

Leaf-Derived Allelopathy in Sweetpotato (*Ipomoea batatas*): Chlorogenic Acid Accumulation and Weed Suppression

Ziming Yue¹, Te-Ming Tseng², Mark Shankle², Yan Meng¹, Victor Njiti¹, Chunquan Zhang¹

¹Department of Agriculture, Alcorn State University, Lorman, USA

²Department of Plant and Soil Sciences, Mississippi State University, Mississippi State, USA

Email: zyue@alcorn.edu

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Abstract

Sweetpotato (*Ipomoea batatas*) is an important food security crop but is highly susceptible to weed interference due to its prostrate growth habit and limited herbicide options. While root-derived allelopathy in sweetpotato has been studied extensively, leaf-derived allelopathy remains poorly understood. This study provides the first formal report of leaf-mediated allelopathy and its role in natural weed suppression. Two cultivars, Heart-O-Gold and 529, were analyzed for chlorogenic acid (CGA) concentrations using HPLC. Results showed that CGA content increased with leaf age, reaching up to 1% of fresh weight, with leaf tissues containing significantly higher levels than roots. Field and greenhouse experiments demonstrated that sweetpotato leaves shed quadratically beginning in the fourth week after planting, contributing an estimated 1.2 - 2.8 t/ha of dry matter across the season. Pot experiments using shed leaves as mulch revealed complete suppression of Palmer amaranth and grasses, with only minimal purple nutsedge emergence at pot edges. These findings indicate that sweetpotato leaf shedding and decomposition release substantial amounts of allelopathic compounds, particularly CGA, creating a natural mulch that extends the weed-free period beyond the critical 2 - 6-week window after transplanting. Leaf-derived allelopathy thus represents a sustainable, above-ground mechanism of weed management, with potential applications in cultivar selection, organic mulch development, and eco-friendly cropping systems.

Keywords

Sweetpotato, Allelopathy, Chlorogenic Acid, Weed Suppression, Leaf Shedding, *Ipomoea batatas*

1. Introduction

Sweetpotato (*Ipomoea batatas*) is a widely cultivated crop valued for its adaptability and nutritional benefits. It is the world's seventh most important food crop and the most efficient staple in terms of calories produced per unit area [1], making it a vital food security crop. However, its canopy architecture and prostrate growth habit make it particularly vulnerable to weed interference.

Seem *et al.* [2], working with the “Beauregard” cultivar and local weed populations in North Carolina, demonstrated that sweetpotato fields must remain weed-free from the second to the sixth week after transplanting to prevent yield and quality losses—this period is referred to as the critical weed-free period. Effective weed management is therefore essential, as weeds compete with sweetpotato for nutrients, water, and sunlight, ultimately impairing yield and quality.

Commercial producers largely rely on herbicides to manage troublesome weed species. In Mississippi, major weeds include yellow nutsedge, purple nutsedge, goosegrass, common cocklebur, redroot pigweed, and Palmer amaranth [3] [4]. However, herbicide options are limited. Currently registered products include clomazone, flumioxazin, and S-metolachlor [5]. Clomazone provides insufficient control of Palmer amaranth, while flumioxazin is highly effective against Palmer amaranth but not against nutsedges. S-metolachlor controls yellow nutsedge and Palmer amaranth but often causes significant crop injury, reducing both yield and storage root quality. Moreover, post-emergence herbicide use is largely restricted to row middles, leaving weeds within the crop rows unmanaged.

Given these limitations, there is a pressing need for alternative weed management strategies that minimize weed pressure while safeguarding yield and storage root quality. One promising approach is to exploit the inherent weed-suppressive potential of certain crop cultivars, a phenomenon known as allelopathy.

Allelopathy is a natural phenomenon in which secondary metabolites produced by one plant species inhibit the growth and development of neighboring species. It represents the external, chemically mediated aspect of plant-plant interactions and is often regarded as a defensive strategy. Since [6] reported that sweetpotato leaf extracts suppressed alfalfa root growth, several studies have explored the allelopathic potential of sweetpotato [7]-[9]. However, most of these investigations have concentrated on root-mediated allelopathy, with the exception of [10] and [11], who examined sweetpotato—*Mikania micrantha* interactions and identified specific allelopathic compounds in sweetpotato leaves. Similarly, [12] investigated the allelopathic effects of aqueous sweetpotato extracts on the seed germination of *Ageratum conyzoides* and found that high concentrations inhibited, while low concentrations promoted, germination. The present study focuses on a different mechanism—leaf shedding—and the allelopathic effects derived from this process.

