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Ph.D. dissertation

Physiological Responses and Functional Traits of some Willow, Poplar and Bamboo taxa under Cadmium Stress

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ABBREVIATIONS

PES	Plant Economics Spectrum
LES	Leaf Economics Spectrum
RES	Root Economics Spectrum
TF	Translocation factor
BCF	Bioconcentration factor
PFT	Plant functional traits
RN	Root nitrogen content
RK	Root potassium content
BN	Branch nitrogen content
BK	Branch potassium content
LN	Leaf nitrogen content
LK	Leaf potassium content
SN	Soil nitrogen content
SK	Soil potassium content

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1 INTRODUCTION

1.1Background of the Study

Human activities have caused a multitude of environmental problems, among which heavy metal pollution is particularly concerning. Cd pollution is one of the most widespread and harmful issues, posing significant and often irreversible risks to human health and the environment (Six & Smolders, 2014). Panagos et al., (2013) estimated that over 2.5 million potentially contaminated sites exist within the European Union (EU), based on an analysis of the European Environmental Information and Observation Network for Soils (EIONET-SOIL) data. Urban and industrial waste accounts for approximately 38% of these sites, with mineral oils and heavy metals comprising 60% of the associated pollutants. The primary sources of Cd contamination in soils include vehicle emissions, mining activities, smelting operations, and the excessive application of pesticides and fertilizers. In recent years, environmental legislation aimed at mitigating Cd accumulation in soils has led to a 40% reduction in the use of phosphate fertilizers over the past 15 years. This reduction is projected to decrease soil Cd levels in cereal and potato cropping systems by approximately 15% over the next century (Ballabio et al., 2024). Despite these efforts, an estimated 5.5% of soils in the EU still exhibit Cd concentrations exceeding the critical threshold of 1 mg kg^{-1}.

In China, agricultural practices such as fertilization and sewage irrigation have exacerbated Cd pollution. In the rice-producing regions of southern China, approximately 1.46×10^8 kg of agricultural products are contaminated with Cd, including roughly 5.0×10^7 kg of rice (Mu et al., 2020). Although Cd is not an essential element for plant growth, it is readily absorbed by plants due to its chemical similarity to divalent metal ions such as zinc (Zn), iron (Fe), and calcium (Ca). Once extracted, Cd can replace the active centers of various enzymes or bind to the hydrophilic groups of proteins, altering the structure of biological macromolecules. These interactions disrupt enzyme systems, impairing plant growth and development. Cd's ability to enter the food chain poses severe health risks to humans, including kidney failure and bone fractures (Bautista et al., 2024). As such, mitigating Cd exposure and limiting its mobility in the natural environment are critical measures for ensuring food and ecological safety. These efforts are essential to protect both food consumers and agricultural practitioners from the hazardous effects of heavy metals. Addressing Cd pollution is therefore imperative for safeguarding public health and maintaining environmental integrity.

The adsorption of heavy metals by plants is primarily influenced by the concentration of free heavy metal ions in the soil. Cd exists in the environment predominantly as an oxide ion (Kubier et al., 2019). Anthropogenic sources of Cd in soil are largely derived from phosphate fertilizers (Wielgusz et al., 2022), as Cd is a common impurity in phosphate minerals and phosphate rocks. It can substitute for Ca in apatite, which constitutes the main component of phosphate (Gnandi & Tobschall, 2002). Cd concentrations in unpolluted soil solutions typically range between 40 and 300 nM (Lux et al., 2011). The concentration and dissolution order of active metals in soil plays a critical role in determining the accumulation of metals in plants (Gupta & Sinha, 2007). Cd exhibits a weak adsorption effect in environments where it competes with other metals and persists in soil solutions with a pH of less than 6.5, unlike other heavy metals which tend to be more readily fixed. Furthermore, Cd often forms stable dissolved coordination complexes with inorganic and organic ligands, inhibiting adsorption and precipitation processes (Kubier et al., 2019). Soil organic matter and pH are key factors controlling the distribution of heavy metals (Qishlaqi & Moore, 2007). The pH of the soil significantly influences the chemical form of heavy metal ions, directly impacting their uptake by plants (Han et al., 2017). Mechanisms such as adsorption, precipitation, and complexation with minerals and soil organic matter mediate these effects (Stein et al., 2021).

Cd concentrations in agricultural and horticultural soils should not exceed 3 $\mu g\ g^{-1}$ to ensure safe plant cultivation (Lawlor, 2004). Plants are more likely to absorb Cd in acidic soils (Tudoreanu & Phillips, 2004). In addition, plants can release root exudates, increasing the bioavailability of Cd (Chen et al., 2016). Mlangeni et al., (2022) observed that rice accumulated high levels of Cd in acidic soils, a phenomenon attributed to the enhanced mobility and bioavailability of Cd at lower pH levels, which facilitates the conversion of Cd from fixed to bioavailable forms. Willow seedlings, which thrive under moderately acidic conditions, also demonstrate significant growth responses to soil pH. Gu et al., (2015) reported that willow seedlings exhibited optimal root length, seedling length, and vigor at a soil pH of 4.8.

Phytoremediation has emerged as a prominent research area in recent years within the broader domains of bioremediation and sustainable remediation. This approach encompasses various mechanisms, including phytoextraction (the absorption of pollutants from the soil by plants, followed by their transport and storage in above-ground organs), phytostabilization (the immobilization of pollutants in the soil to prevent their environmental mobility), phytovolatilization (the absorption of pollutants from the soil and their subsequent release into the atmosphere as volatile compounds), phytodegradation (the metabolism of organic pollutants through plant or rhizosphere microbial activity), and rhizofiltration (the use of plant roots in aquatic systems to filter contaminants from sewage) (Mocek-pł et al., 2023). For non-degradable heavy metals, certain plants can either concentrate them in their accessible above-ground parts or immobilize them in their roots (Liang et al., 2024).

Compared to traditional remediation methods, phytoremediation offers several advantages, including its in situ applicability, cost-effectiveness, and the absence of secondary pollutants (Ciadamidaro et al., 2022). Current research predominantly focuses on the absorption and enrichment capacities of crops (An et al., 2022), cash crops (Alamer et al., 2022), and aquatic plants (Dalla Vecchia et al., 2020). However, studies on woody plants, particularly forest timber species, ornamental green plants, and economic forest species, remain in their nascent stages. Unlike herbaceous plants, woody plants possess deep root systems, high biomass, and enhanced tolerance to heavy metal stress (Nong et al., 2023). Among woody plants, the genera *Salix* and *Populus* within the *Salicaceae* family are of particular interest. *Salix* encompasses approximately 520 species worldwide, primarily distributed in the temperate and frigid zones of the Northern Hemisphere, while *Populus* comprises around 30–40 species (Dickmann & Kuzovkina, 2014). These genera are prominent energy tree species and are typically cultivated using short-rotation forestry models. They exhibit high nutrient-use efficiency, elevated transpiration rates, rapid growth, substantial biomass production, and the ability to regenerate above-ground parts following harvesting. Furthermore, they hold significant potential for genetic improvement (Christersson, 2010).

The United States initiated research and application of woody plant remediation technology as early as the 1980s, utilizing short-rotation hybrid poplar trees to remediate soils contaminated with petroleum hydrocarbons (Ile et al., 2021). As this technology evolved, tree remediation methods were expanded to encompass water and atmospheric pollution control. The conceptual framework of tree remediation extends beyond the trees themselves to include the soil and associated microbiome as an integrated system. The root systems of most tree species can establish symbiotic associations such as mycorrhizae and nodules with soil microorganisms, thereby enhancing the synergistic effects of plant and microbial remediation. Through the regular harvesting of biomass, pollutants can be effectively removed from the soil. Additionally, fast-growing trees cultivated under a short-rotation model can generate biomass while simultaneously restoring ecosystems. This approach offers the dual benefits of ecological rehabilitation and contributing to the alleviation of the energy crisis (Espada et al., 2022).

In 2023, Europe experienced an increase of approximately 950 MW in total installed biomass energy capacity. This growth was predominantly driven by the demand for industrial and district heating, particularly in Finland and the UK, where several large-scale projects have been recently launched. By 2032, it is projected that new biomass energy installations in Europe will exceed 19.1 GW (http1). Economically, the EU's solid biomass sector generated a turnover of 38.45 billion euros in 2022. Germany was a major contributor, producing approximately 14.38 million tons of oil equivalent in solid biomass energy. Furthermore, Spain supported biomass development through dedicated auctions, resulting in projects with a combined capacity of approximately 50 MW (http2). In Sweden, short-rotation biomass forests have been successfully employed for phytoremediation to eliminate harmful compounds from waste. Large-scale implementation of such systems provides an ecologically advantageous and cost-effective solution for waste treatment while simultaneously promoting bioenergy production (Christersson, 2010).

As the application of this technology deepens, researchers are exploring the remediation potential of various hybrids while evaluating the capacity of other energy plants to act as sinks for soil pollutants, thereby expanding the species bank. Bamboo, a widely distributed economic tree species in tropical and subtropical regions, has emerged as a potential alternative material for phytoremediation. Beyond its ecological significance, bamboo offers additional benefits in terms of landscape aesthetics, energy production, building materials, and ecological restoration (Liang et al., 2023). Globally, there are over 1,300 species of bamboo, with China hosting more than 500 species, making it the country with the largest area of bamboo forests. According to the results of the ninth national forest resources inventory in China, the area of bamboo forests spans 6.4116 million hectares, accounting for 2.94% of the total forest area. The average biomass of these forests is 65.81 t ha^{-1}, significantly surpassing that of hyperaccumulators (Li & Feng, 2019). Bamboo, as one of the most primitive subfamilies of the *Poaceae*, represents a highly diverse group within this family. It is characterized by a woody stem, well-developed root systems, complex branching, and infrequent flowering. Bamboo exhibits rapid growth, with moso bamboo (*Phyllostachys edulis*) typically reaching heights of 15–20 m within approximately 60 days. The bamboo sheath plays a critical role in supporting and protecting the growth of bamboo shoots (Chen et al., 2022).

Furthermore, the annual biomass output of moso bamboo is noteworthy, reaching 6.0–7.6 Mg C ha^{-1} per year, highlighting its substantial carbon sequestration potential (Zheng et al., 2022). Studies indicate that the absorption capacity of bamboo plants is primarily determined by the underground root system and the whiplash root system. A larger root surface area facilitates the uptake of heavy metals and nutrients (Liu et al., 2014). For instance, the root systems of moso bamboo and Lei bamboo (*Phyllostachys praecox*) concentrate approximately 80% of their length and volume within the 0–40 cm soil layer, optimizing their ability to absorb heavy metals (Zhou et al., 2022; Gao et al., 2024)

Some studies have reported cases of in situ phytoremediation in different regions of Hungary, but these studies are usually based on wastewater irrigation and mixed pollutant treatment (Tőzsér et al., 2018; Tóth et al., 2024). However, there are many hybrids of willow and poplar, and studies on the absorption and accumulation of a heavy metal by different hybrids of native poplar and willow are still lacking, especially on the application potential of different poplars and willows in the remediation of Cd-contaminated soil. On the other hand, due to the long growth cycle of woody plants, not much is known about the heavy metal distribution strategies of woody plants, especially the nutritional element response under Cd stress. Although the genome sequence of poplar and willow has been published, providing valuable references for molecular biology research, there are still many differences in the mechanisms of response to heavy metals (Dos Santos Utmazian et al., 2007).

In addition, bamboo has strong adaptability and can not only survive in poor soil but also effectively absorb and fix heavy metals such as Cd, Pb, and Zn through its well-developed root system (Bian et al., 2017). In tropical and subtropical regions, bamboo has been widely used to remediate polluted soil and has performed well in rapidly restoring ecological functions (Tong et al., 2020). For Hungary, bamboo is not only an important species in horticulture but also offers a new option for the remediation of polluted soil. Bamboo's high biomass and multiple harvesting characteristics make it economically and ecologically valuable. However, there are currently few studies on the adaptability of bamboo in the local environment of Hungary, especially in Central European climatic conditions. The cold tolerance and heavy metal absorption efficiency of bamboo have not been fully evaluated. In addition, compared with willows and poplars, there are even fewer studies on the molecular mechanisms involved in the phytoremediation of bamboo. There is a gap in research on nutrient allocation and metabolic regulation of bamboo under heavy metal stress. This provides important scientific value for exploring the gene regulation mechanism of bamboo and its interaction with the environment. At the same time, the introduction of bamboo may also enrich Hungary's phytoremediation technology and provide more diverse options for soil remediation of different pollution types. Therefore, the introduction of bamboo as a phytoremediation material in Hungary not only provides a useful supplement to the current phytoremediation strategy but also provides an innovative direction for solving the problem of heavy metal pollution. This process not only requires collaborative research in ecology, botany, and molecular biology but also the accumulation of practical experience to achieve the sustainable application of bamboo in soil remediation in Hungary.

The types of plants utilized in heavy metal phytoremediation can be broadly categorized into hyperaccumulators and those with high biomass. Hyperaccumulators are defined as species that naturally grow in specific environments and are capable of accumulating exceptionally high concentrations of heavy metals or their ions in the aboveground tissues (Boyd, 2012). It is important to note that the threshold for hyperaccumulation varies depending on the specific heavy metal involved. To date, more than 450 hyperaccumulating plant species have been identified globally, with a predominant focus on nickel (Ni) accumulators within the Brassicaceae family. Notable hyperaccumulators include genera such as *Thlaspi*, *Lyssum*, *Brassica*, and *Psychotria*. The hyperaccumulation thresholds for common heavy metals and relevant studies on hyperaccumulators are summarized in Table 1 (Boyd, 2012).

Table 1. Heavy metal enrichments of some hyperaccumulator plants

Heavy metals	Threshold value μg^{-1}	Hyperaccumulator	Concentration	Above-ground accumulation	References
Ni	1000	*Odontarrhena chalcidica*	85-150 g kg^{-1}	20.2g	(Tognacchini et al., 2020)
		Brassica juncea	40 mg kg^{-1}	3.36mg kg^{-1}	(V. Sharma et al., 2024)
Zn	3000	*Sisymbrium lipskyi*	80mg kg^{-1}	114 mg kg^{-1}	(Drozdova et al., 2024)
		Vesicularia montagnei	0.094 mg L^{-1}	8 mg kg^{-1}	(Taeprayoon et al., 2024)
Cu	300	*Azolla filiculoides*	25 mg L^{-1}	6.03 mg kg^{-1}	(Valderrama et al., 2013)
		Verbascum thapsus	375 mg L^{-1}	492.8 mg kg^{-1}	(Kavousi et al., 2021)
As	1000	*Pteris vittata*	0.05 mM	4598 mg kg^{-1}	(L. M. De Oliveira et al., 2014)
		Pteris vittata	131 mg kg^{-1}	4100 mg kg^{-1}	(Fayiga et al., 2004)
Pb	1000	*Brassica cultivars*	1000 mg kg^{-1}	4,011.7 μg pot^{-1}	(Kaur et al., 2025)

		Bermudagrass	3000 mg kg^{-1}	1352.76 mg kg^{-1}	(Xie et al., 2021)
Cd	100	*Youngia japonica*	120 mg kg^{-1}	314.29 mg kg^{-1}	(Yu et al., 2021)
		Bidens pilosa	49.79 mg kg^{-1}	290 mg kg^{-1}	(Dai et al., 2021)

Expanding the catalog of hyperaccumulating plant species is crucial for advancing phytoremediation applications across diverse environmental contexts. The ability of plants to hyperaccumulate heavy metals in their aboveground tissues allows for the removal of these contaminants from the soil through the regular harvesting of the biomass. However, the majority of the currently identified hyperaccumulators are annual herbaceous species with relatively small biomass, which results in low extraction efficiency and restricts their practical application in phytoremediation. Consequently, the identification and development of plant species that exhibit both high heavy metal tolerance and absorption capacity, coupled with large biomass, has become a critical challenge in the advancement of phytoremediation technologies. Figure 1 shows the three mechanisms of heavy metal phytoremediation, including phytostabilization, phytoextraction and phytovolatilization.

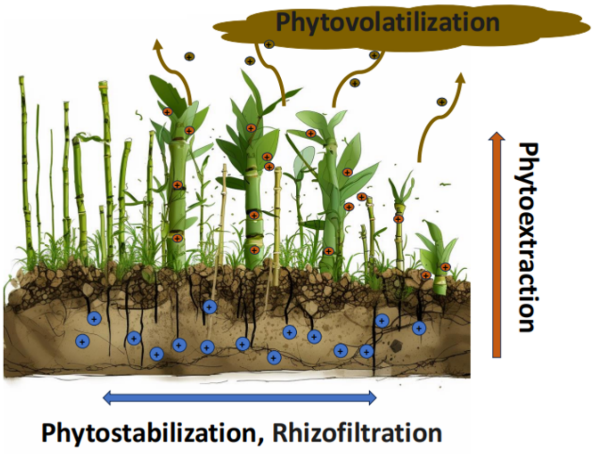


Figure 1: Mechanism of heavy metals phytoremediation

The BCF is defined as the ratio of the concentration of a substance in an organism to its concentration in the surrounding environment, and it serves as an indicator of a plant's ability to absorb and accumulate a particular heavy metal (Rahmani & Sternberg, 1999). Similarly, the TF is the ratio of the metal content in the above-ground parts of a plant to that in the below-ground parts, providing insight into the efficiency of heavy metal translocation within the plant (Zacchini et al., 2008). In comparative studies, willow clones have been shown to exhibit greater tolerance to Cd than poplars. However, when assessing transport capacity, the mean TF for willows was found to be twice that of poplars, whereas the total BCF for poplar was significantly higher than that of the willow clones (Zacchini et al., 2008).

Certain plants, known as hyperaccumulators, possess the ability to absorb and concentrate specific elements at concentrations 10 to 100 times greater than those found in typical plants. These species can translocate elements from the soil to the above-ground tissues when the metal concentration in the soil is unusually high (Yang et al., 2004). However, van der Ent et al., (2013) raised concerns regarding the limitations of the BCF, noting that it does not significantly differ when plants are grown in soil or hydroponically, in relation to metal concentrations in the leaves. They suggested that the threshold for hyperaccumulation should be defined in two ways: either as 2–3 orders of magnitude higher than the concentration in plant leaves grown in normal soil, or at least one order of magnitude higher than the usual concentration of metals in plants grown in metal-contaminated soils. For example, while the natural Cd concentration in plants is typically very low (ranging from 0.03 to 5.0 μg g^{-1}), plants with Cd concentrations greater than 100 μg g^{-1} are Cd hyperaccumulators (Baker et al., 1995). Two halophytes from the *Cressaceae* family, *Sesuvium portulacastrum* and *Mesembryanthemum crystallinum*, have been reported to accumulate Cd in their shoots at concentrations as high as 350–700 μg g^{-1} (Ghnaya et al., 2005).

Typically, the TF value for hyperaccumulators exceeds 1 (Jatin G. Italiya, 2012). However, TF values alone are not sufficient to define a hyperaccumulator, although they serve as a useful supporting indicator in the identification of such plants (van der Ent et al., 2013). Baker et al., (1995) argued that hyperaccumulators should be sourced from natural populations, cautioning against the use of isolated biotic enrichment factors to define hyperaccumulation, as these factors reflect the interaction between genotype and environmental conditions. To date, several hundred hyperaccumulators have been identified. For instance, *Lysimachia deltoides* is considered a potential Cd hyperaccumulator with a TF value of up to 3.2 (Wang et al., 2009), while *Silene viscidula* exhibits a TF value of 1.1 for Cd. It is important to note that Cd contamination in soil is often accompanied by elevated levels of Zn, necessitating that hyperaccumulators also possess the ability to tolerate and accumulate Zn (van der Ent et al., 2013).

Many hyperaccumulators have developed specialized uptake mechanisms for specific elements. In addition, Wang et al., (2024)introduced the concept of "biomass cost," proposing that high concentrations of heavy metals in plant tissues often result in reduced biomass. This is aligned with the growth-defense hypothesis, which quantifies defense-related investment as biomass units (BC). The BC is calculated as 1000 divided by the concentration of a single metal in plant tissue. This framework, grounded in the plant economic spectrum, may offer a more direct theoretical basis for quantifying the efficiency of heavy metal phytoremediation.

1.2 Significance of the study

Expanding the inventory of phytoremediation species and selecting plants suited to local environments is crucial for advancing and optimizing phytoremediation technologies. The considerable variation in BCF, TF, and Cd tolerance and accumulation capacity across different genotypes of poplar and willow provides a solid theoretical foundation for selecting effective remediation plants. Through comparison, genotypes that efficiently absorb and transport Cd can be identified for intensive remediation in heavily polluted areas, while genotypes with high Cd tolerance may be selected for ecological restoration and greening in less contaminated regions.

From the perspective of functional traits and the PES, studying the performance of these plants in various restoration contexts helps to elucidate the key characteristics underlying their remediation mechanisms. The theory of PES posits that plants optimize resource allocation along a continuum of acquisition and conservation strategies. This differentiation in functional traits offers a novel perspective for selecting and matching plants for restoration purposes. Furthermore, by examining functional traits, the growth responses and remediation capacities of plants under Cd stress can be quantified, providing insights into how plants allocate resources under stressful conditions. The integration of functional traits and economic spectra not only classifies the remediation functions of plants but also enables the prediction of the ecological and functional benefits of plant species combinations through modeling.

For bamboo species, a member of the grass family, there are notable differences in Cd tolerance and accumulation capacity among different species. For instance, moso bamboo and lei bamboo exhibit significant disparities in their ability to accumulate and distribute Cd. Bamboo, due to its unique growth form and biomass potential, represents a promising avenue for research into Cd pollution remediation. Bamboo species could offer additional plant options for pollution remediation in this region, improving overall remediation efficiency and broadening the possibilities for utilizing biomass resources.

From a molecular perspective, investigating the Cd enrichment and transport mechanisms in various plant genotypes not only uncovers the expression patterns of key genes but also provides a theoretical basis for molecular breeding and genetic engineering applications. Research on the genetic foundations of functional traits related to Cd tolerance could inform the selection or improvement of plant genotypes. Additionally, the impact of essential nutrients such as N, K, and P on plant responses to Cd stress is significant. Understanding nutrient balance mechanisms under Cd stress can optimize fertilizer management during phytoremediation, enhancing the growth and remediation efficiency of plants. Moreover, the synergy between functional traits—such as the relationship between leaf nitrogen content and photosynthetic rate—may be critical to understanding the remediation mechanisms.

Poplars, willows, and bamboo species not only perform remediation functions but also contribute to environmental beautification and soil quality improvement, thereby indirectly enhancing the quality of life for surrounding communities. The non-edible parts of Cd-contaminated plants can be repurposed for biomass fuel and other applications, reducing resource waste during the remediation process and achieving the dual objectives of pollution control and resource recycling. These additional benefits further underscore the promising applications of remediation strategies based on the study of PFT and economic spectra. Figure 2 shows the functional traits as a quantitative tool to link ecosystem restoration at different levels.

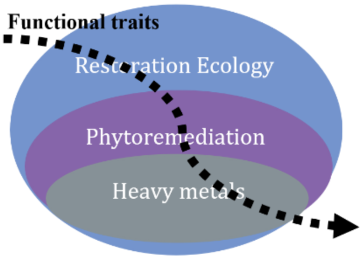


Figure 2: A functional-trait-based approach links the solution of environmental restoration problems at different scales.

1.3 Objectives to achieve

1) The characteristics of Cd extraction and accumulation by poplar, willow and bamboo, and the distribution of Cd in different organs
2) The contents of N and K in the organs and the physiological changes in the leaves of poplar, willow and bamboo under Cd treatment
3) Changes in soil nitrogen content of poplar, willow and bamboo under Cd treatment
4) Phytoremediation from the perspective of PFT and PES
Figure 3 shows the technical route and research objectives of this dissertation.

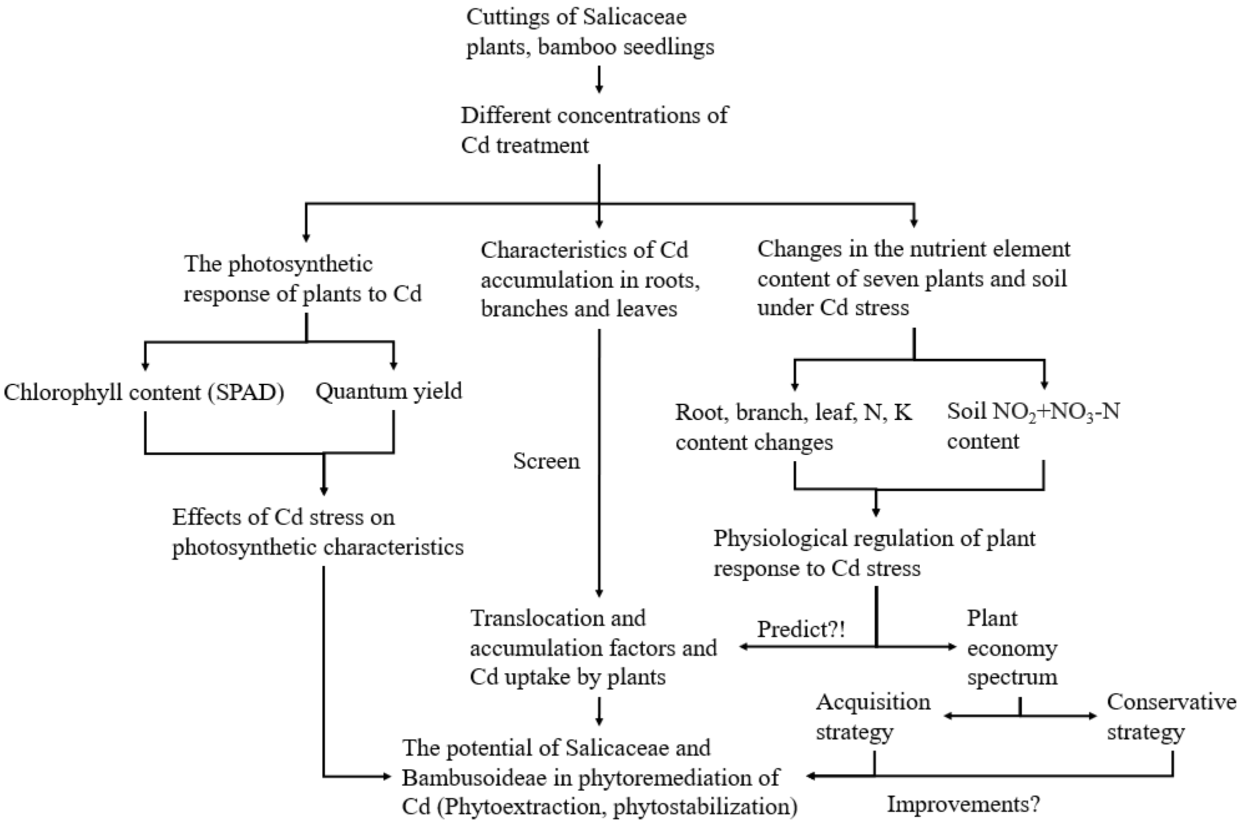


Figure 3. Technical route and research objectives

2 LITERATURE OVERVIEW

2.1 Poplar and Willow Heavy Metal Phytoremediation

Poplars and willows are among the most representative energy plants and have become key research subjects in the field of heavy metal-contaminated soil remediation. These species are widely utilized for the restoration of agricultural soils, abandoned mining sites, and industrial areas (Zalesny et al., 2019), primarily due to their remarkable ability to absorb and tolerate various heavy metals, such as Cd, Pb, Zn, and Ni, as well as their capacity for large-scale cultivation (Tőzsér et al., 2023). Over the past decade, with the increasing emphasis on sustainability, research focused on poplar and willow-based phytoremediation has expanded significantly (Figure 4). Key research areas include the identification and screening of genotypes with high metal tolerance and accumulation capabilities (Li et al., 2024; Pilipović et al., 2019), exploration of intercropping systems and plant interactions (Zhang et al., 2024; Gómez-Sagasti et al., 2021), the use of additives or microbial inoculants to enhance remediation efficiency (Wang et al., 2020; Nandillon et al., 2019), and genetic engineering approaches to improve heavy metal uptake and tolerance (Ma et al., 2023; Guan et al., 2023).

Figure 4. Trends in the number of research documents on the use of poplar and willow trees for phytoremediation of heavy metals from 2014 to 2024 (Source: Web of Science, the search queries included all fields: TS = phytoremediation AND TS = Salix (TS= Poplar) AND TS = “heavy metals”)

2.1.1 Poplar and willow trees with high tolerance/accumulation genotypes selection

Testing different genotypes of poplar and willow trees across various polluted environments is a crucial strategy for identifying plant species with high tolerance and accumulation capacities. For instance, under flooding conditions, Cao et al., (2022) assessed the accumulation of Cd, Zn, and Pb in 15 willow genotypes. The genotypes J1010, P54, and P667 demonstrated significant potential for multi-metal remediation. While flooding conditions reduced Cd concentrations in all plant organs, they notably increased Zn and Pb levels in the roots. Similarly, Li et al., (2024) conducted field experiments on 15 poplar hybrids to evaluate their remediation efficiency for Cd, mercury (Hg), Pb, and arsenic (As). In comparison to intra-specific hybrids, interspecific hybrids, such as QHQ, QHB, and 107, exhibited higher remediation efficiency, greater biomass, higher cellulose content, and lower lignin content, making them more suitable for pulpwood production.

Beyond testing for single heavy metals, examining the effects of mixed pollutants, such as sewage sludge (Guidi Nissim et al., 2018), dredged river sediments (Pilipović et al., 2019), and landfill leachate (Zalesny et al., 2019), provides a more comprehensive understanding of plant responses under realistic conditions. For example, Guidi Nissim et al., (2018) compared the removal capacities of four energy plant species (*Salix matsudana* cv Levante, *P. deltoides* × *P. nigra* cv Orion, *Eucalyptus camaldulensis*, and *Helianthus annuus*) in the treatment of municipal sewage sludge. Both poplar and willow species showed superior capacities to accumulate As in their leaves and chromium (Cr) in their roots, compared to *Helianthus annuus*. Furthermore, in short-rotation phytoremediation systems, the interaction between poplar genotypes and their environment led to substantial variations in biomass. Biomass values for phytoremediation trees in the Midwestern United States ranged from 4.4 to 15.5 Mg ha^{-1} y^{-1}, which was approximately 20% lower than the biomass of bioenergy trees. However, certain genotype × environment interactions resulted in significant increases in growth and productivity. For example, genotypes such as 'DN34', 'NM6', and '7300501' exhibited enhanced tolerance to various pollutants. Similarly, Italian poplar short-rotation restoration forests successfully reduced the concentrations of Cd, Se, As, Pb, and Zn in polluted soils, with these metals being accumulated in the rhizosphere of the plants (Zalesny et al., 2019). Phytoremediation strategies using 'Monviso' clones were particularly effective in removing overall heavy metal contamination (Ancona et al., 2021; Barra Caracciolo et al., 2020; Pietrini et al., 2017).

Despite the progress made, the screening of tolerant and high-accumulating genotypes remains an unresolved challenge, both in laboratory and field settings. Montesinos, (2024) argues that there is a trade-off between field and pot experiments. Field studies may be hindered by uncontrollable environmental factors, and replication can be difficult. In contrast, pot experiments allow for better control over specific experimental treatments, making them ideal for detecting plant responses. However, Zhu et al., (2024) emphasize that only field studies that include mixed-species approaches can reliably identify traits that predict the future abundance and persistence of species in contaminated environments.

2.1.2 Intercropping poplar, willow and other plants

Intercropping systems, such as forest-forest and forest-grass combinations under woody plants, have emerged as effective strategies for soil pollution remediation (Zhang et al., 2024). These cropping patterns alter soil nutrients, pH, enzyme activity, and microbial communities, which can enhance interspecific interactions and promote ecological balance (Xu et al., 2023). Song et al., (2023) reviewed the growing body of research on multi-plant symbiotic phytoremediation systems, highlighting plant diversity, interspecific relationships, and plant gender as key research areas in this field. These symbiotic systems encompass both facilitative and competitive interactions; however, under stress conditions, the facilitative effects typically prevail.

For instance, intercropping willows with *Lolium perenne* L., *Iris lactea* Pall., and

Bidens pilosa L. enhanced plant photosynthesis, boosted antioxidant responses, and significantly increased the biomass of willows. Additionally, this intercropping improved the uptake of bioavailable Cd and Pb by both the willow and the herbaceous plants. Notably, the willow exhibited a significant competitive advantage in this system (Zhang et al., 2024). In a greenhouse study, co-cultivation of *Salix interior* and *Trifolium pratense* resulted in an increase in the As, Cr, and Cu concentrations in the willow roots. However, this intercropping did not lead to a significant increase in biomass, underscoring the complexity of interspecies interactions in phytoremediation systems.

Although the forest-forest plant restoration system has demonstrated potential value in practical applications, its implementation is not without challenges. The establishment of many trees can result in high costs, and tree survival rates may decline due to competition among individual trees (Xu et al., 2023). As a result, forest-grass intercropping systems present significant advantages in terms of both practicality and restoration effectiveness.

Common herbaceous plants intercropped with poplar and willow include species such as *Medicago sativa* (Gómez-Sagasti et al., 2021), *Lolium perenne* (Zhang et al., 2024), and *Trifolium* spp. (Lachapelle et al., 2021); hyperaccumulators like *Sedum* spp. (Zhou et al., 2023); and certain cash crops such as *Brassica napus* (Massenet et al., 2021). However, no studies were identified that investigated the intercropping of food crops, such as maize, rice, or wheat, with poplars or willows. Several factors may explain this gap in research: i:) Poplars and willows, with their extensive root systems, tend to compete with shallow-rooted crops for essential resources such as water, nutrients, and light. This competition may lead to reduced crop yields, which could negatively impact the economic viability of intercropping systems. ii:)The primary goal of remediation efforts involving poplars and willows is often ecological restoration of contaminated soils, making hyperaccumulating or nitrogen-fixing plants more suitable for intercropping than food crops. These plants are better equipped to contribute to soil decontamination and nutrient cycling. iii:) Phytoremediation experiments involving poplars and willows typically require extended periods (several years) to evaluate their effectiveness. In contrast, food crops have relatively short growth cycles (several months), limiting their utility within the longer timeframes typically associated with restoration efforts. Thus, while forest-grass intercropping systems hold promises for improving soil restoration outcomes, further research is needed to optimize these systems and explore their potential integration with food crop cultivation.

2.1.3 Restoration of poplar and willow trees with heavy metals and research on additives

Table 2 provides a summary of several types of additives commonly employed in the phytoremediation of heavy metals using poplars and willows.

Table 2. Several common poplar and willow heavy metal phytoremediation additives

Additive type	Main function	Common example	Applicable scenario	References

Chelate	Enhancing the bioavailability of heavy metals	EDTA, DTPA, citric acid, oxalic acid	Deeply contaminated soil remediation	(Arsenov et al., 2019c Dai et al., 2020)
Biological additive	Enhances plant stress resistance and absorption capacity	Mycorrhizal fungi, rhizobium, phosphate-solubilizing bacteria, actinomycetes, arbuscular mycorrhizal fungi	Ecological restoration of farmland	(Virk et al., 2023; Liu et al., 2022; De Oliveira et al., 2020)
Soil conditioner	Reduce heavy metal toxicity and improve soil quality	lime, humic acid, biochar	Remediation of lightly to moderately contaminated soil	(Salam et al., 2019; Al-Lami et al., 2022; Lebrun et al., 2021)
Hormone and anti-stress agent	Enhance phytoremediation capacity and resistance	Indole-3-acetic acid (IAA)	Highly polluted and stressful environment	(Schmidt et al., 2018)
Redox regulator	Alter the valence state and toxicity of heavy metals	Fe^{2+}	Specific heavy metal (Cr)	(Mokarram-Kashtiban et al., 2019; Li et al., 2022)
Surfactant	Improve heavy metal mobility and absorption efficiency	SDS (sodium dodecyl sulphate)	Low-soluble metal contamination	(Pierattini et al., 2018)

These additives target three primary objectives: (1) improving plant physiological growth, (2) enhancing the soil microbial community structure, and (3) increasing the bioavailability of heavy metals in the soil. While the application of organic amendments such as manure and sewage sludge is often categorized as an additive in phytoremediation strategies (Wang et al., 2020), it is important to note that these materials may contain polluting properties. Consequently, their use can potentially diminish the overall effectiveness of phytoremediation and introduce additional environmental risks. Thus, careful evaluation of additive selection is crucial to optimizing remediation outcomes while minimizing potential adverse effects.

Chelating agents and soil conditioners have proven effective in enhancing the accumulation and transport efficiency of heavy metals in poplar and willow trees. These additives demonstrate high adaptability to variations in soil pH, heavy metal types, and pollution levels while contributing to the improvement of the soil ecosystem with relatively low environmental risk. Su et al., (2024) conducted a comparative study on the effects of organic and synthetic additives on the uptake of Cu and Pb in poplar trees. The results indicated that organic conditioners citric acid increased root Cu content by

2.68–48.61% and root Pb content by 6.60–49.51%, whereas synthetic amendments EDTA and EGTA led to more substantial increases, with root Cu content rising by 65.94–260% and root Pb content by 12.50–103%. Similarly, the organic amendment citric acid enhanced Cd extraction in willows growing in alkaline soil, improving photosynthetic rates and gas exchange capacity. The highest Cd accumulation occurred after 60 days of growth (Arsenov et al., 2020). Biochar has also gained prominence in phytoremediation applications. In contrast to chelating agents, biochar reduces the bioavailability of metals in the soil. However, Lebrun et al., (2021) observed that biochar addition increased Pb concentration in the aboveground parts of plants, with results varying based on biochar particle size. The study found that the application of 5% biochar generally supported better plant development.

Moreover, combining biosolids with biochar or humus has demonstrated potential in managing vegetation in tailings ponds, enhancing heavy metal extraction, and promoting biomass production (Al-Lami et al., 2022). Although synthetic amendments are more effective, they pose potential risks of contaminant migration. To mitigate these risks, Su et al., (2024) recommend optimizing the concentration of synthetic additives and implementing measures such as proper collection of fallen leaves to minimize environmental impact.

A significant component of the detoxification mechanisms in phytoremediation is the symbiotic relationship between plants and microorganisms, which markedly enhances the efficiency of heavy metal absorption, transformation, and stabilization in contaminated environments. Microorganisms in the rhizosphere play a crucial role in increasing the bioavailability of heavy metals by secreting organic acids, such as citric acid and oxalic acid, as well as chelating agents. These substances mobilize heavy metals bound to soil particles, thereby facilitating their uptake by plant roots (Schmidt et al., 2018). For instance, Schmidt et al., (2018) isolated *Alphaproteobacteria* from the roots and leaves of hybrid poplars (*P. nigra* × *P. maximowiczii*, clone Max-4) at a contaminated site, demonstrating the critical role of rhizosphere microorganisms in enhancing phytoremediation processes.

In addition to enhancing metal bioavailability, certain microorganisms, such as sulfate-reducing bacteria, can mitigate the toxicity of heavy metals by altering their chemical forms or precipitating them as insoluble compounds, such as CdS and PbS. This process effectively reduces the harmful effects of heavy metals on plant systems (Liu et al., 2024). Furthermore, microorganisms contribute to plant growth under heavy metal stress by producing phytohormones, such as indole-3-acetic acid (IAA) and gibberellins, or by enhancing nutrient availability through processes like nitrogen fixation and phosphate solubilization (Kidd et al., 2021). Conversely, plants actively support microbial communities by providing carbon substrates in the form of root exudates, including sugars, amino acids, and organic acids, which serve as essential energy sources for microbial metabolism (Gladysh et al., 2023). Additionally, plants regulate the rhizosphere environment by altering pH levels and releasing specific compounds that promote microbial proliferation and activity.

The synergistic interactions between plants and microorganisms facilitate detoxification through various mechanisms, including the co-adsorption and accumulation of metals, enzymatic transformations mediated by microbial enzymes (e.g., metallothionein and glutathione-S-transferase), and plant antioxidants. Moreover, microbial signaling molecules activate plant defense pathways, further enhancing detoxification (Barra Caracciolo et al., 2020). Collectively, these interactions significantly improve the efficiency of heavy metal phytoremediation while simultaneously restoring soil health and ecosystem functionality.

2.1.4 Genetic engineering

Genetic engineering enables the transfer and integration of external genes into the genome of target plants, allowing the expression and inheritance of foreign traits. Unlike traditional hybridization methods, genetic engineering can achieve the precise expression of transgenes and confer novel traits on plants within a significantly shorter timeframe (Yan et al., 2020). Advanced techniques such as miRNAs, non-coding RNAs, and CRISPR/Cas9 have become integral tools in genetic engineering. Among these, CRISPR technology is particularly noteworthy due to its ability to perform precise genome editing through RNA-guided Cas proteins without requiring the introduction of foreign DNA. This feature alleviates public concerns regarding genetically modified organisms.

Through genetic engineering, plants' stress tolerance or heavy metal accumulation capacity can be modified by overexpressing or downregulating specific genes. For instance, overexpression of the *PyWRKY75* gene in poplar enhances the synthesis of glutathione (GSH) and phytochelatins (PCs), thereby improving stress tolerance and Cd accumulation (Wu et al., 2022). Similarly, the overexpression of the *SsIRT9* gene from *Salix suchowensis* in tobacco increased Cd accumulation in tobacco leaves by 152–364% compared to wild-type plants. Cd accumulation in the aboveground parts of the transgenic plants increased by 135–444%, highlighting the gene’s high Cd transport activity relative to other *SsIRT* genes (Guo et al., 2024).

