



Article

An Integrated Green Control System: Combining Immune Inducer ZNC and Microbial Consortium Recharge for Sustainable Yam Production

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Abstract

The sustainable production of *Dioscorea polystachya* (Chinese yam) is severely compromised by a vicious cycle of excessive chemical dependency and complex biotic stresses including anthracnose, nematodes, thrips and other associated pests and diseases. Moreover, the efficacy of single biocontrol agents in field applications often proves unstable, and balancing the growth–defense trade-off remains challenging. To break these impasses, we established a novel “ZR Integrated Green Control System” (ZR-IGCS) by coupling an active plant immune inducer ZNC with a functional microbial agent Recharge. This system establishes a dual defense barrier, orchestrating internal immune activation with external micro-ecological regulation to engineer ecological synergy. Field trials demonstrated that the ZR-IGCS significantly accelerated seed tuber germination and seedling biomass accumulation. It established a spatiotemporal complementary defense network, exhibiting excellent integrated pest and disease control efficacy. The system maintained over 60% efficacy against foliar diseases such as anthracnose and brown spot, while enhancing the control of soil-borne diseases like wilt and root-lesion nematodes by more than 60% and 30%, respectively. It also achieved ~48% specific control of thrips. Crucially, ZR-IGCS alleviated the growth–defense conflict, significantly delaying plant senescence and synchronously optimizing yield structure for aerial beans and underground tubers. This synergy increased the proportion of high-quality yam beans, yielded a 51.66% surge in high-quality tubers, and improved total economic benefits by ~30%. The combined system successfully bridges the gap between laboratory potential and field stability for yam production, offering a robust and sustainable strategy to mitigate continuous cropping obstacles and reduce chemical inputs.

Keywords: *Dioscorea polystachya*; integrated system; growth–defense trade-off; micro-ecological regulation; sustainable agriculture



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1. Introduction

Yam (*Dioscorea* spp.) is a globally distributed crop of profound economic and medicinal significance, holding substantial agronomic importance across Asia, Africa, and Latin America. As the world's fourth-largest tuber crop, global yam production reaches approximately 90 million tons across over 10 million hectares [1]. Beyond providing a staple food source for millions, yam is a representative “medicine-food homology” plant whose bioactive secondary metabolites possess potent anti-inflammatory and antioxidant properties for pharmacological applications [2–4].

However, sustainable yam production is increasingly threatened by a complex interplay of biotic and abiotic stressors. Diseases and pests, including anthracnose, brown spot, root-lesion nematodes, beet armyworm, and thrips, severely compromise crop viability. Yam anthracnose causes devastating foliage and vine necrosis, precipitating yield losses of 50–90% [1,5]. Concurrently, soil-borne nematode infections reduce tuber weight by 20–30% and degrade market value [1], particularly with root-lesion nematodes inducing 24–80% yield reductions and cultivar degeneration in China [6]. Herbivorous pests further cause global yield reductions of 18–20%, totaling nearly \$500 billion in annual economic losses [7]. Compounding these biotic threats, long-term continuous monocropping deteriorates the rhizosphere micro-environment. Continuous cropping exceeding three years induces drastic soil pH fluctuations, degrading the rhizosphere microbial habitat and causing nutrient depletion [8,9]. This convergence of stresses collapses the underground defense of tuber crops, undermining yield quality and grower economic stability. Although chemical pesticides offer transient mitigation, their indiscriminate application drives soil degradation, eradicates non-target beneficial microbiota, and accelerates pesticide resistance [7]. Crucially, as a medicinal crop, yam is subject to stringent maximum residue limits [10]. These issues not only undermine the sustainability of yam cultivation but also severely compromise its export potential and medicinal value. Therefore, exploring green and sustainable alternatives to chemical pesticides is an urgent imperative for the yam industry.

In response to these challenges, biological control agents (BCAs) have garnered widespread attention as alternatives to synthetic agrochemicals. Nevertheless, a critical bottleneck remains in their practical application. While single-strain formulations like *Trichoderma* spp. and *Bacillus* spp. demonstrate potent antifungal and nematicidal activities under controlled laboratory conditions, their field efficacy is frequently inconsistent [11–15]. This “lab-to-field” translational gap presents a significant challenge to green plant protection. Because yam faces a complex network of pathogenic microorganisms and insect pests, solitary BCAs, due to their narrow target spectra and environmental susceptibility, often fail to provide comprehensive protection [11,16]. Thus, developing adaptive and integrated control strategies is required. Plant immune inducers have emerged as an eco-friendly disease control pathway by activating systemic defenses [17,18]. However, their deployment is constrained by the physiological “growth–defense trade-off”, where constitutive defense activation diverts metabolic energy away from biomass accumulation, compromising yield potential [19–22]. Therefore, current strategies remain insufficient, warranting adaptive and enhanced systems to reconcile these limitations.

To bridge these gaps, we propose a novel control system integrating the active plant immune inducer “ZNC” with the composite microbial agent “Recharge”. ZNC, a bio-stimulant derived from *Paecilomyces variotii*, operates at ultra-low concentrations and exhibits dual regulation of growth and immunity [17,23,24]. It orchestrates a dose-dependent mechanism that finely balances the growth–defense trade-off. Low concentrations (1–5 ng/mL) remodels root architecture via auxin signaling to promote growth, whereas higher concentrations (>5 ng/mL) trigger a reactive oxygen species burst and activate the salicylic acid pathway to prime plant immunity [23,25,26]. Although ZNC has demonstrated efficacy in potato

(increasing yield by 18–26%) [25] and pepper (enhancing resistance to bacterial wilt) [27], its application in the sustainable production of tuber crops, specifically Chinese yam, remains unvalidated. Complementing this internal regulation, we utilized the commercial microbial consortium Recharge as a practical vehicle to introduce an external ecological component, constructing a holistic defense barrier from the rhizosphere to the phyllosphere. Specifically, *Beauveria bassiana* combines contact insecticidal activity against piercing–sucking pests with endophytic hormonal modulation to simultaneously drive vegetative growth and suppress pathogens like *Botrytis* [28–30]. *Metarhizium anisopliae* delivers broad-spectrum virulence against early-instar larvae [31,32], while *Bacillus subtilis*, a core plant growth-promoting rhizobacterium (PGPR), inhibits *Fusarium* and nematodes via antibiosis and primes host immunity through induced systemic resistance [1,11,13]. Additionally, *Purpureocillium lilacinum* disrupts nematode life cycles and reinforces insecticidal efficacy, broadening the scope of Integrated Pest Management (IPM) [33–36]. Despite the individual promise of these components, their combined stability and efficacy within the yam agro-ecosystem lack systematic empirical validation.

Predicated on these theoretical underpinnings, this study established a green control system integrating ZNC with the microbial consortium Recharge, herein designated as the “ZR Integrated Green Control System” (ZR-IGCS). This framework aims to couple ZNC-mediated endogenous physiological modulation with Recharge-based external ecological optimization. This combination primes immunity, enhances nutrient uptake, improves the crop micro-environment, and directly controls pests. Through rigorous field experimentation, we demonstrated that the ZR-IGCS significantly improved key agronomic traits, including emergence rate, plant height, stem diameter, and dry matter accumulation. Simultaneously, it significantly reduced the disease indices of anthracnose, brown spot, *Fusarium* wilt, and root-lesion nematode disease, while enhancing resistance against thrips infestation. Notably, the system delayed plant senescence and significantly boosted the yield of high-quality tubers and aerial beans. Aligning with the need for sustainable agriculture and reduced chemical reliance in yam, the ZR-IGCS establishes a practical framework that accommodates ecological sustainability with economic profitability. This system provides pivotal technical support for IPM strategies to enhance crop resilience and market competitiveness in the face of multiple environmental pressures.