2. Materials and Methods

2.1. Plant Materials and Growth Conditions

Sweetpotato cultivars Heart-O-Gold and 529 were grown in the greenhouse with

without fertilization at North Farm, Mississippi State University fall to winter, 2021. These cultivars were kept there for continuation of the germplasm, on the other hand, only vines with all leaves intact were selected to sample in early December. Hence their growth time was estimated between one and three months. Along each vine, every other leaf was sampled for analysis. Field images of sweetpotato leaf shedding and residual traces were obtained from a deer repellent project conducted in Pontotoc in 2022, while images showing canopy closure and the leaf mulch layer following de-vining were collected at Alcorn State University in September 2025. A leaf allelopathy assay on the alluvial soil was performed at Alcorn State University from July to September 2025 (see 2.4).

2.2. High Pressure Liquid Chromatography (HPLC) Analysis

An Agilent 1100 series HPLC (Agilent, Santa Clara, CA) was used to analyze chlorogenic acid. The HPLC consisted of a diode array detector (DAD), a fluorescence detector (FLD), an online vacuum degasser, a quaternary pump, an autosampler and a thermostatted column compartment. The Agilent Chemstation A.10.02 software with a spectral module (Agilent Technologies Inc., Wilmington, DE, USA) was used to process the data. Separation was achieved on an ACE reverse phase C18 column (150 mm × 4.6 mm, ACE) with particle size 3 µm. Chlorogenic acid (CGA) was detected at 430 nm (fluorescence with excitation: 325 nm), with a flow rate of 1 mL/min and column temperature of 30°C. Peaks were identified using standard compounds (chlorogenic acid). The injection volume of 5 µL was used. Isocratic elution program was developed as follows: Eluent was mixed by acetonitrile (40%) with water (60%) (modified with 0.02% acetic acid). The CGA detection limit was 0.03 ppm and quantification limit was 0.1 ppm. The standard CGA was purchased from Fisher Scientific with 98% purity. Stock standard solution of 200 ppm was made from it without further purification. Calibration curve was made by analyzing series dilutions 200, 100, 50, 10, 5.0, 1.0 ppm with $r^2 > 0.999$. All analyses were conducted in triplicates. If the results are beyond the calibrations, the sample is diluted and reanalyzed.

2.3. Sample Preparation

Fresh sweetpotato leaf tissue 0.10 g was weighed into 2 mL plastic tube, followed by addition of 0.9 mL methanol + water mixture (1:1) and three beads and capped, loaded onto Precellys Evolution Touch sample homogenizer and mixing at 4500 rpm for 1 minute. The tube was centrifuged at $16,100 \times g$ for 10 min at room temperature. The resulting supernatant was filtered (0.2 µm pore size) and loaded onto the HPLC sample tray for chlorogenic acid analysis.

2.4. Sweetpotato Leaf Mulching Experiment

Three pots were filled with field soil containing a natural seed bank of weeds and assumed to be homogeneous. The pots were labeled 0, 1, and 2, and were placed outdoors to receive daily dew and natural precipitation. Pot 0 remained bare,

while pots 1 and 2 were covered with fallen sweetpotato leaves at ratios of 1:2. The leaves were collected from two benches of sweetpotato plants five weeks after planting. Previous studies indicate that sweetpotato leaf drop begins around the fourth week and increases quadratically thereafter. Within 20 days, enough fallen leaves had accumulated to completely cover the soil surface in pots 1 and 2, at which point no additional leaves were added.

3. Results

3.1. Sweetpotato Leaf Chlorogenic Acid Concentration

Table 1. Chlorogenic acid concentrations of series of leaves on a vine for each cultivar.

