

Dual-Benefit Breeding in Sweetpotato (*Ipomoea batatas*): Leveraging Secondary Metabolites for Crop Resilience and Human Nutrition

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Abstract

Sweetpotato (*Ipomoea batatas* (L.) Lam.) is a globally important crop valued for its adaptability, nutritional contribution, and role in food security. However, persistent agronomic constraints—particularly weed pressure and increasing input limitations—continue to challenge sustainable production. At the same time, sweetpotato is increasingly recognized as a functional food crop due to its abundance of phenylpropanoid-derived secondary metabolites, especially chlorogenic acid, which has demonstrated antioxidant, metabolic regulatory, and anti-obesity potential. Despite these attributes, secondary metabolites have historically received limited attention as direct breeding targets. This paper proposes a dual-benefit breeding framework that intentionally integrates the nutritional and ecological functions of secondary metabolites into sweetpotato cultivar development. We argue that phenylpropanoid metabolites represent multifunctional traits capable of simultaneously enhancing human metabolic health and crop ecological competitiveness through residue-mediated weed suppression. By synthesizing evidence from plant ecology, polyploid genetics, and ideotype-based breeding theory, we demonstrate how secondary metabolites can be reframed as selectable, dosage-responsive traits rather than incidental metabolic by-products. Special attention is given to the opportunities and challenges associated with sweetpotato's autohexaploid genome, including allele dosage effects, environmental plasticity, and threshold-based trait expression. We further discuss breeding strategies that integrate functional phenotyping, canopy dynamics, and agronomic performance within ideotype-guided selection pipelines. The proposed framework highlights how cultivar-embedded ecological functions can reduce reliance on external inputs while preserving yield stability and nutritional value. By positioning secondary metabolites at the intersection of nutrition, ecology, and breeding, this conceptual analysis provides a foundation for developing multifunctional sweet-

potato cultivars and offers a transferable model for polyploid crop improvement under sustainability-driven agricultural systems.

Keywords

Sweetpotato, Chlorogenic Acid, Secondary Metabolites, Dual-Benefit Breeding, Weed Suppression, Anti-Obesity, Sustainable Agriculture

1. Introduction

Sweetpotato (*Ipomoea batatas* (L.) Lam.) is a globally important root crop that plays a central role in food security, nutrition, and rural livelihoods, particularly in sub-Saharan Africa, Asia, and parts of Latin America [1] [2]. Its high caloric productivity, adaptability to marginal soils, and vegetative propagation have positioned sweetpotato as a strategic crop for addressing both hunger and micronutrient deficiencies. Large-scale breeding and dissemination programs, especially those focused on orange-fleshed sweetpotato, have demonstrated that targeted nutritional improvement can translate into measurable public-health benefits, including reductions in vitamin A deficiency [2] [3].

Despite these successes, sweetpotato production systems continue to face persistent agronomic constraints. Weed pressure remains one of the most significant yield-limiting factors, particularly during early growth stages when canopy establishment is slow [4]. In many production regions, effective weed management relies on repeated hand weeding, mechanical cultivation, or herbicide applications, all of which impose increasing labor, economic, or environmental costs [5]. As labor availability declines and chemical control options become constrained by regulation or resistance, weed management is increasingly recognized as a challenge that cannot be solved by management alone but must also be addressed through genetic and physiological improvement.

Secondary metabolites occupy a unique position at the intersection of nutritional and agronomic challenges. In sweetpotato, phenylpropanoid-derived compounds—particularly chlorogenic acid (CGA) and related caffeoylquinic acids—are among the most abundant phenolics in both leaves and storage roots [6] [7]. From a human-health perspective, CGA has been widely studied for its antioxidant, anti-inflammatory, and metabolic regulatory properties. Experimental and clinical studies indicate that CGA can modulate lipid metabolism, suppress adipocyte differentiation, improve insulin sensitivity, and reduce body-weight gain under high-fat dietary conditions, highlighting its relevance to obesity and metabolic syndrome [8]-[10].

Importantly, the biological significance of CGA extends beyond human nutrition. In plants, phenylpropanoid metabolites function as defense compounds, oxidative buffers, and allelochemicals that mediate interactions with competing vegetation [11] [12]. In sweetpotato, these compounds accumulate preferentially in

vegetative tissues, particularly leaves, where they contribute to stress tolerance and ecological competitiveness [6]. This convergence of nutritional and ecological functions within the same metabolic pathway presents an opportunity for a new breeding paradigm—one that treats secondary metabolites as multifunctional traits rather than incidental by-products of metabolism.