2. Materials and Methods

2.1. Geographical Location and Cultivation Conditions

The field experiment was conducted at the Yam Planting Base in Wenjia Street, Shouguang City, Shandong Province, China (36°51′ N, 118°42′ E) from April to October 2021. During the growing season, the region experienced a typical warm temperate monsoon climate, with an average mean temperature of 21.36 °C and cumulative precipitation of approximately 782.2 mm. The experimental field spanned 10,000 m², characterized by well-drained black soil with a pH of 7.5. Given that yam yields typically decline by the second year of continuous cultivation due to accumulated biotic stressors and soil degradation [37], a field with a three-year cropping history was selected to rigorously evaluate the biological agents under fully established continuous cropping obstacles. Prior to the experiment, crop residues and weeds were removed, and the land was plowed and sun-exposed. A double-furrow planting pattern was adopted. The furrow spacing was 1.7 m, plant spacing was 17–18 cm, and planting depth was 3.5–5.0 cm, resulting in a planting density of approximately 6000 plants per 1000 m².

2.2. Plant Materials and Biological Agents

The yam cultivar “*Dioscorea polystachya* cv. Japanese White Jade” was selected as the experimental subject. Two biological agents were utilized for the treatments. ZNC (Zhinengcong) is a plant immune inducer whose main component is the ethanol crude extract of *Paecilomyces variotii*, with an active ingredient content of 5 mg/mL. The composition and biological activity of this extract have been well-characterized in previous studies [23,24]. The composite microbial agent “Recharge” (a powder formulation) was produced by Russell IPM Ltd. (Deeside, Manchester, UK) and contains a microbial consortium including *Beauveria*, *Metarhizium*, *Bacillus subtilis*, *Purpureocillium lilacinum*, and *Bacillus amyloliquefaciens*. Because it is a proprietary commercial product, the exact quantitative composition—including the specific viable propagule counts and standardized concentrations for each constituent microorganism—is protected as a commercial trade secret and was not disclosed by the manufacturer.

2.3. Experimental Design

The experiment was arranged in a randomized block design comprising four main treatment groups. To ensure reproducibility, the experimental field was divided into three distinct blocks, which corresponded to the three biological replicates. Within each block, the treatments were randomly allocated to independent field plots, with each plot serving as a distinct biological replicate (the experimental unit). Based on the double-furrow planting pattern (furrow spacing of 1.7 m, plant spacing of 17–18 cm), each experimental plot was appropriately sized to accommodate the subsequent yield sampling areas, which covered 9.1 m² (with dimensions of 10 m by 0.91 m) per plot. Group A served as the conventional control and received standard local management consisting of biweekly irrigation at a volume of 30 m³ per 667 m² and the application of a balanced water-soluble fertilizer with an N:P:K ratio of 20:20:20 at a rate of 10 kg per 667 m² throughout the growth period. Additionally, plants in Group A received mock treatments with equivalent volumes of water devoid of active ingredients, matching the precise application methods used for the biological agent treatments. Group B, designated as Recharge single treatment, incorporated the microbial agent Recharge into the conventional protocol at three distinct stages: soil pre-treatment via drip irrigation using a 1.67 g/L solution one week prior to planting; seed tuber soaking in a 3 g/L solution for 30 s before sowing; and a combined application of drip irrigation at 1000 g per 667 m² coupled with foliar spraying using a 1000-fold dilution at the germination, vining, and tuber swelling stages. Group C, representing ZNC single treatment, involved ZNC application via root irrigation at concentrations of 1, 2.5, and 5 ng/mL, which were coded as Ca0, Cb0, and Cc0 respectively. These were applied either alone or coupled with a fixed 50 ng/mL foliar spray, coded as Ca1, Cb1, and Cc1 respectively. Finally, Group D represented the Recharge and ZNC Combination, where the varying ZNC application protocols of Group C were superimposed onto the full Recharge regimen of Group B, with treatments coded as Da0 through Dc1 as detailed in Supplementary Table S8.

2.4. Determination of Growth-Promoting Indicators

Eighteen days after planting, random sampling was conducted at five points within uniform growth areas for each treatment, with 20 plants surveyed per point. The emergence rate was calculated as the ratio of the number of emerged plants to the total number of surveyed plants, multiplied by 100%. One month after planting, five points were randomly selected per treatment, and two plants per point were assessed to determine plant height, measured from the ground level to the growing point, and stem diameter, measured at a height of 1.00 cm above the soil surface. Subsequently, at 60 days during the vining stage

and 160 days during the tuber swelling stage, sampling was performed at three random points with five plants per point. The collected plants were separated into above-ground stems and leaves and underground tubers, which were then washed, subjected to enzyme inactivation, and dried to determine the dry matter weight.

2.5. Assessment of Disease and Pest Resistance and Plant Senescence

Upon the natural occurrence of anthracnose and brown spot in the field, disease severity was evaluated by surveying 20 leaves at each of five randomly selected points per treatment. Subsequently, the Disease Index (DI) and relative control efficacy were calculated, with the experiment conducted in triplicate. The disease grade was classified as follows: grade 0: no lesions; grade 1: lesion area < 5%; grade 3: 5–10%; grade 5: 10–25%; grade 7: 25–50%; and grade 9: >50%. The disease index (DI) was calculated using the formula: $DI = [\sum(\text{number of leaves of each grade} \times \text{grade value}) / (\text{total leaves} \times 9)] \times 100$. Control efficacy was determined using the formula: Control Efficacy (%) = $(1 - DI_{\text{treatment}} / DI_{\text{control}}) \times 100$. For *Fusarium* wilt, 20 plants were surveyed at each of five random points to calculate the incidence rate, defined as (number of diseased plants/total plants) $\times$ 100. For root-lesion nematode disease assessments, twenty tubers were randomly sampled from each of five distinct points per treatment. Disease severity was graded based on the percentage of tuber surface area covered by galls (black skin): grade 0: no galls; grade 1: <5%; grade 3: 5–10%; grade 5: 10–20%; grade 7: 20–33%; and grade 9: >33%. The DI and control efficacy were calculated using the same formulas described above. Because the biological agents were applied prior to pest outbreaks, initial baseline populations were not recorded. To accurately assess treatment efficacy against thrips, infestation severity was evaluated by randomly sampling five plants at each of three points per treatment and visually counting the populations of relatively immobile, highly destructive thrips nymphs congregating on the upper tender leaves. Finally, plant mortality was recorded when the death rate in the control group exceeded 33% by surveying 100 plants at each of three points per treatment, calculated as (number of dead plants/total plants) $\times$ 100. The experiments above were performed with three biological replicates.

2.6. Assessment of Yield, Commercial Quality, and Economic Benefits

Aerial beans (yam beans) and underground tubers were classified into two grades based on customized commercial morphological standards established for this study: Grade I (high quality) and Grade II (Secondary or inferior). Grade I beans were defined as having a diameter greater than 1.0 cm, whereas Grade II beans had a diameter of less than 1.0 cm. For tubers, the morphological quality assessment incorporated both qualitative shape parameters and quantitative dimensions. Grade I samples were characterized by a straight shape, a length exceeding 40.00 cm, and a growing point diameter greater than 3.00 cm. Conversely, Grade II tubers exhibited a curved shape or deformed growing points, with a length of less than 40.00 cm and a growing point diameter of less than 3.00 cm. Following harvest, yield assessment was conducted in three randomly selected sampling plots per treatment, each covering an area of 9.1 m² with dimensions of 10 m by 0.91 m. The yields of Grade I and Grade II beans and tubers were recorded and standardized to a unit area of 0.91 m² (1 m $\times$ 0.91 m) with three replications.

The net income per mu (667 m²) was calculated by integrating the market values of graded products with the input costs of the biological agents. The actual income generated from aerial beans (I_{beans}) and underground tubers (I_{tubers}), as well as the total net income (I_{net}), were derived using the following equations:

$$I_{\text{beans}} = (Y_{b1} \times P_{b1} + Y_{b2} \times P_{b2}) \times 733$$

$$I_{tubers} = (Y_{t1} \times P_{t1} + Y_{t2} \times P_{t2}) \times 733$$

$$I_{net} = I_{beans} + I_{tubers} - C_{ZNC} - C_{Recharge}$$

where Y_b and Y_t represent the yields of beans and tubers, respectively, within the 0.91 m² sampling area; the subscripts 1 and 2 denote Grade I and Grade II classifications; P indicates the corresponding market unit price; 733 serves as the conversion factor to scale production from 0.91 m² to 667 m²; and C represents the specific input costs for ZNC and Recharge agents.