Leaf plastochon index (LPI)	Cultivar 5 (Heart-O-Gold) Leaf chlorogenic acid concentration (ppm)	Cultivar 39 (529) Leaf chlorogenic acid concentration (ppm)
2	871.1 ± 4.7	1378.1 ± 7.8
4	2471.4 ± 5.3	1514.7 ± 3.7
6	10351.8 ± 5.9	2080.5 ± 5.8
8	16234.2 ± 6.6	4137.8 ± 8.4
10		4941.6 ± 2.9
12		6736.3 ± 9.8

As shown in **Table 1**, leaf chlorogenic concentrations of cultivar Heart-O-Gold increased from 871 ppm to 16,234 ppm from second leaf from the vine tip to the eighth leaf from the vine tip while leaf chlorogenic acid concentrations of cultivar 529 increased from 1378 ppm to 6736 ppm from the second leaf from tip of the vine to the 12th leaf from the tip of the vine. Leaf tissues showed chlorogenic acid (CGA) concentrations significantly higher than roots [13].

3.2. Quadratically Increased Fallen Leaf Number

This paragraph should be arranged in the discussion part, but it is so fundamental and influences other experiments, we have to move it forward as part of our work. The sweetpotato leaf shedding phenomena had been studied using the “Jewel” cultivar in Georgia State in 1990s [14] [15]. Their data showed the missing (here we refer to as fallen) leaves started from the fourth week after transplanting and increased quadratically (see **Figure 1**) following fallen leaf number $N = 1.50 - 2.75t + 0.72t^2$. t -time in weeks. The accumulated dry matter in the fallen leaves over a growth season was estimated as 1.2 - 2.8 t/ha.

3.3. Images of Sweetpotato Fields with Shed Leaves

Leaf shedding is uncommon during the first month after transplanting, a period when weed suppression is primarily achieved through the combined effects of root-exuded allelopathic compounds and canopy shading. By the ninth week (**Figure 2**), leaf shedding becomes evident. The fallen leaves typically contract in size

and, after absorbing nighttime dew, remain moist—conditions that may enhance their allelopathic activity.

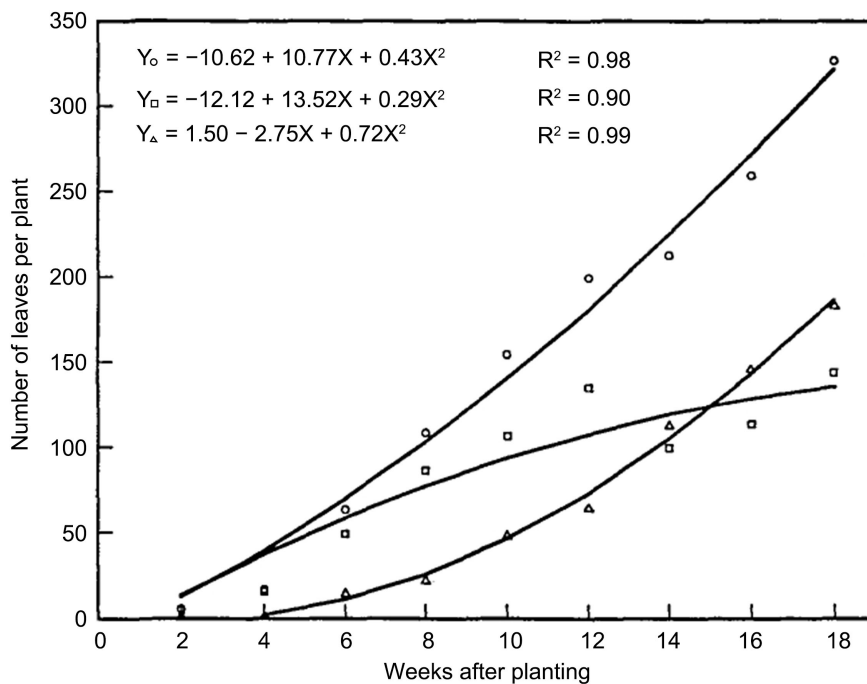


Figure 1. Total number of leaves produced (circle), leaves present (square), and missing leaves (triangle) of sweetpotato plants at 2-week intervals throughout the growing season. (modified from [14]).



Figure 2. Early shedding, 57 days after planting on Sep 16, 2022; soil surface breakage was also shown.

Figure 3 shows the fallen leaves (decayed away) during the thirteenth week. Although the fallen leaves are gone, their previous existence can be figured out: the brownish leaf leach color, leaf print on the soil surface, the bare old vines (used to be equipped with full leaves).



Figure 3. Showed leaf shedding imaged on the 86th day after transplanting on October 14, 2022. The bare soil surfaces without shading under the Sun at this season are a miracle, as such surfaces are usually covered by weeds.