Despite this potential, secondary metabolites have historically received limited attention in sweetpotato breeding programs. The crop's autohexaploid genome complicates genetic analysis, obscuring allele-dosage effects and weakening genotype-phenotype associations for quantitative traits [13] [14]. Moreover, metabolite accumulation is often perceived as environmentally plastic and difficult to select, reinforcing the assumption that such traits are unsuitable breeding targets [15]. As a result, breeding priorities have traditionally emphasized yield, root quality, and disease resistance, while metabolite variation has been treated as peripheral.

Here, we propose a dual-benefit breeding framework for sweetpotato that intentionally integrates the nutritional and ecological functions of secondary metabolites into cultivar development. We argue that phenylpropanoid-derived compounds—particularly CGA—represent ideal dual-benefit targets because they simultaneously contribute to human metabolic health, including anti-obesity effects, and to crop ecological competitiveness through weed suppression and stress resilience. By reframing secondary metabolites as selectable, dosage-responsive traits, this framework bridges nutritional improvement, agronomic sustainability, and modern polyploid breeding theory.

2. Conceptual Framework of Dual-Benefit Breeding

2.1. Rethinking Secondary Metabolites as Breeding Targets

Conventional crop improvement has largely treated secondary metabolites as ancillary traits, relevant mainly to postharvest quality, sensory attributes, or niche nutritional value. In this paradigm, breeding success is measured primarily by yield, stability, and resistance to major pests and diseases, while metabolite profiles are considered either too complex or too environmentally variable to warrant direct selection [15]. This perspective has been reinforced by the logistical difficulty of metabolite phenotyping and the historical separation between plant breeding and functional food research.

Ideotype theory provides a conceptual basis for challenging this assumption. Rather than optimizing individual traits in isolation, ideotype-based breeding emphasizes the deliberate integration of trait combinations that collectively enhance crop performance in target environments [16] [17]. When secondary metabolites contribute measurably to plant fitness or resource-use efficiency, excluding them from ideotype design represents a conceptual omission rather than a technical limitation.

Within a dual-benefit framework, secondary metabolites are elevated from passive chemical features to functional agronomic traits. The key criterion is not bi-

ochemical activity per se, but whether variation in metabolite accumulation translates into consistent, selectable outcomes in the field and in the diet. Phenylpropanoid metabolites in sweetpotato meet this criterion by influencing both post-harvest nutritional value and in-field ecological interactions.

2.2. Dual-Benefit Metabolites: Linking Human Health and Crop Fitness

Dual-benefit metabolites are defined here as compounds that simultaneously enhance human health outcomes and crop ecological performance. In sweetpotato, CGA exemplifies this duality. From a nutritional perspective, CGA has been shown to regulate lipid metabolism, reduce adipogenesis, and improve glucose homeostasis, supporting its relevance to obesity prevention and metabolic health [8] [9]. These effects are particularly important in regions where sweetpotato serves as a staple food and diet-based interventions are more feasible than pharmaceutical approaches.

From a plant-centered perspective, the same metabolites participate in defense-related processes, including allelopathy and stress mitigation [11] [12]. This convergence allows a single biosynthetic pathway to influence outcomes that are traditionally addressed by separate breeding or management strategies. **Figure S1** illustrates this framework by positioning secondary metabolites at the intersection of nutrition-focused improvement and ecological function, emphasizing shared metabolic origins and shared selection leverage.

While chlorogenic acid contributes to metabolic health benefits, high polyphenol intake has also been associated with reduced mineral bioavailability under certain dietary contexts due to chelation effects. These considerations reinforce the importance of threshold-based selection strategies that maximize functional benefits while avoiding excessive accumulation that could compromise nutritional balance.

2.3. Above-Ground Ecological Delivery via Leaf Dynamics

A defining feature of dual-benefit breeding in sweetpotato is the ecological deployment of metabolites through above-ground tissues. Comparative analyses consistently demonstrate that CGA and related phenolics accumulate at substantially higher concentrations in sweetpotato leaves than in storage roots [6]. As the canopy develops, mature leaves undergo senescence and abscission, depositing metabolite-rich residues onto the soil surface [18].

This leaf-shedding process creates a natural mulch layer that serves both physical and chemical functions. Physically, leaf residues contribute to soil coverage and microclimate moderation. Chemically, they act as a reservoir of soluble phenolics that are gradually released during decomposition, generating sustained allelopathic pressure against germinating weeds [12]. This mechanism extends weed suppression beyond early canopy closure and provides a biological explanation for long-observed but poorly quantified weed suppression in vigorous sweet-

potato stands.

Recent metabolomic profiling studies further confirm that sweetpotato leaves exhibit substantially higher phenylpropanoid diversity and abundance than storage roots, with genotype- and environment-dependent variation that supports their role as primary sites of ecological metabolite deployment [19] [20].