2.7. Statistical Analysis

Statistical analysis was performed using GraphPad Prism 8.0.2. All figures were generated using Adobe Photoshop CC 2019. Data were presented as means $\pm$ standard error (SE) of three biological replicates for each treatment. For indicators where multiple plants or leaves were sampled within a single plot, the raw measurements were first averaged to calculate a single plot mean. These plot means were then utilized as the independent replicate values for the subsequent statistical analysis. Differences between experimental groups were compared using one-way ANOVA followed by Duncan's multiple range test. Prior to the one-way ANOVA, the assumptions of normality and homogeneity of variances were verified. A p -value greater than 0.05 was considered not statistically significant. Data processing was conducted using t Processing System (DPS, version 7.05).

3. Results

3.1. The Integrated System of ZNC and Recharge Enhances Seedling Emergence and Vegetative Growth

To evaluate the combined impact of the immune inducer ZNC and microbial consortium Recharge on emergence, yam seed tubers received various treatments (Supplementary Table S8). Compared to 87% emergence rate in the conventional control (Group A), ZNC root irrigation alone at 1 ng/mL (Ca0) and 2.5 ng/mL (Cb0) significantly improved emergence, reaching 93% at 2.5 ng/mL (Figure 1, Supplementary Table S1). However, 5 ng/mL treatment (Cc0), even with a 50 ng/mL foliar spray (Cc1), yielded no significant increase. Recharge single-agent treatment (Group B) significantly increased emergence to 90%. Combining Recharge with 2.5 ng/mL ZNC irrigation and a 50 ng/mL spray (Db1) further raised emergence to >94% (Figure 1A). Thus, appropriate concentrations of both agents can promote emergence, whereas excessive ZNC may inhibit it.

To evaluate the effects of both agents on field growth at the seedling stage, plant height and stem diameter were measured 30 days after planting. ZNC irrigation at 2.5 ng/mL (Cb0) significantly increased seedling height by 7.69%. While 1 and 5 ng/mL irrigation alone lacked growth-promoting effects, combining 1 ng/mL irrigation with a 50 ng/mL spray (Ca1) enhanced height by 9.42%. Conversely, the high-concentration combination (Cc1 treatment) significantly inhibited vertical growth by 5.34% (Figure 1B, Supplementary Table S1), suggesting a negative impact of excessive ZNC concentrations on plant height. Furthermore, Recharge alone did not significantly enhance seedling height or stem diameter under any conditions (Figure 1B,C). Although high-concentration ZNC inhibited vertical growth, it dose-dependently promoted stem thickening. The combination of Recharge, 5 ng/mL ZNC irrigation, and a 50 ng/mL spray (Dc1) achieved the greatest stem diameter increase (20.13%) (Figure 1C, Supplementary Table S1). Collectively, these findings demonstrate that ZNC treatment effectively enhances vegetative growth of the aerial parts.

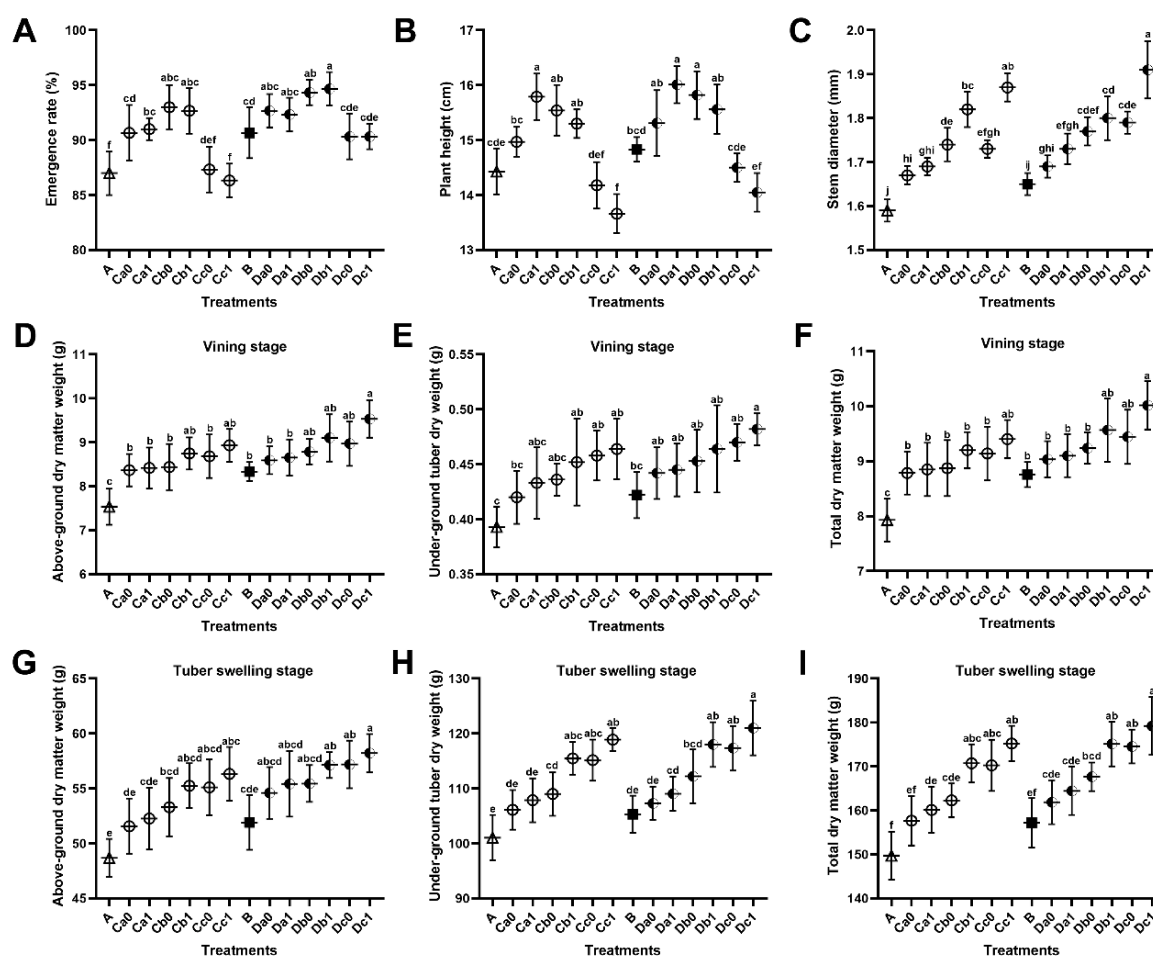


Figure 1. Enhanced effects of the immune inducer ZNC and the microbial agent Recharge on the seedling emergence and vegetative growth of *Dioscorea polystachya*. (A) Emergence rate recorded 18 days after planting. (B) Plant height and (C) stem diameter at the seedling stage (30 days after planting). (D–F) and (G–I) Aerial, tuber, and total dry weights during the vining stage (60 days after planting) and the tuber swelling stage (160 days), respectively. Treatments include conventional control (group A), Recharge alone (group B), ZNC alone (groups Ca0–Cc1), and the combined application of ZNC and Recharge (groups Da0–Dc1) at varying concentrations (see Materials and Methods for detailed descriptions). Data are means $\pm$ standard error (SE) of three biological replicates ($n = 3$). Different lowercase letters above the bars indicate statistically significant differences among treatments ($p < 0.05$).

At the vining stage (60 days post-planting), most ZNC treatments significantly increased aerial and tuber dry matter accumulation compared to the control (Group A), whereas Recharge single-agent application yielded no significant tuber biomass improvement (Figure 1D–F). Without Recharge, the 5 ng/mL root irrigation plus 50 ng/mL foliar spray treatment (Cc1) maximized biomass, increasing aerial, tuber, and total dry weights by 18.55%, 18.07%, and 18.58%, respectively. The 2.5 ng/mL combination (Cb1) performed comparably (Figure 1D–F, Supplementary Table S2). Recharge amplified this effect, and the Dc1 treatment achieved optimal accumulation, increasing aerial, tuber, and total dry weights by 26.50%, 22.65%, and 26.31%, respectively. These results indicate that Recharge significantly enhances the efficacy of ZNC in promoting dry matter accumulation.

