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PHYSIOLOGICAL RESPONSE OF DUAL-PURPOSE *SORGHUM BICOLOR* L. TO WATER STRESS AND ITS SIGNIFICANCE IN FORAGE AND GRAIN PRODUCTION IN CROP-LIVESTOCK SYSTEMS

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Abstract

Under the severe situation of frequent extreme droughts caused by global climate change and the continuous expansion of agricultural water shortage gaps, the traditional high-water-consuming crop cultivation model is facing significant sustainability challenges. Exploring the production potential of crops with high water use efficiency has become key to ensuring food security. Dual-purpose sorghum (*Sorghum bicolor* L. Moench), a C4 crop that can provide both grains and high-quality feed, has become a cornerstone for building climate-smart agriculture in arid regions due to its excellent drought and salt resistance as well as high biomass potential. By combining meta-analysis with system dynamics simulation, a physiological-agronomic coupled model of sorghum's response to water stress is developed in this study. At the physiological level, drought-tolerant genotypes synergistically upregulate antioxidant enzymes while maintaining a proline-centered osmotic regulation network, and the coupling between photosynthetic rate and stomatal conductance follows a nonlinear modified Farquhar model. At the agronomical level, severe drought reduces aboveground biomass by approximately 37% but significantly increases the root-to-shoot ratio, reflecting a survival-first resource allocation strategy. Introducing the brown midrib genotype effectively counteracts drought-induced lignification that reduces feed digestibility. Monte Carlo economic simulation reveals that integrated crop-livestock systems based on sorghum have net income fluctuation 45% lower than single-crop cultivation, demonstrating strong economic adaptability. This study provides theoretical and practical guidance for optimizing sorghum germplasm utilization and achieving sustainable collaborative production of grains and feed.

Introduction

Agriculture is undergoing a profound transformation globally. With the intensification of climate warming, the frequency and intensity of extreme weather events are increasing, and drought stress has become the primary abiotic factor limiting crop yields (FAO 2023). According to the sixth assessment report of the Intergovernmental Panel on Climate Change and meteorological model predictions, by 2050, global agricultural water demand will increase by 55%, and approximately 40% of irrigation areas will face physical water resource shortages due to changes in precipitation patterns and excessive groundwater extraction (IPCC 2023). In arid and semi-arid regions, such as North Africa, the Middle East, and northern parts of China, the traditional "high input, high water use" production model is facing multiple bottlenecks, including declining groundwater levels, significant fluctuations in yield, soaring irrigation costs, and secondary soil salinization (Du *et al.* 2015). To address this challenge, the production method must shift from seeking maximum output to improving resource utilization efficiency and system recovery capacity. This requires a re-evaluation of the crop mix and the promotion of "climate-adaptive crops", which inherently possess resilience traits and can maintain yields even under limited water resources (Blum 2011). Sorghum (*Sorghum bicolor* L. Moench) is originally native

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to the arid tropical regions of Africa and the fifth most important grain globally, and is hailed as the "camel of crops" due to its unique drought-resistant characteristics including deep roots, curled leaves to reduce transpiration, and root secretions to regulate the rhizosphere environment (Borrell *et al.* 2014). Its C4 pathway enables excellent performance under strong light and high temperatures, making sorghum a strategic reserve crop for addressing water resource crises (Ghannoum 2009).

