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Influence of Humidity Control on Disease Occurrence in Cucumber Production

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Abstract Humidity management is a critical environmental factor influencing disease occurrence, crop health, and productivity in cucumber (*Cucumis sativus* L.) production systems. Excessive humidity, prolonged leaf wetness, and unstable microclimatic conditions create favorable environments for pathogen survival, spore germination, and infection, resulting in severe losses caused by fungal and bacterial diseases. With the rapid development of protected cultivation and precision agriculture technologies, humidity regulation has become an important strategy for sustainable disease prevention and improved crop performance. This review systematically summarizes the mechanisms underlying humidity-mediated disease development in cucumber production, focusing on the interactions among environmental humidity, plant physiological responses, and pathogen infection processes. The effects of humidity conditions on major cucumber diseases, including powdery mildew, downy mildew, gray mold, and bacterial diseases, are discussed from ecological and physiological perspectives. Furthermore, current humidity control approaches, such as ventilation management, irrigation optimization, dehumidification technologies, and integrated greenhouse climate regulation, are evaluated for their effectiveness in reducing disease risks. Advances in computational modeling, machine learning-based disease prediction, and sensor-driven environmental control systems are also highlighted as emerging tools for real-time disease forecasting and precision management. A case study framework is presented to demonstrate how humidity monitoring, disease assessment, and predictive modeling can be integrated to optimize greenhouse cucumber production. Despite significant progress, challenges remain in accurately defining humidity thresholds across cultivars and production environments, improving model interpretability, and integrating multi-factor environmental regulation strategies. Future research combining artificial intelligence, digital agriculture, and plant-microbe interaction studies will provide new opportunities for developing sustainable and intelligent disease management systems in cucumber production.

Keywords Humidity control; Cucumber production; Disease occurrence; Greenhouse microclimate management; Precision agriculture

1 Introduction

Cucumber is a major greenhouse vegetable crop, and its productivity depends heavily on precise microclimate regulation in protected cultivation systems. Greenhouse production enables high yields through environmental control, but the same stable environment can also favor pathogen establishment when humidity, temperature, and ventilation are not well managed (Fanourakis et al., 2026). This dual role makes humidity management especially important in cucumber production, where crop performance is shaped not only by resource-use efficiency and yield optimization but also by the need to suppress disease-conducive conditions. Long-term greenhouse observations further show that cucumber yield is significantly associated with environmental variables including relative humidity, with average nighttime humidity emerging as a meaningful correlate of production outcomes in semi-closed systems. Humidity control is therefore not a secondary engineering detail, but a central production factor linking plant growth, fruit yield, and crop health. In practical terms, managing humidity affects leaf wetness duration, canopy moisture, and air exchange, all of which influence whether greenhouse cucumber systems operate near optimal physiological conditions or drift toward environments that increase production risk.

The importance of humidity management becomes even clearer when considering disease epidemiology in cucumber crops. Across greenhouse vegetables, warm and humid conditions consistently promote fungal and

bacterial pathogens, and cucumber is particularly characterized by foliar fungal diseases favored by high relative humidity (Fanourakis et al., 2026). In cucumber specifically, downy mildew remains one of the most destructive diseases, and its development is tightly linked to moisture availability. Experimental work has shown that *Pseudoperonospora cubensis* forms abundant sporangia when infected tissues are wetted or exposed to 100% relative humidity, whereas only a few sporangia are produced at 90% relative humidity. These findings indicate that relatively small differences in humidity can determine whether pathogen reproduction is strongly amplified or constrained. More broadly, humidity interacts with temperature to regulate infection timing, sporulation intensity, and epidemic development, which explains why disease outbreaks in cucumber houses often occur rapidly once favorable microclimatic thresholds are reached. Because greenhouse cultivation often involves dense canopies and restricted air movement, unmanaged humidity can quickly create persistent infection windows that are difficult to reverse after symptoms appear.

Research over the last decade has strengthened the case for humidity-based disease prevention by identifying actionable thresholds and revealing similar moisture dependence across multiple cucumber pathogens. In greenhouse trials on cucumber downy mildew, relative humidity above 90% favored disease development, whereas keeping humidity below 89% protected plants from infection; under early infection, ventilation-based humidity reduction decreased infection percentage by 95.8% and disease severity by 70% (Khudhair and Aljarah, 2023). Comparable patterns have also been reported for cucumber target leaf spot caused by *Corynespora cassiicola*, for which moisture had a stronger effect than temperature on sporulation on living plants, maximum spore production occurred at 100% relative humidity, and only a few spores formed at 75% relative humidity (Zhao et al., 2022). Together, these studies suggest that humidity regulation is not relevant to a single disease only, but is a broader mechanism for suppressing inoculum production and secondary spread in cucumber production systems. At the same time, reliance on fungicides alone is increasingly problematic because repeated use raises concerns about residues, environmental contamination, and resistance development, which further motivates non-chemical strategies centered on environmental control (Abdelfatah et al., 2025).

Against this background, current research is moving from descriptive observation toward predictive and automated humidity management. Forecasting models for cucumber downy mildew have already been proposed to reduce epidemic risk by combining records of pathogen presence with temperature and relative humidity in greenhouse and field settings, highlighting the value of climate-informed decision support. At the production level, modern protected cultivation is also beginning to use sensor-based and AI-assisted control systems, with remotely managed greenhouse compartments showing that artificial intelligence can perform well in cucumber climate regulation, and IoT-based microclimate systems maintaining more favorable humidity conditions while increasing yield by 41.6% per vine under protected cultivation. Therefore, the objective of this paper is to examine how humidity control influences disease occurrence in cucumber production by integrating evidence on microclimate regulation, humidity-pathogen interactions, and emerging predictive control strategies. Particular attention is given to the role of relative humidity in shaping disease-conducive environments, to the potential of ventilation and automated monitoring as preventive tools, and to the broader significance of humidity management for sustainable cucumber health and quality control.

2 Humidity Characteristics and Microclimatic Regulation in Cucumber Production Systems

2.1 Sources and dynamics of humidity variation in cultivation environments

Humidity variation in cucumber production systems arises from the interaction of greenhouse enclosure, crop transpiration, soil or substrate evaporation, and external weather forcing. Protected cultivation stabilizes the environment for year-round production, but that same enclosed microclimate can also retain moisture and increase the probability of pathogen-favorable conditions (Fanourakis et al., 2026). In cucumber houses specifically, total radiation, air temperature, and humidity show strong seasonal variation, and average nighttime relative humidity is significantly associated with yield, indicating that humidity is not static but part of a continuously shifting greenhouse climate system. The temporal pattern of humidity is especially important because many cucumber diseases respond to short periods of high moisture rather than daily averages alone. For downy mildew, infection

and sporulation depend on temperature and moisture together, and lesions produce abundant sporangia when leaves are wetted or exposed to 100% relative humidity, but only a few at 90% relative humidity. Field-oriented greenhouse observations similarly show that downy mildew initiation is favored by relative humidity above 90% for several hours, with disease increasing under humid, cooler conditions and declining in dry-hot periods (Khudhair and Aljarah, 2023).

Humidity dynamics also differ among disease types because the relevant moisture source may be aerial or soil-based. Greenhouse reviews indicate that cucumber disease pressure is dominated by phytopathogenic fungi favored by high relative humidity as well as soilborne pathogens, showing that both canopy moisture and root-zone wetness contribute to disease risk (Fanourakis et al., 2026). This distinction is supported by *Fusarium* wilt experiments, where soil moisture played an important role in disease initiation and development, with maximum incidence observed at 45% soil moisture and no disease at 15% soil moisture. Crop architecture and air exchange further shape local humidity accumulation within cucumber houses. Greenhouses with elevated humidity and restricted airflow create optimal conditions for diverse fungal pathogens, including mixed infections involving *Fusarium*, *Botrytis*, *Alternaria*, and *Cladosporium*, which suggests that poor ventilation can intensify both single-pathogen and multi-pathogen problems. Broader greenhouse monitoring likewise shows that cucumber diseases under covered production are strongly influenced by temperature and humidity, with many pathogens remaining active within roughly 15°C-20°C and 80%-100% relative humidity.

2.2 Effects of humidity on cucumber growth and physiological processes

Humidity affects cucumber growth not only through disease pressure but also through direct regulation of photosynthesis, water relations, and biomass accumulation. Under greenhouse conditions, environmental management is important for improving resource-use efficiency and yield, and long-term modeling shows that nighttime relative humidity has a significant relationship with cucumber production. However, high humidity becomes physiologically harmful when combined with low temperature, as young cucumber plants exposed to low temperature plus 95% humidity showed reduced shoot and root biomass, lower photosynthetic rate and chlorophyll fluorescence, and greater oxidative stress (Amin et al., 2024). Recent physiological work indicates that the effect of high humidity depends on the broader stress context and developmental stage. In cucumber seedlings, combined low temperature and high relative humidity reduced chlorophyll a, chlorophyll b, total chlorophyll, and carotenoids, while also impairing chlorophyll biosynthesis and increasing oxidative damage. At the same time, older plants at the six-leaf stage showed greater tolerance than plants at the two- and four-leaf stages, suggesting that humidity-related stress sensitivity is developmentally regulated rather than uniform across crop stages (Amin et al., 2024).

Humidity also shapes disease severity in ways that feed back onto cucumber growth and yield. Downy mildew can spread rapidly under favorable heat and humidity and may cause severe productivity and quality losses, making humidity control relevant to both plant health and harvest performance (Abdelfatah et al., 2025). Seasonal surveys likewise found that increased relative humidity combined with low or moderate temperature increased downy mildew severity, and these disease changes were accompanied by differences in fresh weight, dry weight, fruit number, and yield. Not all cucumber pathogens respond to humidity in the same way, but moisture remains a core physiological and epidemiological driver. For target leaf spot caused by *Corynespora cassicola*, maximum spore production occurred at 100% relative humidity, and moisture explained a large share of spore-size variation, which matters because larger spores were more virulent (Zhao et al., 2022). By contrast, powdery mildew showed best development under intermediate humidity ranges of 50-70%, whereas very low relative humidity suppressed germination and very high relative humidity favored germination but limited continued lesion growth, underscoring that humidity management must consider pathogen-specific responses rather than assuming a single threshold for all diseases (Saad and Khalifa, 2021).

2.3 Environmental monitoring and humidity control technologies

Because humidity fluctuates rapidly and disease responses can be threshold-based, effective cucumber production increasingly depends on continuous monitoring and active control technologies. Climate-informed decision

systems are emerging in greenhouse horticulture, and reviews emphasize that adaptive climate regulation combined with environmental sensing offers a preventive pathway for pest and disease management (Fanourakis et al., 2026). Forecasting studies on cucumber downy mildew further show that recording temperature and relative humidity can support epidemic prediction and reduce disease risk, input costs, and fungicide residues when linked to timely intervention. Ventilation remains one of the most direct humidity-control methods in cucumber houses. In greenhouse trials, relative humidity above 90% promoted downy mildew, whereas keeping humidity below 89% was protective, and adding ventilation openings reduced infection percentage by 95.8% and disease severity by 70% under early infection conditions (Khudhair and Aljarah, 2023). This practical effect is consistent with the broader principle that microclimatic stability determines infection probability and host susceptibility, so active air exchange can disrupt disease-conducive moisture regimes before epidemics intensify (Fanourakis et al., 2026).

More advanced systems combine sensors with automated actuators to maintain target humidity conditions. In small- and medium-scale protected houses, IoT-based systems used digital temperature and humidity sensors together with foggers and exhaust fans to control relative humidity, maintained more favorable daytime humidity conditions, and increased cucumber yield by 41.6% per vine compared with conventional management. At the high-technology end, AI-controlled greenhouse compartments for cucumber production integrated ventilation, screens, heating, fogging, CO₂ supply, irrigation, and continuous sensing, and overall AI performed well in greenhouse climate control. Humidity management technologies can also be integrated with environmentally safer disease suppression methods. For diseases strongly affected by humidity such as cucumber downy mildew, thermal fogging with chlorine dioxide achieved 80.9% control efficacy and outperformed conventional diluted spray approaches, suggesting that delivery methods interacting with greenhouse moisture conditions can materially change control success (Kim et al., 2021). Older greenhouse disease-control work likewise showed that successful biological control depends on abiotic conditions such as vapor pressure deficit and humidity, indicating that future cucumber protection systems will work best when humidity regulation, monitoring, and biological or low-residue interventions are designed together rather than separately.

3 Mechanisms Linking Humidity Conditions to Cucumber Disease Occurrence

3.1 Effects of humidity on pathogen survival and infection processes

Humidity influences cucumber disease occurrence first by controlling whether propagules can survive, germinate, and complete infection on plant surfaces. In *Pseudoperonospora cubensis*, abundant sporangia are produced when infected tissue is wetted or held at 100% relative humidity, whereas only a few sporangia form at 90% relative humidity, showing that small increases near saturation can sharply increase inoculum pressure. Infection also depends on the interaction between moisture duration and temperature, with minimum wetness requirements dropping to about 1 h at 20°C-25°C but becoming much longer at cooler or hotter temperatures, which explains why short humid periods can still trigger outbreaks under favorable thermal conditions. Humidity also affects the later stages of pathogen release and dispersal rather than only germination. For cucumber target leaf spot, alternating wet and dry conditions coupled with wind were necessary for spore discharge and spread to neighboring plants, while constant high or low humidity without wind did not produce infection in healthy plants. A similar principle has been shown for angular leaf spot, where high relative humidity increased the release amount, survival time, and infectivity of *Pseudomonas amygdali* pv. *lachrymans* aerosols, with the highest survival recorded at 18°C and 95% relative humidity (Chai et al., 2023).

Not all cucumber pathogens respond to humidity in the same way, but most show humidity-sensitive windows for successful infection. Powdery mildew conidia germinated poorly at 20-40% relative humidity, developed best at intermediate humidity of 50%-70%, and showed limited continued lesion growth under prolonged 80%-90% relative humidity, indicating a nonlinear moisture response rather than a simple “more humidity, more disease” pattern (Saad and Khalifa, 2021). By contrast, *Didymella bryoniae* infection under experimental conditions depended strongly on surface wetness duration, which was a more important determinant of infection than temperature once leaves and petioles were exposed to saturated humidity. Humidity effects also extend belowground, where soil water status governs survival and infection by vascular wilt pathogens. In cucumber

Fusarium wilt, disease incidence was highest at 45% soil moisture and absent at 15% soil moisture, indicating that pathogen activity and host invasion require an intermediate-to-high soil moisture range rather than dry substrates (Figure 1). Fruit pathogens show a similarly broad but humidity-responsive capacity for infection, because *Phytophthora capsici* formed lesions across all tested relative humidities, yet water-soaking and pathogen growth increased as humidity increased, demonstrating that elevated atmospheric moisture can intensify symptom expansion even when infection is already possible.

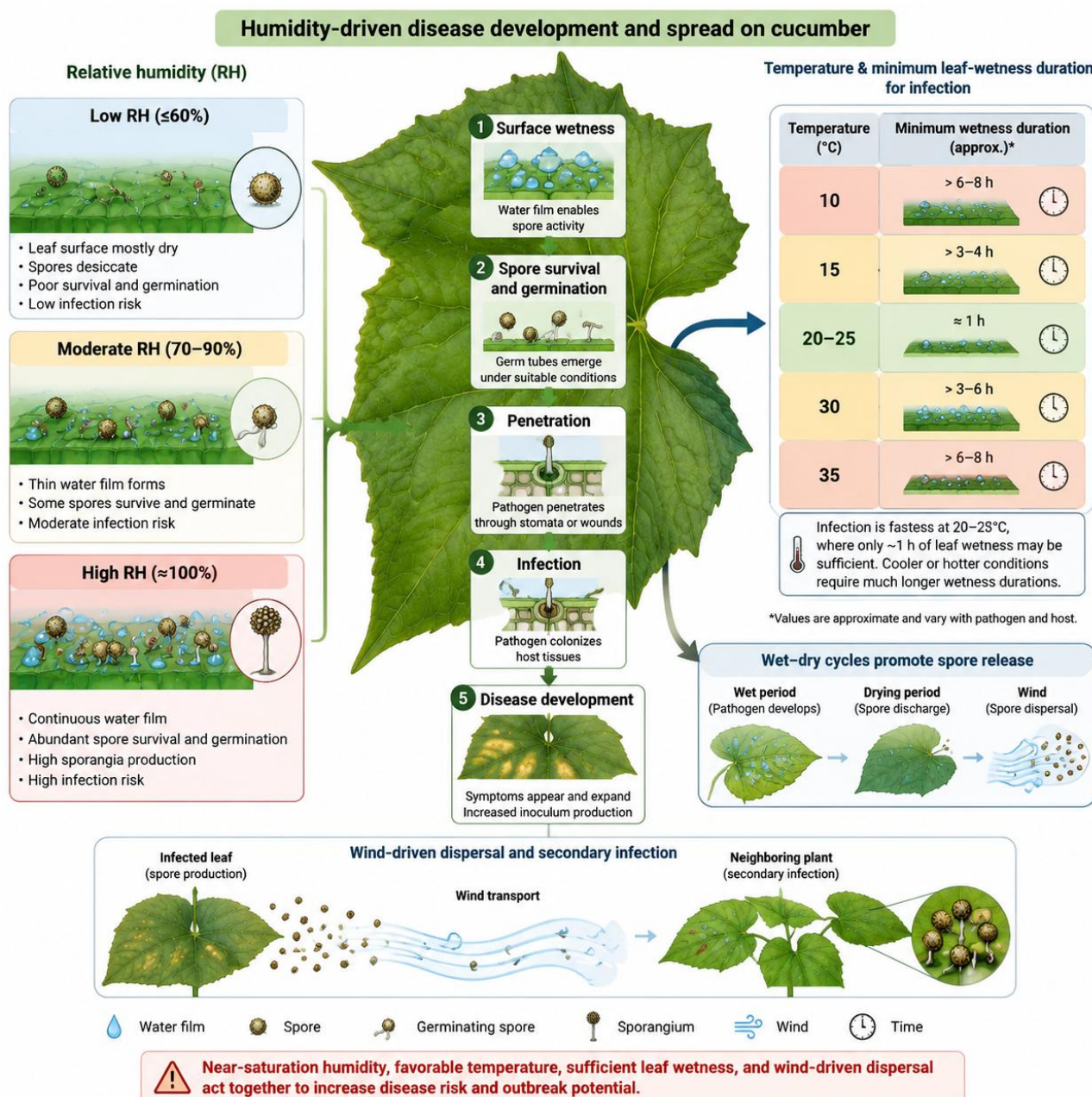


Figure 1 Conceptual framework illustrating the effects of relative humidity, leaf wetness duration, temperature, and wind-driven dispersal on cucumber pathogen survival, germination, infection, and disease development

3.2 Humidity-mediated changes in plant-pathogen interactions

Humidity conditions modify plant-pathogen interactions not only by favoring the pathogen, but also by changing cucumber physiology and defense capacity. Under low temperature plus 95% humidity, young cucumber plants showed reduced photosynthesis, chlorophyll content, and biomass together with increased oxidative stress markers, indicating that humid stress environments can weaken host performance at the same time that they favor disease development. Later work similarly showed that low temperature and high relative humidity reduced

chlorophyll pigments and precursor levels while increasing oxidative damage, which provides a physiological basis for greater vulnerability under prolonged humid stress (Amin et al., 2024). These humidity-driven physiological changes are not uniform across development, which means disease susceptibility can shift with plant stage. Seedlings at earlier leaf stages were more sensitive to high-temperature high-humidity stress, with larger reductions in biomass, net photosynthesis, and photosynthetic electron transfer than older seedlings, while four-leaf plants showed the greatest tolerance (Wang et al., 2024). Comparable stage dependence was observed under low-temperature high-humidity stress, where six-leaf plants were more tolerant than two- and four-leaf plants, suggesting that humidity-mediated disease risk partly reflects the developmental capacity of the host to maintain antioxidant and hormonal balance.

Humidity-mediated disease outcomes also depend on how effectively cucumber defense pathways are activated after pathogen challenge. In downy mildew resistance, increased lignin and hydrogen peroxide accumulation were associated with reduced germination and extension of *P. cubensis*, and transcriptome profiling identified defense functions involving pathogen recognition, signal transduction, reactive oxygen species, and transcriptional regulation (Gao et al., 2021). In gray mold, the resistant cucumber genotype showed shorter hyphae and lower spore germination than the susceptible mutant, together with stronger activation of redox, jasmonic acid, and ethylene signaling pathways, indicating that host biochemical responsiveness can counteract pathogen establishment even under favorable greenhouse humidity (Yang et al., 2020). At the greenhouse scale, humidity therefore acts as a regulator of both infection probability and host susceptibility. Greenhouse syntheses indicate that microclimatic stability determines infection probability and host vulnerability, while warm humid conditions generally promote fungal and bacterial pathogens in cucumber systems (Fanourakis et al., 2026). This interaction becomes agronomically important because greenhouse environments with elevated humidity and restricted airflow support mixed infections by *Fusarium*, *Botrytis*, *Alternaria*, and *Cladosporium*, so humidity stress can coincide with exposure to multiple pathogens rather than a single disease agent.

3.3 Major cucumber diseases associated with humidity conditions

Among humidity-associated cucumber diseases, downy mildew remains the clearest example of a pathogen tightly governed by moist air and leaf wetness. Greenhouse observations found that relative humidity above 90% was sufficient to trigger downy mildew development, whereas keeping humidity below 89% protected plants and sharply reduced infection and severity under early epidemic conditions (Khudhair and Aljarah, 2023). This strong moisture dependence is consistent with the infection biology of *P. cubensis*, whose sporangia germinate in free water and penetrate through stomata after zoospore release, making saturated leaf-surface conditions central to epidemic onset. Field and survey data also show that downy mildew severity rises under cooler, more humid conditions. Increased relative humidity together with low or moderate temperature increased disease severity in Egyptian production environments, and disease initiation elsewhere has been linked to high night relative humidity above 93% combined with prolonged night leaf wetness. The importance of downy mildew in cucumber production is amplified by its economic impact, because it is among the most destructive foliar diseases of cucurbits and has caused annual yield losses of up to 80% in European greenhouse and field production.