Similar trends emerged at the tuber swelling stage (160 days post-planting). Without Recharge, Cc1 remained highly effective, increasing aerial, tuber, and total dry weights by 15.73%, 17.65%, and 17.03%, respectively (Figure 1G–I). While Recharge single-agent application did not significantly enhance biomass, it considerably improved ZNC efficacy.

Combined treatments Dc1 and Db1 demonstrated superior performance, reaching total dry weights of 179.206 g (+19.69%) and 175.124 g (+16.97%), respectively (Figure 1I, Supplementary Table S3). In conclusion, while Recharge alone has limited impact on biomass during tuber expansion stage, it acts collectively with ZNC to significantly maximize biomass accumulation in both aerial vines and underground tubers.

3.2. The Integrated System Significantly Enhances Disease Resistance

To evaluate the impact of ZNC and the Recharge agent on disease resistance, the disease indices (DIs) for anthracnose, brown spot, and root-lesion nematode disease were assessed to determine control efficacy. Field surveys revealed that ZNC treatment significantly enhanced anthracnose resistance regardless of Recharge application. Combining 5 or 2.5 ng/mL ZNC root irrigation with a 50 ng/mL foliar spray (Cc1/Dc1 and Cb1/Db1) demonstrated optimal efficacy, significantly reducing leaf lesion area (Figure 2A). Control efficacy reached 56.23% (Cc1) and 54.36% (Cb1) in the absence of Recharge, rising to 64.27% (Dc1) and 61.94% (Db1) with Recharge application, showing no significant difference between these optimal treatments (Figure 2B). Interestingly, Recharge suppressed anthracnose with low-concentration ZNC (1 ng/mL). Moreover, superimposing a ZNC foliar spray consistently improved resistance across all root irrigation treatments, mostly exceeding 50% improvement (Figure 2B, Supplementary Table S4).

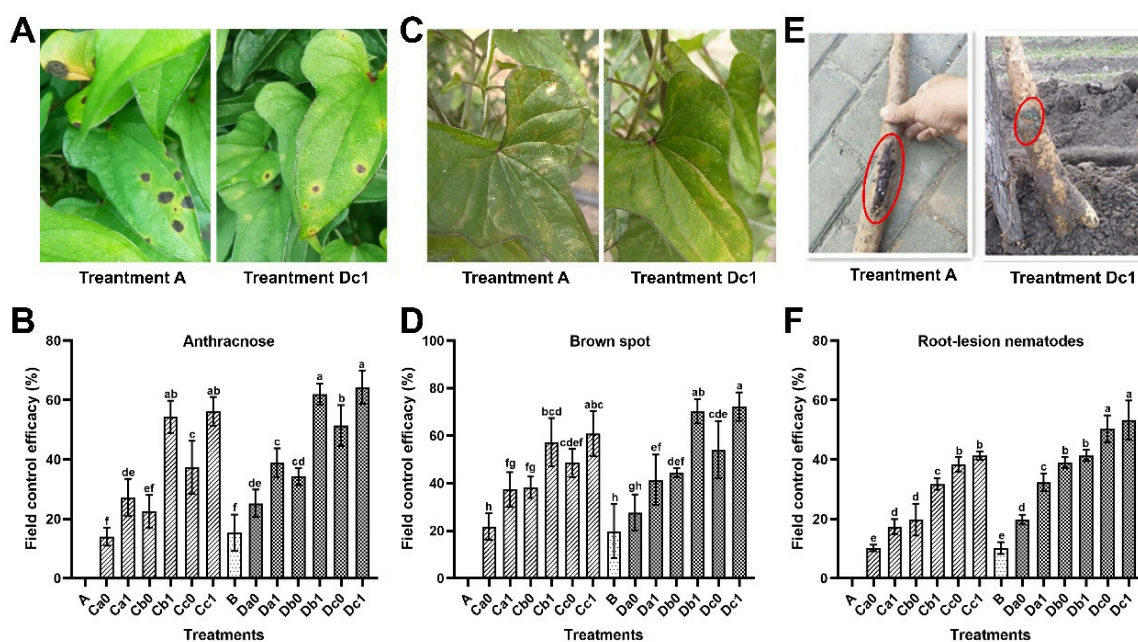


Figure 2. Enhanced field control efficacy against anthracnose, brown spot, and root-lesion nematode diseases mediated by the combined application of ZNC and Recharge. (A,C,E) Representative disease symptoms of anthracnose (A), brown spot (C), and root-lesion nematodes (E). Comparisons are shown between the conventional control (Treatment A, exhibiting severe symptoms) and the combined application of Recharge with 5 ng/mL ZNC root irrigation plus 50 ng/mL foliar spray (Treatment Dc1, showing significantly reduced symptoms). Red circles in (E) highlight the characteristic black lesions caused by nematode infection. (B,D,F) Field control efficacy (%) for the respective diseases. Data are means $\pm$ standard error (SE) of three biological replicates ($n = 3$). Different lowercase letters above the bars indicate statistically significant differences among treatments ($p < 0.05$).

Regarding brown spot, trends mirrored those of anthracnose. The combinations of 5 ng/mL and 2.5 ng/mL root irrigation with a 50 ng/mL foliar spray yielded superior results, markedly reducing disease severity (Figure 2C). With Recharge, these treatments achieved control efficacies of 72.24% (Dc1) and 70.31% (Db1), significantly outperforming

other groups (Figure 2D, Supplementary Table S4). In contrast to the broad efficacy observed with ZNC, Recharge alone showed limited efficacy against brown spot, but it could provide minor enhancement to ZNC treatments (Figure 2D).

Regarding underground tuber health, root-lesion nematode incidence decreased as ZNC concentration increased. Specifically, the Dc1 treatment significantly reduced tuber galls area (black skin), achieving 53.28% control efficacy (Figure 2E, Supplementary Table S4). Crucially, unlike foliar diseases, Recharge application significantly amplified ZNC efficacy against nematodes across all treatment groups (Figure 2F). This amplification was particularly pronounced at lower ZNC concentrations (1 ng/mL), where efficacy improved by over 80%, while high-concentration groups showed ~30% improvement (Supplementary Table S4). Furthermore, the integrated system also significantly inhibited *Fusarium* wilt, with maximum control efficacy exceeding 60% (Supplementary Figure S1, Table S4). Ultimately, while the immune inducer ZNC effectively suppresses both aerial and tuber diseases, Recharge agent exhibits specific therapeutic efficacy against underground pathogens, generating combined overall disease control.

3.3. Recharge Significantly Reduces Thrips Infestation, Whereas ZNC Shows No Control Efficacy

Thrips represent a major pest threatening yam foliage. To evaluate the pest control efficacy of ZNC and Recharge, infestation levels were monitored via random field sampling during the growing season. Compared to the control (Group A), none of the six ZNC treatment combinations (Ca0–Cc1) significantly reduced thrips populations (Figure 3B, Supplementary Table S4). In sharp contrast, all plants treated with Recharge exhibited enhanced resistance, with infestation levels significantly mitigated (Figure 3A,B). Specifically, Recharge application reduced the average thrips population per plant from 36.14 to 18.76, achieving a control efficacy of 48.09% (Supplementary Table S4). These findings demonstrate that the Recharge agent possesses superior efficacy compared to ZNC in controlling thrips.