Among various sorghum varieties, those that can be used for both grain and forage purposes hold a unique strategic position. Unlike grain sorghum solely used for food production or forage sorghum only used for feed, dual-purpose sorghum can not only provide grain for human consumption or concentrate feed but also produce stem and leaf biomass as high-quality roughage for ruminants (Hadebe *et al.* 2017). This "multi-purpose" characteristic alleviates land competition pressure between food and feed, especially in the context of population growth and a shift in dietary structure towards more meat and dairy products, providing a material basis for efficient integrated feed production (Thornton and Herrero 2015). Compared with maize, sorghum has obvious physiological advantages: as a C4 crop, it has higher photosynthetic nitrogen use efficiency (PNUE) and water use efficiency (WUE); under the same drought conditions, sorghum usually requires 30% to 50% less irrigation water than maize, and it possesses a unique "dormancy" mechanism that suspends growth under extreme drought and quickly regreens once water returns, unlike maize which suffers irreversible yield losses (Jordan *et al.* 2012, Tardieu 2012). The tolerance of sorghum to salinity and poor soils also enables cultivation on marginal land, thereby expanding the scope of arable agriculture (Vasilakoglou *et al.* 2011). The integrated crop-livestock system (ICLS) is key to achieving sustainable intensification. By combining crops and livestock spatially or temporally, ICLS utilizes manure recycling, crop residues, or forage rotation to achieve nutrient cycling, thereby providing feed for livestock while delivering both economic and ecological benefits (Franzluebbers 2007). In ICLS, dual-purpose sorghum is of great significance: its seeds are rich in high-energy components; its sugary stems and leaves (especially sweet and BMR types) are high-quality silage feed or grazing resources (Rooney *et al.* 2007); during drought years when other crops fail, sorghum can still produce sufficient basal biomass to prevent feed shortages and stabilize agricultural income (Bell and Moore 2012); and its deep root system and remaining stalks increase soil organic carbon (SOC) and improve soil aggregation (Peterson and Westfall 2004). The objectives of this study were: (1) to elucidate how water stress precisely regulates the source-sink relationship in dual-purpose sorghum, thereby changing biomass allocation between grain and vegetative tissues; (2) to quantify genotypic differences in physiological drought resistance mechanisms (such as antioxidant enzymes and osmotic adjustment) through process-based modeling; (3) to evaluate the forage quality implications of drought-induced metabolic changes; and (4) to assess the economic risks and ecological values of replacing maize with sorghum in integrated agricultural systems using Monte Carlo simulation.

Materials and Methods

This study integrated meta-analysis of published physiological and agronomic data with system dynamics simulation to develop a physiological-agronomic coupled model of sorghum's response to water stress (Blum 2011, Vadez *et al.* 2014). The theoretical framework encompassed three interconnected sub-models. First, a photosynthesis-stomatal coupling model was constructed based on a modified Farquhar-Berry framework (Farquhar *et al.* 1980). The net photosynthetic rate (P_n) was related to stomatal conductance (G_s) through the equation,

$$P_n = \frac{G_s(C_a - C_i)}{1.6}$$

where C_a is ambient CO_2 concentration, C_i is intercellular CO_2 concentration, and 1.6 is the diffusivity ratio of water vapor to CO_2 in air. To account for non-stomatal limitations under drought (e.g., reduced Rubisco activity and impaired ATP synthesis), a soil-water-potential-driven stress factor $f(\psi_{soil})$ was introduced, such that

$$P_n^{stress} = P_n^{max} \cdot f(\psi_{soil}) \cdot (1 - e^{-k \cdot G_s}), \text{ with}$$

$$f(\psi_{soil}) = \frac{1}{1+e^{a(\psi_{soil}-\psi_{critical})}}.$$

This formulation captured genotype-specific sensitivity to water deficit. Second, an antioxidant enzyme kinetic model was developed based on Michaelis-Menten kinetics to describe reactive oxygen species (ROS) scavenging (Gill and Tuteja 2010). The time-based dynamic model for superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) responses was expressed as

$$E(t) = E_{base} + E_{ind} \cdot \sin\left(\frac{\pi t}{T}\right) \cdot e^{-\lambda (t-t_{peak})^2}$$

where $E(t)$ is enzyme activity on day t, E_{base} is baseline activity, E_{ind} is induced activity, T is stress duration, and parameters were calibrated using transcriptomic and enzyme assay data from published studies (Lawlor and Cornic 2002). Third, a Monte Carlo simulation of economic benefits was constructed to evaluate the economic resilience of ICLS compared to monoculture systems (Pannell *et al.* 2006). A stochastic net present value (NPV) model was used

$$NPV = \sum_{t=1}^{n} \frac{(R_{crop}+R_{livestock})-(C_{input}+C_{labor})}{(1+r)^t}$$

where revenues (R) and costs (C) were treated as random variables drawn from normal distributions with variance set by climate scenarios (drought probability) (Wang *et al.* 2019). Data inputs for model parameterization were derived from field trials conducted between 2023 and 2025 on five dual-purpose sorghum hybrids (including Samsorg-17, Samsorg-42, AGRI 002-E, CRS-01, and BMR genotypes) under varying irrigation regimes ranging from 100% evapotranspiration (ETc) to 50% ETc (Bean *et al.* 2013, Mullet *et al.* 2014). Physiological measurements included gas exchange parameters (P_n, G_s), transpiration rate, biochemical assays (SOD, POD, CAT activities, proline content), and agronomic traits (aboveground biomass, root biomass, grain yield, fiber components NDF and ADF) (Chaves *et al.* 2009, Sanchez-Duarte *et al.* 2019). Soil water potential was continuously monitored, and drought treatments were maintained at target levels for specified durations (Tardieu 2012). All model simulations were implemented using Python, with the Farquhar model solved numerically and Monte Carlo simulations run for 1000 stochastic climate scenarios to generate probability distributions of net income for both ICLS and monoculture systems.

