglądzie literatury, selekcji i wytypowaniu metod kontroli obcych gatunków roślin wodnych, wytypowaniu zbiorników nadających się do przetestowania pilotażowych metod kontroli, przeprowadzeniu monitoringów przyrodniczych przed, w trakcie i po zabiegach przeprowadzeniu dokumentacji zdjęciowej, ocenie efektywności podjętych działań, przygotowanie manuskryptu kompedium, wykonanie precyzyjnych pomiarów i zdjęć na rzecz pierwszego rozdziału pracy, edycji i poprawek tekstu zgodnie z zaleceniami zamawiającego.



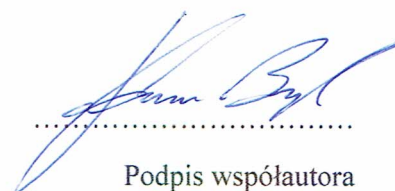
Podpis współautora

Poznań 16.09.2024

Oświadczenie współautora pracy

Ja, Łukasz Bryl, oświadczam, że jestem współautorem pracy pt. **„Opracowanie metod zwalczania dla minimum 10 inwazyjnych gatunków obcych wraz z przeprowadzeniem działań pilotażowych w terenie. Kompendium - dotyczące metod zwalczania kabomby karolińskiej (*Cabomba caroliniana*)”** autorstwa: Macieja Gąbki, Łukasza Bryła, Mateusza Dragi, Daniela Liska, Stanisława Rosadzińskiego, Krzysztofa Dominiaka, Weroniki Ciężyńskiej oraz Piotra Leperowskiego, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Mój udział polegał na: konceptualizacji pracy, komunikacji z zamawiającym, wytypowaniu zbiorników nadających się do przetestowania pilotażowych metod kontroli, kierowanie pracami terenowymi polegających na przeprowadzeniu pilotażowych metod kontroli inwazyjnych gatunków obcych, wykonanie dokumentacji zdjęciowej, przygotowanie manuskryptu kompendium, stworzeniu kosztorysu, ocenie pracochłonności przeprowadzonych metod, edycji i poprawek tekstu zgodnie z zaleceniami zamawiającego.



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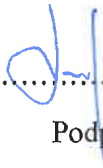
Podpis współautora

Poznań 16.09.2024

Oświadczenie współautora pracy

Ja, Daniel Lisek, oświadczam, że jestem współautorem pracy pt. „**Opracowanie metod zwalczania dla minimum 10 inwazyjnych gatunków obcych wraz z przeprowadzeniem działań pilotażowych w terenie. Kompendium - dotyczące metod zwalczania kabomby karolińskiej (*Cabomba caroliniana*)**” autorstwa: Macieja Gąbki, Łukasza Bryła, Mateusza Dragi, Daniela Liska, Stanisława Rosadzińskiego, Krzysztofa Dominiaka, Weroniki Ciężyńskiej oraz Piotra Leperowskiego, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Mój udział polegał na: konceptualizacji pracy, komunikacji z zamawiającym, selekcji i wytypowaniu metod kontroli obcych gatunków roślin wodnych, wytypowaniu zbiorników nadających się do przetestowania pilotażowych metod kontroli, przygotowanie manuskryptu kompendium, edycji i poprawek tekstu zgodnie z zaleceniami zamawiającego.


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Podpis współautora

Poznań 16.09.2024

Oświadczenie współautora pracy

Ja, Stanisław Rosadziński, oświadczam, że jestem współautorem pracy pt. „**Opracowanie metod zwalczania dla minimum 10 inwazyjnych gatunków obcych wraz z przeprowadzeniem działań pilotażowych w terenie. Kompendium - dotyczące metod zwalczania kabomby karolińskiej (*Cabomba caroliniana*)**” autorstwa: Macieja Gąbki, Łukasza Bryła, Mateusza Dragi, Daniela Liska, Stanisława Rosadzińskiego, Krzysztofa Dominiaka, Weroniki Ciężyńskiej oraz Piotra Leperowskiego, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Mój udział polegał na: wytypowaniu zbiorników nadających się do przetestowania pilotażowych metod kontroli oraz przeprowadzeniu części monitoringów przyrodniczych.