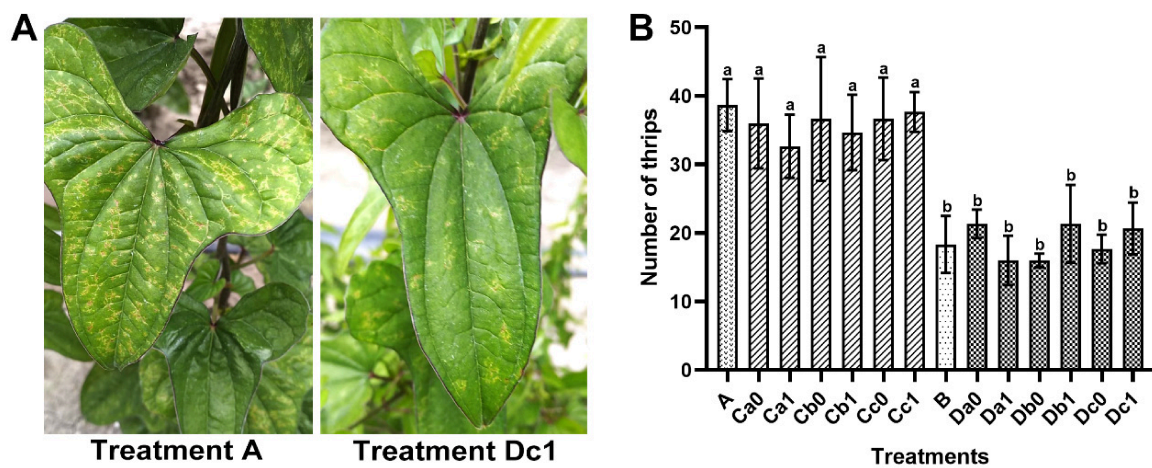


Figure 3. Significant reduction in thrips infestation in *Dioscorea polystachya* mediated by Recharge. (A) Representative thrips damage symptoms in the control (Treatment A, exhibiting severe chlorotic spotting and feeding damage) and the combined application of Recharge with 5 ng/mL ZNC root irrigation plus 50 ng/mL foliar spray (Treatment Dc1, showing significantly reduced symptoms). (B) Number of thrips per plant across treatments. Treatments containing Recharge (Group B and Groups Da0–Dc1) significantly reduced the thrips population. In contrast, ZNC alone (Groups Ca0–Cc1) showed no significant efficacy against thrips infestation. Data are means $\pm$ standard error (SE) of three biological replicates ($n = 3$). Different lowercase letters above the bars indicate statistically significant differences among treatments ($p < 0.05$).

3.4. The Integrated System Significantly Delays Plant Senescence

Six months post-sowing, as the yams entered the late growth stage, an interesting phenomenon was observed. In contrast to the extensive mortality (>33%) in the control group (Group A), all treated plants maintained vigor and exhibited significantly delayed senescence (Figure 4). While the control mortality rate reached 44.33%, combining 5 or 2.5 ng/mL ZNC root irrigation with a 50 ng/mL foliar spray reduced mortality to 14.33% (Cc1) and 16.67% (Cb1), respectively. Even 1 ng/mL ZNC root irrigation alone (Ca0) mitigated vine death, reducing mortality by 22.56% compared to the control (Figure 4B, Supplementary Table S4). Crucially, Recharge application further suppressed mortality across all groups. Combining Recharge with 5 or 2.5 ng/mL ZNC irrigation plus a 50 ng/mL spray (Dc1 and Db1) optimally maintained plant vigor (Figure 4A), lowering mortality to 10.33% and 12.00%, respectively, representing reductions of 76.70% and 72.93% relative to the control (Supplementary Table S4). Significant suppression also occurred in other treatments (Figure 4B). Collectively, these results demonstrate that the combined ZNC and Recharge system effectively delays vine senescence, resulting in a pronounced “stay-green” effect.

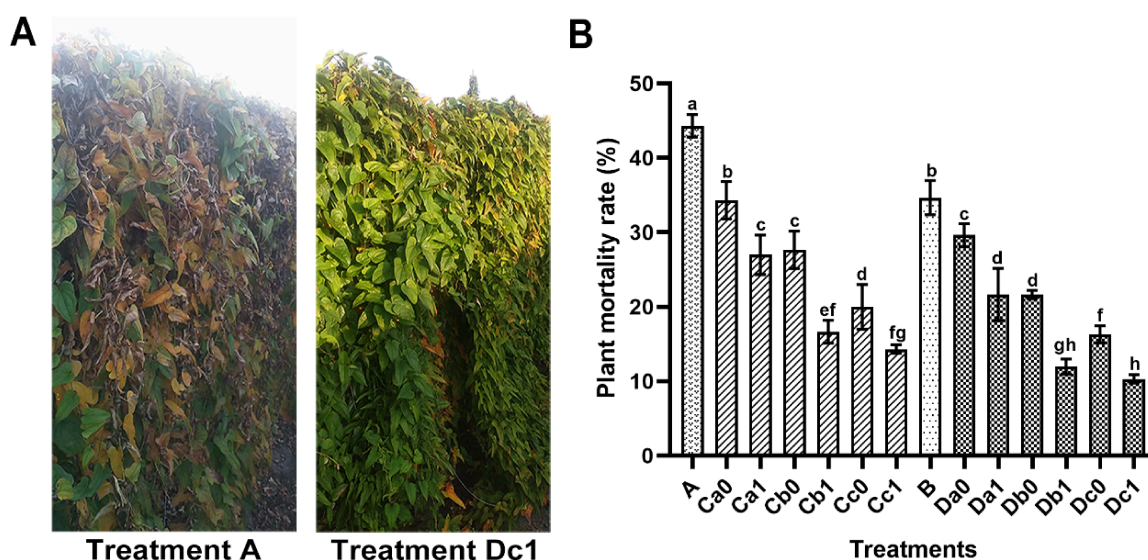


Figure 4. Significant delay of vine senescence in *Dioscorea polystachya* mediated by the combined application of ZNC and Recharge. (A) Representative senescence status of yam vines at the late growth stage in the control (Treatment A, exhibiting severe withering and leaf browning) and the combined application of Recharge with 5 ng/mL ZNC root irrigation plus 50 ng/mL foliar spray (Treatment Dc1, showing vigorous growth and a stay-green phenotype). (B) Plant mortality rate across treatment groups. The single-agent treatments (Group B and Groups Ca0–Cc1) and combined application (Groups Da0–Dc1) significantly inhibited vine mortality, effectively prolonging the functional growth period. Data are means $\pm$ standard error (SE) of three biological replicates ($n = 3$). Different lowercase letters above the bars indicate statistically significant differences among treatments ($p < 0.05$).

3.5. The Integrated System Significantly Improves Yield and Quality of Aerial Yam Beans

Aerial yam beans were classified into Grade I (high quality, diameter > 1.00 cm) and Grade II (Secondary or inferior, diameter < 1.00 cm). Six months post-sowing, aerial beans were harvested, and the yields of both grades were quantified via random sampling within a 0.91 m² area. Statistical analysis revealed that ZNC and Recharge treatments significantly increased bean size and weight compared to the control (Figure 5A). Without Recharge, all ZNC treatments (Ca0–Cc1) significantly increased Grade I yield and reduced Grade II yield. The Cb1, Cc0, and Cc1 treatments achieved relatively optimal Grade I yields of 0.95, 0.91,

and 0.96 kg/0.91 m², respectively, significantly outperforming other groups (Figure 5B, Supplementary Table S5). The significant increase in Grade I yield was accompanied by a concurrent reduction in Grade II yield (Figure 5C), indicating that ZNC treatment optimizes quality structure by allocating assimilates toward superior-quality commercial beans.