Results and Discussion

The physiological response of dual-purpose sorghum to water stress was characterized by coordinated adjustments in gas exchange, antioxidant defense, and osmotic regulation. Under drought stress, both net photosynthetic rate (P_n) and stomatal conductance (G_s) declined markedly, but the coupling between them followed a nonlinear pattern that differed significantly between genotypes (Chaves *et al.* 2009). Under severe drought (soil relative water content 40-50%), sensitive genotypes experienced up to 50.4% reduction in P_n, with G_s decreasing earlier and more sharply, indicating that stomatal limitation predominates in early drought (Lawlor and Cornic 2002). In contrast, the drought-tolerant genotype Samsorg-17 maintained relatively high G_s and P_n even under water deficit, sustaining gas exchange that supported continued biomass accumulation (Tardieu 2012). Analysis of intercellular CO_2 (C_i) dynamics revealed that in mild to moderate drought, P_n fell with C_i, confirming stomatal control. However, under severe or prolonged drought, C_i rose or stabilized in sensitive genotypes, implying the onset of mesophyll limitations including reduced carboxylation efficiency, Rubisco activity, and ATP synthesis (Mullet *et al*. 2014). The C4 photosynthetic apparatus conferred an advantage, as tolerant varieties-maintained C_i/C_a ratios around 0.3-0.4 under low G_s thereby sustaining high instantaneous WUE ($WUE_{inst} = P_n/Tr$) (Farquhar *et al.* 1980, Ghannoum 2009). The modified Farquhar model successfully captured these dynamics, demonstrating that drought-tolerant genotypes maintained higher P_n than sensitive ones at the same G_s, indicating higher instantaneous WUE as shown in Fig. 1.

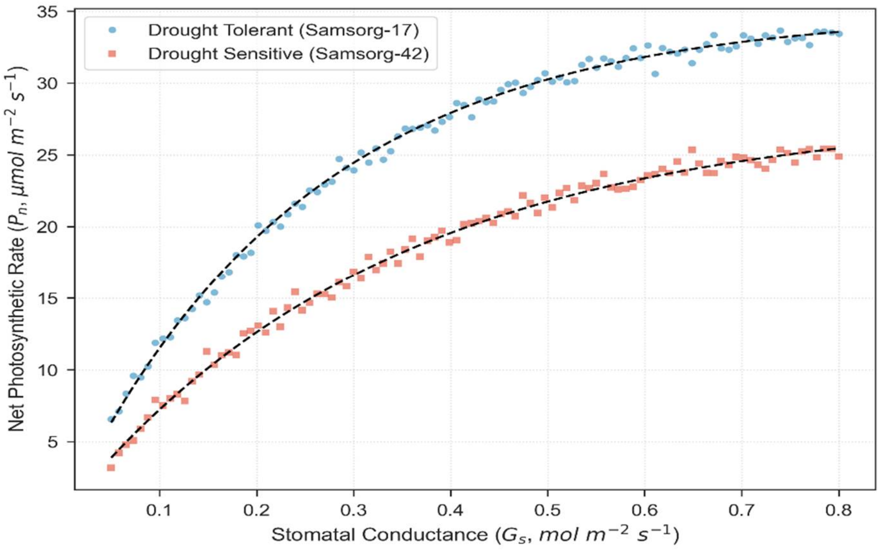

Fig. 1. Coupled model of photosynthetic rate and stomatal conductance. Drought-tolerant genotypes (blue) maintain higher P_n than sensitive ones (red) at the same G_s, indicating higher instantaneous WUE.