Podpis współautora

Poznań 16.09.2024

Oświadczenie współautora pracy

Ja, Krzysztof Dominiak, oświadczam, że jestem współautorem pracy pt. „**Opracowanie metod zwalczania dla minimum 10 inwazyjnych gatunków obcych wraz z przeprowadzeniem działań pilotażowych w terenie. Kompendium - dotyczące metod zwalczania kabomby karolińskiej (*Cabomba caroliniana*)**” autorstwa: Macieja Gąbki, Łukasza Bryła, Mateusza Dragi, Daniela Liska, Stanisława Rosadzińskiego, Krzysztofa Dominiaka, Weroniki Ciarzyńskiej oraz Piotra Leperowskiego, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Moja praca polegała na udziale w pracach terenowych mających za zadanie przetestowanie pilotażowych metod kontroli inwazyjnych gatunków obcych.

Krzysztof Dominiak

Podpis współautora

Poznań, 16.09.2024 r.

Oświadczenie współautora pracy

Ja niżej podpisana, Weronika Ciążyńska, oświadczam, że jestem współautorem pracy pt. „**Opracowanie metod zwalczania dla minimum 10 inwazyjnych gatunków obcych wraz z przeprowadzeniem działań pilotażowych w terenie. Kompendium - dotyczące metod zwalczania kabomby karolińskiej (*Cabomba caroliniana*)**” autorstwa: Macieja Gąbki, Łukasza Bryła, Mateusza Dragi, Daniela Liska, Stanisława Rosadzińskiego, Krzysztofa Dominiaka, Weroniki Ciążyńskiej oraz Piotra Leperowskiego, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Mój udział polegał na: komunikacji z zamawiającym i z właścicielami zbiorników na terenie których przeprowadzono próbne metody kontroli, pracach terenowych oraz na edycji tekstu manuskryptu zgodnie z zaleceniami zamawiającego.



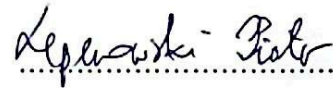
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Podpis współautora

Poznań 16.09.2024

Oświadczenie współautora pracy

Ja, Piotr Leperowski, oświadczam, że jestem współautorem pracy pt. „Opracowanie metod zwalczania dla minimum 10 inwazyjnych gatunków obcych wraz z przeprowadzeniem działań pilotażowych w terenie. Kompendium - dotyczące metod zwalczania kabomby karolińskiej (*Cabomba caroliniana*)” autorstwa: Macieja Gąbki, Łukasza Bryła, Mateusza Dragi, Daniela Liska, Stanisława Rosadzińskiego, Krzysztofa Dominiaka, Weroniki Ciężyńskiej oraz Piotra Leperowskiego, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Mój udział polegał na edycji tekstu manuskryptu zgodnie z zaleceniami zamawiającego.

Handwritten signature of Piotr Leperowski in black ink, written over a dotted line.

Podpis współautora

Chapter 5

Opracowanie metod zwalczania dla minimum 10 inwazyjnych gatunków obcych wraz z przeprowadzeniem działań pilotażowych w terenie. Kompendium dotyczące metod zwalczania moczarki delikatnej (*Elodea nuttallii*)