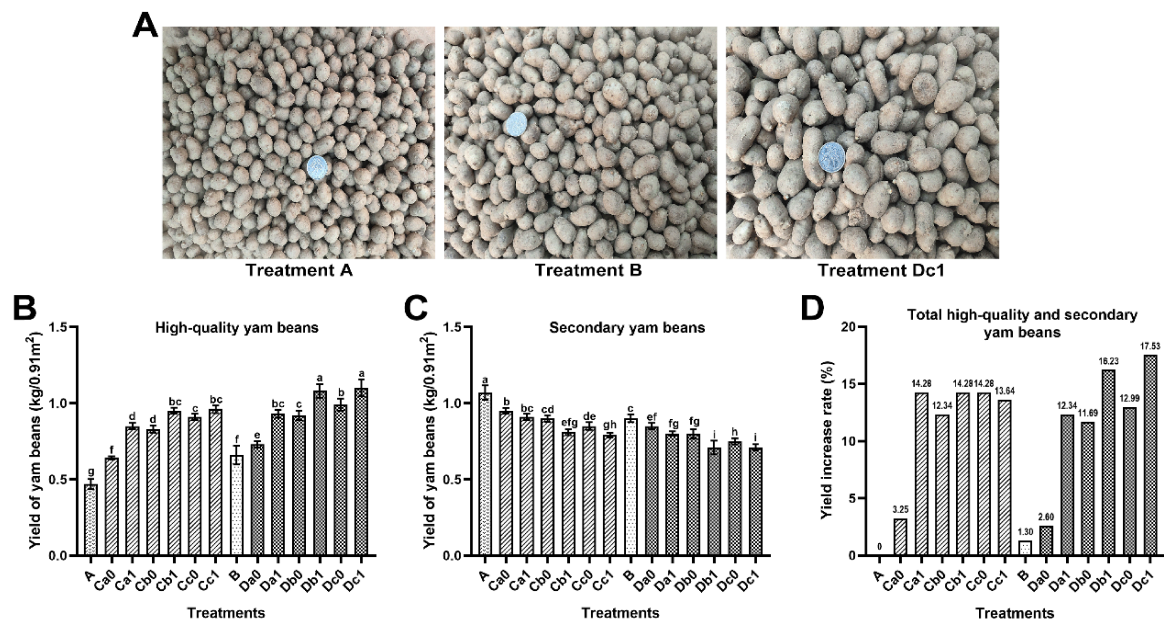


Figure 5. Improvement of yield and quality structure in aerial yam beans mediated by the combined application of ZNC and Recharge. (A) Representative harvest quality of yam beans in Treatment A (exhibiting smaller size and lower quality), the Recharge-only Treatment B (showing intermediate improvement in bean size), and the combined Treatment Dc1 (showing significantly increased size and volume). A coin is used as a scale marker. (B–D) The yield classification and increase rate across different treatment groups. The combined Groups Da0–Dc1 significantly increased the yield of high-quality beans (diameter > 1.00 cm) (B) and the total yield increase rate (D), while significantly reducing the proportion of secondary inferior beans (diameter < 1.00 cm) (C), effectively optimizing yield composition. Data are means $\pm$ standard error (SE) of three biological replicates ($n = 3$). Different lowercase letters above the bars (B,C) indicate statistically significant differences among treatments ($p < 0.05$). Values above the bars (D) represent the calculated percentage increase based on mean yield of total beans per 0.91 m².

Recharge application further amplified these benefits. The Db1 and Dc1 combinations proved most effective, raising Grade I yields to 1.08 kg/0.91 m² and 1.10 kg/0.91 m², increasing 13.68% and 14.58% over their non-Recharge counterparts, demonstrating integrated quality enhancement (Figure 5, Supplementary Table S5). Within Recharge-treated groups, foliar spraying proved valuable. For instance, Db1 increased Grade I yield by 17.39% and reduced Grade II yield by 11.25% compared to root irrigation alone (Db0) (Figure 5B,C and Supplementary Table S5). Most treatments increased total yield by >10%, with Dc1 and Db1 achieving 17.53% and 16.23% increases, respectively (Figure 5D). Consequently, these results confirm that the combined green cultivation strategy utilizing ZNC and Recharge effectively boosts the yield and quality of aerial beans.

3.6. The Integrated System Significantly Increases Yield and Quality of Underground Tubers

Similar to aerial beans, yam tubers were categorized into superior Grade I (straight, length > 40.00 cm, and growing point diameter > 3.00 cm) and inferior Grade II (curved or malformed, length < 40.00 cm, and diameter < 3.00 cm) (Figure 6A,B). Systematic analysis revealed that ZNC treatment significantly optimized yield composition by promoting biomass allocation toward Grade I tubers. Without Recharge, all ZNC treatments opti-

mized yield composition by increasing Grade I and decreasing Grade II tuber yields. The 5 ng/mL root irrigation plus 50 ng/mL foliar spray (Cc1) proved most effective, increasing Grade I yield to 9.82 kg/0.91 m² (+42.11% vs. Control A) and reducing Grade II yield to 0.87 kg/0.91 m² (−65.34%). Treatments including Cb1 and Cc0 also significantly improved Grade I yields (Figure 6D,E and Supplementary Table S6). These results indicate ZNC modulates source–sink relationships to favor high-quality tuber formation.

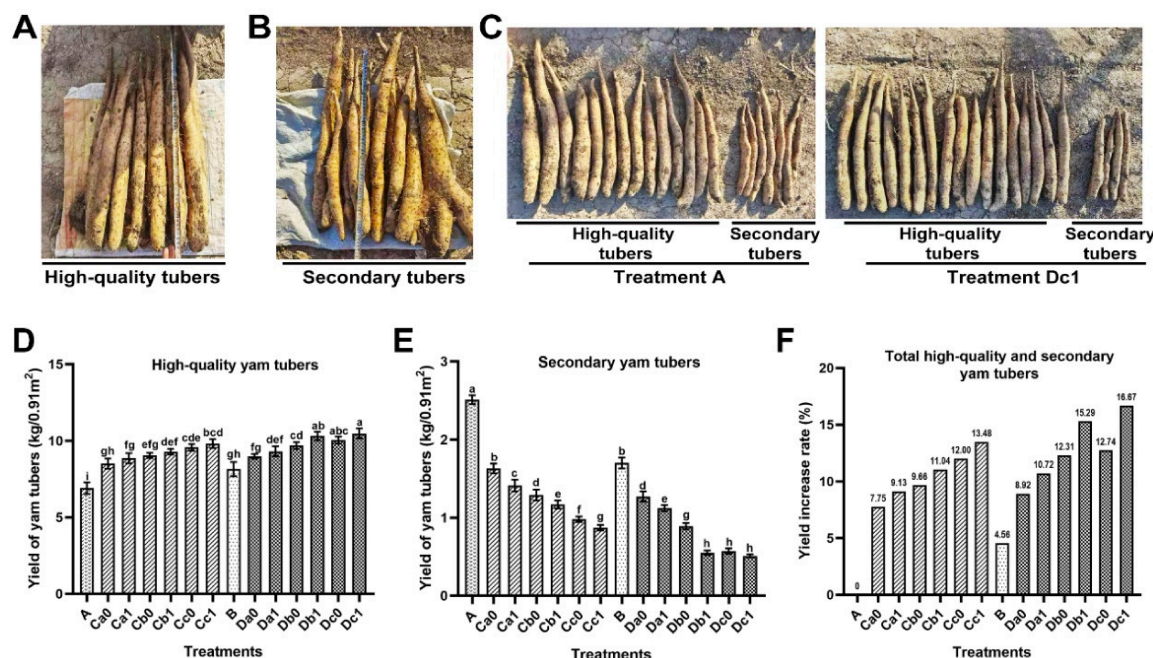


Figure 6. Enhanced optimization of tuber quality and yield structure mediated by the combined application of ZNC and Recharge. (A,B) Representative morphological classification of yam tubers: (A) high-quality tubers (a straight shape, length > 40.00 cm, and diameter > 3.00 cm), and (B) secondary inferior tubers (a curved or malformed shape, length < 40.00 cm, and diameter < 3.00 cm). (C) Visual comparison of harvested tubers between the control Treatment A and the optimized combined Treatment Dc1, demonstrating a marked shift towards the formation of high-quality tubers. (D–F) The yield of high-quality tubers (D), secondary inferior tubers (E), and the total yield increase rate (F). The combined system significantly increased the yield of high-quality tubers while reducing the proportion of secondary inferior tubers. Data are as means $\pm$ standard error (SE) of three biological replicates ($n = 3$). Different lowercase letters above the bars indicate statistically significant differences among treatments ($p < 0.05$). Values above the bars (F) represent the calculated percentage increase based on mean yield of total tubers per 0.91 m².

Further analysis demonstrated Recharge amplified these quality and total yield improvements. The optimal combination (Dc1) elevated Grade I yield to 10.48 kg/0.91 m² (+51.66%) and suppressed Grade II yield to 0.51 kg/0.91 m² (−79.68%) (Figure 6C–E and Supplementary Table S6). Although individual treatments of Recharge or low-concentration ZNC increased Grade I tuber yield, combined applications produced significantly greater gains, confirming robust synergy. Regarding total yield, the combined strategy also achieved maximum production potential. The Dc1 treatment reached a total yield of 10.99 kg/0.91 m², representing a 16.67% increase and significantly outperforming other groups (Figure 6F, Supplementary Table S6). Taken together, the green system developed in this study not only increases total unit yield but, more critically, achieves “quality-efficient” production by significantly shifting the ratio of yield components in favor of superior Grade I tubers.