2.4. From Metabolic Function to Breeding Interpretation

Translating the dual-benefit concept into breeding practice requires reframing secondary metabolites as quantitative traits with threshold-dependent effects. In a polyploid crop such as sweetpotato, metabolite accumulation reflects the combined influence of multiple alleles across homologous chromosomes, resulting in dosage-responsive expression rather than binary presence or absence [14]. While environmental conditions influence absolute concentrations, consistent genotype-dependent differences indicate that these traits are heritable and amenable to selection [21].

Crucially, dual-benefit breeding does not assume that maximal metabolite accumulation is desirable. Excessive investment in secondary metabolism may impose carbon costs that compromise yield or storage-root development. Instead, the breeding objective is to identify functional thresholds at which metabolite levels are sufficient to deliver nutritional and ecological benefits without incurring disproportionate trade-offs. This threshold-based perspective aligns metabolite selection with ideotype design rather than trait maximization.

3. Ecological Expression of Secondary Metabolites in Sweetpotato

3.1. Secondary Metabolites as Drivers of Crop-Weed Interactions

Weed suppression in sweetpotato has traditionally been attributed to rapid canopy closure and shading. While shading plays an important role, it does not fully explain the persistence of weed suppression later in the season or the inhibition of aggressive weed species capable of penetrating physical barriers. These observations necessitate chemical mediation as a complementary mechanism [4].

Field studies in multiple cropping systems have demonstrated that residue-mediated allelopathic effects persist beyond canopy closure and cannot be explained by physical shading alone, particularly when inhibitory effects are observed after residue incorporation or under reduced canopy cover [11] [12]. These observations support a chemical contribution to weed suppression in addition to morphological interference.

Phenylpropanoid metabolites released from senescing sweetpotato leaves contribute to this chemical dimension of crop–weed interactions. By interfering with weed germination and early seedling growth, these compounds enhance crop competitiveness beyond what can be achieved through morphology alone [11] [12]. In this sense, allelopathy in sweetpotato is best understood as an emergent canopy-level trait rather than a discrete root-level phenomenon.

3.2. Leaf Accumulation, Senescence, and Residue-Mediated Effects

Sweetpotato exhibits vigorous vine growth followed by progressive leaf senescence as canopy density increases [18]. Mature and senescing leaves act as major sinks for phenylpropanoid metabolites, particularly CGA, reflecting their defensive role in vegetative tissues [6]. As leaves abscise, accumulated metabolites are transferred to the soil surface, where they are gradually released during decomposition.

Residue-mediated delivery provides a sustained source of allelochemicals, in contrast to transient root exudates. This temporal persistence is particularly advantageous in low-input systems, where extended weed suppression reduces reliance on repeated cultivation or chemical control [12]. The magnitude of these effects depends on leaf biomass production, senescence timing, and environmental conditions that regulate decomposition and phenolic mobility.

3.3. Environmental Modulation and Functional Limits

The ecological effectiveness of metabolite-mediated weed suppression is modulated by moisture, temperature, and microbial activity, which influence residue breakdown and allelochemical availability [11]. As a result, allelopathic effects may vary across environments and seasons. Recognizing these limitations is essential for realistic breeding expectations and reinforces the importance of selecting for robust, threshold-based metabolite expression rather than maximal accumulation.

Recent syntheses of allelopathy in cropping systems emphasize that residue-mediated chemical interference frequently operates in tandem with physical suppression and remains detectable under variable moisture and microbial regimes, reinforcing the relevance of chemically mediated weed suppression under field conditions [22].

4. Breeding Challenges and Opportunities in a Hexaploid Crop

4.1. Polyploid Genome Complexity and Trait Inheritance

Sweetpotato is an autohexaploid species ($2n = 6x = 90$), a genomic condition that fundamentally alters the inheritance, expression, and selection of quantitative traits. Unlike diploid crops, in which alleles are typically present in two copies, hexaploidy introduces a continuum of allele dosage states ranging from zero to six copies at a given locus. This dosage complexity weakens simple genotype–phenotype associations and has historically limited the application of classical Mendelian analysis and marker-assisted selection in sweetpotato breeding programs [13] [14].

Secondary metabolite accumulation exemplifies these challenges. Phenylpropanoid biosynthesis involves multiple enzymatic steps distributed across interconnected pathways, each potentially influenced by allele dosage, regulatory variation, and epistatic interactions. As a result, metabolite-related traits often display quantitative, rather than discrete, inheritance patterns that are difficult to

capture using selection strategies optimized for monogenic traits such as disease resistance [15]. This complexity has contributed to the historical marginalization of secondary metabolites as direct breeding targets in sweetpotato.

Recent advances in polyploid quantitative genetics have introduced dosage-aware statistical models that explicitly account for multi-allelic inheritance, providing improved resolution for complex traits such as secondary metabolite accumulation in autopolyploid crops [23].