However, not all genetic modifications result in simultaneous improvements in stress resistance and heavy metal accumulation. For example, overexpression of the *SlPCR6* gene in poplar enhanced resistance to Cd and Cu but reduced the accumulation of these metals in transgenic poplar plants (Hu et al., 2022). Additionally, the overexpression of the *PtoHMA5* gene from *Populus tomentosa* Carr. in tobacco led to increased Cd accumulation in the leaves of transgenic plants but significantly compromised the plants’ Cd resistance. These findings emphasize the dual challenges in genetic engineering: balancing the enhancement of stress tolerance with the optimization of heavy metal accumulation in target plants.

2.2 Phytoremediation of heavy metals by bamboo

According to the Web of Science database, research on phytoremediation of heavy metals using bamboo is still lacking (Figure 5). However, this research has gradually attracted widespread attention in the past five years.

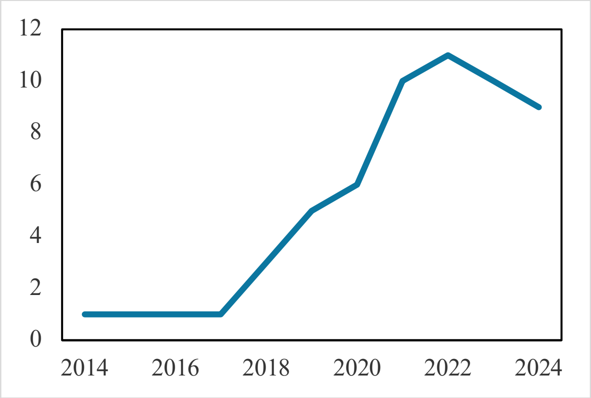


Figure 5. Trends in the number of research documents on the use of bamboo for heavy metal phytoremediation from 2014 to 2024 (Source: Web of Science, the search queries included all fields: TS = phytoremediation AND TS = bamboo AND TS = “heavy metals”)

Bamboo's unique biological characteristics present significant challenges for hybridization and breeding. Unlike poplar and willow, bamboo has a prolonged generation cycle and irregular flowering patterns, typically flowering only once every few decades or even a century. This infrequent flowering greatly complicates the process of hybrid breeding. Even when flowering occurs, seed production is minimal, limiting the availability and cultivation of hybrids. Furthermore, bamboo predominantly propagates vegetatively through rhizomes, a reproductive strategy that facilitates the expansion of bamboo forests but restricts genetic variation. This lack of genetic diversity hinders the development of new bamboo varieties with enhanced heavy metal phytoremediation capabilities through hybridization and selection.

Given these constraints, research on bamboo forest phytoremediation systems primarily focuses on evaluating the remediation potential of various bamboo species, understanding their influence on soil properties and microbial communities, and assessing the effects of additives within the bamboo remediation framework. These efforts aim to optimize the use of bamboo in addressing heavy metal contamination while leveraging its ecological and structural advantages (Liang et al., 2022).

2.2.1 Bamboo species selection for Phytoremediation

Investigating the physiological responses of various bamboo species under heavy metal stress is crucial for understanding their adaptive mechanisms and stress resistance in polluted environments. Such studies not only elucidate the physiological and molecular mechanisms involved in heavy metal uptake, transport, accumulation, and detoxification within bamboo plants but also provide a scientific foundation for identifying species with high tolerance and remediation potential. Table 3 summarizes key studies on heavy metal phytoremediation using different bamboo species.

Table 3. Research on common bamboo species in phytoremediation of heavy metals

Bamboo species	Heavy metals	Treatment concentration	Mainly accumulative organ	Accumulation of vital organs	References

Phyllostachys pubescens	Cu	125.0 mg L^{-1}	Rhizomes	67mg kg^{-1}	(Emamverdian, Ding, et al., 2023)
	Cu	200 µM	Roots	810 mg kg^{-1}	(Chen et al., 2014)
	Cd	400 µM	Roots	377 mg kg^{-1}	(Li et al., 2015)
	Pb	400µM	Roots	4282.8 mg kg^{-1}	(Liu et al., 2015)
	Zn	400 µM	Roots	8642 mg kg^{-1}	(Chen et al., 2015)
	Cr	200 mg L^{-1}	Roots	1.31 mg g^{-1}	(Ranieri et al., 2023)
Dendrocalamus asper	Cu	20 ppm	Roots	0.65 mg g^{-1}	(Go et al., 2019)
Sasa argenteostriata	Pb	900 mg L^{-1}	Roots	9969.46 mg g^{-1}	(Jiang et al., 2020)
	Zn	600 mg L^{-1}	Roots	17883.33 mg kg^{-1}	(Liao et al., 2022)
Bambusa. vulgaris	Pb	72 mg L^{-1}	Roots	0.41 mg kg^{-1}	(Pooja et al., 2023)

Bamboo species such as *Phyllostachys* spp., *Dendrocalamus* spp., *Sasa* spp., and *Bambusa* spp. are commonly used for the remediation of heavy metal-contaminated soils. Bian et al., (2020) systematically reviewed the potential of bamboo in heavy metal remediation, highlighting its unique advantages compared to poplar and willow. These advantages include strong tolerance to heavy metal-contaminated soils, rapid growth, ease of renewal, well-developed root systems, soil and water conservation capabilities, and low maintenance requirements. Field experiments further demonstrate the feasibility of bamboo in phytoremediation. For instance, Shakeel et al., (2024) investigated four bamboo species (*Bambusa balcooa*, *B. vulgaris* 'wamin', *B. bambos*, and *B. vulgaris*) planted in a disused fly ash dump. The study revealed significant improvements in the physicochemical properties of the contaminated site. Specific species were identified for targeted remediation roles: *B. bambos* as ideal for the phytoextraction of Cr and Zn; *B. balcooa* for the stabilization of Pb, As, and Zn; *B. vulgaris* 'wamin' for stabilizing Cu, Ni, Zn, and As; and *B. vulgaris* for stabilizing Cu, Cr, and Ni.

Additionally, Zhang et al., (2022) conducted a two-year study on contaminated farmland soil and found that three bamboo species (*Sasa auricoma*, *Indocalamus tessellatus*, and *Shibataea chinensis*) accumulated significant amounts of Cd, Zn, and Pb in their roots. Notably, *S. auricoma* accumulated 157.14 g hm^{-2} of Cd, 363.3 g hm^{-2} of Zn, and 7.18 g hm^{-2} of Pb, with root BCFs exceeding 1 for all species. Moreover, Moso bamboo has been successfully utilized in situ in constructed wetlands for treating wastewater and extracting heavy metals from oil sludge. This dual-purpose application, combining biomass production with heavy metal phytoextraction, underscores its practicality in environmental management (Mulama et al., 2020; Nast et al., 2022).

Transmission electron microscopy (TEM) is a powerful tool for examining subcellular changes and alterations in organ structures within plant cells. Li et al. (2018) used TEM to observe that excessive copper (Cu) exposure caused significant abnormalities in the chloroplasts of Moso bamboo leaves, including alterations in the structure of the endoplasmic reticulum, which was either transformed or completely disappeared.

Similarly, Chen et al. (2015) observed that Cu stress had detrimental effects on the cell walls, mitochondria, and xylem parenchyma in the roots of *Moso bamboo*, highlighting the cellular damage caused by heavy metal exposure.

Cd also induces notable changes in Moso bamboo under stress. Li et al., (2018) reported that Cd exposure led to irregular or triangular chloroplasts, dissolution of the thylakoid membranes, deformation of the cell wall, and significant disruption of the regularity of the cell structure. Additionally, Cd stress resulted in a marked reduction in the size of mitochondria in comparison to control plants. Under Zn stress, Moso bamboo exhibited a thickening of the cell walls and ruptured nucleoli; however, neither the grain membrane nor the mitochondria were significantly affected, suggesting that Moso bamboo possesses a degree of tolerance to high Zn concentrations (Chen et al., 2015). Beyond Moso bamboo, Jiang et al., (2020) revealed in TEM that the root cell walls of *S. argenteostriata* became distorted under Pb stress. The cell spaces expanded, and high-electron-density granular and needle-like deposits accumulated on the cell walls and plasma membranes. Similarly, Pb exposure caused the formation of needle-like crystals and blocky precipitates in the root cells of *Sasaella glabra* and *Indocalamus decorus*, along with thickening of the cell walls and noticeable damage to the chloroplasts in the leaves, including distorted thylakoids (Liao et al., 2022).

2.2.2 Soil properties and changes in soil microorganisms

The bamboo root system is the primary organ for the accumulation of heavy metals, making it crucial for understanding the plant's role in phytoremediation. Investigating soil properties and the activity of rhizosphere microorganisms is essential for elucidating the mechanisms behind bamboo's stabilization of heavy metals. Numerous studies have explored these aspects, shedding light on the interaction between bamboo and the soil environment in contaminated areas (Wu et al., 2024; Bian et al., 2018; Bian et al., 2017). Wu et al., (2024) found that in soil contaminated with Cd and Pb, the α-diversity of the microbial community remained like that of uncontaminated soil, while β-diversity showed significant differences. The relative abundance analysis revealed that *α- proteobacteria* (37%) and actinobacteria (31%) were dominant in the contaminated soil, whereas *γ- proteobacteria* (40%) and *α- proteobacteria* (22%) were dominant in the uncontaminated soil. The most important environmental factors influencing microbial community structure were found to be available phosphorus, organic matter, and available Pb (Wu et al., 2024).

Additionally, intercropping bamboo with hyperaccumulating plants has been shown to enhance the phytoremediation process and alter the soil microbial community. For instance, intercropping Moso bamboo with *Sedum plumbizincicola* resulted in an increase in the α-diversity index of bacteria, a reduction in the content of organic matter, available nutrients, and heavy metals (Cd and Cu) in the rhizosphere soil. This intercropping system also decreased the metal content in *Sedum* tissues but enhanced the accumulation of heavy metals in bamboo roots (Bian et al., 2021; Bian et al., 2017). Moreover, intercropping increased soil organic matter and elevated levels of polysaccharide C-O, carbonate C-O, and aliphatic methyl and methylene groups (Bian et al., 2023). Bian, et al., (2023) and Bian, et al., (2018) also reported that intercropping

P. praecox with *S. plumbizincicola* led to a 10.8% reduction in total nitrogen content compared to monocropping bamboo, while total organic carbon increased by 12.3%. Furthermore, intercropping significantly enhanced the heavy metal concentration, BCF, and TF in bamboo shoots. Key microbial biomarkers, including *Gemmatimonadetes*, *Actinobacteria*, *Chloroflexi*, and *Kaistobacter*, were identified as significantly increased in the intercropping system. These findings highlight the potential of intercropping to optimize bamboo's role in heavy metal remediation while altering the rhizosphere microbiome to support the phytoremediation process.

2.2.3 Effect of additives on phytoremediation by bamboo

Ethylene diamine tetra acetic (EDTA) is widely recognized as one of the most effective chelating agents for enhancing the accumulation of heavy metals in various plant organs. For example, EDTA has been shown to promote the absorption and transport of Pb in the stems of four bamboo species: *Indocalamus latifolius* (Keng) McClure (LA), *Indocalamus hunanensis* B.M. Yang (HU), *Indocalamus chishuiensis* Y.L. Yang and Hsueh (CH), and *Indocalamus lacunosus* Wen (LC). Although EDTA facilitated Pb uptake and translocate to the stems of these species, the BCF and TF remained below 1, classifying these species as non-hyperaccumulators of Pb (Liao et al., 2024).

Further research by Yang et al., (2022a) and Yang et al., (2022b) examined the effects of various chelating agents, including EDTA and nitrilotriacetic acid (NTA), on Pb extraction in *I. decorus* QH Dai and *S. argenteostriata* respectively. These studies demonstrated that all tested chelating agents enhanced the enzymatic activity of rhizosphere soil, thereby promoting the absorption and transport of heavy metals by plants. Zhang et al., (2018) reported that while the combined application of EDTA and citric acid had no significant impact on the biomass of Moso bamboo, the application of EDTA (10 mmol kg^{-1}) significantly increased the Cu content in the roots and aboveground parts by 56.5% and 84.9%, respectively. Similarly, Pb content in the roots and aboveground parts increased by 51.8% and 210.8%, respectively. These findings indicate that EDTA is more effective than citric acid in improving the phytoremediation potential of Moso bamboo.

Sodium nitrite (SNP), a small signaling molecule, has also been utilized to alleviate plant stress. A study by Emamverdian et al., (2023) demonstrated that treatment with 400 μM SNP reduced Mn and Cr concentrations in the leaves, stems, and roots of *Pleioblastus pygmaea* L. The reductions were 55% and 48% in leaves, 61% and 48% in stems, and 59% and 50% in roots, respectively. Additionally, the application of SNP increased the contents of proline (Pro), betaine (GB), GSH, and relative water content in bamboo tissues. This was accompanied by a significant increase in the dry weight of both aboveground and underground organs.

However, it is important to note that excessive concentration and frequent applications of chelating agents can lead to a reduction in plant biomass and an increased risk of heavy metal migration in the environment. These findings highlight the need to carefully optimize the concentration and application frequency of chelating agents to maximize remediation efficiency while minimizing adverse effects (Yang et al., 2022).

2.3 Effect of Cd stress on the physiological and biochemical characteristics of plants

2.3.1 Effect of Cd stress on photosynthesis

Cd has detrimental effects on photosynthetic organs and chloroplast structures, inhibiting chlorophyll synthesis and reducing biomass accumulation. This inhibition exerts a pronounced negative impact on photosynthesis. Key indicators such as photosynthetic pigment content, gas exchange parameters, and chlorophyll fluorescence induction parameters are often employed to evaluate plant photosynthetic performance under stress conditions (Chen et al., 2008). Elobeid et al., (2012) investigated the effects of Cd exposure by subjecting poplar trees to 50 μM $CdSO_4$ for 24 days. Their findings indicated significant reductions in carbon assimilation and photochemical quantum yield. However, contrasting results were observed by He et al., (2011), who reported that poplar trees exhibited resilience to Cd stress at the same concentration. Over time, the net photosynthetic rate of poplar seedlings partially recovered, with notable improvements in stomatal conductance and transpiration rate after 20 days of Cd exposure. Despite the initial decline, reductions in chlorophyll and carotenoid levels were relatively minor, at 17% and 15%, respectively.

To further understand the impacts of Cd on photosynthesis, Qian et al., (2011) compared the Chl *a* fluorescence induction parameter of three willow species—*Salix babylonica*, *Salix jiangsuensis* CL. 'J172', and *S. leucopithecia*'—under varying Cd treatments. The study revealed that ΦPSII decreased across all species under Cd stress, with F_0 and Fm peaking in the second week of exposure. *S. babylonica* primarily dissipated excess photons by enhancing non-photochemical quenching (NPQ), thereby protecting the PSII reaction center and improving Cd tolerance. In contrast, *S.*'J172' and *S. leucopithecia* adapted through photochemical conversion and efficient light energy utilization.

The combined effects of cultivar and Cd treatment on photosynthesis were significant, as reported by Wang et al., (2021). Most plants exhibited reduced Chl *a* and *b* pigment concentrations under all Cd treatment levels. However, specific cultivars, including FC185, FC187, FC189, and SX67, demonstrated either increased or unchanged Chl *a* and *b* concentrations compared to the control under 10 μM and 30 μM Cd treatments. Carotenoid concentrations followed a similar trend, showing no significant interaction with cultivar or treatment. Touati et al., (2019) further investigated the effects of Cd gradients on *Salix alba* and *S. viminalis*. They found that total chlorophyll and carotenoid contents in both species decreased with increasing Cd concentrations, though the reductions were not statistically significant compared to controls. Notably, *S. viminalis* demonstrated greater Cd tolerance in its leaves than *S. alba*, maintaining stomatal conductance under high Cd levels.

2.3.2 Effect of Cd stress on the concentration of plant nutrients

Adequate nutrition is fundamental to the normal development and growth of plants. Currently, 17 elements are recognized as essential nutrients for plants, classified into macronutrients (e.g., N, P, K, Ca, Mg) and micronutrients (e.g., Zn, Cu, Fe, and Mn) (Xu et al., 2019). Among these, nitrogen and potassium are the most abundant elements acquired by plants, absorbed through the roots, stored, and subsequently transported to the aerial parts of the plant. Nitrogen primarily exists in soil as ammonium (NH_4^+) and nitrate (NO_{3-}), serving as crucial sources for plant uptake. Once assimilated through root transport proteins, nitrogen participates in various metabolic processes, including the synthesis of amino acids, proteins, nucleic acids, and hormones, all of which are essential for plant growth and development (Zhang et al., 2024). Similarly, potassium (K^+) is the most significant cation in plant cells, playing a critical role in regulating osmotic balance, enzymatic activity, stomatal function, and photosynthesis. However, Cd stress significantly impairs the ability of plant roots to absorb and transport these nutrients (Yasin et al., 2018). Cd disrupts nutrient distribution in plants by competitively inhibiting the uptake of cations such as potassium and Ca by the roots (Li et al., 2012). Moreover, Cd alters nitrogen metabolic pathways, resulting in reduced activity of key enzymes such as nitrate reductase and glutamine synthetase, thereby diminishing nitrogen use efficiency (Pilipović et al., 2019). Cd^{2+} may interfere with nutrient uptake by competing for binding with root transport proteins, leading to decreased nutrient content in plants and disruption of ion homeostasis (Li et al., 2023). Cd^{2+} can enter root cells through Zn and Fe transport proteins (ZIP) located on the plasma membrane, and its transport mechanism mimics that of Ca^{2+} channels (Zou et al., 2023), low-affinity cation transporter 1 (LCT1) (K. Kumar et al., 2023), and Nramp proteins (Mohabubul Haque et al., 2022), all of which are regulated by specific proteins.

To mitigate Cd toxicity, plants employ exclusion mechanisms to expel some absorbed Cd^{2+} back into the rhizosphere environment. This process is facilitated by two types of proteins: P1B-type ATPases on the plasma membrane (Adams et al., 2011) and ABC transporters (Ghuge et al., 2023). Additionally, Cd^{2+} can be sequestered within root cell vacuoles via a cation/H^+ antiporter located on the vacuolar membrane, thus reducing cytoplasmic Cd concentrations (Yang, et al., 2022). Further, Cd translocate from roots to aboveground plant parts is mediated by three primary protein types: P1B-type ATPases (Smith et al., 2014), ABC transporters (Sun et al., 2018), and YSL transporters (Huang et al., 2023). These proteins facilitate the movement of Cd^{2+} from the root symplasm into the xylem, promoting Cd migration to aerial tissues and lowering Cd concentrations in root cells. Such mechanisms highlight the sophisticated strategies employed by plants to maintain nutrient balance and mitigate heavy metal toxicity under Cd stress.

2.3.3 Oxidative stress caused by Cd

Under Cd stress, plants exhibit reduced water and nutrient absorption. Prolonged exposure to heavy metals results in clear symptoms of toxicity, particularly in sensitive plant species, including reduced biomass, chlorosis, decreased transpiration, and eventual plant mortality (Touati et al., 2019). At elevated concentrations, heavy metal stress causes a metabolic shift from normal growth to defense mechanisms, severely inhibiting plant development (Jiang & Zhao, 2001). However, at lower Cd concentrations, plant uptake of Cd exhibits a linear relationship with soil Cd levels. Notably, Cd accumulation in plants correlates positively with total and bioavailable soil Cd concentrations (Yang et al., 2018).

Heavy metal accumulation within plants involves several intricate processes, including metal ion activation, root absorption, root cell compartmentalization and sequestration, xylem loading and transport, and storage in leaf cells (Gupta & Sinha, 2007). Hyperaccumulators typically display elevated metal loading in the stem xylem, whereas non-accumulators preferentially sequester metals within root cell vacuoles, leading to high root metal concentrations (Luo et al., 2016). Cd uptake through Ca channels has been identified as a key pathway for Cd^{2+} entry into plant cells (Rodriguez-Hernandez et al., 2015). For instance, poplar roots exhibit a net influx of Ca^{2+} in the absence of Cd stress (Zhang. et al., 2017). Upon entering cells via Ca channels, Cd disrupts mitochondrial function, activates caspase pathways, or accumulates within vacuoles. The depletion of Ca ions induces endoplasmic reticulum stress, destabilizes Ca homeostasis, and ultimately leads to programmed cell death (Kapoor et al., 2021).

The root cell wall serves as the primary barrier to heavy metal entry into plant cells and comprises cellulose, hemicellulose, lignin, suberin, and pectin (Chen et al., 2013). Exposure to Cd significantly alters the ultrastructure of root cells, resulting in reduced mitochondrial and endoplasmic reticulum integrity and invagination or rupture of the plasma membrane (Ge et al., 2012). A hallmark physiological response to Cd stress is a sharp increase in reactive oxygen species (ROS), including hydroxyl radicals (-OH), superoxide anions (O_2^-), and hydrogen peroxide (H_2O_2). While ROS are critical in activating signaling pathways, excessive ROS production leads to oxidative stress, characterized by an imbalance between ROS generation and antioxidant capacity, culminating in damage to cellular components and cell death (Qin et al., 2020). Lipid peroxidation, often indicated by malondialdehyde (MDA) content, is a critical measure of oxidative damage (Yan et al., 2010). To mitigate oxidative stress, plants activate enzymatic and non-enzymatic defense mechanisms that scavenge ROS and alleviate their deleterious effects. Enzymes such as superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) are recognized as reliable biomarkers for Cd ecotoxicological assessments (Ge et al., 2012).

Cd detoxification within plant cells is primarily mediated through vacuolar compartmentalization. This process involves the sequestration of Cd in the vacuole, facilitated by complex formation between Cd ions and ligands such as organic acids or mercaptoacetic acid (Wang et al., 1991). The coordination complexes thus formed are sequestered in vacuoles, rendering the metal ions inactive and limiting their cytoplasmic concentration (Morel et al., 2009). Vacuolar compartmentalization is critical for metal tolerance and detoxification, particularly in hyperaccumulator species. The transport efficiency of vacuolar carrier proteins directly influences the plant's capacity to absorb or restrict heavy metal ions, underscoring the importance of this mechanism in mitigating Cd toxicity.

2.4 Link between functional traits and phytoremediation

The concept of the PES was first introduced by Wright et al., (2004) and has since evolved through extensive research on plant leaf functional traits. PFT refers to measurable characteristics, such as morphology, physiology, and phenotype, that are directly associated with a plant's environmental adaptation and ecological functions. In their seminal study, Wright et al., (2004) analyzed the leaf economic properties of various plant species across the globe and proposed the "Global Leaf Economics

Spectrum," which established a continuous framework for understanding plant strategies related to resource acquisition and utilization. The LES is defined by six key leaf traits: leaf lifespan, leaf area, leaf mass per area (LMA), rates of photosynthesis and respiration, and concentrations of nitrogen and phosphorus. These traits exhibit strong covariation along a single principal axis, forming a spectrum of trait combinations. This spectrum spans from species with high rates of photosynthesis and respiration, high nutrient content in leaves, low LMA, and short leaf lifespans, to species with low rates of photosynthesis and respiration, low nutrient content in leaves, high LMA, and long leaf lifespans. This framework has since been expanded to include other plant organs, such as roots and stems, as well as additional ecological functional traits related to resource acquisition and storage, thereby broadening the scope to encompass a general plant economic spectrum. The PES can be broadly summarized into two strategies: the acquisition strategy and the conservation strategy.

With the advancement of research in this field and the growing application of plants in environmental remediation, the PES theory provides valuable insights into the performance and growth patterns of plants under stress conditions. It also serves as a useful tool for screening plant species suitable for phytoremediation of contaminated sites. For example, Massante et al., (2023) conducted a screening of 203 tree species for 78 functional traits on mining land, identifying 16 species that can optimize restoration outcomes. In another study, Colin et al., (2019) used PFT to investigate the key factors influencing soil bacterial diversity. They found that specific traits related to root structure and leaf decomposability were key drivers of soil bacterial community succession, suggesting that selecting plant species based on functional traits can promote beneficial changes in soil microbial communities and enhance soil microbial-mediated ecosystem services in mining areas. Table 4 summarizes the strategic performance of several PFT within the economic spectrum, drawing on the works of (Wright et al., 2004; Reich, 2014; Lavorel & Grigulis, 2012).

Table 4. Some traits expressed under acquisition and conservation strategies

Functional traits category	Resource-Acquisitive Strategy	Resource-conservative Strategy
Growth rate	High	Low
Specific Leaf Area (SLA)	High	Low
Leaf nitrogen content	High	Low
Photosynthetic Rate	High	Low
Nutrient Use Efficiency	Low (rapid resource cycling)	High (slow resource cycling)
Root Morphology	High root surface area; fine roots	Low root surface area; coarse roots
Respiration Rate	High	Low
Water Use Efficiency	Low	High
Seed Size	Small	Large
Tolerance to Stress	Low (sensitive to poor conditions)	High (adapted to stress or nutrient-poor soils)

Although the PES approach has been widely applied in the screening of plant species for contaminated sites (focusing on traits rather than species) (Massante et al., 2023; Laffont-Schwob et al., 2020; Navarro-Cano et al., 2018), two key unresolved issues persist.

i): the concept of a root economic spectrum (RES) remains ambiguous. Some researchers argue that the RES is not yet clearly defined, citing a nonlinear relationship between root system diameter, tissue density, and root nitrogen concentration in woody plants, which complicates predictions regarding the RES (Kong et al., 2019). Moreover, Mommer & Weemstra, (2012) highlighted that *the resource economics syndrome observed in leaves cannot be directly extrapolated to roots, nor can it be compared straightforwardly between roots and shoots*. This suggests that applying the same principles of resource economics to roots may not be appropriate.

ii): the applicability of functional traits as indicators for monitoring and predicting plant performance in ecosystems remains uncertain. While functional traits are commonly used to assess plant responses to environmental conditions, identifying which traits can serve as predictive indicators for ecological outcomes remains a challenge. Hodgson et al., (1999) proposed a classification of functional traits into "soft" traits, which are easy to measure, and "hard" traits, which are more difficult to quantify. By identifying traits that correlate with a wide range of plant responses and ecosystem effects, a trait framework could be established to predict restoration outcomes. However, the selection of such indicators is not without difficulty.

Gervais-Bergeron et al., (2024) investigated a willow short rotation coppice forest restoration system by measuring ten functional traits, including specific leaf area, leaf area, leaf dry matter content, leaf pH, leaf nitrogen content, leaf carbon content, root dry matter, root nitrogen content, root carbon content, and stem specific density. Their findings indicated that plant extraction was generally associated with a fast to moderate aboveground growth strategy and rapid underground tissue development, while the TF correlated with slower root growth. Plant stabilization, on the other hand, was linked to the stress tolerance of rapidly growing roots and above-ground tissues. However, in a separate study, Charles et al., (2022) found that leaf functional traits were not suitable for monitoring wetland ecological restoration, particularly the traits of leaf area and leaf dry matter content. The discrepancy in these findings underscores the need for further research to resolve the issues surrounding the selection of functional traits as reliable indicators for ecosystem monitoring and restoration.

Research on PFT and the PES provides a crucial theoretical framework for the remediation of contaminated sites. Investigating the variation in PFT from diverse perspectives is essential for understanding the adaptive mechanisms plants employ in response to environmental stressors. PFT directly influence the physiological characteristics of individual plant growth and play a key role in studying plant adaptation strategies to environmental conditions and ecosystem functions. Liang et al., (2024) summarized the role of functional traits in transitioning from laboratory to field applications in phytoremediation, particularly for heavy metal contamination. They classified traits into two categories: response traits and impact traits and emphasized that PFT can aid in screening plants suitable for specific pollution conditions, offering predictive potential for plant performance in contaminated environments.

Further studies have highlighted the significance of root morphological traits in determining plant strategy performance in contaminated environments. For example, in abandoned Pb-Zn tailings, analysis of 16 root characteristics across 11 tree and shrub species revealed that species with a lower root surface area ratio or root length ratio and higher root tissue mass density tended to adopt a resource conservation strategy. In contrast, species with a higher root surface area ratio, richer nitrogen content, and lower root tissue mass density were more aligned with a resource acquisition strategy (Wang et al., 2024). Similarly, in a short-rotation willow restoration system, specific leaf area, leaf nitrogen content, and root nitrogen content were associated with a resource acquisition strategy, while leaf dry matter content, root dry matter content, and root carbon content were linked to a resource conservation strategy. These findings highlighted a clear trade-off between the two strategies (Gervais-Bergeron et al., 2021). Current plant trait databases, such as *TRY* (Kattge et al., 2020) and *BiolFlor* (Kühn et al., 2004), offer researchers and practitioners a broad and flexible selection of species based on specific plant traits, facilitating the identification of suitable candidates for targeted phytoremediation. Despite these advancements, the complexity of plant responses to environmental conditions and their broader ecological implications still limits the full understanding of these processes. Consequently, small-scale pot experiments remain necessary to assess plant performance and refine restoration strategies before proceeding with large-scale field applications.

There is no doubt that soft traits that are easily measurable in the field—offer significant advantages in terms of efficiency and cost-effectiveness. They reduce the need for expensive soil and tissue analyses, minimize labor intensity, and have the potential to predict community-level characteristics, thus providing valuable ecophysiological insights (Gervais-Bergeron et al., 2024). However, the study of hard traits that are more challenging to measure in the field—can yield important information regarding the dynamic changes occurring at the molecular or cellular level within plants. Understanding how the content of elements and compounds in various plant tissues changes under environmental stress can enhance the optimization of field-based remediation strategies, ultimately improving the overall efficiency of phytoremediation processes.

Consequently, research focusing on PFT and the PES represents a major area of investigation within the interdisciplinary fields of resource management, environmental science, and biology. These approaches are particularly valuable for addressing some of the technical challenges faced in phytoremediation, offering a deeper understanding of plant responses to environmental stress and contributing to the refinement of remediation practices in the field.

Functional traits offer a quantitative and macroscopic approach to elucidate plant responses and mechanisms in various environmental contexts, presenting a promising tool for advancing phytoremediation practices. Although this method has garnered increasing attention in recent years, studies exploring its application remain limited. A search of the Web of Science database using the keywords *'TS = phytoremediation AND TS = "Functional traits"* yielded only 46 articles, highlighting the nascent stage of research in this area.

Recent findings underscore the significance of leaf functional traits in plant responses to air pollutants, particularly particulate matter (PM) and polycyclic aromatic hydrocarbons (PAHs). For instance, traits associated with trichomes have demonstrated a positive correlation with daily PM uptake, while the physical and chemical characteristics of the leaf cuticle are crucial for the phytoremediation of PAHs (Prigioniero et al., 2022; Prigioniero et al., 2023). Variations in plant surface morphology and chemical leaf traits, such as cuticular properties, enhance our understanding of plant efficiency in air pollution absorption. These traits are instrumental in explaining the mechanisms underlying plant interactions with air pollutants.

The functional trait-based approach also holds potential for elucidating plant responses to heavy metal contamination and their subsequent extraction effects. Ilyas et al., (2022) revealed that invasive plants growing in Cd-contaminated soils exhibited significantly higher structural leaf traits, chlorophyll content, and flavonoid content compared to native plants. Moreover, the decline in fluorescence parameters under Cd stress was more pronounced in invasive plants than in native species. Similarly, Sharma et al., (2021) investigated 21 functional traits of *Solanum nigrum* under Pb stress, encompassing aboveground traits (e.g., leaf number, specific leaf area, branch length), belowground traits (e.g., root length, root diameter), reproductive traits (e.g., fruit number, flower dry mass), and photosynthetic traits (e.g., chlorophyll and carotenoid content). Their findings demonstrated the utility of morphological and functional traits in determining the phytoremediation efficiency of plants. Wang et al., (2024) further highlighted the role of root morphological traits in the remediation of mining tailings, emphasizing their effectiveness in practical applications.

Despite advancements in trait-based research at the macro level, including studies on microbial community structure (Gil-Martínez et al., 2018), root morphological traits (Wang et al., 2024), leaf morphological traits (V. Kumar & Babu, 2022), and chemical traits (Liang et al., 2024), the practical application of these insights in phytoremediation remains insufficient. Several challenges hinder broader implementation:

Variability in Plant Response Mechanisms: Significant differences in the adaptability and response mechanisms of various plant species to remediation conditions have impeded the development of universal predictive models based on functional traits. Each species demonstrates unique responses to environmental stressors, complicating model standardization.

Complex Trait-Environment Interactions: The interaction between functional traits and environmental factors, such as soil pH, organic matter content, heavy metal concentrations, and water availability, is intricate. These variables significantly influence the expression of plant traits and the efficacy of phytoremediation, necessitating a more nuanced understanding of their interrelationships.

While the functional trait-based approach presents a valuable framework for understanding and improving phytoremediation practices, addressing the outlined limitations will require a more integrated and comprehensive research effort. Future studies should focus on evaluating the synergistic effects of multiple traits, standardizing predictive models across diverse plant species, and deciphering the complex interplay between plant traits and environmental factors. Such advancements will enhance the practical applicability of trait-based methods in phytoremediation and contribute to more efficient and sustainable remediation strategies.

3 MATERIALS AND METHODS

3.1 Material Cultivation and Processing

The pot experiment was carried out in a ventilated small plastic tunnel with open ends on the farm of the University of Agriculture and Life Sciences in Hungary (47°58′N, 19°37′E) in 2022 and 2023 for 90 days (June to September). Each plastic pot was 15 cm high, with an upper diameter of 19 cm and a lower diameter of 13 cm. The pots were filled with 1 kg of soil for rooting the plants. The soil used in the experiment was purchased from Florimo and its physical and chemical properties are shown in Table 5.

Table 5. Experimental soil properties

Parameters	Examination result	Unit
K_A	> 60	
Ph_{KCl}	6.74	
pH_{H2O}	6.70	
Humus content	7.02	%
P_2O_5	1291.62	mg kg^{-1}
K_2O	2905.98	mg kg^{-1}
NO_2+NO_3-N	1368.00	mg kg^{-1}
Zn	9.96	mg kg^{-1}
SO_4	5137.33	mg kg^{-1}
Ni	8.11	mg kg^{-1}
Cd	0.29	mg kg^{-1}

Poplar and willow cuttings from a short rotation coppice plantation (latitude 47°58′, longitude 19°37′). Two willow genotypes: ‘Csala’ (*Salix triandra* × *S. viminalis*), ‘Tora’ (*Salix schwerinii* × *S. viminalis*), two poplar genotypes: ‘Pegaso’ (*Populus* × *Generosa* × *P. nigra*), ‘AF2’ (*Populus deltoides* × *P. nigra*) (diameter: 3±1 cm, length: 20 cm). Three types of bamboo: *Phyllostachys edulis* (Moso), *Dendrocalamus asper*, *Dendrocalamus strictus* were purchased from Yunnan Bamboo Industry Co., Ltd. in August 2021 and 2022, and germinated in pots under greenhouse conditions for 8 months.

The temperature of 2022 and 2023 in experiment site shown in Figure 6 and Figure 7. In April 2022 and April 2023, 30 cuttings of each poplar and willow cuttings were planted in pots for rooting and acclimatization. Because of high temperatures in 2022 (Fig.6), only five plants survived in numbers greater than the experimental setup (3 x 6 pots), and ‘AF2’ and *D. strictus* only survived in 5 and 3 pots each and were therefore not experimented with. Meanwhile, six well-grown bamboo plants were selected separately, transplanted into pots to ensure proper rooting and acclimatization. After two months, Cd treatment was carried out.

The tested plants showed below:
2022: ‘Csala’, ‘Tora’, ‘Pegaso’, Moso, *D. asper*
2023: ‘Csala’, ‘Tora’, ‘Pegaso’, ‘AF2’, Moso, *D. asper*, *D.strictus*

3.2 Experimental design

The experiment was carried out from June to September in 2022 and 2023. For the Cd treatment, 1 liter of $CdCl_2 \cdot 2.5H_2O$ solution with concentrations of 50 mg kg^{-1} and 100 mg kg^{-1}, respectively, was divided into 12 equal parts and evenly sprayed on the soil surface. The soil was then allowed to equilibrate for three days. The resulting final total Cd concentrations were therefore 0.29 mg kg^{-1} (CK) original Cd concentration in the soil, 4.17 mg kg^{-1} (T1) and 8.33 mg kg^{-1} (T2). In a completely randomized block design, there were six replicates of each treatment per plant, 90 pots in the first year and 126 pots in the second year. Humidity was maintained at 60–65% during growth, and no fertilizer was applied. At the end of the experiment, the roots, branches and leaves of each plant were harvested. Soil samples were taken from the entire soil profile in each pot using a stainless-steel spatula. The soil samples were thoroughly homogenized, sieved through a 2 mm sieve, and then divided equally into 3 random sub-samples (n=3). The plant root systems were rinsed with deionized water and then dried in an oven at 70°C for 72 hours before being analyzed.

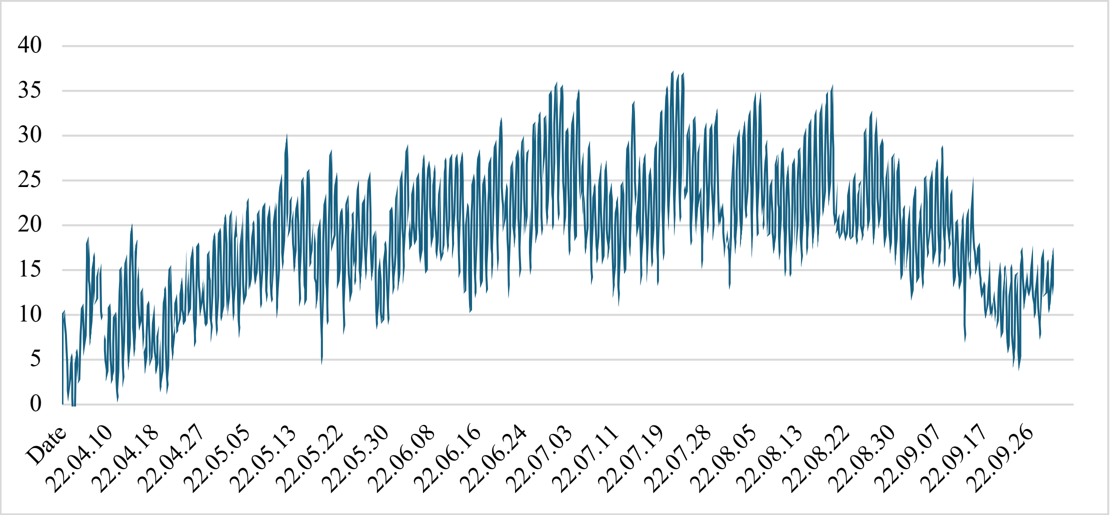


Figure 6. Measured temperatures at the test site from April to September 2022

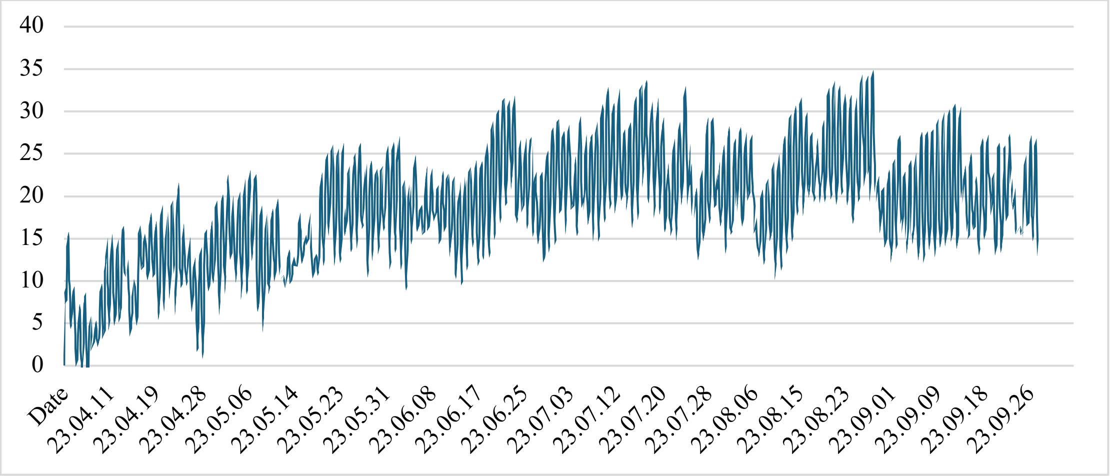


Figure 7. Measured temperatures at the test site from April to September 2023

3.3 Measurement methods

3.3.1 Quantitative analysis of elements in plant organs

To determine the total elemental content in plant organs, a stainless steel pulverize was used to grind a dried sample of biomass. Total nitrogen content was determined using the Kjeldahl method (Hungarian standard: MSZ-08-1783-6:1983). The potassium content of the finely ground and dried plant sample was determined after acid digestion (Hungarian standard: MSZ-08-1783-29:1985). The resulting solution was diluted and analyzed using a Shimadzu UV-1800 spectrophotometer. The concentration of potassium was determined by measuring the absorbance and comparing it to a calibration curve. For Cd analysis, the samples were digested using nitric acid (HNO_3) and hydrogen peroxide (H_2O_2) according to the Hungarian standard MSZ 21470-50:2006:4.1 using a VELP DK20 digestion block. After digestion, the solution was diluted and analyzed using an inductively coupled plasma optical emission spectrometer (ICP-OES; JY Ultima 2). The Cd content was quantified using instrumental reading and calibration curve.

3.3.2 Quantitative analysis of soil NO_2+NO_3-N and K

The concentration of nitrate (NO_2+NO_3-N) in the soil was determined using a FIAStar 5000 analyzer in accordance with the Hungarian standard MSZ 20135:1999 5.4.3. Soil samples were collected, air-dried and sieved through a 2 mm sieve. An amount of 10 g of prepared soil sample was extracted with 100 ml of 1 M KCl solution. After extraction, the mixture was filtered to obtain a clear filtration. The filtrate was then analyzed using the FIAStar 5000, which uses flow injection analysis (FIA) and a chemical colorimetric reaction.