4. Discussion

4.1. The Paradigm Shift from Chemical Dependency to Ecological Synergy via the ZR-IGCS

Long-term yam production is constrained by excessive chemical inputs and soil micro-ecological imbalances, which intensify pest and disease pressures while reducing yield and quality. Continuous monoculture exacerbates co-infections of biological stressors such as anthracnose, brown spot, *Fusarium* wilt, root-lesion nematodes, and thrips, ultimately leading to tuber deformity and rot, and causing a dual decline in yield and quality (Figure 7A). While chemical models offer short-term control, they cause severe soil pollution. To address this, we integrated the plant immune inducer ZNC with the functional microbial agent Recharge to construct the “ZR Integrated Green Control System” (ZR-IGCS), which realizes a paradigm shift from the “adversarial killing” of chemical pesticides to the “systemic ecological regulation” of green biological agents.

Impact of ZNC and Recharge on Chinese Yam Production: Traditional vs. Green Planting

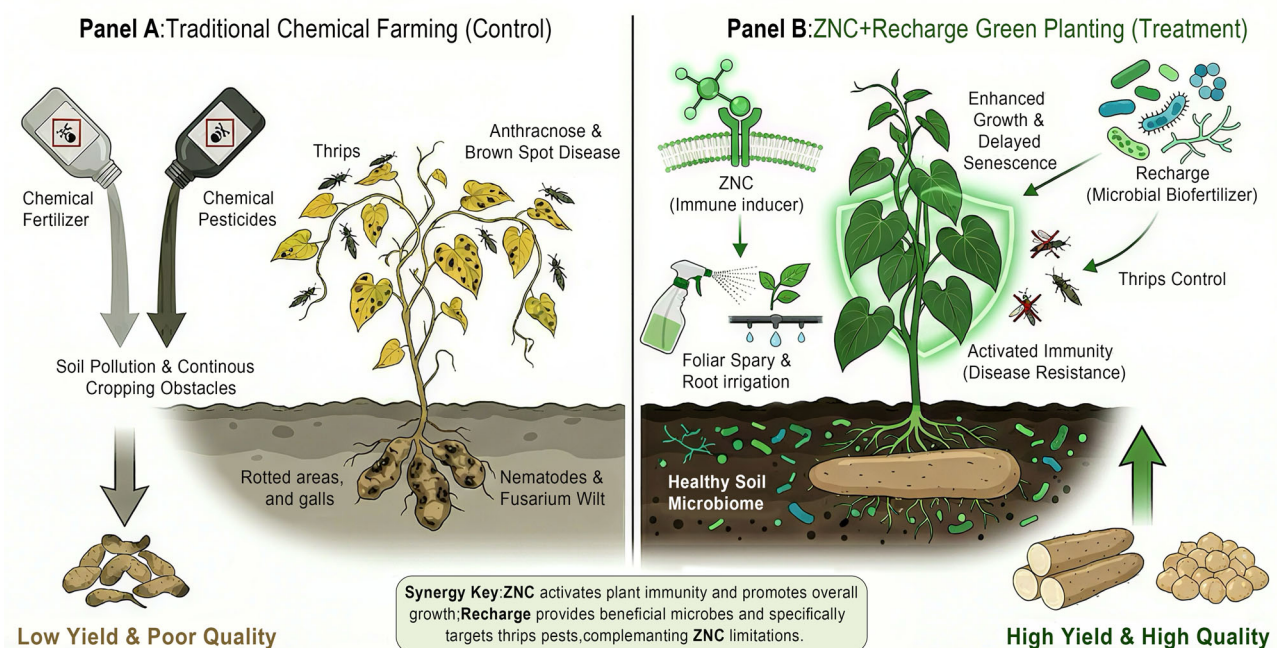


Figure 7. Schematic illustration of the ZR-IGCS-mediated ecological system for sustainable *Dioscorea polystachya* production. (A) The traditional chemical farming relies on excessive chemical fertilizer and pesticide inputs, which induces soil pollution, continuous cropping obstacles, and severe biotic stress, ultimately resulting in rotted tubers and compromised yield quality. (B) The ZR Integrated Green Control System (ZR-IGCS) establishes a dual defense barrier defined by “internal immunity activation combined with external ecological regulation”. ZNC acts as an active immune inducer applied via foliar spray and root irrigation to activate endogenous plant immunity, enhance disease defense, and delay senescence. Concurrently, Recharge functions as a microbial biofertilizer to optimize the external rhizosphere microbiome, suppressing soil-borne pathogens and providing specific control against thrips infestation. This integration promotes a virtuous cycle that ensures healthy soil microbiomes, thereby achieving high yield, superior quality, and sustainable production capabilities.

As illustrated in the model, the ZR-IGCS establishes a dual defense barrier characterized by internal immune activation coupled with external ecological regulation. Internally, ZNC acts as a potent elicitor. Based on previous molecular characterizations of its primary active component, 2'-deoxyguanosine (2-dG), ZNC is proposed to be perceived by cell-surface pattern-recognition receptors (PRRs)/coreceptors and ATP receptors (e.g., P2K1). This receptor-mediated recognition subsequently activates endogenous immunity to enhance disease defense and promote vegetative growth, an assumption supported by

previous molecular studies [17,23,24]. Externally, Recharge microbial agent optimizes the external micro-ecology to manage soil-borne diseases like nematodes and above-ground pests like thrips (Figure 7B). Previous studies have reported that single biological agents often exhibit field instability [11,12]. In contrast, our empirical field study demonstrates the ZR-IGCS successfully overcomes the efficacy instability in complex field environments. It achieves an enhancement of crop yield, quality, and multiple stress resistance, serving as a prime example of translating laboratory research into field practice. For instance, the system significantly increased premium Grade I tuber yield by 51.66% (Figure 6, Group Dc1). Meanwhile, control efficacy exceeded 60% for foliar diseases like anthracnose and brown spot (Figure 2, Groups Db1 and Dc1), surpassed 30% and 60% for tuber diseases like root-lesion nematodes and *Fusarium* wilt, respectively (Figure 2, Group Dc1 and Supplementary Figure S1, Group Db1), and approached 50% for thrips (Figure 3, Groups B-Dc1). Additionally, the system significantly promoted early seed tuber germination (94%, Figure 1, Group Db1) and dry matter accumulation. These results confirm that the ZR-IGCS offers a robust, sustainable agricultural solution to reduce reliance on chemical pesticides.

4.2. Establishment of the Optimal ZR-IGCS Strategy via Alleviation of the “Growth–Defense Trade-Off”

Activating plant immunity typically incurs high metabolic costs, diverting photosynthates to defense and inhibiting vegetative growth, which is known as the “Growth–Defense Trade-off” [20,38,39]. However, the combined ZNC and Recharge treatment achieved simultaneous high-level disease resistance and biomass accumulation, effectively alleviating this traditional trade-off. We hypothesize that this combined effect is not a simple mixture of two agents but a systemic integration, likely attributable to the putative dose-dependent dual regulatory mechanism of ZNC and the energy compensation function of Recharge, as suggested by earlier physiological research [23,40–42].

First, ZNC exhibited a significant hormesis effect: low concentration (1 ng/mL) enhanced emergence and plant height, likely via auxin signaling activation [23]. Conversely, high concentration (5 ng/mL) inhibited growth (Figure 1), likely due to resource reallocation caused by the induction of systemic acquired resistance [23,25,27]. Second, plant growth-promoting rhizobacteria (e.g., *Bacillus subtilis*) in Recharge may provide additional nutritional support through phosphate solubilization, potassium release, and plant growth regulator secretion [40–42]. This microbe-driven nutrient compensation likely effectively supplements the metabolic demands of the ZNC-triggered immune response, thereby avoiding the common “yield penalty” and ensuring that the crop maintains strong disease resistance alongside material accumulation. Our study provides evidence that while single ZNC treatments (Groups Cb1 and Cc1) significantly improved resistance against diseases like anthracnose, the introduction of Recharge did not significantly alter disease control efficacy ($p > 0.05$). Instead, the microbial consortium significantly increased the yield of high-quality Grade I aerial beans and tubers following ZNC application (Figures 5 and 6, Group Db1 vs. Cb1 or Group Dc1 vs. Cc1), ultimately achieving dual improvements in defense and biomass.