Other major cucumber diseases also show strong but distinct humidity relationships. Target leaf spot caused by *Corynespora cassiicola* produced the most spores at 100% relative humidity, and moisture explained most of the variation in spore size, which mattered because larger spores were more virulent than small spores (Zhao et al., 2022). Gray mold caused by *Botrytis cinerea* is similarly favored by greenhouse conditions of high humidity and 20°C-30°C, helping explain its persistence in continuously cropped protected systems (Yang et al., 2020). Humidity associations extend to powdery mildew, *Fusarium* wilt, and fruit rots, showing that cucumber disease risk spans both foliar and root or fruit pathogens. Powdery mildew is one of the major fungal diseases of cucumber and can recur annually, while its epidemic development is optimized at intermediate humidity rather than saturation, distinguishing it from downy mildew and target leaf spot (Saad and Khalifa, 2021). *Fusarium* wilt becomes more severe in warm, moist soil, and greenhouse disease monitoring has further shown that cucumber

pathogenic activity commonly clusters within 15°C-20°C and 80%-100% relative humidity, emphasizing that humidity control influences a broad disease complex rather than only one pathogen.

4 Influence of Humidity Control Strategies on Disease Prevention and Crop Health

4.1 Ventilation and airflow regulation for disease suppression

Ventilation is the most direct humidity-control strategy for suppressing cucumber diseases in protected cultivation because it reduces leaf-surface moisture and shortens periods of pathogen-favorable saturation. Greenhouse evidence shows that relative humidity above 90% promotes cucumber downy mildew, whereas keeping humidity below 89% protects plants, and ventilating greenhouses during early infection can reduce infection percentage by 95.8% and disease severity by 70% (Khudhair and Aljarah, 2023). This aligns with broader greenhouse epidemiology showing that cucumber is especially vulnerable to fungi favored by high relative humidity, and that adaptive climate regulation is a central preventive strategy rather than a secondary management step (Fanourakis et al., 2026). Airflow design matters as much as simply opening vents, because ventilation configuration influences both cooling and pathogen dispersal pathways. CFD-based greenhouse simulations showed that ventilation mode determined how *Corynespora cassiicola* spores moved through cucumber houses, and a hybrid ventilation strategy alternating full and bottom openings balanced cooling with pathogen containment by blocking aerial spread routes. At the production scale, adding mechanical ventilation and internal air circulation to a traditional high tunnel improved heat and humidity uniformity, and the ventilated house achieved markedly better cucumber growth and a 126% higher total yield than natural ventilation alone.

The disease-suppression effect of ventilation also appears under different greenhouse designs and climates. In a semi-closed greenhouse, relative humidity was maintained below 95% with nighttime air circulation, and fungal diseases were largely absent, particularly downy mildew, while slight positive pressure also helped block airborne pathogens and pests. Similarly, in Mediterranean greenhouses, combining a double-roof system with increased natural ventilation consistently lowered disease severity for cucumber powdery mildew, downy mildew, and gummy stem blight compared with the control sector. Ventilation can also reduce dependence on chemical control while improving production outcomes. A greenhouse with three ventilation openings produced 3000 kg of cucumber versus 1800 kg in a regular house, and the same study concluded that ventilation at disease onset functioned as a natural control strategy for downy mildew. This fits evidence from Japanese greenhouse cucumber production, where humid closed-house cultivation is used to promote growth before noon, but the same practice also promotes plant diseases, illustrating the tradeoff between moisture retention for vigor and disease suppression through airflow.

4.2 Irrigation management and humidity regulation

Irrigation management affects disease prevention partly by regulating how much water enters both the root zone and the greenhouse air. In greenhouse cucumber, full irrigation without disease produced the best gas-exchange performance, while downy mildew infection reduced photosynthesis, transpiration, and stomatal conductance, and additional irrigation deficits further depressed growth and leaf area (Wang et al., 2024). A similar interaction was reported for powdery mildew, where nutrient-solution deficits combined with disease sharply reduced plant height, stem diameter, and leaf area, indicating that water stress and pathogen stress reinforce each other rather than acting independently. Well-calibrated irrigation can therefore support crop health by avoiding both excessive humidity generation and plant weakening from water deficit. A cucumber transpiration model developed for semi-closed greenhouses was proposed as a tool to optimize irrigation and greenhouse relative humidity control, because reducing overestimated transpiration and irrigation lowers unnecessary water input into the air. Complementing this, optimization experiments across air temperatures found that the best irrigation amount for integrated cucumber growth typically stayed close to crop evapotranspiration demand, with optimal ranges shifting from 87%-91% ET_c at cooler temperatures to 107%-114% ET_c at the hottest range.

Irrigation strategy also interacts with greenhouse structure and cooling regime. In hot arid regions, a naturally ventilated polyhouse combined with normal irrigation at 100% ET gave the most reliable commercial performance, whereas even moderate deficit irrigation caused significant yield losses across structures. Under

Mediterranean soilless cucumber production, fan ventilation improved transpiration by 60% relative to fan-pad cooling and reduced drainage outflows by 95%, while an irrigation regime of 0.24 L/m² minimized nutrient losses without compromising growth. Irrigation can also be part of a broader disease-resistance strategy when linked with plant material and resource-saving delivery systems. Greenhouse work on grafted cucumbers reported that combining an appropriate irrigation regime with a suitable rootstock prolonged fruiting by about 38-40 days and increased yield, suggesting that water management can strengthen crop persistence under stress-prone production conditions. More generally, reviews of sustainable greenhouse vegetable systems identify irrigation system choice, irrigation timing, and drainage-water management as key low-input tools for controlling the production environment while improving resource efficiency (Argento et al., 2024).

4.3 Integrated environmental control strategies

The strongest disease-prevention outcomes come from integrated environmental control, where humidity is managed together with temperature, airflow, light, and crop monitoring rather than in isolation. Greenhouse reviews emphasize that microclimatic stability determines infection probability and host susceptibility, and that integrating environmental sensing, biological control, and adaptive climate regulation offers a preventive pathway toward climate-smart pest and disease management (Fanourakis et al., 2026). This systems view is reinforced by general greenhouse-control research, which treats temperature, humidity, light, and CO₂ as jointly regulated variables and identifies multi-scale model coupling as the next step for more reliable environmental control. Sensor networks, automation, and predictive control are increasingly central to this integrated approach. Intelligent environmental control systems use real-time sensor data to continuously maintain target growing conditions, while AI can predict plant responses and support proactive rather than purely reactive climate management. At the control-algorithm level, model predictive control using heaters, humidifiers, and ventilation fans reduced relative RMS error for temperature and humidity deficit to 23.5% and 13.1%, respectively, and humidity control in this framework is explicitly expected to support photosynthesis while helping prevent plant disease (Ito and Tabei, 2021).

Integrated systems are also becoming more effective by linking environmental control with disease detection. AI-based greenhouse management platforms have been developed to combine disease-image classification with environmental information such as humidity, temperature, and light, and these systems can feed back into vent and screen control to improve greenhouse sustainability and intervention timing. In real greenhouse conditions, such an integrated system achieved 94% classification accuracy and was proposed as a way to reduce labor, lower pesticide use, and improve productivity through more precise pest and disease control (Kim et al., 2021). For cucumber production specifically, integrated control is most effective when disease suppression and crop performance are optimized together. In semi-closed greenhouse production, yield models showed that average nighttime relative humidity was significantly associated with cucumber yield, while the overall environmental dataset supported improved greenhouse management and forecasting. Across protected agriculture more broadly, internet-based remote control, efficient water management, temperature regulation, and optimized IPM are now treated as complementary parts of sustainable greenhouse operation, suggesting that next-generation cucumber disease prevention will depend on coordinated humidity control rather than single-factor interventions (Argento et al., 2024).

5 Computational and Predictive Approaches for Humidity-Based Disease Management

5.1 Data-driven modeling of humidity-disease relationships

Data-driven modeling has made humidity-based disease management in cucumber production more operational by converting greenhouse climate measurements into early-warning indicators of infection risk. An early warning model for primary cucumber downy mildew in solar greenhouses was built from monitoring data, epidemiological theory, and a limited set of practical inputs, and it could issue warnings more than two days before symptoms appeared, with a positive warning raising estimated disease occurrence probability from 0.68 to 0.96 (Zhao et al., 2022). This emphasis on parsimonious environmental variables is important because growth-environment data are relatively easy to collect at scale in facility agriculture, making them well suited for broad predictive use in

greenhouse disease management (Lee and Yun, 2023). A central variable in these models is leaf wetness duration, because humidity affects disease not only through bulk air moisture but through condensation and persistence of wet surfaces. Early warning work for cucumber downy mildew treated leaf wetness duration as a key variable and combined leaf-wetness sensing with a relative-humidity threshold approach to create a practical estimation method when direct monitoring was difficult. Later greenhouse studies confirmed that leaf wetness duration is an important disease-model input related to infection and pathogen development, and showed that a back-propagation neural network estimated it more accurately than a simple relative-humidity model, reaching accuracies of 0.90 and 0.92 in two greenhouses (Liu et al., 2020).

Recent modeling has also moved from point estimates toward spatially explicit representations of humidity-related infection conditions inside greenhouses. A CFD transient model showed that canopy condensation caused by high humidity is a major cause of leaf wetness duration formation and could estimate the temporal and spatial distribution of wetness across cucumber canopies with good agreement to observations. Spatial heterogeneity studies likewise found that leaf wetness duration varied systematically within solar greenhouses, with longer wetness in the south and east zones and on rainy days, patterns that are closely related to the occurrence of high-humidity cucumber diseases (Liu et al., 2020). Another advance is the coupling of climate prediction with disease-process models so that warning systems can anticipate risk before unfavorable humidity conditions fully develop. A model-based methodology combined a mechanistic greenhouse climate model with a disease model, first predicting indoor climate 72 hours ahead and then using that forecast to detect downy mildew occurrence in advance. This integration is strengthened by machine-learning humidity forecasting, where a stacking ensemble for greenhouse indoor humidity achieved an R^2 of 0.96515 and high predictive precision, showing that accurate humidity prediction itself is now feasible enough to support downstream disease-risk models (Melal et al., 2024).

5.2 Machine learning prediction of disease risk

Machine learning has improved cucumber disease-risk prediction by exploiting the sequential structure of greenhouse environmental data rather than relying only on static thresholds. In cucumber downy mildew, an LSTM neural network was built from IoT-acquired time-series data on temperature, relative humidity, soil temperature, and solar radiation, and the resulting disease prediction model achieved 90% accuracy, 94% precision, 89% recall, and an AUC of 90.15%. The advantage of this approach is that classic machine-learning methods often handle long-term sequence dependence poorly, whereas LSTM better captures previous environmental feature information that is closely tied to disease onset (Liu et al., 2022). Prediction performance has improved further when environmental data are fused with direct disease indicators. A CNN-LSTM model for cucumber downy mildew integrated greenhouse and outdoor environmental records with airborne spore counts and observed diseased leaf area, reaching an R^2 of 0.9127 with low mean absolute and root mean square errors. The same study argued that future real-time prediction should integrate online spore detection with environmental big data, indicating that disease forecasting is moving toward multimodal monitoring rather than climate-only inference (Wang et al., 2024).

Broader deep-learning evidence suggests that humidity-based risk prediction can generalize beyond a single crop or pathogen when sufficient environmental data are available. A recent sequential deep-learning framework used previous growth-environment information, including air temperature, relative humidity, dew point, and CO_2 concentration, to predict crop disease risk and achieved an average AUROC of 0.917 across multiple crops and facilities. This wider applicability is plausible because environmental data are comparatively easy to collect in facility farms, and the authors argue that such data-driven learning frameworks could be used broadly for disease and pest prevention in controlled agriculture (Lee and Yun, 2023). At the same time, current machine-learning prediction still depends on stable management conditions and high-quality sensor streams. In the cucumber LSTM study, abrupt human-driven changes in greenhouse climate could disrupt data acquisition and degrade prediction accuracy, so venting schedules and field operations had to remain orderly for reliable modeling (Liu et al., 2022). Related greenhouse IoT reviews similarly note that high-detail monitoring in space and time is what enables more

accurate predictive models and their coupling with advanced control architectures such as model predictive control, underscoring that model quality depends on sensing quality (Bersani et al., 2022).

5.3 Smart agriculture systems for real-time disease control

Smart agriculture systems extend prediction into real-time action by linking humidity sensing, data transmission, and automated control of greenhouse conditions. An IoT- and wireless-sensor-network platform collected temperature, humidity, and soil-moisture data, sent them to a Raspberry Pi processing unit, and used a fuzzy-logic controller to generate climate and irrigation decisions, with testing showing effective platform performance (Benyezza et al., 2023). This type of architecture is attractive for cucumber disease prevention because it supports continuous regulation of humidity-sensitive microclimates rather than intermittent manual correction. Recent IoT greenhouse research also shows that remote management and cloud-connected sensing are now technically mature enough for practical humidity control. Web-based and smartphone-linked systems can display greenhouse status and send commands to actuators for humidity, temperature, and irrigation management, while NB-IoT sensor nodes can upload environmental data such as humidity in real time with stable transmission success rates that meet management requirements (Bersani et al., 2022). These capabilities matter for disease control because they enable timely response to short-lived humidity spikes that often precede infection events.

A further step is the integration of monitoring, forecasting, and disease detection into one control loop. IoT reviews describe automated systems that monitor temperature and humidity while also inspecting crop health by image analysis, and these systems have been reported to enhance yield through immediate control and monitoring without requiring direct farmer analysis. More generally, IoT-based greenhouse monitoring provides high-detail spatial and temporal data at reasonable cost, which supports more accurate models of plant environments and better control decisions at the level of individual crops or zones (Bersani et al., 2022). The emerging frontier is digital-twin disease control, although evidence here is still early. A recent digital-twin framework for greenhouse downy mildew combined intelligent air-quality sensing, optimization, and a three-dimensional disease model to generate real-time hotspot maps, and simulation experiments reported 96.7% hotspot coverage together with a 31% reduction in spraying path length and a 53% decrease in fungicide use. However, those gains remain simulation-based and require real-world validation, so digital twins appear promising for adaptive humidity-linked disease control but are not yet established as routine production tools (Wu, 2026).

6 Case Study: Humidity Control Strategies for Reducing Disease Occurrence in Greenhouse Cucumber Production

6.1 Experimental design and environmental data collection

A case-study design for greenhouse cucumber humidity control should combine continuous environmental sensing with repeated disease observation from transplanting to symptom onset. In solar-greenhouse downy mildew studies, indoor monitoring nodes have been placed at fixed canopy-relevant heights, with temperature, relative humidity, soil temperature, and water-related variables recorded at 15 min intervals, while disease surveys were conducted weekly before symptom appearance and then every 3-4 days after onset (Liu et al., 2022). A related early-warning experiment coupled climate monitoring from transplanting to primary infection with model-based forecasting, showing that short-horizon climate prediction can be directly linked to disease detection workflows in production greenhouses.

To strengthen spatial representativeness, environmental data collection should also account for within-greenhouse heterogeneity in humidity and leaf wetness. A chessboard deployment of sensors across nine sampling points in solar greenhouses showed that leaf wetness duration varies systematically by position, with longer wetness in southern canopy zones and on rainy days, which is directly relevant because wetness duration is a key input for cucumber disease forecasting (Liu et al., 2020). Field trials for cucumber powdery mildew likewise used hourly inside and outside greenhouse weather measurements across multiple seasons, with disease onset recorded when first symptoms appeared and fungicides withheld to allow natural epidemic development, providing a strong template for unbiased humidity-disease assessment.

6.2 Effects of different humidity regimes on disease development

Different humidity regimes produce clear differences in cucumber disease development, but the response depends on the pathogen and its interaction with temperature and leaf wetness. For cucumber downy mildew, sporangial germination and infection are favored by very high humidity, with infection commonly requiring relative humidity above 90% for several hours, and greenhouse observations showed that maintaining humidity below about 89% sharply reduced disease incidence and severity (Khudhair and Aljarah, 2023). Controlled-environment work supports this threshold behavior: downy mildew lesions produced abundant sporangia under leaf wetness or 100% RH, but only a few at 90% RH, and the minimum wetness duration needed for infection varied strongly with temperature.

Other cucumber pathogens show related but not identical humidity responses, which means that humidity targets should be set for multi-disease suppression rather than a single disease alone. For target leaf spot, maximum spore production occurred at 100% RH and moisture explained most of the variation in spore size, while larger spores were more virulent, indicating that saturated air not only increases inoculum quantity but can also increase its aggressiveness (Zhao et al., 2022). For powdery mildew, by contrast, intermediate RH of 50%-70% optimized disease development, while low RH of 20%-40% reduced lesion growth and short daily exposure to 35°C suppressed disease development by 70%-92%, showing that not all foliar pathogens peak under the same humidity regime (Figure 2) (Saad and Khalifa, 2021).

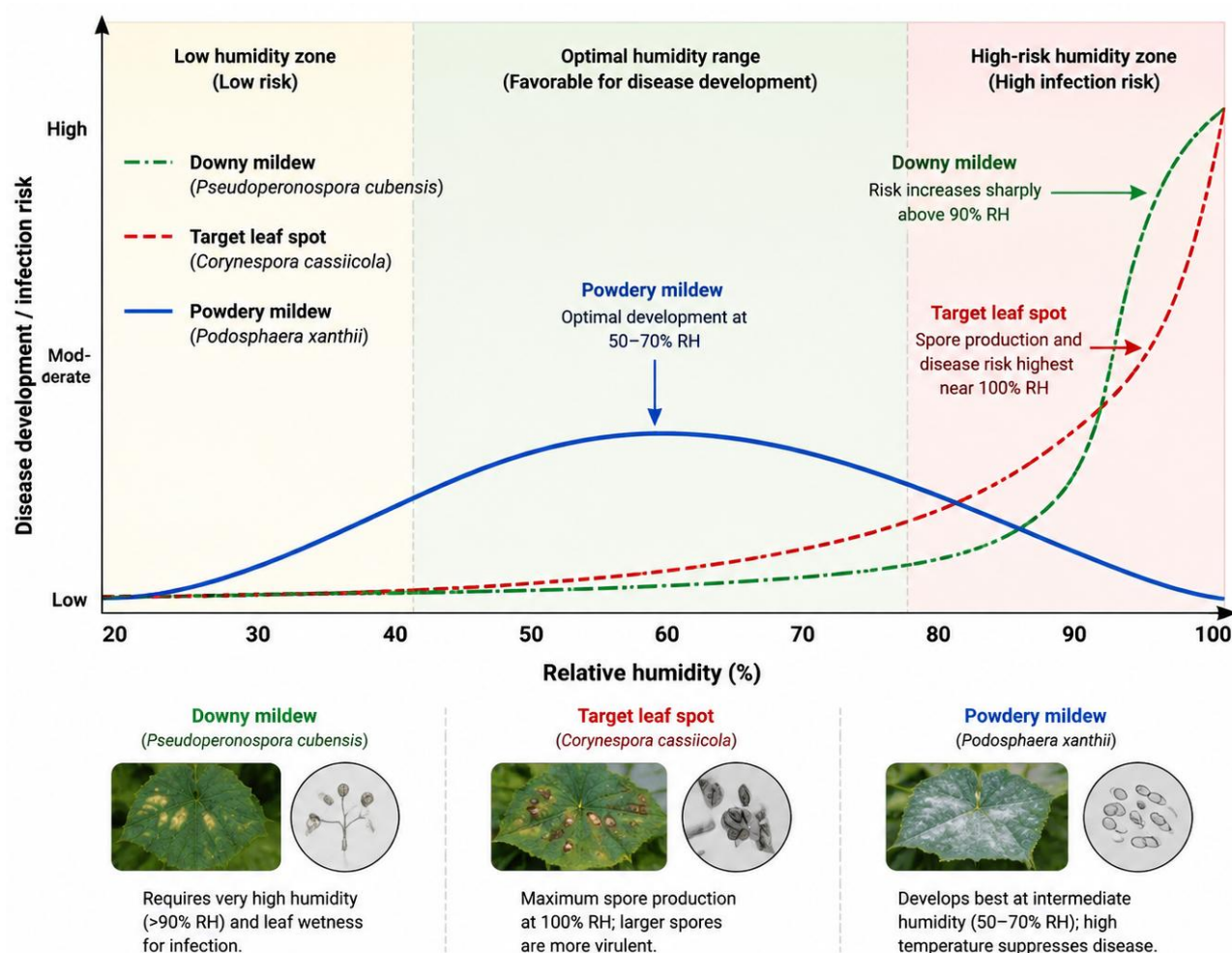


Figure 2 Conceptual humidity-response patterns of major cucumber foliar diseases. Different pathogens exhibit distinct humidity-sensitive infection windows, with downy mildew and target leaf spot showing increased disease risk under near-saturated humidity, whereas powdery mildew develops optimally under intermediate relative humidity conditions

6.3 Development of optimized humidity management strategies

Optimized humidity management in greenhouse cucumber production should prioritize ventilation-led control while integrating forecasting and disease thresholds. In a greenhouse case study on downy mildew, adding three ventilation openings reduced infection percentage and disease severity by 95.8% and 70%, respectively, and increased total fruit production relative to the regular greenhouse, indicating that relatively simple structural ventilation can serve as an effective non-chemical suppression strategy (Khudayer1 and Ahmed, 2025). Broader greenhouse engineering evidence supports this approach: ventilation is the most common dehumidification method because of its simple infrastructure, and the central operational goal is to prevent condensation on plant surfaces while keeping operating costs acceptable for growers.

A more advanced strategy is to combine temperature-relative humidity control with predictive analytics so that dehumidification is activated before long humid periods produce persistent leaf wetness or disease onset. Dehumidification modeling recommends integrated T-RH control rather than humidity control alone, and in cold regions suggests ventilation as the main control method, supplemented by mechanical dehumidification when ambient humidity is high or heating costs are limiting. On the disease side, greenhouse prediction studies show that environmental time-series data can forecast downy mildew occurrence with strong performance, and coupled climate-disease models have matched first field observation after early warnings, supporting a management framework in which ventilation, dehumidification, and monitoring are triggered by forecasted risk rather than calendar schedules (Liu et al., 2022).

7 Challenges and Future Perspectives

7.1 Limitations in current humidity-based disease management

Humidity control remains necessary in greenhouse cucumber disease suppression, but it is not sufficient because disease risk is shaped by a broader microclimatic system that includes temperature, vapor pressure deficit, light, host susceptibility, and pathogen-specific biology (Khudhair and Aljarah, 2023). This matters in cucumber because high relative humidity strongly favors fungal diseases such as downy mildew, yet humidity thresholds alone do not capture the full epidemiological variability across greenhouse conditions (Fanourakis et al., 2026).