The concentration of total potassium in the soil was determined using an ICP-OES analyzer in accordance with the Hungarian standard MSZ 21470-50:2006 4.1. A 0.5 g portion of the prepared soil sample was digested with a mixture of HNO_3 and H_2O_2 using a high-temperature digestion system. After complete digestion, the solution was filtered and diluted to a final volume of 50 mL with deionized water. The potassium concentration in the digest was then measured using ICP-OES.

3.3.3 Measurement of physiological parameters of leaves

The chlorophyll content (SPAD value) and quantum yield (Q_y) of three mature leaves of each plant were measured every 15 days using the SPAD-502 Konica Minolta portable chlorophyll meter and the PAR-FluorPen FP110 portable fluorometer (due to equipment acquisition, Q_y data will only be available in the 2023 experiment). Chlorophyll content is expressed as a chlorophyll index without units. Measurements were taken from 10:00 a.m. to 3:00 p.m. and followed the operating procedures of the instrument.

3.3.4 Phytoremediation efficiency parameters

The accumulation of Cd was assessed by calculating the bioconcentration factor values for the root (BCF_r), shoot (BCF_b) and leaf parts (BCF_l) using the following formula:

$$BCF_l = C_{leaf}/C_{Soil}$$

$$BCF_b = C_{branch}/C_{Soil}$$

$$BCF_r = C_{root}/C_{Soil}$$

The ability of Cd to translocate from the roots to the aboveground part was evaluated by calculating the translocation factor (TF) of the aboveground part. The calculation formula is as follows:

$$TF = C_{leaf+branch}/C_{root}$$

3.4 Data processing

3.4.1 Difference analysis

Analyses and plots were carried out in SPSS (IBM SPSS 27) and Excel (Microsoft 365), respectively. The individual effects of treatment concentration, species, and plant organ and the interactions of the three were assessed using multi-way ANOVA and expressed in the form of graphs and tables. Prior to the ANOVA, the normality of the data and the homogeneity of variances were assessed using Levene's test to confirm the applicability of the ANOVA. Duncan's post-hoc test was used to detect differences between means. If the data did not meet the requirements of homogeneity, the Games-Howell test was used as a non-parametric alternative, statistical significance was defined as $p \leq 0.05$, and bar charts were used to visualize the results. The data from the experimental results are always presented as mean ± standard deviation.

3.4.2 Correlation analysis

The differences in the physiological functions of leaves under Cd treatments of different concentrations were studied using one-way ANOVA (SPSS 27) and linear fitting and expressed as line graphs (Excel Microsoft 365).

R is used for analysis and plotting; Euclidean distance is used to represent the linear distance between two points in multidimensional space. The similarity or difference between different variables is calculated, and a heat map is generated using the *pheatmap* function. A dendrogram is generated by recursively merging or splitting variables to reveal the potential relationships between variables. The formula is as follows: x represents the functional form of each nutrient element, and y represents each bioaccumulation and translocation parameter.

$$d(x,y) = \sqrt{\sum_{i=1}^{n}(x_i - y_i)^2}$$

R is used for analysis and plotting; Principal component analysis (PCA) is used to project high-dimensional data onto a few orthogonal principal components while retaining as much of the data's primary variation information as possible. The principal components are eigenvectors of the data covariance matrix. The first principal component captures the maximum amount of variation, the second principal component captures the maximum amount of the remaining variation, and so on. The *prcomp* function is used to perform principal component analysis, and the *factoextra* package is used for visualization.

R was used for analysis and plotting; redundancy analysis (RDA) was performed using the *vegan* package. Redundancy analysis is a method that combines multiple regression and principal component analysis to investigate how the response variable (bioaccumulation parameters) is affected by the combined influence of the explanatory variables (nutritional characteristics). The main objective of our study was to explore the potential role of all candidate variables, rather than to construct a simplified predictive model. Therefore, we did not remove collinear variables.

Mantel's test (Pearson's correlation coefficient) from the vegan package was used to explore the relationship between plant nutritional traits and organ bioaccumulation and translocation parameters in plants in the bamboo and willows families. This is a non-parametric statistical method based on a distance matrix that is used to compare the correlation between two matrices. Since the results in the first year varied greatly due to the influence of natural temperature, we used the data from the second year for analysis. The formula is:

$$r = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n}(\sum X_{ij} - \bar{X})(\sum Y_{ij} - \bar{Y})}{\sqrt{\sum_{i=1}^{n}\sum_{j=1}^{n}(\sum X_{ij} - \bar{X})^2(\sum Y_{ij} - \bar{Y})^2}}$$

The statistical significance of the mantel test is set to $p \leq 0.05$. Considering the different units of nitrogen and potassium and their large variability, all data were standardized using Z-scores before analysis. The Z-score formula is shown below, where X is the original data, μ is the mean and σ is the standard deviation.

$$Z = \frac{\mathrm{X} - \mu}{\sigma}$$

Fisher discriminant analysis (FDA) is used to determine whether nutritional functional traits can be used as the basis for plant classification and their position on the economic spectrum. The method of analysis of variance is used, which not only uses the classification of known samples and the extremum method of multivariate functions to maximise the variance between groups and minimise the variance within groups, but also to find the discriminant function. Data processing and analysis were carried out using SPSS. Eight characteristics of the seven plants from the second year were selected: RN (X1), RK (X2), BN (X3), BK (X4), LN (X5), LK (X6), SN (X7) and SK (X8) for statistical classification and Fisher's discriminant analysis to obtain the discriminant function coefficients and construct the discriminant model. Finally, the discriminant model for the corresponding plants was verified using the five plants grown in the first year. The principle is as follows: Suppose that *nt* samples are taken from *k* populations G_t *(t = 1, ..., k)*, and each sample is described by m feature values, forming an m-element vector *x(i)(t)=(xi l(t),...xim(t)), t=1,...k; i=1,...,nt)*, where *nt* is the number of samples taken from population *Gt*. If a= (a_1, …,a_m) is a specified vector in m-dimensional space, then *u(x)=a'x* is the projection of the sample x in the direction normal to a. After each sample is projected, it is converted from a multivariate array to univariate data. An overall population contains n t such univariate projections, and k overall populations contain k sets of projections. The analysis of variance for these k sets of univariate data is performed, and the sum of the squares between groups is:

$$B_0 = \sum_{t=1}^{k} \mathrm{n}_t(a'\bar{x}^{(t)}\ \overline{a'})^2 \ \ = \mathrm{a}'[\sum_{t=1}^{k} \mathrm{n}_t\ (\bar{x}^{(t)} - \ \bar{x})\ \ (\bar{x}^{(t)} - \ \bar{x})']\mathrm{a} = \mathrm{a}'\mathrm{Ba}$$

The mean vector of the *nt* samples of *Gt* is:

$$\bar{x}^{k} = \frac{1}{\mathrm{n}_{k}} \sum_{j=1}^{\mathrm{n}_{k}} x_{j}{}^{(k)}$$

The overall sample mean vector for k is:

$$\bar{x}^{k} = \frac{1}{\mathrm{n}_{k}} \sum_{t=1}^{k} \sum_{j=1}^{\mathrm{n}_{k}} x_{j}{}^{(k)}$$

B is the intergroup variance matrix.

$$\mathrm{B}=\textstyle\sum_{t=1}^{k} \mathrm{n}_{t}\, (\bar{x}^{(t)}-\ \bar{x})\ \ (\bar{x}^{(t)}-\ \bar{x})'$$

The sum of the squares within the merged group is:

$$A_{0}=\textstyle\sum_{t=1}^{k} \sum_{j=1}^{\mathrm{n}_{t}} (a' x_{j}{}^{(t)} - a\bar{x})^{2} = a' [\sum_{t=1}^{k} \sum_{j=1}^{\mathrm{n}_{t}} (x_{j}{}^{(t)} - \bar{x}^{(t)})(x_{j}{}^{(t)} - \bar{x}^{(t)})'] a = a' A a$$

The combined within-group variance matrix A is:

$$\mathrm{A}=[\textstyle\sum_{t=1}^{k} \sum_{j=1}^{\mathrm{n}_{t}} (x_{j}{}^{(t)} - \bar{x}^{(t)})(x_{j}{}^{(t)} - \bar{x}^{(t)})']$$

Therefore, if the mean of the population (class) in group *k* is significantly different, then the ratio $\Delta(a) = \frac{\mathrm{a}' B a}{\mathrm{a}' A a}$ should be sufficiently large. Using analysis of variance, this problem becomes finding the projection direction a such that $\Delta(a)$ reaches its maximum. Since *a* that makes it reach the maximum is not unique, a constraint is added to a, namely *a*=1. Therefore, the above condition extremum problem is transformed into a problem of finding the maximum eigenvalue of $\frac{B}{A}$ and the corresponding eigenvector. Assume $\frac{B}{A}$ have non-zero eigenvalues $\gamma_1 \geq \gamma_2 \geq \ldots \geq \gamma_r > 0$, and let its corresponding eigenvectors that satisfy the constraint conditions be $a_1, a_2, \cdots, a_r$. This is called: $P1 = \frac{\gamma_1}{\sum_{i=1}^{r} \gamma_i}$ is the discriminant ability of the linear discriminant function $u_1(x)=a_1'x$, and $P_i = \frac{\gamma_1+\cdots+\gamma_l}{\sum_{i=1}^{r} \gamma_i}$ is the cumulative discriminant ability of the first l ($l \leqslant r$) linear discriminant functions $u_1(x) = a_1'x, \ldots, u_l(x) = a_l'x$. The stronger the discriminant ability, the higher the discrimination accuracy.

4 RESULTS AND DISCUSSION

4.1 Difference analysis

4.1.1 Differences in the content of plant organs in different years

The analysis of variance for total Cd, N, and K content in plants across years shown in Table 6 revealed that high-temperature years significantly influenced Cd and K content, while the impact on N content varied among plant species.

Table 6. Analysis of variance for total Cd, N, and K content of plants between different years

Plants	Elements	Sum of Squares	df	Mean squares	F value	P value
Moso	N	70515.994	1	70515.994	8.153	0.006
	K	40.463	1	40.463	2.462	**0.122**
	Cd	73.211	1	73.211	15.147	<0.001
D. asper	N	4140.527	1	4140.527	8.274	0.006
	K	286.763	1	286.763	8.827	0.004
	Cd	318.293	1	318.293	28.279	<0.001
‘Csala’	N	0.143	1	0.143	0.149	**0.701**
	K	884.760	1	884.760	19.910	<0.001
	Cd	452.431	1	452.431	19.895	<0.001
‘Tora’	N	0.213	1	0.213	0.144	**0.705**
	K	2758.804	1	2758.804	275.186	<0.001
	Cd	1957.567	1	1957.567	25.990	<0.001
‘Pegaso’	N	0.027	1	0.027	0.009	**0.924**
	K	2967.308	1	2967.308	102.682	<0.001
	Cd	1760.644	1	1760.644	75.389	<0.001

Cd content was significantly affected by heating ($P < 0.001$) across all plants, with high F-values indicating the strong sensitivity of Cd accumulation to environmental changes, likely due to plant responses to high-temperature stress. Similarly, K content exhibited significant year-to-year variability in most plants, excluding Moso, with notable effects observed in ‘Tora’ and ‘Pegaso’. The corresponding F-values for K content, 275.186 and 102.682 respectively, underscore the high sensitivity of potassium accumulation mechanisms to climatic fluctuations. In contrast, variations in N content were significant in bamboo species but not in ‘Csala’, ‘Tora’, or ‘Pegaso’, suggesting that nitrogen uptake and metabolism are relatively stable and species-dependent. These results may suggest that high-temperature years exert a pronounced influence on Cd and K content by altering soil nutrient availability and plant metabolic processes, while the effect on N content is modulated by species-specific physiological characteristics.

4.1.2 Cd distribution characteristics in plants

Table 7 shows the results of a two-way analysis of variance of total plant Cd accumulation by plant species, Cd treatment and plant organs for different years, revealing the significant effects of each main effect and interaction on Cd accumulation.

Table 7. Two-way ANOVA table for Cd treatment, plant species and plant organ on total Cd accumulation in plants

Years	Variant Source	Sum of Squares	df	Mean squares	F value	P value
2022	Plants	2899.069	4	724.774	46.164	<0.001
	Treatments	3408.898	2	1704.449	108.565	<0.001
	Organs	173.634	2	86.817	44.255	<0.001
	Plants ×Treatments	1649.125	8	206.141	13.130	<0.001
	Plants× Organs	843.167	8	105.396	53.726	<0.001
	Treatments× Organs	120.246	4	30.062	15.324	<0.001
	Plants× Treatments× Organs	570.375	16	35.648	18.172	<0.001
2023	Plants	340.065	6	56.678	214.149	<0.001
	Treatments	306.860	2	153.430	579.715	<0.001
	Organs	4.530	2	2.265	8.558	<0.001
	Plants ×Treatments	147.720	12	12.310	46.512	<0.001
	Plants× Organs	77.151	12	6.429	24.292	<0.001
	Treatments× Organs	5.166	4	1.292	4.880	<0.001
	Plants× Treatments× Organs	44.153	24	1.840	6.951	<0.001

In the first year, plant species, Cd treatment and plant organ all showed significant effects (*P<0.001*), with F values of 46.164, 108.565 and 44.255, respectively. This indicates that there are significant differences in the Cd accumulation capacity between different cultivars, that Cd treatment concentration significantly promotes Cd accumulation, and that there are also significant differences in the distribution of Cd in different organs. In addition, all interactions (e.g., cultivars × treatments, cultivars × organs) were significant, especially the three-factor interaction with an F value of 18.172, indicating that Cd accumulation is affected by the coupling of multiple factors. In the second year, although the trend was like the first year, the Cd treatment effect (F = 579.715) and the plant species effect (F = 214.149) significantly increased, while the difference between organs (F = 8.558) decreased. The response of different plant species to Cd treatment was more significant in the second year, which may be due to the stable experimental environment and the lack of high temperatures. At the same time, the effect of interactions generally weakened, e.g. the F value for variety × treatment increased from 13.130 to 46.512, while the F value for three-factor interactions decreased to 6.951. In the second year of the experiment, due to the increase in the number of plant varieties and the stability of environmental conditions, the variety × treatment effect increased significantly, indicating that under stable environmental conditions, the response of different varieties to Cd treatment became more significant. At the same time, the significance of the three-way interaction effect decreased because the Cd distribution pattern among organs tended to converge with a larger sample size and the environmental stressor (high temperature) disappeared. This result shows that in a stable environment, the response of plants to Cd stress is mainly reflected in the physiological differences between varieties, while the difference in distribution among organs shows a marginal diminishing effect.

Table 8. Difference in total Cd accumulation in plants under Cd treatment and plant species

Years		Total Cd (mg kg^{-1})		
		CK	T1	T2
2022	Moso	7.86±0.06bB	14.33±1.49aC	13.5±2.26aD
	D. asper	7.98±0.15bB	19.26±0.57aBC	23.7±1.32aD
	‘Csala’	9.84±0.19cB	25.37±1.23bB	47.32±4.15aC
	‘Tora’	8.45±0.04cB	48.35±3.24bA	86.88±3.82aA
	‘Pegaso’	18.2±2.4cA	42.53±1.7bA	65.47±4.22aB
2023	Moso	0.97±0.17bCD	3.59±1.36aD	3.75±0.67aC
	D. asper	0.87±0.17aCD	1.3±0.3aD	1.98±0.74aC
	D. strictus	0.62±0.08bD	1.26±0.25bD	5.29±0.72aC
	‘Csala’	3.05±0.34cA	9.44±0.35bC	17.58±1.91aA
	‘Tora’	2.25±0.45bB	15.1±1.94aA	18.98±1.34aA
	‘Pegaso’	1.51±0.06bC	12.65±0.74aAB	13.39±1.6aB
	‘AF2’	0.99±0.2bCD	11.33±1.17aBC	13.57±0.25aB

Note: Different lowercase letters indicate significant differences between different concentrations of the same plant, and different uppercase letters indicate significant differences between different plants at the same concentration. The results for each year are marked separately ($p < 0.05$).

During the first year, *Salicaceae* species demonstrated a pronounced capacity for Cd accumulation, particularly in Tora and ‘Pegaso’, with Cd concentrations reaching 86.88 ± 3.82 mg kg^{-1} and 65.47 ± 4.22 mg kg^{-1} , respectively, significantly exceeding those of other treatments. Similarly, ‘Csala’ exhibited notable Cd accumulation during the first year, especially under the T2 treatment (47.32 ± 4.15 mg kg^{-1}). In contrast, *Bambusoideae* species, such as Moso and *D. asper*, displayed significantly lower Cd accumulation capacities, with concentrations of 14.33 ± 1.49 mg kg^{-1} and 23.7 ± 1.32 mg kg^{-1}, respectively.

In the second year, the Cd accumulation in all plants generally declined and stabilized, attributed to the absence of high-temperature conditions. *Salicaceae* species maintained a relatively high Cd accumulation capacity, with ‘Tora’ and ‘Csala’ achieving concentrations of 18.98 ± 1.34 mg kg^{-1} and 17.58 ± 1.91 mg kg^{-1}, respectively, under the T2 treatment, indicating sustained Cd enrichment potential. Conversely, the *Bambusoideae* species continued to exhibit low Cd accumulation, with Moso and *D. asper* reaching only 3.75 ± 0.67 mg kg^{-1} and 1.98 ± 0.74 mg kg^{-1}, respectively, under the T2 treatment.

The results showed that in the first year, high temperatures significantly enhanced the ability of each plant to accumulate Cd.

4.1.3 Accumulation of different Cd concentrations in different organs (2022)

Figure 8 illustrates that Cd concentration significantly increased ($P < 0.05$) across plant organs with increasing treatment concentrations. However, the Cd accumulation and distribution characteristics varied among different plant species.

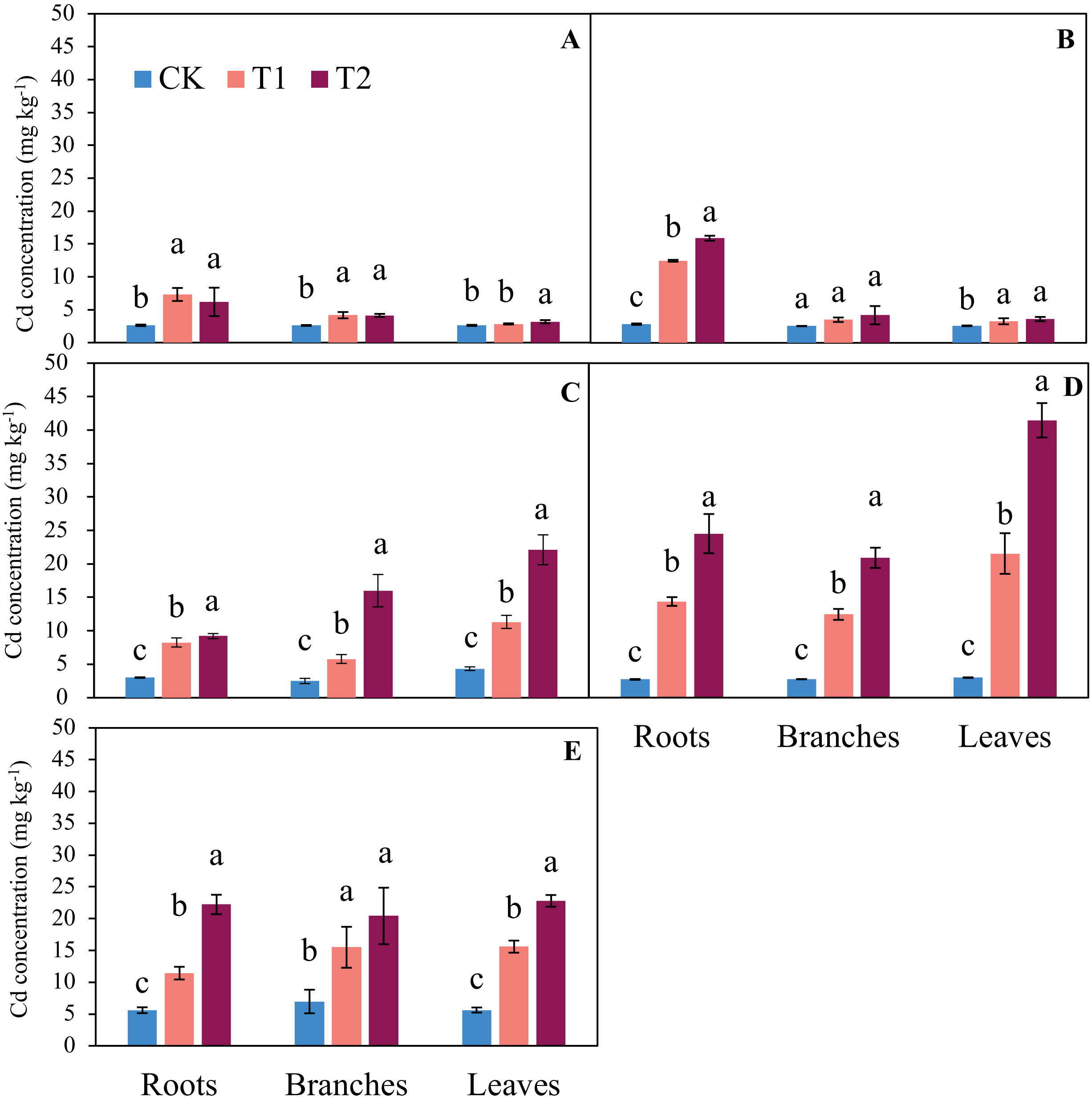


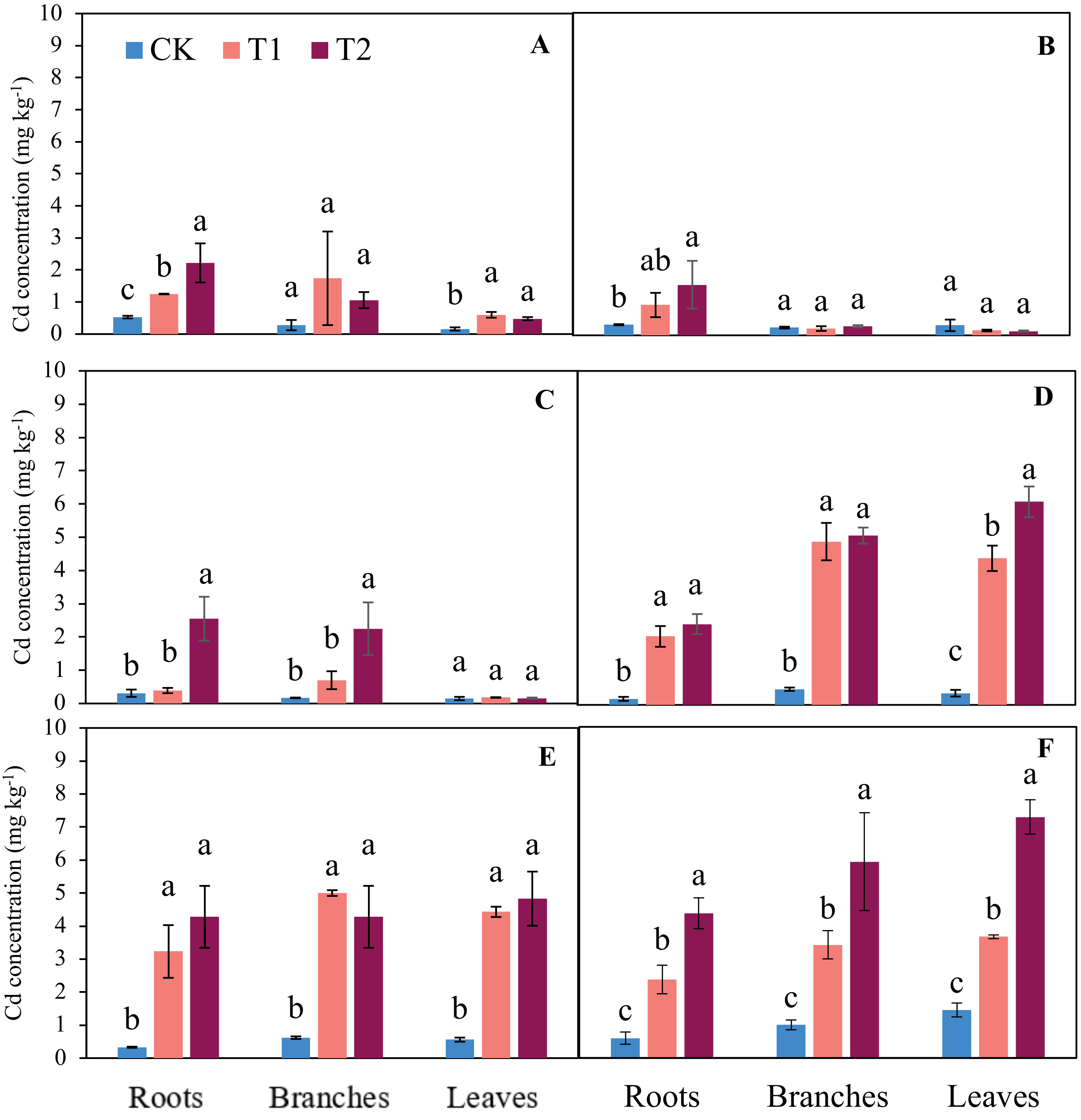
Figure 8. Cd concentration in roots, branches and leaves of each plant in the first year, (A: Moso, B: *D. asper*, C: 'Csala', D: 'Tora', E: 'Pegaso'), different lowercase letters indicate significant differences ($p < 0.05$) in the same organ at different concentrations.

In Moso and *D. asper*, Cd primarily accumulated in the roots, with significantly lower concentrations observed in the branches and leaves. This pattern indicates a limited Cd transport capacity in these species. Under T1 and T2 treatments, the Cd concentration in the roots of *D. asper* was 4.39 and 5.59 times higher than in the CK, respectively.

In contrast, *Salicaceae* species such as 'Csala', 'Tora', and 'Pegaso' exhibited significantly higher Cd concentrations in their aboveground parts, particularly in the leaves, indicating a strong Cd transport capacity. Notably, 'Tora' demonstrated the highest Cd concentration in leaves under the T2 treatment, underscoring its exceptional Cd uptake and transport potential. The Cd concentrations in ‘Tora’'s leaves under T1 and T2 treatments were 7.2 and 13.86 times higher than in the CK, respectively. These results emphasize the superior performance of *Salicaceae* species in Cd enrichment in aboveground tissues, while Moso and *D. asper* predominantly accumulated Cd in their roots.

4.2.2 Accumulation of different Cd concentrations in different organs (2023)

Figure 9 shows the organ Cd accumulation content and differences of seven plants in 2023.



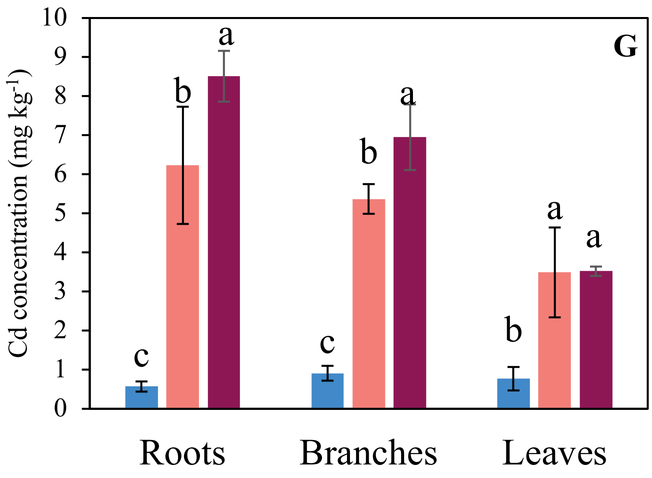


Figure 9. Cd concentration in roots, branches and leaves of each plant in the second year, (A: Moso, B: *D. asper*, C: *D. strictus*, D: 'AF2', E: 'Pegaso', F: 'Csala', G: 'Tora'), different lowercase letters indicate significant differences ($p < 0.05$) in the same organ at different concentrations.

Like the results of the first year, Cd treatments significantly increased Cd accumulation across various plant organs. In bamboo species (Moso, *D. asper*, and *D. strictus*), roots were the primary Cd-accumulating organs, with concentrations of 2.22 ± 0.61, 1.57 ± 0.74, and 2.55 ± 0.66 mg kg^{-1}, respectively, representing increases of 4.18, 4.75, and 8.22 times compared to the CK. Moso and *D. strictus* demonstrated some capacity for Cd translocation to the branches (Fig. 9C), while the Cd accumulation in the aboveground parts of *D. asper* did not differ significantly (Fig. 9B).

In *Salicaceae* species, under T1 and T2 treatments, no significant differences were observed in Cd accumulation between roots and branches (Fig. 9D, E), suggesting that these treatment concentrations had limited effects on Cd accumulation in these organs. However, Cd concentrations in the leaves of 'Pegaso' and 'AF2' were significantly elevated, reaching 8.62 and 17.37 times higher than the CK, respectively. Unlike the first year, 'Tora' exhibited a shift in Cd accumulation patterns under increasing Cd concentrations, with roots accumulating a substantial amount of Cd (Fig. 9G) rather than the leaves. Additionally, in 'Csala' (Fig. 9F), increasing Cd concentrations under T2 treatment significantly enhanced Cd accumulation in the leaves, reaching 7.28 ± 0.52 mg kg^{-1}, which was 5.02 and 1.99 times higher than CK and T1, respectively.

4.1.4 Cd treatments effects on N,K elements within plants

Table 9 shows the N,K content differences between plants, treatments and organs in a two-way ANOVA.

Table 9. Cd treatments, plant species and organs (two-way ANOVA) analysis of variance for total N, K

Years		Variant Source	Sum of Squares	df	Mean squares	F value	P value
2022	N	Plants	13.191	4	3.298	89.789	<0.001

		Treatments	0.609	2	0.304	8.286	<0.001
		Organs	35.172	2	17.586	478.799	<0.001
		Plants ×Treatments	2.856	8	0.357	9.721	<0.001
		Plants× Organs	2.562	8	0.320	8.719	<0.001
		Treatments× Organs	0.031	4	0.008	0.212	**0.931**
		Plants× Treatments× Organs	1.886	16	0.118	3.208	<0.001
	K	Plants	1469.265	4	367.316	99.498	<0.001
		Treatments	33.324	2	16.662	4.513	0.014
		Organs	1862.386	2	931.193	252.240	<0.001
		Plants ×Treatments	273.220	8	34.153	9.251	<0.001
		Plants× Organs	1584.584	8	198.073	53.654	<0.001
		Treatments× Organs	9.858	4	2.464	0.668	**0.616**
		Plants× Treatments× Organs	190.697	16	11.919	3.228	<0.001
2023	N	Plants	86.336	6	14.389	649.302	<0.001
		Treatments	0.428	2	0.214	9.668	<0.001
		Organs	29.040	2	14.520	655.204	<0.001
		Plants ×Treatments	0.687	12	0.057	2.583	0.004
		Plants× Organs	2.480	12	0.207	9.324	<0.001
		Treatments× Organs	0.037	4	0.009	0.419	**0.794**
		Plants× Treatments× Organs	1.701	24	0.071	3.199	<0.001
	K	Plants	1631.977	6	271.996	148.614	<0.001
		Treatments	1.857	2	0.929	0.507	**0.603**
		Organs	841.348	2	420.674	229.848	<0.001
		Plants ×Treatments	271.931	12	22.661	12.382	<0.001
		Plants× Organs	1090.222	12	90.852	49.640	<0.001
		Treatments× Organs	33.007	4	8.252	4.509	0.002
		Plants× Treatments× Organs	275.242	24	11.468	6.266	<0.001

During the first year, Cd treatment significantly influenced both total N and total K content. For total N content, the variety effect was highly significant ($F = 89.789$, $P < 0.001$), indicating substantial differences among plant species. Additionally, treatment and organ effects were also significant ($P < 0.001$), whereas the treatment × organ interaction was not significant ($P = 0.931$). For total K content, the effects of variety, treatment, and organ were all significant ($P < 0.001$), with variety contributing the most to total K variability ($F = 99.498$), reflecting species-specific differences in K accumulation during Cd exposure. Moreover, the interaction between variety × treatment had a significant effect on total K content ($P < 0.001$), suggesting that Cd treatment impacted K content differently across plant species, while the treatment × organ interaction was not significant ($P = 0.616$).

In the second year, the ANOVA for total N content indicated that variety and organ effects remained significant ($P < 0.001$), but the influence of Cd treatment was minimal

(P = 0.794). Notably, the interactions of variety × treatment and variety × organ were significant (P < 0.001), highlighting species-specific responses and organ-level variations in N accumulation. For total K content, the variety effect remained significant (P < 0.001), while treatment had no significant impact (P = 0.603). However, organ effects on total K content were significant, and the interactions of variety × treatments and plant species × organs were also significant (P < 0.001).

Overall, Cd treatment significantly affected the total nitrogen and potassium content of plants during the two-year study, and the treatments × organs interaction was not significantly different.

Table 10. Total N and K content of plants in each year

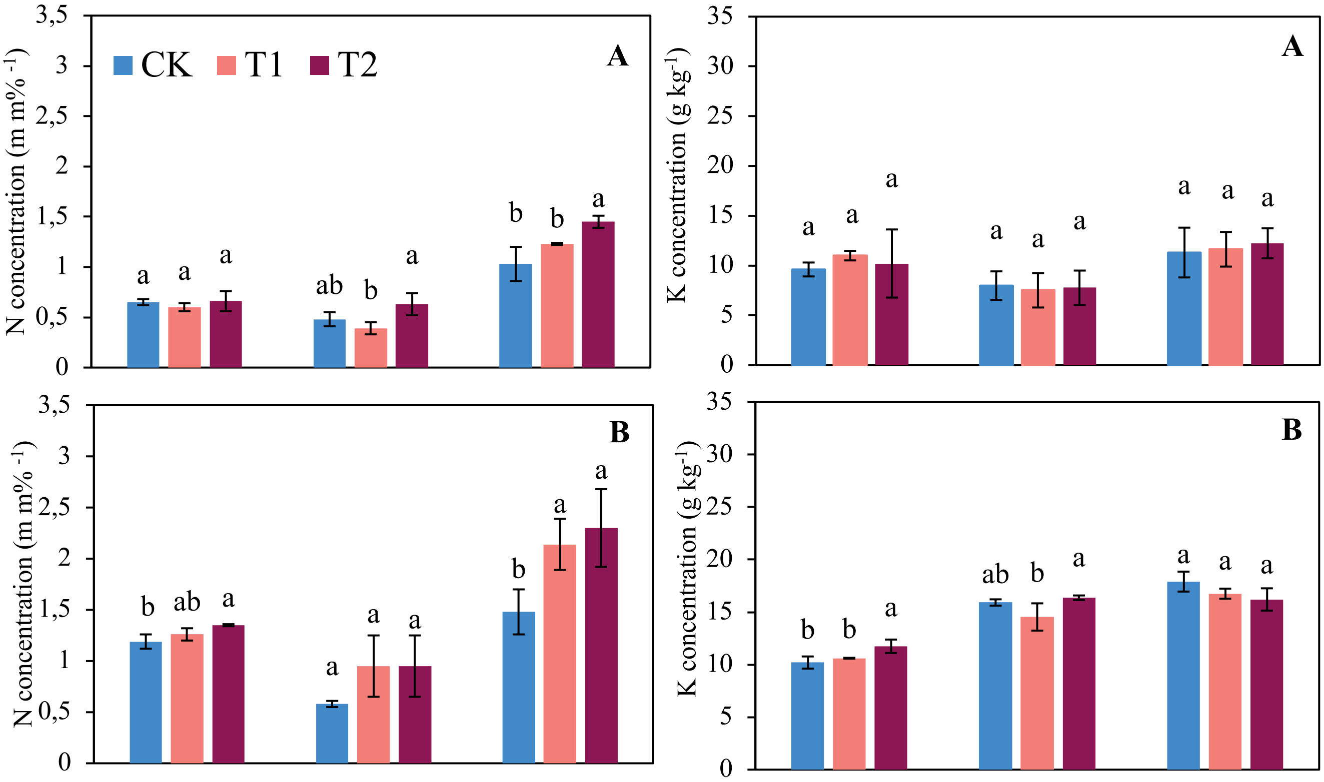
Years	Elements	Plants	CK	T1	T2
2022	N	Moso	2.16±0.19aC	2.22±0.02aB	2.75±0.14aB
		D. asper	3.25±0.24aC	4.35±0.12aA	4.59±0.29aA
		'Csala'	4.68±0.25aAB	5.34±0.13aA	4.68±0.1aA
		'Tora'	3.5±0.2aBC	4.26±0.14aA	5.04±0.31aA
		'Pegaso'	5.57±0.49aA	4.99±0.5aA	4.35±0.25aAB
	K	Moso	28.88±2.27aB	30.13±0.99aC	30.19±5.08aB
		D. asper	44.04±0.37aAB	41.91±0.86aBC	44.33±0.3aAB
		'Csala'	43.7±1.38aAB	37.4±1.29aBC	32.12±5.09aB
		'Tora'	41.52±1.56bAB	53.03±0.41aAB	59.36±1.89aA
		'Pegaso'	51.43±3.53aA	63.16±7.5aA	59.13±1.44aA
2023	N	Moso	5.11±0.24aB	5.45±0.2aB	5.21±0.81aB
		D. asper	6.54±0.36aA	6.1±0.23aAB	5.9±0.1aB
		D. strictus	7.69±0.13aA	7.03±0.19aA	7.26±0.54aA
		'Csala'	3.2±0.06aC	2.74±0.25aC	2.5±0.07aC
		'Tora'	2.27±0.19aC	2.12±0.09aC	2.19±0.34aC
		'Pegaso'	2.35±0.16aC	1.92±0.07aC	1.78±0.05aC
		'AF2'	2.37±0.26aC	2.03±0.15aC	2.61±0.13aC
	K	Moso	26.72±0.92bBC	40.16±5.34aA	28.71±5.97bBC
		D. asper	46.43±6.17aA	30.42±2.83bAB	41.51±2.78abA
		D. strictus	33.98±2.2aB	39.6±0.78aA	37.91±4.18aAB
		'Csala'	22.18±0.54aCD	18.12±1aBC	17.89±0.74aCD
		'Tora'	13.73±1.56aD	14.2±1.4aC	15±0.49aCD
		'Pegaso'	21.57±0.92aCD	22.65±0.13aBC	19.48±2.13aCD
		'AF2'	23.35±0.56aCD	24.02±2.17aBC	23.72±1.31aCD

Note: Different lowercase letters indicate significant differences between different concentrations of the same plant, and different uppercase letters indicate significant differences between different plants at the same concentration. The results for each year are marked separately (p <0.05).

The results of the two-year experiment showed that Cd treatment had no significant effect on the total nitrogen content of the plant species. Although the nitrogen content changed with the increase of Cd concentration, the change increased or decreased depending on the species, and the difference between the treatment groups was not significant (Table 10).

The first-year results revealed that Cd treatment significantly increased the total K content in Tora. However, in another willow species, Csala, the K content exhibited a declining trend as Cd concentrations increased, although this decline did not reach statistical significance. During the second year, significant changes in K content were limited to Moso and *D. asper*. The response patterns of these species were notably distinct. Moso exhibited an initial increase in K content at moderate Cd concentrations (T1), followed by a decline at higher concentrations (T2), suggesting that moderate Cd exposure may have stimulated K uptake and accumulation, while higher concentrations impaired this ability. Conversely, *D. asper* showed a contrasting pattern, with an initial decline in K content at T1, potentially reflecting the inhibitory effects of Cd stress. At higher Cd concentrations (T2), however, the K content rebounded, indicating a possible activation of compensatory mechanisms that allowed the plant to partially restore its K absorption capacity.