<https://www.gov.pl/web/gdos/kompendia-zwalczania-wybranych-igo>

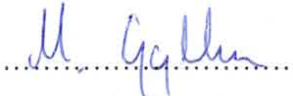
Oświadczenie współautora pracy

Ja, Mateusz Draga, oświadczam, że jestem współautorem pracy pt. „**Opracowanie metod zwalczania dla minimum 10 inwazyjnych gatunków obcych wraz z przeprowadzeniem działań pilotażowych w terenie. Kompendium - dotyczące metod zwalczania moczarki delikatnej (*Elodea nuttallii*)**” autorstwa: Macieja Gąbki, Łukasza Bryła, Mateusza Dragi, Daniela Liska, Stanisława Rosadzińskiego, Krzysztofa Dominiaka, Piotra Dynowskiego, Weroniki Ciężyńskiej oraz Piotra Leperowskiego, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Mój udział polegał na: konceptualizacji pracy, przeglądzie literatury, selekcji i wytypowaniu metod kontroli obcych gatunków roślin wodnych, wytypowaniu zbiorników nadających się do przetestowania pilotażowych metod kontroli, udziale w pracach terenowych polegających na przeprowadzeniu pilotażowych metod kontroli inwazyjnych gatunków obcych, przeprowadzeniu monitoringu przyrodniczych przed, w trakcie i po zabiegach wraz ze zebraniem i pomiarem podstawowych danych morfometrycznych osobników *Elodea nuttallii* oraz oceną efektywności podjętych działań, przeprowadzeniu dokumentacji zdjęciowej, przygotowanie manuskryptu kompendium (w szczególności rozdziałów „3. Metody zapobiegania rozprzestrzenianiu się i zwalczania moczarki delikatnej” oraz „4. Zalecenia dotyczące sposobu prowadzenia monitoringu”), wykonanie i edycji i poprawek tekstu zgodnie z zaleceniami zamawiającego.



Podpis współautora



Podpis promotora

Poznań 16.09.2024

Oświadczenie współautora pracy

Ja, Maciej Gąbka, oświadczam, że jestem współautorem pracy pt. „**Opracowanie metod zwalczania dla minimum 10 inwazyjnych gatunków obcych wraz z przeprowadzeniem działań pilotażowych w terenie. Kompendium - dotyczące metod zwalczania moczarki delikatnej (*Elodea nuttallii*)**” autorstwa: Macieja Gąbki, Łukasza Bryła, Mateusza Dragi, Daniela Liska, Stanisława Rosadzińskiego, Krzysztofa Dominiaka, Piotra Dynowskiego, Weroniki Ciążyńskiej oraz Piotra Leperowskiego, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Mój udział polegał na: konceptualizacji pracy, komunikacji z zamawiającym, przeglądzie literatury, selekcji i wytypowaniu metod kontroli obcych gatunków roślin wodnych, wytypowaniu zbiorników nadających się do przetestowania pilotażowych metod kontroli, przeprowadzeniu monitoringów przyrodniczych przed, w trakcie i po zabiegach przeprowadzeniu dokumentacji zdjęciowej, ocenie efektywności podjętych działań, przygotowanie manuskryptu kompendium, wykonanie precyzyjnych pomiarów i zdjęć na rzecz pierwszego rozdziału pracy, edycji i poprawek tekstu zgodnie z zaleceniami zamawiającego.



Podpis współautora

Poznań 16.09.2024

Oświadczenie współautora pracy

Ja, Łukasz Bryl, oświadczam, że jestem współautorem pracy pt. „**Opracowanie metod zwalczania dla minimum 10 inwazyjnych gatunków obcych wraz z przeprowadzeniem działań pilotażowych w terenie. Kompendium - dotyczące metod zwalczania moczarki delikatnej (*Elodea nuttallii*)**” autorstwa: Macieja Gąbki, Łukasza Bryla, Mateusza Dragi, Daniela Liska, Stanisława Rosadzińskiego, Krzysztofa Dominiaka, Piotra Dynowskiego, Weroniki Ciężyńskiej oraz Piotra Leperowskiego, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Mój udział polegał na: konceptualizacji pracy, komunikacji z zamawiającym, wytypowaniu zbiorników nadających się do przetestowania pilotażowych metod kontroli, kierowanie pracami terenowymi polegających na przeprowadzeniu pilotażowych metod kontroli inwazyjnych gatunków obcych, wykonanie dokumentacji zdjęciowej, przygotowanie manuskryptu kompendium, stworzeniu kosztorysu, ocenie pracochłonności przeprowadzonych metod, edycji i poprawek tekstu zgodnie z zaleceniami zamawiającego.