A second limitation is that humidity-based management is often operationally fragile because greenhouse climate can shift abruptly under routine human actions or external weather changes, which reduces the stability of environmental measurements and weakens disease prediction reliability (Liu et al., 2022). Even where ventilation lowers downy mildew infection substantially, successful control still depends on timely implementation and coordinated regulation of temperature and humidity rather than ventilation as an isolated intervention (Khudhair and Aljarah, 2023).

7.2 Integration of artificial intelligence and precision agriculture

The next step is to embed humidity management within AI-enabled forecasting systems that combine sensor networks, time-series learning, and greenhouse decision support. In cucumber downy mildew, long short-term memory models have shown strong performance for forecasting greenhouse environmental variables and subsequent disease occurrence, which supports earlier intervention than symptom-based control (Liu et al., 2022). More broadly, AI, IoT, and machine learning are increasingly positioned as core tools for proactive disease forecasting and precision crop management under variable environmental conditions (Delfani et al., 2024).

The main constraint is not proof of concept but deployment quality. Current systems still face problems with data availability, validation, transparency, and real-world usability, while greenhouse sensors can suffer from communication interference, environmental noise, and mismatch between training conditions and commercial conditions (Delfani et al., 2024). Even so, the trajectory is promising because machine-learning models can predict greenhouse humidity with high accuracy, and future cucumber systems can extend from binary outbreak alerts toward severity prediction and dynamic visual decision platforms (Liu et al., 2022; Melal et al., 2024).

7.3 Sustainable disease management under climate change

Under climate change, sustainable cucumber disease management must move beyond reactive spraying toward climate-informed integrated management. Rising temperatures, shifting moisture regimes, and combined abiotic stresses are changing host-pathogen interactions and increasing the unpredictability of disease outbreaks, which makes traditional single-factor control less reliable. In greenhouse cucumber specifically, erratic humidity promotes downy mildew outbreaks, and combined thermal and RH fluctuations can also reduce fungicide efficacy, further increasing the value of preventive environmental regulation (Fanourakis et al., 2025).

Future strategies therefore need to combine adaptive surveillance, precision agriculture, structural greenhouse adaptation, and economically viable cleaner production. Reviews of climate-resilient disease management emphasize early warning systems, precision tools, and resilient cultivars, while protected-cultivation research highlights smart climate control, insulation, and sustainable energy integration as practical adaptation pathways (Hossain et al., 2024). For greenhouse cucumber production, the most durable path is a preventive, data-driven IPM framework that couples humidity control with broader climate sensing, biological and agronomic measures, and farmer-usable decision tools.

8 Conclusions

Humidity regulation remains one of the clearest environmental levers for suppressing cucumber downy mildew in greenhouses because infection develops under high relative humidity and moderate temperatures, while drier conditions slow epidemic progress. Experimental evidence further shows that keeping greenhouse humidity below about 89% can protect cucumber plants from downy mildew, making RH control a practical disease-prevention target rather than only a descriptive risk factor. The practical value of humidity regulation is strongest when it is implemented through ventilation and integrated greenhouse management. Ventilation-based reduction of humidity lowered downy mildew infection and severity substantially, and in one greenhouse comparison the ventilated house also produced more fruit than the regular greenhouse. This matters agronomically because downy mildew can spread rapidly and cause major economic loss under favorable humid conditions, so environmental control reduces both disease pressure and dependence on repeated chemical intervention.

For precision cucumber production, the main implication is that humidity must be treated as part of a multi-sensor microclimate system rather than as a standalone variable. Greenhouse studies have shown that wireless nodes can collect temperature, humidity, soil, and external weather data at short intervals for disease-linked monitoring, while IoT platforms can automatically maintain target humidity ranges inside cucumber houses. This supports a production model in which disease prevention, crop growth, and resource control are managed through the same data infrastructure. That same infrastructure also improves production outcomes beyond disease suppression. IoT-based cucumber houses maintained more favorable daytime temperature and RH conditions and achieved a 41.6% yield increase per vine over conventional management, while cloud-based automated control improved cucumber yield, fruit quality, water-use efficiency, and energy performance. In this sense, humidity control contributes to precision production not only by lowering infection risk, but by stabilizing the broader greenhouse environment needed for consistent crop performance.

The strongest future opportunity is to shift from reactive humidity management toward predictive, AI-assisted prevention. LSTM-based greenhouse models have already predicted cucumber downy mildew occurrence with 90% accuracy from environmental time-series data, and CNN-LSTM models that combine disease and environmental information have also shown good agreement between predicted and observed disease severity. These results indicate that future systems can move from fixed RH thresholds to dynamic disease-risk forecasting. A second opportunity is to build smart prevention systems that combine environmental sensing with automated control, image analysis, and low-cost deployment. Emerging greenhouse platforms now integrate feedback loops for fans, pumps, and lighting, while future designs explicitly propose machine-learning image analysis for early disease detection and autonomous decision-making. At the same time, low-cost validated sensor systems and IoT-fuzzy control platforms suggest that smart disease prevention can be made technically feasible for smaller greenhouse operations rather than only high-capital facilities. Humidity regulation, then, is not just a

disease-control measure in cucumber production. It is the environmental backbone of a broader precision and smart-management strategy that can reduce disease, improve yield, and support more sustainable greenhouse production.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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Research Insight

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Effects of Fruit Bagging on Microclimate and Grape Quality

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Abstract Fruit bagging is an important horticultural practice widely applied in grape production to improve fruit appearance, reduce environmental stress, and enhance market value. The microenvironment created by fruit bags plays a crucial role in regulating temperature, humidity, light conditions, and gas exchange around grape clusters, thereby influencing fruit development and quality formation. This review summarizes recent advances in the effects of fruit bagging on grape microclimate, physiological responses, and quality characteristics. Different bag materials, colors, and covering periods modify light distribution, thermal conditions, and moisture dynamics, which subsequently affect fruit growth, sugar accumulation, organic acid metabolism, anthocyanin biosynthesis, and flavor compound formation. At the physiological and molecular levels, bagging regulates source-sink carbon allocation, hormone signaling pathways, and secondary metabolic processes involved in fruit maturation and coloration. In addition, optimized bagging strategies combined with canopy management, precise timing, and environmental monitoring can improve disease resistance and promote high-quality grape production. Case studies demonstrate that appropriate selection of bag types and management practices effectively enhances grape quality under diverse climatic conditions. Future research should focus on developing intelligent and sustainable bagging technologies, integrating microclimate monitoring systems, and establishing precision management strategies for efficient and environmentally friendly viticulture.

Keywords Fruit bagging; Grape quality; Microclimate regulation; Sugar accumulation; Anthocyanin biosynthesis

1 Introduction

Table grapes are a globally important fruit crop, valued both economically and nutritionally, and improving grape quality has become a central goal of modern viticulture as consumer demand increasingly emphasizes appearance, sweetness, acidity, flavor, and other market-defining traits. At the same time, conventional efforts to raise yield and quality have often increased reliance on agrochemicals, creating pressure to develop production systems that better balance fruit quality, food safety, and environmental sustainability (Luca et al., 2023). This challenge is especially important because grape quality is shaped not only by genotype, but also by environmental and agronomic factors that regulate berry color, sugar accumulation, acidity, flavor, and secondary metabolites during development. In grapes, light and other abiotic conditions strongly influence these traits, making canopy- and fruit-zone microclimate management a key pathway for quality improvement in both fresh-market and specialty production systems (Wang et al., 2022).

Within this context, fruit bagging has emerged as an increasingly important physical protection technology in viticulture. Pre-harvest bagging is widely recognized as a good agricultural practice that can create a modified microenvironment around the fruit, reduce damage from pests, pathogens, birds, sunburn, and mechanical injury, and lower agrochemical residues while also influencing visual and internal quality attributes. Its adoption across fruit industries in Asia, Australia, Europe, and the Americas reflects growing demand for safer and more environmentally friendly cultivation methods, although the benefits of bagging remain dependent on bag material, timing, cultivar, and local climatic conditions. In grapes specifically, bagging has been studied and developed as a low-environmental-impact technique in Mediterranean production areas and elsewhere, with the aim of integrating it into existing vineyard management systems to improve commercial quality while reducing the need for chemical treatments. Even so, reported outcomes remain variable, which has sustained interest in optimizing bagging protocols for specific cultivars and production environments (Pisciotta et al., 2020).

Research on grape bagging has progressively moved from simple protection trials to more detailed analyses of berry microclimate, ripening physiology, and metabolite regulation. Earlier work showed that bagging can alter the temperature and humidity conditions surrounding grape clusters, increase day-night thermal differences, reduce fruit shrinkage, and in some systems improve carbohydrate assimilation, yield, and economic return, indicating that the bag acts not merely as a barrier but as a microenvironmental regulator. More recent studies have shown that the effects of bagging on grape quality are highly dependent on the light environment created inside the bag. Because different bag materials and colors transmit light differently, they can alter berry ripening, sugar accumulation, anthocyanin synthesis, phenolics, and aroma compounds in distinct ways, with some treatments improving sensory or compositional quality and others delaying maturation or suppressing coloration (Wang et al., 2022).

Current evidence therefore supports a nuanced view of fruit bagging in grapes: it can improve fruit protection, reduce pesticide residues, and in some cases enhance bunch weight, berry appearance, flavor-related compounds, or marketability, but it can also delay ripening or inhibit color development under low-light conditions. For example, bagging has been shown to reduce pesticide residues while improving some quality traits in white table grapes, yet other studies report lower soluble sugars and delayed anthocyanin accumulation in shaded berries unless bags are removed before harvest to restore light exposure (Luca et al., 2023). Against this background, the objective of the present paper is to examine how fruit bagging modifies the grape cluster microclimate and how those microclimatic changes translate into effects on berry development and final fruit quality. Particular attention is given to the interactions among bag type, light transmission, temperature and humidity conditions, and cultivar-specific berry responses, with the broader aim of clarifying how bagging can be optimized as a sustainable viticultural practice.

2 Characteristics of Fruit Bagging Microenvironment in Grape Production

2.1 Effects of bagging on temperature regulation around fruit clusters

Fruit bagging modifies the thermal environment around grape clusters, but the magnitude and direction of change depend strongly on bag material and local radiation load. In Mediterranean table grapes, air temperatures around unbagged clusters were slightly higher than those inside paper bags, while a broader review of grape bagging reported that temperatures inside paper bags were modestly lower during July to September, with only a slight reversal in October (Pisciotta et al., 2020; Ali et al., 2021). These results indicate that paper-based bagging does not necessarily create overheating; under field conditions, it can instead buffer fruit clusters from direct solar heating and smooth short-term thermal extremes.

Temperature effects are nonetheless not uniform across bag types, because plastic and highly enclosed systems can trap more heat than ventilated or paper-based coverings. In organic grape production, clear plastic bags advanced ripening relative to brown paper bags and also caused abnormal overgrowths and sunburn, whereas in colored polypropylene bagging systems, lower temperature inside the bag was proposed as one factor contributing to larger berry size under white bags (Kiran et al., 2020). Taken together, these findings suggest that temperature regulation by bagging is best understood as a balance between radiation interception and heat retention, with breathable paper or light-colored bags generally providing a milder thermal microclimate than transparent plastic enclosures.

2.2 Influence of bagging on humidity and gas exchange conditions

Bagging also changes the moisture environment around grape bunches, although humidity responses vary with bag permeability and ventilation design. In Cabernet Sauvignon, temperature inside bags was only slightly elevated while relative humidity was slightly decreased compared with the canopy environment, likely because the two-layer Kraft bags were fitted with ventilation support; by contrast, postharvest plastic-film bag studies in table grapes showed that non-perforated bags maintained the highest relative humidity and reduced weight loss most effectively (Amorim et al., 2020). This contrast shows that bag structure, especially whether it is ventilated or tightly sealed, determines whether the cluster microenvironment shifts toward moisture retention or toward a more balanced exchange with outside air.

The gas environment created by bagging is equally important because restricted permeability can alter respiration and transpiration around the fruit. Plastic-film bags for table grapes were explicitly described as atmosphere-modifying packages that hinder CO₂ escape and O₂ entry, while perforation-controlled packaging work in other fruits showed that adjusting the number of perforations can stabilize favorable O₂, CO₂, and humidity levels by regulating fruit respiration and transpiration (Amorim et al., 2020; Herrera et al., 2024). Although most direct grape evidence here comes from postharvest systems, the same principle applies to preharvest bagging: gas exchange is not simply blocked, but engineered by material permeability and venting, which in turn influences water loss, condensation risk, and fruit metabolic activity.

2.3 Regulation of light environment by different bagging materials

The most consistent microenvironmental effect of fruit bagging in grapes is the modification of the light regime reaching the berry surface. Cluster bagging in Cabernet Sauvignon markedly reduced both photosynthetically active radiation and solar radiation throughout berry development, and work in Muscat-flavored table grapes likewise showed that bags of different materials and colors have different light transmittances that alter the fruit microenvironment and ultimately fruit quality (Wang et al., 2022). Light regulation is therefore the main mechanism by which bagging materials differ biologically, because variation in transmittance changes not only exposure intensity but also the spectral composition of light perceived by berry tissues.

Differences among bag colors and materials produce distinct quality outcomes because high- and low-transmittance bags do not regulate berry development in the same way. In 'Kyoho' grapes, light transmittance ranked white > yellow > blue, and higher transmittance increased soluble solids and anthocyanin content, whereas lower transmittance reduced berry cracking and increased sub-epidermal thickness; similarly, in multi-bag trials on Muscat-flavored grapes, transparent and white bags promoted phenolics and monoterpenes, while pink and blue bags showed inhibitory effects (Wang et al., 2022). These findings show that bagging materials should not be treated as interchangeable coverings, since their optical properties directly shape the balance between visual protection, ripening progress, skin integrity, and the accumulation of flavor- and color-related metabolites.

3 Effects of Fruit Bagging on Grape Growth and Development

3.1 Effects on fruit expansion and morphological development

Fruit bagging can promote berry expansion and improve commercial morphology, but the effect depends strongly on bag material, timing, and cultivar. In Mediterranean table grapes, bagged bunches were heavier than unbagged controls across cultivars, mainly because of higher berry number and berry weight in some seedless varieties, while parchment bags in another study increased berry length, width, and weight more clearly than paper or non-woven materials (Pisciotta et al., 2020; Luca et al., 2023). These results indicate that bagging can support fruit enlargement, but the benefit is not universal across all bag types.

Color-specific and stage-specific bagging studies reach a similar conclusion. In 'Muscat Hamburg', white non-woven polypropylene bags produced the highest bunch weight, berry diameter, berry weight, and yield per vine in both evaluated seasons, whereas in 'Kyoho' grape the highest berry weight was obtained when bagging was applied late, at 7 to 9 weeks after full bloom, rather than throughout the whole development period (Kiran et al., 2020). Together, these findings suggest that moderate microclimate modification during key expansion phases is more favorable for berry growth than prolonged or poorly timed enclosure.

Bagging also affects berry texture and skin-related morphology, which are important components of market quality. In Sicily-grown table grapes, bagging altered mechanical traits, increasing berry hardness in seedless cultivars while lowering skin break force in all varieties, which indicates a softer and easier-to-chew skin; broader reviews similarly note that bagging often improves size uniformity and reduces deformities caused by environmental stress (Pisciotta et al., 2020; K et al., 2025). This combination of improved external uniformity and modified skin mechanics helps explain why bagged grapes often meet fresh-market standards even when compositional effects are mixed.

Not all morphological responses are positive, however. In Cabernet Sauvignon, solar interception by bags had limited effects on berry weight at harvest, suggesting that shading does not necessarily translate into larger berries, while clear plastic bags in organic production caused abnormal overgrowths and sunburn despite advancing ripening. The overall evidence therefore supports a material-sensitive view in which breathable or light-modifying bags can improve fruit expansion, whereas excessive enclosure or inappropriate plastic coverings can impair normal morphological development.

3.2 Influence on fruit ripening process and phenological development

Bagging frequently delays grape ripening because it reduces light exposure during critical phases of sugar accumulation and skin coloration. In two Chinese cultivars, bagging lowered soluble sugar content, delayed pigment development, and therefore delayed maturation, while a recent metabolomic and transcriptomic study in 'Ruidu Kemei' also concluded that bagging inhibited fruit growth and delayed ripening even though some quality indices were higher at the over-mature stage (Yuying et al., 2023). These studies support the view that bagging often shifts berry development toward a later ripening trajectory rather than simply reducing final quality.

The effect on ripening is especially clear for anthocyanin accumulation. In Cabernet Sauvignon, bagging after véraison significantly inhibited skin anthocyanin accumulation, whereas early bagging followed by re-exposure to sunlight increased flavan-3-ol and flavonol concentrations, showing that timing relative to véraison determines whether light exclusion suppresses or redirects phenolic development. This means bagging is not only a protective practice but also a developmental regulator whose phenological effects depend on when berries are re-exposed to light.

Bag removal can partially reverse delayed ripening responses. In 'Shenhua' and 'Shenfeng', fruit color and soluble solids rapidly returned toward normal after bags were removed, and in a teinturier grape, anthocyanin derivatives accumulated rapidly after re-exposure to light, accompanied by increased expression of light-responsive regulators and anthocyanin biosynthetic genes (Li et al., 2023). These results indicate that at least part of the bagging effect is reversible and mediated through light-sensitive metabolic pathways rather than irreversible developmental damage.

At the mechanistic level, the ripening response to bagging interacts with core sugar and hormone pathways that normally regulate grape maturation. Independent ripening studies show that sucrose and abscisic acid promote sugar accumulation, anthocyanin biosynthesis, and ripening-related gene expression, while sucrose concentrations above 2% can induce anthocyanin synthesis even without added ABA, helping explain why light restriction that disrupts sugar signaling can slow normal ripening progression. Bagging effects on phenology therefore appear to arise from altered light conditions that secondarily reshape the metabolic signals driving maturation.

3.3 Effects on fruit surface protection and disease reduction

Fruit bagging provides direct surface protection by forming a physical barrier between the cluster and external hazards. In grapes, this barrier reduces mechanical injury, bird damage, and exposure to whole-canopy agrochemical sprays, while broader reviews of preharvest bagging identify protection against pathogens, insect pests, abrasions, sunburn, and residues as one of its most consistent advantages (Luca et al., 2023; Buthelezi et al., 2021). This protective function is central to the value of bagging in high-quality table grape production because berry surface defects strongly reduce marketability.

Direct field evidence shows that bagging can sharply reduce disease and pest incidence. Under organic conditions, brown paper bags reduced grape berry moth infestation to 1.8-2.3%, black mold to 0.6-2%, gray mold to 1.1-2.2%, and powdery mildew to 0-5.4%, compared with very high damage levels in non-bagged controls; the same study found that pesticide application did not improve protection beyond bagging alone. These results suggest that, when properly applied, bagging can function as an effective non-chemical protective strategy rather than merely a supplement to spraying.

Bagging also reduces surface contamination by pesticide residues, which is an important part of fruit protection in a food-safety sense. In two white table grape cultivars, all bagging treatments greatly reduced agrochemical residues at harvest, and review evidence likewise emphasizes that bags physically block agrochemical deposition onto the fruit surface during preharvest spraying (Luca et al., 2023; Kiran et al., 2020). This residue-reduction effect strengthens the role of bagging as a surface-management tool for residue-sensitive fresh-market grapes.

Protection effects may also extend into postharvest behavior by altering the microbial ecology of the fruit surface. Although demonstrated in pear rather than grape, bagging maintained higher fungal diversity on the fruit surface, increased non-pathogenic or antagonistic fungi, and reduced postharvest decay, suggesting a plausible biological route by which preharvest surface shielding can lower later spoilage risk; in stored grapes, protective packaging systems that better control fungal decay likewise improve fruit preservation during storage (Figure 1) (Gao et al., 2022). Overall, the evidence indicates that fruit bagging protects grape surfaces through combined physical exclusion, residue prevention, and disease-suppression mechanisms.

Fruit bagging protects table grapes from preharvest environmental and biological stresses

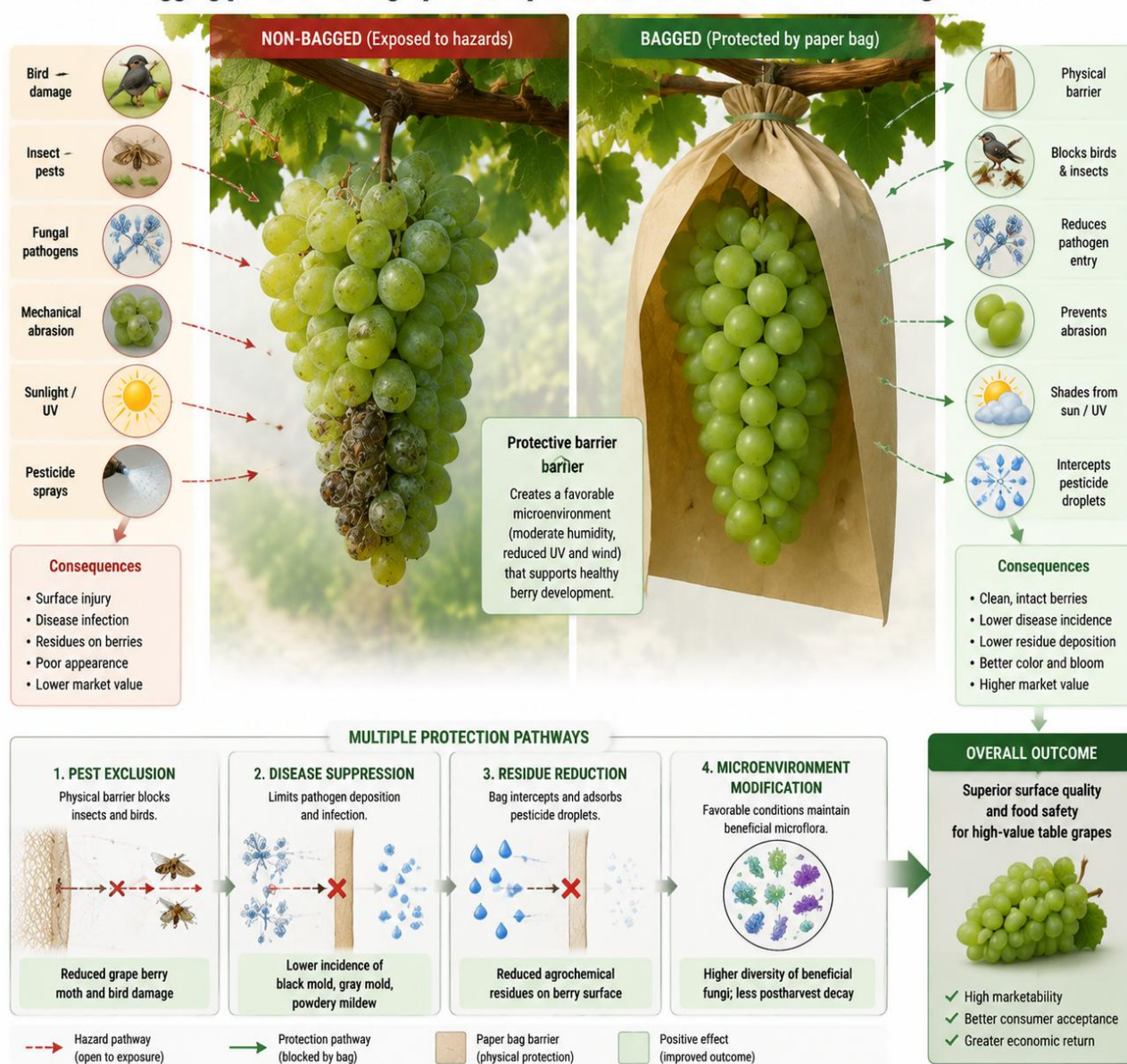


Figure 1 Multifunctional protective mechanisms of fruit bagging in table grapes: physical exclusion, contamination reduction, and surface quality preservation

4 Effects of Fruit Bagging on Grape Quality Attributes

4.1 Regulation of soluble sugar accumulation and carbohydrate metabolism

Fruit bagging alters soluble sugar accumulation in grapes, but the direction of effect depends on cultivar, developmental stage, and light regime. In Muscat-flavored table grapes, several bag types, including transparent, mesh, yellow, white, and blue bags, significantly increased total soluble solids in two cultivars, while in 'Red Globe' bagging raised total sugar content at the late stage of development and increased relative sucrose content and acid invertase activity (Wang et al., 2022). These results suggest that some bagging systems promote carbohydrate accumulation by modifying the berry microenvironment rather than uniformly suppressing ripening.