4.1.5 N and K content of different organs (2022)



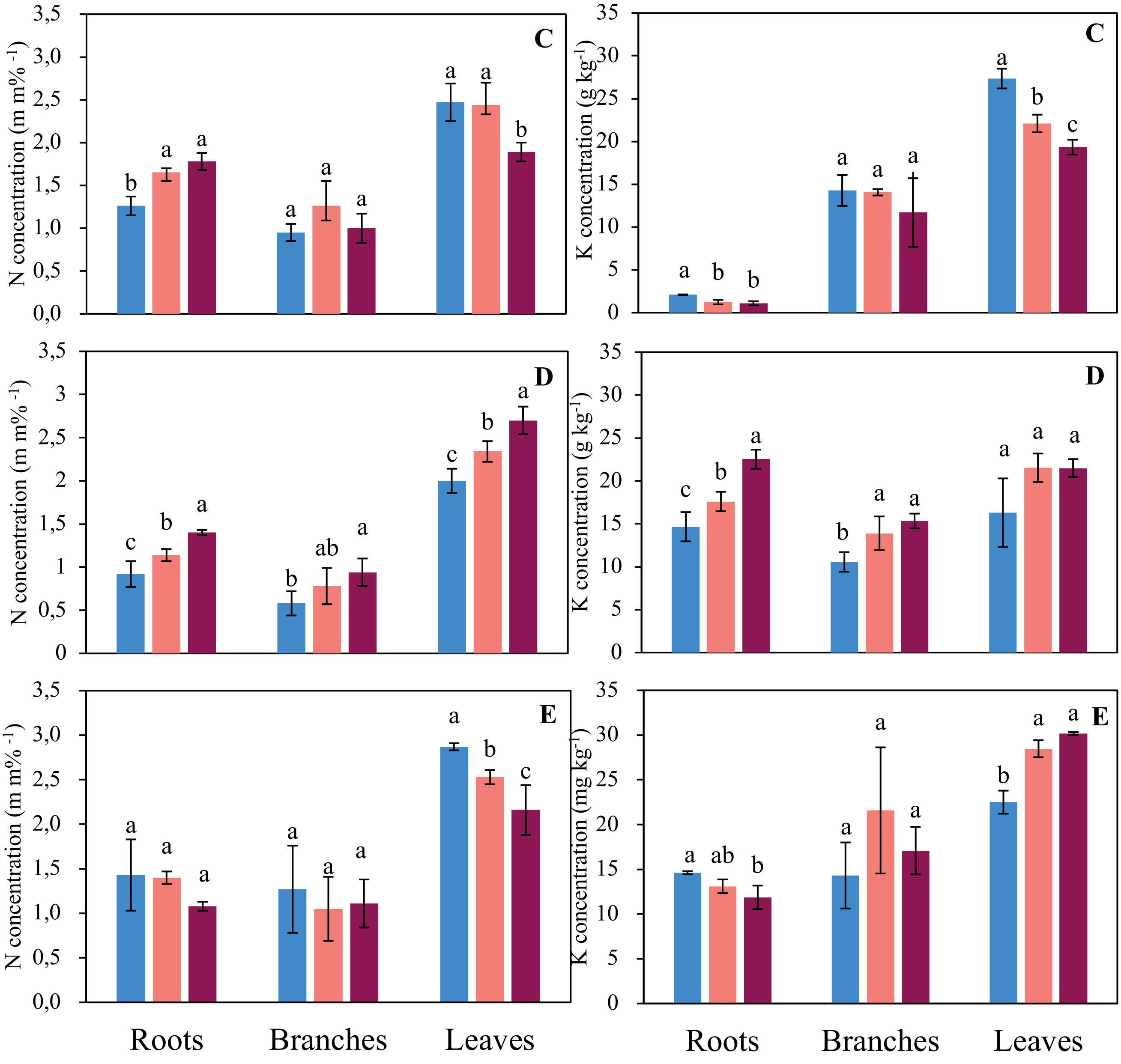
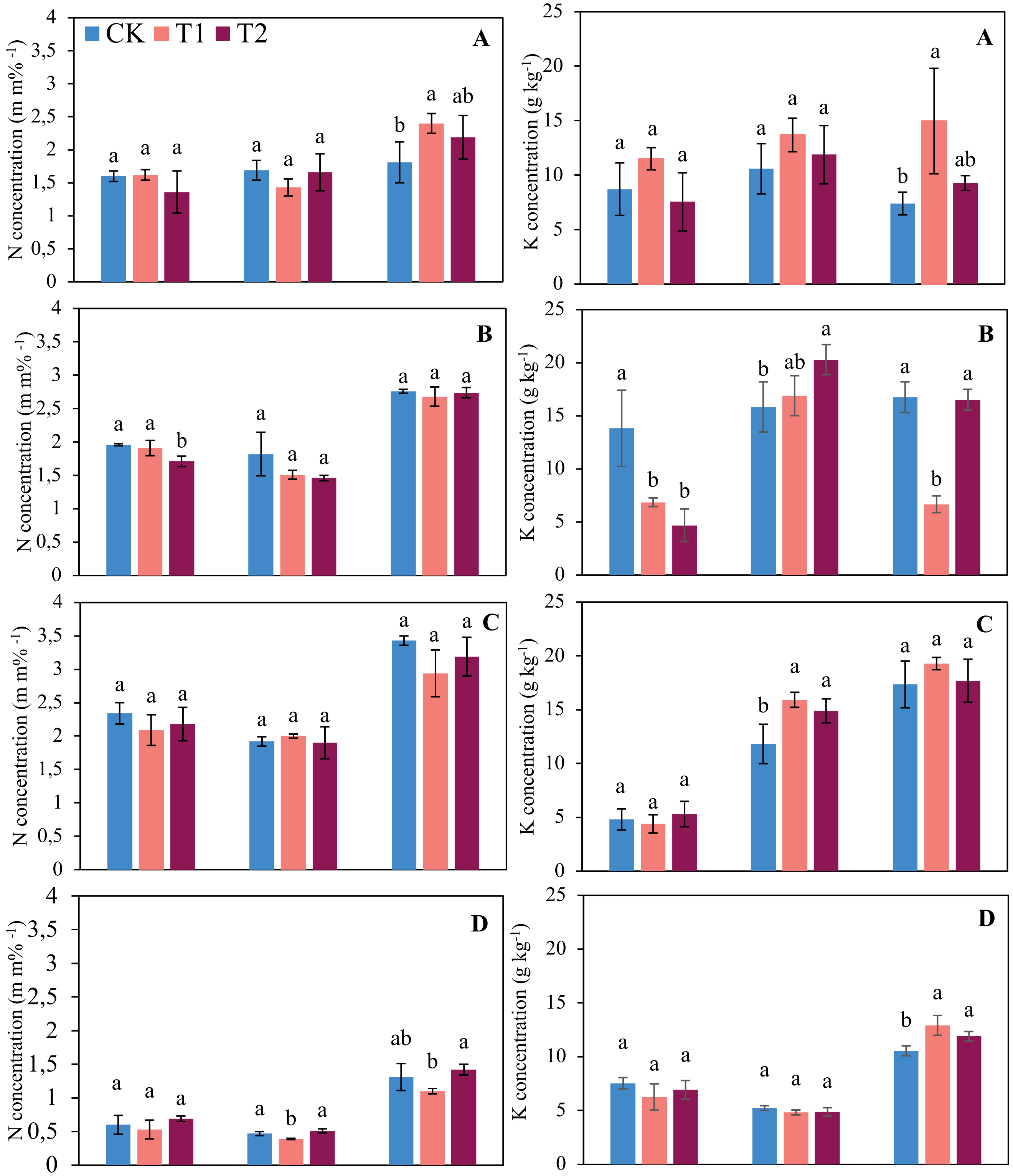


Figure 10. N (left) and K (right) concentrations in the roots, branches and leaves of each plant (A: Moso, B: *D. asper*, C: ‘Csala’, D: ‘Tora’, E: ‘Pegaso’). Different lowercase letters indicate significant differences in the concentration of the same organ ($p < 0.05$).

Figure 10 showed that leaves are the main nutrient regulatory organs of most plants under Cd stress. Except for ‘Csala’, the N and K concentrations in the T2 treatment were higher than those in the other treatments. In contrast, the N and K concentrations in the roots and branches changed slightly, with no significant differences or only slight changes between treatments, indicating their stability under Cd stress. The response patterns of different plants also showed species specificity. For example, Tora showed a strong Cd treatment difference in N and K in all organs (Fig. 10D). Under treatment T2, the leaf N concentration and leaf K concentration increased by 0.35 times and 0.31 times compared to CK, indicating that it has strong adaptability and regulatory ability to Cd stress; while Moso and *D. asper* only showed a significant increase in N concentration in the leaves, but no significant difference in the roots and branches (Fig. 10 A,B left). In addition, the LN concentration of ‘Csala’ and ‘Pegaso’ was significantly lower than that of the other treatments in the T2 treatment, 0.76 times and 0.75 times lower than the CK group, respectively. Overall, the effects of Cd treatment on plant N and K concentrations are organ- and species-specific. The key role of leaves in nutrient transport and metabolic activity makes them the most sensitive part under Cd stress.

4.1.6 N and K content of different organs (2023)



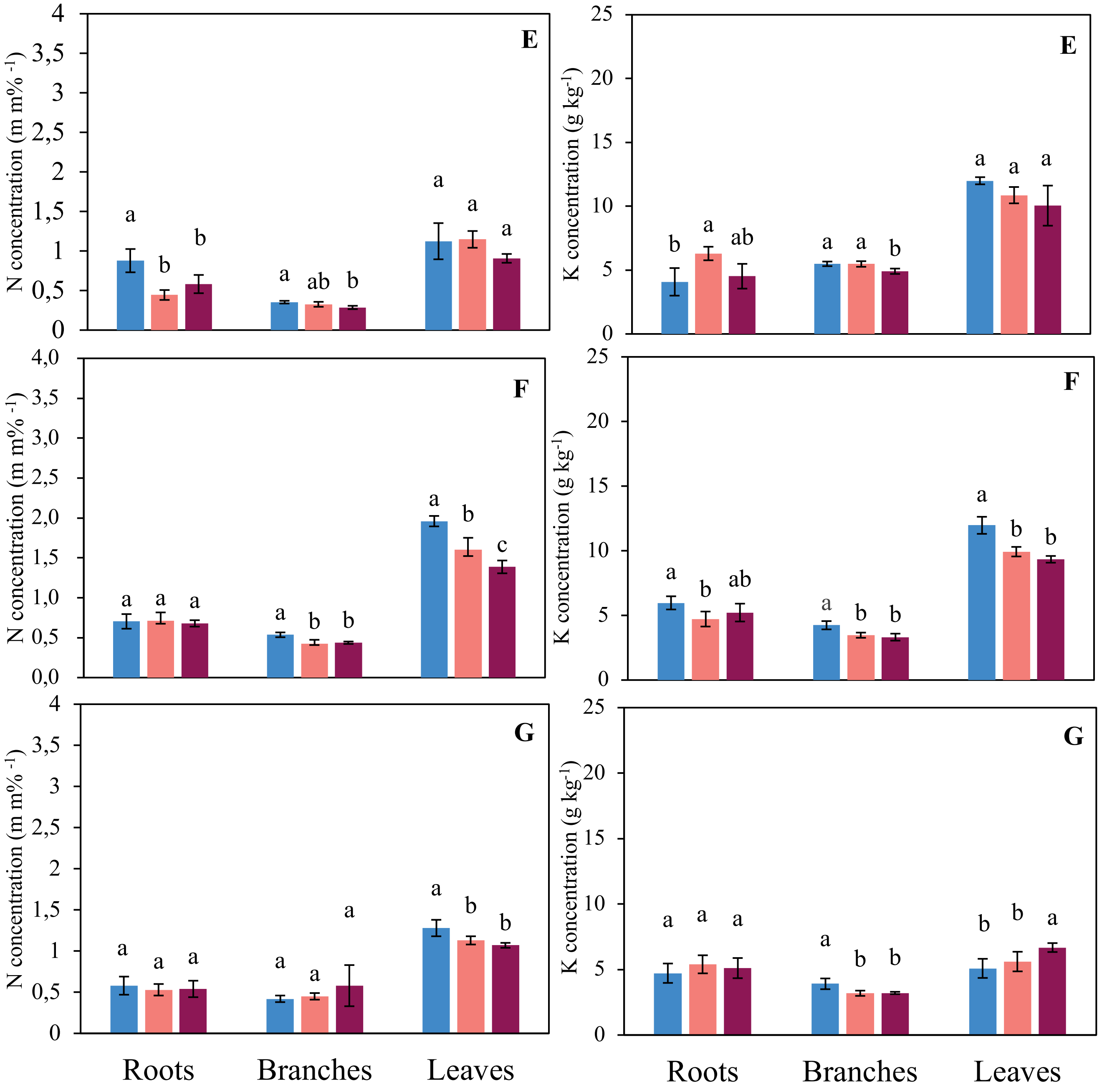


Figure 11. N (left) and K (right) concentrations in the roots, branches and leaves of each plant (A: Moso, B: *D. asper*, C: *D. strictus*, D: 'AF2', E: 'Pegaso', F: 'Csala', G: 'Tora'). Different lowercase letters indicate significant differences in the same organ at different concentrations ($p < 0.05$).

In the second year, the experiment was not affected by high temperatures, the experimental environment was more stable, the data trends were clearer, and most plants did not show significant differences under each treatment. This may be due to the relatively stable mineral element storage and transport functions of roots and branches, which make their response to Cd stress less obvious than that of leaves. The results in Figure 11 show that the significant differences in N and K concentrations were mainly concentrated in the leaves, while the roots and branches showed smaller changes. Among the leaves, only the N content of two willow species ('Csala' and 'Tora') was significantly affected by Cd concentration, which was 0.7 times and 0.83 times lower than that of CK at T2 concentration, respectively. However, the change in K concentration was more significant. The K concentration in the leaves of Moso and *D. asper* showed opposite trends of first increasing and then decreasing, and first decreasing and then increasing, respectively. Under the T1 treatment, the K concentration in Moso was 0.5 times higher than that in CK. Similarly, this opposite trend was also found in 'Csala' and 'Tora', which may be related to the fact that different plants may adopt different mineral nutrient regulation mechanisms to maintain cell ion balance and metabolic needs when responding to Cd stress.

4.1.7 Effect of Cd on NO_2+NO_3-N, K content in rhizosphere soil of different plants

Table 11 shows the effects of different plants, Cd treatments and their interactions on soil NO_2+NO_3-N and K content in the 2022 and 2023 years.

Table 11. Analysis of variance table for the effects of Cd treatment and plant species (two-way ANOVA) on soil NO_2+NO_3-N and K content

	Soil	Variant Source	Sum of Squares	df	Mean squares	F value	P value
2022	NO_2+NO_3-N	Plants	90156.727	4	22539.182	133.160	<0.001
		Treatments	4994.875	2	2497.437	14.755	<0.001
		Plants ×Treatments	15242.388	8	1905.298	11.256	<0.001
	K	Plants	5.047	4	1.262	53.924	<0.001
		Treatments	0.693	2	0.346	14.801	<0.001
		Plants ×Treatments	0.987	8	0.123	5.270	<0.001
2023	NO_2+NO_3-N	Plants	587277.467	6	97879.578	294.118	<0.001
		Treatments	3746.799	2	1873.399	5.629	0.007
		Plants ×Treatments	48761.156	12	4063.430	12.210	<0.001
	K	Plants	7.619	6	1.270	87.823	<0.001
		Treatments	0.017	2	0.008	0.585	**0.561**
		Plants ×Treatments	0.409	12	0.034	2.360	0.020

In the first year, the effects of plants on soil NO_2+NO_3-N and K were both significant ($F = 133.160$ and 53.924, $P < 0.001$), indicating that plants are an important factor affecting soil nutrient cycling. The effects of the Cd treatment were also significant for both nutrients ($F = 14.755$ and 14.801, $P < 0.001$), reflecting the Cd treatment's alteration of the soil nutrient distribution pattern. The significance of the interaction between plants and treatments for the two nutrients ($F = 11.256$ and 5.270, $P < 0.001$) indicates that there are significant differences in the response of different plants to Cd stress, which may be related to species-specific absorption mechanisms and the ability to adapt to Cd stress.

In the second year, the experimental environment was more stable, and the effect of plants was further enhanced. The significance of the effects of plants on soil NO_2+NO_3-N and K content was higher than in the first year ($F = 294.118$ and 87.823, $P < 0.001$), indicating that the dominant role of interspecific differences among plants on soil nutrient dynamics became more obvious. In contrast, the effect of the Cd treatment on NO_2+NO_3-N was significantly weaker ($F = 5.629$, $P = 0.007$), and the effect on K was not even significant ($F = 0.585$, $P = 0.561$), possibly because the stable environmental conditions reduced the direct disturbance of the soil by Cd. In addition, the interaction between plants and treatments increased significantly for NO_2+NO_3-N ($F = 12.210$, $P < 0.001$) and decreased for K ($F = 2.360$, $P = 0.020$). This trend indicates that in the second year, the response of different plants to Cd treatment is more likely to be reflected in changes in NO_2+NO_3-N, while the dynamics of K is more dependent on the characteristics of the plant itself.

4.1.7.1 Soil NO_2+NO_3-N and K content at different Cd treatment concentrations (2022)

Figure 12 shows the changes in NO_2+NO_3-N and K content in the soil of five plants treated with Cd in 2022.

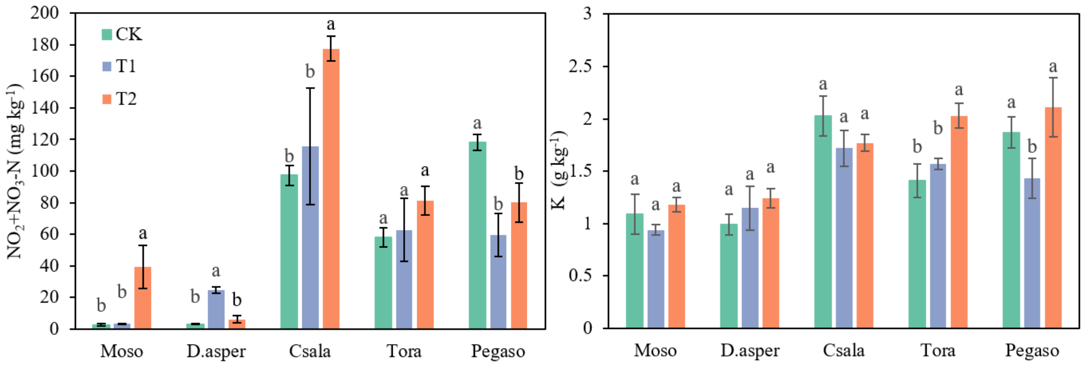


Figure 12. Soil NO_2+NO_3-N (left) and K (right) content under different Cd concentrations. Different lowercase letters indicate significant differences ($p < 0.05$) in the same organ under different concentrations.

The soil NO_2+NO_3-N of *Salicaceae* plants was significantly higher than that of *Bambusoideae* plants. Moso and ‘Csala’ showed a significant increase in response to high Cd concentration (T2) treatment. Under T2 treatment, the $NO_2^- + NO_3^-$-N content of Moso and ‘Csala’ was 10.9 times and 1.53 times higher than that of T1, respectively, reflecting the fact that high Cd concentration may enhance its ability to affect soil nitrogen cycling. In contrast, there was no significant change in soil NO_2+NO_3-N under each treatment of ‘Tora’. In addition, the soil K content of Moso, *D. asper* and ‘Csala’ did not change significantly with the increase of Cd concentration, while the soil K content of Tora increased slightly under treatment T2, which was 1.44 times and 1.29 times higher than that of the CK and T1 groups, respectively, reaching a significant level.

4.1.7.2 Soil NO_2+NO_3-N and K content at different Cd treatment concentrations (2023)

Figure 13 shows the changes in NO_2+NO_3-N and K content in the soil of seven plants treated with Cd in 2023.

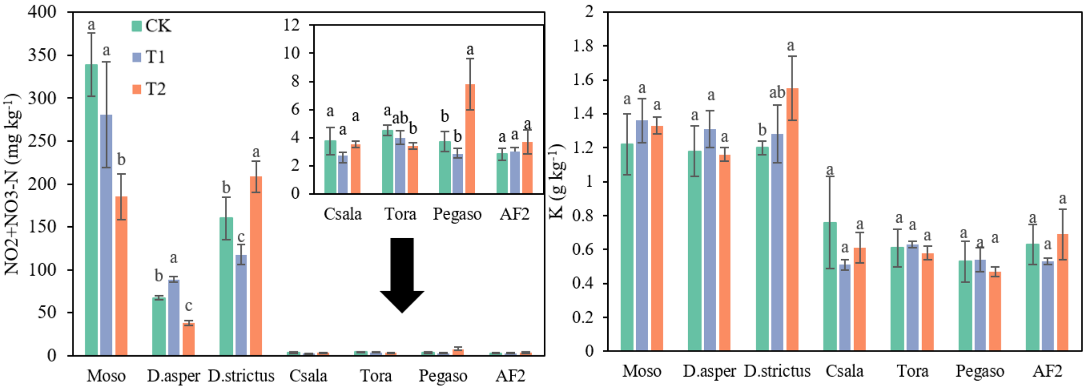


Figure 13. Soil NO_2+NO_3-N (left) and K (right) content under different Cd concentrations. Different lowercase letters indicate significant differences ($p < 0.05$) in the same organ under different concentrations.

Interestingly, the soil NO_2+NO_3-N content in the second year showed the opposite trend to the first year, with the *Bambusoideae* plants showing significantly higher values for both parameters than the *Salicaceae* plants. Among these, Moso had the highest value in the CK group, and decreased significantly with increasing Cd concentration. In addition, *D. asper* and *D. strictus* also showed a trend of first increasing and then decreasing, and first decreasing and then increasing, respectively. Among the *Salicaceae* plants, 'Tora' and 'Pegaso' showed a significant decrease and increase, respectively, at the T2 concentration compared to CK, while the other two plants showed no significant changes. Similarly, the soil K content of the *Bambusoideae* plants was also significantly higher than that of the four *Salicaceae* plants, but only *D. strictus* showed a significant difference at the T2 concentration.

4.1.8 Bioaccumulation and translocation parameters

4.1.8.1 TF and BCF(2022)

Table 12. TF and BCF values of plants under different Cd treatments

		Moso	*D. asper*	'Csala'	'Tora'	'Pegaso'
TF	CK	1.99±0.07a	1.81±0.06a	2.27±0.09b	2.11±0.06a	2.24±0.17ab
	T1	0.96±0.08b	0.55±0.05b	2.09±0.31b	2.38±0.38a	2.74±0.4a
	T2	1.27±0.38b	0.49±0.09b	4.15±0.62a	2.56±0.27a	1.95±0.2b
BCF$_r$	CK	0.97±0.04a	0.99±0.02a	0.98±0.01a	1.01±0.01ab	1.48±0.01a
	T1	0.45±0.09b	0.57±0.04b	0.73±0.12b	1.1±0.09a	1.01±0.05b
	T2	0.14±0.03c	0.45±0.09c	0.41±0.06c	0.86±0.14b	0.86±0.18b
BCF$_b$	CK	0.96±0.04a	0.89±0.03a	0.81±0.14a	1.02±0.02a	1.82±0.32a
	T1	0.26±0.07b	0.16±0.03b	0.51±0.09a	0.95±0.06a	1.39±0.34ab
	T2	0.09±0.01c	0.12±0.04b	0.73±0.2a	0.73±0.07b	0.81±0.3b
BCF$_l$	CK	0.97±0.02a	0.91±0.03a	1.41±0.06a	1.11±0.03a	1.49±0.13a
	T1	0.18±0.06b	0.15±0.02b	1±0.08b	1.64±0.19a	1.39±0.06a

T2	0.07±0.01c	0.1±0.02c	0.99±0.19b	1.46±0.27ab	0.87±0.13b

Note: Different lowercase letters indicate significant differences ($p < 0.05$) in the same plant at different concentrations.

In general, the TF values of *Salicaceae* plants were significantly higher than those of bamboo plants (Table 12). Csala had a TF value (4.15±0.62) under treatment T2 that was much higher than that of other plants, indicating that it has a stronger ability to transport Cd under high Cd concentrations. The TF values of the plants in the *Bambusoideae* decreased significantly under both T1 and T2 treatments. For example, the TF values of Moso under T1 and T2 treatments were 0.96±0.08 and 1.27±0.38, respectively, which were significantly lower than those of the control group (1.99±0.07), indicating that high Cd concentrations inhibit the transport capacity of plants in the bamboo family.

In addition, the increase in Cd concentration resulted in a significant decrease in the BCF values of the roots (BCF_r), branches (BCF_b) and leaves (BCF_l) of all plants, but the trends differed among plants and organs. The BCF_r and BCF_l of *Salicaceae* plants remained at a high level under treatment T1. For example, the BCF_r of 'Tora' under treatment T1 reached 1.1±0.09, which was significantly higher than that of other plants. Similarly, the BCF_l values of the leaves of 'Tora' and 'Pegaso' were also significantly higher than those of the plants in the *Bambusoideae* under treatment T1, indicating their stronger ability to accumulate Cd at low concentrations. In contrast, the BCF values of the plants in the *Bambusoideae* decreased sharply under treatment T2, showing a significant decrease in Cd tolerance. For example, the BCF of Moso decreased from 0.97±0.02 in the control group to 0.07±0.01 in T2, and *D. asper* showed a similar trend.

4.1.8.2 TF and BCF(2023)

Table 13. TF and BCF values of plants under different Cd treatments

		'Pegaso'	'AF2'	'Csala'	'Tora'	*D. strcitus*	*D. asper*	Moso
TF	CK	1.72±0.1a	4.92±1.35a	4.25±1.04a	2.95±0.1a	1.14±0.52ab	1.7±0.65a	0.86±0.45a
	T1	1.44±0.47b	4.56±0.52a	3.07±0.67a	1.49±0.45b	2.36±1.06a	0.46±0.25b	1.88±1.11a
	T2	1.17±0.36b	4.68±0.68a	3.03±0.35a	1.23±0.06b	0.87±0.33b	0.32±0.19b	0.73±0.22a
BCF_r	CK	1.45±0.02a	0.72±0.46a	1±0.35a	2.37±1.31a	1.6±0.79a	2.33±0.4a	2.43±0.73a
	T1	0.48±0.11c	0.33±0.09a	0.89±0.36a	1.28±0.36ab	0.19±0.01b	0.27±0.16b	0.32±0.02b
	T2	0.78±0.18b	0.22±0.01a	0.39±0.1a	0.58±0.11b	0.52±0.27b	0.29±0.15b	0.25±0.07b
BCF_b	CK	2.78±0.28a	1.83±0.65a	1.65±0.34a	3.91±2.54a	0.84±0.18a	1.71±0.11a	1.18±0.51a
	T1	0.74±0.07b	0.79±0.19b	1.3±0.53a	1.1±0.13ab	0.35±0.16b	0.05±0.01b	0.42±0.33b
	T2	0.78±0.18b	0.47±0.02b	0.54±0.21b	0.47±0.1b	0.49±0.18b	0.05±0.01b	0.12±0.03b
BCF_l	CK	2.51±0.18a	1.42±0.81a	2.37±0.18a	3.16±1.75a	0.71±0.1a	2.13±1.08a	0.69±0.12a
	T1	0.66±0.07b	0.7±0.16a	1.37±0.45b	0.72±0.29b	0.09±0.01b	0.04±0.01b	0.15±0.03b
	T2	0.87±0.11b	0.56±0.07a	0.64±0.08c	0.24±0.02b	0.03±0.01b	0.02±0.01b	0.05±0.01b

Note: Different lowercase letters indicate significant differences ($p < 0.05$) in the same plant at different concentrations.

Table 13 reveals the significant species-Cd transport and accumulation capacities of plants under Cd stress. *Salicaceae* plants generally have higher TF values than those of bamboo subfamily plants and exhibit stronger transport capacities at T2 concentrations. 'AF2' and 'Csala', with TF values of 4.68 and 3.03 under the T2 treatment, respectively, showed no significant decreases compared to CK. However, the TF values of plants in the bamboo subfamily decreased more significantly. For example, the TF value of *D. asper* decreased from CK to T2 about 5 times; while the TF value of Moso first increased and then decreased with the increase of Cd concentration, indicating that the transport inhibition of bamboo subfamily plants by high Cd concentration is more significant.

In addition, an increase in Cd concentration generally leads to a decrease in BCF_r, BCF_b, and BCF_l, but the performance of different plants significantly. In the roots, the BCF_r of *Salicaceae* plants at T1 concentration is relatively high. For example, the BCF_r value of 'Tora' decreased from 2.37 in CK to 1.28 in T1, a decrease of about 2 times; it further decreased to 0.58 under T2 treatment, a decrease of about 4 times overall. The BCF_r of the roots of *Bambusoideaed* plants showed a more drastic decrease at high Cd concentrations. The BCF_r of Moso decreased nearly 10 times from CK to T2. The BCF_l value was also significantly inhibited by high Cd concentrations. For instance, 'Csala' decreased 3.7 times from CK to T2. The BCF_l values of bamboo subfamily at high Cd concentrations were close to the lowest levels. Moso decreased from 0.69 in CK to 0.05 in T2, a decrease of about 14 times, and the BCF_l of *D. asper* decreased from 2.13 in CK to 0.02 in T2, a decrease of about 107 times.

4.1.9 Discussion

4.1.9.1Uncertainty in phytoremediation due to differences in field environments

The practical application of phytoremediation technology is often significantly affected by environmental conditions in the field. The physical and chemical properties of the soil, climatic conditions and the composition of the microbial community can lead to significant differences in the efficiency of phytoremediation. For example, due to heavy rainfall, the soil pH in a rapeseed-rice rotation Cd remediation system decreased significantly in the second year of the three-year rotation, resulting in an increase in bioavailable Cd. The Cd accumulated by rice exceeded the threshold of 0.2 mg kg^{-1} (Li et al., 2024). Similarly, the sensitivity of different plants to temperature resulted in large differences in their accumulation capacity in phytoremediation (Rahman et al., 2021). Previous studies have shown that *Sedum alfredii*, under Cd stress, exhibited significantly enhanced heat tolerance. While high temperatures impair stomatal function, chloroplast structure, and photosynthesis, they also increase survival rates and Cd accumulation capacity (Xu et al., 2023). The synergistic effects of heat and metal stress likely activate antioxidant enzymes, promote plant hormone synthesis, and upregulate gene expression. In this dissertation, there was a significant difference in Cd accumulation between the first-year and second-year plants. High temperatures caused high mortality during rooting in two plants (*D. strictus* and 'AF2'), but stimulated Cd accumulation in other plants. In my dissertation, all plants showed high total Cd accumulation in all treatments in the first year, which may be related to the multiple effects of high temperature on plant metabolism and the soil environment. On the one hand, the enhanced transpiration of plants under high temperature conditions accelerates the transport of water and solutes, making it easier for Cd to be transported from the soil to the aboveground parts of the plant (Lin et al., 2024). On the other hand, high temperature may increase the bioavailability of Cd by promoting the secretion of root exudates and changing the rhizosphere environment. Previous studies have shown that Rahman et al., (2021) observed that the three As hyperaccumulating plants, *Pteris multifida*, *Pteris cretica* and *Pteris vittata*, had a significantly increased accumulation capacity at 25°C than at 10°C, and a large amount of As accumulated in the leaves accumulated a large amount of As. In addition, the remediation efficiency of water hyacinth was significantly higher than that at 12–15°C, and the biomass also increased significantly in the range of 15-25°C water temperature (Wang et al., 2013). In addition, the uncertainty of phytoremediation in the field is further exacerbated by the differences in the response of different species to high temperatures. The effects of high temperatures may have stimulated the *Salicaceae* to break through the accumulation threshold. Under treatment T2, the accumulation of *D. asper*, 'Csala', 'Tora' and 'Pegaso' in the first year was significantly higher than that of CK and T1, but in the second year we found that except for Csala, there was no significant difference in accumulation between T2 and T1 (Table 8). This may be due to the different responses of different species to high temperatures. 'Csala' still maintained a significant Cd accumulation capacity in the second year, which may be related to its unique metabolic adaptation mechanism.

It is worth noting that there was a significant difference in soil N and K content between the two years. The N and K content of the rhizosphere soil of *Salicaceae* plants was higher than that of *Bambusoideae* plants in the first year. Temperature not only alters plant uptake of soil nutrients such as nitrogen and potassium but also affects soil potassium mobility. High temperatures accelerate potassium mobility in soil (Guerin et al., 2024). When Cd^{2+} is present, competition between Cd^{2+} and K^+ for uptake increases potassium accumulation and concurrently enhances Cd accumulation in willow and poplar species (Haider et al., 2021). This competitive uptake explains why no significant differences in soil potassium were observed under Cd treatments during non-heat-stress years. Interestingly, bamboo exhibited significantly higher NO_2+NO_3-N content than poplar and willow under non-high-temperature conditions but reversed this trend under high-temperature conditions. It is hypothesized that, under non-heat-stress conditions, bamboo rhizosphere microbiota is dominated by nitrifying bacteria, which promote the conversion of NH_4^+ to NO_3^-, while denitrifying bacterial activity remains low, leading to NO_2^- and NO_3^- accumulation in soil (Bian, et al., 2023). Conversely, poplar and willow likely exhibit higher direct absorption of NO_2^- and NO_3^- and utilize rhizosphere metabolism to convert NO_2^- and NO_3^- into plant-available organic nitrogen, reducing soil accumulation (Istenič & Božič, 2021).

However, the opposite was true in the second year, and the soil N content of *Bambusoideae* plants was much higher than that of *Salicaceae* plants. My finding suggests that this phenomenon may be related to the multiple effects of environmental conditions on the plant rhizosphere microbial community, nutrient cycling, and plant physiological metabolism. The high temperature conditions in the first year may have promoted root activity and the metabolism of rhizosphere microorganisms in *Salix* plants, thereby enhancing the release and transformation of nitrogen and potassium in the soil. This transformation may be achieved through two main mechanisms: first, root exudates (such as organic acids) increase the release of insoluble potassium in the soil and promote the mineralization of organic nitrogen; second, high temperatures accelerate the activity of specific functional bacteria (such as nitrogen-fixing bacteria and potassium-solubilizing bacteria) in the microbial community, thereby further increasing the bioavailability of N and K (Chen et al., 2024). In contrast, the bamboo subfamily may have lower rhizosphere N and K content in the first year due to lower root metabolic activity and relatively conservative resource utilization strategies. However, in the second year, when environmental conditions are milder, the *Bambusoideae* gradually takes advantage of its stronger root system density and absorption capacity. Its rhizosphere microbial community may change under a more stable climate, more effectively converting organic nutrients in the soil into forms that are available to plants, while reducing N and K loss (Lin et al., 2024). Bamboo plants have a denser root network and wider coverage and may be better adapted to lower temperatures than *Salicaceae* plants. In addition, Salix spp. have a lower Cd accumulation capacity in the second year compared to the first year, which may lead to a reduction in the activity of rhizosphere microorganisms and indirectly affect the efficiency of N and K cycling. Studies have shown that the absorption of heavy metals by plants and metabolic stress may change the chemical balance of the rhizosphere environment, thereby affecting the dynamic distribution of nutrients in the rhizosphere (Yuan et al., 2022).

4.1.9.2 Species accumulation specificity of the *Bambusoideae* and *Salicaceae*

Bambusoideae and *Salicaceae* showed significant differences in Cd accumulation capacity and its distribution mode in plants, which reflected the fundamental differences in physiological characteristics and metabolic mechanisms between the two groups of plants. In addition to temperature effects, the total Cd accumulation in plants varies significantly depending on Cd treatment, plant species, and plant organs (Table 7). Specifically, total Cd accumulation increases with higher Cd concentrations. Willow and poplar species exhibit higher Cd accumulation compared to *Bambusoideae* species, with bamboo concentrating Cd primarily in roots, whereas willow and poplar accumulate it in leaves. These findings align with those of Bian et al., (2020) and Liang et al., (2022).

This study showed that the Cd accumulation in *Bambusoideae* was mainly in the roots, and the aboveground accumulation was significantly lower than that in willow plants, which was mainly related to the differences in root structure, metabolic strategies and nutrient allocation mechanisms between the two groups of plants. *Bambusoideae* plants usually have a dense root network with a wider inter-root coverage, which enables them to absorb and fix Cd more efficiently; however, this resource utilization strategy tends to restrict Cd to the roots and reduce the translocation of Cd to the aboveground parts of the plant. This ‘low translocation -high fixation’ mechanism helps bamboo subfamily plants to reduce the toxic effects of Cd on photosynthesis and other physiological processes in polluted environments and thus maintain a high level of tolerance. For example, Li et al., (2016) showed that the concentration of MDA content in Cd-treated moso bamboo leaves increased significantly, and antioxidant enzymes, such as SOD, POD, and CAT, all showed a trend of increasing and then decreasing with the increase of Cd concentration, and that the cytoplasm of the root was the main accumulation site of Cd in moso under the treatment of 25 μM Cd. In addition, Li et al., (2015) observed that moso bamboo transported Cd to aboveground parts via the xylem, with detoxification mechanisms including chelation via plant chelating peptides or vesicular compartmentalization. However, this strategy also limits the amount of Cd accumulated by *Bambusoideae* in above-ground parts, resulting in a relatively low total Cd accumulation capacity. Recent studies have shown that through this mechanism, Emamverdian, et al., (2023) used melatonin and zeolite to significantly increase plant nutrients in soil under Cd stress in *Sasa kongosanensis*, resulting in increased plant nutrient utilization, reduced Cd uptake and increased osmotic pressure accumulation. This study also provides novel insights into the Cd accumulation and translocation capacities of *D. asper* and *D. strictus* under Cd stress. Like Moso bamboo, these species exhibited strong root fixation capacities and low translocation efficiency to aboveground tissues. This behavior may be attributed to the effective fixation of Cd by pectin and the polysaccharide matrix in the cell walls, which restricts Cd mobility. Additionally, vesicular sequestration further mitigates Cd toxicity by chelating it into organic acids or metallothionein within vesicles, thereby protecting organelles from damage. The "low translocation -high fixation" strategy of the bamboo subfamily reflects its conservative resource utilization approach. Instead of promoting Cd translocation to aboveground tissues, these plants prioritize enhanced antioxidant enzyme activity, such as SOD and CAT, to mitigate Cd-induced ROS accumulation.

In contrast to the *Bambusoideae*, *Salicaceae* exhibits a strong capacity for aboveground Cd enrichment, following a ‘high translocation -high accumulation’ strategy. Once Cd enters the root xylem, it is efficiently transported to the aboveground parts of the plant via transpiration pull, a process closely linked to the activity of metal transporter protein systems (Guo et al., 2022). This study demonstrated that Cd treatment did not significantly inhibit plant growth across all concentrations, and a relatively stable proportion of Cd was translocated from roots to aboveground organs. ‘Csala’ consistently displayed stable TF values across years and treatments. Similarly, the BCF_r, BCF_l, and TF values of ‘AF2’ were not significantly affected by Cd exposure, while ‘Pegaso’ and ‘Tora’ showed higher TF and BCF values compared to bamboo plants (Fig. 13).

Cd uptake by root tips and root hairs is primarily regulated by the activities of ZIP/IRT and Nramp proteins. Hu et al., (2022) demonstrated that overexpression of the *SlPCR6* gene from *S. linearistipularis* in transgenic poplar significantly improved Cd resistance. These transgenic poplars exhibited reduced net uptake of Cd and Cu by roots compared to wild-type plants. Similarly, Yu et al., (2022) identified eight putative *PcNRAMP* genes in poplar, most of which were predominantly expressed in roots. Overexpression of *PcNRAMP1* increased net Cd^{2+} influx by 39–52% in poplar roots and boosted Cd accumulation in aboveground parts by 25–29%. Upon Cd entry into the plant, highly expressed transporter proteins, including Zn/Fe-regulated transporter protein-like proteins, natural resistance-associated macrophage proteins, and plasma membrane heavy metal ATPases, facilitate the efficient translocation of Cd to aboveground tissues (Zou et al., 2023).

The specificity of Cd accumulation and translocation in *Bambusoideae* plants and poplar plants reflects their different adaptation strategies. Bamboo subfamily plants show high tolerance by fixing Cd in their roots and are suitable for phytostabilization of contaminated sites. In contrast, poplars can rapidly absorb and translocate Cd and have a significant advantage in phytoextraction.

4.1.9.3 Species-specific response of nutrients between plants and organs

The results showed that there was no significant difference in total N content between the first and the second year in the *Salicaceae* (Table 6), but there was a significant difference in the *Bambusoideae* (Moso and *D. asper*), and both species of bamboos had lower total N content in the first year than in the second year (Table 6), which may be attributed to the fact that high-temperature conditions exacerbate oxidative stress and inhibit the activities of nitrate transporter proteins (NRT) (Xu et al., 2020) and ammonium transporters (AMT) (Wang et al., 2022), thus reducing plant uptake of nitrate N (NO_3^-) and ammonium N (NH_4^+). High temperatures in the first year may also disrupt nitrogen metabolism by inhibiting the activities of key nitrogen metabolism enzymes, such as nitrate reductase and glutamine synthetase, as well as by inducing the accumulation of ROS in Moso and *D. asper*, which reduces the efficiency of nitrate reduction and ammonium assimilation capacity (Pilipović et al., 2019). Plants consume more nitrogen for the synthesis of antioxidant enzymes and heat-stimulating proteins (HSPs) in response to high-temperature stress, thereby reducing the allocation of nitrogen resources for growth and yield formation, which further reduces nitrogen use efficiency (NUE) (Yer et al., 2018).

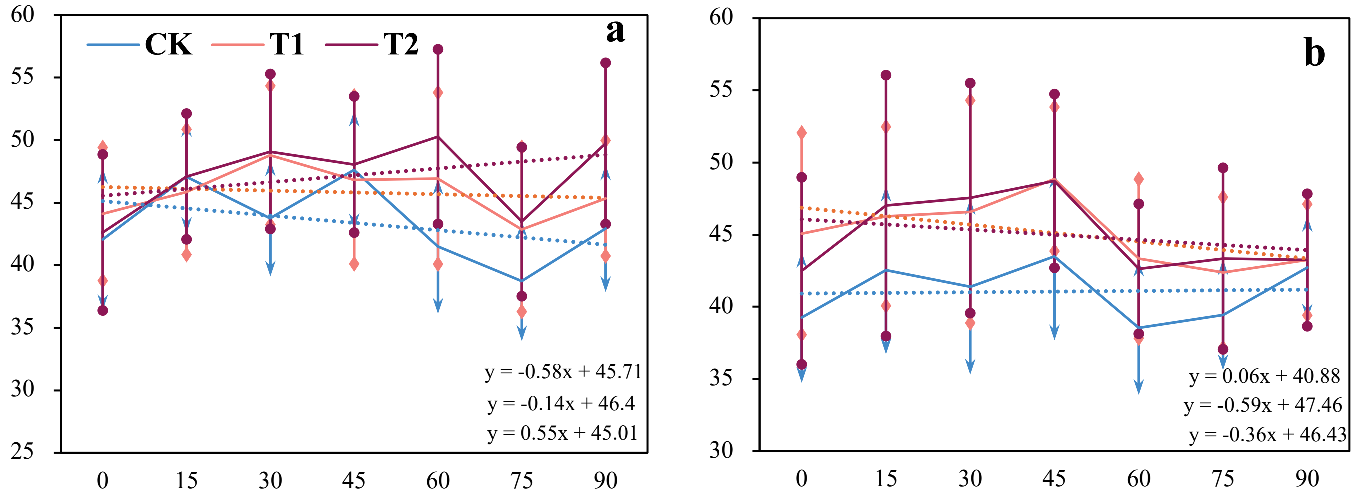
On the other hand, no significant effect of the Cd treatments on the total N content of the plants was found in this study (Table 10), while significant changes in total K content were only found in Moso and *D. asper* in the second year (Table 10). Further comparisons of N and K contents in each plant organ showed that leaves of all plants had higher N and K contents than roots and branches, and that leaves and roots were the most susceptible organs to Cd (Figures 10, 11), because leaves are the main organs of plants for photosynthesis and transpiration and thus have a higher N and K requirement. Nitrogen is an important component of chlorophyll, photosynthesis-related enzymes (e.g. Rubisco), and protein synthesis, while potassium plays a key role in stomatal regulation, water metabolism, and enzymatic reactions. Secondly, roots, as the first barrier to Cd uptake, accumulate large amounts of Cd under Cd stress and are thus directly poisoned. Oxidative damage to root cell membranes and disruption of inter-root microorganisms by Cd may also affect nitrogen cycling and potassium release, further reducing the ability of roots to accumulate N and K. The effects of Cd on root cell membranes and the destruction of inter-root microorganisms may also affect nitrogen cycling and potassium release, further reducing root N and K accumulation capacity.