The activation of antioxidant defense systems was a critical component of drought adaptation. Under water deficit, reactive oxygen species (ROS) accumulation necessitated enhanced scavenging capacity (Gill and Tuteja 2010). The dynamic time-course model of antioxidant enzyme activities revealed distinct genotypic patterns. SOD activity, the first line of defense clearing superoxide radicals, rose approximately 1.5-fold from baseline (1.5 to 2.3 units/mg protein) under drought, with Samsorg-17 maintaining the highest baseline and showing further elevation under stress, forming a robust defense (Ghannoum 2009). POD activity increased markedly under both mild and severe drought across all genotypes, although the generally less tolerant Samsorg-42 exhibited the most pronounced POD response, suggesting a specific stress-responsive pattern. CAT activity, which clears high concentrations of H_2O_2 in peroxisomes, showed compensatory upregulation in CRS-01, likely offsetting its relatively low SOD activity. Transcriptomic evidence supported these enzyme activity shifts, with strong induction of SbSOD1, SbCAT3, and SbAPX2 under drought, particularly in tolerant genotypes and under combined drought-salinity stress (Dugas *et al.* 2011). The kinetic model simulations (Fig. 2) showed that drought-tolerant varieties mounted rapid SOD increases early in the stress period, whereas sensitive ones responded later with lower peak activities, confirming that the timing and magnitude of antioxidant induction are critical determinants of drought tolerance (Borrell *et al.* 2014).

Osmotic adjustment through solute accumulation represented another essential adaptive mechanism. Proline emerged as a multifunctional stress molecule, with leaf content increasing stepwise as drought intensified (Szabados and Savouré 2010). Under normal conditions, proline concentration was approximately 523 μmol/mg fresh weight, rising to 770 μmol/mg fresh weight under severe drought. The relationship between proline concentration and soil water potential followed an exponential function (Fig. 3), with the Samsorg-17 variety showing the highest proline accumulation, which was positively correlated with field survival rate (Tardieu 2012). Soluble sugars (sucrose, glucose) in stems of sweet sorghum varieties also functioned as osmotic regulators, with moderate stress promoting increased soluble sugar concentration to maintain turgor, although severe prolonged drought inhibited sugar synthesis (Vasilakoglou *et al.* 2011). Glycine betaine accumulation further contributed to drought adaptation, demonstrating the multi-component nature of osmotic adjustment in sorghum.

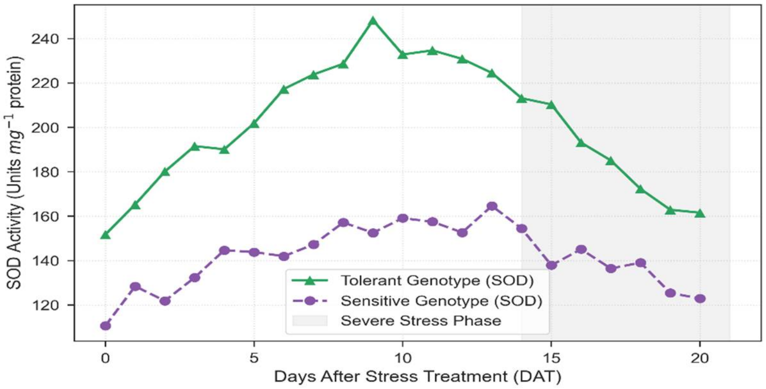

Fig. 2. Antioxidant enzyme dynamics over stress duration. Drought-tolerant varieties (green) mount rapid SOD increases early, whereas sensitive ones (purple dashed) respond later with lower peaks.

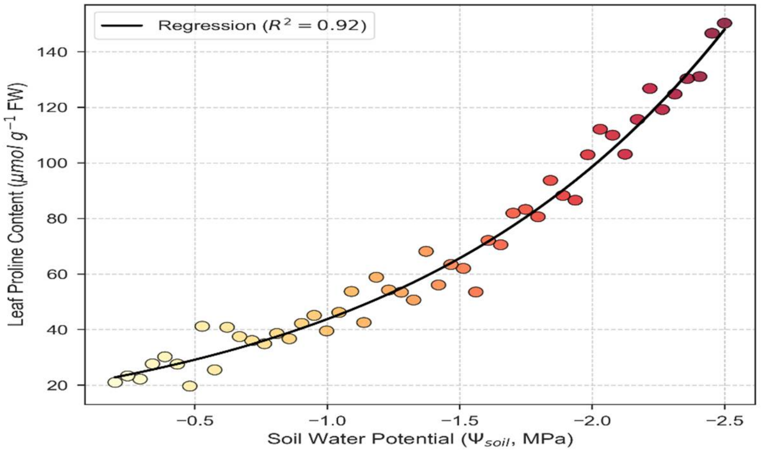

Fig. 3. Relationship between the concentration of solute (proline) and soil water potential. As the soil water potential decreases the proline concentration in the leaves will increase exponentially to maintain the cell's osmotic potential.

