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Chemical composition and ecological adaptation of *Populus* (Salicaceae) species and hybrids depending on soil and environmental conditions

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This review synthesizes two decades of research on the interplay between soil properties and genotype in shaping the chemical composition and adaptive traits of hybrid poplars (*Populus* spp.). The present review is grounded in a comprehensive survey of peer-reviewed literature published from 2000 to 2025. Out of approximately 400 identified documents, 100 were chosen according to their scientific validity, methodological soundness, and pertinence to the study's objectives. The search strategy incorporated databases including PubMed, PubChem, Google Scholar, Scopus, and ResearchGate, using keyword combinations such as *Populus* species & soil, *Populus* species & ecological role, and *Populus* species & pollutant uptake. Unlike previous summaries, it advances the field by highlighting novel insights into genotype soil–metabolite interactions, demonstrating how macro- and micro-nutrient uptake influences the accumulation of flavonoids, salicylates, and other polyphenolic derivatives. It also examines how trees respond to soil pH, organic matter, and contamination, including radionuclides, and how feedback *via* rhizosphere microbiomes and leaf litter decomposition regulates nutrient cycling and microbial biomass. Beyond integration, the review identifies critical gaps, notably the lack of long-term field validation of soil–microbiome–metabolite linkages and the need for directed breeding of poplar varieties with specific metabolite traits. By outlining how selective breeding, metabolomics, and chemical modification of plant-derived compounds can be harnessed for bio-based materials and pharmaceuticals, and by providing region-specific case studies in urban greening, phytoremediation, bioenergy, and agroforestry, this synthesis establishes a framework for translating biochemical insights into applied strategies for ecosystem restoration and sustainable land use.

1. Introduction

1.1 The ecological, pharmacological, and environmental importance of the genus *Populus* (Salicaceae)

The genus *Populus*, comprising around 30 tree species widely distributed across the Northern Hemisphere, plays a pivotal role in various scientific disciplines including ecology, pharmacology, and environmental science. These fast-growing deciduous trees are essential components of riparian and boreal ecosystems, offering a broad range of ecosystem services and biotechnological applications. Their ecological plasticity, rapid vegetative propagation, and rich phytochemical profiles make them valuable biological models for both fundamental and applied research.[1,2] *Populus* species are considered keystone taxa in riverine and temperate forest ecosystems. They contribute to soil stabilization, water regulation, carbon sequestration, and biodiversity enhancement. Their deep root systems reduce erosion and maintain stream bank integrity, while their annual leaf litter plays a critical role in nutrient cycling and microbial activity in forest soils. *Populus* plantations have been shown to have the ability to significantly improve degraded soils through increased microbial biomass and enhanced nitrogen and potassium cycling.[3] Additionally, *Populus* interacts heavily with mycorrhizal fungi and rhizosphere microbiota, forming complex networks that facilitate plant health and tolerance to abiotic stress. Their ability to colonize marginal soils, including post-industrial land and floodplains, makes them ideal candidates for ecological restoration and afforestation initiatives.[4,5]

Traditionally, *Populus* buds, bark, and leaves have been used in folk medicine to treat fever, inflammation, arthritis, and respiratory disorders. These therapeutic effects are attributed to a variety of bioactive compounds, including phenolic glycosides (such as salicin and populin), flavonoids, and terpenoids. Recent studies confirm the pharmacological potential of

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Populus extracts, demonstrating antioxidant, anti-inflammatory, antimicrobial, and even anticancer properties.[5]

For example, black poplar (*P. nigra*) leaf and bud extracts have shown significant inhibition of pro-inflammatory cytokines such as IL-1β, IL-6, and TNF-α *in vitro*. Additionally, balsam poplar (*P. balsamifera*) is rich in *p*-coumaric and caffeic acid derivatives, contributing to its antimicrobial and antioxidative capacity. These findings suggest the genus *Populus* could be an untapped resource in modern phytopharmacy and nutraceutical development.[6]

One of the most promising applications of *Populus* lies in phytoremediation—the use of plants to clean contaminated soils and water. Owing to their high transpiration rates and metal uptake ability, *Populus* species are effective in absorbing and stabilizing heavy metals such as cadmium, lead, and zinc, as well as organic pollutants like PCBs and petroleum hydrocarbons.[7] Hybrid poplars have been used in field-scale remediation projects across Europe and North America.[8]

Furthermore, their high biomass productivity and potential for short-rotation coppicing make them suitable for bioenergy production, aligning with goals of sustainable development and circular economy practices.

Populus species are well established as keystone taxa in forest and riparian ecosystems, valued for their ecological roles (Fig. 1), phytochemical richness, and wide-ranging applications from folk medicine to phytoremediation and bioenergy. While their contribution to soil stabilization, microbial networks, and pollutant uptake is broadly recognized, uncertainties remain regarding long-term effectiveness of large-scale phytoremediation projects and the variability of metabolite profiles across species and environments. We try to link soil factors to specific metabolite pathways and validating *Populus*-based strategies in field conditions to fully harness their ecological and biotechnological potential.

1.2 Relevance of studying chemical composition in relation to environmental and soil conditions

Understanding the chemical composition of *Populus* species in connection with environmental and soil conditions is essential for advancing ecological, pharmacological, and biotechnological applications. *Populus* trees exhibit a remarkable ability to adapt to diverse climatic zones, soil types, and ecological stressors.[9] This plasticity is closely linked to their secondary metabolism, which produces a range of bioactive compounds whose expression is highly sensitive to environmental factors. A number of investigations have illustrated that the phytochemical content of *Populus* species especially the concentration of phenolic compounds, flavonoids, terpenoids, and salicylates can considerably vary as a response to site conditions. For example, nutrient availability, soil pH, organic matter content, and heavy metal pollution all influence the synthesis and accumulation of these compounds in leaves, bark, and buds.[10,11] The regulation of secondary metabolism is mediated by key enzymatic pathways, including the phenylpropanoid pathway, which generates flavonoids, lignans, and salicylates from phenylalanine, and the mevalonate and methylerythritol phosphate pathways, which control terpenoid biosynthesis. These

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pathways are sensitive to environmental cues, allowing plants to modulate metabolite profiles in response to stress.

Soil composition, particularly levels of nitrogen, phosphorus, potassium, and trace elements such as zinc, iron, and manganese, affects enzymatic activity in these biosynthetic routes.[12] For instance, nitrogen fertilization has been shown to enhance flavonoid synthesis in *Populus nigra* leaves by increasing the availability of amino acid precursors for the phenylpropanoid pathway.[13] In contrast, plant growth and the activities of nitrogen-assimilating enzymes were more strongly influenced by nitrate availability and showed a positive association with nitrogen uptake efficiency. Based on shoot dry weight, these classifications were further supported by pronounced differences between the two genotypes in root architecture, nitrogen metabolic traits, and overall nitrogen use efficiencies (NUEs). Conversely, high soil salinity induces oxidative stress, leading to the upregulation of antioxidant phenolics, which function mechanistically as radical scavengers and metal chelators.[14] *Populus* trees growing on metal-contaminated soils accumulate heavy metals in their tissues and respond by elevating polyphenol and glutathione levels, highlighting the link between chemical adaptation and environmental stress.[15]

Beyond accumulation, the structural diversity of these secondary metabolites underlies their functional roles. Flavonoids, with hydroxylated aromatic rings, can chelate metal ions and quench reactive oxygen species. Phenolic acids such as *p*-coumaric and caffeic acids provide both antimicrobial activity and cross-linking in cell walls. Salicylates act as signaling molecules in plant defense, mediating systemic acquired resistance. Understanding these structure–function relationships is critical for predicting how environmental factors modulate chemical properties.

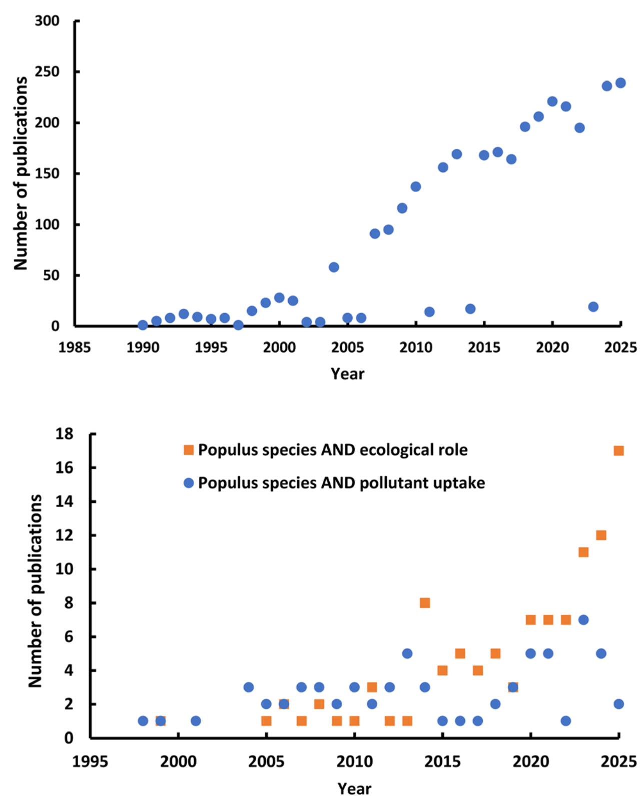

Fig. 1 Annual growth of scientific publications related to combination of keywords search: (A) *Populus* species; (B) *Populus* species AND ecological role; *Populus* species AND pollutant uptake, data extracted from https://pubmed.ncbi.nlm.nih.gov/, 28.9.2025.