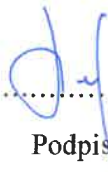
Podpis współautora

Poznań 16.09.2024

Oświadczenie współautora pracy

Ja, Daniel Lisek, oświadczam, że jestem współautorem pracy pt. „**Opracowanie metod zwalczania dla minimum 10 inwazyjnych gatunków obcych wraz z przeprowadzeniem działań pilotażowych w terenie. Kompedium - dotyczące metod zwalczania moczarki delikatnej (*Elodea nuttallii*)**” autorstwa: Macieja Gąbki, Łukasza Bryła, Mateusza Dragi, Daniela Liska, Stanisława Rosadzińskiego, Krzysztofa Dominiaka, Piotra Dynowskiego, Weroniki Ciężyńskiej oraz Piotra Leperowskiego, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Mój udział polegał na: konceptualizacji pracy, komunikacji z zamawiającym, selekcji i wytypowaniu metod kontroli obcych gatunków roślin wodnych, wytypowaniu zbiorników nadających się do przetestowania pilotażowych metod kontroli, przygotowanie manuskryptu kompedium, edycji i poprawek tekstu zgodnie z zaleceniami zamawiającego.

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Podpis współautora

Poznań 16.09.2024

Oświadczenie współautora pracy

Ja, Stanisław Rosadziński, oświadczam, że jestem współautorem pracy pt. „**Opracowanie metod zwalczania dla minimum 10 inwazyjnych gatunków obcych wraz z przeprowadzeniem działań pilotażowych w terenie. Kompendium - dotyczące metod zwalczania moczarki delikatnej (*Elodea nuttallii*)**” autorstwa: Macieja Gąbki, Łukasza Bryła, Mateusza Dragi, Daniela Liska, Stanisława Rosadzińskiego, Krzysztofa Dominiaka, Piotra Dynowskiego, Weroniki Ciężyńskiej oraz Piotra Leperowskiego, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Mój udział polegał na: wytypowaniu zbiorników nadających się do przetestowania pilotażowych metod kontroli oraz przeprowadzeniu części monitoringów przyrodniczych.



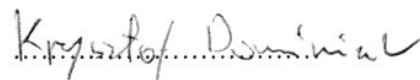
Podpis współautora

Poznań 16.09.2024

Oświadczenie współautora pracy

Ja, Krzysztof Dominiak, oświadczam, że jestem współautorem pracy pt. „**Opracowanie metod zwalczania dla minimum 10 inwazyjnych gatunków obcych wraz z przeprowadzeniem działań pilotażowych w terenie. Kompendium - dotyczące metod zwalczania moczarki delikatnej (*Elodea nuttallii*)**” autorstwa: Macieja Gąbki, Łukasza Bryla, Mateusza Dragi, Daniela Liska, Stanisława Rosadzińskiego, Krzysztofa Dominiaka, Piotra Dynowskiego, Weroniki Ciężyńskiej oraz Piotra Leperowskiego, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Moja praca polegała na udziale w pracach terenowych mających za zadanie przetestowanie pilotażowych metod kontroli inwazyjnych gatunków obcych.



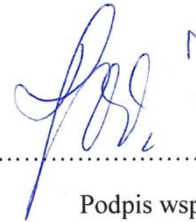
Podpis współautora

Poznań 16.09.2024

Oświadczenie współautora pracy

Ja, Piotr Dynowski, oświadczam, że jestem współautorem pracy pt. „**Opracowanie metod zwalczania dla minimum 10 inwazyjnych gatunków obcych wraz z przeprowadzeniem działań pilotażowych w terenie. Kompedium - dotyczące metod zwalczania moczarki delikatnej (*Elodea nuttallii*)**” autorstwa: Macieja Gąbki, Łukasza Bryła, Mateusza Dragi, Daniela Liska, Stanisława Rosadzińskiego, Krzysztofa Dominiaka, Piotra Dynowskiego, Weroniki Ciężyńskiej oraz Piotra Leperowskiego, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Mój wkład polegał na udziale w pracach terenowych mających za zadanie przetestowanie pilotażowych metod kontroli inwazyjnych gatunków obcych oraz na wykonaniu części monitoringów przyrodniczych, których celem była ocena skuteczności przeprowadzonych działań.



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Podpis współautora

Poznań, 16.09.2024 r.