LN content of all plants in the first year of the experiment was significantly affected by Cd. N content in Moso and *D. asper* leaves increased significantly with increasing Cd concentration, whereas poplars showed different response patterns. Among them, N content in ‘Tora’ leaves increased with increasing Cd concentration, while ‘Csala’ and ‘Pegaso’ showed a decreasing trend. This inconsistency reflects the differentiated response to Cd stress in *Salicaceae* under different physiological mechanisms and adaptive strategies. However, the significant changes in K content were mainly concentrated in the roots, suggesting that roots are the main target of Cd affecting K metabolism. In the second year, changes in nutrient element contents in plant organs stabilized as they were not affected by high temperature stress. Only Moso showed a significant increase in LN content under T1 treatment, whereas N content in *D. asper* and *D. strictus* leaves was insensitive to Cd treatment. In contrast, the response of the *Salicaceae* was more complex. The N content in the leaves of ‘Csala’ and ‘Tora’ decreased significantly under Cd treatment, but the magnitude and trend of the decrease did not show consistency. In addition, the LK contents of ‘Csala’ and ‘Tora’ also showed different trends of increase and decrease, further highlighting the diversity in nutrient metabolism response of poplar and willow plants. This difference may stem from the differences in strategies exhibited by *Bambusoideae* and *Salicaceae* in inter-root Cd uptake, transport and metabolism. *Bambusoideae* plants usually adopt a conservative nutrient utilization strategy by limiting the translocation of Cd to the aboveground and preferentially fixing N and K in the roots, thus reducing the toxicity of Cd to leaf photosynthesis and metabolic activities. However, this ‘high fixation-low translocation’ strategy may also limit the nutrient supply capacity of the leaves of *Bambusoideae*. Willow plants, on the other hand, tend to translocate Cd rapidly to the leaves to avoid the toxicity caused by Cd accumulation in the roots, and at the same time, they may regulate the dynamic distribution of N and K in the leaves to alleviate the disturbance of photosynthesis and metabolic activities by Cd stress.

4.2 Correlation analysis

4.2.1 Effect of Cd on physiological parameters of plant leaves

4.2.1.1 SPAD value (2022)



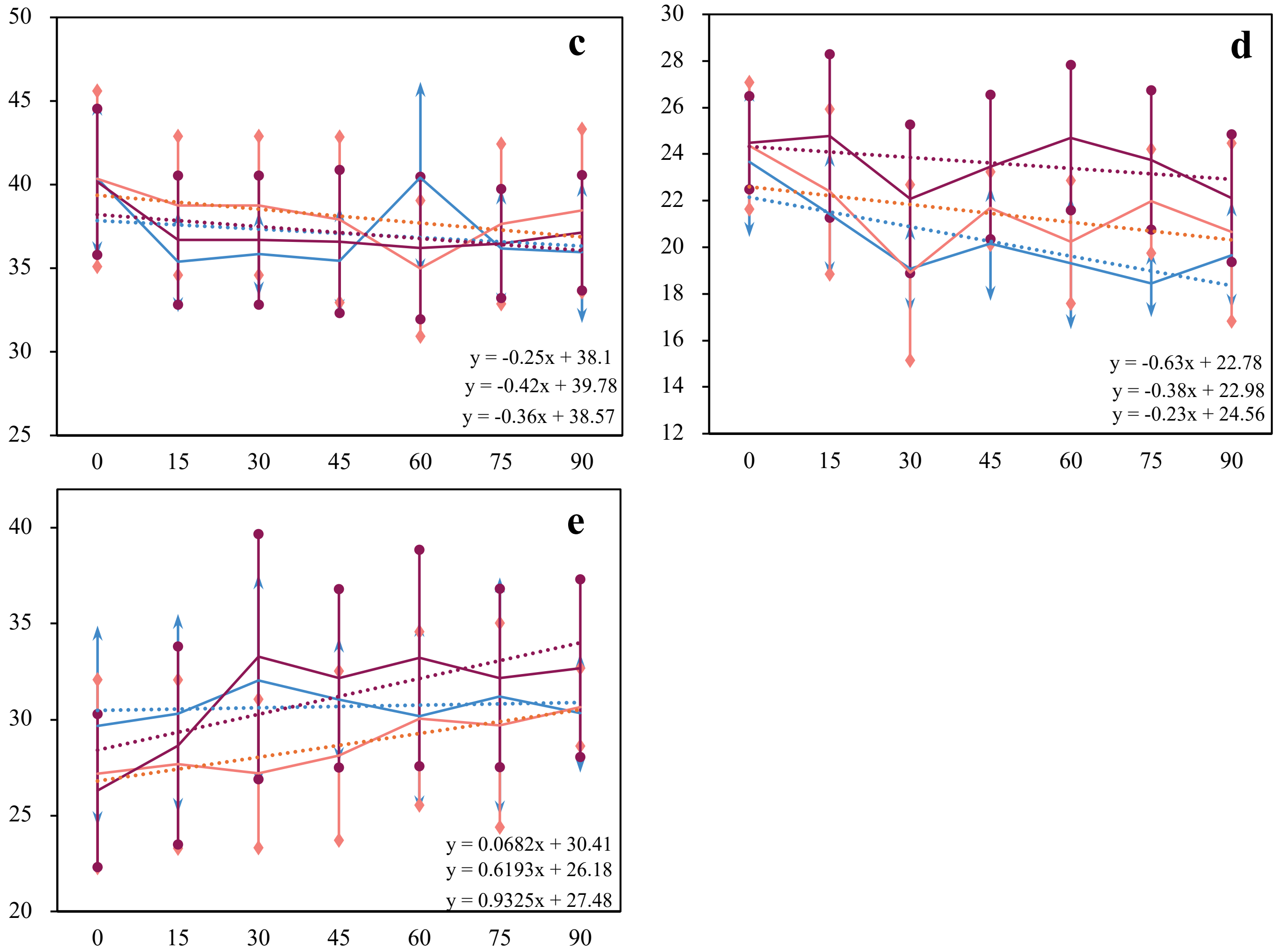
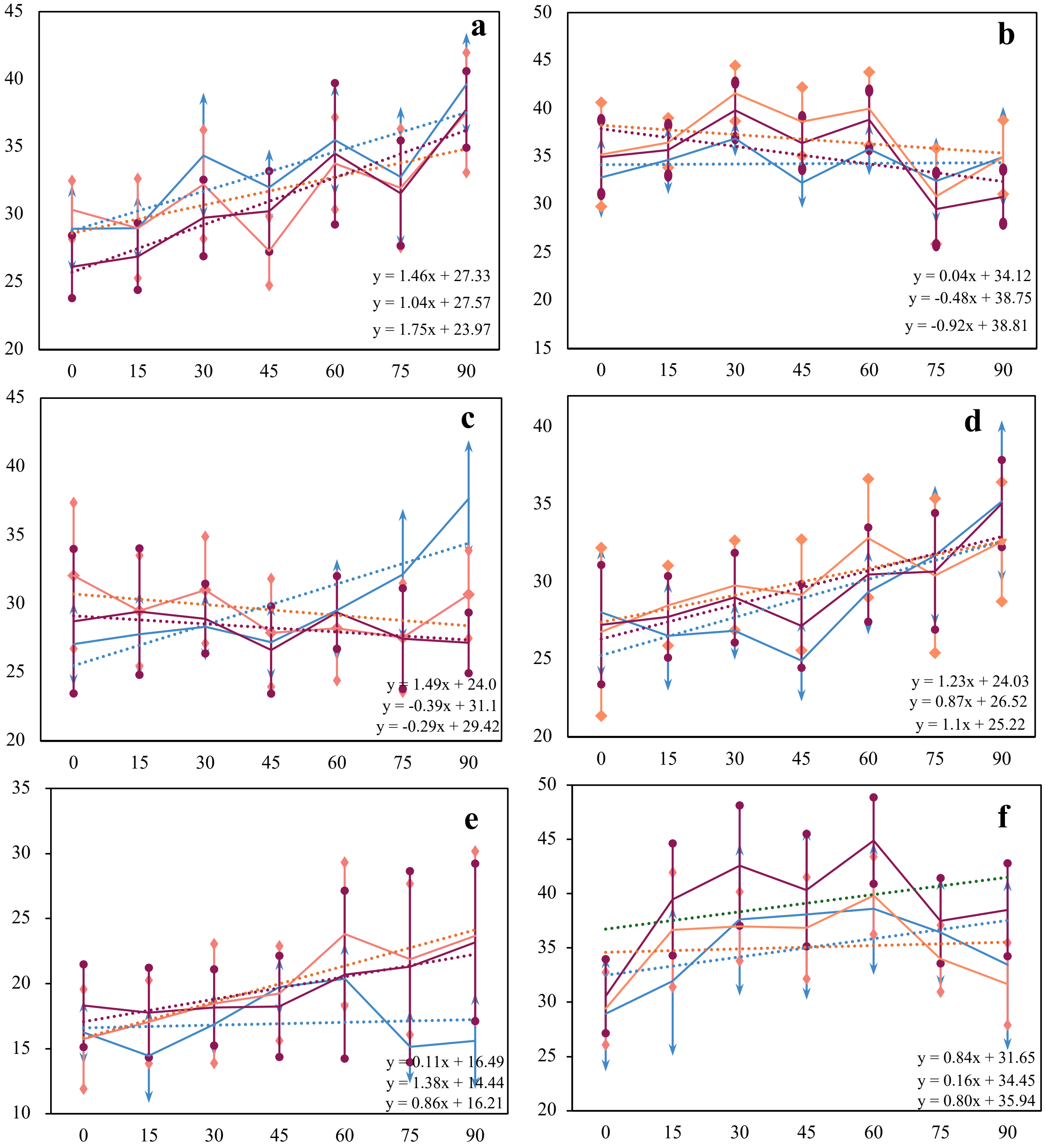


Figure 14. Changes in chlorophyll content (SPAD value) of plants at 0-90 days under different Cd concentration treatments. The values represent the average of 6 replicates n=6, (a: ‘Csala’, b: ‘Tora’, c: ‘Pegaso’, d: Moso, e: *D. asper*), the fitted equations are CK, T1, and T2, respectively.

Figure 14 reveals the different plants’ response to Cd stress. Under the CK treatment, the SPAD values of most plants decreased over time, such as ‘Csala’ (Figure 14 a) and Moso (Figure 14 d), indicating a gradual degradation of chlorophyll under natural conditions. In contrast, the SPAD value of ‘Tora’ (Figure 14 b) remained almost stable under CK, indicating a higher chlorophyll maintenance capacity. Under treatment T1, different plants showed different response mechanisms: the rate of decline in SPAD values of ‘Csala’ slowed significantly (Figure 14 a), while the decline in SPAD values of ‘Tora’ and ‘Pegaso’ was most significant (Figure 14 b and Figure 14 c), indicating that the inhibitory effect of low Cd concentrations on these plants was more . Under treatment T2, high Cd concentrations triggered a compensatory effect in some plants, such as ‘Csala’ and *D. asper* (Figure 14 a and Figure 14 e), with a significant increase in SPAD values over time, possibly due to their resistance to Cd toxicity under stress conditions by enhancing chlorophyll synthesis or antioxidant capacity. In contrast, the SPAD values of ‘Pegaso’ and Moso still showed a downward trend at T2, but the rate of decline slowed. Overall, ‘Csala’ and *D. asper* showed strong adaptability at high Cd concentrations, while ‘Tora’ and ‘Pegaso’ were more sensitive to Cd stress.

4.2.1.2 SPAD value (2023)



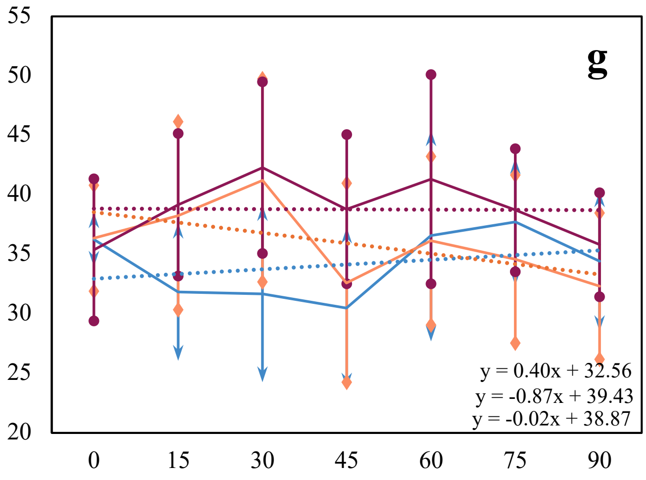
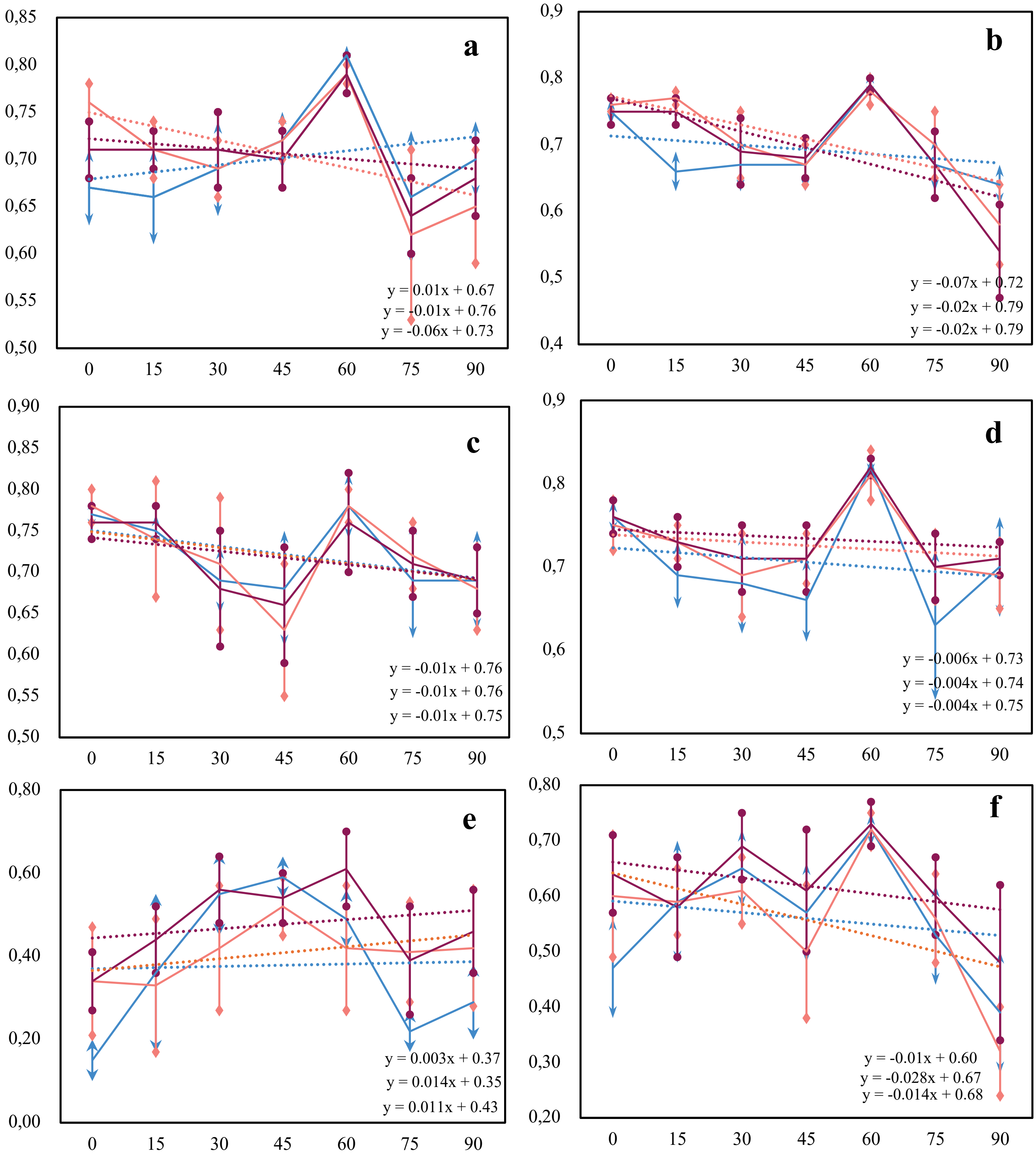


Figure 15. Changes in chlorophyll content (SPAD value) of plants from 0 to 90 days under different Cd concentrations. The values represent the average of 6 replicates n=6, (a: ‘Csala’, b: ‘Tora’, c: ‘Pegaso’, d: ‘AF2, e: Moso, f: *D. asper*, g:*D. strictus*), the fitted equations are CK, T1, and T2, respectively

Figure 15 shows the changes in SPAD values (chlorophyll content) of seven plants over 90 days under different Cd concentration treatments. Most of the plants in the CK group showed a stable increase or slight fluctuation in SPAD values over time, indicating normal accumulation of chlorophyll content under natural conditions. However, under treatments T1 and T2, different plants showed significant differences in response patterns. ‘Csala’ and *D. asper* showed significant Cd tolerance, with the fastest increase in SPAD under treatment T2. This may be related to their resistance to Cd toxicity by enhancing chlorophyll synthesis or activating antioxidant defense systems, indicating that they can effectively maintain or even improve photosynthetic efficiency at high Cd concentrations. In contrast, Tora showed a significant decrease in SPAD values under both T1 and T2, and the decrease was more pronounced at high Cd concentrations, indicating that its chlorophyll stability is more sensitive to Cd stress and has weak adaptability. In addition, ‘Pegaso’ and *D. strictus* also showed high sensitivity, especially under the T1 treatment, their SPAD values decreased significantly, indicating that low Cd concentrations have had a greater impact on their chlorophyll metabolism. In contrast, ‘AF2’ and Moso showed strong adaptability, and their SPAD values maintained an increasing trend under the T1 and T2 treatments, reflecting the fact that these two plants have good tolerance at low to moderate Cd concentrations. ‘Csala’ and *D. asper* showed outstanding Cd tolerance and exhibited a strong compensatory mechanism, while ‘Tora’, ‘Pegaso’ and *D. strictus* were more sensitive to Cd stress, especially at low Cd concentrations, where chlorophyll metabolism was significantly affected.

4.2.1.3 Quantum yield (2023)


a
0,85
0,80
0,75
0,70
0,65
0,60
0,55
0,50
0
15
30
45
60
75
90
y = 0.01x + 0.67
y = -0.01x + 0.76
y = -0.06x + 0.73
b
0,9
0,8
0,7
0,6
0,5
0,4
0
15
30
45
60
75
90
y = -0.07x + 0.72
y = -0.02x + 0.79
y = -0.02x + 0.79
c
0,90
0,85
0,80
0,75
0,70
0,65
0,60
0,55
0,50
0
15
30
45
60
75
90
y = -0.01x + 0.76
y = -0.01x + 0.76
y = -0.01x + 0.75
d
0,9
0,8
0,7
0,6
0,5
0
15
30
45
60
75
90
y = -0.006x + 0.73
y = -0.004x + 0.74
y = -0.004x + 0.75
e
0,80
0,60
0,40
0,20
0,00
0
15
30
45
60
75
90
y = 0.003x + 0.37
y = 0.014x + 0.35
y = 0.011x + 0.43
f
0,80
0,70
0,60
0,50
0,40
0,30
0,20
0
15
30
45
60
75
90
y = -0.01x + 0.60
y = -0.028x + 0.67
y = -0.014x + 0.68

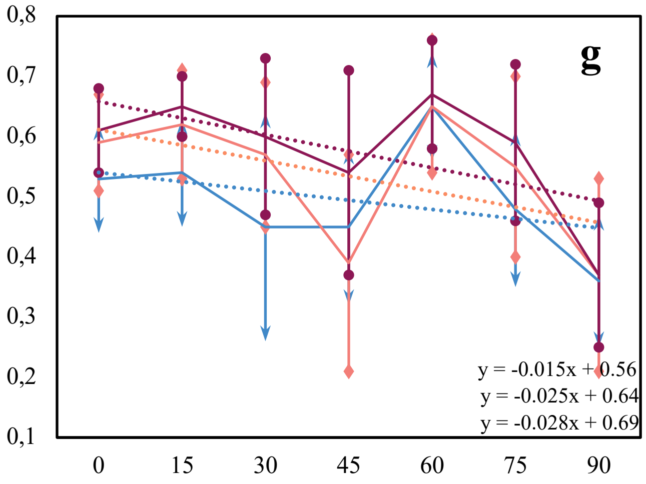


Figure 16. Quantum yield values of plants at 0-90 days under different Cd concentration treatments. The values represent an average of 6 replicates. n=6, (a: ‘Csala’, b: ‘Tora’, c: ‘Pegaso’, d: ‘AF2, e: Moso, f: *D. asper*, g:*D. strictus*), the fitted equations are CK, T1, and T2, respectively.

The trend of quantum yield under each plant treatment from 0 to 90 days is shown in Figure 16. Most plants maintained a stable or slightly fluctuating quantum yield under CK conditions, indicating that the photochemical efficiency of chlorophyll under normal photosynthetic conditions was not disturbed. However, the response patterns of each plant to Cd stress under T1 and T2 treatments showed significant species specificity. ‘Csala’ showed a slight downward trend in quantum yield under T1 conditions, while the decrease under T2 conditions increased significantly, indicating that low Cd concentrations had a limited inhibitory effect on its photosynthetic efficiency, but high Cd concentrations had a more significant negative impact on photochemical efficiency. In contrast, the trends in quantum yield changes for ‘Tora’ and ‘Pegaso’ under T1 and T2 treatments were relatively mild, indicating that these two plants had a certain degree of adaptability, as they showed little change in photosynthetic efficiency under Cd stress. ‘AF2’ and Moso showed stable or increasing trends in quantum yield under T1 and T2 conditions, respectively, indicating strong Cd tolerance. Photosynthetic compensation may have improved photochemical efficiency at low Cd concentrations. However, *D. asper* and *D. strictus* showed obvious sensitivity to Cd stress, especially under T2 conditions, where quantum yield decreased the most. This indicates that high Cd concentrations significantly inhibit the photosynthetic efficiency of these two plants, which may be related to damage to the photosystem and a decrease in photochemical efficiency.

4.2.4 Principal component analysis (PCA)

Figure 17 shows the PCA plot of each plant based on eight functional (LK, LN, BK, BN, RK, RN, SK, SN) traits in 2022 and 2023.

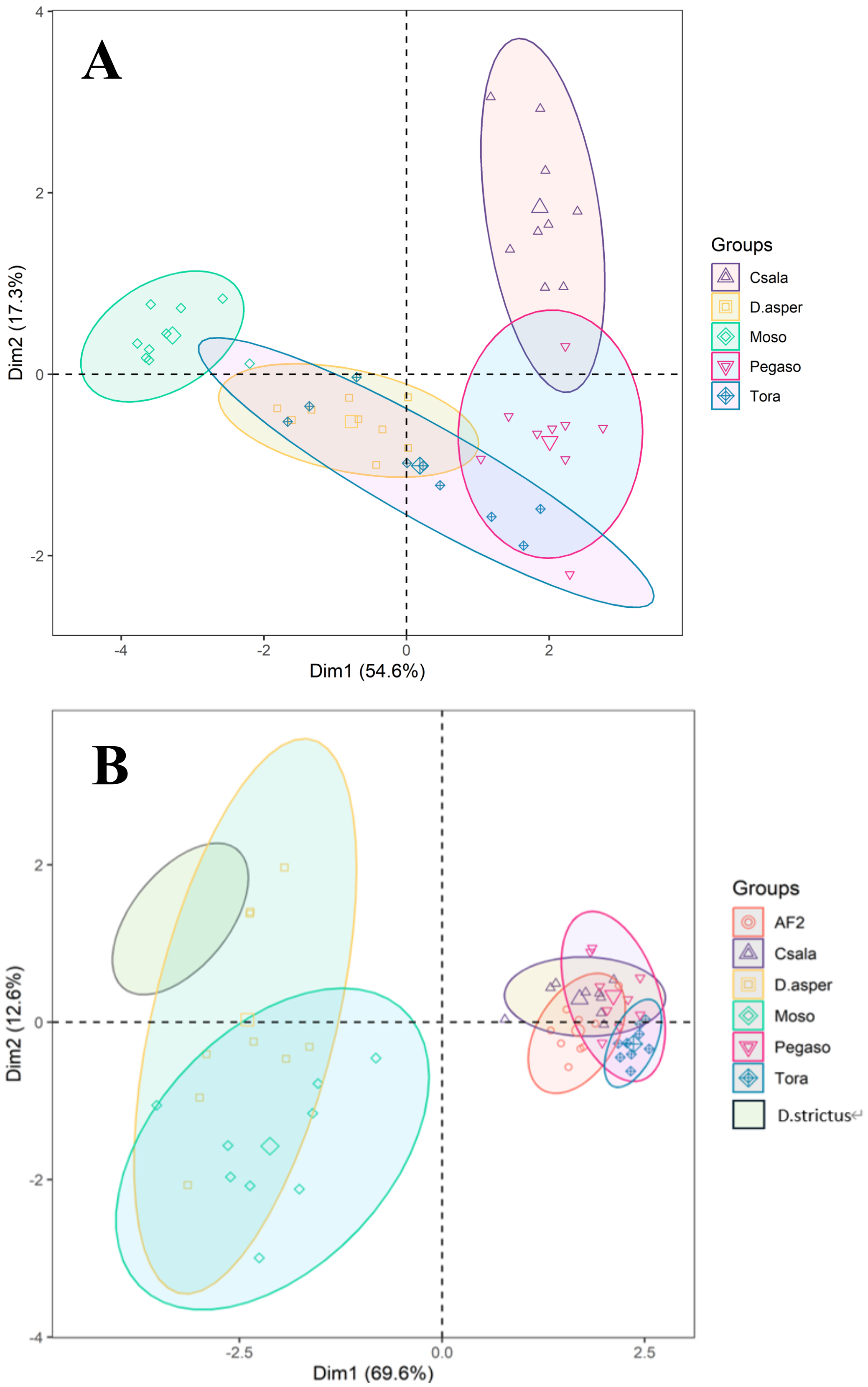


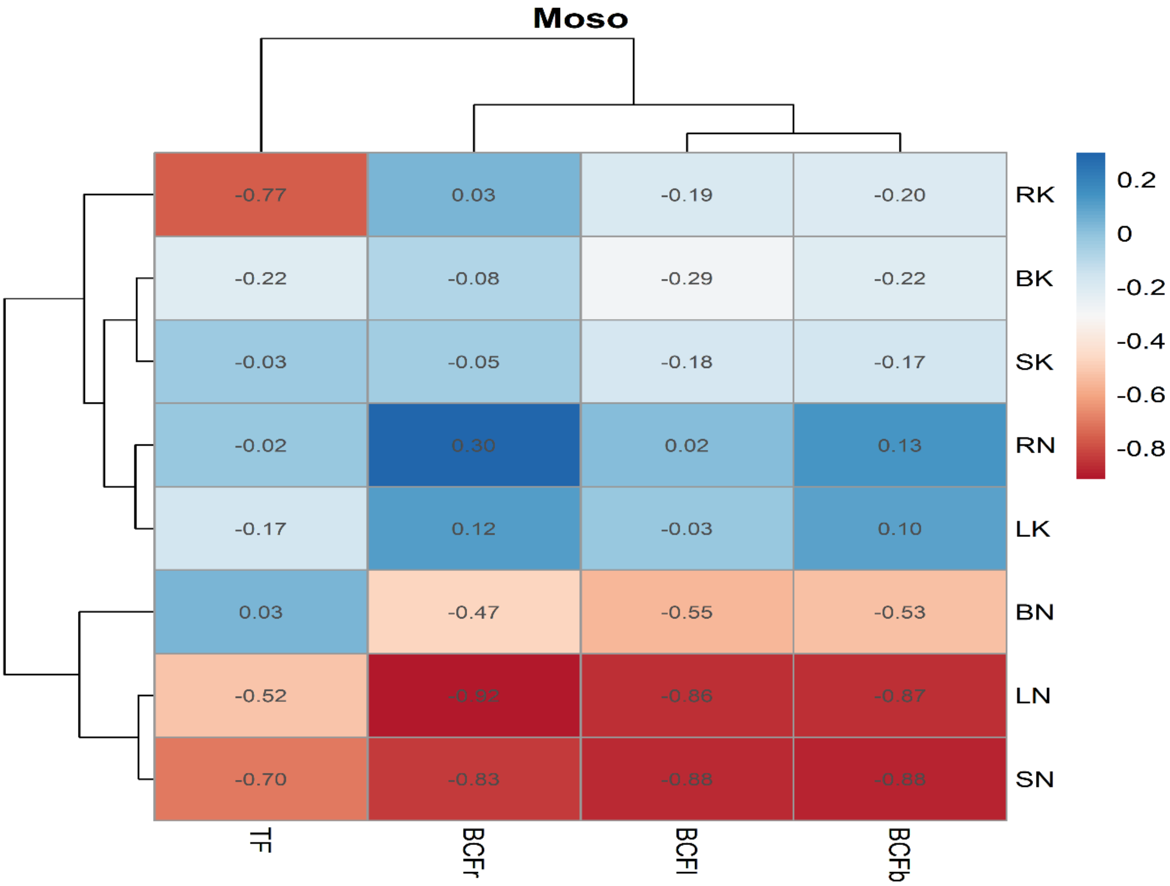
Figure 17. PCA plot for the first year (A) and the second year (B)

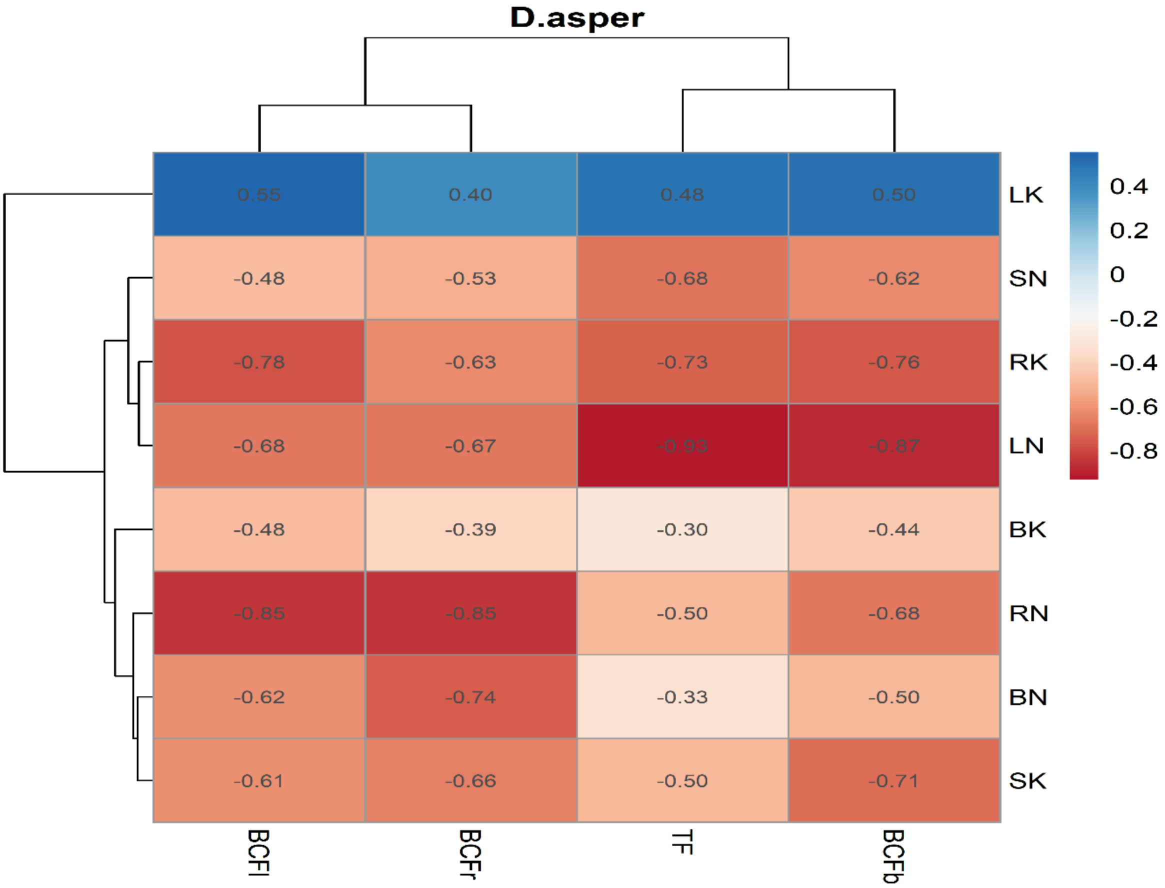
The PCA captures the variability in plant responses to Cd treatment and highlights intergroup differences. In both years, Dim1 and Dim2 accounted for most of the variability in the data. Specifically, in the first year, Dim1 and Dim2 explained 54.6% and 17.3% of the variability, respectively, while in the second year, they accounted for 69.6% and 12.6%, respectively. Significant differences were observed in the PCA results between the two years. In the first year, environmental factors, particularly high temperatures, influenced the data structure, leading to reduced intergroup separation and some overlap in plant distribution patterns. For example, the distribution of *D. asper* and 'Tora' overlapped significantly on both Dim1 and Dim2, suggesting that elevated temperatures may have disrupted the typical Cd absorption and distribution patterns in plants. High temperatures accelerate plant metabolism, directing energy towards maintaining the antioxidant defense system to mitigate Cd-induced oxidative stress rather than enhancing Cd uptake and translocation. Furthermore, elevated temperatures may reduce root activity, increasing variability in Cd concentrations within plant populations. These factors likely contributed to the lower proportion of total variability explained by Dim1 and Dim2 in the first year (72.9%).

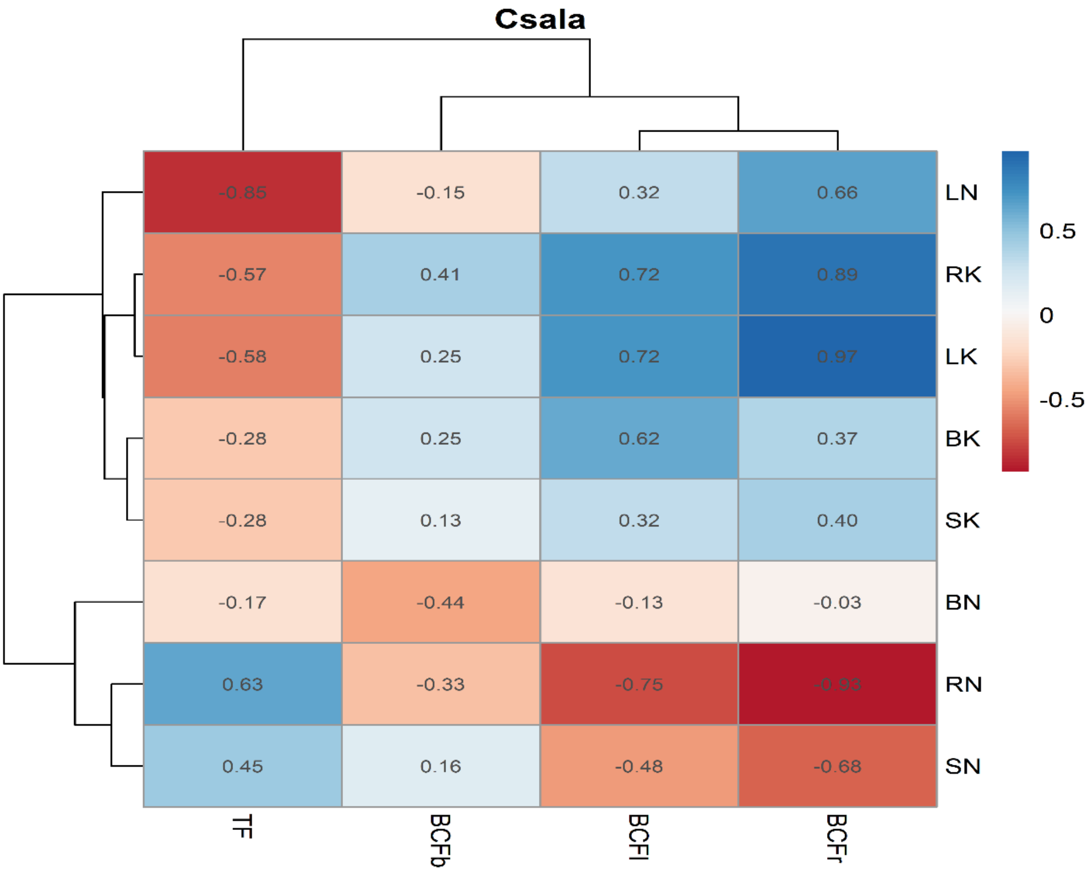
In contrast, the second year was characterized by more stable environmental conditions, which improved the clarity of intergroup separation. Notably, distinct groupings of the bamboo subfamily and willow family were evident, reflecting significant differences in plant responses to Cd treatment under optimal temperature conditions. The total variation explained by Dim1 and Dim2 in the second year reached 82.2%, a marked improvement over the first year. This suggests that under reduced environmental disturbances, the response characteristics of different plant species to Cd treatment became more pronounced, resulting in enhanced differentiation in the PCA.