4.2. Environmental Plasticity versus Genetic Signal

A second major obstacle to breeding for secondary metabolites is their sensitivity to environmental conditions, including temperature, light intensity, nutrient availability, and plant developmental stage. Phenylpropanoid accumulation in sweetpotato leaves has been shown to vary across environments and seasons, reinforcing the perception that metabolite traits lack stability or heritability [6] [7]. Consequently, breeders have often regarded metabolite variation as environmentally driven noise rather than a selectable genetic signal.

However, studies across polyploid crops indicate that while absolute metabolite concentrations may fluctuate, relative genotype rankings and threshold-based expression patterns can remain consistent across environments [21]. From a breeding perspective, this distinction is critical. Dual-benefit breeding does not require precise prediction of metabolite concentrations under all conditions; rather, it requires identification of genotypes that consistently exceed functional thresholds associated with ecological outcomes such as weed suppression or nutritional relevance. Recognizing this distinction reframes environmental plasticity as a manageable feature rather than a prohibitive barrier.

Functional thresholds need not be defined as absolute metabolite concentrations, but as relative performance benchmarks across environments. Genotypes that consistently exceed ecological or nutritional thresholds across locations can be identified through multi-environment trials, even when absolute concentrations vary.

4.3. Dosage Effects as a Breeding Opportunity

Although polyploidy complicates genetic analysis, it also creates unique opportunities for trait optimization through allele dosage manipulation. In autohexaploid crops, incremental increases in favorable allele copy number can generate additive or near-additive effects on quantitative traits without the severe pleiotropic consequences often associated with single-gene overexpression in diploid systems [14] [24].

For secondary metabolites, dosage-responsive regulation provides a mechanism for fine-tuning metabolic flux through biosynthetic pathways such as phenylpropanoid metabolism. Rather than selecting extreme phenotypes with potentially high metabolic costs, breeders can target intermediate dosage classes that balance metabolite-mediated ecological benefits with storage-root yield and can-

opy productivity. This dosage-centric perspective transforms polyploid complexity from a breeding constraint into a selective advantage within a dual-benefit framework.

Emerging genomic selection frameworks developed for polyploid crops further suggest that intermediate allele dosage classes can be intentionally targeted to optimize quantitative traits while minimizing trade-offs, supporting the feasibility of dosage-based selection for secondary metabolites [25].

4.4. Phenotyping Constraints and Functional Proxies

Reliable phenotyping remains a practical bottleneck for breeding programs seeking to incorporate secondary metabolites into selection schemes. Direct chemical quantification of phenylpropanoids requires specialized instrumentation and is often too labor-intensive for large breeding populations. These constraints have reinforced the perception that metabolite traits are impractical targets for routine selection.

Dual-benefit breeding addresses this limitation by emphasizing functional phenotyping rather than chemical quantification alone. Field-level traits such as weed suppression indices, canopy persistence, leaf senescence timing, and residue-mediated inhibition integrate multiple underlying processes into agronomically relevant outcomes [4] [12]. By combining targeted metabolite assays on representative genotypes with high-throughput ecological proxies, breeders can reduce phenotyping costs while maintaining selection accuracy.

Functional phenotyping proxies are not intended to replace chemical quantification, but to complement it. Empirical calibration using representative genotypes demonstrates that traits such as weed suppression indices and residue persistence correlate with underlying phenylpropanoid abundance. Once validated, these proxies enable scalable selection while preserving biological relevance.

4.5. Integrative Breeding Opportunities in Sweetpotato

The challenges described above underscore the need for integrative breeding strategies tailored to polyploid crops. In sweetpotato, recent advances in haplotype-resolved genome assemblies and dosage-aware analytical frameworks have begun to provide tools for dissecting complex quantitative traits, including metabolite accumulation [13] [14]. Importantly, dual-benefit breeding does not depend on the immediate deployment of advanced genomic tools. Instead, it can be implemented incrementally through ideotype-based selection that integrates ecological performance, canopy traits, and nutritional value.

By explicitly incorporating secondary metabolites into selection criteria, breeding programs can expand the definition of cultivar success beyond yield and root quality alone. In doing so, sweetpotato becomes a model for how polyploid crops can be improved for multifunctional performance, aligning nutritional enhancement with ecological resilience and sustainability goals.

Recent integrative metabolomic–genomic studies in sweetpotato and related

crops have begun to identify dosage-sensitive loci and regulatory regions associated with phenylpropanoid accumulation, providing early evidence that these traits can be genetically anchored despite polyploid complexity [19] [20].

5. Dual-Benefit Breeding Strategies and Ideotype Design

5.1. Defining the Dual-Benefit Ideotype

Within a dual-benefit breeding framework, the target cultivar is defined not by the maximization of a single trait, but by balanced performance across nutritional, ecological, and agronomic dimensions. This ideotype-oriented perspective contrasts with conventional selection paradigms that prioritize yield or quality traits in isolation and instead emphasizes functional integration across traits that jointly determine crop performance [16] [17]. In sweetpotato, a dual-benefit ideotype integrates moderate to high accumulation of secondary metabolites with stable storage-root yield, acceptable root quality, and vigorous canopy development capable of sustained leaf turnover.