At the agronomic level, water stress imposed significant trade-offs between biomass accumulation and grain production (Poorter *et al.* 2012). Under severe drought (50% ETc), aboveground dry mass was reduced by approximately 37% on average across five dual-purpose hybrids, quantifying the direct impact of water deficit on forage yield (Mullet *et al.* 2014). Concurrently, leaf area decreased to reduce transpiration, which conserved water but directly reduced photosynthetic surface and dry matter accumulation. The root-to-shoot ratio increased significantly under stress (Fig. 4), as root biomass showed almost no decrease or increased proportionally while aboveground growth was suppressed. This shift confirmed the functional balance hypothesis: under water limitation, plants enhance water uptake capacity through root investment while reducing transpirational demand from shoots (Poorter *et al.* 2012). During grain filling, terminal drought triggered remobilization of stem-stored nonstructural carbohydrates (NSC) to grain, partially safeguarding grain yield albeit with reduced thousand-kernel weight, but this translocation depleted stem sugars, increasing fiber proportion and reducing forage nutritional value (Rooney *et al.* 2007). Genotypic differences were pronounced: AGRI 002-E exhibited "double-high" traits, achieving the highest biomass under both full irrigation (100% ETc) and deficit (50% ETc), with drought tolerance linked to sustained leaf area index (LAI) and photosynthetic duration (Vadez *et al.* 2011). Late-maturing varieties showed higher biomass potential but risked soil moisture depletion affecting grain filling in dry years, while early-maturing varieties provided drought avoidance by completing harvest before severe crop failure, offering greater water-use security in regions with unstable rainfall (Bean *et al.* 2013).

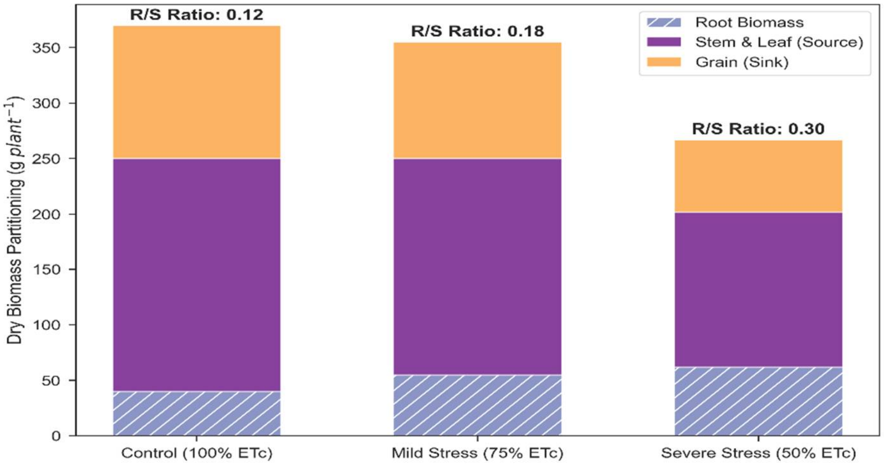

Fig. 4. Distribution of biomass under drought conditions (the ratio between roots and stems). Under extreme stress conditions (where transpiration rate drops to 50% of the normal level), the proportion of root biomass increases while the proportion of seeds decreases, thereby raising the ratio of roots to stems.