4.2.5 Clustered heat map

4.2.5.1 The Clustered heat map of 2022

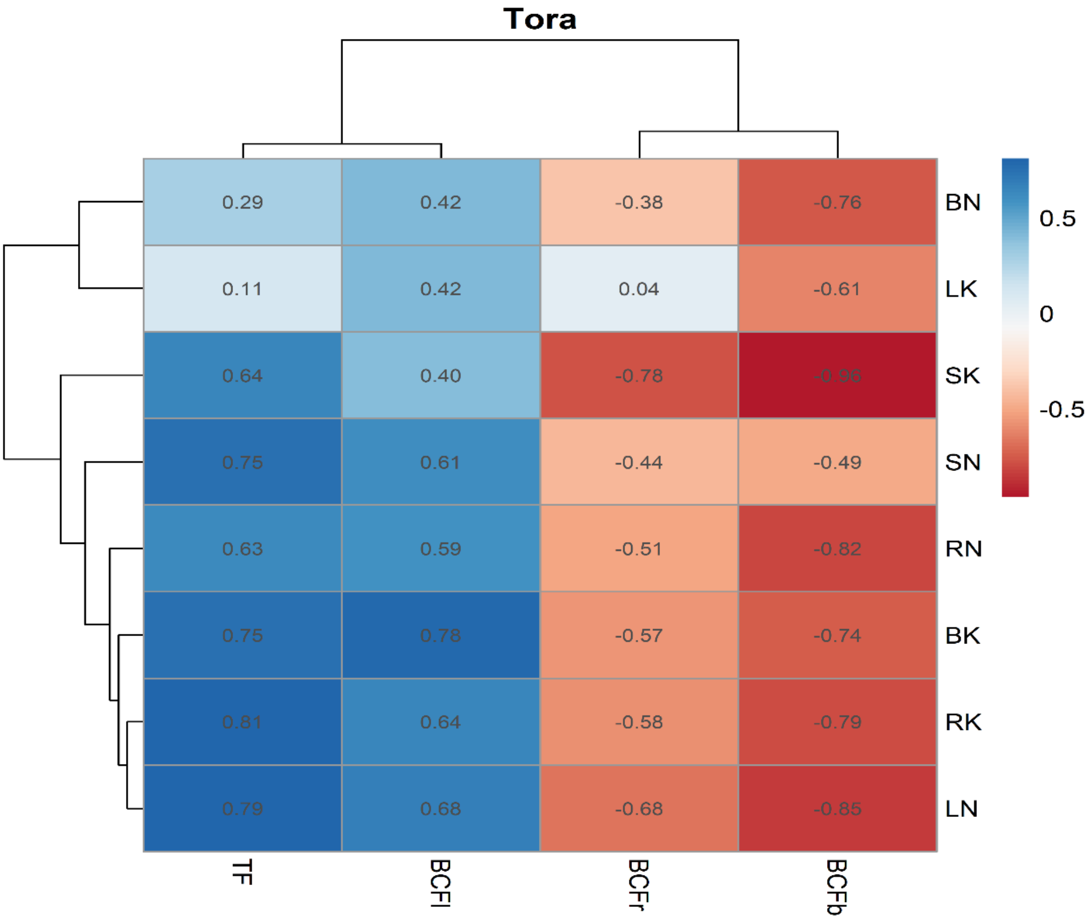

Moso
-0.77
0.03
-0.19
-0.20
RK
-0.22
-0.08
-0.29
-0.22
BK
-0.03
-0.05
-0.18
-0.17
SK
-0.02
0.30
0.02
0.13
RN
-0.17
0.12
-0.03
0.10
LK
0.03
-0.47
-0.55
-0.53
BN
-0.52
-0.92
-0.86
-0.87
LN
-0.70
-0.83
-0.88
-0.88
SN
TF
BCFr
BCFl
BCFb
0.2
0
-0.2
-0.4
-0.6
-0.8


D.asper
0.55
0.40
0.48
0.50
LK
-0.48
-0.53
-0.68
-0.62
SN
-0.78
-0.63
-0.73
-0.76
RK
-0.68
-0.67
-0.93
-0.87
LN
-0.48
-0.39
-0.30
-0.44
BK
-0.85
-0.85
-0.50
-0.68
RN
-0.62
-0.74
-0.33
-0.50
BN
-0.61
-0.66
-0.50
-0.71
SK
BCFl
BCFr
TF
BCFb
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8



Csala

	TF	BCFb	BCFl	BCFr
LN	-0.85	-0.15	0.32	0.66
RK	-0.57	0.41	0.72	0.89
LK	-0.58	0.25	0.72	0.97
BK	-0.28	0.25	0.62	0.37
SK	-0.28	0.13	0.32	0.40
BN	-0.17	-0.44	-0.13	-0.03
RN	0.63	-0.33	-0.75	-0.93
SN	0.45	0.16	-0.48	-0.68



Tora

	TF	BCFl	BCFr	BCFb
BN	0.29	0.42	-0.38	-0.76
LK	0.11	0.42	0.04	-0.61
SK	0.64	0.40	-0.78	-0.96
SN	0.75	0.61	-0.44	-0.49
RN	0.63	0.59	-0.51	-0.82
BK	0.75	0.78	-0.57	-0.74
RK	0.81	0.64	-0.58	-0.79
LN	0.79	0.68	-0.68	-0.85

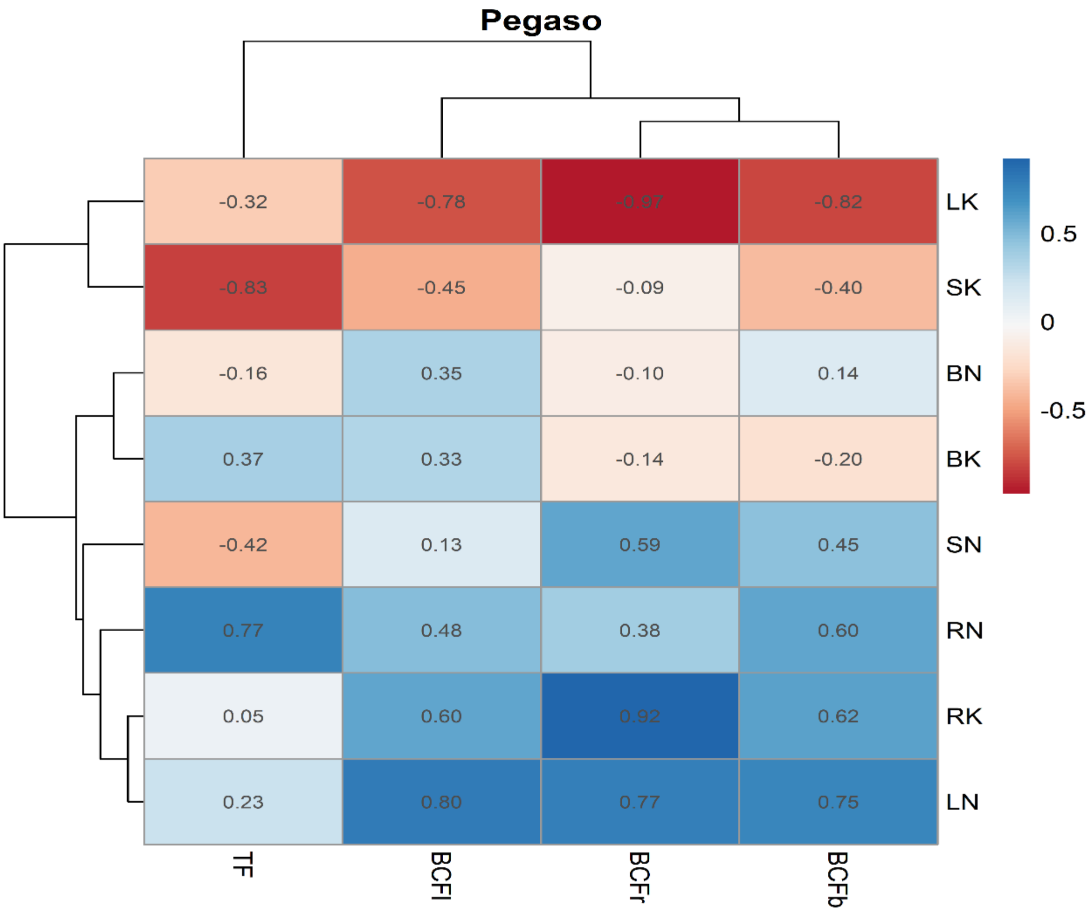
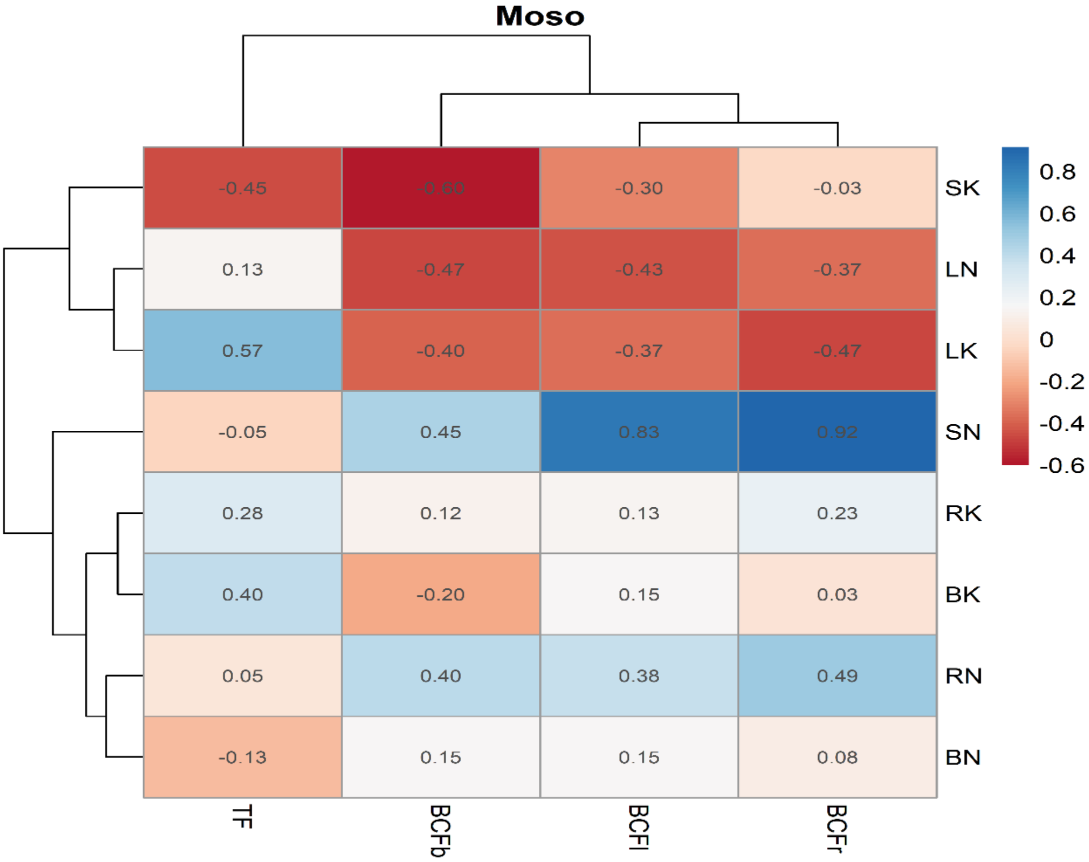


Figure 18. Heat map of the correlation between plant traits and TF, BCF (2022)

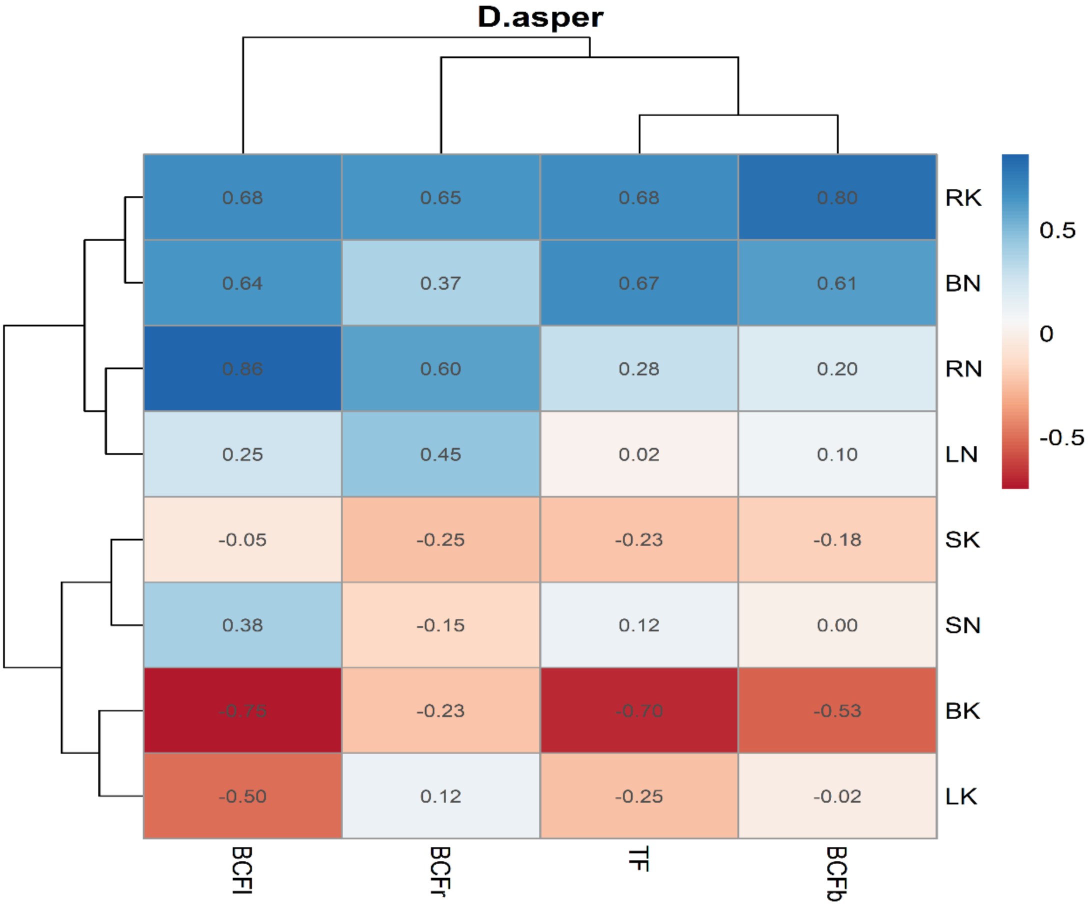
Figure 18 shows the relationship between the 8 plant nutritional traits and the translocation and accumulation parameters under high temperature conditions in the first year. Among them, LN and SN of Moso were negatively correlated with all TF and BCF, which were the main factors limiting phytoextraction and phytoaccumulation. Although RN promoted Cd accumulation in roots, the correlation coefficient was only 0.3. In addition, almost all traits showed a strong negative correlation in *D. asper*. LN negatively correlated with BCF_b and TF by -0.93 and -0.87, respectively, and RN also had a negative correlation with BCF_l and BCF_r of -0.85. For *Salicaceae* plants, RN significantly affected the accumulation of Cd from soil to root in ‘Csala’, but promoted the translocation from root to aboveground part, which also occurred in ‘Tora’. However, ‘Csala’'s LN and TF had a strong negative correlation of -0.85, indicating that the N content of different organs had a significant difference in Cd transport. It is worth noting that each trait in Tora showed a positive correlation with TF and BCF_l and a negative correlation with BCF_r and BCF_b. RK and LN both showed a strong positive correlation with the translocation of Cd to the aboveground, reaching 0.79 and 0.81. In addition, in ‘Pegaso’, RN is the main positive factor for TF, reaching 0.77, while RK and LK show opposite correlations with BCF_r, 0.92 and -0.97, respectively

4.2.5.2 The Clustered heat map of 2023



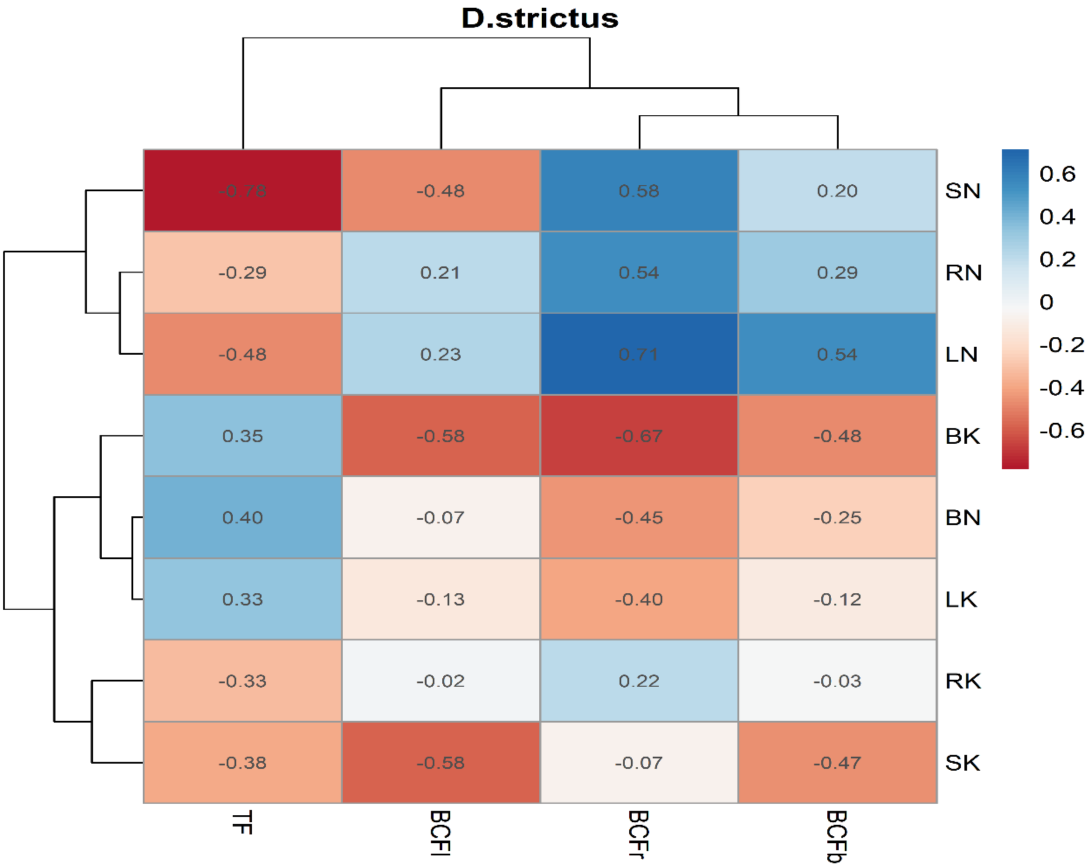
Moso

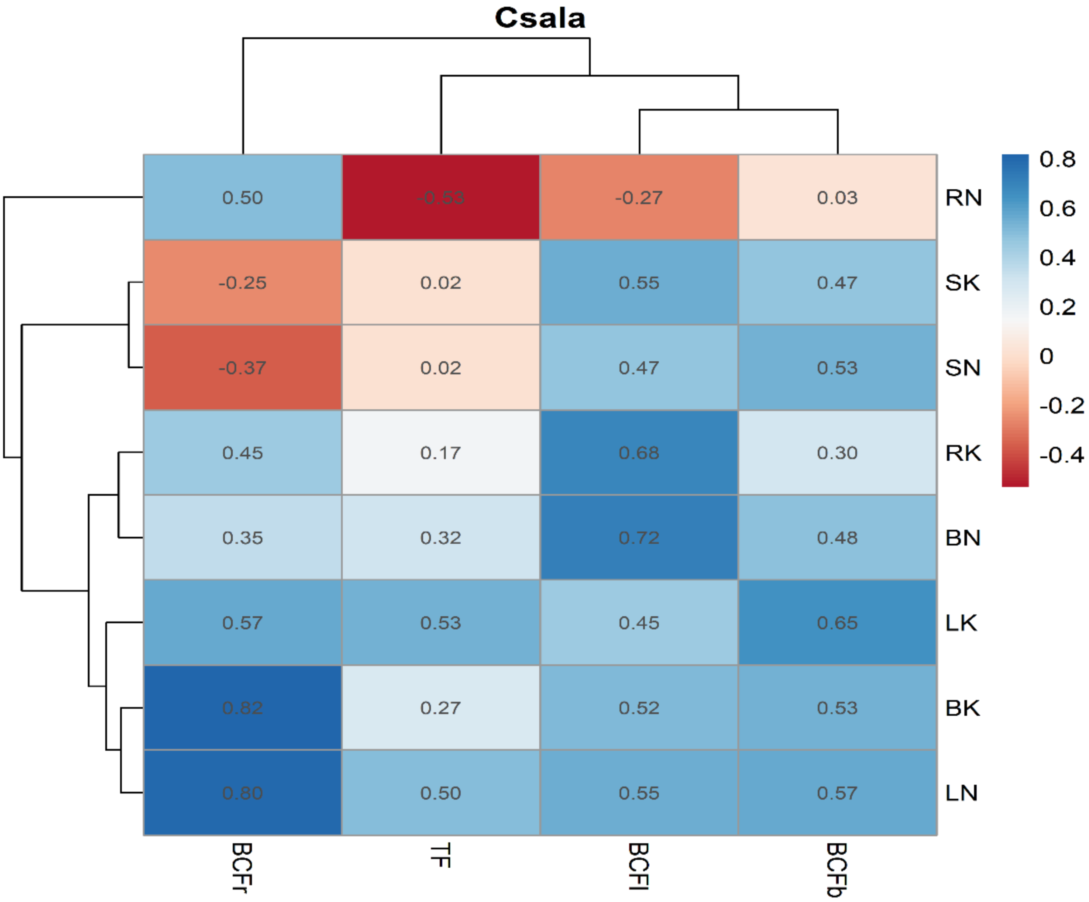
-0.45 -0.60 -0.30 -0.03 SK
0.13 -0.47 -0.43 -0.37 LN
0.57 -0.40 -0.37 -0.47 LK
-0.05 0.45 0.83 0.92 SN
0.28 0.12 0.13 0.23 RK
0.40 -0.20 0.15 0.03 BK
0.05 0.40 0.38 0.49 RN
-0.13 0.15 0.15 0.08 BN
TF
BCFb
BCFl
BCFr
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6

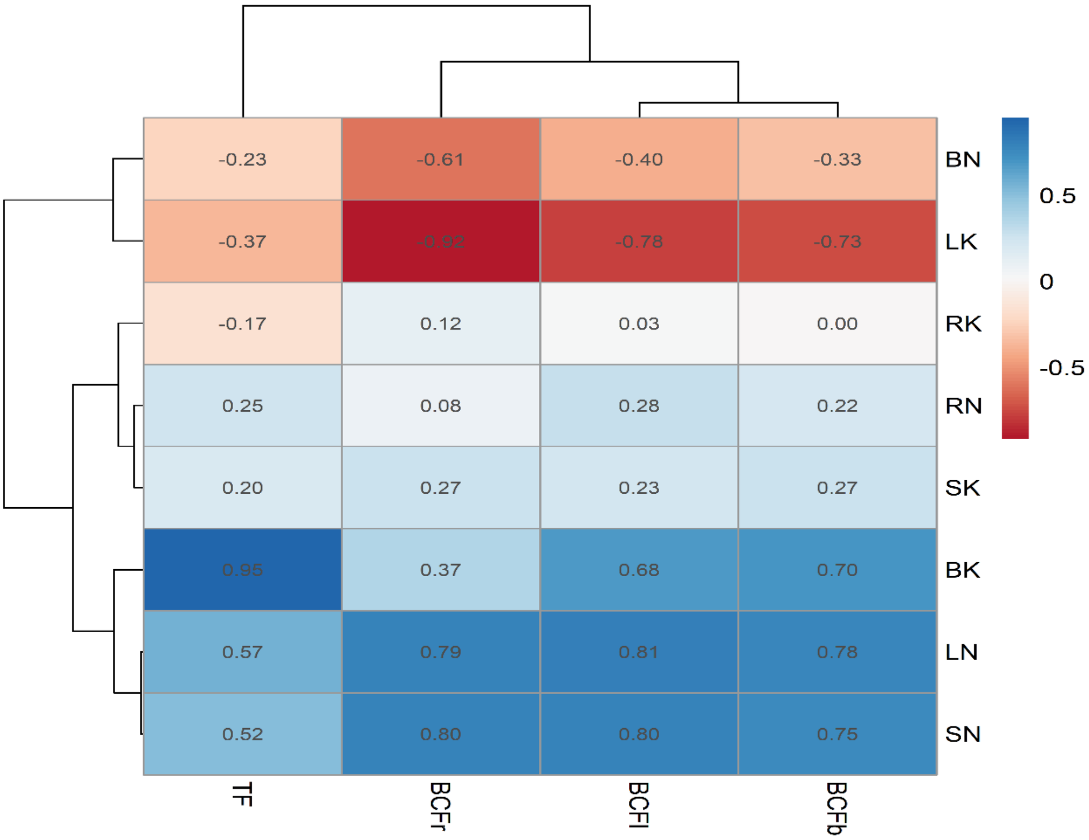


D.asper

0.68 0.65 0.68 0.80 RK
0.64 0.37 0.67 0.61 BN
0.86 0.60 0.28 0.20 RN
0.25 0.45 0.02 0.10 LN
-0.05 -0.25 -0.23 -0.18 SK
0.38 -0.15 0.12 0.00 SN
-0.75 -0.23 -0.70 -0.53 BK
-0.50 0.12 -0.25 -0.02 LK
BCFl
BCFr
TF
BCFb
0.5
0
-0.5

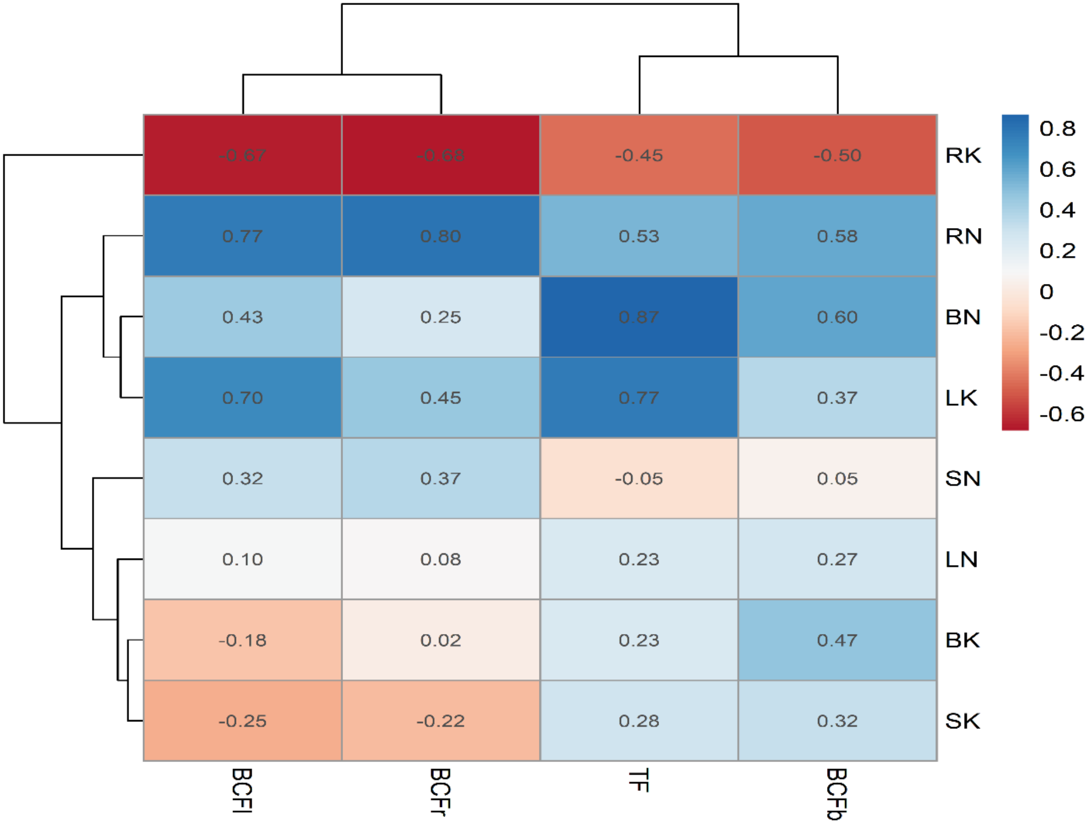

D.strictus
-0.78 -0.48 0.58 0.20 SN
-0.29 0.21 0.54 0.29 RN
-0.48 0.23 0.71 0.54 LN
0.35 -0.58 -0.67 -0.48 BK
0.40 -0.07 -0.45 -0.25 BN
0.33 -0.13 -0.40 -0.12 LK
-0.33 -0.02 0.22 -0.03 RK
-0.38 -0.58 -0.07 -0.47 SK
TF
BCFl
BCFr
BCFb
0.6
0.4
0.2
0
-0.2
-0.4
-0.6


Csala
0.50 -0.53 -0.27 0.03 RN
-0.25 0.02 0.55 0.47 SK
-0.37 0.02 0.47 0.53 SN
0.45 0.17 0.68 0.30 RK
0.35 0.32 0.72 0.48 BN
0.57 0.53 0.45 0.65 LK
0.82 0.27 0.52 0.53 BK
0.80 0.50 0.55 0.57 LN
BCFr
TF
BCFl
BCFb
0.8
0.6
0.4
0.2
0
-0.2
-0.4



Tora

-0.23
-0.61
-0.40
-0.33
BN
-0.37
-0.92
-0.78
-0.73
LK
-0.17
0.12
0.03
0.00
RK
0.25
0.08
0.28
0.22
RN
0.20
0.27
0.23
0.27
SK
0.95
0.37
0.68
0.70
BK
0.57
0.79
0.81
0.78
LN
0.52
0.80
0.80
0.75
SN
TF
BCFr
BCFl
BCFb
0.5
0
-0.5



Pegaso

-0.67
-0.68
-0.45
-0.50
RK
0.77
0.80
0.53
0.58
RN
0.43
0.25
0.87
0.60
BN
0.70
0.45
0.77
0.37
LK
0.32
0.37
-0.05
0.05
SN
0.10
0.08
0.23
0.27
LN
-0.18
0.02
0.23
0.47
BK
-0.25
-0.22
0.28
0.32
SK
BCFl
BCFr
TF
BCFb
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6

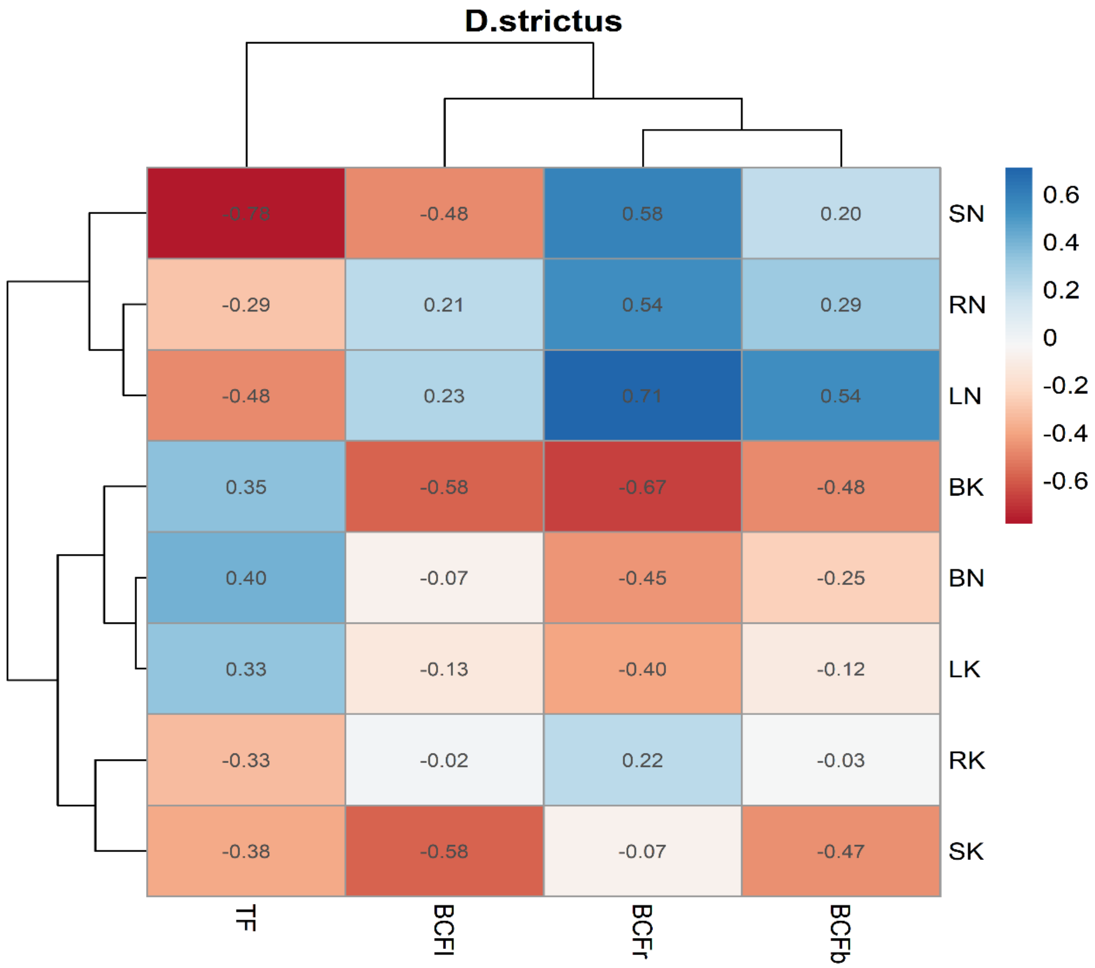


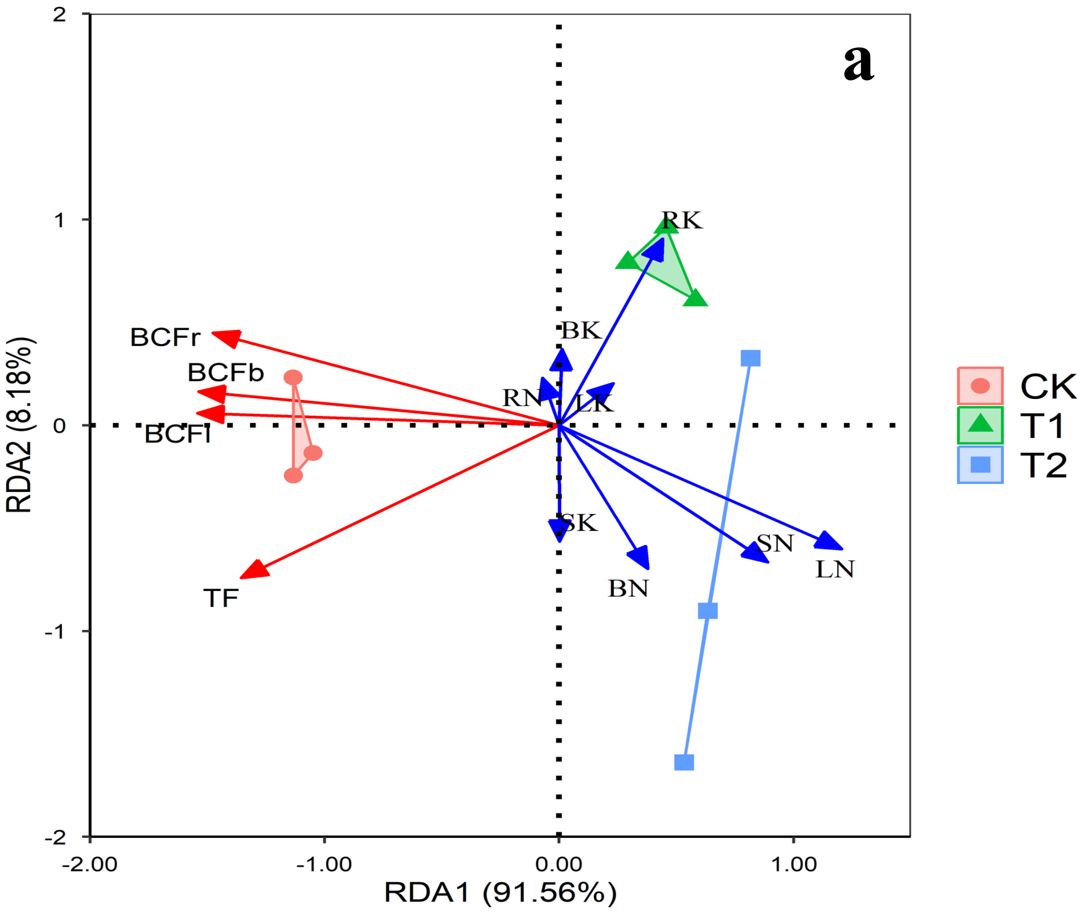
Figure 19. Heat map of the correlation between traits and TF, BCF (2023)

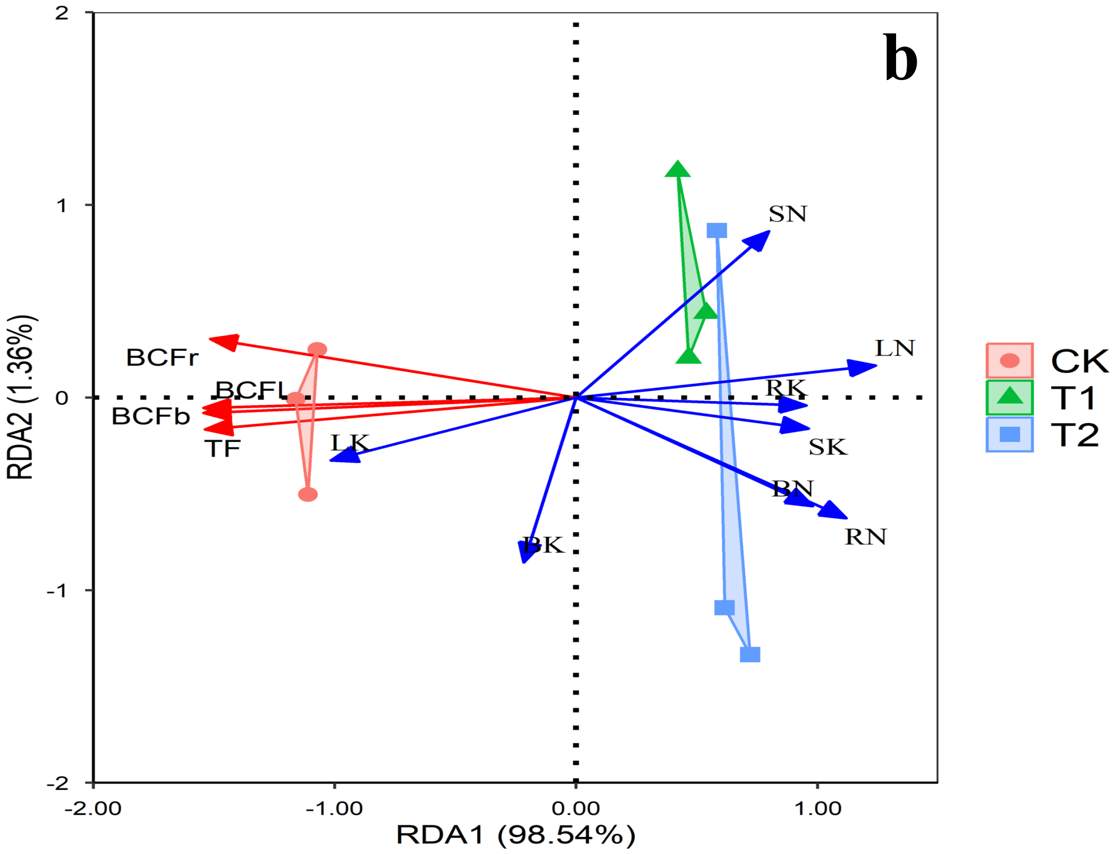
During the second year, a more stable environment revealed distinct trait dominance mechanisms across different plants. For Moso, leaf and soil properties emerged as the primary factors influencing the rhizosphere extraction. SN demonstrated strong positive correlations with BCF_r and BCF_b, reaching values of 0.92 and 0.83, respectively, likely due to interactions between the soil microbial community and plant traits. In contrast, LK and LN acted as limiting factors, restricting the translocate of Cd from soil to aboveground tissues. For *D. asper*, root and branch traits dominated the process of Cd accumulation. BN and RK were positively correlated with various parameters, highlighting their roles in enhancing Cd uptake. However, BK was identified as the primary factor restricting the upward translocation of Cd, thereby limiting its distribution to aerial parts of the plant. In *D. strictus*, SN exhibited a strong negative correlation with TF (-0.76), suggesting its role in impeding the translocation of Cd from roots to shoots. Conversely, LN displayed a significant positive correlation with BCF_r (0.71), emphasizing its contribution to Cd translocation within the plant. These findings indicate that both nitrogen-related traits play pivotal roles in regulating Cd dynamics in this species.

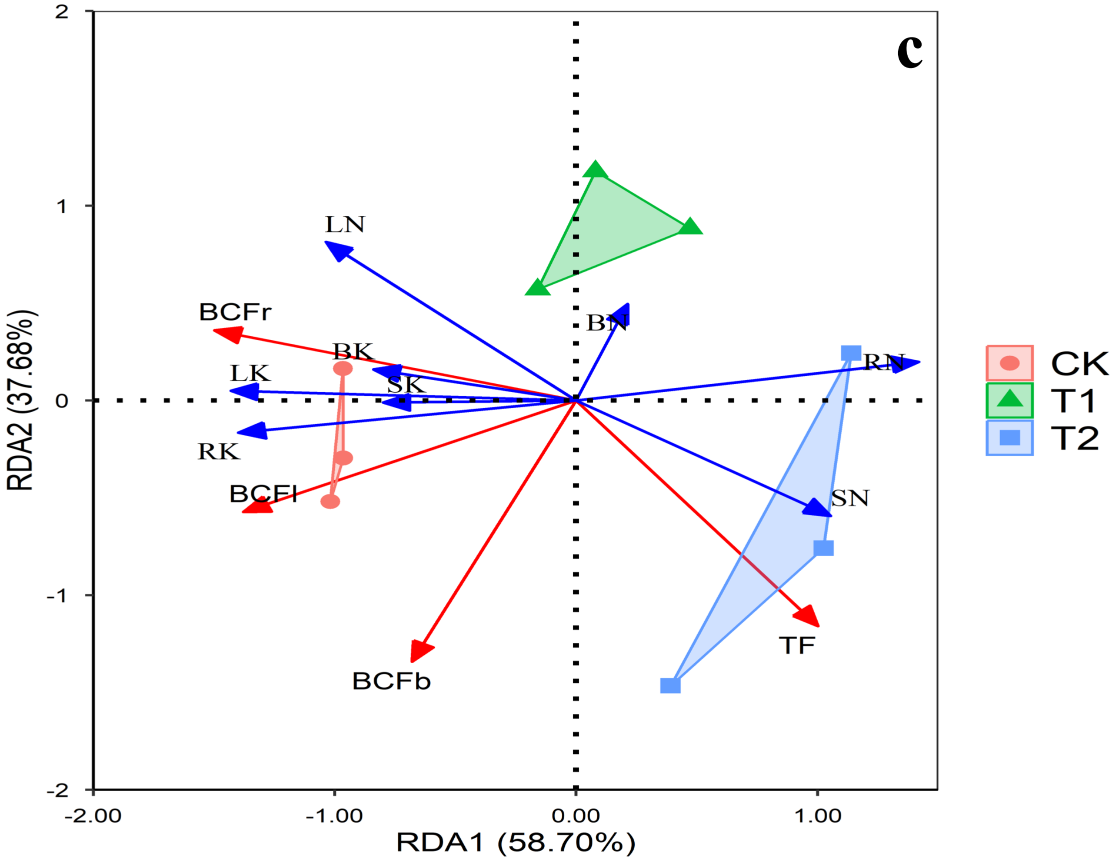
The rhizosphere traits of 'AF2' were central to heavy metal accumulation. RK showed significant positive correlations with BCF_l (0.60) and BCF_b (0.55), underscoring the role of root traits in enhancing heavy metal absorption. Meanwhile, SN exhibited a strong negative correlation with BCF_l (-0.80), potentially inhibiting Cd fixation in the soil or rhizosphere isolation. Additionally, LN and TF demonstrated a strong positive correlation, suggesting their regulatory influence on Cd translocation to aerial tissues through nitrogen metabolic pathways. For ‘Pegaso’, the coordination of overall plant traits was particularly evident. BN was positively correlated with TF (0.87), and RN exhibited a strong positive correlation with BCF_r (0.80), highlighting the roles of BN in Cd translocation and RN in Cd accumulation. In contrast, RK showed negative correlations with all parameters, indicating that root potassium content inhibits Cd translocation to aboveground parts. In ‘Tora’, SN and LN exhibited high positive correlations with all parameters, suggesting their dominant roles in Cd interactions between plants and soil. However, LK showed a strong negative correlation with BCF_r (-0.92), indicating that leaf traits limit Cd translocation upward. This suggests a regulatory effect of aboveground traits in controlling Cd dynamics. For ‘Csala’, RN emerged as the primary factor inhibiting TF, while SN and SK exhibited weak negative correlations with Cd accumulation in roots. Although these correlations were not as pronounced, they highlight potential roles in modulating Cd distribution within the plant.