Other studies show the opposite pattern under stronger shading or prolonged light exclusion. In 'Shenhua' and 'Shenfeng', bagged berries had lower soluble sugar contents than unbagged berries, although sugar levels recovered rapidly after bag removal, while controlled shading in 'Marselan' reduced fructose, glucose, and total sugar accumulation and delayed ripening as light transmission declined (Nan et al., 2024). This indicates that the carbohydrate response to bagging is largely driven by the optical properties of the bag and the duration of reduced light exposure.

At the metabolic level, bagging appears to reshape sugar metabolism through changes in enzyme activity and carbon-partitioning pathways. In 'Red Globe', early changes in invertase activity under bagging were proposed to contribute to later sugar accumulation, and transcriptomic analysis of 'Ruidu Kemei' identified differentially expressed genes linked to starch and sucrose metabolism, glycolysis, and the tricarboxylic acid cycle under bagged conditions (Yuying et al., 2023). These findings support a mechanistic interpretation in which bagging affects not only final sugar concentration but also the regulatory network controlling carbon use during berry development.

This interpretation is consistent with broader evidence on grape carbon economy. Sugar accumulation in grape berries depends on imported carbon and is a core process in ripening, while more general fruit studies show that soluble sugar metabolism is governed by coordinated action of enzymes, transporters, and their spatiotemporal gene expression (Lu et al., 2024; Wu et al., 2025). Bagging therefore influences sweetness and maturity partly by altering the environmental signals that regulate these carbohydrate metabolism systems.

4.2 Effects on organic acids and flavor formation

The effects of fruit bagging on organic acids in grapes are generally weaker and less consistent than its effects on sugars. In 'Ruidu Kemei', bagging increased the sugar-acid ratio but had no significant effect on titratable acidity at the over-mature stage, while in Cabernet Sauvignon, bagging had limited effects on total soluble solids and titratable acidity at harvest despite clear shifts in berry light exposure (Yuying et al., 2023). This suggests that bagging often changes perceived taste balance more through sugar responses than through large changes in acid concentration.

A similar conclusion emerges from broader bagging literature. Reviews note that bagging can increase or decrease sugars and organic acids depending on species and treatment, but grape berries often show relatively small changes in these core compositional traits, and citrus work likewise found that bagging exerted little effect on sugars and organic acids when applied late in fruit development (Ali et al., 2021; Jiang et al., 2022). The available evidence therefore supports a moderate view in which acid metabolism is affected by bagging less consistently than berry color or aroma.

By contrast, flavor-related volatile formation appears highly responsive to bagging, especially to bag color and material. In Muscat-flavored grapes, the dominant volatiles included linalool, geraniol, β -myrcene, and ocimenes, and transparent and white bags promoted phenolics and monoterpenes, whereas pink and blue bags inhibited them (Wang et al., 2022). Because monoterpenes are key contributors to floral and fruity notes in table grapes, these findings indicate that bagging can materially reshape sensory quality even when sugar and acid responses are modest.

More detailed aroma studies confirm that these effects are selective rather than uniform. In 'Kyoho', red, green, blue, and white paper bags promoted ester accumulation but inhibited aldehydes, alcohols, terpenes, ketones, and acids, with green bags showing the strongest effect, while recent Vinalopó data showed that bagged grapes had relatively more aldehydes associated with green and fresh notes, whereas non-bagged grapes contained more alcohols and esters linked to fruity and overripe aromas (Andreu-Coll et al., 2025). Fruit bagging therefore modifies flavor formation mainly by redirecting volatile biosynthesis and volatile-family balance rather than by causing a simple increase or decrease in total aroma.

4.3 Influence on anthocyanins, phenolics and antioxidant compounds

The most consistent quality effect of fruit bagging in colored grapes is the suppression of anthocyanin accumulation under low-light conditions. In 'Shenhua' and 'Shenfeng', bagged berries developed poorer skin color and lower anthocyanin content than unbagged fruit, and in 'ZhongShan-HongYu' bagging without light caused obvious inhibition of anthocyanin accumulation (Li et al., 2023). This agrees with the broader view that berry coloration remains highly dependent on light exposure during ripening.

The inhibitory effect, however, is often reversible after re-exposure to light. In Cabernet Sauvignon, early bagging followed by sunlight re-exposure significantly elevated flavan-3-ol and flavonol concentrations, while in 'ZhongShan-HongYu' malvidin, cyanidin, and delphinidin derivatives accumulated rapidly after bag removal (Li et al., 2023). These findings indicate that bagging does not simply block phenolic metabolism permanently, but instead shifts the timing and composition of phenolic accumulation according to light recovery.

Responses of total phenolics and antioxidant-related compounds vary with bag design. In Muscat-flavored grapes, mesh, transparent, and white bags improved phenolic content to some extent, while a recent study using photoselective bags in teinturier grape showed that red and blue bags enhanced total phenols, anthocyanins, and antioxidant activity by increasing phenylpropanoid-pathway enzyme activities (Wang et al., 2022; Zhang et al., 2025). This suggests that not all bagging-induced shading is equivalent: spectral selectivity can either suppress or enhance phenolic quality depending on the wavelengths transmitted.

At the molecular level, light-responsive regulation explains much of this variability. In Cabernet Sauvignon, light-responsive transcriptional changes in CRY2, HY5/HYHs, MYBA1, and flavonoid-pathway genes coincided with altered phenolic accumulation under bagging, while in 'Shenhua' and 'Shenfeng' anthocyanin biosynthesis was linked to the expression of VvMYB genes together with the light-response factors VvHY5 and VvCOP1. Overall, fruit bagging influences grape quality most strongly through its control of the berry light environment, which in turn regulates sugar accumulation, aroma metabolism, and especially anthocyanin and phenolic biosynthesis.

5 Physiological and Molecular Mechanisms of Bagging-Induced Quality Regulation

5.1 Regulation of photosynthetic carbon allocation and source-sink balance

Fruit bagging regulates grape quality first by altering the local light environment around the cluster, which changes carbon supply to the berry and shifts source-sink relations during ripening. In grapevine, shading decreases carbon assimilation and can maintain vegetative growth at the expense of berries, while cluster bagging in Cabernet Sauvignon intercepted solar radiation but had limited effects on final berry weight and soluble solids at harvest, indicating that bagging modifies carbon economy more through developmental timing than through severe carbon starvation (Poupard et al., 2024). This helps explain why bagged fruit often shows delayed sugar accumulation during véraison but only modest differences at maturity when sink activity and post-bag light recovery compensate part of the early reduction in carbon import.

Whole-vine evidence further shows that grape ripening speed depends on balancing leaf source strength with fruit sink demand. Defoliation experiments delayed véraison and harvest by up to nine weeks and reduced root starch reserves, while bagged Jingyou grape berries showed lower soluble solids and reducing sugars during maturation, with quality improving after bag removal before harvest (Martínez-Lüscher and Kurtural, 2021). Together, these

results suggest that fruit bagging acts as a localized shading treatment that weakens berry sink activity during early ripening, but its final effect depends on how long light exclusion persists and whether the vine retains sufficient whole-plant carbon supply.

At the metabolic level, altered source-sink balance under bagging likely affects both sugar transport and sink conversion within berry tissues. Post-véraison sunlight studies showed that exocarp sugar transport can directly influence skin pigmentation and that flavonoid gene promoters contain sugar-responsive elements, whereas ABA-treated berries up-regulated beta-fructofuranosidase and sucrose transporter genes that support sucrose cleavage and import during ripening (He et al., 2020). This indicates that bagging-induced reductions in light may suppress not only photosynthate delivery but also sugar-responsive signaling networks that couple carbon status to color and flavor development.

More broadly, grape berries function within a dynamic source-sink system in which environmental constraints reshape carbon partitioning priorities rather than simply reducing total assimilate availability. Grapevines are managed around the ratio of leaf area to fruit mass, and over-cropping can delay ripening, while crop studies under periodic shading show that yield penalties are closely tied to disrupted source:sink carbon partitioning and can be mitigated by strengthening reproductive sinks (Martínez-Lüscher and Kurtural, 2021; Liang et al., 2025). Bagging therefore appears to regulate quality through a combined mechanism of reduced irradiance, modified sink strength, and delayed metabolic transition of the berry into a dominant carbon sink.

5.2 Influence of bagging on hormonal regulation during fruit ripening

Bagging-induced ripening delay is closely linked to hormonal reprogramming, especially the balance between ABA, auxin, and ethylene. In grape, ABA is a major positive regulator of ripening onset and promotes sugar metabolism, cell enlargement, softening, and color development, whereas auxin acts as a repressor of véraison and delays ripening at the transcriptional level. This hormonal opposition provides a mechanistic basis for the lower sugar accumulation, delayed coloration, and slower maturation commonly observed under prolonged bagging.

Direct bagging evidence supports this interpretation. In Cabernet Sauvignon, delayed ripening under sunlight exclusion coincided with up-regulation of auxin-related negative biomarkers such as AUX/IAA and ARF, while bagged strawberry fruit also showed delayed ripening associated with reduced ABA accumulation and induction of an ABA catabolism gene, suggesting that light exclusion can shift hormone balance away from ripening promotion (Sun et al., 2024). Although the strawberry work is not grape, it supports a general mechanism by which reduced light under bagging lowers ABA-driven ripening competence through enhanced ABA turnover.

Hormonal control during bagging is not limited to ABA alone, because grape ripening depends on strong crosstalk among several phytohormones. Reviews of non-climacteric fruit show that ABA, auxin, gibberellins, and ethylene act together during ripening, and grape-specific analyses indicate that light-responsive changes in auxin, cytokinin, ABA, brassinosteroid, salicylic acid, and ethylene signaling all occur after bagging or bag removal. Bagging therefore appears to alter a broader signaling network rather than a single pathway, with the timing of re-exposure to light likely determining whether ripening resumes rapidly or remains delayed.

Experimental hormone treatments in grape clarify the direction of these effects. Exogenous ABA increases endogenous ABA, activates ethylene and auxin signaling-related genes, and improves color, sugar accumulation, and softening, whereas NAA lengthens the growth-to-ripening interval and suppresses normal ripening progression (He et al., 2020). In practical terms, bagging likely delays maturation because light exclusion favors auxin-linked repression and reduces ABA-associated ripening signals, while bag removal reverses part of this shift by restoring the environmental cues that support ABA-mediated onset of ripening.

5.3 Molecular regulation of secondary metabolism under altered light conditions

The strongest molecular effect of bagging is on light-regulated secondary metabolism, especially anthocyanin and flavonol biosynthesis in the berry skin. Sunlight exposure during ripening increases flavonoid accumulation and the expression of biosynthetic genes, whereas cluster bagging in Cabernet Sauvignon caused coordinated changes

in CRY2, HY5/HYHs, MYBA1, UFGT, FLS4, LAR, and ANR that tracked changes in flavonoid accumulation under light exclusion and re-exposure. This shows that bagging modifies secondary metabolism mainly through transcriptional light signaling rather than through temperature effects alone.

At the regulatory level, MYB transcription factors occupy the core of the anthocyanin network, but their activity is tightly linked to upstream light-responsive regulators. MYB proteins are dominant regulators of anthocyanin biosynthesis across plants, and recent grape work identified a VvHY5-VvMYB24-VvMYBA1 cascade in which the light-responsive factor VvHY5 activates VvMYB24, which then cooperates with VvMYBA1 to increase VvDFR and VvUFGT expression (Yan et al., 2021; Zhen et al., 2024). Under bagging, reduced light would be expected to weaken this cascade, thereby lowering anthocyanin accumulation and suppressing red coloration.

Bagging also affects the composition of secondary metabolites beyond anthocyanins by changing the timing and extent of re-exposure to light. In Cabernet Sauvignon, re-exposure after early bagging significantly elevated flavan-3-ol and flavonol concentrations, whereas shading studies showed that flavonols were the most drastically reduced flavonoids and that MYB12 and FLS4 responded rapidly to changing light levels. These findings indicate that different branches of phenylpropanoid metabolism have different light sensitivities, with flavonols appearing especially responsive to bagging-induced light restriction.

6 Optimization Strategies for Fruit Bagging Technology in Viticulture

6.1 Selection of bag materials and structural characteristics

The first priority in optimizing grape bagging is to match bag material and structure to the intended balance among protection, microclimate regulation, and fruit quality. Evidence from table grapes shows that bag performance depends on material type, since paper, parchment, and non-woven polypropylene do not produce equivalent quality outcomes, and parchment bags in particular improved berry size and color while all bag types reduced residue accumulation (Luca et al., 2023). More broadly, bagging reviews emphasize that standardization of bag materials remains a major need because material permeability, color, and construction determine whether bagging preserves or improves fruit quality under field conditions (Ali et al., 2021).

Structural traits should be selected to regulate light transmission and ventilation rather than simply maximize enclosure. In grapes, white non-woven UV-stabilized polypropylene bags produced the best berry size and yield attributes, likely because they allowed more favorable light penetration and a suitable internal microclimate (Kiran et al., 2020). Evidence across fruit systems likewise shows that high-transmittance bags are generally preferable to highly opaque ones, because bags with very low light transmission tend to depress sugar accumulation, phenolic content, and antioxidant capacity, whereas moderate light transmission better preserves internal quality.

6.2 Optimization of bagging time and duration

Bagging time and duration should be optimized according to cultivar phenology, because prolonged light exclusion during ripening can delay maturation and suppress desirable skin coloration. In two grape cultivars bagged at 45 days after anthesis, low-light treatments reduced soluble solids and delayed pigment development, but fruit color and sugar levels recovered rapidly after bag removal near maturity, indicating that duration of enclosure is a key controllable variable. This stage dependence is reinforced in Cabernet Sauvignon, where early bagging followed by re-exposure after véraison increased some flavonoids, whereas bagging after véraison markedly inhibited anthocyanin accumulation.

The practical implication is that bagging should usually begin after the fruit becomes sufficiently developed to benefit from protection, but bags should not remain on clusters so long that they impose unnecessary low-light stress during the final ripening phase. In grapes, the effects of bagging on color depend on the stage of development, bagging date, bag type, bag removal date, and climatic conditions, underscoring the need for cultivar-specific scheduling (Pisciotta et al., 2020). Evidence from other fruit crops points in the same direction: early bagging around 15 days after fruit set often outperformed later timing for quality protection, while 30 days after fruit set could favor some compositional traits depending on material, showing that timing must be tuned to crop development rather than fixed as a universal rule (Kumar et al., 2023; Srivastava et al., 2023).

6.3 Integration of bagging with other vineyard management practices

Bagging is most effective when integrated with other vineyard practices that improve cluster-zone microclimate and reduce disease pressure. Reviews of grapevine pest management argue that cultural and physical methods should complement other control tools rather than be treated in isolation, especially as reliance on synthetic pesticides becomes less sustainable (Pavan et al., 2026). This logic fits grape bagging well, because bagging provides direct fruit protection while pruning, irrigation, and canopy management regulate the surrounding environment that still shapes temperature, humidity, and pathogen risk.

Field evidence supports combining bagging with practices such as defoliation, bunch-density reduction, and irrigation control to strengthen disease suppression and quality preservation. In vineyards, defoliation, reduced bunch density, and irrigation cut-off significantly reduced *Aspergillus* occurrence on berries and altered the carposphere microbiome in ways associated with lower disease pressure (Testempasis et al., 2023). At a broader systems level, extensive vineyard management with vegetation cover and low pesticide use increased biodiversity and ecosystem services, including pest control, suggesting that bagging should be positioned within low-input, ecology-based production systems rather than as a stand-alone intervention (Winter et al., 2025).

7 Case Studies: Application of Fruit Bagging in Commercial Grape Production

7.1 Effects of different bag colors on red grape anthocyanin accumulation

Commercial experience with red grapes shows that bag color strongly regulates anthocyanin accumulation by modifying cluster light environment rather than by providing a uniform bagging effect. In three red table grape cultivars, anthocyanin responses differed among seven bag types: mesh bags produced the highest anthocyanin content in RDZH, yellow bags were best in RDHY, and transparent or mesh bags outperformed paper bags in RDHM, showing that the optimal color or material is cultivar-dependent (Wang et al., 2022). A separate production-oriented study in 'Kyoho' likewise found that bagging effects on skin anthocyanins were inconsistent and depended on bag color, bag material, and whether an umbrella was added, confirming that commercial color management must be tailored rather than generalized (Zhou et al., 2020).

The practical lesson from red-grape systems is that some bag colors suppress total anthocyanin accumulation even when they improve uniformity or alter anthocyanin composition. In 'Kyoho', white, green, and yellow bags significantly reduced soluble solids and both total and individual anthocyanin concentrations, with green and yellow bags causing the strongest inhibition (Figure 2) (Zhou et al., 2020). By contrast, in teinturier grape 'Yan 73', red and blue photosensitive bags increased redness and brightness and raised anthocyanin, total phenol, and antioxidant activity, indicating that spectral selectivity rather than simple shading is the key design principle for premium color enhancement (Zhang et al., 2025).

A second case-study pattern is that bagging timing determines whether color suppression is temporary or persistent. In 'Shenhua' and 'Shenfeng', bagging imposed low-light stress, lowered soluble sugars, and delayed pigment development, but fruit color and soluble solids recovered rapidly after bag removal near maturity. Cabernet Sauvignon showed the same stage dependence at higher physiological resolution: bagging during véraison or late ripening inhibited anthocyanin accumulation, whereas early shading followed by sunlight re-exposure could preserve or even enhance final phenolic outcomes.

From a commercial perspective, the best red-grape strategy is therefore not simply “bag or do not bag,” but to choose spectrally appropriate materials and define a removal window that restores light before final coloration. Transparent and white polypropylene micro-perforation bags promoted phenolics and monoterpenes more consistently than pink or blue bags in Muscat-flavored table grapes, while yellow bags specifically increased anthocyanins in RDHY but inhibited certain traits in other cultivars (Wang et al., 2022). More generally, Mediterranean field data indicate that bagging can either promote or inhibit fruit color depending on bag type, bagging date, bag removal date, and climate, which is why color-targeted protocols must be cultivar- and region-specific (Pisciotta et al., 2020).



Figure 2 Mechanistic model illustrating how fruit bag color and material regulate anthocyanin accumulation in red table grapes through modification of cluster light environments

7.2 Bagging management for improving table grape quality under rainy conditions

Under rainy conditions, bagging works best as part of a moisture-exclusion strategy aimed at reducing fruit wetness, surface contamination, and disease pressure. In open-field rain-shelter systems, fruit bagging was reported to prevent fruit surface contamination, reduce pesticide residues, and protect clusters from bird damage, while broader grape studies identify fruit bagging as a physical barrier against microbial pathogens, insects, and mechanical injury (Wang et al., 2022; Luca et al., 2023). This makes bagging especially relevant where frequent rain increases disease incidence and repeated spraying raises residue concerns. Direct disease-control evidence in grapes is strong for paper-bag systems. Brown paper bagging reduced grape berry moth infestation to 1.8%–2.3%, black mold to 0.6%–2.0%, gray mold to 1.1%–2.2%, and powdery mildew to 0.0–5.4%, compared with severe damage in non-bagged controls, and these benefits were achieved even without additional pesticide benefit from spraying. In rainy regions, whole-vine rain shelters further reduced canopy leaf wetness and relative humidity and lowered the severity of ripe rot, white rot, downy mildew, gray mold, and brown spot, showing that cluster bagging and rainfall exclusion address complementary parts of the same moisture-driven disease problem.

Quality improvement under wet conditions also depends on avoiding bag materials that create heat injury or excessive enclosure. Clear plastic bags advanced ripening but caused abnormal overgrowths and sunburn, whereas brown paper bags improved fruit quality and yield while still providing strong physical protection, making breathable paper materials more suitable for humid production environments. This material effect is consistent with Mediterranean table-grape results showing that parchment bags produced larger and better-colored berries and that all tested bags substantially reduced agrochemical residues at harvest (Luca et al., 2023). Commercial rainy-region management also benefits from combining bunch protection with broader protected cultivation. In 'Niagara Rosada', both plastic cover and bunch bagging improved physical and chemical traits across two seasons and delayed maturation, indicating that dual protection can stabilize quality when climate is limiting (Guerios et al., 2021). At larger scale, rain shelter increased grape yield by 110%-176% and farmer income by 80-193% compared with fungicide-based management, suggesting that bagging under rainy conditions is most valuable when integrated with canopy-scale rainfall protection rather than used as an isolated intervention.