Secondary metabolites such as chlorogenic acid (CGA) are central to this ideotype because they contribute simultaneously to postharvest nutritional value and in-field ecological function. However, dual-benefit breeding does not seek to maximize metabolite concentration indiscriminately. Excessive allocation of carbon to secondary metabolism may compromise growth or storage-root bulking, particularly in environments where resources are limiting. Instead, the ideotype is defined by **functional sufficiency**—metabolite levels that exceed thresholds required for nutritional relevance and ecological competitiveness without imposing disproportionate metabolic costs [21].

Key attributes of a dual-benefit sweetpotato ideotype therefore include:

- 1) sustained leaf biomass production during early and mid-season growth,
- 2) predictable timing of leaf senescence and shedding, and
- 3) secondary metabolite accumulation sufficient to suppress weed emergence while maintaining yield stability.

These attributes position secondary metabolites as contributors to whole-plant fitness rather than isolated chemical traits.

5.2. Selection Targets across Developmental Stages

Dual-benefit breeding requires attention to trait expression across plant developmental stages. Unlike traits assessed solely at harvest, metabolite-mediated ecological functions are expressed dynamically over time. Early-stage selection may emphasize rapid canopy establishment, leaf area expansion, and initial metabolite accumulation, which collectively determine the crop's ability to compete with weeds during the critical weed-free period [4].

Mid-season selection focuses on canopy persistence and the onset of senescence, which determine the timing and magnitude of metabolite deployment to the soil surface. In sweetpotato, the transition from active canopy expansion to leaf shedding represents a key developmental window in which ecological effects

are expressed most strongly [18]. Late-stage evaluation integrates agronomic outcomes, including cumulative weed suppression, storage-root yield, and harvest index stability.

This stage-aware selection contrasts with conventional breeding approaches that emphasize end-point measurements alone. By aligning selection targets with the developmental timing of metabolite release, breeders can apply selection pressure where functional benefits are maximized, recognizing that ecological traits often emerge from **developmental trajectories rather than static measurements** [21].

5.3. Managing Trade-Offs and Threshold Effects

A central challenge in ideotype design is managing potential trade-offs between secondary metabolite production and other agronomic traits. Phenylpropanoid biosynthesis requires carbon skeletons and energy, raising concerns that elevated metabolite levels may reduce yield or storage-root development. Such trade-offs have been documented in multiple crops when secondary metabolism is constitutively upregulated without regard to developmental context [26].

In polyploid crops such as sweetpotato, however, dosage-mediated regulation offers a mechanism for incremental trait adjustment rather than binary extremes. Allele dosage variation allows breeders to fine-tune metabolite accumulation through selection on quantitative variation rather than relying on single-gene effects [14]. Dual-benefit breeding therefore prioritizes **threshold-based selection**, identifying metabolite levels sufficient to confer ecological functions—such as weed suppression—beyond which additional increases yield diminishing returns.

In addition to agronomic trade-offs, elevated phenylpropanoid accumulation may influence sensory attributes such as bitterness or astringency, particularly in edible leaves or processed products. Excessive chlorogenic acid has been associated with reduced palatability in some leafy vegetables and beverages. Dual-benefit breeding therefore emphasizes functional sufficiency rather than maximal accumulation, allowing breeders to balance sensory quality with nutritional and ecological benefits.

This threshold-based perspective reframes secondary metabolites from liabilities to tunable contributors to plant fitness. Rather than asking whether higher metabolite concentration is always better, the breeding question becomes: *What level of metabolite accumulation delivers the greatest net benefit when nutritional, ecological, and agronomic outcomes are considered together?*

5.4. Integrating Phenotyping and Selection Tools

Effective implementation of dual-benefit breeding strategies depends on scalable phenotyping approaches that balance precision with practicality. Direct chemical quantification of secondary metabolites remains valuable for calibration and validation, but its routine application across large breeding populations is often impractical due to cost and labor requirements [6].

Dual-benefit breeding addresses this limitation by integrating **functional phenotyping proxies** into selection pipelines. Field-level traits such as weed suppression indices, canopy persistence, leaf senescence timing, and residue-mediated inhibition capture the integrated outcome of metabolite accumulation and deployment rather than chemical abundance alone [4] [12]. When combined with targeted metabolite assays on representative genotypes, these proxies enable breeders to maintain selection accuracy while reducing phenotyping burdens.