Investigating these chemical environmental relationships provides insights into the ecological strategies of *Populus* species and their role as bioindicators of soil health. Because biochemical composition reflects local soil conditions, *Populus* trees are increasingly used in phytomonitoring and environmental diagnostics.[16] Variation in metabolite profiles among genotypes and hybrids also offers potential for selecting and breeding lines optimized for specific environmental or industrial purposes. From a pharmacological perspective, environmental modulation of secondary metabolite production is highly relevant. Bioactive compounds such as salicin, populin, and *p*-coumaric acid the key constituents of *Populus* extracts – exhibit anti-inflammatory, antioxidant, and antimicrobial activities.[17] Understanding of their biosynthesis, structural features, and stress-induced accumulation can inform strategies to optimize growth conditions, enhance yields, and improve the chemical quality of *Populus*-based pharmaceuticals.

Moreover, in the context of climate change, evaluating chemical responses to soil and environmental shifts becomes even more critical. Drought, soil degradation, and pollution can alter enzymatic fluxes in secondary metabolic pathways, ultimately impacting flavonoid, phenolic, and salicylate profiles. Such knowledge supports the development of resilient tree-based systems for land restoration, urban greening, and phytoremediation, while linking ecological insights with the chemical properties of plant-derived compounds for broader applications in biochemistry and industrial chemistry.[18]

Current evidence firmly establishes that the chemical composition of *Populus* is strongly modulated by soil and environmental conditions, with secondary metabolites acting as both adaptive responses and valuable bioactive compounds (Fig. 2).

While numerous studies confirm links between nutrient status, pH, contamination, and metabolite accumulation, the consistency and predictability of these responses across genotypes and long-term field conditions remain less clear. Following research focuses on integrating soil chemistry, genotype variation, and metabolomic profiling to identify stable biochemical markers, support phytomonitoring applications, and guide breeding programs aimed at enhancing both ecological resilience and pharmaceutical value.

1.3 Phytochemical composition of *Populus* species

Poplars are renowned for their abundant phenolics and flavonoids, which are key players in antioxidant, anti-inflammatory, antimicrobial, and antitumor activities. In-depth analyses of *P. nigra* buds reveal a complex mix of phenols, phenolic acids, phenylpropanoids, flavones (*e.g.*, apigenin, chrysin), flavanones

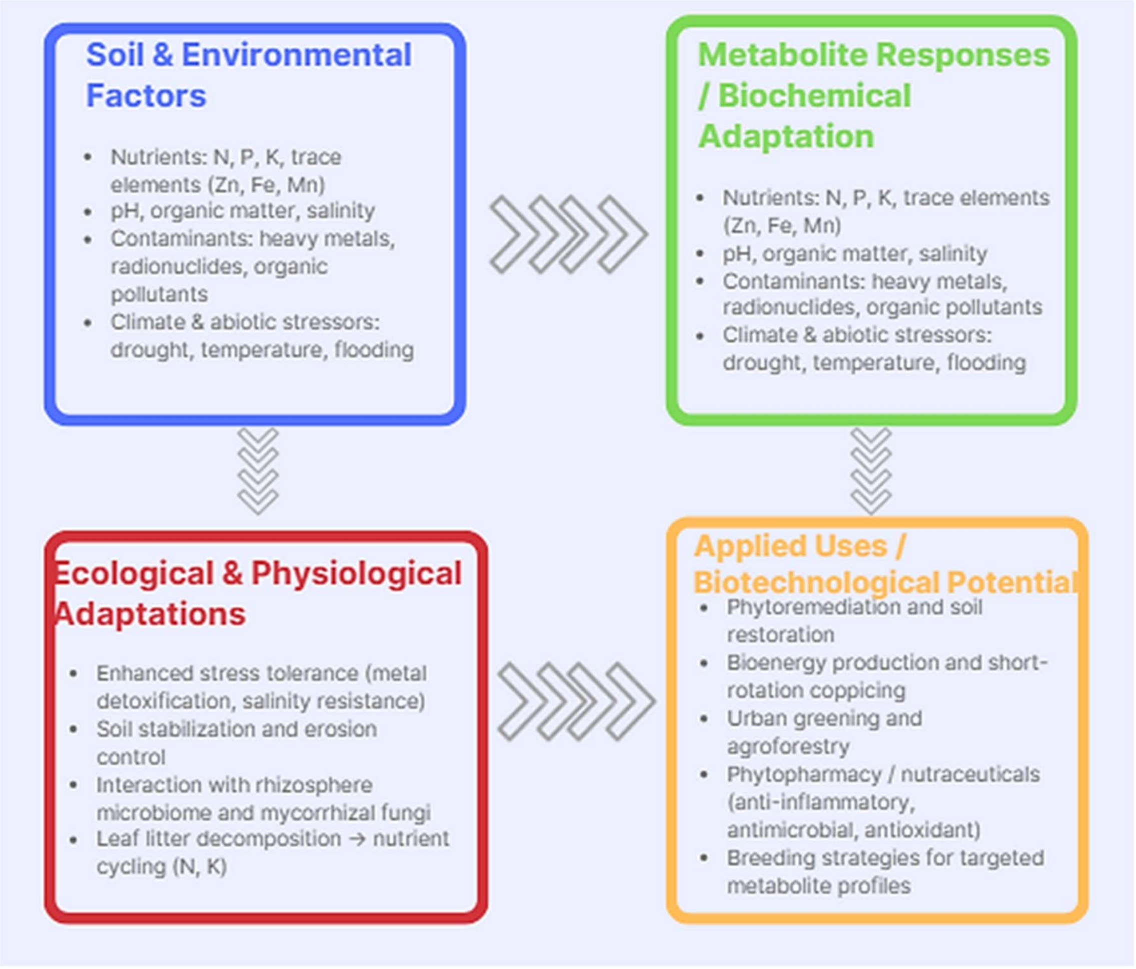

Fig. 2 Conceptual diagram: soil & metabolite & adaptation & application in *Populus*.

(pinocembrin, pinostrobin), caffeic and ferulic acids, and over 48 essential oil components.[19] These compounds collectively contribute to the bud's effectiveness in complementary medicinal uses such as anti-inflammatory and antimicrobial treatments.

A comprehensive review summarized 159 constituents phenolics, flavonoids, terpenoids from various parts of *Populus* species, indicating that many remain biologically untested.[20] *P. balsamifera* buds contain polyphenols like *p*-coumaric acid (as much as ~13 mg g^{-1}), cinnamic acid, pinobanksin, and salicin.[21] The extract composition in 27 samples of *Populus* buds covering different taxa was examined using ultra-high-performance liquid chromatography. The antibacterial activity noted is likely associated with the flavonoid content (*e.g.*, pinobanksin, pi-nobanksin-3-acetate, chrysin, pinocembrin, galangin, isosakuranetin dihydrochalcone, pinocembrin dihydrochalcone, and 2′,6′-dihydroxy-4′-methoxy-dihydrochalcone), hydroxycinnamic acid monoesters (*e.g.*, cinnamyl ester of *p*-methoxycinnamic acid, phenethyl caffeate, and prenylated isomers), and trace components such as the balsacones (Fig. 3).[22]

The majority of the identified compounds were phenolic and polyphenolic in nature, including free hydroxycinnamic acids, salicylate-like phenolic glycosides, monoesters and glycerides of hydroxycinnamic acids, as well as other polyphenols and a few non-polyphenolic substances. Among these, flavonoids constituted the largest group, with 73 compounds identified. This was followed by hydroxycinnamic acid monoesters (35 compounds), other polyphenols (22 compounds), hydroxycinnamic acid glycerides (13 compounds), salicylate-like glycosides (9 compounds), and free phenolic acids (6 compounds) (Fig. 4). Only four compounds were categorized as non-polyphenols, although most of the unidentified substances were likely to belong to this group as well.[22]

The shikimate pathway leads to the formation of shikimic acid, a central metabolic intermediate that serves as the primary precursor for the biosynthesis of the aromatic amino acids L-phenylalanine, L-tyrosine, and L-tryptophan, as well as a wide range of phenolic compounds. The pathway originates from intermediates of primary metabolism, namely phosphoenolpyruvate derived from glycolysis and erythrose-4-phosphate from the pentose phosphate pathway (Fig. 5). The condensation of these two substrates produces 3-deoxy-D-arabino-heptulosonate-7-phosphate, which is subsequently converted into shikimic acid through a series of enzyme-catalyzed reactions. Further metabolic transformations of shikimic acid lead