7.3 Integrated bagging strategies for premium grape production

Premium grape production uses bagging not only for protection but to coordinate appearance, compositional quality, and food safety. In Sicily, paper, parchment, and non-woven bags applied from BBCH 75 to harvest all reduced agrochemical residues, while parchment bags also produced bigger and better-colored berries, demonstrating how bag choice can align residue reduction with premium visual standards (Luca et al., 2023). The same study showed that bagging can be developed as a protocol added to existing table-grape management in Mediterranean climates rather than as a stand-alone replacement for vineyard practices (Pisciotta et al., 2020). Integrated premium systems also rely on matching bag design to target quality traits such as sweetness, phenolics, and aroma. In Muscat-flavored grapes, transparent polypropylene micro-perforation bags, followed by white polypropylene bags, were the most effective for sweet-sour balance, phenolics, and monoterpene accumulation, whereas pink and blue bags had the strongest negative effects (Wang et al., 2022). In 'Ruidu Kemei', bagging increased total soluble solids and sugar-acid ratio at the over-mature stage but also delayed ripening and altered hundreds of metabolites and thousands of genes, showing that premium-quality gains can come with a developmental trade-off that must be managed operationally (Yuying et al., 2023).

A further premium-production lesson is that bagging should be integrated with timing control rather than maintained continuously until harvest in every market class. In Cabernet Sauvignon, early bagging followed by sunlight re-exposure increased flavan-3-ols and flavonols, whereas bagging after véraison inhibited skin anthocyanins, showing that staged removal can improve secondary-metabolite profiles without sacrificing final color. Similarly, in 'Niagara Rosada', protected plants or bagged bunches outperformed the untreated control for all evaluated traits, but both plastic cover and bagging delayed maturation, which means harvest scheduling is part of quality optimization in commercial premium programs (Guerios et al., 2021).

8 Perspectives and Conclusions

Future grape bagging technologies will likely move beyond passive protection toward smart, sustainable, and crop-specific systems. Recent reviews identify biodegradable and sensor-enabled bags as the main innovation directions, arguing that conventional materials create environmental concerns while next-generation designs can combine fruit protection with lower ecological impact. This transition is also supported by broader packaging research, which highlights growing use of biodegradable, edible, and smart packaging platforms that can preserve fruit quality while reducing waste and environmental burden. Material innovation is especially important because future grape bagging must achieve both field durability and end-of-life sustainability. Reviews of fruit packaging emphasize bio-based films derived from cellulose and starch as practical alternatives to petroleum plastics, while recent film-engineering work shows that recyclable cellulose-containing systems can improve moisture resistance, structural integrity, and fruit freshness retention under humid conditions. For viticulture, this means that future bags should be designed not only for spectral selectivity and ventilation, but also for recyclability or biodegradability after field use.

Smart bagging will also depend on embedding microclimate-responsive sensing into the bag itself. Sensor-oriented reviews propose bags capable of real-time tracking of temperature, relative humidity, ethylene, and light flux, allowing growers to adjust irrigation, canopy operations, or bag removal timing according to the fruit's actual microenvironment. More general fruit-monitoring literature reaches the same conclusion, noting that smart packaging can continuously monitor temperature, humidity, and gas composition and use wireless communication to improve freshness control and traceability. A second innovation frontier is the automation and customization of bagging operations. Recent reviews point to robotic applicators, autonomous platforms, and machine-vision-guided deployment as ways to reduce the labor bottleneck that currently limits commercial adoption, while customizable bag dimensions and materials are expected to better match cultivar-specific and market-specific requirements. This is particularly relevant because current grape studies already show that bag performance differs by material, shape, color, and closing system, so technical standardization will require adaptable rather than uniform designs.

The next step for grape bagging is to integrate it with precision viticulture, where bagging decisions are guided by sensor data rather than fixed calendars. Precision viticulture relies on reliable climatic and soil information to support site-specific actions, and grape quality is especially sensitive to local variation in temperature, humidity, and radiation at both microclimate and mesoclimate scales. Because bagging directly modifies the cluster microenvironment, its optimization should be linked to these same variables instead of being treated as an isolated practice. Sensor networks also make it possible to connect bagging with water, disease, and harvest management. IoT-focused viticulture surveys show that even relatively simple sensor sets can support disease monitoring, phenological tracking, and vineyard water-regime assessment, while more integrated systems combining humidity, radiation, soil water, and imaging data can assist irrigation management, canopy decisions, stress monitoring, and harvest timing. In practice, this creates a framework in which growers could decide when to bag, ventilate, or remove bags based on dynamic risk and ripening signals.

Non-destructive sensing is especially promising for evaluating whether bagging is improving or impairing quality development. Portable fluorescence sensing has already shown strong utility for tracking grape flavonols, estimating sugar content, and predicting optimal harvest time under different vineyard microclimates and canopy treatments. Smartphone-based thermal imaging and canopy apps also offer low-cost routes for assessing vine water status, canopy architecture, and spatial variability, which could make bagging adjustments more feasible in commercial vineyards without requiring highly specialized equipment. Bagging should therefore be viewed as one component of a broader digital decision-support system. Reviews of smart viticulture emphasize that sensing technologies, AI, and user-friendly software are valuable only when they improve decisions on canopy architecture, pests, water status, yield, and fruit composition, while climate-adaptation work similarly argues for integrated technological systems that help growers respond rapidly to variable weather and quality risks. The most useful future bagging systems will likely combine in-bag sensing, vineyard-scale monitoring, and predictive analytics to manage fruit microclimate from bagging through harvest and storage.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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Research Insight

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Effects of Drought Stress on Photosynthesis and Water Use Characteristics of *Chrysanthemum morifolium*

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Abstract *Chrysanthemum morifolium* is an important medicinal and ornamental crop with high economic value; however, its growth and productivity are increasingly threatened by drought stress caused by climate change and limited water availability. Drought stress directly affects plant water balance, photosynthetic performance, carbon assimilation, and water use efficiency, thereby limiting biomass accumulation and flower yield formation. This review systematically summarizes the effects of drought stress on photosynthesis and water use characteristics of *C. morifolium*, with emphasis on physiological, biochemical, and molecular regulation mechanisms. Under drought conditions, reduced soil moisture availability induces declines in leaf relative water content, stomatal conductance, transpiration rate, and net photosynthetic rate, resulting from both stomatal limitation and non-stomatal inhibition. Meanwhile, drought stress alters chlorophyll metabolism, damages photosystem II activity, and affects electron transport efficiency, leading to reduced light energy conversion capacity and carbon fixation efficiency. To cope with water deficiency, *C. morifolium* plants employ multiple adaptive strategies, including stomatal regulation, osmotic adjustment through accumulation of proline and soluble sugars, enhancement of antioxidant defense systems, and modulation of drought-responsive gene expression. Changes in water use efficiency reflect the trade-off between carbon gain and water conservation, providing important indicators for evaluating drought adaptation. A case study approach is presented to analyze the dynamic responses of photosynthetic parameters and water use traits under different drought intensities, identifying key physiological indicators associated with drought tolerance. Furthermore, this review discusses practical strategies for improving drought resilience, including optimized irrigation management, application of soil amendments and biostimulants, and development of drought-tolerant cultivars through molecular breeding. Future integration of multi-omics technologies, high-throughput phenotyping, and intelligent irrigation systems will provide new approaches for enhancing water-saving production and sustainable cultivation of *Chrysanthemum morifolium* under increasingly variable climatic conditions.

Keywords *Chrysanthemum morifolium*; Drought stress; Photosynthetic characteristics; Water use efficiency; Drought adaptation mechanisms

1 Introduction

Chrysanthemum morifolium is a globally important horticultural crop with substantial ornamental, economic, ecological, and medicinal value. As one of the world's leading ornamental flowers and among the most valuable cut flowers in international floriculture, *Chrysanthemum* supports commercial production as cut flowers, potted plants, and landscape ornamentals across diverse cultivation systems (Luo et al., 2023). Beyond its ornamental role, *C. morifolium* has long been used as a medicinal and food-homology plant in East Asia, where its dried capitula and related products are valued in traditional medicine, tea, and functional foods because of their rich flavonoids, phenolic acids, volatile oils, polysaccharides, and other bioactive compounds (Hao et al., 2022; Liu et al., 2024). This dual-use identity means that stable *Chrysanthemum* production is important not only for the flower industry, but also for the sustained supply of plant material with nutritional and pharmacological relevance. As a result, environmental stresses that reduce biomass, flowering quality, or phytochemical accumulation can diminish both commercial value and downstream medicinal utility.

Among abiotic constraints, drought is one of the most serious factors limiting *Chrysanthemum* growth, production, and market performance. Studies consistently show that water deficit reduces plant growth and flower yield,

restricts planting area and geographical distribution, and lowers ornamental quality by impairing water relations and developmental performance (Xu et al., 2020). In commercial production systems, drought can also delay marketability and reduce profitability, while physiological symptoms commonly include dehydration, wilting, membrane damage, and suppressed gas exchange, indicating that *Chrysanthemum* is highly sensitive to inadequate water supply (Gogoláková and Paganová, 2020; Huang et al., 2026). More broadly, drought acts as a complex whole-plant stress that disrupts transpiration, photosynthesis, respiration, and cellular homeostasis, so its effects extend beyond visible growth inhibition to fundamental metabolic processes that determine survival and productivity. This is especially important under current climate trends, because increasing drought frequency and severity are likely to intensify water limitation during nursery, field, and postharvest phases of *Chrysanthemum* production.

Research on drought-induced photosynthetic regulation in *Chrysanthemum* has shown that photosynthesis is among the earliest and most sensitive processes affected by water deficit. Under drought conditions, net photosynthetic rate, stomatal conductance, transpiration rate, chlorophyll concentration, chlorophyll fluorescence, and PSII performance decline, with stronger or earlier reductions typically observed in drought-sensitive cultivars, indicating that both stomatal limitation and damage to the photosynthetic apparatus contribute to performance loss (Sahithi et al., 2020). At the same time, comparative physiological studies indicate that cultivar differences in drought tolerance are associated with variation in leaf structure, antioxidant capacity, and maintenance of photosynthetic function, while water-regime experiments show that reduced water availability significantly depresses stomatal conductance, transpiration, and photosynthesis and can alter intercellular CO₂ dynamics (Gogoláková and Paganová, 2020). These findings have established a useful physiological framework for understanding how drought reshapes carbon assimilation and water use in *Chrysanthemum*, and they also highlight the close coupling between leaf water status, oxidative stress, and photosynthetic stability.

Recent work has expanded this framework from whole-plant physiology to molecular and regulatory mechanisms, but important knowledge gaps remain. Drought-response studies in *Chrysanthemum* have identified genes and pathways related to ABA signaling, stomatal adjustment, cuticle formation, ROS detoxification, and stress-responsive transcriptional regulation, while genome-wide and transcriptomic analyses have emphasized that drought tolerance is a complex multigenic trait whose causal architecture remains incompletely resolved (Yang et al., 2020). Likewise, dehydration transcriptomics has shown large-scale reprogramming of hormone signaling, metabolism, and protective pathways, yet the integration of these molecular responses with dynamic changes in photosynthesis and water use efficiency under different drought intensities is still insufficiently characterized. In particular, more work is needed to link gas-exchange traits, chlorophyll fluorescence, leaf water status, and biochemical protection systems into a unified model of drought adaptation in *C. morifolium*. Therefore, examining the effects of drought stress on photosynthesis and water use characteristics is necessary for clarifying the physiological basis of drought injury and for supporting the breeding and cultivation of more water-efficient, drought-resilient *Chrysanthemum* cultivars.

2 Physiological Responses of *Chrysanthemum morifolium* to Drought Stress

2.1 Effects of drought stress on plant growth and biomass accumulation

Drought stress consistently suppresses vegetative growth and biomass accumulation in *Chrysanthemum*. Comparative physiological studies show that water deficit reduces biomass, flower development, transpiration, stomatal conductance, and photosynthetic performance, while cultivar-specific responses indicate that tolerant genotypes maintain growth better than sensitive ones under the same drought regime (Sahithi et al., 2020). This inhibitory effect is also evident at the production level, where drought decreases leaf increment, leaf area, and total biomass, although some cultivars partially compensate by increasing the root-to-shoot ratio to improve soil water use (Gogoláková and Paganová, 2020).

Growth reduction under drought is closely associated with impaired water status and declining physiological quality. Across diverse *Chrysanthemum* genotypes, relative water content, membrane stability, chlorophyll traits, fluorescence, and biomass are strongly correlated under stress, indicating that biomass loss reflects coordinated

disruption of hydration, membrane integrity, and carbon assimilation (Namita et al., 2025). Repeated osmotic stress experiments further show that initial drought episodes can inhibit microshoot growth more strongly than subsequent moderate stress, whereas severe repeated stress causes cumulative growth inhibition, suggesting that biomass responses depend on both stress intensity and stress history.

2.2 Morphological and anatomical adaptations to water deficit

Chrysanthemum responds to water deficit through structural adjustments that reduce transpirational water loss and improve dehydration avoidance. In a cultivar comparison, the drought-tolerant ‘Nannong Xuefeng’ developed denser trichomes, lower stomatal density, and much greater leaf wax deposition than the sensitive ‘Nannong Jingyan’, whereas transgenic evidence showed that enhanced drought resistance is likewise associated with reduced stomatal opening and a thicker epidermal cuticle (Wang et al., 2021). These traits fit the broader pattern of drought adaptation in leaves, where smaller effective evaporative surfaces, altered stomatal traits, and thicker cuticular barriers limit water loss while sustaining leaf function under drying conditions (Yavas et al., 2023).

The drought response of *Chrysanthemum* leaf morphology is also shaped by the growth environment and by long-term water relations rather than by acute soil drying alone. Plants grown under low vapor pressure deficit developed larger stomata and higher stomatal density, but their leaves lost water more rapidly during subsequent desiccation because stomatal closure was less effective, showing that preconditioning can alter later drought sensitivity. At the whole-plant level, drought commonly reduces leaf area and can shift biomass allocation toward roots, and these morphological changes are considered adaptive because they lower evaporative demand and improve water acquisition relative to shoot demand (Gogoláková and Paganová, 2020).

2.3 Osmotic regulation and antioxidant defense under drought conditions

Osmotic adjustment is a central component of *Chrysanthemum* drought tolerance. Under water deficit, *Chrysanthemum* commonly accumulates proline, soluble proteins, and soluble sugars to maintain cell turgor, and tolerant materials generally show stronger or more stable osmoprotective responses than sensitive ones (Zhang et al., 2022). Experimental mitigation studies support this interpretation, showing that exogenous melatonin increases soluble sugars and soluble protein under drought, while robinin plus chitosan promotes the accumulation of carbohydrates, proline, K^+ , and Ca^{2+} to sustain osmotic balance and turgor pressure (Elansary et al., 2020; Luo et al., 2023).

Antioxidant defense is equally important because drought-induced dehydration promotes reactive oxygen species accumulation, membrane lipid peroxidation, and loss of cellular stability. In *Chrysanthemum*, drought-sensitive plants accumulate more superoxide radicals and malondialdehyde, whereas tolerant genotypes or stress-alleviated plants maintain higher activities of SOD, POD, CAT, and APX, thereby limiting oxidative damage (Huang et al., 2026). Gene-level evidence is consistent with these physiological patterns: drought tolerance increases when ABA- and ROS-related defense pathways are activated, as shown by higher antioxidant enzyme activity in CmWRKY10-overexpressing lines and stronger proline accumulation and ROS-scavenging capacity in CmBBX22-repressed plants.

3 Effects of Drought Stress on Photosynthetic Characteristics of *Chrysanthemum* Leaves

3.1 Changes in photosynthetic pigments and light capture capacity

Drought stress generally weakens pigment accumulation and leaf light-harvesting capacity in *Chrysanthemum morifolium*, although the magnitude depends on stress severity and genotype. In *Chrysanthemum*, chlorophyll concentration declines as soil water content falls, and these decreases appear earlier and more strongly in drought-sensitive cultivars than in tolerant ones; multivariate screening across diverse spray *Chrysanthemum* genotypes similarly identifies chlorophyll a, chlorophyll b, total chlorophyll, carotenoids, and chlorophyll fluorescence as core drought-response traits linked to biomass and reproductive performance.

The physiological significance of these pigment changes is that reduced chlorophyll lowers the capacity for light absorption, while altered carotenoid dynamics help buffer stress-induced excess excitation. Ground-cover

Chrysanthemum showed a slight chlorophyll increase under light drought but a decline under moderate and heavy drought, indicating a threshold response rather than a simple monotonic loss, whereas broader pigment research shows that chlorophyll content and the chlorophyll a/b ratio directly influence antenna size, light distribution, and the balance between efficient capture and photodamage avoidance (Figure 1) (Simkin et al., 2022).

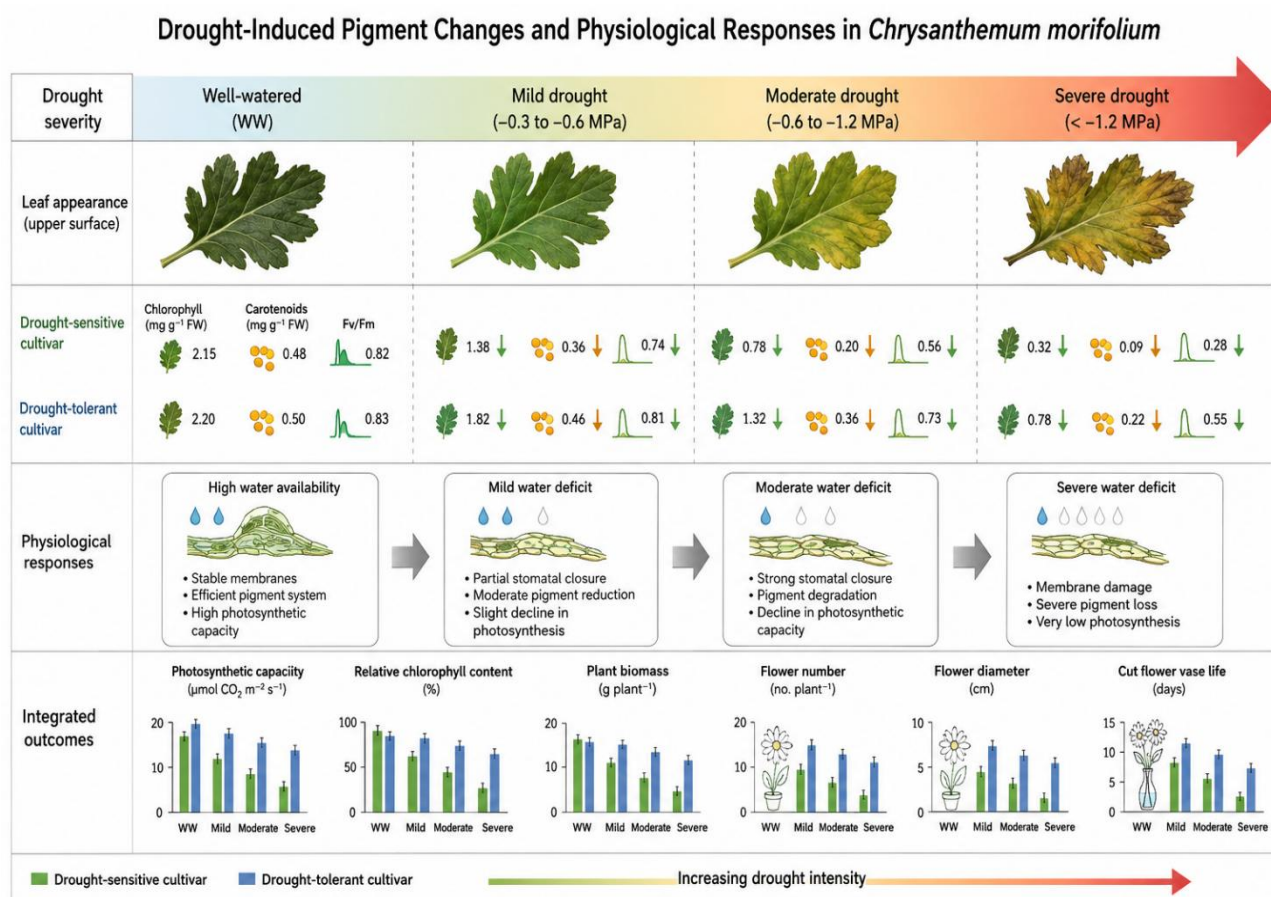


Figure 1 Phenotypic and physiological responses of *Chrysanthemum morifolium* leaves under progressive drought stress

3.2 Effects of drought stress on gas exchange parameters

Drought stress consistently suppresses the major gas-exchange parameters of *Chrysanthemum* leaves, especially net photosynthetic rate, stomatal conductance, and transpiration rate. In *Chrysanthemum* seedlings exposed to PEG-induced drought, net photosynthetic rate, stomatal conductance, and transpiration rate all decreased significantly while intercellular CO₂ concentration increased, and similar patterns were observed in ground-cover *Chrysanthemum*, where light drought reduced intercellular CO₂ but heavy drought increased it by 30.6% (Luo et al., 2023).

These patterns indicate a transition from stomatal limitation under milder drought to stronger non-stomatal limitation as stress intensifies. General drought physiology supports this interpretation: when leaf water status remains relatively higher, declines in photosynthesis track parallel declines in stomatal conductance and intercellular CO₂, but under more severe water deficit photosynthesis continues to fall even as intercellular CO₂ rises, implying biochemical impairment beyond stomatal closure; *Chrysanthemum*-focused analysis likewise notes that stomatal closure is typically the main determinant under mild to moderate drought, although metabolic damage becomes increasingly important as stress deepens (Gogoláková and Paganová, 2020).

3.3 Regulation of photosynthetic electron transport and carbon fixation

Beyond gas exchange, drought stress disrupts the photochemical machinery that supports electron transport and carbon assimilation in *Chrysanthemum* leaves. Comparative work in *Chrysanthemum* shows declines in PSII yield

and chlorophyll fluorescence under drought, with earlier and stronger reductions in sensitive cultivars, while severe drought in other model systems causes disassembly of PSII supercomplexes, degradation of the PSII core, and reduced operative quantum efficiency, indicating that the light reactions themselves become structurally and functionally compromised (Sahithi et al., 2020; Hu et al., 2023).