Importantly, this approach allows dual-benefit breeding to be implemented even in programs with limited access to advanced analytical infrastructure. This flexibility is particularly relevant for public-sector and resource-constrained breeding programs, including those operating within 1890 land-grant institutions, where practical field performance remains a primary criterion for cultivar advancement.

5.5. Ideotype-Guided Breeding Pipelines

Implementing dual-benefit breeding at scale requires a shift from trait-by-trait selection toward **ideotype-guided breeding pipelines**. Such pipelines begin with explicit ideotype definition, followed by targeted phenotyping and selection cycles that reinforce both nutritional and ecological performance. Rather than treating secondary metabolites as ancillary traits, they are incorporated directly into selection indices alongside yield, root quality, and stress tolerance.

Ideotype-guided selection also accommodates diversity in production systems and market classes. For example, the optimal balance between metabolite accumulation and yield may differ between subsistence-oriented systems and commercial production, or between fresh-market and processing cultivars. Dual-benefit breeding does not impose a single optimal ideotype, but rather provides a framework for tailoring trait integration to specific agroecological and socioeconomic contexts [17].

By embedding secondary metabolites into ideotype design, breeding programs can intentionally align cultivar development with sustainability goals. Dual-benefit cultivars thus represent a convergence of nutritional enhancement and ecological function, offering a practical pathway toward resilient sweetpotato production systems under increasing environmental and management constraints.

6. Agronomic and Sustainability Implications

6.1. Cultivar-Embedded Weed Suppression as an Agronomic Strategy

One of the most immediate agronomic implications of dual-benefit breeding is the potential to reduce reliance on external weed control inputs by embedding weed suppression capacity directly within the cultivar. Sweetpotato production systems are particularly vulnerable to early-season weed pressure due to slow initial canopy establishment and limited availability of selective post-emergence herbicides [4]. Consequently, weed management often represents a major source

of labor demand and production cost, especially in smallholder and low-input systems.

Cultivars capable of metabolite-mediated weed suppression complement traditional morphological mechanisms such as canopy shading. While rapid vine growth and leaf expansion reduce light availability to competing weeds, chemical interference extends suppression beyond physical shading and into later developmental stages [11] [12]. By suppressing weed emergence and early growth through residue-mediated allelopathy, dual-benefit cultivars provide a layered defense that operates across multiple temporal windows of crop development.

From an agronomic standpoint, even partial reductions in weed pressure can translate into meaningful gains in yield stability and management efficiency. This is particularly relevant in systems where perfect weed control is neither economically feasible nor environmentally desirable. Embedding weed suppression capacity within the cultivar thus shifts weed management from a purely operational challenge to a genetic attribute of the cropping system.

6.2. Compatibility with Low-Input and Organic Production Systems

Dual-benefit breeding is especially well aligned with the needs of low-input and organic production systems, where access to chemical weed control options is limited and labor availability often constrains management intensity. In such systems, cultivar traits that enhance ecological competitiveness are critical determinants of success [27].

Residue-mediated weed suppression derived from leaf senescence offers a biologically based control mechanism that requires no additional inputs beyond standard crop establishment. This feature is particularly valuable for organic producers, who rely heavily on mechanical cultivation and manual weeding, both of which can disrupt soil structure and increase erosion risk. By reducing weed pressure later in the season, dual-benefit cultivars may decrease the frequency or intensity of cultivation, contributing to improved soil health and reduced labor demands.

Importantly, these benefits do not depend on complete weed elimination. Ecological weed management frameworks emphasize suppression to levels that minimize yield loss rather than eradication [4]. Dual-benefit cultivars align naturally with this philosophy by reducing weed competitiveness through sustained chemical and physical interference rather than acute control measures.

6.3. Contribution to Sustainable Intensification

At broader scales, dual-benefit breeding contributes to sustainable intensification by aligning productivity gains with reduced environmental impact and input dependence. Sustainable intensification seeks to increase or maintain agricultural output while minimizing negative externalities, including chemical runoff, soil degradation, and greenhouse gas emissions [5].

By reducing the need for herbicides and repeated mechanical operations, cultivar-level weed suppression decreases fossil fuel use and associated emissions. Moreover, the retention of leaf residues on the soil surface contributes organic matter, enhances soil moisture retention, and moderates temperature fluctuations, providing ancillary benefits that extend beyond weed management alone [27]. These effects are particularly relevant under climate variability, where soil moisture conservation and system resilience are increasingly important.

Dual-benefit breeding also aligns with sustainability goals by integrating nutritional quality into agronomic performance. Cultivars that deliver both functional food value and ecological services maximize the return on breeding investment, supporting public-sector breeding mandates that emphasize societal benefit alongside productivity.