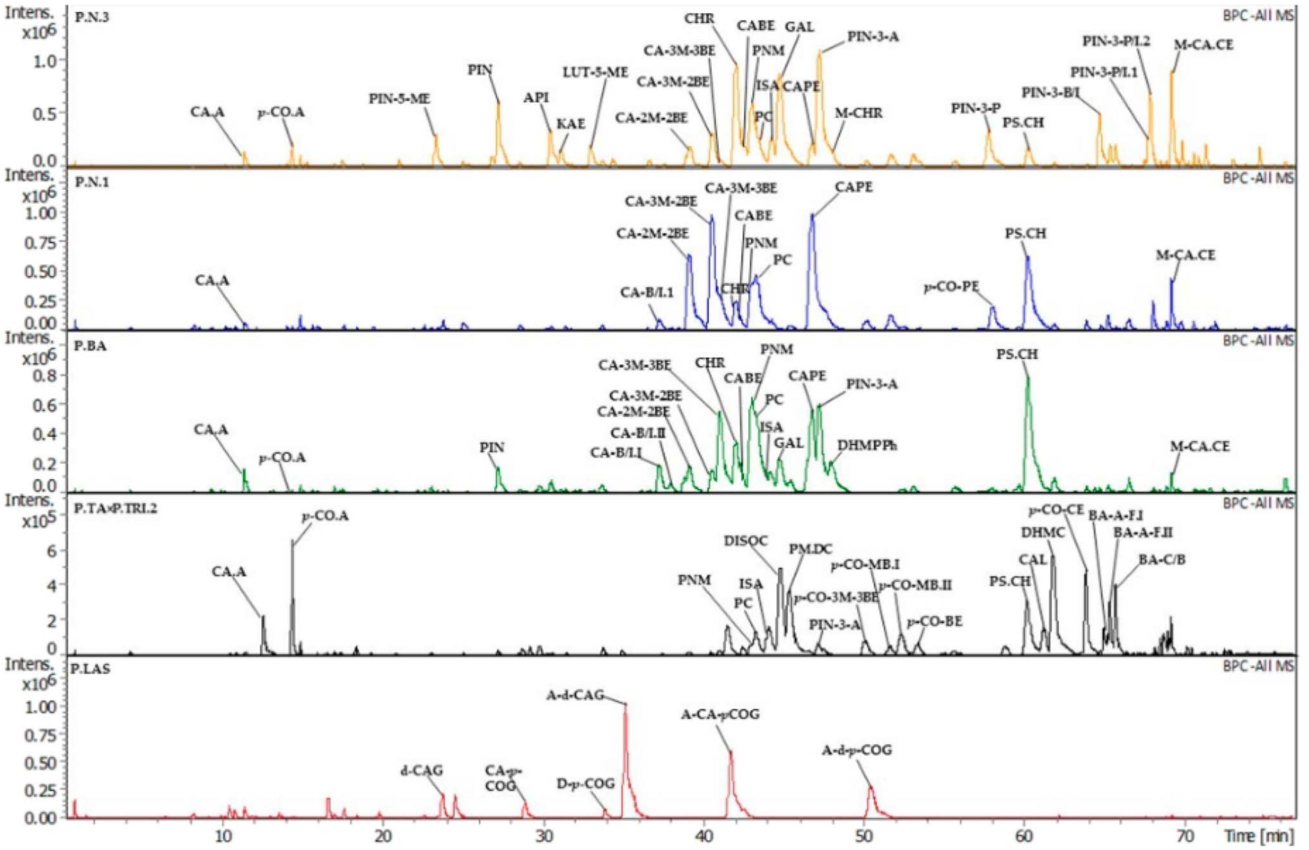

Fig. 3 Representative LC-MS chromatograms of ethanol extracts from *Populus* buds, illustrating five different chemical groups of detected compounds, reproduced from ref. 22 with permission from MDPI,[22] copyright 2024.

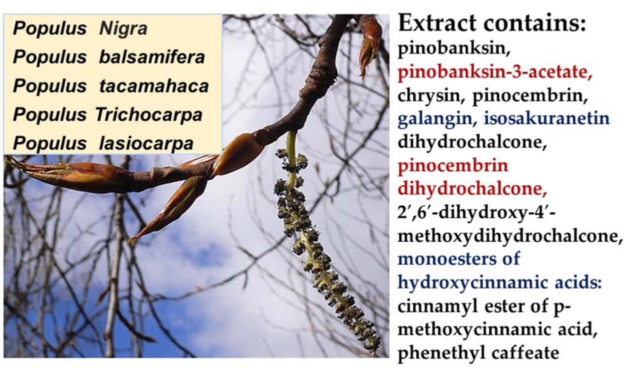

Fig. 4 Illustration of found antibacterial activity associated compounds in *Populus nigra*, *Populus balsamifera*, *Populus tacamahaca*, *Populus trichocarpa*, *Populus lasiocarpa* extracts.

to the formation of various hydroxybenzoic acids, including *p*-hydroxybenzoic acid, protocatechuic acid, and gallic acid.[23]

Meanwhile, bark and leaf extracts of multiple *Populus* species showed salicylate content up to 10% w/w and elevated flavonoid levels evaluated by advanced IR/Raman spectroscopy.[24] Poplar (*Populus*, Salicaceae) bark was used to obtain a series of extracts using five different solvents in sequential extraction over 24 h each in a Soxhlet apparatus. The chemical profile revealed a wide variety of compounds, including hydrolyzable tannins, phenolic monomers (*e.g.*, catechol and vanillin), pentoses and hexoses, and other organic compounds such as long-chain alkanes, alcohols, and carboxylic acids (Fig. 5).[25] Quite often researches reports all data from GC-MS analysis without critical evaluation of each component, it is often one can see contamination with plastificators due to storage in plastic material. For example, natural occurrence of cyclohexane-1,2-diol (**2**) (*i.e.*, cyclohexan-1,2-diol) in plant extracts is extremely rare (Fig. 6). The compound has been documented in castoreum, a secretion from beavers, rather than in plant sources.[26] No definitive role has been demonstrated for 2,4-di-*tert*-butylphenol (**14**) (2,4-DTBP) as a metabolic intermediate in plant biochemical pathways (Fig. 6).[25] Instead, available evidence points to its function as a defensive or allelopathic compound rather than a biosynthetic metabolite. In certain medicinal plants and grasses, 2,4-DTBP has been shown to induce oxidative stress in competing plants, causing lipid peroxidation, membrane damage, reduced chlorophyll content, and activation of antioxidant enzymes—suggesting an allelochemical role in plant–plant interactions.[27,28]

To date, no studies have demonstrated a specific metabolic role for free phenol (C_6H_5OH the compound **3**) in plant biochemical pathways. Phenol itself is rarely found in its free form in plant tissues, as most plant phenolic content exists as

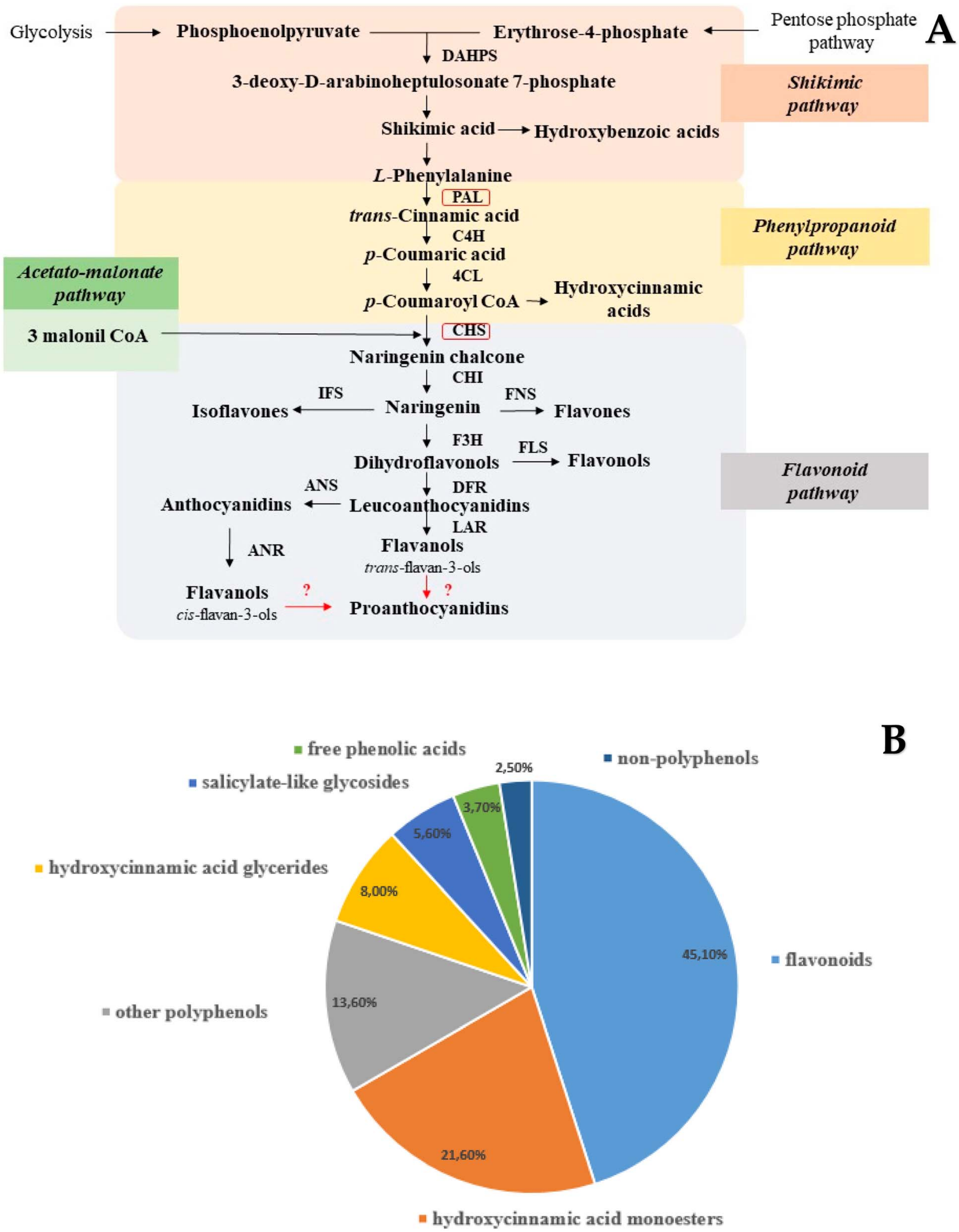

Fig. 5 (A) Biosynthesis pathway of phenolic compounds reproduced from ref. 23 with permission from MDPI,[23] copyright 2023. (B) Relative distribution of identified compounds in *Populus* bud extracts.