The estimated fallen leaf dry matter over a growing season was 1.2 - 2.8 t/ha, taking the average as 2 t/ha, assuming the growth season as 17 weeks (119 days), leaf shedding from the fourth week to the thirteenth week almost accounts for 0.390 (from curve $N = 1.50 - 2.75t + 0.72t^2$) of the total leaf shedding for the whole season, *i.e.*, 0.78 t/ha, equivalent to 78 g dry matter/m².

3.4. Pot Allelopathy Experiments

To simulate natural leaf fall, sweetpotato leaves used in this experiment were collected from two greenhouse benches five weeks after planting. These leaves were divided into two groups at a 1:2 ratio. Group 1 was applied to Pot 1, and Group 2 to Pot 2. The results are shown in **Figure 4**.





Figure 4. The top image was taken on July 16, 2025, and the bottom image on August 4, 2025. The pots were filled with field soil, each assumed to contain a similar weed seed bank. They were numbered 0, 1, and 2 from right to left and placed in the field to receive daily dew and natural precipitation. Although no main crop was planted, the emerging plants are referred to as weeds in this context.

Weed counts (August 11):

- Pot 0: nutsedge—3; grasses—20; Palmer amaranth—1
- Pot 1: nutsedge—2; grasses—0; Palmer amaranth—0
- Pot 2: nutsedge—0; grasses—0; Palmer amaranth—0

The results show that leaf mulch was effective: all grasses and Palmer amaranth were completely suppressed. The two purple nutsedge plants in Pot 1 appeared along the pot edge, an area not fully exposed to leaf leachate in the early stage. Originally, only one nutsedge was present; the second emerged later through propagation.

September 16 final weed counts and weed harvest:

Pot 0: purple nutsedge (*Cyperus rotundus*)—6; barnyard grasses (*Echinochloa crus-galli*)—8; *Dichanthelium oligosanthes*—2; Palmer amaranth (*Amaranthus palmeri*)—1; spurge (*Euphorbia nutans*)—2. Some weeds on August 11 didn't survive due to drought. Total fresh above-ground biomass = 50.9 g;

Pot 1: purple nutsedge (*Cyperus rotundus*)—5. Total fresh above-ground biomass = 15 g;

Pot 2: Total fresh above-ground biomass = 0 g;

Weed above-ground biomass ratios: pot 0:pot 1:pot 2 = 50.9:15:0.

The weed biomass reduction of Pot 1 = $1 - 15/50.9 = 70.5\%$ compared to the control of Pot 0.

In addition, the quadratically increasing fallen leaves (from July 16 to August 5) seem to have special effects on weed suppression: Pot 2 had no weed emergence until September 16 even though the fallen leaves accumulation stopped on August 5, soil surface around the pot edge was exposed although a 10-gallon pot was adequately covered with fallen leaves (1 inch of thick fallen leaves) on August 14, there were two purple nutsedge plants that had penetrated the mulch on September 16 (nutsedge in the plot was dominated by purple nutsedge).

4. Discussions

4.1. Why Chlorogenic Acid?

In our previous study on sweetpotato allelopathy [9], chlorogenic acid (CGA)

emerged as the dominant allelopathic compound. Similarly, in the book *Allelopathy* [16], CGA was highlighted as a representative allelopathic compound across numerous systems. This evidence supports CGA as the primary candidate for investigating sweetpotato allelopathy.

4.2. Chlorogenic Acid Concentration Increases with Leaf Age

Our data (**Table 1**) show that older leaves contain higher concentrations of CGA. Leaf senescence usually begins with older leaves, but the primary reason for leaf shedding is shading [14]. Shading is most serious along the main (old) vines where the canopy closes first, leading to shading. That is why the main vines became bare (**Figure 3**) approaching harvest. Fallen leaves tend to have greater allelopathic potential, sometimes containing up to 1% of fresh weight in CGA.

4.3. Quadratic Accumulation of Fallen Leaves Maintains Allelopathic Pressure

Although fallen leaves are subject to decomposition and environmental degradation, their quadratic increase throughout the season ensures a sustained allelopathic pressure on weed germination and growth.