6.4. Extension and Adoption Considerations

For dual-benefit cultivars to achieve impact, their benefits must be visible, interpretable, and valued by producers. Extension programs play a critical role in translating breeding innovations into adoption by framing cultivar traits in terms of tangible management outcomes, such as reduced weeding frequency, improved yield stability, or enhanced market value associated with nutritional attributes.

Residue-mediated weed suppression offers a particularly accessible entry point for extension messaging, as it aligns with observable field phenomena that producers can readily recognize. Demonstration trials highlighting differences in weed pressure, labor requirements, or soil coverage between cultivars can reinforce the value of dual-benefit traits without requiring producers to engage directly with biochemical or genetic concepts.

Furthermore, dual-benefit breeding supports diversified value chains by linking agronomic performance with nutritional messaging. In regions where sweetpotato is marketed as a health-promoting food, cultivars with elevated phenylpropanoid content may command added value, further incentivizing adoption. Extension strategies that integrate agronomic and nutritional narratives can therefore amplify the impact of dual-benefit cultivars across production and consumption domains.

6.5. Limitations and Context-Dependent Performance

While the agronomic and sustainability advantages of dual-benefit breeding are substantial, they are not universal. Environmental factors such as soil type, moisture regime, and microbial activity influence residue decomposition and allelochemical availability, potentially modulating the magnitude of weed suppression effects [11]. Additionally, weed community composition affects sensitivity to allelopathic interference, with some species exhibiting greater tolerance than others.

Recognizing these limitations is essential for realistic deployment and evaluation of dual-benefit cultivars. Rather than positioning metabolite-mediated weed suppression as a standalone solution, it should be viewed as one component of

integrated weed management systems that combine genetic, cultural, and mechanical approaches [4]. Breeding programs should therefore assess cultivar performance across representative environments and management regimes to identify contexts in which dual-benefit traits deliver the greatest benefit.

7. Conclusions and Future Directions

7.1. Reframing Secondary Metabolites as Agroecological Assets

This conceptual analysis advances a dual-benefit breeding framework that reframes secondary metabolites from ancillary chemical traits into **multifunctional agroecological assets**. In sweetpotato, phenylpropanoid-derived compounds—particularly chlorogenic acid—illustrate how a single metabolic class can simultaneously enhance human nutritional quality, including anti-obesity potential, and crop ecological competitiveness through residue-mediated weed suppression. By integrating these functions within ideotype design, dual-benefit breeding challenges the traditional separation between nutrition-focused improvement and agronomic performance.

A central contribution of this framework is the recognition that secondary metabolites need not be maximized to be valuable. Instead, **threshold-based expression** provides sufficient functionality while avoiding excessive metabolic costs. This perspective aligns metabolite selection with whole-plant fitness and yield stability, reinforcing the idea that breeding objectives should prioritize integrated performance rather than isolated trait optimization [16] [17].

7.2. Implications for Polyploid Crop Improvement

Sweetpotato's autohexaploid genome has long been viewed as a barrier to breeding for complex quantitative traits. However, the dual-benefit framework demonstrates that polyploidy can be leveraged as an advantage rather than a constraint. Dosage-responsive regulation enables incremental adjustment of metabolite accumulation, allowing breeders to fine-tune trait expression without incurring severe pleiotropic penalties [14].

More broadly, this framework has implications beyond sweetpotato. Many polyploid crops—such as potato, sugarcane, and certain forage species—exhibit rich secondary metabolite profiles with underexplored agronomic and nutritional functions. Dual-benefit breeding provides a conceptual template for integrating these traits into breeding pipelines, particularly in crops where environmental resilience and low-input performance are increasingly valued.

7.3. Integrating Nutrition, Ecology, and Breeding Pipelines

Dual-benefit breeding also offers a pathway for aligning crop improvement with public-health and sustainability objectives. The inclusion of metabolites with documented anti-obesity and metabolic regulatory effects positions sweetpotato as a functional food crop capable of contributing to dietary strategies for chronic disease mitigation [8]-[10]. Importantly, these nutritional benefits are achieved with-

out compromising agronomic performance, as the same metabolites support ecological functions that reduce reliance on external inputs.

From a breeding-pipeline perspective, the framework emphasizes **functional phenotyping**, ideotype-guided selection, and stage-aware evaluation rather than reliance on high-resolution molecular tools alone. This approach enhances accessibility for public-sector breeding programs and resource-constrained institutions, where field performance and adoption potential are paramount.

7.4. Research Priorities and Methodological Needs

Several research priorities emerge from this analysis. First, greater emphasis is needed on defining functional metabolite thresholds associated with both nutritional relevance and ecological outcomes. This requires coordinated field trials that integrate metabolite profiling, canopy dynamics, and weed suppression metrics across diverse environments.

Second, improved phenotyping strategies that link chemical composition with field-level ecological proxies will be critical for scaling dual-benefit breeding. Advances in high-throughput phenotyping, coupled with targeted metabolite assays, offer promising avenues for balancing precision and practicality [21].