As photochemical efficiency declines, plants appear to increase protective energy dissipation and reroute electron flow, but these defenses are only partly effective under stronger stress. Drought studies across species show that PSII electron transport declines, non-photochemical quenching rises to relieve excitation pressure, and cyclic electron flow around PSI is activated to generate proton motive force and protect both photosystems; however, prolonged or severe stress also impairs carbon fixation by limiting ATP supply, RuBP regeneration, and Rubisco-related assimilation capacity, which helps explain why photosynthesis remains depressed even after stomatal effects are no longer the dominant constraint.

4 Water Relations and Water Use Characteristics under Drought Stress

4.1 Changes in plant water status and hydraulic regulation

Drought stress directly impairs plant water status in *Chrysanthemum morifolium*, primarily through a mismatch between water uptake and transpirational demand. Physiological studies show that reduced soil moisture lowers leaf water potential and relative water content, and varietal comparisons indicate that drought-tolerant materials maintain hydration more effectively than sensitive ones under stress (Sahithi et al., 2020; Zhang et al., 2022). This pattern is consistent with broader *Chrysanthemum* experiments showing that leaf relative water content declines progressively as drought intensifies, making tissue hydration one of the clearest indicators of water deficit severity and tolerance differences among cultivars (Luo et al., 2023).

Hydraulic regulation under drought depends strongly on stomatal control and epidermal barriers that limit water loss from leaves. In *Chrysanthemum*, transgenic and physiological evidence shows that reduced stomatal opening and thicker cuticles slow water loss, while exogenous ABA rapidly decreases stomatal conductance and delays wilting, indicating that hormonal and structural regulation act together to stabilize plant water balance during dehydration (Wang et al., 2021). Substrate-drying studies further show that more drought-tolerant cultivars conserve water by closing stomata earlier and retaining more water in the growing medium, suggesting that hydraulic regulation in *Chrysanthemum* is not only a leaf trait but also a whole-plant water conservation strategy.

4.2 Effects of drought stress on transpiration and water consumption patterns

Drought stress consistently suppresses transpiration in *Chrysanthemum*, and this response is closely tied to reduced stomatal conductance. Under reduced water availability, *Chrysanthemum* plants show marked declines in transpiration rate, while comparative cultivar studies confirm that transpiration decreases earlier and more strongly in drought-sensitive genotypes than in tolerant ones (Gogoláková and Paganová, 2020). Pot studies also show that both transpiration and stomatal conductance decrease as drought severity increases, and that tolerant cultivars maintain relatively higher gas exchange capacity under the same stress level.

Water consumption patterns in *Chrysanthemum* are shaped not only by soil drying but also by organ-specific and environmental controls on water loss. In cut *Chrysanthemum*, leaf transpiration decreases during desiccation because of stomatal closure, whereas stems and flowers show little active regulation, and leaf transpiration strongly predicts whole-cut-flower water loss (Fanourakis et al., 2021). Long-term growth under low vapor pressure deficit also alters later drought behavior: plants formed larger, denser stomata and then lost water faster during desiccation, showing that prior humidity conditions can modify subsequent transpiration control and wilting risk.

4.3 Water use efficiency responses to drought stress

Water use efficiency in *Chrysanthemum* generally increases under moderate drought because transpiration declines proportionally more than carbon assimilation during the early phase of stress. Ground-cover *Chrysanthemum* showed a progressive increase in water use efficiency with increasing drought, reaching 1.34-fold

the control level under moderate stress, while cyclical water-deficit studies indicate that controlled reduction of water supply can improve tolerance and post-stress performance (Gogoláková and Paganová, 2020). These findings suggest that moderate drought can trigger a conservative water-use strategy that improves instantaneous efficiency even while overall growth remains constrained.

However, improved water use efficiency under drought does not necessarily indicate superior productivity, because severe stress eventually restricts both water loss and photosynthetic carbon gain. In *Chrysanthemum* seedlings, exogenous melatonin increased transpiration, net photosynthesis, and stomatal conductance while also attenuating declines in relative water content, indicating that higher efficiency under mitigation can arise from better coordination between hydration and carbon assimilation rather than from extreme stomatal restriction alone (Luo et al., 2023). Likewise, drought-tolerant *Chrysanthemum* types maintain photosynthesis with less water-status disruption than sensitive ones, implying that the most favorable drought response is not simply low water use, but balanced water conservation with sustained metabolic activity (Zhang et al., 2022).

5 Molecular and Biochemical Mechanisms Regulating Drought Adaptation

5.1 Hormonal regulation of drought responses

Abscisic acid is the central hormonal signal regulating drought adaptation in *Chrysanthemum*, primarily by coordinating stomatal behavior, water conservation, and downstream stress-responsive gene expression. In *Chrysanthemum*, ABA treatment maintains higher leaf water content under water deficit by reducing transpiration through stomatal closure, while broader mechanistic work identifies ABA as the core signal that activates guard-cell drought responses through receptor-mediated signaling cascades that control stomatal movement (Hsu et al., 2020). This role is consistent with the general view that ABA is not only a physiological regulator of drought avoidance, but also a transcriptional signal that links water deficit perception to biochemical and molecular defense programs (Ali et al., 2020; Aslam et al., 2022).

Hormonal regulation in *Chrysanthemum* also depends on crosstalk between ABA and other phytohormones rather than on ABA alone. Exogenous melatonin under drought decreases endogenous ABA, jasmonate, and ethylene while increasing auxin, gibberellin, salicylic acid, and cytokinin levels, indicating that improved drought tolerance can result from a rebalanced hormonal network rather than from uniformly elevated ABA signaling (Parwez et al., 2022; Luo et al., 2023). At the gene-regulatory level, this network includes ABA-responsive transcriptional modules, because CmBBX19 interacts with the master ABA signaling component CmABF3 and suppresses ABA-dependent downstream genes, thereby negatively affecting *Chrysanthemum* drought tolerance (Xu et al., 2020).

5.2 Gene expression and molecular regulation of photosynthetic responses

Drought adaptation in *Chrysanthemum* involves large-scale transcriptional reprogramming that affects both protective stress pathways and photosynthesis-related metabolism. Genome-wide expression profiling under dehydration identified 8,558 responsive transcripts, including hundreds of transcription factors and protein kinases, and showed that drought alters hormone response, amino acid metabolism, secondary metabolism, and light- and photoperiod-related pathways. Proteomic evidence further indicates that drought changes the abundance of proteins associated with stress response, physiological transport, gene regulation, and secondary metabolism, alongside declines in photosynthesis, PSII yield, and stomatal conductance (Sahithi et al., 2020).

Several transcription factor families now appear central to the molecular regulation of *Chrysanthemum* drought responses that indirectly stabilize photosynthetic performance. *Chrysanthemum* and related germplasm studies have identified drought-responsive bZIP, MYB, and NAC candidates, including 28 bZIP family members in *C. mongolicum*, 51 stress-related MYB candidates in *C. nankingense*, and NAC subfamily genes involved in drought-responsive growth regulation (Ai et al., 2023). Functional evidence is stronger for some regulators than others: *CmbZIP9* overexpression increases stress-related gene expression and antioxidant enzyme activity under drought, whereas *CmbHLH112* overexpression elevates ABA levels, antioxidant defenses, and proline accumulation, together supporting photosynthetic tissues by reducing oxidative damage and water loss (Wang et al., 2024; Huang et al., 2026).

5.3 Metabolic regulation under water deficit conditions

Metabolic adjustment under drought centers on osmoprotection, antioxidant defense, and maintenance of carbon and energy balance. In *Chrysanthemum*, melatonin treatment increases soluble sugars, soluble proteins, and antioxidant enzyme activities under drought, while transcriptomic analyses show that dehydration significantly affects pathways related to sugars, amino acids, lipids, hormones, and secondary metabolites (Luo et al., 2023). This pattern matches broader drought biology, in which osmotic adjustment depends on the accumulation of compatible solutes such as soluble sugars, proteins, and proline to maintain cell turgor and protect macromolecular structures under low water potential (Ozturk et al., 2020; Pamungkas et al., 2022).

Reactive oxygen species metabolism is another key biochemical layer of drought adaptation because water deficit disrupts the balance between light absorption and carbon assimilation. Drought commonly increases ROS and membrane lipid peroxidation, but tolerant plants counter this through stronger enzymatic scavenging and osmotic buffering; in *Chrysanthemum* relatives, ABA accumulation promotes proline and trehalose biosynthesis, activates SOD and POD, and supports water retention, while broader redox signaling studies show that ABA-induced stomatal closure is reinforced by ROS-dependent signaling loops (Yang et al., 2020; Ge et al., 2026). More specifically, evidence across plant systems suggests that soluble sugars can contribute more strongly than proline to osmotic adjustment in some drought contexts, which is relevant for interpreting *Chrysanthemum* responses where sugar metabolism repeatedly emerges as a major regulated pathway (Gurrieri et al., 2020).

6 Case Study: Comprehensive Evaluation of Photosynthesis and Water Use Characteristics of *Chrysanthemum morifolium* under Different Drought Intensities

6.1 Experimental design and physiological measurements

A comprehensive evaluation of drought effects in *Chrysanthemum morifolium* is best built on graded water-deficit treatments that capture both intensity and duration effects. Existing *Chrysanthemum* studies have used several complementary designs, including pot experiments with defined soil water contents for moderate and severe drought, and irrigation-withholding trials followed by rewatering to assess stress progression and recovery. These approaches are useful because they separate immediate drought injury from reversible acclimation and make it possible to compare tolerant and sensitive cultivars under the same decline in water availability.

Physiological measurements in such case studies should integrate gas exchange, water status, pigments, and stress-defense traits rather than relying on photosynthesis alone. *Chrysanthemum* screening experiments under hydroponic PEG stress and pot culture drought have measured chlorophyll content, carotenoids, relative water content, membrane stability index, canopy temperature depression, chlorophyll fluorescence, biomass, and reproductive traits, while proteophysiological studies additionally included leaf water potential and stress markers to depict tolerance level (Figure 2) (Sahithi et al., 2020). Together, these variables provide a multidimensional framework for evaluating how drought intensity alters both carbon assimilation and whole-plant water relations.

6.2 Dynamic responses of photosynthesis and water use efficiency under drought stress

As drought intensifies, *Chrysanthemum* leaves show a characteristic sequence of declining photosynthetic activity. Across cultivar-based experiments, net photosynthetic rate, stomatal conductance, and transpiration rate all decrease with increasing stress, and these reductions appear earlier and more strongly in drought-sensitive cultivars than in tolerant ones. This pattern indicates that the dynamic response is not only a function of drought severity, but also of genotype-specific capacity to maintain stomatal regulation and leaf physiological stability.

Water use efficiency often increases during mild to moderate drought, but this does not indicate unchanged photosynthetic performance. In ground-cover *Chrysanthemum*, water use efficiency rose with drought intensity and reached 1.34 times the control under moderate stress, while repeated water-regime studies showed that monitored cyclical deficit can improve tolerance and support rapid recovery after drying (Gogoláková and Paganová, 2020). At the same time, the shift in intercellular CO₂ from an initial decrease to a later increase under stronger drought supports the view that responses move from mainly stomatal limitation toward combined stomatal and non-stomatal inhibition as stress deepens.

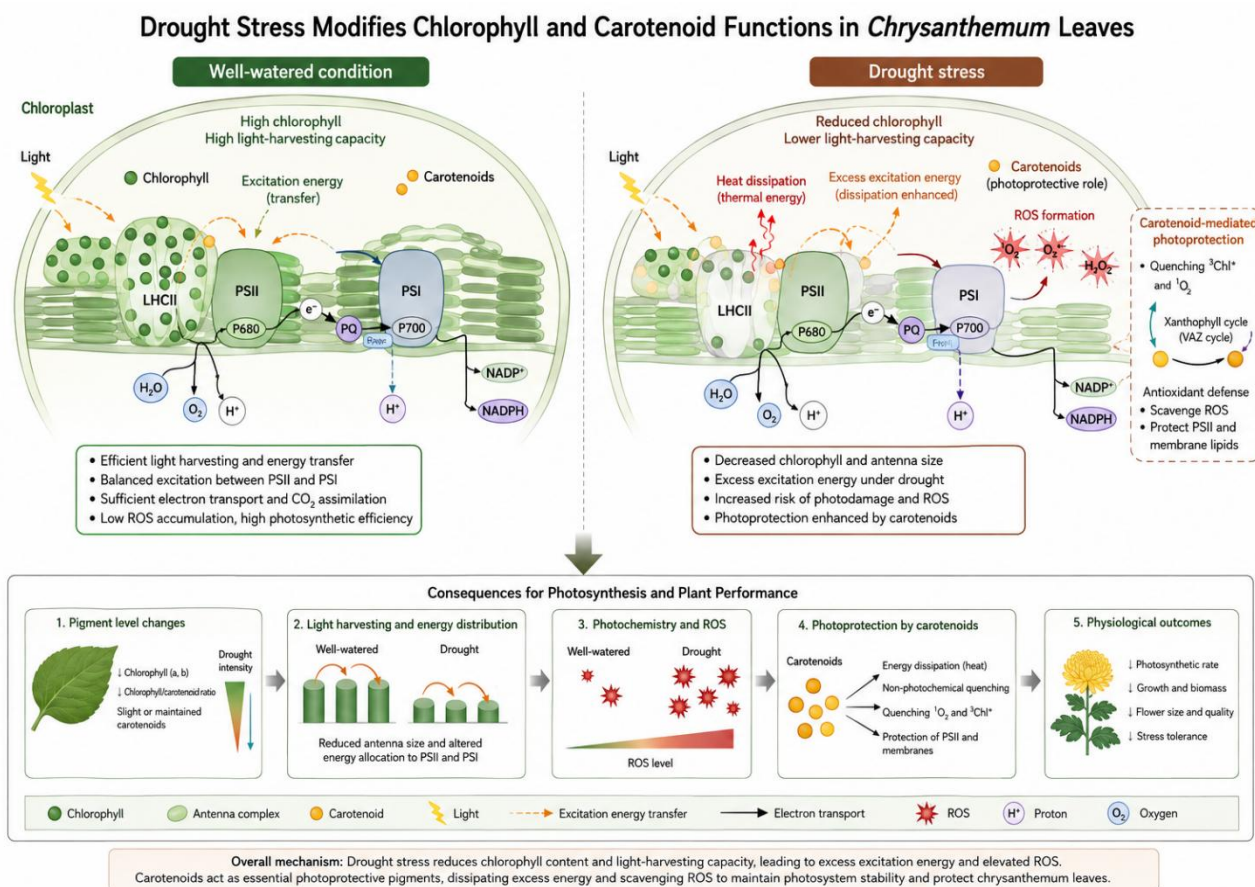


Figure 2 Mechanistic model of drought-induced regulation of chlorophyll and carotenoid functions in *Chrysanthemum morifolium*

6.3 Identification of key physiological indicators for drought adaptation

The most robust physiological indicators for drought adaptation in *Chrysanthemum* are traits that jointly reflect hydration status, photosynthetic integrity, and cellular protection. Multivariate analyses in standard and spray *Chrysanthemum* identified relative water content, membrane stability index, chlorophyll a and b, total chlorophyll, carotenoids, and chlorophyll fluorescence as major contributors to drought-related phenotypic variation and as practical selection indices for tolerant genotypes (Namita et al., 2025). These traits are especially useful because they integrate both functional performance and accumulated damage across different stress environments.

Biochemical indicators further refine this evaluation by distinguishing plants that merely endure dehydration from those that actively maintain homeostasis. Tea *Chrysanthemum* studies showed that increasing drought raised malondialdehyde, proline, and soluble protein while reducing growth and gas exchange, whereas comparative species analysis found that the more tolerant *Chrysanthemum* type maintained better water status, stronger antioxidant enzyme activity, less membrane damage, and less compromised photosynthesis (Zhang et al., 2022). Taken together, a comprehensive case-study assessment should prioritize relative water content, chlorophyll fluorescence, gas-exchange traits, membrane injury indices, and antioxidant or osmotic markers as the key physiological indicators of drought adaptation.

7 Agronomic Strategies for Improving Drought Tolerance and Water Use Efficiency in *Chrysanthemum* Production

7.1 Optimized irrigation management under water-limited conditions

Optimized irrigation management in *Chrysanthemum* production should aim to conserve water without causing irreversible drought injury. Regulated and sustained deficit irrigation are already recognized in ornamental crops as practical tools for controlling growth, hardening plants, and increasing water use efficiency, provided the strategy is adjusted to species-specific tolerance thresholds. In *Chrysanthemum* specifically, irrigation scheduling

and water input level strongly affect yield and efficiency, with field evidence showing that an intermediate irrigation regime of 0.75 Epan produced the highest water use efficiency among tested treatments under semi-arid conditions (Gouthami et al., 2025).

This optimization must also consider substrate and root-zone water dynamics rather than irrigation amount alone. Simulation-based work under protected cultivation showed that a 1.0 lph emitter combined with a 48-hour interval maintained optimal root-zone moisture while limiting deep percolation, indicating that irrigation design can improve water-use efficiency by keeping water available where *Chrysanthemum* roots can use it most effectively. At the same time, excessive deficit remains risky, because garland *Chrysanthemum* exposed to strong water restriction showed leaf chlorosis, reduced fresh and dry mass, and visible drought injury, whereas a moderate deficit treatment was more compatible with maintaining yield while improving efficiency (Chang et al., 2021).

7.2 Application of biostimulants and soil improvement measures

Among biostimulant approaches, exogenous melatonin has the clearest direct evidence for improving *Chrysanthemum* drought tolerance. Under PEG-induced drought, melatonin increased net photosynthesis, transpiration, and stomatal conductance, while also reducing the decline in chlorophyll and relative water content, indicating better coordination between water status and photosynthetic performance under stress. Melatonin also enhanced osmotic adjustment and antioxidant defense by increasing soluble sugars, soluble proteins, and antioxidant enzyme activities, which helps explain its protective effect on seedling vigor under water deficit (Luo et al., 2023).

Brassinolide and rhizosphere-oriented measures provide additional routes for stress mitigation and soil-related improvement. In *Chrysanthemum*, brassinolide treatment increased relative water content, net photosynthetic rate, chlorophyll fluorescence, Rubisco activity, and enzymes of the ascorbate-glutathione cycle, while reducing hydrogen peroxide accumulation, especially under drought conditions (Yang et al., 2020). Beyond plant growth regulators, review evidence indicates that *Chrysanthemum* production can also benefit from biological soil improvement, including rhizosphere inoculation strategies and beneficial microorganisms such as *Pseudomonas putida*, which have shown potential to improve plant growth and flowering and may support more resilient production systems.

7.3 Breeding and biotechnology approaches for drought-resistant *Chrysanthemum*

Breeding drought-resistant *Chrysanthemum* remains a high priority because drought tolerance is a complex trait controlled by many genes and strongly influenced by the species' polyploid and heterozygous genome. Transcriptome profiling under dehydration identified thousands of responsive transcripts, including transcription factors and kinases, and these datasets have been proposed as candidate-gene and marker resources for future breeding of drought-tolerant cultivars. More recent reviews likewise conclude that conventional breeding now needs to be integrated with marker-assisted selection, transgenic methods, genome editing, and multi-omics approaches to accelerate stress-tolerance improvement in *Chrysanthemum*.

Functional genetics and association mapping now provide more direct routes to cultivar improvement. Several drought-related regulators have already been characterized in *Chrysanthemum*, including CmSCL4 and CmR1MYB1, which synergistically enhance drought tolerance through ABA-responsive signaling, showing that targeted manipulation of signaling genes can improve stress adaptation (Zhang et al., 2022). At the population level, GWAS and integrative mapping studies identified favorable alleles, elite donor cultivars, and co-localized loci linked to drought tolerance, providing practical pre-breeding materials and genetic markers for developing cultivars with stronger drought resistance and more efficient water use (Lu et al., 2025).

8 Conclusions and Future Perspectives

Drought stress consistently depresses core photosynthetic processes in *Chrysanthemum* leaves, including net photosynthetic rate, stomatal conductance, transpiration, chlorophyll content, and PSII-related performance, and these declines become stronger as soil water deficit intensifies. Across graded drought treatments, intercellular CO₂ commonly decreases at earlier or milder stress and then rises under more severe stress, indicating a transition

from primarily stomatal limitation to combined stomatal and non-stomatal inhibition of photosynthesis. Water relations are impaired in parallel with photosynthesis, because declining leaf hydration, reduced water uptake relative to transpiration demand, and membrane injury all constrain physiological stability under drought. Even so, *Chrysanthemum* shows meaningful adaptive variation: tolerant genotypes or related species maintain better water status, less membrane damage, stronger antioxidative protection, and less compromised photosynthesis than sensitive materials.

For sustainable *Chrysanthemum* production, the main implication is that water-saving management should reduce unnecessary irrigation while avoiding severe stress that causes visible quality loss, depressed growth, and lower marketability. Moderate or monitored deficit appears more useful than uncontrolled drying, because *Chrysanthemum* can recover rapidly from cyclical water shortage and, in some systems, moderate deficit improves adaptation and post-production performance. Production strategies should also combine irrigation control with physiological protection and genotype choice. Exogenous melatonin and brassinolide both improved relative water content, photosynthetic performance, antioxidant capacity, and biochemical homeostasis under drought, while grafting onto *Artemisia annua* helped maintain gas exchange, photosynthesis-related gene expression, and Rubisco activity. At the cultivar level, multivariate screening now supports the use of chlorophyll traits, relative water content, membrane stability, canopy temperature depression, fluorescence, biomass, and reproductive traits as practical indicators for selecting drought-resilient production materials.