Oświadczenie współautora pracy

Ja niżej podpisana- Weronika Ciężyńska, oświadczam, że jestem współautorem pracy pt. **„Opracowanie metod zwalczania dla minimum 10 inwazyjnych gatunków obcych wraz z przeprowadzeniem działań pilotażowych w terenie. Kompendium - dotyczące metod zwalczania moczarki delikatnej (*Eloдея nuttallii*)”** autorstwa: Macieja Gąbki, Łukasza Bryła, Mateusza Dragi, Daniela Liska, Stanisława Rosadzińskiego, Krzysztofa Dominiaka, Piotra Dynowskiego, Weroniki Ciężyńskiej oraz Piotra Leperowskiego, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Mój udział polegał na: komunikacji z zamawiającym i z właścicielami zbiorników na terenie których przeprowadzono próbne metody kontroli, pracach terenowych oraz na edycji tekstu manuskryptu zgodnie z zaleceniami zamawiającego.



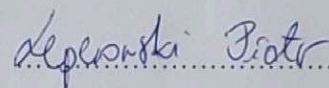
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Podpis współautora

Poznań 16.09.2024

Oświadczenie współautora pracy

Ja, Piotr Leperowski, oświadczam, że jestem współautorem pracy pt. „Opracowanie metod zwalczania dla minimum 10 inwazyjnych gatunków obcych wraz z przeprowadzeniem działań pilotażowych w terenie. Kompendium - dotyczące metod zwalczania moczarki delikatnej (*Elodea nuttallii*)” autorstwa: Macieja Gąbki, Łukasza Bryła, Mateusza Dragi, Daniela Liska, Stanisława Rosadzińskiego, Krzysztofa Dominiaka, Piotra Dynowskiego, Weroniki Ciężyńskiej oraz Piotra Leperowskiego, która jest częścią rozprawy doktorskiej Mateusza Dragi.

Mój udział polegał na edycji tekstu manuskryptu zgodnie z zaleceniami zamawiającego.



Podpis współautora

Summary

In summary, the key findings of my research include: (1) The identification of distribution patterns for 15 alien aquatic plant species and an explanation of the mechanisms behind the expansion of individual species based on precisely defined environmental gradients. The research demonstrated the significant role of low temperatures (mean minimum air temperature) in determining the occurrence of specific plant species across the country, with predictions for their future spread. (2) Drawing on literature data, unpublished findings, herbarium records, and numerous own observations, the history of the development of alien aquatic plants in Poland was traced, identifying over 300 locations distributed across the country. (3) Based on the collected data, a unique database was created that tracks the history of alien aquatic plants spread in Poland, along with various factors associated with their sightings. This database is continuously updated with new findings. (4) Through experimental studies, the behavior and response of *Cabomba caroliniana*, *Elodea nuttallii* and *Vallisneria spiralis* to varying thermal and light conditions were characterized. These findings provide new insights into the potential for growth and development of these species under low to medium light and temperature values. A particularly significant discovery was the high tolerance of these species to low light conditions and the accelerated growth in warm water conditions. (5) Experimental studies showed that barley straw extract has no negative effect on the growth of both *Elodea nuttallii* and *Cabomba caroliniana*, indicating that this method is not suitable for controlling alien aquatic plant species populations. However, these findings also indicate that the use of barley straw extracts as a method for controlling harmful cyanobacterial blooms carries a low environmental risk. (6) Performed pilot studies on the control methods for *Cabomba caroliniana* and *Elodea nuttallii* demonstrated that reducing the populations of alien aquatic plants is feasible, although it requires significant effort and likely the integration of multiple control techniques. Particularly noteworthy is the method of shading alien aquatic plants with jute mats, which not only effectively eradicated the targeted species but also promoted the rapid recolonisation by native macrophytes. The research also highlighted the substantial potential of diving-based methods, both for the implementation of control methods as well as for ecological monitoring.

Funding

- 1) The pilot testing of control methods for managing selected invasive species was funded by the following project: ‘POIS.02.04.00-00-0100/16 pn. Opracowanie zasad kontroli i zwalczania inwazyjnych gatunków obcych wraz z przeprowadzeniem pilotażowych działań i edukacją społeczną ze środków Unii Europejskiej w ramach Programu Infrastruktura i Środowisko 2014-2020’.
- 2) The research on the potential use of barley straw extract for controlling invasive macrophyte species was funded by ID-UB project: ‘Inicjatywa Doskonałości - Uczelnia Badawcza (017/02/SNP/0029)’.

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