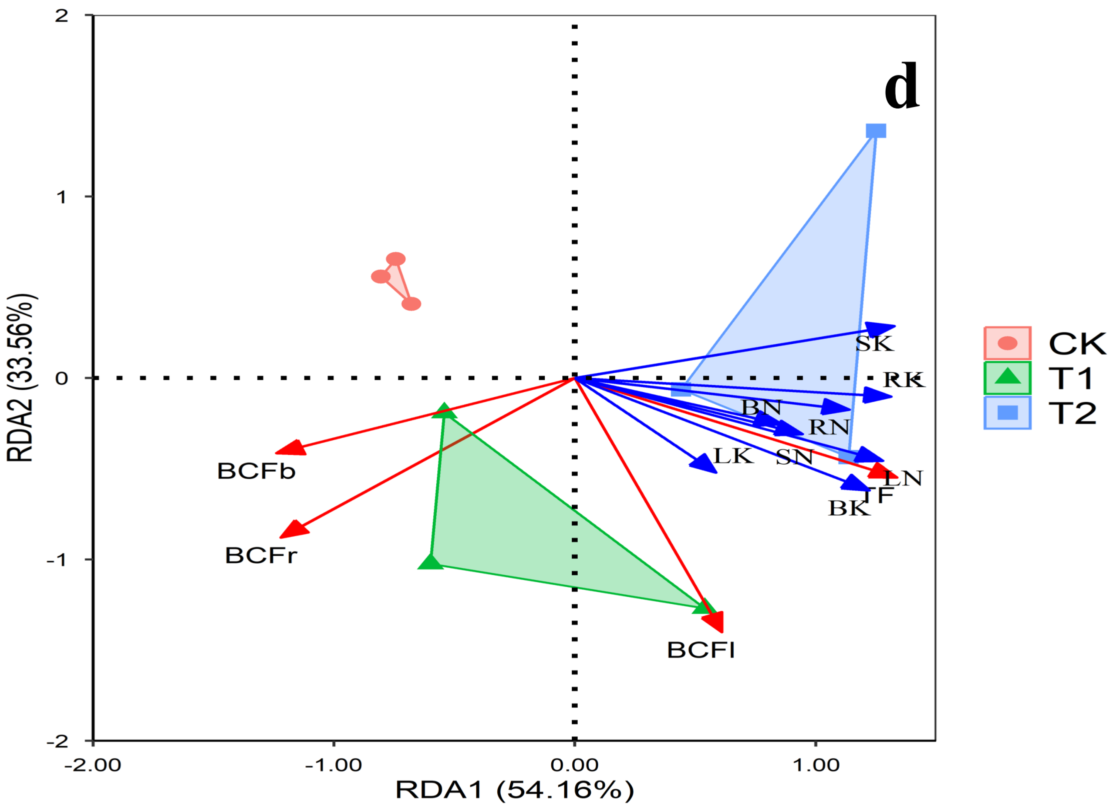
4.2.3 Redundancy Analysis (RDA)

4.2.3.1 The RDA of 2022




b
RDA2 (1.36%)
RDA1 (98.54%)
2
1
0
-1
-2
-2.00
-1.00
0.00
1.00
BCFr
BCFL
BCFb
TF
LK
BK
SN
LN
RK
SK
BN
RN
CK
T1
T2


c
RDA2 (37.68%)
RDA1 (58.70%)
2
1
0
-1
-2
-2.00
-1.00
0.00
1.00
LN
BCFr
BK
LK
SK
RK
BCFl
BCFb
BN
RN
SN
TF
CK
T1
T2


d
2
1
0
-1
-2
RDA2 (33.56%)
-2.00
-1.00
0.00
1.00
RDA1 (54.16%)
SK
RK
BN
RN
LK
SN
LN
TF
BK
BCFb
BCFr
BCFl
CK
T1
T2

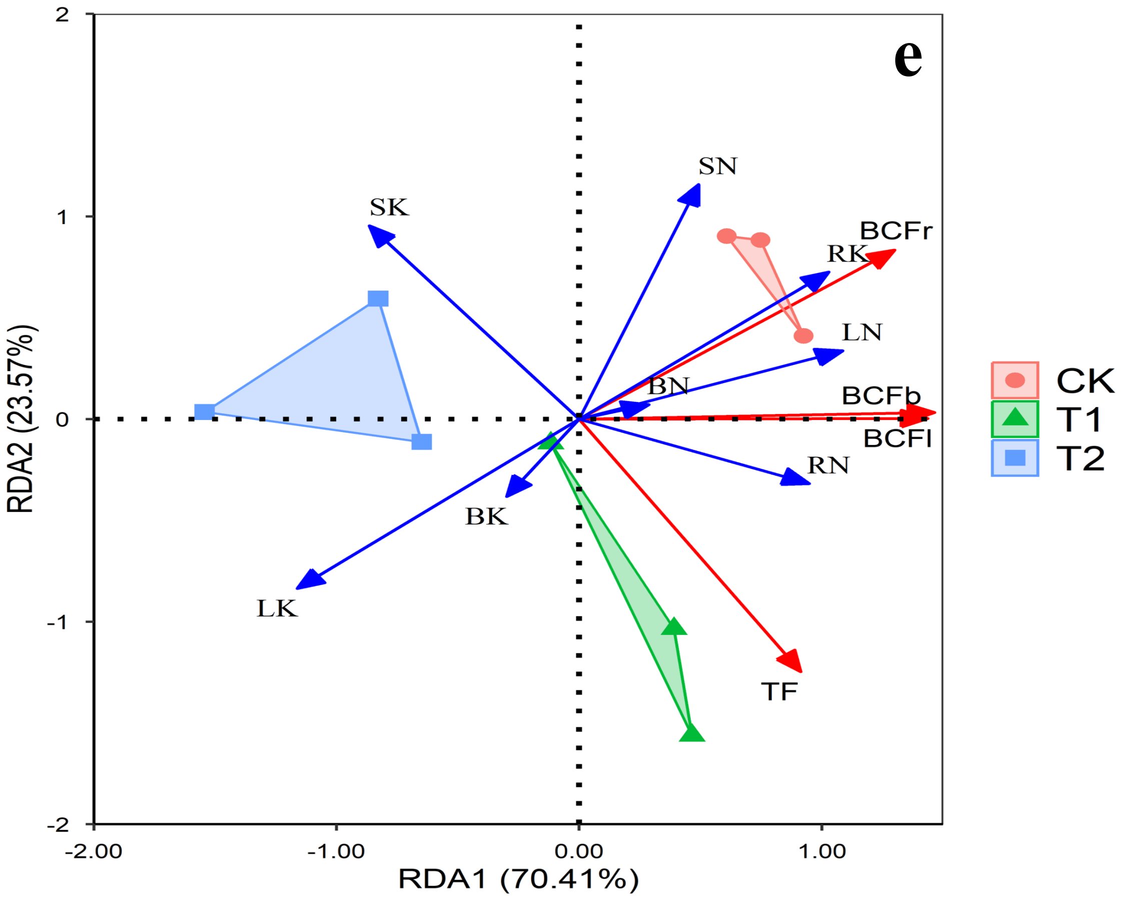
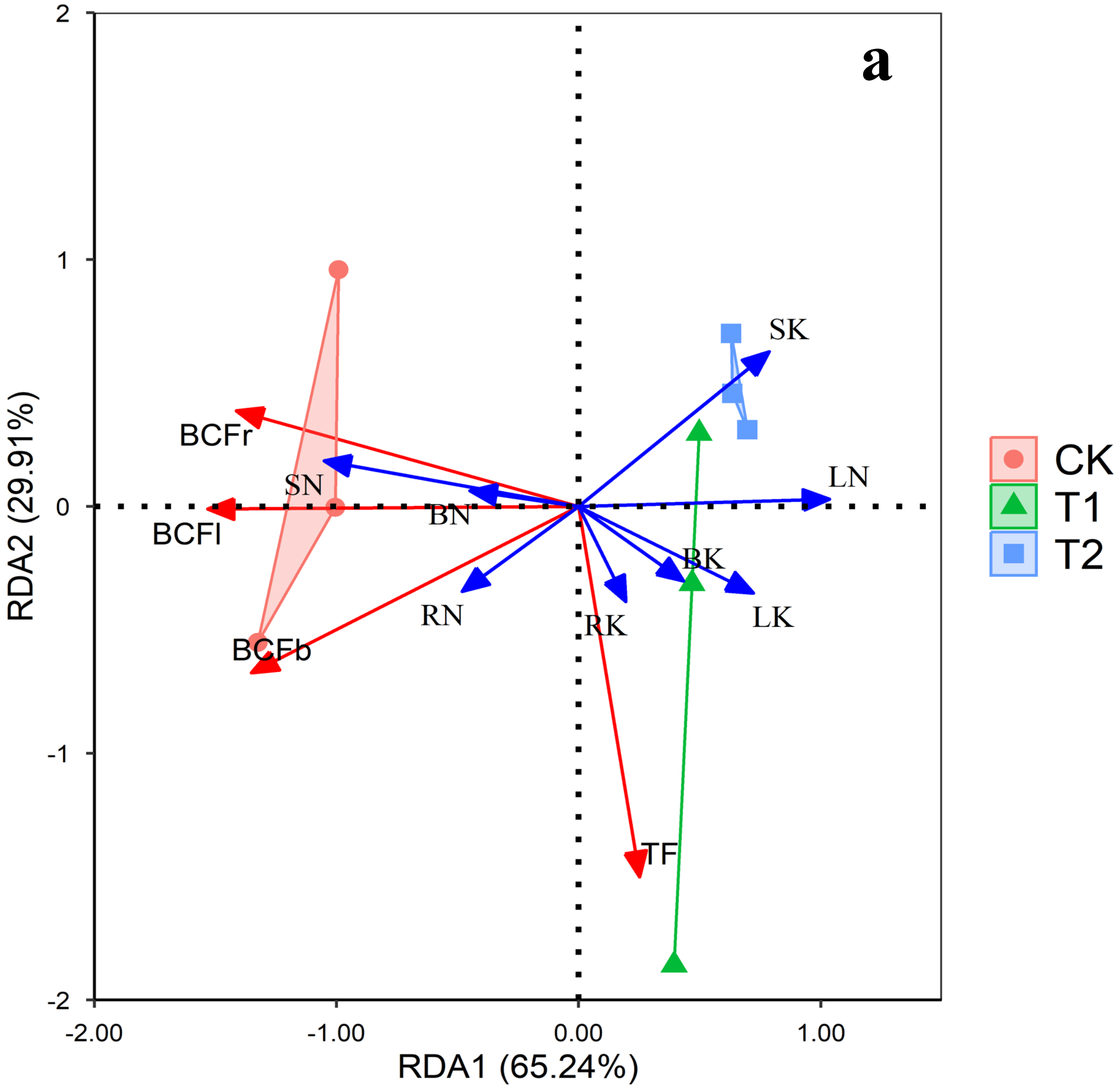
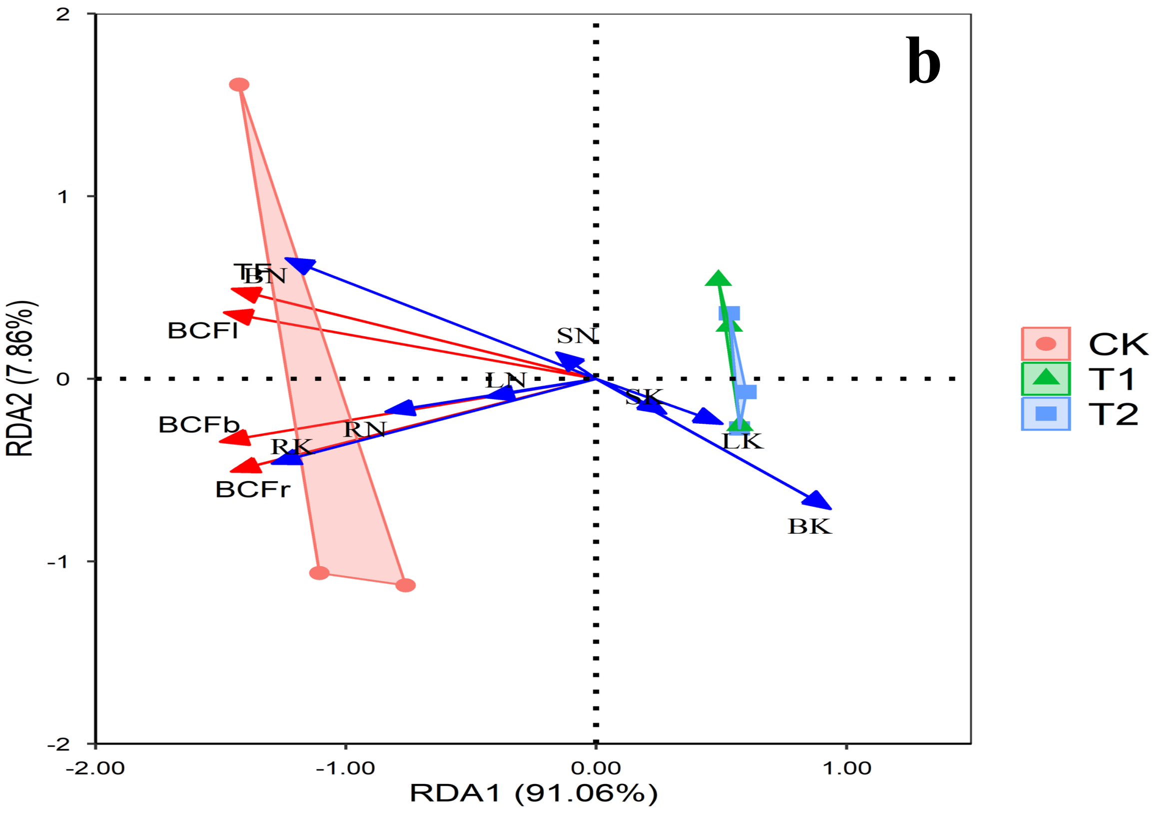

e
2
1
0
-1
-2
RDA2 (23.57%)
-2.00
-1.00
0.00
1.00
RDA1 (70.41%)
SN
SK
BCFr
RK
LN
BN
BCFb
BCFl
RN
BK
LK
TF
CK
T1
T2

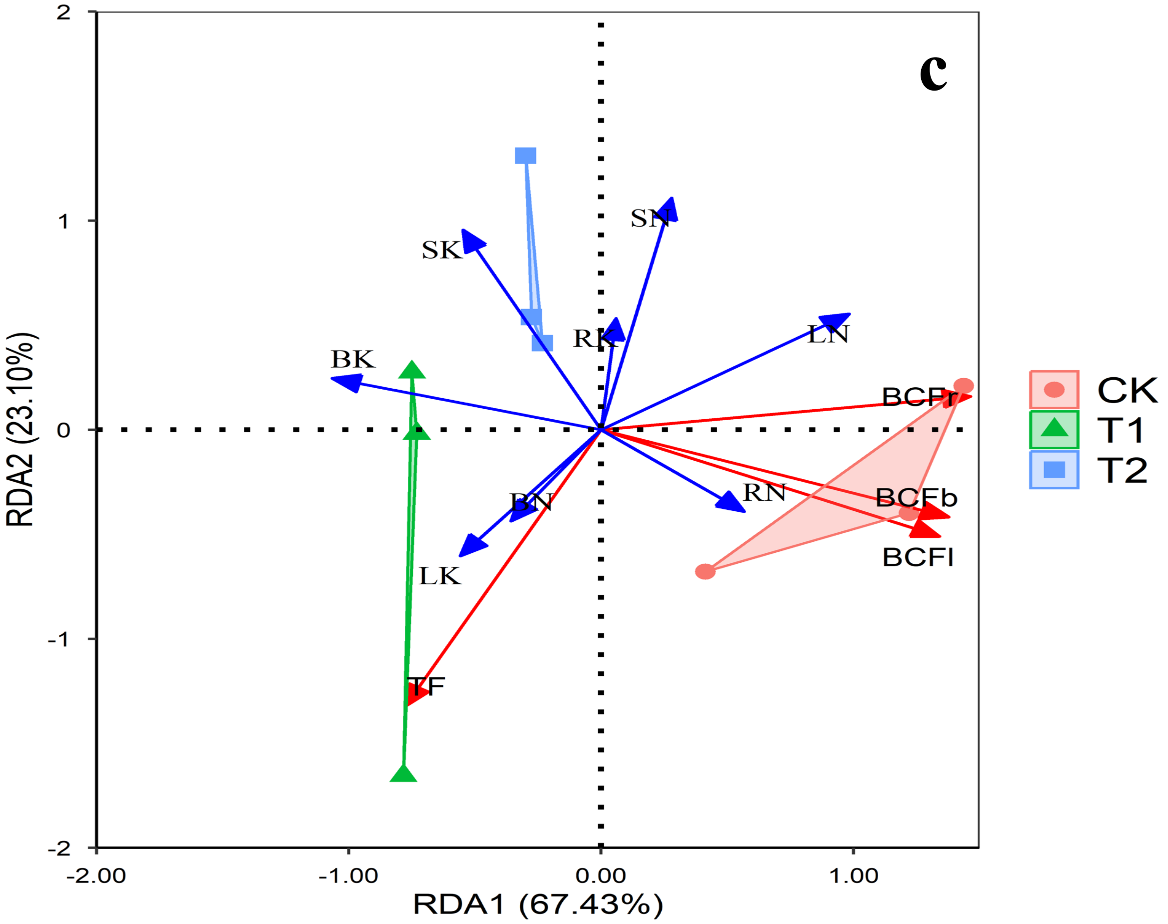
Figure 20. RDA analysis of nutritional traits and TF and BCF for each organ (a: Moso, b: *D. asper*, c: ‘Csala’, d: ‘Tora’, e: ‘Pegaso’)

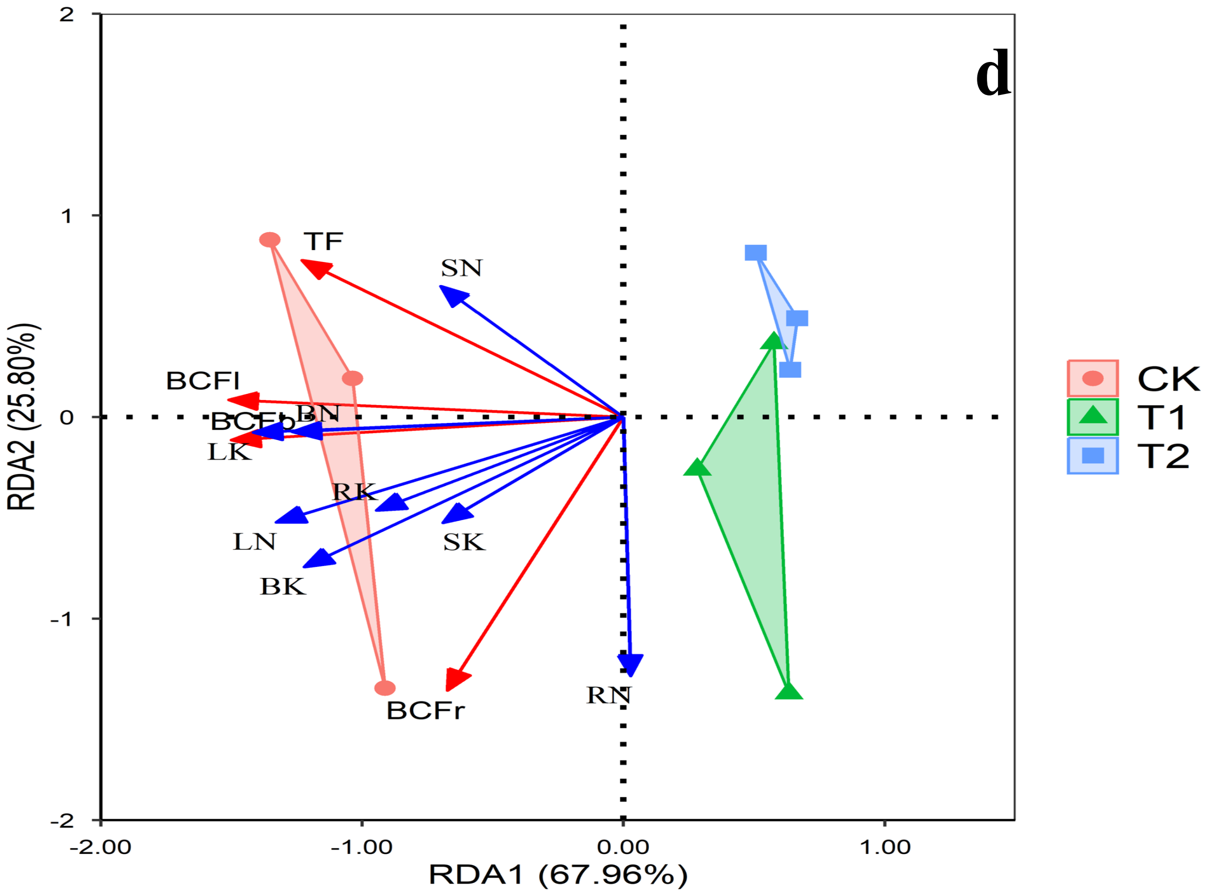
Figure 20 reveals the relationship between the nutritional traits of the five plants and the Cd TF and BCF in the first year through RDA. RDA1 of Moso and *D. asper* explained 91.56% and 98.54% of the variation, respectively (Figure 20 a,b). LN contributed most to this axis and was a negative factor for both BCF and TF, possibly in high temperature environments, LN may affect Cd fixation and transport by regulating the plant's nitrogen metabolic pathway, while inhibiting Cd migration from the roots to the aboveground. RDA1 of ‘Csala’ and ‘Tora’ explained 58.70% and 54.16% of the variation, respectively (Figure 20 c,d). LK was a positive factor of BCF_r and BCF_l and a negative factor of TF. ‘Tora’'s SK was also only a positive factor of TF. In ‘Pegaso’, RDA1 explains 70.41% of the variation, and LK is a significant negative factor for BCF_r and BCF_l.

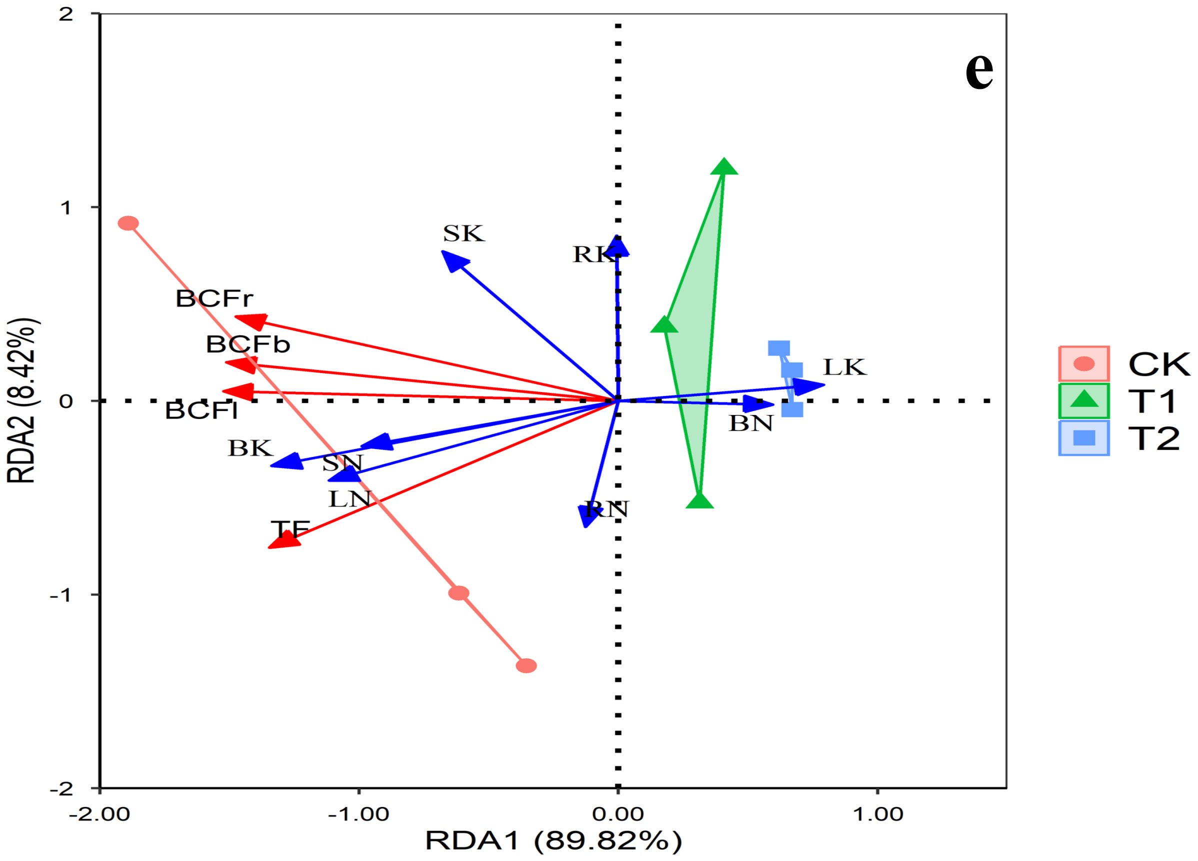
4.2.3.2 The RDA of 2023

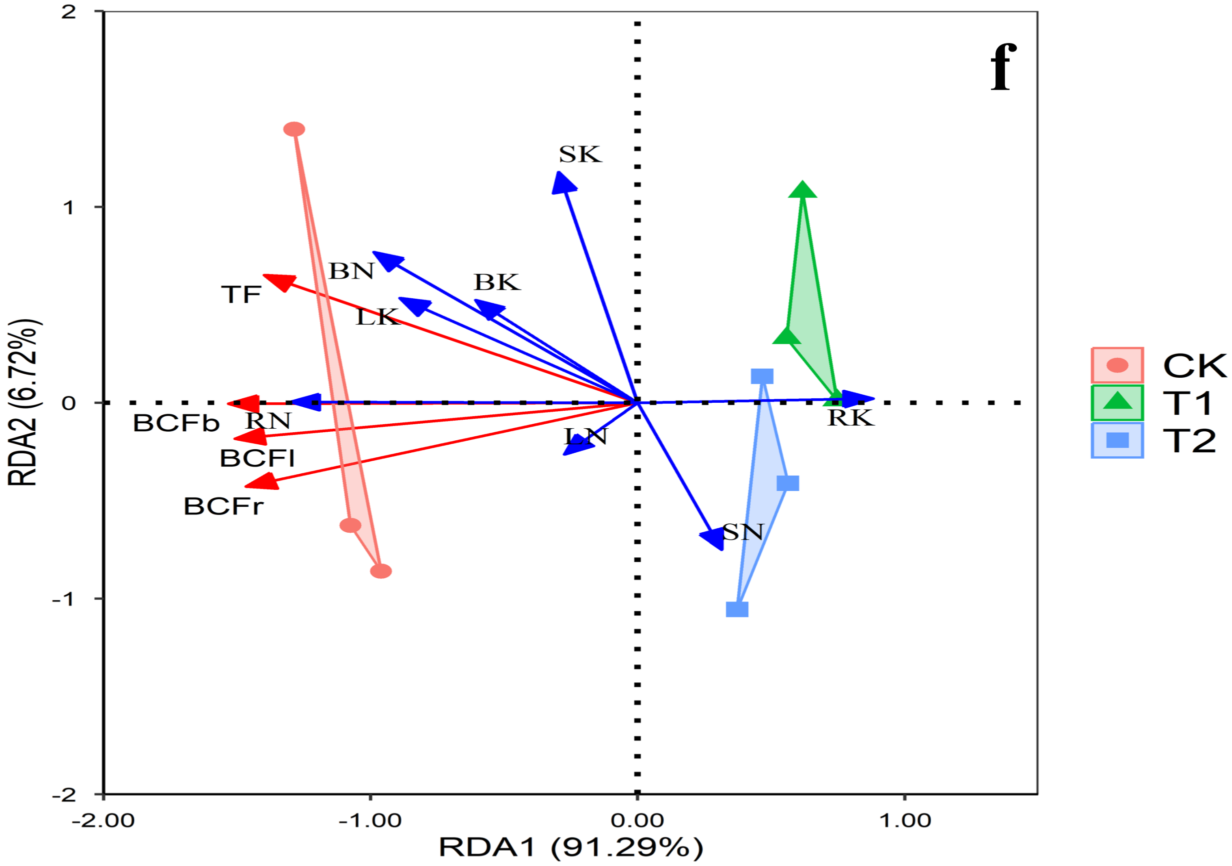



b
RDA2 (7.86%)
RDA1 (91.06%)
2
1
0
-1
-2
-2.00
-1.00
0.00
1.00
TF
BN
BCFl
SN
LN
SK
BCFb
RN
RK
LK
BCFr
BK
CK
T1
T2


c
RDA2 (23.10%)
RDA1 (67.43%)
2
1
0
-1
-2
-2.00
-1.00
0.00
1.00
SN
SK
RK
LN
BK
BCFr
BN
RN
BCFb
LK
BCFl
TF
CK
T1
T2


d
2
1
0
-1
-2
-2.00
-1.00
0.00
1.00
RDA1 (67.96%)
RDA2 (25.80%)
TF
SN
BCFl
BN
BCFb
LK
RK
LN
SK
BK
BCFr
RN
CK
T1
T2


e
2
1
0
-1
-2
-2.00
-1.00
0.00
1.00
RDA1 (89.82%)
RDA2 (8.42%)
SK
RK
BCFr
BCFb
BCFl
LK
BN
BK
SN
LN
TF
RN
CK
T1
T2


f
SK
BN
BK
TF
LK
BCFb
RN
BCFl
BCFr
LN
SN
RK
CK
T1
T2
2
1
0
-1
-2
-2.00
-1.00
0.00
1.00
RDA2 (6.72%)
RDA1 (91.29%)

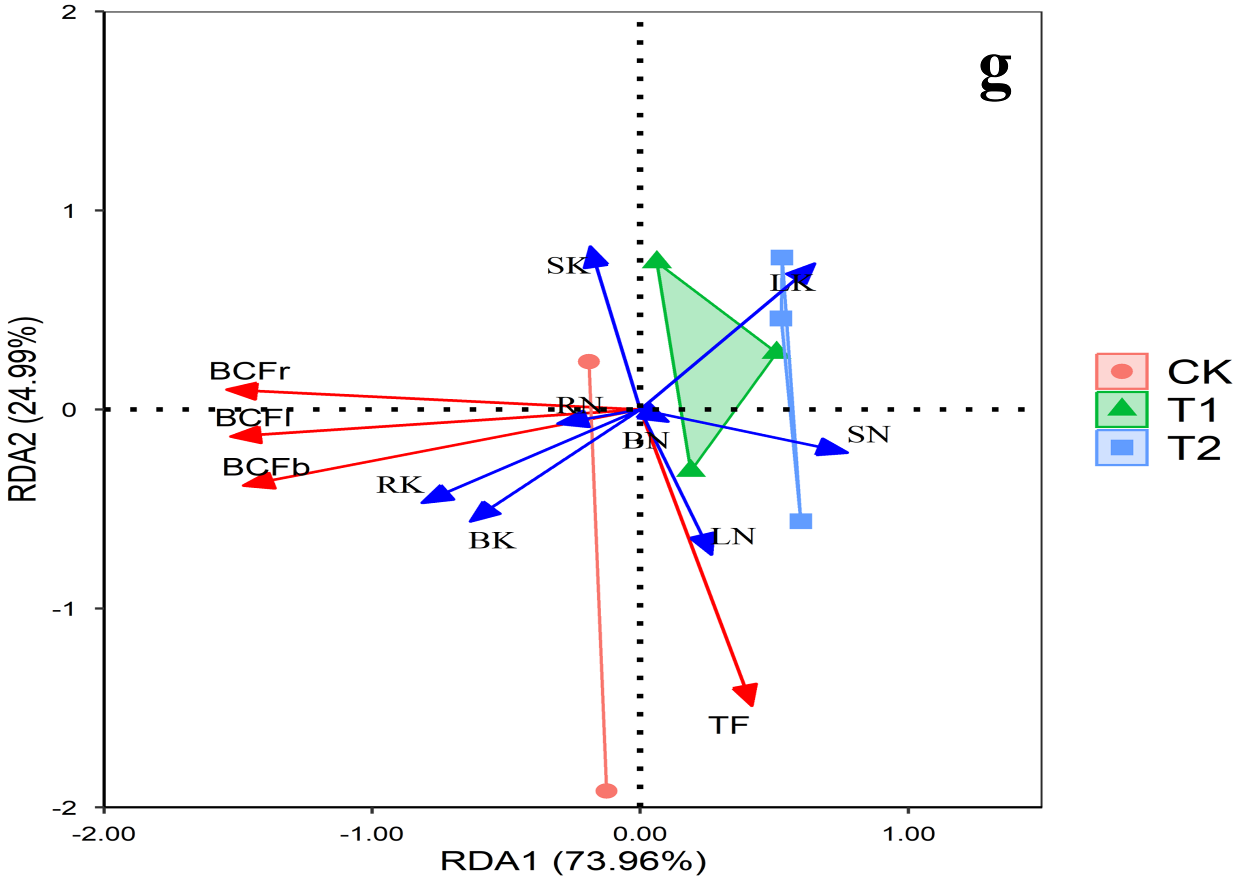
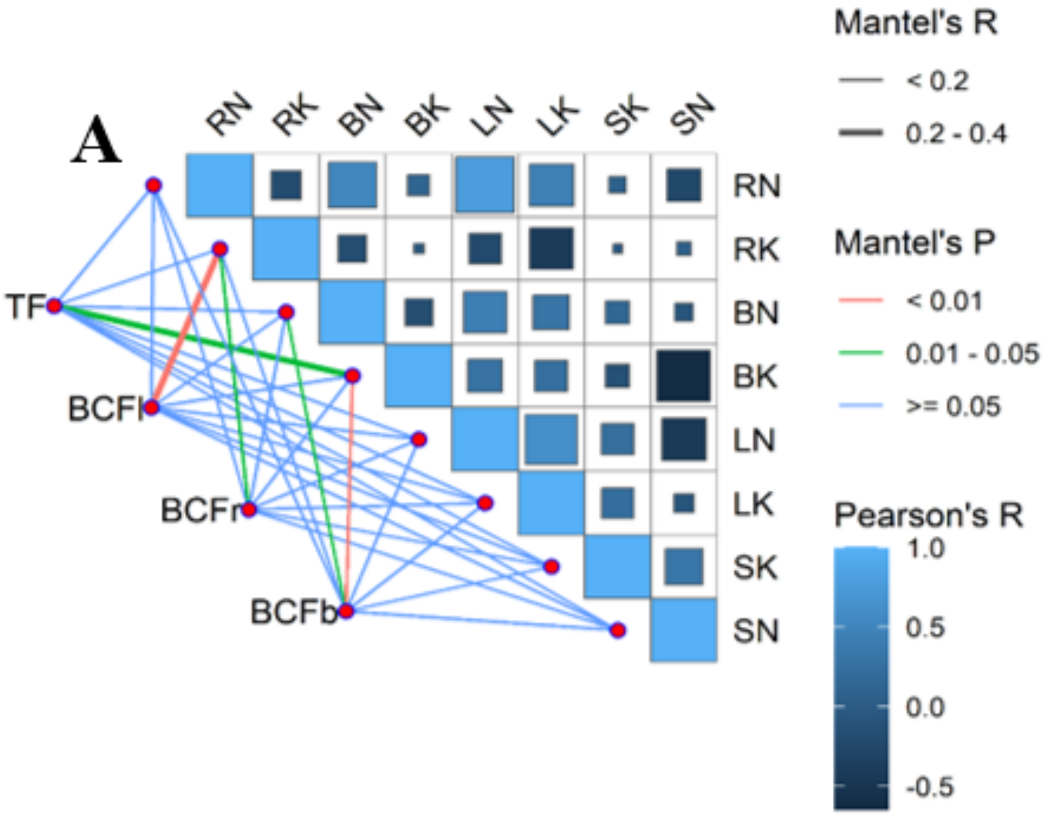

g
SK
LK
BCFr
RN
BCFl
BN
SN
BCFb
RK
BK
LN
TF
CK
T1
T2
2
1
0
-1
-2
-2.00
-1.00
0.00
1.00
RDA2 (24.99%)
RDA1 (73.96%)

Figure 21. RDA analysis of nutritional traits and TF and BCF for each organ (a: Moso, b: *D. asper*, c: *D. strictus*, d: ‘Csala’, e: ‘Tora’, f: ‘Pegaso’, g: ‘AF2’)

Figure 21 shows the relationship between each trait and TF and BCF for the seven plants in the second year. The results show that RDA1 and RDA2 of Moso explained 65.24% and 29.91% of the variation, respectively. LN was a negative factor of BCF, but SN was a significant contributing factor of RDA1 and a positive factor of BCF_r. As in the first year, the parameters of *D. asper* were still in the negative direction of the RDA1 axis, which still explained most of the variation, reaching 91.06%. RK was a significant positive factor of BCF_r, and BN was a significant positive factor of TF. Similarly, in *D. strictus*, RDA1 and RDA2 explained 67.41% and 23.1% of the variation, respectively. BK was a significant negative factor for each BCF, and LN was a negative factor for TF, significantly inhibiting the translocation of Cd.

For *Salicaceae*, RDA1 and RDA2 explained 67.96% and 25.8% of the variation in ‘Csala’, respectively, and LK, RN and LN were significant positive factors for BCF. The RDA1 axis of the other willow, ‘Tora’, explained most of the variation, at 89.82%, while BK was a significant positive factor for BCF_l and TF and LK was a negative factor, but not significant. In addition, the RDA1 axis of ‘Pegaso’ also explained most of the variation, reaching 91.29%, and RN and BN were significant positive factors of BCF_b and TF, respectively. However, in ‘AF2’, RDA1 and RDA2 explained 73.69% and 24.99% of the variation, respectively, and RK was a significant positive contributor to the RDA1 axis, but not significant.

4.2.4 Translocation and accumulation parameters in correlation with plants in the *Bambusoideae* and *Salicaceae*



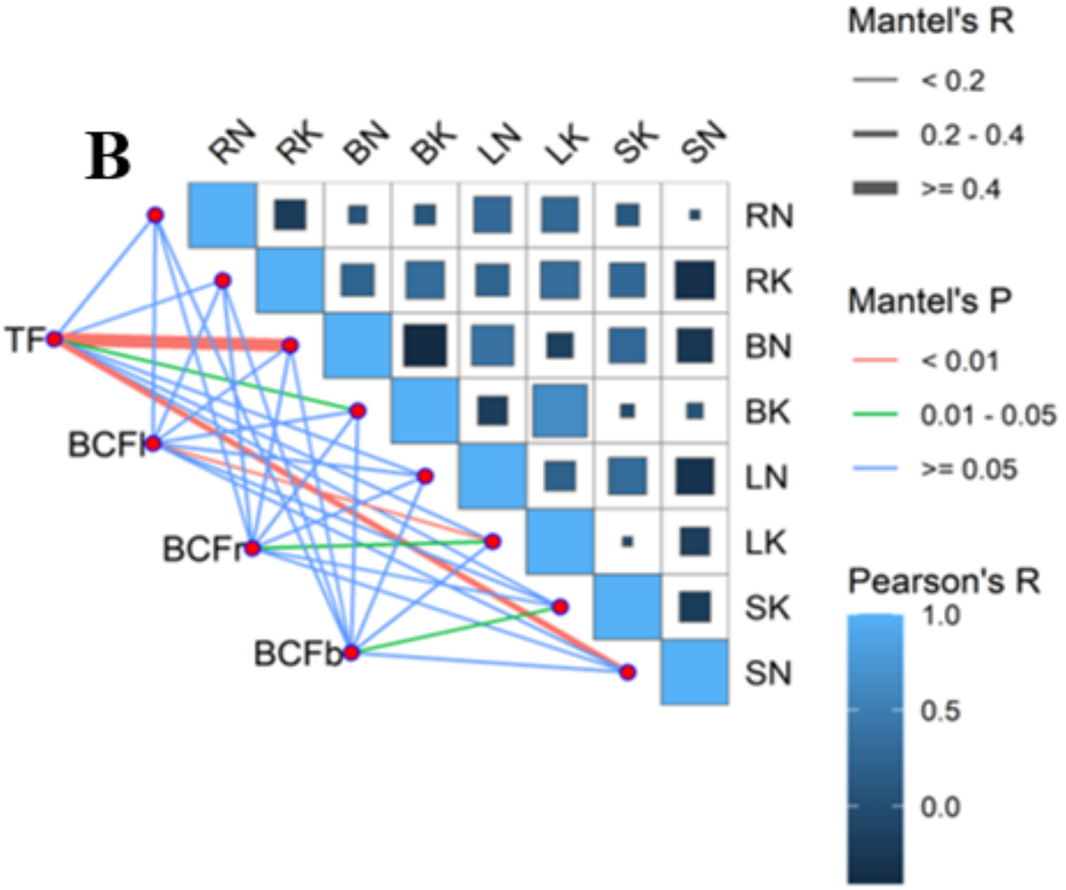


Figure 22. Mantel tests the importance values of the different translocation and accumulation parameters for different plant nutritional functional traits. The color gradient represents the Spearman correlation coefficient under pairwise comparisons of environmental factors. Edge width corresponds to Mantel's r statistic of distance correlation, and edge color indicates statistical significance (A: *Bambusoideae*, B: *Salicaceae)* .

Figure 22 reveals significant differences in the mechanisms of Cd transport and enrichment between the two plant families. The correlation of bamboo plants was generally low. The results of the Mantel analysis showed that most variables had a weak correlation with TF and BCF (R value <0.2), and only a few parameters (such as TF and BK, BCF_l and RK) had a moderate correlation (R value = 0.2-0.4). In terms of statistical significance, most of the correlations were not significant ($P \geq 0.05$), indicating that the Cd transport and accumulation of bamboo plants is less dependent on nutritional traits and may be more affected by external environmental factors. In addition, the Pearson correlation matrix shows that the leaf traits LN and RN, LN and LK of bamboo plants are strongly positively correlated, while BK and SN are strongly negatively correlated.