Future research should move from single-trait descriptions toward integrated multi-omics and phenomics frameworks that connect drought physiology with underlying genes, proteins, metabolites, and high-throughput phenotypes across developmental stages and environments. This need is especially pressing in *Chrysanthemum* because current omics applications remain relatively early, full-genome resources are still limiting, and large-population phenotyping under environmental variation remains one of the major bottlenecks for breeding progress. A second priority is to translate genetic discovery into usable breeding tools for drought-tolerant cultivars with stable photosynthesis and efficient water use. Association mapping, multi-locus GWAS, and integrative linkage mapping have already identified favorable alleles, pre-bred tolerant cultivars, colocalized loci, and validated candidate genes, but these resources still need functional validation and deployment in cultivar development. More broadly, future experiments should compare mild, moderate, and severe drought with rewatering phases, because stress intensity-dependent designs are better suited to linking dynamic physiological responses with transcriptomic regulation and to defining agronomically useful tolerance rather than survival alone.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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Research Insight

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Growth Characteristics of Sword Bean under Different Management Practices

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Abstract Sword bean (*Canavalia gladiata*) is an important leguminous crop with high nutritional value, strong environmental adaptability, and potential applications in sustainable agricultural systems. However, its growth performance and productivity are strongly influenced by cultivation conditions and management practices. This review summarizes the effects of different management strategies, including nutrient management, water regulation, cultivation practices, and environmental control, on the growth characteristics of sword bean. The morphological development, physiological responses, biomass accumulation, and yield formation processes of sword bean under different management conditions are systematically discussed. Nutrient management, particularly the balanced application of nitrogen, phosphorus, potassium, and organic amendments, plays a critical role in promoting vegetative growth, improving photosynthetic efficiency, and enhancing nutrient use efficiency. Water availability and environmental factors such as temperature and light intensity further regulate root development, physiological activity, and stress adaptation capacity. In addition, cultivation practices, including planting density, tillage methods, intercropping, and crop rotation, influence canopy structure, resource utilization, and final productivity. A case study based on integrated management practices demonstrates that optimized combinations of fertilization, irrigation, and field management can significantly improve sword bean growth traits, yield performance, and agricultural sustainability. Despite these advances, further research is needed to clarify the interactions among genotype, environment, and management practices using physiological, molecular, and digital agricultural approaches. Future efforts should focus on developing precise and sustainable cultivation systems to maximize the production potential of sword bean. Overall, improving management practices provides an effective pathway for enhancing sword bean growth, productivity, and ecological benefits in modern agricultural systems.

Keywords Sword bean; Growth characteristics; Management practices; Nutrient management; Sustainable cultivation

1 Introduction

Sword bean (*Canavalia gladiata*) is an underutilized legume with clear potential for sustainable agriculture because it combines nutritional value with agronomic resilience. It has been described as a cheap source of protein and calories, and it also shows favorable agronomic traits for tropical cultivation, with average yields reported as comparable to soybean in suitable environments. Its broader significance lies in the fact that underutilized legumes can diversify food systems while improving resilience and food security, and sword bean has specifically been noted as having good agronomic properties that make it resilient to adverse climate conditions in the tropics.

Beyond its direct food value, sword bean also fits the ecological logic of low-input farming systems because, like other legumes, it can contribute to soil fertility and reduce reliance on synthetic nitrogen inputs. Reviews of legumes in sustainable systems emphasize that symbiotic nitrogen fixation is a major pathway by which legumes support environmentally friendly production and crop diversification, while bean-based systems more broadly can buffer productivity under variable weather and reduce dependence on environmentally unfriendly inputs. Sword bean itself has been described as a high-biomass, drought-tolerant, pest-resistant species with nitrogen-fixing ability expressed through root nodulation, traits that make it attractive not only as a grain crop but also as forage, green manure, and a multipurpose component of integrated farming systems.

Crop growth in legumes is strongly shaped by management, and sword bean is unlikely to be an exception. Across legume systems, phosphorus application and rhizobial inoculation consistently increase grain yield, biomass yield,

and biological nitrogen fixation, while response size varies with species, soil organic carbon, and soil pH, indicating that management recommendations must be adapted to local conditions rather than generalized (Muoni et al., 2022). Parallel evidence from grain legumes shows that crop performance is also influenced by sowing density, irrigation, fertilization, tillage, and inoculation strategy, and that these factors interact with genotype and developmental stage to determine both yield and crop quality (Karavidas et al., 2022).

The available sword bean literature already points to several management-sensitive growth responses that justify dedicated study. Climatic adaptation is one major issue: sword bean tolerates drought better than many legumes but does not tolerate waterlogging, prolonged low temperatures during flowering reduce growth, and low light reduces flower and pod number; in cooler regions, transplanting may be needed to compensate for a shorter growing season. Experimental work also shows that management alters crop performance in more specific ways: moderate urea application changed forage quality more than biomass production, suggesting partial replacement of fertilizer N by biological fixation, while vesicular-arbuscular mycorrhiza and rock phosphate improved nutrient uptake pathways, especially nitrogen and phosphorus acquisition.

Research on sword bean growth has progressed, but it remains fragmented and much less developed than work on major legumes. Existing studies have examined seed production in non-native environments, forage production under nitrogen fertilization, nutrient uptake under mycorrhiza and phosphate application, and seed maturation physiology. These studies show, for example, that early cultivars can produce well-germinating seed under Polish conditions whereas late cultivars fail to mature fully, and that physiological seed maturity occurs around 80 days after anthesis with maximum germination and seed vigor at that stage. Even so, the crop remains underutilized and comparatively overlooked despite the recognized protein potential of *Canavalia* species and their possible contribution to future food strategies.

Against this background, the objective of a study on the growth characteristics of sword bean under different management practices is clear. A focused experiment can help determine how key agronomic variables influence vegetative growth, biomass accumulation, reproductive development, and yield formation in this species, while also clarifying which management combinations best express its potential under specific production conditions. Such work is needed because legume responses to management are often species- and environment-dependent, and because broader reviews show that improved agronomic practice, together with breeding and adaptation to stress conditions, is central to making legumes more productive and sustainable in modern agriculture.

2 Growth Characteristics and Physiological Development of Sword Bean

2.1 Morphological characteristics and growth dynamics

Sword bean is a vigorous climbing legume with a pronounced vegetative habit, and its morphology helps explain its adaptation to diverse tropical production systems. It is described as a perennial climbing plant with stems that can reach about 3-10 m, while its leaves are trifoliate and relatively large, supporting an expansive canopy during vegetative development. Broader agronomic descriptions likewise characterize sword bean as a tropical legume with favorable agronomic features and distinct morphological attributes, indicating that vegetative growth is one of its defining biological strengths .

Growth dynamics in sword bean show both species-level regularity and substantial genotypic variation. Field characterization of 20 genotypes found clear variation in days to germination, pod size, pod weight, and seed weight, with germination ranging from 3 to 6 days and pod length from 16.45 to 32.87 cm, which indicates that early establishment and subsequent structural development are strongly genotype-dependent (Debbarma et al., 2023). Quantitative growth analysis also showed that whole-plant weight increased early after sowing, leaf area expanded markedly after 50 days, and the reddish type expressed stronger early growth than the white type because specific leaf area, leaf area ratio, and leaf weight ratio were higher in the initial stage.

2.2 Photosynthetic characteristics and biomass accumulation

Sword bean appears to have strong biomass-forming ability because of its capacity to build large vegetative structures and convert intercepted radiation into dry matter. Agronomic work describes the crop as rapidly

growing and capable of converting solar light energy into chemical energy, which helps explain its reputation for high biomass production under tropical conditions. Evidence from closely related *Canavalia* systems also shows that higher photosynthetically active radiation increases biomass, photosynthesis, and water use, supporting the view that light capture is a central driver of canopy development and dry matter accumulation in this genus.

Biomass accumulation is also strongly shaped by growth stage, season, and nutrient-acquisition processes. In *Canavalia*, biomass production rises toward later vegetative-reproductive stages, with the highest fresh forage yield recorded at pod development rather than at earlier growth stages, indicating continued assimilate accumulation beyond flowering. Nutrient-management studies in sword bean further show that vesicular-arbuscular mycorrhiza increased nitrogen uptake and interacted with rock phosphate to affect phosphorus uptake, although dry matter itself was not significantly altered, suggesting that management can modify physiological efficiency even when visible biomass responses are limited.

2.3 Reproductive growth and yield formation processes

Sword bean reproductive development is relatively prolonged, and yield formation depends on successful transition from flowering to pod filling and seed maturation. Morphological field observations indicate that the vegetative phase lasts about 4-5 months before flowering begins, while pod maturation may continue for 5-6 months or longer, showing that reproductive growth extends over a large part of the crop cycle. Reproductive ecology studies add that the species flowers throughout the year, with more prominent flowering and fruiting during the rainy season, and that year-long prolific flowering helps sustain continual seed production.

Yield formation in sword bean is constrained not only by flowering intensity but also by pollination biology, fruit set, and the timing of seed physiological maturity. Comparative reproductive work found high pollen viability in *Canavalia gladiata* but a low seed-set percentage relative to flower number, likely because of abscission of young floral buds, while ecological study showed that the crop is pollinator-dependent and sets relatively low fruit numbers that are partly compensated by high seed set per successful fruit. Seed maturation data further show that pods and seeds reach physiological maturity around 80 days after anthesis, when pod and seed dry weight, germination, seedling vigor, and seed protein content are maximal, making this stage critical for harvest decisions aimed at maximizing yield quality.

3 Effects of Nutrient Management on Sword Bean Growth

3.1 Influence of nitrogen fertilization on vegetative growth

Nitrogen fertilization can stimulate vegetative growth in legumes, but the response is often moderate and depends strongly on dose. A global meta-analysis showed that nitrogen enrichment increased total legume biomass by 30.9% and tissue nitrogen content by 13.2%, while a pot study on long bean found that higher nitrogen input increased plant biomass and leaf greenness during reproductive onset (Tang et al., 2024). For sword bean, this broader pattern suggests that supplemental nitrogen can enhance canopy development and plant vigor, especially in nutrient-poor systems, but the benefit is unlikely to increase indefinitely with fertilizer rate.

At the same time, excessive nitrogen can weaken the root-nodule system that supports biological nitrogen fixation in legumes. Across legume datasets, nitrogen enrichment reduced nodule number by 21.2%, nodule weight by 29.3%, and the proportion of plant nitrogen derived from fixation by 27.1%, while field research in common bean showed that nitrogen fertilizer significantly reduced root length, secondary roots, and nodulation in most varieties (Figure 1) (Tang et al., 2024). This tradeoff is especially relevant to sword bean because the crop has inherent nitrogen-fixing capacity, so large nitrogen inputs may favor short-term shoot growth at the expense of longer-term physiological efficiency.

Evidence from sword bean itself indicates that modest nitrogen inputs may be more useful for improving forage quality than for substantially increasing biomass. In a urea-fertilization experiment, different nitrogen rates produced similar fresh and dry matter production, but crude protein and crude fiber changed significantly, and the 50 kg/ha treatment was judged most efficient because it saved urea while allowing rhizobial activity to function effectively. This indicates that, under some management conditions, sword bean vegetative growth is not strongly

limited by nitrogen alone, likely because symbiotic fixation can supply part of the crop demand once nodulation is established. A similar conclusion emerges from rotational *Canavalia* research, where the legume derived 69% of its nitrogen from the atmosphere, yet soil nitrogen replenishment was still gradual and mineral nitrogen remained necessary in the short term to sustain production. Together, these findings suggest that nitrogen management for sword bean should emphasize moderate starter or supplemental application rather than heavy fertilization, balancing early vegetative support with preservation of nodulation and biological nitrogen fixation.

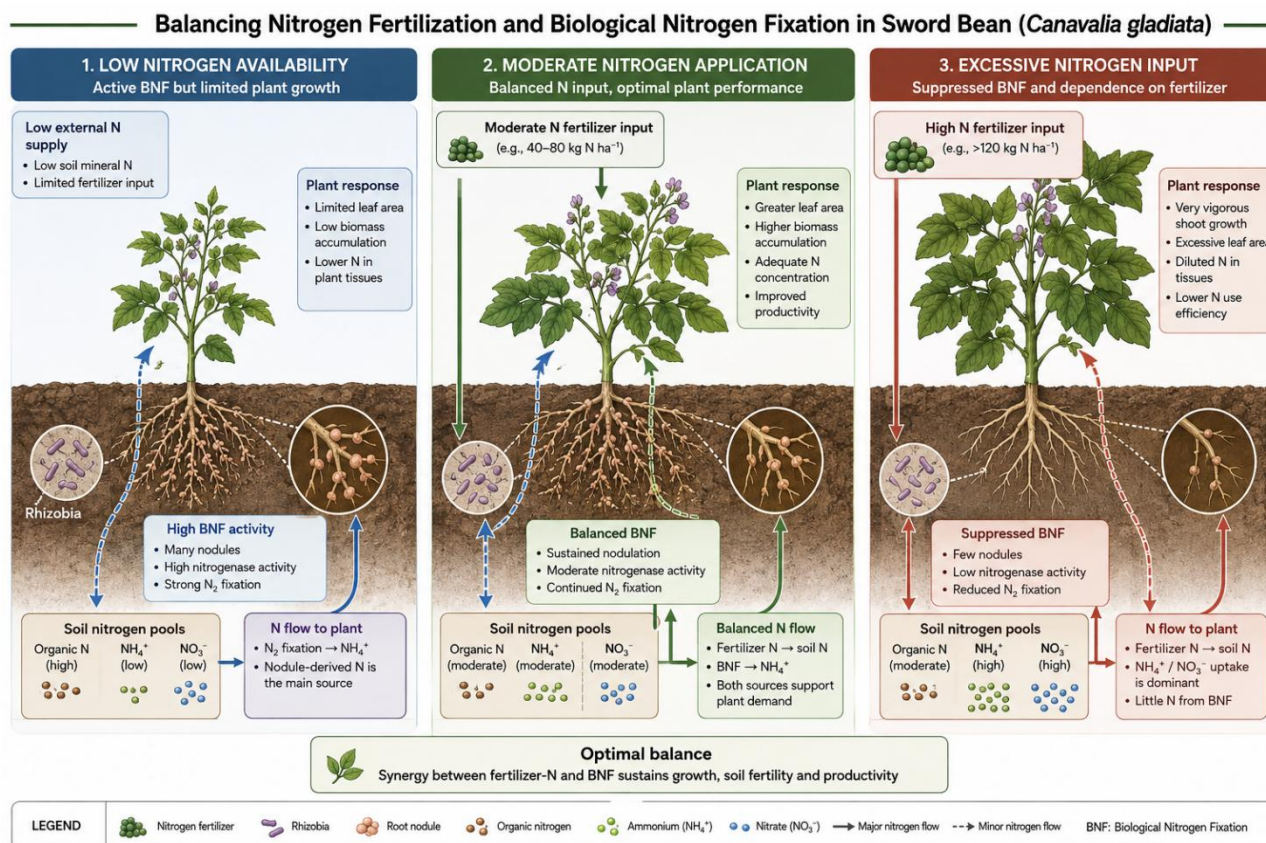


Figure 1 Conceptual model illustrating the effects of different nitrogen application levels on sword bean growth, root nodulation, and biological nitrogen fixation efficiency

3.2 Effects of phosphorus and potassium application on root development and yield

Phosphorus is central to root development, nodulation, and productive growth in sword bean, particularly in acidic or phosphorus-deficient soils. Experimental work on sword bean in acid upland soil showed that phosphorus fertilization significantly affected leaf phosphorus concentration, overall growth, and yield, while broader legume evidence indicates that phosphorus supports root proliferation and the energy-demanding process of biological nitrogen fixation. These responses are physiologically important because improved phosphorus nutrition strengthens the belowground structures that regulate nutrient acquisition and nitrogen fixation. Sword bean-specific yield data show that phosphorus application is essential for effective pod and seed formation, but the response can plateau above moderate rates. In East Lampung, increasing phosphorus increased sword bean yield, yet beyond 50 kg/P₂O₅ hthere was no further increase in biomass or pod weight, and crops receiving no phosphorus formed pods but failed to produce seed. A related study found that rock phosphate interacted with vesicular-arbuscular mycorrhiza in determining phosphorus uptake, with lower rates sometimes more efficient than higher ones. This indicates that optimizing phosphorus availability, rather than simply maximizing fertilizer dose, is more important for sword bean productivity.

Potassium complements phosphorus by supporting photosynthesis, enzyme activation, sugar transport, and nitrogen-use processes that ultimately influence legume growth and yield. In bean systems, adequate potassium improves nitrogen use efficiency and enhances nodulation and nitrogen fixation, indicating a strong functional

link between potassium supply and legume physiological performance. Field evidence from common bean further showed that crops responded strongly to combined phosphorus and potassium fertilization, reaching grain yields up to 3,600 kg/ha and requiring calibration of both nutrients even where soil tests suggested relatively high availability. However, potassium effects in *Canavalia* appear to be more pronounced in reproductive traits than in early vegetative growth. In jack bean, potassium source and timing did not significantly affect plant height, leaf number, or productive branches, although the study identified flower and pod drop as a major production constraint and recommended further work on potassium management during the generative phase (Eklemis et al., 2025). Consistent with this, cowpea achieved its highest nodulation and grain yield when inoculation was combined with both phosphorus and potassium, showing that potassium is most effective when integrated with other nutrient and biological inputs rather than applied in isolation (Emmanuel et al., 2020).

3.3 Organic fertilizers and integrated nutrient management strategies

Integrated nutrient management generally outperforms sole reliance on mineral fertilizers because it improves nutrient availability, root-rhizosphere function, and fertilizer-use efficiency. In faba bean, the combined application of organic and inorganic fertilizers produced the highest yield when organic nitrogen accounted for about half of total nitrogen, and this treatment also increased seed nitrogen accumulation and nitrogen harvest efficiency (Liu et al., 2023). Similarly, French bean studies report broad agreement that integrated plant nutrient systems are superior to exclusive chemical-input strategies for sustaining production and soil health. The mechanism behind this advantage is that organic inputs create a more favorable rhizosphere for nodulation and nutrient assimilation while mineral inputs provide readily available nutrients during periods of rapid demand. In faba bean, the 50% organic treatment increased total nodule number by 52.5%, fresh nodule weight by 55.8%, and nitrate reductase activity by 70.7%, while integrated nutrient use in French bean was associated with higher growth and better yield attributes than unfertilized controls (Liu et al., 2023). This mechanism is highly relevant to sword bean, whose growth depends on balancing external nutrient supply with its inherent biological nitrogen-fixing capacity.

Recent legume research also supports combining organic amendments, inoculation, and moderate phosphorus rather than increasing single-input rates alone. In haricot bean, the sole and combined application of vermicompost, phosphorus, and *Rhizobium* significantly improved growth, yield, and nitrogen fixation, and the combination of 30 kg P/ha with 5 t vermicompos/ha gave the highest yield among tested treatments. Long-term practical recommendations from vegetable legumes point in the same direction, with integrated nutrient management treatments combining inorganic fertilizer with vermicompost producing the highest plant height, pod number, and yield under acidic soil conditions (Changkiri et al., 2023). For sword bean, integrated strategies are especially promising because they can reduce overdependence on mineral nitrogen while improving phosphorus availability and biological nutrient capture. Research on root-focused nutrient management in French bean argues that sustainable production requires combining chemical, organic, and biofertilizer sources, and that biofertilizers with organic manure enhance root biomass and nutrient absorption. Sword bean studies also show that mycorrhizal inoculation increased nitrogen uptake and that phosphorus uptake depended on its interaction with rock phosphate, supporting the view that coordinated nutrient and biological management is more effective than single-factor fertilization.

4 Effects of Water Management and Environmental Conditions on Sword Bean Growth

4.1 Responses of sword bean growth to water availability

Water availability strongly regulates legume growth, and sword bean is expected to follow the general pattern seen across related species in which water deficit suppresses vegetative development, photosynthetic function, and final productivity. In grain legumes, drought reduces leaf area, shoot and root growth, chlorophyll content, stomatal conductance, CO₂ influx, nutrient uptake, and water-use efficiency, while severe stress also causes stunted growth and damage to the photosynthetic apparatus (Khatun et al., 2021). Because sword bean is managed for vigorous canopy growth and prolonged reproductive development, these drought-driven reductions in assimilatory capacity are likely to translate directly into lower biomass accumulation and weaker yield formation

when water supply is inadequate. The effect of drought on growth is closely tied to root performance, since deeper and more extensive root systems improve access to subsoil moisture and support better recovery under episodic stress. Across legumes, deep rooting, greater root length, and higher rooting density are repeatedly identified as promising traits for drought avoidance, whereas drought in common bean reduced rooting depth by 14%, root biomass by 29%, and total root length by 35%, with parallel declines in pod set and pod weight. For sword bean, this suggests that irrigation practices and soil-water management that maintain root activity during both vegetative and early reproductive stages will be essential for sustaining aboveground growth and reproductive success.

Water stress effects also depend on stress timing, intensity, and recovery opportunities rather than on soil moisture status alone. Reviews of legume drought responses note that yield loss varies by species and variety according to phenology, soil texture, and agro-climatic conditions, while intermittent drought can differ biologically from terminal drought because recovery capacity becomes part of the response (Khatun et al., 2021). This distinction is important for sword bean because a long growth cycle increases the chance that the crop will encounter both short-term water deficits and later-season moisture decline, making stage-specific water management more relevant than a single uniform irrigation strategy. Some legume responses to limited water are adaptive rather than purely damaging. Drought escape through faster development, early flowering, and earlier seed set is recognized as a major legume strategy, and plants with indeterminate growth can partly compensate after short drought by producing new organs during recovery. In practical terms, sword bean management under water-limited environments may benefit from synchronizing planting date and moisture availability so that the most drought-sensitive phases do not coincide with severe soil drying.

4.2 Effects of temperature and light conditions on physiological performance

Temperature and light conditions have major effects on legume physiological performance, and both factors interact strongly with water relations. Legume cover crop experiments that included jack bean (*Canavalia ensiformis*) showed that increasing light intensity significantly increased leaf, shoot, and root growth, while also increasing net assimilation rate, SPAD index, net photosynthesis, stomatal conductance, and transpiration (Baligar et al., 2020). These findings indicate that sword bean performance under different management systems will be highly sensitive to canopy light environment, especially in intercropping or shaded production settings where reduced irradiance can constrain carbon gain. Reduced light does not simply lower growth; it also changes leaf structure and biomass partitioning. Under shade, legumes developed thinner but larger leaves, had higher leaf-to-stem and leaf-to-total dry weight ratios, and accumulated more chlorophyll per unit area, yet final biomass still declined by about one-third relative to full sun. For sword bean, this suggests that shaded plants may show morphological adjustment that helps maintain light capture, but this acclimation is unlikely to fully offset losses in dry matter production where radiation is substantially limited.