Third, long-term evaluations are needed to assess the stability of dual-benefit traits under climate variability. Because residue-mediated allelopathy depends on environmental conditions that influence decomposition and microbial activity, understanding context-dependent performance will be essential for responsible deployment [11] [12].

7.5. Toward a Broader Vision of Crop Improvement

Ultimately, dual-benefit breeding represents a shift in how crop improvement is conceptualized. Rather than treating nutritional quality, agronomic performance, and ecological function as competing objectives, this framework demonstrates that they can be mutually reinforcing when mediated by multifunctional traits such as secondary metabolites. In sweetpotato, this integration offers a practical pathway toward cultivars that support healthier diets, reduced input dependence, and resilient production systems.

Recent perspectives in crop science increasingly emphasize the integration of metabolomics into ideotype-guided breeding pipelines, highlighting secondary metabolites as actionable traits rather than descriptive end points [28]. These developments reinforce the relevance of dual-benefit breeding frameworks that align nutritional, ecological, and genetic objectives.

As global agriculture confronts the combined challenges of climate change, labor scarcity, and diet-related chronic disease, breeding strategies that deliver multiple benefits from a single genetic investment will become increasingly important. Dual-benefit breeding provides one such strategy, positioning sweetpotato not only as a staple crop, but as a model for multifunctional, sustainability-oriented crop improvement.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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Supplement

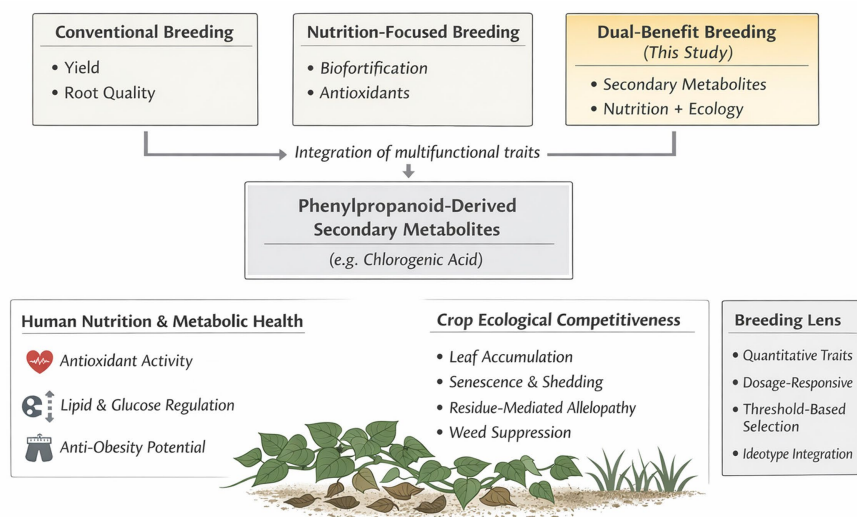


Figure S1. Dual-benefit breeding framework in sweetpotato. The framework positions secondary metabolites, particularly chlorogenic acid (CGA), as multifunctional breeding targets that enhance both human metabolic health—including anti-obesity relevance in the United States—and crop ecological competitiveness. Accumulation of these metabolites in leaves followed by senescence and shedding results in residue-mediated allelopathic effects that contribute to weed suppression. Treating secondary metabolites as dosage-responsive quantitative traits enables ideotype-guided breeding that integrates nutrition, ecology, and agronomic performance (Table S1).

Table S1. Dual-benefit and single-benefit secondary metabolites in sweetpotato.

Metabolite/Metabolite Class	Chemical Class	Primary Tissue Accumulation	Human Health Relevance	Ecological/Breeding Interpretation
Chlorogenic acid (CGA)	Phenylpropanoid	Leaves > storage roots	Antioxidant; lipid and glucose regulation; anti-obesity relevance	Core dual-benefit trait; residue-mediated allelopathy and weed suppression; dosage-responsive selection target
Caffeoylquinic acids (3-CQA, 4-CQA, 5-CQA)	Phenylpropanoid	Leaves	Antioxidant and metabolic regulatory effects	Complementary dual-benefit metabolites supporting allelopathic function
Caffeic acid derivatives	Phenylpropanoid	Leaves	Anti-inflammatory and antioxidant properties	Secondary dual-benefit contributors linked to CGA biosynthesis
Flavonoids (general class)	Phenylpropanoid	Leaves and vines	Antioxidant activity; metabolic health support	Supportive dual-benefit traits enhancing stress tolerance and canopy resilience
Carotenoids (e.g., β -carotene)	Terpenoid (tetraterpenoid, C40)	Storage roots > leaves	Vitamin A nutrition; antioxidant activity	Nutrition-focused single-benefit trait; limited ecological or allelopathic function