derivatives or conjugates.[29] Most probably it is secondary derivative of polyphenol degradation by microorganism. Environmental stressors such as UV-B exposure have been linked to increased phenolic and flavonoid levels in *P. trichocarpa* leaves, illustrating ecological responsiveness at the biochemical level.[30] Terpenoids and salicylates comprise another significant

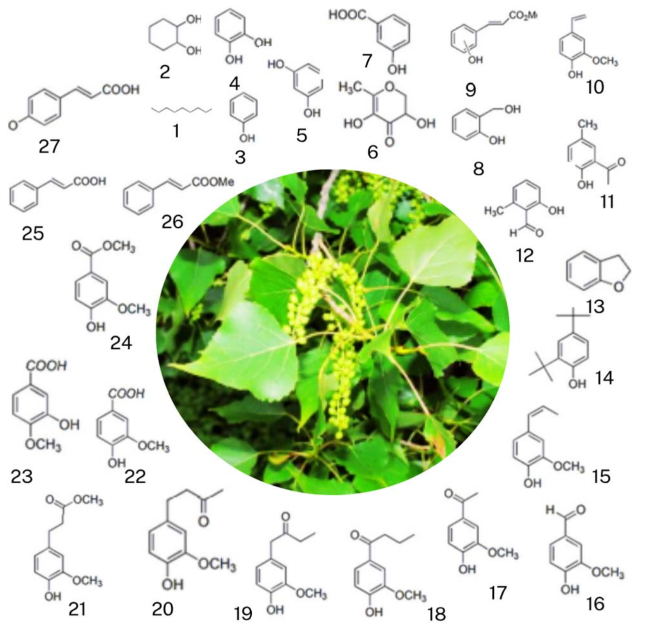

Fig. 6 Representative chemical structures of analytes detected in *Populus* bark extracts *via* GC-MS.

fraction of *Populus* phytochemistry. Essential oils extracted from *P. balsamifera* buds contained mono- and sesquiterpenoids, including alpha-bisabolol (a major cytotoxic agent).[19] Other terpenes such as cadinenes, cineol, curcumene, bisabolene, and humulene were also detected. Notably, six novel cinnamoylated dihydrochalcones (balsacones D–I) were isolated from *P. balsamifera* buds, demonstrating antibacterial potential, along analgesic and antioxidant activities (Fig. 7).[31]

Salicylates are abundant in poplar tissues; salicin and its derivatives are responsible for the familiar medicinal qualities analgesic and anti-inflammatory that have been known historically. Quantitative studies report salicylate levels up to 10% w/w in bark and leaves, which can be rapidly measured using spectroscopic techniques.[32] Phytochemical content varies significantly between *Populus* species and hybrids, driven by genetic background and environmental factors. For instance, *P. nigra* buds are particularly rich in apigenin and chrysin, whereas *P. balsamifera* shows higher levels of *p*-coumaric acid, salicin, and alpha-bisabolol. These differences are influenced both by genetic factors and by environmental conditions, including soil nutrient availability, pH, temperature, humidity, UV exposure, and stressors such as heavy metal contamination or drought. Several studies explicitly considered environmental influences, for example by correlating metabolite content with soil nutrient status, UV exposure, or climatic conditions.[10,30] However, many reports focus primarily on compound identification without fully integrating ecological or climatic data, indicating a need for further systematic investigations to clarify how environmental factors shape species-specific chemical profiles. For quantitative assessment, the main phytochemical compounds of the studied poplar species and hybrids are summarized in Table 1, with concentrations expressed as μg g^{-1}. This allows for direct comparisons between species and the identification of significant interspecific differences in phenolic, flavonoid, and salicylate content (Table 1).

Inter-species differences are also seen in solvent extraction profiles hexane *vs.* ether extracts show unique chemotaxonomic compositions between *P. balsamifera* and *P. nigra*.[33] Hybrid species like *P. trichocarpa* × deltoides are noted for high phenolic glycoside production, which confers pest resistance.[32] Emerging hybrids, such as *P. tomentiglandulosa*, have yielded novel flavonoids (*e.g.*, luteolin derivatives), showcasing the genetic reservoir of *Populus*.[34] *Populus* species are rich in phenolic and polyphenolic compounds, including flavonoids,

Fig. 7 *P. balsamifera* buds extract main phyto compounds and synergetic biological activity.

Table 1 Comparative phytochemical profiles of *Populus* species (buds)

Species	Key phytochemicals in buds	Notable features
Populus nigra	Apigenin, chrysin, pinocembrin, catechin derivatives	Rich in phenolics; strong antioxidant and therapeutic activity[19]
Populus balsamifera	*p*-Coumaric acid (496–13.3 μg g^{-1}), salicin, cinnamic acid, alpha-bisabolol (in essential oil)	High in phenolic acids and salicylates; precursors for propolis production[21]
Populus trichocarpa	Flavonoids and phenolic compounds (responsive to UV-B and environmental stress)	High metabolic plasticity under stress; indicative of strong adaptive biochemical mechanisms[30]

hydroxycinnamic acids, salicylates, and terpenoids, which contribute to their antioxidant, antimicrobial, and anti-inflammatory properties. Flavonoids represent the largest chemical group, with notable variation across species and hybrids. Soxhlet extraction of bark identified tannins, phenolic monomers, sugars, and fatty compounds. Environmental stressors influence phytochemical profiles, especially in *P. trichocarpa*. Hybrid species exhibit unique metabolic traits, emphasizing *Populus* as a chemically diverse and pharmacologically promising genus.

Populus species are rich in phenolics, flavonoids, terpenoids, and salicylates, which contribute to antioxidant, anti-inflammatory, antimicrobial, and antitumor activities. Analyses of buds, leaves, and bark show that most compounds are polyphenols, including flavonoids, hydroxycinnamic acids, salicylate-like glycosides, and their derivatives, with content strongly influenced by genotype and environmental factors such as UV stress. Key terpenoids and salicylates, including α-bisabolol, cadinenes, and salicin derivatives, underlie the traditional medicinal properties of poplars, highlighting their potential for pharmacological and biotechnological applications.

1.4 Influence of soil properties on chemical composition

Soil nutrient content plays a central role in shaping the secondary metabolite profiles of *Populus* species. The availability of macronutrients such as nitrate, ammonium, phosphorus (P), and potassium (K), as well as micronutrients like zinc (Zn), manganese (Mn), and iron (Fe), directly impacts the biosynthesis of flavonoids, salicylates, and phenolic acids.[35] These compounds are crucial for plant defense and have well-documented antioxidant and antimicrobial activities.[36]

In nutrient-rich soils, poplars typically exhibit enhanced levels of polyphenols, as nutrient availability supports the phenylpropanoid pathway.[37] Conversely, nutrient-deficient soils often trigger stress-induced metabolic shifts, resulting in the accumulation of certain flavonoids and phenolic glycosides as protective responses. Research suggests that nitrogen fertilization, in particular, can enhance phenolic biosynthesis, although excessive nitrate content may suppress salicylate levels due to metabolic trade-offs.[38]

It is worth taking into consideration the composition of soil, as it affects the content of biologically active compounds, ultimately influencing both ecological fitness and pharmacological potential.[39]

Soil pH is a critical determinant of nutrient solubility and microbial activity. Acidic soils tend to limit the uptake of calcium and magnesium, while alkaline soils can restrict the availability of iron and manganese due to insoluble oxides formation both of which are cofactors in enzymatic steps of polyphenol biosynthesis.[40] Furthermore, soil texture (*e.g.*, sandy, loamy, clay) and organic matter content affect water retention and cation exchange capacity, shaping root-zone nutrient dynamics. High levels of organic matter promote beneficial microbial communities and support a balanced F : B (fungi-to-bacteria) ratio, which in turn can modulate phytohormone levels and stimulate the production of defense-related compounds.[41] In highly organic soils, *Populus* species may upregulate the production of phenolic glycosides such as salicin and tremulacin, enhancing their therapeutic potential. Differences in microbial-derived elicitors across soil types also influence the induction of stress-response pathways and metabolite accumulation.[42]

Differences in soil texture and organic matter content significantly influence the biosynthesis and accumulation of secondary metabolites such as flavonoids and salicylates in *Populus* tissues. A comparative summary of phytochemical content across various soil types is presented in Table 2.