In contrast, *Salicaceae* plants showed higher correlations and significance. The results of the Mantel analysis showed that SN and BN were moderately or highly correlated with TF and were significantly correlated. In addition, LK was significantly correlated with BCF_l and TF, indicating that LK content played a key role in the aboveground transport of Cd in *Salicaceae* plants. Meanwhile, the Pearson correlation matrix showed that BK was strongly positively correlated with LK, while BN was strongly negatively correlated with BK, indicating that the Cd transport and enrichment capacity of *Salicaceae* plants is highly dependent on aboveground organ traits, maintaining the nitrogen and potassium balance under Cd stress to maintain Cd transport to the aboveground parts.

4.2.5 Nutritional functional traits and discriminant analysis of plants in the *Salicaceae* and *Bambusoideae* (Discriminant model construction)

A sample set of 8 nutrient functional traits using 7 plant organs was subjected to Fisher discriminant analysis in the SPSS 27 program to obtain discriminant function coefficients and construct a discriminant model. The discriminant model established is as follows:

$Y1(\text{Moso}) = 28.129X1+0.252X2+98.178X3+6.833X4+38.582X5+(-1.123X6)+0.278X7+32.665X8-237.627$

$Y2(\textit{D. asper}) = 28.87X1+(-0.711)X2+91.313X3+9.923X4+71.404X5+(-0.865X6)+0.069X7+28.903X8-281.585$

$Y3(\textit{D. strictus}) = 49.640X1+0.705X2+119.238X3+7.190X4+63.989X5+(-3.295X6)+0.206X7+30.714X8-353.741$

$Y4(\text{Csala}) = 26.167X1+0.609X2+27.208X3+0.835X4+14.401X5+(-0.586X6)+0.016X7+20.663X8-44.574$

$Y5(\text{Tora}) = 14.615X1+0.193X2+25.34X3+1.329X4+14.8X5+(-0.067X6)+0X7+23.299X8-30.348$

$Y6(\text{Pegaso}) = 11.857X1+0.276X2+18.812X3+2.073X4+20.122X5+0.054X6+0.001X7+17.943X8-29.369$

$Y7(\text{AF2})= 15.899X1+0.457X2+25.548X3+1.701X4+14.794X5+0.222X6+0.007X7+22.095X8-36.911$

The nutritional traits of the eight plant species in the training sample set were substituted into the corresponding discriminant models to test their discriminant effect, as shown in Table 14.

Table 14. Discriminate Function predicted Classification Results of training Samples of 7 species of Plants

	D.strictus	'Tora'	'AF2'	Moso	*D.asper*	'Csala'	'Pegaso'
D. strictus	100.0	0	0	0	0	0	0
'Tora'	0	100.0	0	0	0	0	0
'AF2'	0	0	88.9	0	0	11.1	0
Moso	0	0	0	100.0	0	0	0
D. asper	0	0	0	0	100.0	0	0
'Csala'	0	11.1	0	0	0	88.9	.0
'Pegaso'	0	0	22.2	0	0	0	77.8

a : 93.7% of original group cases correctly classified.

The discriminant scatter plot of the classification results for the training sample set of seven plant species (Fig. 21) shows that the classification centers of the four *Salicaceae* plants are relatively close to each other; there are misclassifications between ‘AF2’ and ‘Csala’, ‘Csala’ and ‘Tora’, and ‘Pegaso’ and ‘AF2’, but the overall accuracy is high.

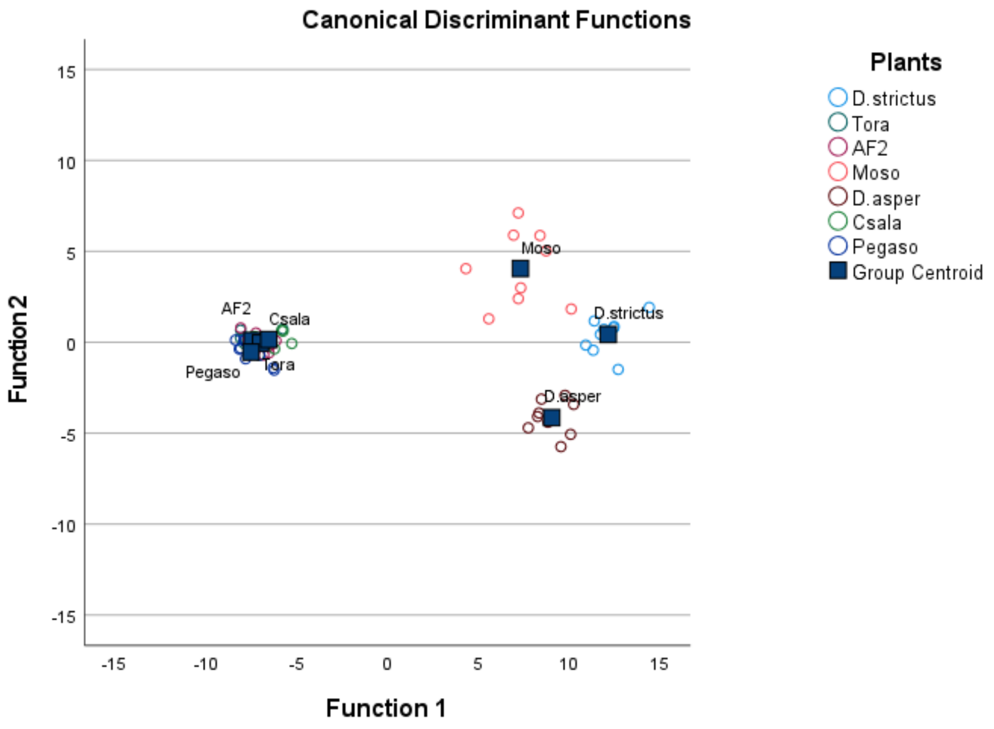


Figure 23. Canonical Discriminate Functions of training Samples of 7 species of plants

The test sample set identification model was further verified using the five plants from the first year, and the results are shown in Table 15.

Table 15. Results of testing Samples of first year 5 species verify Discriminate Function

	‘Tora’	Moso	*D.asper*	‘Csala’	‘Pegaso’
‘Tora’	0	100.0	0	0	0
Moso	0	33.3	55.6	0	11.1
D. asper	0	100	0	0	0
‘Csala’	0	100	0	0	0
‘Pegaso’	0	100	0	0	0

a : 6.66% of original group cases correctly classified.

The results of the classification model prediction using the training sample set of 7 plants in the second year and the test sample set of 5 plants in the first year showed that the identification model based on Fisher discriminant analysis of nutritional functional traits had a low accuracy in distinguishing plants, with a correct recognition rate of only 6.66%. This result reflects the limitations of the Fisher discriminant analysis model based on nutritional functional traits in plant classification applications. My finding suggests that the main reason for this result is the significant differences in field conditions, especially the severe impact of high temperatures in the first year. Such extreme climatic conditions have caused considerable disruption to the plant growth environment, which may have led to increased volatility in the data on nutritional traits, thereby affecting the stability and accuracy of the discriminant model. In addition, changes in the physical and chemical properties of the soil, nutrient supply and other microenvironmental conditions in the field in different years may have further exacerbated the differences in plant functional traits, resulting in poor model performance when applied across years. Therefore, the applicability of the model in the complex field environment needs to be further optimized.

Due to the milder climatic conditions in the second year, the variability of the field environment was smaller, the data on the nutritional traits of plants were more consistent, and the prediction accuracy of the model for the classification results was relatively improved. This shows that under stable environmental conditions, the Fisher discriminant analysis model based on nutritional functional traits can better capture the classification characteristics of plants and has certain application value. Therefore, although the model has limited performance across years and under external interference, it can still be used as an effective tool for plant classification and identification when the climate and field environment are relatively stable. In the future, the model should be optimized using long-term monitoring data to enhance its applicability and robustness under complex field conditions.

4.2.6 Discussion

4.2.6.1 The stimulating effect of Cd on plant photosynthesis

Cd is considered to have an inhibitory effect on plant growth and photosynthesis. However, under certain conditions, low concentrations of Cd have been observed to stimulate photosynthesis in some plants. This contradiction is often attributed to the dual role of Cd as both a stressor and a potential enhancer of metabolic processes (Li et al., 2015; Jia et al., 2015; Liu et al., 2017). For example, 2.0 mg kg $^{-1}$ of Cd treatment increased the photosynthetic rate of rice (Shennong 265) as well as the photosynthetic rate, intercellular CO_2 concentration, stomatal conductance, and transpiration efficiency of rice (Shenda 6) (Liu et al., 2017). Zn and Cd transcribed 161 common genes for photosynthesis in *Sedum alfredii* up-regulation, and Cd treatment at 5 μM had a significant stimulatory effect on plant chlorophyll fluorescence parameters, chloroplast size and chlorophyll content (Tang et al., 2016). In another study, Cd treatment below 10 mg kg^{-1} significantly increased the net photosynthetic rate (P_n), chlorophyll carotenoid content, effective quantum yield, and photochemical burst coefficient qP of *Lonicera japonica* Thunb. but significantly suppressed it above 25 mg kg^{-1} (Jia et al., 2015). In addition, *Elsholtzia argyi* leaves also exhibited significant increases in F_v/F_o, F_v/F_m, and qP within 5-15 μmol L^{-1} concentrations (Li et al., 2015).

In this study, a positive stimulation of chlorophyll content by Cd was observed in the first year in three plants 'Csala', Moso and *D. asper* (Fig. 12). Similarly, this effect was still observed in Moso and 'Csala' under T2 treatments in the second year (Fig. 13), suggesting that these two plants have strong adaptive capacity and metabolic regulatory mechanisms to Cd stress. In addition, we also observed an increase in quantum yield of

Moso (Fig. 14). This may be due to its ability to maintain higher photosystem II (ΦPSII) efficiency at high Cd concentration, which is related to the enhancement of photoprotective mechanism and electron transport chain of Moso, which maintains higher light energy conversion efficiency under Cd stress by accelerating the repair of ΦPSII reaction center and reducing photochemical damage. However, the degree of response to Cd-induced photosynthetic stimulation varied significantly among species. The response of different plants to Cd stress was not only reflected in changes in chlorophyll content, but also significantly affected their photochemical efficiency (Fig. 14). For Moso, this Cd-stimulating effect may be associated with its strong antioxidant capacity and root regulation, characteristics that may help it to effectively cope with Cd-induced ROS accumulation, thereby reducing damage to the photosynthetic organs (Pokora & Tukaj, 2010). At the same time, Cd may enhance the uptake and partitioning of key nutrients (Mg^{2+}, Fe^{2+}), which play an important role in maintaining chlorophyll structure and photosynthetic processes, by affecting metabolic pathways in Moso (Yang et al., 2023). Although 'Csala' did not significantly change quantum yield in the second year despite still showing an increase in chlorophyll content and even had a decreasing trend under T2 treatment (Fig. 14), which may reflect the gradual inhibitory effect of Cd on ΦPSII under long-term exposure. Overall, Cd has a positive stimulatory effect on plant photosynthesis under specific conditions, but this effect is significantly dependent on species, stress concentration, and environmental conditions. The outstanding performance of Moso demonstrated its adaptability and photosynthetic efficiency advantage in Cd-contaminated environments.

4.2.6.2 The connection between the functional traits of nutrients and phytoremediation

While past studies have typically analyzed the physiological and ecological responses of plants under stress conditions, the theory of leaf and root economic profiles suggests significant variability in resource utilization and allocation by different organs (Kramer-Walter et al., 2016). This theory emphasizes that different organs of a plant may adopt different functional strategies when adapting to stressful environments, such as leaves tend to fast acquisition and efficient use of resources to maintain photosynthesis and transpiration, which are the main ways for plants to acquire external energy and matter, while roots show more efficient fixation and storage capacity of resources to enhance the acquisition of below-ground resources and the soil's isolation of harmful substances in the soil (de la Riva et al., 2018). This functional differentiation among different organs is not only one of the basic adaptive mechanisms for plants to cope with environmental stresses, but also an important survival strategy developed during their long-term evolution (Lozano et al., 2022). In addition, resource allocation among organs and functional trait responses are also regulated by the overall metabolic strategies of plants. For example, acquisitive plants usually exhibit high photosynthesis rates and rapid growth, but their root systems are weak in resource fixation and often require more external resource support, whereas conserved plants are characterized by lower photosynthesis rates and slow growth, but their root systems are able to efficiently fix resources and sequester harmful substances, which reduces physiological and metabolic stresses under stress conditions (Kong et al., 2019). This trade-off between conservation and acquisition strategies not only reflects the differences in plant adaptation to environmental conditions but also provides a theoretical basis for exploring the accumulation and translocation mechanisms of plants under stress conditions.

In this article, a great number of correlation analyses were conducted with the aim of exploring the trends and correlations between changes in various nutrient-functional traits in response to Cd stress. Here, my dissertation is based on the theoretical framework of plant economic spectrum and functional traits (Reich, 2014) and combines experiments to propose three queries: 1) Are the tested plants accumulation-dominant or translocation-dominant? How does each organ perform? 2) Are the plants dominated by conservative or acquisition strategies? How did each organ perform? and 3) Do nutrient functional traits have the potential to predict phytoremediation?

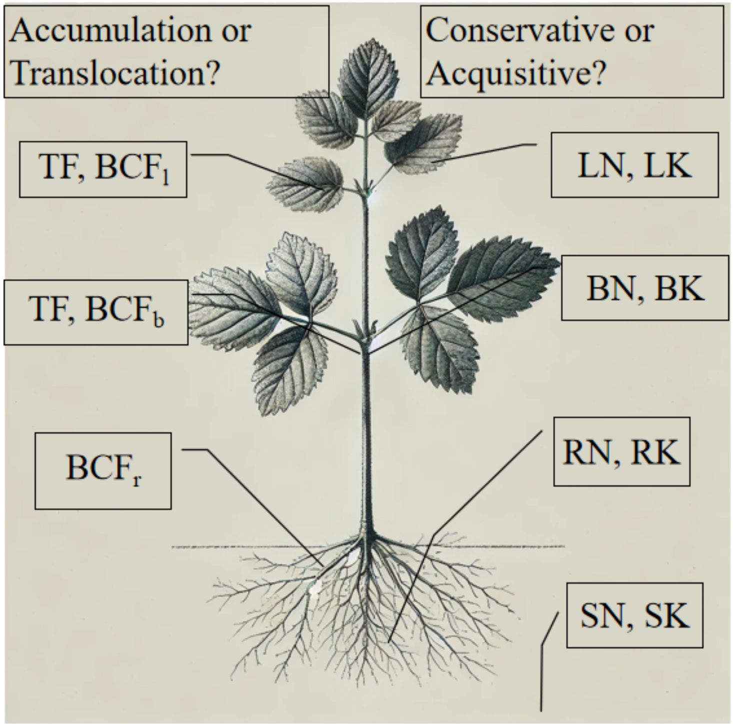


Figure 24. Bridging the gap between functional traits and phytoremediation

4.2.6.3 Accumulation or translocation?

The previous conclusions indicate that the roots and leaves of the tested *Bambusoideae* and *Salicaceae* plants are the main organs of Cd accumulation, respectively. However, the consistency and variability of the strategies exhibited among the organs have not yet been clarified. The theory of the economic spectrum of plants suggests that rapid acquisition and processing of carbon, water, or nutrients by leaves, stems, or roots is advantageous only if all organ systems can rapidly acquire and process all resources, otherwise plants would have excess capacity, which would be both expensive and wasteful (Reich, 2014). Therefore, for the *Bambusoideae*, my dissertation hypothesis are: 1) the fixation of Cd in the roots by bamboo is a result of the root organs' dominance in order to protect the plant, and 2) after fixation of Cd in the roots by bamboo, the aboveground organs are repulsed by the transport of Cd, and therefore, the Cd accumulates mainly in the roots. For *Salicaceae*, my dissertation hypothesis are: 3) the extraction capacity of *Salicaceae* is a result of the dominance of the root organ, and the upper limit of extraction in the root determines the lower limit of accumulation in the aboveground parts; 4) the amount of aboveground accumulation in *Salicaceae* is related to the aboveground organ, and the stronger the physiological ability of the aboveground organ is the more it accumulates. These hypotheses imply that it is clear whether the organ response of plants under Cd stress is aboveground dominant or belowground dominant. In my dissertation, the clustered heat map (Fig. 16) obtained in the second year of the previous context is used as an example to explain the above hypotheses for each plant and is represented by Table 16.

Table 16. Hierarchical Table of Plant Translocation and Accumulation Parameters in the Clustered Heatmap of second Year

Plants	TF	BCF_r	BCF_b	BCF_l
Moso	1	3	2	3
D. asper	3	2	3	1
D.strictus	1	3	3	2
‘Csala’	2	1	3	3
‘Tora’	1	2	3	3
‘Pegaso’	2	2	2	2
‘AF2’	1	3	3	2

Note: 1 is the highest tier, 3 is the lowest tier

Because the smallest sets in a clustered heat map are categorized as a group of variables or samples at the bottom level. These elements have the highest similarity at a specific distance metric, usually reflecting direct relationships between variables or common characteristics of samples, and thus the smallest set can be considered to play a major role in the plant Cd allocation strategy. Thus, from Table 16,

Moso can be interpreted as: the root contributes the most, although leaves have the same level of action as roots, e.g. transpiration tension, but branches prevent upward transport of Cd.

D. asper can be interpreted as: the stem plays more contribution, but the root's ability to accumulate restricts more Cd accumulation.

D. strictus can be interpreted as: both roots and stems can accumulate more Cd, but leaves have a transporter inhibitory effect on Cd.

‘Csala’ can be interpreted as a strong inhibition of Cd accumulation by roots, but a strong facilitation of Cd transport by stems and leaves.

‘Tora’ can be interpreted as: moderate inhibition of Cd accumulation by roots, but strong positive effect of Cd transport by stems and leaves.

‘Pegaso’ can be interpreted as a balanced strategy with a balanced distribution of Cd among roots, stems and leaves, with no significant functional trait dominance.

‘AF2 can be interpreted as: strong promotion of Cd accumulation by roots and stems, but inhibition of Cd translocation by leaves.

From the above explanation, my dissertation further derived from the following table 17.

Table 17. Strategic performance of each organ

Plants	Roots	Branches	Leaves	Hypothetical
Moso	+	-	+	2
D. asper	-	+	-	1
D.strictus	+	+	-	2
‘Csala’	-	+	+	4
‘Tora’	-	+	+	4
‘Pegaso’	/	/	/	/
‘AF2’	+	+	-	3

Note: “+” represents an acquisitive strategy, “-”represents a conservative strategy, and “/” represents a balanced strategy.

Table 17 shows the strategy of each plant organ in Cd accumulation, and it can be found that this performance has a large difference at the organ level, although from the initial finding that the *Bambusoideae* has roots as the main organ of accumulation, and the *Salicaceae* has the aboveground as the main organ of accumulation. This difference reflects the significant differentiation of plants in resource allocation and functional traits among different organs. It has been shown that trait differentiation and opposing aboveground and belowground strategies may facilitate the invasion of Moso bamboo into subtropical broad-leaved evergreen forests, strongly supporting the ‘phenotypic divergence hypothesis’ (Wang et al., 2022). Although there are few studies on heavy metal phytoremediation-dominated traits, my dissertation suggests that this approach will help to understand the stress resistance and transport mechanisms of different plants and provide theoretical guidance for species selection for phytoremediation on real sites.

4.2.6.4 Conservative or Acquisitive?

After understanding the differences in performance on organs, further exploration of the role played by nutrient elements (N,K) in organs can help to understand the mechanisms. In dissertation, the experimental results of the second year are used as an example to explain the differences in the strategies of nutrient element traits in organs in combination with clustering heatmap (Fig. 16) and redundancy analysis (Fig. 19).

Moso's LN, LK were strongly negatively correlated with the three BCF parameters (Fig.

16), LN explained most of the variation in the RDA1 axis and was significantly negatively correlated with the three BCF parameters (Fig. 19 a), and Moso counteracted the upward translocation of Cd from the roots by increasing the N,K content of the leaves (acquisitive strategy), with a stronger role for N than K. This ‘high acquisition-low translocation’ strategy was reflected in the allocation of functional traits to Moso, particularly in the leaves, which showed a clear pattern of resource preferential utilization. This pattern may be realized through the following mechanisms: firstly, the increase in LN may have enhanced the efficiency of photosynthesis and transpiration, thus providing more energy and material support to the plant. However, the negative correlation of LN on BCF suggested that, despite the positive effect of increased LN on physiological metabolism, it might simultaneously inhibit further Cd translocate from roots to above-ground organs by enhancing the segregation of Cd by leaves. Secondly, the increase in LK provides critical support for cellular osmotic pressure regulation and ion homeostasis, and the important role of potassium in plant stress tolerance includes maintaining cell membrane stability and regulating Cd uptake by the root system.

The RDA plots revealed that RK and BN of *D. asper* explained most of the variation in the RDA1 axis (Fig. 19 b) and were significantly positively correlated with each parameter (Fig. 16, Fig. 19 b), suggesting that the plant exhibited a conservative strategy under stress. In addition, *D. asper* showed a conservative strategy for both root N,K, with Cd accumulating more in the roots rather than being translocated upwards. Stem N and K showed opposite strategies, revealing the adaptive functional differentiation of *D. asper* to Cd stress in different organs. The conservative strategy in roots was mainly reflected in the fixation and sequestration of Cd, with N and K content providing antioxidant capacity and osmotic pressure regulation support to root cells, thus mitigating the direct effects of Cd toxicity on root physiological functions. In contrast, the functional strategies of the stem were more diverse. The conserved strategy of N may be to support the structural and metabolic stability of the stem under Cd stress conditions. In contrast, the acquisitive strategy of K emphasizes the reduction of upward transport of Cd by the stem by increasing the K^+ concentration to modulate the activity of transporter proteins.

BK and LN of *D. strictus* explained most of the variation in the RDA1 axis (Fig. 19 c), where BK was significantly negatively correlated with each parameter, and LN was negatively correlated with TF, implying that the Cd accumulation capacity of *D. strictus* is mainly regulated by the above-ground organs. The acquisitive strategy of BK increased the accumulation of Cd at the roots of the plant but suppressed the transport of Cd in the plant. However, LN showed a conservative strategy probably to prioritize the protection of photosynthetic and transpiration functions of leaves, thus reducing the toxic effects of Cd on key physiological processes in leaves. This strategy reduces the accumulation of Cd in leaves by limiting the transport of Cd to aboveground organs, thus maintaining the stability of photosynthetic efficiency. This ‘low-translocation-high-protection’ strategy enabled *D. strictus* to maintain high metabolic stability in a Cd-stressed environment, while reducing interference with photosynthesis and transpiration.

The performance of poplars is more complex, with aboveground traits, especially LN, explaining more variation in both willows (‘Csala’ and ‘Tora’) (Fig. 19 d, e) and positively correlating with both TF and BCF (Fig. 16, Fig. 19 d, e), which is the same as that found by Gervais-Bergeron et al., (2021). This implies that by increasing the LN, willow promotes the upward translocation of Cd and aboveground accumulation, showing a clear ‘high translocation-high accumulation’ strategy. The increase in LN may be achieved by the following mechanisms: higher LN content indicates higher levels of proteins and enzymes in the leaves and branches, which may provide the basis for the expression of heavy metal transporter proteins. This may provide metabolic support for the expression of heavy metal transport proteins, thus enhancing the efficiency of Cd transport from roots to aboveground organs. In addition, high LN content may enhance Cd transport in plants by promoting transpiration pull in xylem conduits. The expression of this functional trait was also closely related to the stronger resource acquisition ability of willow. The increase in LN may provide more energy and carbon resources to the plant for coping with the metabolic demands under Cd stress conditions by enhancing the efficiency of photosynthesis. Meanwhile, the significant positive correlations of LN with TF and BCF indicated that willow could not only transport Cd efficiently but also achieve higher enrichment in leaves and branches. This property may reduce the toxic effects of Cd through leaf vesicle sequestration and chelation mechanisms, thus maintaining normal physiological functions in the aboveground. The significant role of LN reflects the priority of willow in resource allocation, showing a unique adaptive strategy to Cd-stressed environments. Notably, the organs in ‘Pegaso’ showed a balanced strategy, with RN and BN explaining most of the variation in the RDA1 axis and facilitating the accumulation and translocation of Cd to the stem, a phenomenon that is a result of the combined action of both belowground (roots) and aboveground organs (stems) (Fig. 19 f). The increase in RN may have enhanced the Cd trapping capacity of the root system. The higher nitrogen content of the roots indicated their strong metabolic activity and ion uptake capacity, which effectively promoted the uptake of Cd from the soil to the roots by regulating ion channels and transport proteins. Meanwhile, the vesicle sequestration mechanism in the stem may reduce the toxicity of Cd to cellular metabolism by chelating Cd into metallothionein or organic acids. In addition, the increase in BN may have supported the activity of transporter proteins, which further enhanced the efficiency of Cd partitioning. This balanced strategy of synergistic action between below- and aboveground organs enables ‘Pegaso’ to efficiently allocate resources under Cd stress while mitigating the toxicity of Cd on key physiological functions. Similar root, stem co-promotion as ‘Pegaso’ can be found in another poplar ‘AF2’, such as RK, BK was positively correlated with Cd accumulation capacity, and the acquisitive strategy of LK inhibited further Cd translocation from stems to leaves.

4.2.6.5 Do nutrient functional traits serve as a predictor of phytoremediation?

A significant number of studies have used functional traits as a tool for species screening in restoration ecology in a variety of range contexts (Fort & Freschet, 2020; Grimond et al., 2023; Kramer-Walter et al., 2016). However, the prediction of plant responses under stress from this range of quantitative trait data remains constrained by uncertain environmental changes (Anderegg, 2023). Liu et al., (2021) suggested that improving the predictive power of functional traits for ecosystems requires matching between individuals and ecosystems to screen for appropriate traits rather than measuring them broadly. As a result, trait screening in the context of phytoremediation is gaining attention and is being incorporated as a tool to address this prediction problem (Wang et al., 2024; Liang et al., 2024; Gervais-Bergeron et al., 2021).

Recent studies have shown that willow predicts phytoremediation services better than traditional taxonomy by means of traits, and that leaf nitrogen content is a valid predictor of phytoextraction (Gervais-Bergeron et al., 2024). In dissertation, we extend this prediction to the poplar and bamboo subfamilies to identify valid predictors. Mantel analysis (Figure 22) revealed that the stem potassium content of *Bambusoideae* was significantly correlated with TF of the three bamboo species, which had the potential to be used as a predictor. Whereas the transit silver of *Salicaceae* was significantly correlated with BN content, along with $R \geq 0.4$, which can be used as a predictor. This result may support the potential application of functional traits in predicting phytoremediation efficiency. The possibility of BK as a valid predictor in the bamboo subfamily suggests that potassium distribution in plants has an important influence on Cd transport mechanisms. This may be due to the critical role of potassium in regulating osmotic pressure in plants, maintaining stability of cellular stress response and facilitating ion transport. When Cd enters the plant root system, high potassium levels within the stems may promote efficient Cd transport from roots to aboveground by increasing transpiration pull and maintaining ionic balance in xylem conduits. The discovery of this functional trait not only provides a more targeted screening index for the restoration potential of *Bambusoideae* plants but also provides a theoretical basis for further optimizing their planting management.

Meanwhile, BN was significantly correlated with the Cd TF in *Salicaceae*, further revealing the importance of branches as an intermediate station for Cd accumulation and transport. The high BN content may reflect the higher protein and enzyme activities of branches, which provide stronger metabolic support for Cd sequestration, transport and sequestration. This phenomenon also suggests that branches not only serve as temporary storage organs for Cd but also may mitigate the direct toxicity of Cd to leaf photosynthesis by regulating the partitioning of Cd between branches and leaves. The prominence of this trait in *Salicaceae* makes BN an important predictor for screening *Salicaceae* species for efficient remediation of Cd pollution. In addition, the analyses in my dissertation show that the screening and application of functional traits are not static, but are closely related to specific plant species, remediation targets and environmental conditions. However, the results of this dissertation are still preliminary, and future studies need to test more plants to identify generic predictive traits.

5 CONCLUSIONS AND RECOMMENDATIONS

5.1 Effect of high temperature in pot plant experiments

The results of this study demonstrate that temperature exerts a significant impact on the phytoremediation capacity of plants, with different species exhibiting distinct responses under varying thermal conditions. Overall, high temperatures exerted both promoting and inhibitory effects on the remediation efficiency, which contributed to the interannual variations observed during the experiment.

In the first year, elevated temperatures enhanced the Cd accumulation capacity of most plants, leading to a significant improvement in overall remediation efficiency. Under high-temperature conditions, plant metabolism accelerated, facilitating the transport of water and solutes, which in turn promoted the translocation of Cd from soil to aboveground tissues. Consequently, the total Cd accumulation across treatment groups was generally higher in the first year. However, high temperatures also negatively affected the survival and rooting rates of certain species, such as *D. strictus* and 'AF2,' resulting in increased mortality during the early growth stages and constraining further improvements in remediation performance.

In the second year, when temperatures were milder, significant interspecies differences in Cd accumulation capacity became apparent. Some taxa, such as 'Csala' and *P. edulis* (Moso), maintained high levels of Cd accumulation, whereas others experienced a decline in their remediation performance. These variations likely stem from the differential adaptability of species to changing thermal conditions. For instance, 'Csala' continued to exhibit high Cd accumulation in the second year, reflecting its robust adaptive mechanisms to environmental variability. Conversely, other species may have lacked sufficient adaptive traits or experienced reduced stimulation under milder conditions, leading to diminished remediation efficiency. Additionally, moderate temperatures appeared to enhance root development in certain species. For example, *Bambusoideae* plants exhibited higher SN in the second year, likely due to their enhanced root absorption capacity and more efficient resource utilization under stable environmental conditions.

The differential responses of species to temperature variations significantly influenced the outcomes of this study. Certain plants exhibited stimulated photosynthesis under high-temperature conditions, characterized by increased chlorophyll content and improved photochemical efficiency. For example, Moso demonstrated exceptional photosynthetic efficiency and remediation performance under combined heat and Cd stress. However, as the experiment progressed, prolonged exposure to high temperatures and Cd stress began to exert inhibitory effects on some species. For instance, while 'Csala' maintained increased chlorophyll content in the second year, its photochemical efficiency began to decline, indicating that prolonged stress might have compromised the stability of its photosynthetic system.

5.2 Species-specificity of Cd accumulation

The results of this study indicate significant differences in Cd accumulation capacity and distribution patterns between *Bambusoideae* plants and *Salicaceae* plants, reflecting their distinct strategies for adapting to polluted environments. *Bambusoideae* plants primarily accumulate Cd in their roots, with significantly lower accumulation observed in aboveground organs compared to *Salicaceae*. This "low translocation-high fixation" strategy enables *Bambusoideae* plants to effectively reduce the toxic effects of Cd on photosynthesis and other physiological processes, thereby maintaining high tolerance levels in contaminated environments. However, this approach also limits the translocation of Cd to aboveground tissues, resulting in relatively lower overall Cd accumulation capacity.

In contrast, *Salicaceae* plants exhibit a strong capacity for Cd translocation and accumulation in aboveground organs, adopting a "high translocation-high accumulation" strategy. In polluted environments, *Salicaceae* plants rapidly translocate absorbed Cd from roots to aboveground tissues, maintaining high accumulation efficiency. Experimental results demonstrated that some *Salicaceae* species maintained stable translocation factors and accumulation coefficients under varying Cd treatment conditions, highlighting their strong adaptability in Cd uptake and translocation.

The differences in Cd accumulation characteristics between bamboo subfamily and *Salicaceae* plants determine their suitability for different applications in phytoremediation. *Bambusoideae* plants are well-suited for phytostabilization, effectively immobilizing Cd and preventing its migration and dispersion in the environment. In contrast, *Salicaceae* plants, with their superior Cd absorption and translocation capabilities, are better suited for phytoextraction applications. These species-specific characteristics provide diverse options for addressing varying scenarios in pollution management.

5.3Effect of Cd on the content of N and K in plants

The results of the study indicate that the impact of Cd on N and K content in plants varies significantly and exhibits distinct patterns across different plant species and organs. Overall, Cd treatment had no significant effect on the total N content in plants but caused notable changes in the distribution of N and K among plant organs. Leaves, as the primary organs for photosynthesis and transpiration, consistently exhibited higher N and K content compared to roots and branches. Furthermore, leaves and roots were the most sensitive organs to Cd stress.

In the first year of the experiment, Cd significantly influenced leaf N content in Moso and *D. asper*, with LN increasing significantly as Cd concentration rose. In contrast, *Salicaceae* plants displayed diverse response patterns. For instance, the leaf N content of ‘Tora’ increased with increasing Cd concentration, whereas ‘Csala’ and ‘Pegaso’ showed a decreasing trend. These differences reflect the distinct adaptive strategies employed by *Salicaceae* plants under Cd stress. Additionally, Cd had a pronounced effect on K content in roots, underscoring the role of roots as the primary target for Cd-induced disruption of potassium metabolism.

In the second year, as high-temperature stress diminished, nutrient content changes in plant organs became more stabilized. While Moso exhibited an increase in leaf N content under certain treatments, the leaf N content of *D. asper* and *D. strictus* showed low sensitivity to Cd treatment. Compared to *Bambusoideae*, *Salicaceae* plants exhibited more complex changes in N and K content. For example, the leaf N content of ‘Csala’ and ‘Tora’ decreased significantly under Cd treatment, but the extent and pattern of this decrease were inconsistent. Similarly, leaf K content displayed contrasting trends, with ‘Csala’ showing an increase and ‘Tora’ a decrease.

5.4 Understand plant strategies of Cd stress from functional traits

This research indicated that functional traits provide a deeper understanding of plant adaptive strategies under Cd stress and reveal differences in Cd accumulation and distribution among species and plant organs. The experimental results demonstrate that different plants exhibit distinct trait differentiation and resource allocation strategies under Cd stress, which directly influence their remediation capacity in polluted environments.

Bambusoideae, such as Moso, adopted a "high acquisition-low translocation" strategy by increasing the N and K content in leaves, thereby limiting the upward translocation of Cd from roots to aboveground parts. This reduces the toxic effects of Cd on critical physiological functions in leaves. In contrast, *D. asper* employed a "conservative strategy" by enhancing N and K accumulation in roots, fixing more Cd in the root zone, and slowing its upward translocation. Additionally, different organs exhibit distinct adaptive differentiation, with roots primarily focused on maintaining stability, while stems display more diverse resource allocation strategies.

Salicaceae plants exhibited more complex adaptations. For instance, functional traits of ‘Csala’ and ‘Tora’ emphasized the rapid translocation of Cd to aboveground parts, with leaf N content showing a significant positive correlation with Cd translocation and accumulation. This "high translocation-high accumulation" strategy enhances remediation capacity in aboveground organs while alleviating Cd toxicity in roots. ‘Pegaso’ adopted a "balanced strategy," utilizing coordinated action between roots and stems to achieve efficient Cd accumulation and distribution.

Furthermore, the study revealed that functional traits can serve as important predictors of plant remediation capacity. For example, stem K content in *Bambusoideae* plants showed a significant correlation with Cd translocation factors, while branch N content in *Salicaceae* plants correlates with Cd accumulation capacity. These findings highlight the predictive potential of functional traits in assessing plant responses to Cd stress, providing a scientific basis for optimizing phytoremediation strategies and applications.

6 NEW SCIENTIFIC RESULTS

6.1 Differences in Cd accumulation of bamboo, poplar and willow

This study presents the first scientific investigation into the significant differences in Cd accumulation capacity and distribution patterns between *Bambusoideae* and *Salicaceae* taxa under Cd stress. Based on adaptive strategies and functional trait performance, *Bambusoideae* species primarily adopted a "low translocation-high fixation" strategy, with Cd predominantly accumulated in the roots. In contrast, *Salicaceae* taxa exhibited a "high translocation-high accumulation" strategy, rapidly translocating Cd from roots to leaves and branches, thus achieving higher Cd extraction efficiency.

6.2 The first time using new bamboo plant material in Cd phytoremediation

According to our findings two *Bambusoideae* species, *Dendrocalamus asper*, and *D. strictus* were used for the first time for phytoremediation purposes and proved that under high temperature conditions *D. asper* was more suitable for phytoremediation experiments especially for phytostabilization by the roots.

6.3 The role of functional traits in heavy metal phytoremediation

In my dissertation, the concept of functional traits is introduced for the first time in heavy metal phytoremediation, and the understanding and application of plant economic spectrum in heavy metal phytoremediation are discussed at three levels: plant, organ and nutrient element. These traits influenced the uptake, translocation and accumulation capacity of heavy metals by modulating the resource acquisition, allocation and utilization strategies of plants.

6.4 Nutrient functional traits as predictors of heavy metal phytoremediation

This dissertation concluded that branch potassium(BK)and branch nitrogen(BN) have the potential to serve as effective predictors of heavy metal transport efficiency in *Bambusoideae* and *Salicaceae* taxa, respectively. The results demonstrate that functional traits such as BK and BN are closely linked to the translocation and accumulation of heavy metals, providing a practical tool for assessing phytoremediation potential. Additionally, leaf nitrogen has been identified as a viable predictor for translocation factor in willow, highlighting its significance in evaluating the phytoextraction capacity of specific taxa.

7 SUMMARIES

7.1 Introduction

This study focuses on the impact of heavy metal Cd contamination on plants, investigating their adaptive strategies and remediation capabilities under varying environmental conditions and Cd stress. Cd pollution is a global environmental issue, primarily originating from agricultural practices, industrial activities, and waste disposal, posing a severe threat to soil health and ecosystem stability. Phytoremediation, known for its cost-effectiveness and environmental friendliness, has gained significant attention, with *Bambusoideae* and *Salicaceae* taxa demonstrating notable potential in heavy metal remediation.

Bambusoideae taxa, characterized by high biomass and extensive root systems, are suitable for stabilization-based remediation strategies, effectively immobilizing Cd in the soil. In contrast, *Salicaceae* species, such as willows and poplars, are recognized as ideal candidates for extraction-based remediation due to their rapid growth and high Cd accumulation capacity. However, significant differences in functional traits, nutrient allocation, and Cd accumulation capacities among species influence their remediation efficiency and adaptability.

This study aims to explore the patterns of Cd accumulation and distribution in *Bambusoideae* and *Salicaceae* plants from the perspective of functional traits, considering field environmental factors and nutrient dynamics. By elucidating the underlying mechanisms and optimizing strategies for phytoremediation, this research provides scientific insights and practical guidance for the remediation of Cd-contaminated soils.

7.2 Material and Methods

This study employed a combination of pot plant experiments and laboratory analyses to systematically evaluate the remediation capabilities and functional traits of *Bambusoideae* and *Salicaceae* plants under Cd stress. Field experiments were conducted in Cd-contaminated soils, with representative *Bambusoideae* species (*P. edulis*, *D.asper*, *D.strictus*) and *Salicaceae* taxa ('Csala', 'Tora', 'pegaso', 'AF2') selected as the research subjects. Experimental groups were established with varying Cd concentrations to facilitate comparative analyses.

Plant organ samples (leaves, stems, roots) were collected at the regular end of the experiments, and standardized experimental methods were used to measure Cd content, N, and K levels. Functional trait data, including TF and BCF, were calculated to assess the Cd translocation and accumulation capacities of the selected plants.

Furthermore, environmental factors such as temperature and soil nutrient variations were incorporated into the analysis. RDA and clustering heatmap analysis were performed to elucidate the relationship between functional traits and Cd remediation efficiency. Statistical analyses were applied to validate the significance of the results, providing quantitative evidence for the predictive potential of functional traits. The systematic and comprehensive approach of this study provides robust technical support for advancing phytoremediation research.

7.3 Results and Discussion

This study systematically revealed significant differences in Cd accumulation and distribution patterns, as well as functional trait characteristics, between *Bambusoideae* and *Salicaceae* taxa. The findings demonstrate that *Bambusoideae* species adopt a "low translocation-high fixation" strategy by enhancing root Cd fixation, thereby limiting Cd translocation to aboveground parts. This strategy effectively mitigates Cd toxicity to leaf photosynthesis and metabolic functions, enhancing the stabilization-based remediation capacity of *Bambusoideae* species in polluted soils and their resistance to Cd stress. In contrast, *Salicaceae* species exhibit a "high translocation-high accumulation" strategy, rapidly translocating Cd from roots to leaves and branches, thus achieving higher Cd extraction efficiency. However, this approach also increases the risk of Cd toxicity in aboveground tissues, necessitating functional trait adjustments to maintain physiological stability.

Functional trait analyses further highlighted the critical role of key nutrients in Cd accumulation and distribution. In *Bambusoideae* species, BK showed a significant correlation with Cd TF, indicating that high BK contributes to root Cd fixation and reduces the risk of Cd migration to aboveground parts. In *Salicaceae* taxa, BN and LN significantly influenced Cd accumulation and translocation. LN was identified as a crucial predictor of Cd translocation efficiency in *Salicaceae* taxa. Moreover, increased BN enhanced the dynamic balance of Cd distribution in aboveground parts, alleviating Cd toxicity in leaves.

Environmental factors, such as temperature fluctuations, also had a significant impact on the remediation capacity of plants. Under high-temperature conditions, increased plant transpiration accelerated the translocation of Cd from soil to aboveground tissues. *Bambusoideae* species exhibited greater sensitivity to climatic variations, with their remediation efficiency more susceptible to environmental fluctuations, whereas *Salicaceae* taxa demonstrated higher adaptability and stability under varying environmental conditions.

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APPENDICES

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