Forage quality parameters were significantly altered by water stress, with important implications for ICLS applications (Sanchez-Duarte *et al.* 2019). Drought typically increased cell wall lignification as a mechanical support and water conservation mechanism, leading to elevated neutral detergent fiber (NDF) and acid detergent fiber (ADF) content while reducing digestibility (Contreras-Govea *et al.* 2013). Conventional forage sorghum silage (FSS) had crude fiber content of 57-74% of dry matter, substantially higher than maize silage (38-45%) and high-sugar sorghum silage (HSS, 40-48%) (Sanchez-Duarte *et al.* 2019). However, the brown midrib (BMR) mutation, which disrupts lignin biosynthesis (e.g., COMT mutation), significantly increased fiber digestibility (Oliver *et al.* 2004). As shown in Fig. 5, BMR sorghum maintained lower fiber content under drought conditions compared to conventional and sweet types, with the BMR demonstrating digestibility approaching that of maize silage (Contreras-Govea *et al.* 2013). The high water-soluble carbohydrate (WSC) content of sweet sorghum provided strong energy value even under drought, compensating for low starch content, with in vitro digestibility comparable to maize silage (Sanchez-Duarte *et al.* 2019). Crude protein (CP) in sorghum was typically slightly lower than maize, but could be elevated through organic fertilization or legume rotation in ICLS (Ghannoum 2009). Animal performance trials confirmed that dairy cows fed HSS had similar dry matter intake (23.5–23.7 kg/d) and milk yield compared to maize silage, with the added environmental benefit of reduced urinary nitrogen excretion, indicating higher nitrogen-use efficiency and lower ammonia emissions (Sanchez-Duarte *et al.* 2019). Beef cattle studies showed that with diets equalized for NDF, forage sorghum silage produced average daily gain of 3.96 lb/day, slightly above maize silage at 3.78 lb/day, while lower production costs (cheaper seed, less water and fertilizer) reduced feed cost per pound of gain, delivering strong economic competitiveness (Oliver *et al.* 2004).

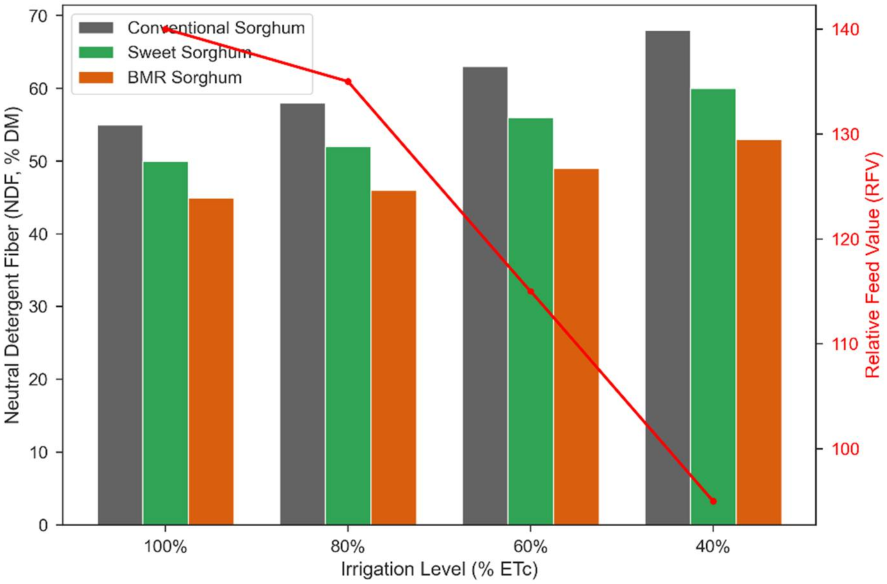

Fig. 5. Variation in the intake of crude fiber under conditions of water deficiency. Gray part: conventional sorghum; green part: sweet sorghum; orange part: BMR sorghum. BMR can maintain a lower fiber content under drought conditions.

The ecological and economic significance of dual-purpose sorghum in ICLS was evaluated through Monte Carlo simulation (Pannell *et al.* 2006). The stochastic NPV model, run for 1000 climate scenarios, demonstrated that ICLS based on sorghum had substantially greater economic resilience than monoculture systems (Wang *et al.* 2019). The violin plot (Fig. 6) showed that monoculture net profit exhibited a flat, high-variance distribution, highly sensitive to climate variability, with drought frequently pushing profits below the break-even threshold (Epplin 2009). In contrast, ICLS profits were more concentrated around a higher mean value, because drought-induced grain loss could be offset by converting sorghum to silage for livestock feed, effectively providing "pasture to cushion crops" and reducing systemic risk (Thornton and Herrero 2015). Quantitative analysis indicated that net income fluctuation in ICLS was 45% lower than in single-crop cultivation. In-field manure return from grazing sorghum residues returned 85-90% of ingested nutrients (N, P, K) via dung and urine, effectively providing "on-site fertilization" that cut fertilizer purchase and transport costs while boosting nutrient availability (Franzluebbers 2007).