Urban and post-industrial soils often contain elevated levels of heavy metals such as cadmium (Cd), lead (Pb), and arsenic (As). *Populus* species are known for their phytoremediation capacity and can tolerate high concentrations of these toxicants, partly due to their ability to sequester metals in cell walls and vacuoles. However, such stress conditions can also induce oxidative stress, leading to increased production of antioxidants such as flavonoids and tannins.[48] In contaminated sites, the expression of genes involved in phenolic biosynthesis may be enhanced. For instance, *Populus nigra* and *P. canescens* have been shown to accumulate higher levels of phenolic acids 1.5–3.0-fold and flavonoid levels rising by up to 2-fold, depending on exposure duration and species under metal stress, possibly as a detoxification mechanism.[49]

L. Karliński *et al.* found that soil conditions, depth, and poplar genotype along with their interactions significantly influenced soil microbial biomass and composition, with site conditions being the most influential factor. At site 3 (Fig. 8), genotype effects were especially pronounced, likely due to soil contamination. Poplar genotype notably affected the fungi-to-bacteria (F : B) ratio and microbial distribution, with fungi more closely tied to genotype and bacteria more influenced by site. The AMF to saprotrophic fungi biomass ratio also varied

Table 2 Comparative phytochemical content by soil type (mg g^{-1} DW)

Soil type	Flavnoids (mg g^{-1})	Salicylates (mg g^{-1})	Phenolic acids (mg g^{-1})	Total polyphenols (mg g^{-1})	Source
Rich organic	7.8	42.0	15.2	75.0	43 and 44
Sandy	4.2	22.5	8.4	45.0	45
Clay	5.5	28.3	12.3	55.0	45 and 46
Contaminated	6.9	47.1	14.8	80.0	43 and 44
Urban mixed	6.0	38.0	13.0	68.0	43 and 47

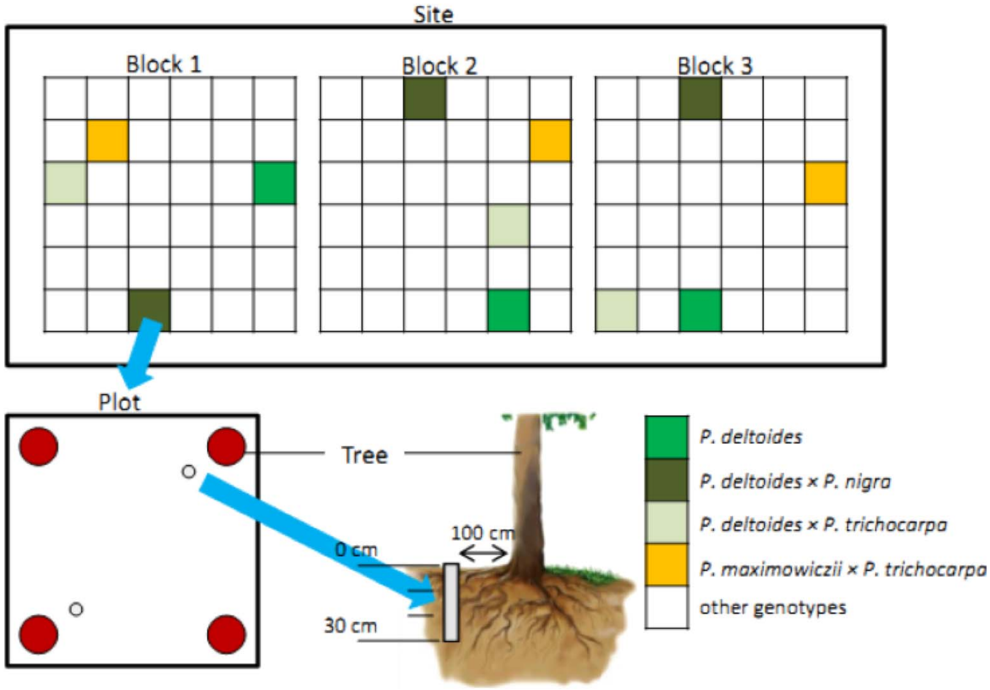

Fig. 8 Sites and sampling scheme of *Populus* spp. reproduced from ref. 43 with permission from MDPI publishing, copyright 2020.

with genotype, shaping microbiome structure. Despite site differences, microbial communities remained relatively stable, highlighting poplars' adaptability to diverse soils.[43]

Soil nutrient content, pH, texture, and organic matter strongly influence the secondary metabolite profiles of *Populus* species. Macronutrients (N, P, K) and micronutrients (Zn, Mn, Fe) affect the biosynthesis of flavonoids, salicylates, and phenolic acids, which are essential for plant defense and antioxidant activity. Nutrient-rich soils generally enhance polyphenol production, while nutrient deficiency or metal contamination can trigger stress responses, increasing certain flavonoids and phenolic glycosides. Soil properties also shape root-zone microbial communities, fungi-to-bacteria ratios, and mycorrhizal interactions, which in turn modulate metabolite accumulation. Poplar genotypes interact with soil conditions to determine both microbial structure and the concentration of bioactive compounds, highlighting their ecological adaptability and pharmacological potential.

1.5 Genotype-by-environment interactions

Expanding green urban and suburban areas with well-adapted tree species like hybrid poplars (*Populus* spp.) is key to improving environmental quality and public health. Hybrids offer high growth rates, phytochemical richness, and environmental resilience. Their genetic diversity allows them to thrive in various soil types, including disturbed and nutrient-poor substrates.[50] An estimation of 20 hybrid poplar cultivars showed that environmental conditions during vegetative propagation significantly influenced growth, biochemical traits, and long-term adaptability in field trials. Notably, hybrids such as *P. balsamifera* × *P. trichocarpa* and *P. trichocarpa* × *P. trichocarpa* displayed the strongest biochemical responses, indicating that early propagation conditions can shape resilience to climate change. These findings underscore the importance of genotype–environment interactions during the formative stages of development.[51] Vegetative propagation conditions including light exposure, rooting substrate, humidity, and nutrient supply have been shown to affect gene expression and metabolite accumulation in poplars. Stress conditions during rooting can act as early elicitors, stimulating defense pathways that persist throughout the plant's lifespan.[52] In the above-cited study, hybrids with elevated salicylate and flavonoid synthesis were found to possess higher adaptability to environmental stresses. Polish researchers reported that the leaves of *Populus* nigra contained the most flavonoids (8 mg g^{-1}), and the leaves of *P.* × *berolinensis* contained the most salicylic compounds (47 mg g^{-1}). These biochemical signatures were strongly correlated with the environmental conditions during the early developmental stages, showing that physiological programming during propagation influences mature plant vigor.[53]

Poplars exert a strong influence on rhizosphere microbial communities, not only through root exudates but also *via* the deposition of phenolic-rich leaf litter. These compounds can selectively support symbiotic fungi (such as AMF) or inhibit pathogenic microbes, thereby shaping microbial diversity and function.[54]

Geraldes *et al.* established that different poplar genotypes differentially affect soil microbial biomass and the fungi-to-bacteria ratio, with some genotypes promoting a fungal-dominated microbiome, which is generally associated with forest health and carbon retention. For instance, the genotype of *P. trichocarpa* significantly influenced the structure of microbial communities in contaminated soils, promoting fungal taxa capable of degrading phenolic compounds.[55]

These microbial shifts, in turn, feed back into plant health, affecting nutrient uptake, stress resistance, and metabolite synthesis closing the loop in the plant–soil–microbe interaction cycle.

Hybrid poplars (*Populus* spp.) are promising for urban and suburban greening due to rapid growth, environmental resilience, and rich phytochemical content. Studies indicate that genotype–environment interactions during vegetative propagation light exposure, nutrient availability, humidity, and rooting substrate strongly influence metabolite accumulation (salicylates, flavonoids), growth, and long-term adaptability. While elevated flavonoid and salicylate levels correlate with increased stress resilience, most studies are limited to a few genotypes and controlled propagation conditions, leaving uncertainties about how these responses translate across diverse urban soils and climates. Additionally, although poplars modulate rhizosphere microbial communities *via* root exudates and phenolic-rich litter, the causal mechanisms remain poorly resolved, and long-term ecological impacts on microbial diversity and soil health are not fully understood. These gaps highlight the need for broader, multi-site field studies to clarify how genotype, propagation practices, and environmental conditions interact to determine both biochemical traits and ecological outcomes.

1.6 Soil feedback and litter decomposition

Leaf litter represents a major pathway of nutrient return from forest vegetation to the soil. In poplar (*Populus* spp.) plantations, this process is particularly dynamic due to the fast growth and nutrient-rich biomass of the trees. According to Jonczak *et al.*, approximately 80% of total litterfall in poplar stands is composed of fallen leaves. These leaves are rich in nitrogen and potassium, but relatively poor in phosphorus, making them a key driver of nitrogen and potassium cycling in managed ecosystems.[56] The rapid decomposition of poplar leaf litter accelerates nutrient turnover. The decomposition rate varies significantly among poplar genotypes due to differences in leaf chemistry primarily nitrogen content, lignin levels, and the C/N ratio. Leaves of Hybrid 275, for example, decompose faster than those of the Robusta clone.[57] Over a 20 month period, more than 70% of Hybrid 275 leaf mass decomposed, compared to only 50% of Robusta. This difference was attributed to higher nitrogen content and lower lignin levels in Hybrid 275 leaves. Importantly, the decomposing litter exhibited nitrogen accumulation during early stages, a progressively declining C/N ratio, and faster loss of potassium than overall biomass.[58] Such patterns are consistent with rapid microbial colonization and efficient nutrient release.