Regarding the optimal application regimen within the ZR-IGCS, the high-concentration combination (Recharge + 5 ng/mL ZNC irrigation + 50 ng/mL foliar spray) showed the best numerical trends for dry matter accumulation, disease control, and yield quality. However, these results were not statistically different from the medium-concentration treatment (Recharge + 2.5 ng/mL ZNC irrigation + 50 ng/mL foliar spray) ($p > 0.05$). Balancing the risk of growth inhibition induced by high-concentration ZNC against marginal benefits and input costs, the combination of Recharge, 2.5 ng/mL ZNC root irrigation, and a 50 ng/mL foliar spray (Group Db1) is established as the optimal implementation strategy.

4.3. Construction of a Spatiotemporally Complementary Defense Network via the ZR-IGCS

Single agents are often limited by narrow target spectra, whereas the ZR-IGCS establishes a spatiotemporally complementary defense network. Spatially, the two components exhibit significant functional complementarity. Although individual ZNC and Recharge treatments comparably inhibited anthracnose and brown spot ($p > 0.05$), their combination significantly enhanced control of root-lesion nematodes (Figure 2). Furthermore, ZNC exhibited minimal efficacy against thrips (Figure 3), highlighting the limitations of immune inducers against specific insects. Conversely, Recharge displayed excellent insecticidal efficacy, likely mediated by entomopathogenic fungi within the consortium (e.g., *Beauveria bassiana*, *Metarhizium anisopliae*) or by triggering specific anti-insect signaling pathways [28,30–32]. This target complementarity across diverse biological stresses (fungi, nematodes, and insects) confirms the necessity of ZNC and Recharge synergy. Temporally, the ZR-IGCS significantly delayed plant senescence. Compared to the 44.33% mortality rate in the control group, the optimal treatment (Group Db1) reduced vine mortality by ~73% (Figure 4). Furthermore, incorporating Recharge resulted in a further 28% reduction in mortality compared to treatment with ZNC alone (Db1 vs. Cb1, Supplementary Table S4). This pronounced “stay-green” effect extended the late-stage photosynthetic window, ensuring continuous photosynthate transport to underground tubers, which is critical for final yield formation.

4.4. Optimization of Source–Sink Relationships and Enhancement of Quality and Profitability

Modern agriculture emphasizes “marketable yield” over mere biomass accumulation. The ZR-IGCS significantly optimized the yield-quality structure, substantially increasing the proportion of Grade I high-quality tubers and aerial beans while drastically reducing Grade II inferior produce. This qualitative improvement can be reasonably explained by an optimized source–sink relationship. At the source, enhanced seedling biomass, reduced foliar pest and disease stress, and delayed senescence ensured a robust and sustained supply of photosynthates from the functional source leaves. At the sink, the effective control of tuber diseases like root-lesion nematodes and *Fusarium* wilt by Recharge maintained the integrity of the root system and tuber epidermis. This prevented pathogen-induced deformity and rot, thereby enhancing the sink’s capacity for expansion [43–46]. Economically, based on post-harvest prices from the experimental year, the ZR-IGCS (Groups Db1 and Dc1) generated revenues exceeding 20,000 RMB per 667 m², achieving a ~30% improvement in total economic return (Supplementary Figure S2, Table S7). However, it is important to acknowledge that this economic analysis is based on a single harvest year and does not account for year-to-year market price volatility or potential fluctuations in input costs. Nevertheless, regardless of annual price fluctuations, the significant shift toward higher commercial-grade tubers achieved by this system will consistently yield a relative increase in grower profitability for any given year. Ultimately, this healthy source–sink interaction directly improves both the total yield and the commercial grade of yam tubers, significantly increasing grower income and demonstrating the substantial application value of this cultivation system.

4.5. Study Limitations and Future Perspectives

While the ZR-IGCS presents a viable strategy to reduce reliance on synthetic agrochemicals, it is necessary to explicitly address the limitations of the current study. First, the designation of this system as a “green” cultural practice in this context strictly denotes the substitution of chemical pesticides and fertilizers with biological alternatives. It is important to acknowledge that the microbial consortium Recharge has the potential to synthesize secondary metabolites and antibiotics to suppress pathogens, and similarly,

ZNC, as a potent physiological modulator, might alter the crop micro-environment. While we must remain cautious about their long-term environmental effects, our empirical data demonstrate that their practical application yields highly effective and stable field performance without observable adverse effects on the crop. Furthermore, although we observed significant phenotypic improvements and the targeted suppression of specific pathogens, establishing a scientifically rigorous definition of a “healthy” soil state requires comprehensive and measurable criteria, such as metagenomic profiling of microbial community structures and soil physio-chemical stability assessments. These current limitations will be addressed through more in-depth, long-term ecological evaluations in our future research. Nevertheless, despite these methodological boundaries, the robust field efficacy achieved by the ZR-IGCS demonstrates that it remains a highly feasible, effective, and practically valuable framework for promoting the sustainable development of agricultural ecosystems.

5. Conclusions

In summary, the novel ZR-IGCS proposed in this study couples endogenous plant immune regulation with external micro-ecological optimization, providing a sustainable strategy to reduce pesticide reliance. By establishing a spatiotemporally complementary defense barrier, the system balances biological stress inhibition with the promotion of crop growth and tuber quality. This system not only provides an innovative strategy for alleviating severe continuous cropping obstacles in tuber crops but also sets a successful example for translating laboratory basic research to field application, offering strong technical support for the sustainable development of agricultural ecosystems. Future research will further integrate multi-omics technologies, such as transcriptomics, metabolomics, and microbiomics, to deeply elucidate the molecular mechanisms underlying ZR-IGCS-mediated immune regulation and rhizosphere microbiome remodeling to fully reveal its ecological effects.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/horticulturae12080947/s1>, Supplementary Figure S1. Statistical analysis of the disease index of yam *Fusarium* wilt mediated by the combined application of ZNC and Recharge. Supplementary Figure S2. Relative enhancement of economic benefits in *Dioscorea polystachya* cultivation mediated by the combined application of ZNC and Recharge. Supplementary Table S1. Enhanced effects of immune inducer ZNC and microbial agent Recharge on the emergence rate and seedling growth parameters of *Dioscorea polystachya*. Supplementary Table S2. Enhanced effects of immune inducer ZNC and microbial agent Recharge on dry matter weight of *Dioscorea polystachya* during vining stage. Supplementary Table S3. Enhanced effects of immune inducer ZNC and microbial agent Recharge on dry matter weight of *Dioscorea polystachya* during tuber swelling stage. Supplementary Table S4. Enhanced effects of immune inducer ZNC and microbial agent Recharge on disease resistance, thrips infestation, and plant mortality of *Dioscorea polystachya*. Supplementary Table S5. Enhanced effects of immune inducer ZNC and microbial agent Recharge on the yield assessment and quality optimization of *Dioscorea polystachya* beans. Supplementary Table S6. Enhanced effects of immune inducer ZNC and microbial agent Recharge on the yield assessment and quality optimization of *Dioscorea polystachya* tubers. Supplementary Table S7. Enhanced benefits analysis and revenue breakdown of *Dioscorea polystachya* mediated by the combined application of ZNC and Recharge. Supplementary Table S8. Instructions for the combined application of ZNC and Recharge.

Author Contributions: X.D., Q.C. and D.W. designed the experiments and wrote the manuscript. S.L. (Shengchen Li) and G.Y. carried out the field experiments. S.L. (Shengjie Li), J.L., N.S., S.L. (Shuyan Liu), T.L., T.H. and W.W. provided suggestions on the writing of manuscripts. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: Authors Jilin Liu and Guangwei Yu were employed by the company Zaozhuang Wangda Agricultural Science and Technology Co., Ltd., and Green IPM AI Biotech (Hong Kong) Institute Limited, respectively. The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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