In the pot experiments (**Figure 4**), Pots 1 and 2 were covered with high-quality organic mulch derived from shed sweetpotato leaves. Unlike conventional organic mulches, which often contain weed seeds, sweetpotato leaf mulch is free of such contamination while releasing allelopathic compounds such as CGA into the soil surface. In Pot 1, two nutsedge plants grew larger than those in Pot 0, likely because the mulch conserved soil moisture, while Pot 0 (bare soil) lost moisture more rapidly. Additionally, the two nutsedge plants in Pot 1 grew at the pot edges, where early in the experiment fewer leachates penetrated the soil. Importantly, no nutsedge plant penetrated the central mulch layer until August 14, demonstrating that sweetpotato leaf mulch can suppress even nutsedges to some extent, which typically grow through fabric, plastic, or standard organic mulch.

4.4. Field Observations

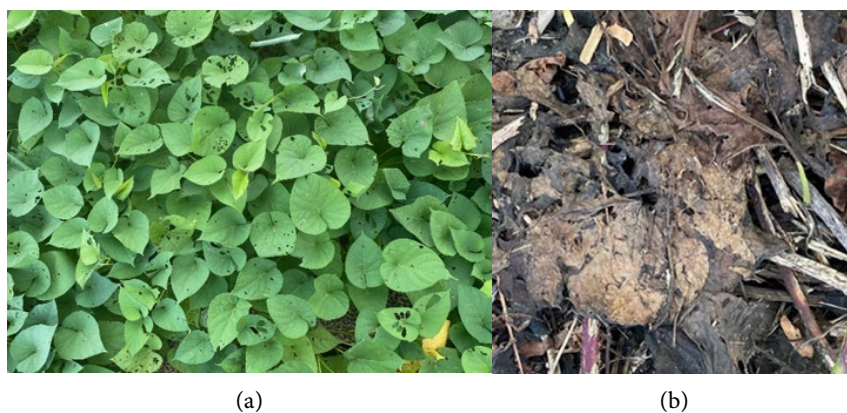


Figure 5. The fallen leaf mulch layer was formed under the closed canopy. (a) Closed canopy; (b) under the canopy the fallen leaves form a mulch layer.

In field conditions, the mulch layer is less obvious (**Figure 5(a)**). However, after de-vining, the mulch layer becomes obvious (**Figure 5(b)**). Similarly, **Figure 2** shows a visible mulch layer on the soil surface, while **Figure 3** shows leaf prints and leach stains on bare soil—evidence of rapid decomposition. The disappearance of mulch does not mean an absence of allelopathy; rather, it reflects rapid compound release. Without such allelopathy, the bare soil surfaces would likely be covered with weeds.

4.5. Leaf Biomass Shedding and Nutrient Remobilization

Sweetpotato leaves contain the highest CGA concentrations compared to other plant parts [13] [17]. Over a growing season, leaf shedding can be substantial: 48% - 63% of total leaves are shed depending on cultivar [14] [15] [18]. Prior to shedding, leaves lose about 63% of dry matter, with the remainder remobilized to the plant [14]. Across cultivars, leaf dry matter loss ranges from 1.2 - 2.8 t/ha. Significant amounts of phosphorus, potassium, and magnesium are also remobilized. While leaf shedding correlates positively with vine dry weight, it shows no negative relationship with storage root yield [15].

From these estimates, old leaves contained 0.73% CGA (fresh weight), equivalent to ~2% on a dry weight basis (assuming 63% water content). This translates to 24 - 36 kg/ha of CGA being released into the field—an amount greater than what is typically contributed via root exudates. Importantly, this release begins at the fourth week after transplanting, increases quadratically, and becomes significant by the sixth week, coinciding with the end of the critical weed-free period [2].

4.6. Cultivar Differences and Future Work

Preliminary results (**Table 1**) suggest that cultivars such as Heart-O-Gold and 529 differ in their patterns of CGA accumulation, leaf size, internode length, and allelopathic delivery potential. A separate study is being designed to evaluate these cultivar-specific traits more comprehensively.

Additionally, we observed that sweetpotato leaves sometimes excrete crystalline deposits along veins. To our knowledge, this phenomenon has not been documented. Given that leaf CGA levels can reach 1%, it is possible that these crystals contain allelopathic compounds. If so, they may provide an additional pathway for early allelopathic release, activated simply by dew or rainfall, even before leaf senescence. This finding warrants further investigation and will be addressed in a follow-up paper.