The accumulation of nitrogen in decomposing litter may indicate active microbial immobilization early in the decay process, followed by nitrogen mineralization and release into the soil. Rapid potassium leaching from fresh litter is also typical of broadleaved species, but its extent in poplars especially hybrids—underscores their role in potassium enrichment of the topsoil.[59] The influence of poplar plantations on soil fertility extends beyond litter decomposition. Continuous input of organic matter, root exudates, and symbiotic microbial activity can reshape soil biochemical profiles over time. Several studies have reported increases in total nitrogen, available potassium, and microbial biomass in soils under poplar cultivation, particularly when organic amendments or nitrogen fertilization are applied.[60,61] Niksa *et al.* evaluated the impact of three years of short rotation forestry on soil nutrient content under *Populus* 'Max-5' and willow cultivars. Their findings revealed that soils beneath Max-5 experienced significant increases in phosphorus, potassium, and magnesium (Mg), especially under annual harvest regimes. The effect was most pronounced in plots receiving high nitrogen fertilizer, either mineral or organic.[62] In combination with the willow cultivar Ekotur, nitrogen application led to the highest phosphorus accumulation, suggesting potential synergies between species in mixed plantations.[63]

Soils under poplar also demonstrated elevated potassium levels, which were enhanced by both organic and mineral inputs. This increase aligns with observed patterns of potassium release during litter decomposition, suggesting that both above- and belowground processes contribute to the nutrient status of these soils. Magnesium accumulation, although more prominent under willow, was also noticeable in *Populus* plots receiving nitrogen-rich amendments.[64] These results emphasize the positive feedback loop between fast-growing poplar genotypes, soil nutrient enrichment, and plantation management practices. In particular, annual harvest cycles though often considered nutrient-depleting can support sustained or even enhanced soil fertility when coupled with appropriate fertilization regimes. Comparative studies of poplar genotypes provide further insight into how genetic background influences litter quality, decomposition, and soil feedbacks. As noted above, Hybrid 275 demonstrates faster litter breakdown than Robusta, a consequence of its higher leaf nitrogen and lower lignin content. These traits not only improve decomposition efficiency but also foster greater microbial biomass in the rhizosphere, which in turn enhances nutrient cycling.[65]

Furthermore, biochemical differences among clones may affect the soil microbiome *via* secondary metabolites such as flavonoids and phenolic glycosides.[66] *Populus* × *berolinensis*, for example, is characterized by high flavonoid concentrations in its leaves and buds, including salicin, chrysin, and pinocembrin. These compounds can exhibit antimicrobial, allelopathic, or symbiotic effects in the soil environment. Elevated levels of flavonoids have been linked to shifts in microbial community structure, particularly in rhizosphere-associated fungi and bacteria, which may have downstream effects on nutrient availability and decomposition rates.[67] While most studies have focused on aboveground biomass production and leaf litter characteristics, emerging research emphasizes the integrative role of genotype, secondary metabolism, and soil feedback mechanisms. Poplar genotypes with higher phenolic content not only influence soil chemistry but may also shape microbial pathways involved in nutrient mineralization and organic matter turnover.[68] Soil microbial communities are highly responsive to both litter quality and root exudates, which vary considerably among poplar genotypes. As reported by Karliński *et al.*, the interaction between soil contamination levels and poplar genotype significantly shaped both biochemical parameters and microbial diversity in the rhizosphere. In particular, poplar hybrids such as *Populus* × *canadensis* 'Marilandica' and *P. nigra* × *P. maximowiczii* 'NE-42' modified the abundance of nitrogen-fixing bacteria (*e.g.*, *Bradyrhizobium* spp.) and stimulated microbial enzymatic activity even in heavy-metal-contaminated soils.[69]

This suggests that genetically controlled differences in leaf chemistry and root exudation patterns affect the composition and functional capacity of soil microbiota. For example, increased concentrations of phenolic glycosides such as salicin and salicortin in *Populus balsamifera* and *P.* × *berolinensis* have been associated with shifts in fungal : bacterial ratios and increased microbial biomass.[70,71] These compounds may act as selective substrates or microbial regulators, depending on their solubility, redox activity, and bioavailability.

The chemical composition of poplar leaf litter plays a central role in its decomposition dynamics and subsequent impact on soil. In addition to basic components like cellulose, hemicellulose, and lignin, poplar leaves contain a rich suite of secondary metabolites, including flavonoids (apigenin, pinocembrin, chrysin), hydroxycinnamic acids (*p*-coumaric acid, ferulic acid), and salicylates.[72]

According to Okińczyc *et al.*, the total phenolic content in *Populus* bud extracts can range from 1000 to over 13 000 $\mu g\ g^{-1}$ DW, with flavonoid profiles strongly depending on both species and growth site.[70] These compounds contribute to antimicrobial activity and also influence litter palatability and decay rates. For instance, high levels of pinocembrin and chrysin may inhibit certain microbial decomposers while supporting others that co-metabolize lignin derivatives.[70] Moreover, flavonoids released during litter breakdown or root exudation may impact nitrogen mineralization rates and microbial nitrogen use efficiency. This may help explain the observed nitrogen accumulation during early litter decay stages in fast-decomposing genotypes such as Hybrid 275. In contrast, more recalcitrant genotypes like Robusta retain higher lignin and tannin levels, which can delay microbial colonization and reduce the speed of nutrient release.[73] Soil feedback effects of poplar litter are not only genotype-dependent but also strongly mediated by edaphic conditions. Soil pH, clay content, and organic matter levels influence the stability and availability of compounds released during litter decay. Karliński with colleagues demonstrated that microbial biomass and enzymatic activity (*e.g.*, dehydrogenase, phosphatase) were highest in slightly acidic soils with intermediate organic carbon levels under hybrid poplar plantations.[69] Soils with pH values between 5.5 and 6.5 supported optimal microbial performance, which was further enhanced by the presence of nitrogen-rich litter.[74] Furthermore, nutrient enrichment effects may be more pronounced in nutrient-poor or degraded soils. The ability of poplars to improve soil phosphorus and magnesium levels as shown by Niksa *et al.* suggests that plantation management on marginal lands could be strategically optimized through clone selection and fertilization regimes. For example, combining high nitrogen input with clones exhibiting fast decomposition and high secondary metabolite content could accelerate restoration of soil fertility and biological function.[75]

Taken together, the evidence suggests that hybrid poplars play a multifaceted role in ecosystem nutrient cycling. Through rapid litter turnover, active root exudation, and modulation of soil microbial communities, they contribute to enhanced nitrogen and potassium availability, improved microbial biomass, and faster organic matter transformation.

Clone-specific traits such as lignin content, nitrogen concentration, and flavonoid richness serve as key determinants of decomposition rates and feedback strength. Genotypes like Hybrid 275 and *P.* × *berolinensis* offer particular promise for agroforestry or phytoremediation due to their favorable biochemical profiles and soil-enhancing capabilities.[76]

Importantly, the combination of litter chemistry, root–microbe interactions, and targeted management (*e.g.*, fertilization or harvest regime) can be tailored to optimize soil function and resilience. This aligns with broader goals in sustainable forestry and bioeconomy strategies, where soil health is increasingly recognized as a critical component of long-term productivity and environmental quality.[77] A comparative summary of selected *Populus* genotypes in terms of leaf

Table 3 Comparative traits of selected *Populus* genotypes related to leaf litter decomposition and soil feedbacks

	Leaf chemistry				Decomposition	Soil nutrients	Microbial response	
Genotype/clone	Leaf N ($mg\ g^{-1}$)	Lignin (% DW)	C/N	Dominant phenolics/flavonoids	Mass loss (%)	Nutrient effects	Biomass/activity	Source
Hybrid 275	High (25–28)	Low (13–15)	∼18	Salicin, pinocembrin, apigenin	>70%	↑ N, ↑ K during decay	↑ Microbial activity, rapid colonization	78 and 79
Robusta	Moderate (18–20)	High (18–20)	∼28	Low flavonoid content	∼50%	Slower nutrient release	Moderate increase	78
P. × *berolinensis*	High (>25)	Moderate (∼16–17)	∼20	Chrysin, salicin, pinocembrin, apigenin	∼60–65%	↑ N, possible ↑ P under certain soils	↑ Bacterial : fungal ratio	70
Populus 'Max-5'	Moderate	Moderate	N/A	Not reported	N/A	↑ P, ↑ K, ↑ Mg with high N input	↑ Biomass with fertilization	75
P. balsamifera	High (22–26)	Moderate (∼16)	∼18–20	*p*-Coumaric acid, salicin, cinnamic acid	N/A	Enhanced microbial turnover potential	↑ With phenolics and flavonoids	71

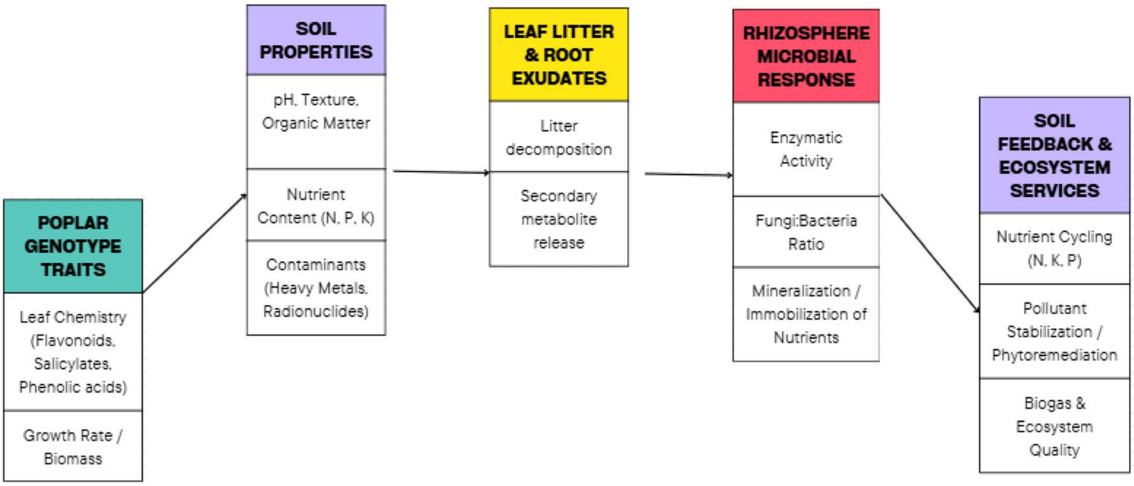

Fig. 9 Poplar genotype–soil feedbacks: linking metabolites to ecosystem services.

chemistry, decomposition rates, and soil feedback effects is presented in Table 3.