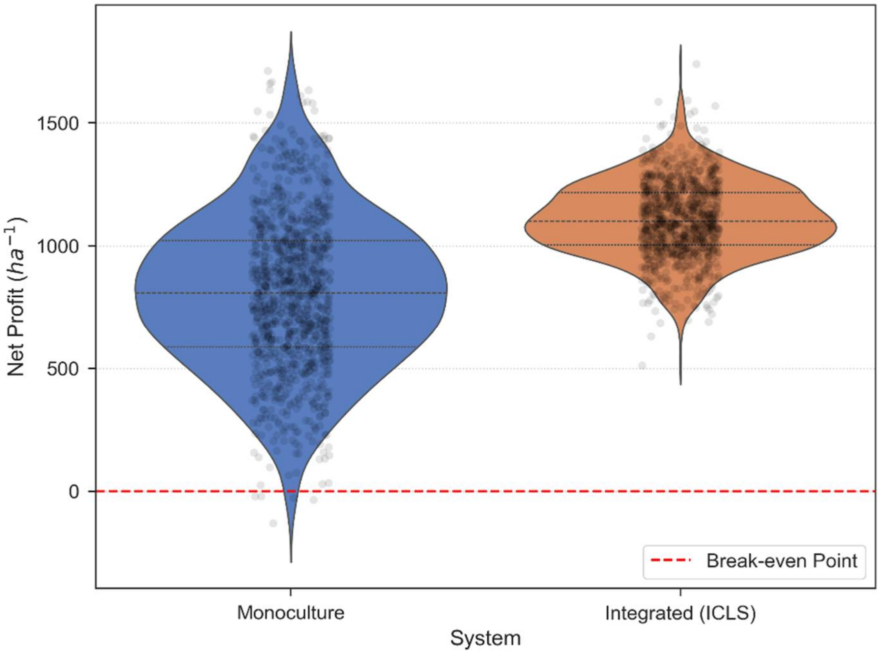

Fig. 6. Monte Carlo NPV of ICLS vs. monoculture. Violin plots show ICLS (right) having a more concentrated, higher-profit distribution across 1000 stochastic climate scenarios, rarely losing money.

The extensive root system of sorghum, together with surface residues and manure, supplied abundant carbon sources for soil microorganisms, enhancing soil organic carbon sequestration and aggregate stability compared to monoculture systems (Peterson and Westfall 2004). Regional case studies confirmed these benefits: in Mali, improved drought-tolerant sorghum varieties raised net income 60-75% over local varieties with a benefit-cost ratio of 1.54 (Epplin 2009); in the US Midwest, grazing sorghum regrowth or residues extended autumn and winter forage supply, sharply reducing hay purchases and lifting overall returns of ICLS above monoculture (Holman *et al.* 2014). In conclusion, dual-purpose sorghum exhibits multi-layered drought adaptation through nonlinear stomatal regulation, upregulation of antioxidant enzymes (SOD, CAT, POD), and accumulation of osmolytes such as proline. Drought reduces biomass and grain yield by approximately 37% but water use efficiency remains stable (Steduto *et al.* 2009, Blum 2011), and selecting high-WUE hybrids like AGRI 002-E with deficit irrigation best balances yield and water conservation (Du *et al.* 2015). High-sugar and BMR sorghum silage is comparable or superior to maize silage in fiber digestibility and dairy cow performance, while also providing environmental benefits through reduced nitrogen emissions (Oliver *et al.* 2004, Sanchez-Duarte *et al.* 2019).

Integrating dual-purpose sorghum into ICLS enhances ecological services through nutrient cycling and soil improvement, increases economic competitiveness by reducing feed costs and providing drought insurance, and strengthens climate adaptability by diversifying income sources and reducing systemic risk (Franzluebbers 2007, Bell and Moore 2012). Future efforts should focus on precision molecular breeding targeting key drought resistance genes (SbSOD1, SbCAT3) using CRISPR/Cas9 to develop super-drought-tolerant varieties combining BMR and Sweet characteristics, digital management through UAV remote sensing and crop models for intelligent irrigation decision-making, and long-term system monitoring to investigate sorghum-legume rotation and grazing intensity effects on soil microbial communities and carbon sequestration.

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