4.7. Implications for Weed Management

Figure 1 illustrates the dynamics of leaf production, retention, and shedding across the season (adopted from [14]). Although leaves are a stronger source of allelopathic compounds than stems or roots, natural shedding begins only at the fourth week, leaving the first six weeks—the critical weed-free period—insufficiently protected. In Mississippi, transplanting typically begins after mid-June,

meaning that an April planting could provide two months of leaf growth. Cultivars with strong allelopathic potential could be grown specifically for leaf harvest, producing mulch for newly transplanted fields. Such leaves, while not extreme in CGA content (>1%), would be sufficient to suppress weeds if pest-free. These leaves could even be produced in greenhouses to ensure quality and punctuality.

As mentioned earlier, during a growing season, 48% - 63% of total leaves are shed, depending on the cultivar [14] [15] [18]. This means that 37% - 52% of the total leaves remain on the vines at harvest. These retained leaves are typically older and contain higher concentrations of allelopathic compounds such as chlorogenic acid. If this strong allelopathic potential can be preserved—by drying and powdering the leaves—it could be applied to newly transplanted fields during the first six weeks of the critical growth period in spring. The vines themselves also contain allelopathic compounds, though in lower amounts, and can be dried and powdered together with the leaves. Thus, de-vined plant material collected before harvest could be processed into a natural amendment for suppressing weeds in the following sweetpotato growing season.

4.8. Summary

Sweetpotato allelopathy appears to function primarily through above-ground mechanisms—particularly leaf shedding and subsequent compound leaching. With CGA as one of the dominant compounds, this mechanism offers a natural and sustainable form of weed suppression. This shifts the focus from root-based to foliar-based allelopathy, with important implications for cultivar selection, organic mulch development, and sustainable weed management strategies.

5. Conclusions

This paper reports on leaf-derived allelopathy in sweetpotato, a relatively late-occurring phenomenon. [6] demonstrated that leaf extracts exerted stronger inhibitory effects on alfalfa root growth than extracts from stems or roots, while [17] and [13] showed that sweetpotato leaves contain higher concentrations of chlorogenic acid (CGA) compared to roots.

Leaf-derived allelopathy manifests later in the crop cycle because sweetpotato leaf shedding typically begins around the fourth week after transplanting and increases quadratically thereafter [14]. Once leaves are shed, allelopathic effects become active. Shedding is mainly driven by canopy closure and shading near the main vine, as well as leaf senescence. Although shedding at the fourth week is generally insufficient to have a strong effect, cumulative leaf loss by the sixth week becomes significant, coinciding with the end of the critical weed-free period [2].

This process is analogous to pine needle-mediated allelopathy around pine trees [19], but with distinct advantages: sweetpotato leaves decompose more rapidly, releasing allelopathic compounds such as chlorogenic acid, caffeic acid, coumarin, trans-cinnamic acid, hydroxycinnamic acid [9], as well as linoleic acid, palmitic acid, and ethyl palmitate [11]. Because of this rapid decay, a persistent mulch layer

is rarely visible. Instead, evidence of allelopathic activity may be inferred from the brownish leachate staining and leaf print on soil surfaces, bare old vines (**Figure 3**), and the estimated dry matter contribution of up to 2.8 t/ha of shed leaves for a growth season [14].

Allelopathy represents an external component of plant-plant interaction, activated only once the leaves are shed and no longer physiologically controlled by the parent plant. The accumulation of shed leaves between weeks four and six thus feeds back to benefit the mother plant by suppressing weeds and helping to close the critical weed-free period.

Because leaf-derived allelopathy occurs relatively late in the crop cycle, there is potential to advance its effectiveness. A practical strategy could involve spreading pre-grown sweetpotato leaves in newly planted fields to provide early-season allelopathic cover during the critical 2 - 6-week window after transplanting [2]. The de-vining product before harvest can be dried and powdered and be applied to suppress weeds for the critical weed-free period the next season.

In summary, sweetpotato leaves are a major source of allelopathic compounds, particularly CGA. Their capacity to suppress weeds through leaf shedding and rapid decomposition provides a natural, sustainable mechanism for weed management. Harnessing this process offers new opportunities for developing low-input, eco-friendly cropping systems.

Conflicts of Interest

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

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