Poplar leaf litter plays a pivotal role in shaping soil nutrient dynamics, particularly through rapid decomposition and the release of nitrogen and potassium. Genotype-specific differences in litter chemistry especially nitrogen content, lignin levels, and flavonoid profiles determine the rate and efficiency of nutrient cycling.[80] Hybrid 275 and *P.* × *berolinensis* revealed favorable traits for promoting microbial biomass and enhancing soil quality, making them suitable candidates for short-rotation forestry and ecological restoration.[81] These effects are further modulated by soil type, fertilization regime, and harvesting practices. Understanding the interactions among genotype, litter composition, and microbial communities is essential for optimizing soil feedbacks and sustaining productive, resilient plantation ecosystems. Fig. 9 illustrates the interactions between poplar genotype traits, soil properties, leaf litter chemistry, rhizosphere microbial communities, and ecosystem-level feedbacks, emphasizing the chemical mechanisms underlying nutrient cycling and pollutant stabilization.

Poplar species shape nutrient cycling and soil function through the chemical composition of their leaf litter and root exudates. Genotype-specific traits such as nitrogen content, lignin, and secondary metabolites including flavonoids and salicylates govern decomposition rates and nutrient release. During litter breakdown, nitrogen-rich compounds undergo microbial mineralization, while lignin and tannins modulate the accessibility of carbon substrates. Flavonoids and phenolic glycosides can act as redox-active molecules, influencing microbial enzymatic activity, stabilizing reactive oxygen species, and selectively inhibiting or promoting certain microbial taxa. These chemical interactions create feedback loops in the rhizosphere, where secondary metabolites regulate microbial pathways involved in organic matter turnover and nutrient availability. Consequently, the biochemical profiles of poplar genotypes drive both decomposition dynamics and soil fertility, illustrating the central mechanistic role of plant chemistry in ecosystem functioning.

1.7 Environmental and biotechnological implications

Poplar species, particularly fast-growing hybrids such as *Populus* × *canadensis*, *Populus deltoides* × *nigra*, and *Populus* × *berolinensis*, have proven to be valuable components of urban forestry programs due to their tolerance to abiotic stress, capacity for pollutant uptake, and high transpiration rates.[82] Urban greening with poplars improves air quality by capturing particulate matter and volatile organic compounds through leaf surfaces rich in cuticular waxes and phenolic compounds.[46] Furthermore, their rapid canopy development supports microclimatic regulation by providing shade and reducing the urban heat island effect.

Phytoremediation potential is a significant driver of poplar deployment in disturbed urban sites. Several studies indicate that hybrid poplars can uptake and sequester heavy metals such as cadmium, lead, and zinc through both root absorption and translocation to aerial tissues. For instance, Czerniawska-Kusza *et al.* demonstrated the effectiveness of *Populus alba* and its hybrids in the reclamation of fly ash ponds, where high levels of boron and selenium were mitigated through biological uptake. Moreover, root exudates of poplars may stimulate rhizospheric microbial communities, thereby enhancing degradation of polycyclic aromatic hydrocarbons and other organic contaminants.[83] *In vitro* cultures of aspen (*Populus tremula* × *tremuloides*) and poplar (*Populus simonii*) were shown to absorb significant quantities of radionuclides from growth media, accumulating up to 16% of ^{63}Ni and 41% of ^{137}Cs after 32 and 16 days, respectively.[84] These radionuclides were primarily localized in metabolically active tissues such as young leaves, mesophyll, shoot meristems, and nodes, reflecting the strong affinity of fast-growing tissues for water and nutrient uptake. Similarly, environmental and experimental exposure of forest trees such as *Populus* alba revealed that ^{137}Cs migrates inward from bark to heartwood *via* apoplastic and symplastic pathways, with a preferential accumulation in meristematic zones. The transport mechanisms may be linked to potassium uptake systems, though this remains to be clarified.[85] Over two growing seasons, *Salix caprea* exhibited higher ^{137}Cs uptake than *Populus tremula*, particularly in root tissues, likely due to increased surface adsorption and reduced translocation. In contrast, ^{90}Sr displayed greater mobility, accumulating predominantly in leaves and stems, with transfer factors (TFs) significantly exceeding those of ^{137}Cs, indicating its higher bioavailability. Notably, uptake of ^{137}Cs was stable in spiked soil but increased in disposal soil with greater root biomass, underscoring the importance of biomass development in phytoremediation efficiency. While short-rotation coppice (SRC) species like *Populus* hold potential for radionuclide phytoextraction, this approach remains constrained by the limited bioavailability of ^{137}Cs suggesting that soil amendments and selection of biomass-optimized genotypes may improve outcomes.[86]

Inter-species comparisons further emphasize the role of growth rate and physiology in radionuclide accumulation. For instance, *Populus* species showed lower TFs for ^{210}Pb and ^{226}Ra than *Quercus* spp., according to Charro & Moyano, suggesting that bioaccumulation is influenced more by plant metabolic traits than soil concentrations.[87] Supporting this, *Populus* nigra leaves washed post-harvest showed 62% lower ^{137}Cs activity, indicating substantial surface adsorption. Similarly, studies by Djingova & Kuleff confirmed that ^{60}Co levels were below detection in poplar samples, while ^{40}K uptake far exceeded ^{137}Cs, reflecting natural selectivity for potassium.[88] Environmental events such as wildfires can dramatically increase the mobility of radionuclides. Field and laboratory studies have shown that burning biomass releases large fractions of radioactive elements into the atmosphere particularly iodine (80–90%) and cesium (40–70%) depending on combustion temperature (160–1000 °C). The residual ash becomes enriched in radionuclides, especially ^{137}Cs, increasing their solubility and environmental bioavailability. If radionuclides such as ^{129}I, ^{137}Cs, or ^{36}Cl are present, wildfires pose a serious radiological risk *via* inhalation, skin contact with ash, or uptake by crops. To mitigate the risks associated with contaminated ash from biomass combustion, as studied by Rantavaara & Moring, it is essential to monitor ^{137}Cs and ^{40}K concentrations, which tend to be highest in fly ash. Management strategies such as landfilling, controlled forest fertilization, or reuse must comply with radiation protection standards (*e.g.*, STUK ST-guide 12.2). In cases where ash is reused, radiation-shielding measures may be required to ensure environmental safety.[89] However, the application of wood ash in forest ecosystems remains controversial. While it may enhance tree growth on nitrogen-rich peatlands, studies have shown that it can reduce productivity on mineral soils and affect vegetation, fungi, and soil biota depending on ash dose, site conditions, and chemical stabilization. Of particular concern is the potential biotoxicity due to heavy metals (*e.g.*, cadmium) and shifts in soil and water chemistry.[90] Long-term field trials revealed that a single application of ^{137}Cs-contaminated or uncontaminated ash had minimal and inconsistent effects on ^{137}Cs uptake by forest vegetation. Co-application with KCl reduced cesium accumulation in some species and years by up to 45%, yet the results were not universally reproducible. These findings caution against relying on wood ash as a countermeasure for radionuclide transfer in forests without site-specific validation.[91] To prevent radionuclide leaching from ash and ensure long-term containment, solidification technologies such as cement binding, geopolymerization, or vitrification are employed. According to Chervonnyi & Chervonnaya, geopolymer-based stabilization offers an environmentally friendly and cost-effective method for immobilizing radioactive ash. The technique avoids liquid waste and high-temperature processing and reduces leaching rates to approximately 10^{-6} g per cm^2 per day. Stabilized ash can, in some cases, be reused in construction or forestry applications provided dose assessments and regulatory approvals confirm its safety.[92]

Therefore, immobilization of radionuclides in ash is considered using binders like cement, geopolymers, or vitrification to prevent leaching into the environment. In some cases, stabilized ash can be reused in construction or forestry with radiation dose assessments and regulatory approval.

Urban landscape planners increasingly integrate poplars along transportation corridors and brownfields due to their ease of vegetative propagation, low management requirements, and proven performance under compacted or nutrient-poor soils. In Poland, ongoing trials in the Silesian region have tested hybrid clones for use on slag heaps and mining areas, reporting successful establishment and improved soil aggregation within three growing seasons.[93] The role of poplars as a sustainable bioenergy crop has gained attention within circular economy frameworks. Short-rotation coppice systems using *Populus* hybrids yield high biomass productivity (10–15 Mg per ha per year under temperate conditions), making them suitable feedstock for bioethanol, biogas, and pyrolysis-based biochar production. Notably, clones such as 'Max4' and 'Skado' exhibit superior lignocellulosic profiles low lignin-to-cellulose ratios and high hemicellulose content facilitating enzymatic saccharification.[94]

Mixing SRC with land remediation presents a synergistic solution, where polluted or degraded areas are remade and utilized for biomass production. Several experimental trials in Central and Eastern Europe show that poplars grown on marginal soils contaminated with petroleum hydrocarbons or heavy metals can produce biomass without compromising their remediation effectiveness.[95] Further, poplar biomass biochar was reported to immobilize pollutants in the soil and increase cation exchange capacity, therefore supporting long-term soil health. Phytostabilization, plant-mediated immobilization of pollutants *in situ*, is another strategy that takes advantage of the deep root systems of poplars. Poplars reduce mobile ion leaching to groundwater through rhizofiltration and hydraulic regulation mediated by transpiration. Field trials conducted in Eastern Slovakia revealed that *Populus* × *euramericana* reduced nitrate leaching by 48% on intensively fertilized agricultural lands due to increased nitrogen retention and uptake efficiency.[96]

Aside from remediation and energy, poplars play multifunctional roles in agroforestry systems, such as biodiversity conservation, microclimate regulation, and farm productivity. Their fast growth and development into a windbreak reduce soil erosion and evapotranspiration from surrounding croplands.

Table 4 Representative applications of hybrid poplars across regions, illustrating multifunctional uses in phytoremediation, urban greening, bioenergy, and ecosystem services

Country/region	Land-use context	Primary ecosystem service	Poplar species/clones	Key environmental outcome	Source
Poland (Silesia)	Post-mining and degraded soils	Phytoremediation, soil stabilization	*Populus* × *canadensis*, *P. nigra*	Improved soil structure and stabilization of contaminated substrates	99
Canada (Ontario)	Riparian buffer strips	Water protection, biodiversity support	*Populus deltoides* × *nigra*	Reduced nutrient runoff and increased bird diversity	98
Germany (Bavaria)	Marginal agricultural land (SRC)	Biomass production, bioenergy	'Max4', 'Skado', *P. trichocarpa* hybrids	High biomass yield under low-input conditions	100
Hungary	Agroforestry with cereal crops	Agroecology, land-use efficiency	*Populus* × *euramericana*	Enhanced crop–tree interactions and system productivity	101
Slovakia (Eastern)	Cropland buffer zones	Nitrate biofiltration	*Populus* × *euramericana*	Reduced nitrate leaching and improved nutrient retention	95
France	Urban and peri-urban green infrastructure	Air quality improvement, climate mitigation	*Populus* × *berolinensis*, *P. deltoides*	Reduced particulate matter (PM) and VOC concentrations	46
China (Hebei, Shaanxi)	Industrial and agricultural waste sites	Biomass, bioremediation	*Populus tomentosa*, *Populus alba* hybrids	Enhanced organic waste degradation and biofuel potential	102
Belgium	Metal-contaminated soils (SRC)	Bioenergy + phytoremediation	*Populus trichocarpa* × *Populus deltoides*	Cd and Zn uptake with sustainable biomass production	95
Kazakhstan (Petropavlovsk)	Chernozem and solonetz soils (experimental plots)	Biomass production, soil stabilization	*Populus balsamifera*, *Populus* × *berolinensis*	Improved soil structure and adaptive growth under saline conditions	103

Agroforestry plans involving hybrid poplars mixed with annual crops (wheat, barley) or pasture offer enhanced land-use efficiency and total system yield, as proven in Hungarian and southern German pilot farms.[97]

Ecosystem services provided by poplar-based systems include carbon sequestration—both in aboveground biomass and soils as well as enhancement of soil microbial diversity. Recent metagenomic studies[46] suggest that the rhizosphere of *Populus* × *canescens* hosts a functionally diverse microbial community, including nitrogen-fixing bacteria (*Bradyrhizobium*, *Azospirillum*) and arbuscular mycorrhizal fungi, which together enhance nutrient cycling and soil resilience.

Additionally, poplar-based systems contribute to the provisioning of pollinator resources when intercropped with herbaceous flowering species. In riparian zones, poplars stabilize stream banks, reduce nutrient runoff, and provide critical habitat for insects and birds. A notable example is the multifunctional buffer strip system in southern Ontario, where *Populus deltoides* × *nigra* hybrids planted along waterways were associated with a 20% increase in avian species richness compared to control sites.[98]

The multifunctionality of hybrid poplars is increasingly recognized across diverse environmental and climatic contexts, where they are integrated not only for biomass production but also for ecological restoration, pollution mitigation, and landscape enhancement. Numerous regional case studies across Europe, Asia, and North America have demonstrated the adaptability of specific clones to different soil types, contamination levels, and agroclimatic conditions. These applications reflect both their biotechnological value and the ecosystem services they provide. Table 4 summarizes selected examples of how hybrid poplars have been deployed in various countries, highlighting their roles in phytoremediation, urban greening, bioenergy production, and agroforestry systems.

Hybrid poplars influence urban and degraded ecosystems primarily through their biochemical and physiological traits. Their leaf surfaces, rich in cuticular waxes, flavonoids, and phenolic compounds, capture particulate matter and volatile organic compounds, contributing to air purification (Table 4). The uptake and translocation of heavy metals (*e.g.*, Cd, Pb, Zn) and radionuclides (*e.g.*, ^{137}Cs, ^{63}Ni) involve both apoplastic and symplastic pathways, with metabolically active tissues acting as primary accumulation sites, often mediated by mechanisms analogous to potassium transport systems.[95] Root exudates and litter secondary metabolites, including flavonoids, phenolic glycosides, and salicylates, chemically interact with rhizosphere microbes, modulating enzymatic activity, nutrient mineralization, and pollutant degradation. In contaminated soils, aforementioned compounds facilitate phytostabilization and rhizofiltration by promoting selective microbial communities that enhance immobilization or breakdown of organic and inorganic pollutants. Lignocellulosic composition of biomass, particularly cellulose, hemicellulose, and lignin ratios, governs chemical accessibility for enzymatic hydrolysis, influencing bioenergy conversion efficiency.[102] Overall, poplar-mediated ecosystem services rely on chemical interactions at multiple scales: pollutant adsorption and chelation, redox reactions mediated by secondary metabolites, nutrient cycling *via* mineralization, and modulation of microbial-mediated chemical transformations. These chemical processes underpin their effectiveness in phytoremediation, urban air quality improvement, bioenergy production, and soil fertility enhancement.

In sum, the integration of poplars into biotechnological applications exemplifies a nature-based solution with wide-ranging ecological and economic benefits. Their versatility supports climate mitigation, land rehabilitation, and sustainable biomass production, aligning with global goals for carbon neutrality and ecosystem restoration.

2. Conclusions and future prospects

We reviewed current evidence on the relationship between soil parameters and genotypic diversity in *Populus* hybrids, focusing on their biochemical plasticity and environmental adaptability. Particular emphasis was placed on flavonoids, salicylates, and other phenolic compounds that play a central role in plant defense, microbial signaling, and phytoremediation capacity. Hybrid poplars exhibit wide ecological amplitude, making them suitable for growth on nutrient-deficient, contaminated, or urban soils. Many studies devoted on the influence of macro- and micronutrients, pH, organic matter, and soil texture on the expression of bioactive secondary metabolites in different *Populus* genotypes. Poplar leaf litter and rhizodeposition also influence soil microbial communities and contribute to nitrogen and potassium cycling. However, much of reviewed research is based on short-term greenhouse or laboratory experiments, with limited replication under field conditions. One of the main gaps in current knowledge is the need to explore long-term genotype soil microbiome interactions across diverse climates and land-use scenarios.

Following research should prioritize the integration of metabolomics, metagenomics, and transcriptomics to unravel the complex interactions among soil, plants, and microbial communities. Long-term field experiments under combined stresses such as salinity, hazard metals, and drought are essential to assess the stability of metabolite expression and ecological performance. In parallel, targeted breeding strategies anchoring on metabolite traits, combined with controlled manipulation of soil microbiomes and light conditions, could enhance the production of high-value compounds. Engineered microbial consortia, plant biostimulants, and precision agronomic practices represent promising tools to maximize both ecological resilience and biochemical output. Beyond ecological applications, poplarderived compounds hold substantial potential for chemical and industrial uses. Flavonoids, phenolics, and salicylates could be developed into pharmaceuticals, bio-based materials, and bioenergy sources, linking the environmental role of hybrid poplars with broader chemical and economic relevance. The implementation of circular bioeconomy approaches, including the valorization of leaf litter, biomass, and ash, can further increase sustainability. In the northern region of Kazakhstan, where *Populus* spp. are widely present and soils are heavily contaminated with heavy metals and radionuclides due to uranium mining,[104,105] these strategies could mitigate secondary contamination of the agricultural sector and reduce human exposure risks. Overall, the future of poplar-based systems lies in the integration of omics-driven research, climate-resilient cultivation, and chemical valorization, which together can optimize ecological, health, and economic outcomes while supporting sustainable biotechnologies.

Author contributions

Conceptualization, D. B. and A. M.; methodology, A. M.; software, D. B.; validation, D. B., A. M. and V. P.; formal analysis, D. B. and V. P.; investigation, A. M. and D. B.; data curation, A. M. and D. B.; writing—original draft preparation, A. M.; writing—review and editing, D. B.; visualization, D. B.; supervision, D. B. and V. P.; project administration, D. B.; funding acquisition, D. B. All authors have read and agreed to the published version of the manuscript.

Conflicts of interest

The authors declare no conflict of interest.

Data availability

This article is a review and did not generate new experimental data. All data referred to are from previously published studies, which are cited throughout the text. Data supporting the findings of this review are available from the referenced publications.

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