Temperature stress imposes a parallel physiological burden because extreme heat alters water relations, photosynthesis, and reproductive metabolism. In legumes, high temperature increases transpiration and water loss, disturbs turgor and physiological processes, and impairs osmotic adjustment partly through damage to photosystem II, increased respiration, and reduced sugar concentrations. More generally, each legume species has specific minimum, maximum, and threshold temperatures, and extreme deviations can disrupt every stage of plant development and cause severe productivity loss. The interaction of temperature and light is especially important because hotter environments often increase evaporative demand at the same time that radiation drives canopy function. Greenhouse work on tropical perennial legumes was conducted near 30/28°C to reflect warmer tropical conditions, and the same study showed that increasing photosynthetic photon flux density improved water-use efficiency as well as nutrient-use efficiency across species (Baligar et al., 2020). This implies that sword bean physiological performance will be best when adequate radiation is matched with sufficient soil moisture, since light can promote carbon gain and efficiency, but high temperature without water supply is more likely to shift the balance toward dehydration and stress.

4.3 Adaptation mechanisms under abiotic stress conditions

Under abiotic stress, legumes activate integrated morphological, physiological, and biochemical defense systems

that help maintain cellular function but often at the cost of growth rate. Plants exposed to drought, salinity, or extreme temperatures adjust growth strategically rather than passively, and stress signaling can actively suppress anabolic activity and plant growth even before energy status collapses. For sword bean, this means that slower growth under adverse conditions should not be interpreted only as injury, but also as part of an adaptive reallocation of resources toward survival and stress resistance. A central adaptation mechanism is osmotic adjustment, in which plants accumulate solutes to maintain turgor and protect sensitive cellular processes during dehydration. Compatible solutes such as proline, soluble sugars, and other osmolytes help maintain water uptake, cell turgor, and redox balance, and across 26 studies in 12 crops osmotic adjustment was positively associated with yield under drought in 24 cases. This evidence supports the view that osmotic adjustment is not merely a survival response, but a trait with direct relevance to sustained growth and productivity under water-limited conditions.

Antioxidant defense is another key mechanism because abiotic stress commonly triggers oxidative damage through excess reactive oxygen species. Drought reduces CO₂ fixation through stomatal closure and is associated with increased ROS production, while major enzymatic antioxidants such as superoxide dismutase, catalase, ascorbate peroxidase, and glutathione reductase are central to restoring ROS homeostasis. In legumes broadly, oxidative burst, membrane instability, and metabolic disruption are early features of stress exposure, so stronger antioxidant capacity is likely to support more stable sword bean physiological performance under heat or drought (Furlan et al., 2021). Morphological escape and avoidance traits also contribute substantially to tolerance in stressed legumes. Early maturity, small leaves, deep rooting, strong remobilization under stress, and stomatal control can combine to improve drought resistance, while reduced leaf number and size, improved root system architecture, and stress-induced hormonal signaling are recognized as major tolerance traits in grain legumes (Khatun et al., 2021). Taken together, these mechanisms suggest that sword bean adaptation under different management practices will depend on combining water-conserving morphology, efficient physiological adjustment, and stress-mitigating field management to preserve growth under variable environments.

5 Effects of Cultivation Practices on Sword Bean Growth Performance

5.1 Influence of planting density and spatial arrangement

Planting density and spatial arrangement strongly influence legume growth by regulating canopy light interception, dry matter accumulation, and competition among neighboring plants (Musana et al., 2020). In soybean, higher density increased canopy light interception and dry matter accumulation and raised seed yield by 22.8%, while in common bean optimized density improved growth rate and yield by increasing light capture and reducing unnecessary competition. Uniform spatial arrangement is as important as plant number because it reduces plant-to-plant variability and improves population-level resource use (Xu et al., 2021). Soybean under uniform spacing increased seed yield by 9.5% and reduced variation in seed weight per plant by 71.5%, while faba bean evidence shows that very low density limits yield through too few plants and very high density reduces yield through pod abortion and barren stalks, indicating that sword bean should also have an optimum intermediate density rather than a simple “more plants is better” response.

Plant density also changes plant architecture, with dense stands often producing taller but less individually vigorous plants. In common bean, the highest density increased plant height, but biomass was greatest at 250,000 plants/ha and pod number per plant declined as density increased, while high-density stands can also raise risks of lodging, disease, and reduced photosynthetic efficiency under low within-canopy light (Musana et al., 2020). More detailed spacing studies show that within-row arrangement affects both vegetative growth and reproductive output. In common bean, intra-row spacing significantly altered leaf area, branch number, shoot dry weight, pods per plant, seeds per pod, and grain yield, and a 5 cm spacing gave the highest yields in the tested environments, showing that spatial precision can influence multiple components of crop performance at once (Bakure et al., 2025). For sword bean, which forms a vigorous canopy and climbing habit, these findings imply that spacing should be optimized not only for stand establishment but also for light penetration, branching pattern, and support of sustained biomass production.

5.2 Effects of tillage and soil management practices

Tillage affects legume growth mainly through its effects on soil structure, aeration, moisture, temperature, and microbial activity, all of which influence nodulation and nitrogen fixation. Conservation tillage often improves soil quality and biological processes by preserving structure and microbial diversity, but its effects on performance are not universally positive because reduced tillage can also lower pH or increase compaction under some conditions. Across legume systems, conservation tillage tends to enhance nodulation and nitrogen fixation by improving soil moisture retention and microbial biomass. Residue retention strengthens this effect by conserving soil moisture, lowering soil temperature, and improving seed emergence, suggesting that sword bean growth may benefit most where reduced tillage is combined with mulch or retained residues rather than implemented alone (Virk et al., 2024).

However, field yield responses to tillage remain context-dependent. A three-year legume experiment found that no-till gave lower average yields (2.24 t/ha) than standard tillage (2.58 t/ha) and deep tillage (2.62 t/ha), and deep tillage also reduced soil stiffness and improved seed nitrogen content. Mediterranean evidence likewise notes contradictory year-to-year responses between conventional and conservation tillage, partly because plowing can improve drainage and spring warming in poorly drained soils, which may favor early crop growth in some environments. These mixed results indicate that the best soil management system for sword bean will depend on local constraints rather than ideology. Where moisture conservation, erosion control, and long-term soil biological quality are priorities, reduced tillage is likely advantageous, but where compaction or slow warming restricts establishment, some soil loosening may still be necessary (Virk et al., 2024). This is consistent with broader rotation evidence showing that tillage interacts with residue management and soil properties, so cultivation systems should be designed as integrated packages rather than as single isolated practices (Zhao et al., 2022).

5.3 Effects of intercropping and rotation systems

Intercropping and rotation improve legume-based systems by increasing biodiversity in space or time, which enhances soil fertility, pest regulation, and input efficiency while sustaining productivity (Liu et al., 2023). In global synthesis, legume-based rotations increased the main crop yield by 20% on average, and the benefits were strongest in low-input, low-diversity systems, which is highly relevant to sword bean as a multipurpose legume suited to sustainable production (Zhao et al., 2022).

Intercropping benefits arise partly from complementary resource capture. Vertical stratification reduces competition for light and nutrients, row and strip arrangements improve sunlight interception and resource distribution, and effective spatial design can raise yields by 10%~20% in intercrop systems (Akchaya et al., 2025). A broader meta-analysis also found that cereal-grain legume intercrops had higher yield stability than sole legume crops, with lower yield variation than the respective monocultures, indicating that sword bean intercropping could improve system reliability as well as mean output.

Rotation effects are not uniform, because the identity of the legume species, background fertility, and fertilization regime all shape the strength of the legacy effect on following crops (Zhao et al., 2022). In a seven-year field experiment, legume inclusion increased subsequent wheat yield by 52% without fertilization and 26% with fertilization, while also improving yield stability, resilience, and topsoil multifunctionality, showing that legume rotations can strengthen both productivity and soil performance over time (Liu et al., 2023).

At the same time, intercrops can impose early competition if species combinations or root interactions are poorly matched. Some systems showed a 15%~20% reduction in legume shoot dry matter during early growth, which means sword bean mixtures will require careful choice of companion crop, row arrangement, and planting density (Akchaya et al., 2025). Overall, the evidence favors intercropping and rotation as effective cultivation strategies for sword bean, especially when designed to exploit complementarity, reduce external inputs, and match local soil and climate conditions (Liu et al., 2023).

6 Case Study: Evaluation of Sword Bean Growth under Integrated Management Practices

6.1 Experimental design and management treatments

A suitable case study should use a field-based comparative design that tests integrated management as a treatment package rather than as isolated inputs. In legumes, integrated crop management is defined as a site-specific combination of nutrient management, residue recycling, tillage, water management, crop diversification, varietal choice, and crop protection, and recent synthesis shows that the strongest benefits arise when rotation, conservation tillage, organic amendments, and microbiome management are combined rather than evaluated separately (Choudhary et al., 2020; Liang et al., 2025). For sword bean, this supports an experimental framework in which a control treatment is compared with several integrated packages differing in fertilizer source, irrigation regime, soil management, and cropping arrangement.

The treatment structure can be modeled on established legume experiments that compare organic, inorganic, and mixed nutrient strategies under replicated field conditions. A split-plot chickpea study used four nitrogen-management strategies-100% organic, 50:50 organic-inorganic, 75:25 organic-inorganic, and 100% inorganic RDF-with three replications, while a long-term maize-chickpea experiment tested 12 combinations of recommended NPK, FYM, poultry manure, compost, residues, and soil-test-based fertilization in a randomized complete block design. In sword bean, a comparable design could assign management packages to main plots and, where relevant, plant density or cropping system to subplots so that both main effects and interactions can be evaluated clearly.

Management treatments should also include practices beyond fertilization, because integrated performance depends on coordinated control of water, weeds, and soil physical condition. Legume reviews identify irrigation, sowing density, tillage, rhizobia application, and biostimulants as major agronomic levers affecting growth and quality, while integrated weed management remains important because weed competition can reduce legume yield by about 10-35% if not controlled during critical early growth stages (Karavidas et al., 2022). A sword bean case study is therefore strongest when nutrient treatments are paired with standardized weed control, stage-specific irrigation, and a clearly defined tillage or residue regime (Figure 2).

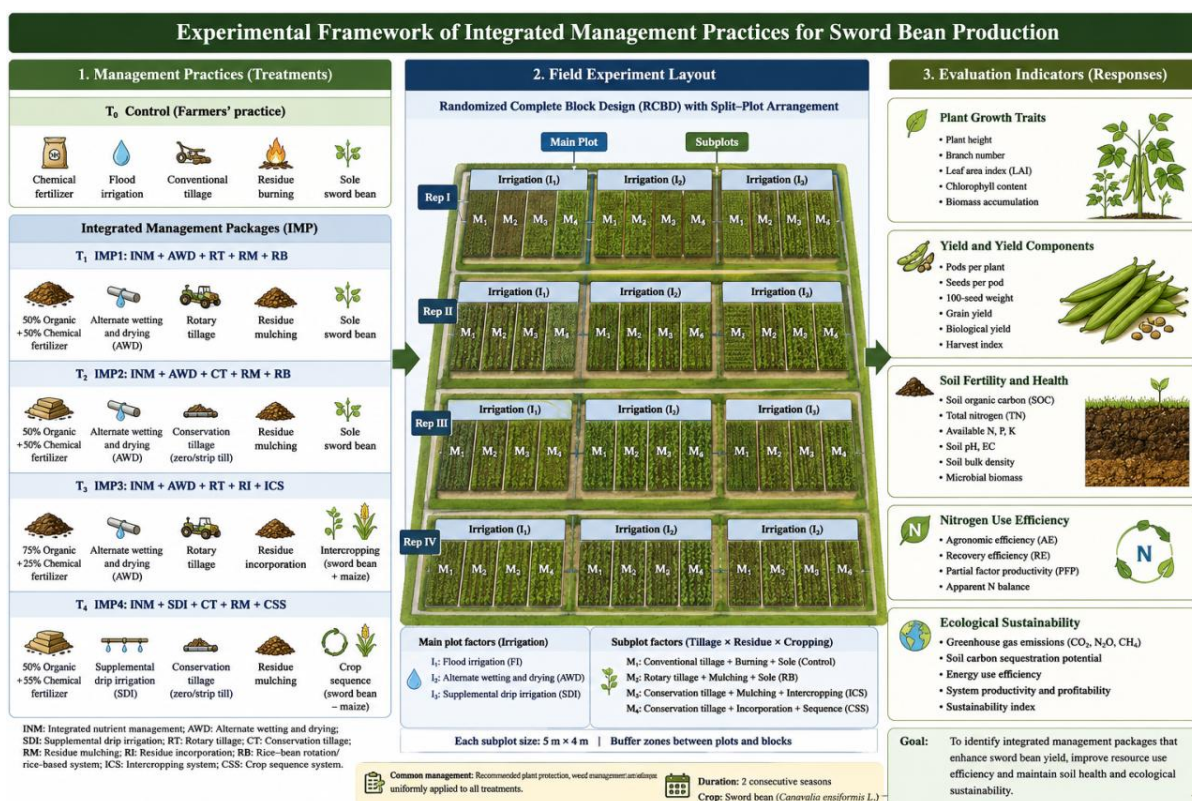


Figure 2 Experimental framework for evaluating integrated management strategies in sword bean production through combined manipulation of nutrient management, water regulation, soil practices, and cropping systems

Intercropping or rotation can be incorporated as an additional integrated-management factor where the objective

includes system productivity and resilience rather than sole-crop growth alone. Meta-analysis shows that intercropping often reduces legume grain and biomass yield relative to sole cropping but increases total land-equivalent productivity, with total LER values of 1.2-1.9, while broader review evidence shows that optimized row arrangement in legume intercrops can improve land productivity and resource-use efficiency. In a sword bean case study, this justifies comparing sole-crop sword bean with a carefully designed intercrop or rotational sequence if the aim is to assess integrated management at both crop and system level.

6.2 Effects of management practices on growth and physiological traits

Integrated management tends to improve vegetative growth and physiological vigor when balanced organic and inorganic nutrient sources are combined. In chickpea, the 50% organic plus 50% inorganic nitrogen treatment produced the highest plant height, dry matter accumulation, crop growth rate, relative growth rate, branch number, nodule number, and SPAD chlorophyll reading, outperforming both fully organic and 75: 25 treatments, and common bean reviews likewise conclude that reducing mineral nitrogen dependence through better biological fixation and stage-adjusted agronomy is central to optimizing crop performance. For sword bean, similar responses would be expected as improved nutrient synchrony promotes canopy development, chlorophyll retention, and nodulation without the inefficiencies of excessive single-source fertilization. Physiological improvements under integrated management are not limited to shoot growth, because belowground responses are equally important. Organic and inorganic nutrient combinations improve soil physical, chemical, and biological properties, which enhances nutrient availability and microbial conversion of less available forms, while biofertilizer inoculation can further stimulate nutrient supply and crop growth through rhizosphere colonization. In a sword bean experiment, these mechanisms would likely appear as stronger root development, more active nodulation, and improved nitrogen and phosphorus capture, especially where management includes microbial inoculants or residue-based amendments.

Water and soil management can further amplify these growth responses when integrated with nutrient treatments. Conservation tillage with crop-residue retention and organic manures improves macro-aggregation, soil-water storage, and bulk density, and legume intercropping systems can improve water-use efficiency by about 20-25% and nutrient-use efficiency by about 25%~30% across diverse environments (Choudhary et al., 2020; Akchaya et al., 2025). In sword bean, such conditions would be expected to support steadier physiological performance during vegetative and reproductive transition phases by buffering short-term water stress and maintaining more favorable root-zone conditions. Growth responses should still be interpreted cautiously because management effects vary with species, soil, and companion crop. A meta-analysis across smallholder legume systems found that inoculation and phosphorus application consistently increased grain and biomass yield, whereas minimum tillage showed no clear productivity effect and intercropping reduced legume biomass to varying extents depending on the associated non-legume crop. A sword bean case study should therefore analyze interactions carefully, since an integrated package that improves chlorophyll status and biomass in one soil or cropping context may not produce the same magnitude of response in another.

6.3 Impacts on yield, quality and agricultural sustainability

Integrated management usually improves yield most when nutrient supply is balanced and matched to crop demand over time. In the long-term maize-chickpea system, 75% soil-test-based NPK plus FYM at 5 Mg/ha increased mean grain yield by 20.9% in maize and 13.08% in chickpea over the general recommended dose, while broader INM evidence reports crop-yield gains ranging from 1.3% to 66.5% over conventional nutrient management across major cropping systems (Paramesh et al., 2023). For sword bean, this supports the expectation that integrated packages can improve pod and seed yield more reliably than either low-input or fully mineral-fertilizer strategies alone. Quality responses are also important because integrated nutrient supply can improve protein and nutrient accumulation rather than only total biomass. Reviews of pulse seed quality report that combining organic and inorganic nutrient sources with biofertilizer inoculation significantly increased phosphorus uptake, protein content, nitrogen, and potassium compared with other treatments, and integrated legume-management reviews identify yield and quality together as major targets of fertilization, irrigation,

inoculation, and density management (Karavidas et al., 2022). In a sword bean case study, measurements of seed protein, crude fiber, and nutrient concentration would therefore be as informative as yield alone for assessing treatment value.

The sustainability case for integrated management is stronger than the yield case alone because it includes soil health, resource efficiency, and environmental protection. Balanced organic-inorganic fertilization is widely described as the most logical strategy for sustaining long-term soil health and productivity, and integrated systems can increase crop yields by up to 15%~30% while also improving soil organic carbon and broader ecosystem services (Liang et al., 2025). In sword bean production, this means the most desirable treatment may not be the one with the absolute highest short-term yield, but the one that maintains soil function and resource-use efficiency while producing stable biomass and seed output. System-level sustainability also depends on how integrated management uses legumes to reduce external inputs and strengthen agroecosystem resilience. Legume-based systems improve soil health by reducing bulk density, increasing soil organic matter, fixing substantial atmospheric nitrogen, and reducing the need for inorganic N fertilizer, while legumes more broadly are valued because they support crop diversity, conserve resources, and fit low-input and conservation systems (Akchaya et al., 2025). Overall, a sword bean case study should evaluate integrated management not only by growth and yield, but by its capacity to deliver stable productivity, better seed quality, and more sustainable use of soil, water, and nutrient resources.

7 Advances and Future Perspectives in Sword Bean Production Management

7.1 Application of precision agriculture technologies in sword bean cultivation

Precision agriculture offers a practical pathway for improving sword bean management because it uses data-driven tools to optimize inputs while reducing resource waste and environmental impact (Mansoor et al., 2025). Across field crops, remote sensing, IoT, GIS, GPS, big-data analytics, and AI are increasingly used to monitor crop status, characterize spatial variability, and support site-specific management decisions that improve production efficiency. For sword bean, these tools are especially relevant where growth varies across fields because of uneven soil moisture, nutrient supply, or pest pressure. Recent sensor platforms suggest that sword bean cultivation could benefit from real-time monitoring of soil, canopy, and weather conditions linked to automated responses. IoT-enabled systems can integrate soil-moisture sensing, air sensing, automatic watering, pesticide application, and crop-health diagnostics, while bean-specific AI models have already shown accurate real-time discrimination between healthy and diseased leaves with lower computation time (Devi et al., 2023). More broadly, soil-moisture sensors, automated irrigation, and predictive analytics can improve water management and help forecast yield, pest outbreaks, and disease occurrence before losses become severe.

Remote sensing is likely to become one of the most useful precision tools for sword bean because it can monitor crop status across space and time without destructive sampling. Multispectral and hyperspectral imaging already support crop-health monitoring and spatially variable input application, and the fusion of spectral data with LiDAR can detect changes even within different parts of individual plants. Proximal sensing and UAV-based sensing also improve the fidelity of structural and physiological measurements by reducing environmental noise and increasing spatial resolution, which is valuable for detecting subtle stress responses in legumes (Berlingeri et al., 2025). The main future challenge is not the lack of digital tools, but their adaptation to real farm conditions and smallholder systems. Reviews of smart agriculture emphasize that broader adoption still depends on solving problems of startup cost, connectivity, data integration, real-time decision support, and farmer-friendly interfaces. For sword bean, future research should therefore move beyond technology demonstration and develop affordable, field-validated decision systems that translate sensor data into clear management recommendations for irrigation, fertilization, disease control, and planting windows.

7.2 Integration of physiological, molecular and ecological approaches

Future sword bean improvement will depend on integrating physiological understanding with molecular tools rather than treating them as separate research domains. In legumes, integrated frameworks that combine genomics, systems biology, physiology, breeding, and crop modeling are proposed as the most effective way to improve

biomass production, stress tolerance, and adaptation under climate change (Palit et al., 2020). This is especially relevant for sword bean because its growth performance is shaped by strong genotype $\times$ environment $\times$ management interactions across water, nutrient, and cropping-system conditions. Systems biology strengthens this integration by linking multiple biological layers to complex field traits. Multi-omics datasets from genomes, transcriptomes, proteomes, metabolomes, and epigenomes are now generated routinely, but they need integrated analysis and predictive modeling to explain the biological networks underlying yield and stress tolerance. A broader plant-systems perspective also argues that conventional gene-centered improvement is inadequate for multiscale stress responses, and that predictive crop design requires integrating molecular control, physiology, ecology, and biotechnology.

For sword bean breeding and management, this means selecting not only for yield potential but also for traits that function well in diversified and low-input systems. Legume breeding literature emphasizes the value of genetic variability for architecture, phenology, cycle duration, root development, stress tolerance, and symbiosis with rhizobia and mycorrhiza, all of which influence adaptation to intercropping, nutrient capture, and water use. It also argues that future ideotypes should be designed holistically across cropping systems and stakeholder needs, using models to predict performance from climate, soil, input, and management conditions. Ecological integration is equally important because crop performance depends on interactions with soils, microbes, companion crops, and climate. Legume inclusion in diversified systems supports ecosystem services linked to soil fertility, greenhouse-gas mitigation, weed and pest control, and yield stabilization, while ecological and evolutionary perspectives show that plant-microbe interactions help shape adaptive capacity along environmental gradients (Liu et al., 2023). For sword bean, future research should therefore connect physiological screening and molecular selection with ecological testing under intercropping, rotation, and climate-stress scenarios rather than relying only on isolated station trials.

7.3 Optimization strategies for sustainable sword bean production

Sustainable sword bean production will likely depend on integrated optimization rather than maximizing any single input. Reviews of legume management consistently argue for site-specific integrated crop management that combines nutrient management, residue recycling, tillage, water management, crop diversification, varietal selection, and crop protection (Choudhary et al., 2020). A broader systems perspective similarly concludes that legumes can deliver their full production and soil-health benefits only when managed through integrated system approaches rather than compartmentalized interventions. Among field-level strategies, legume-based diversification remains one of the strongest routes to sustainability. Intercropping with legumes improves soil health by reducing bulk density, erosion, and fertilizer dependence while increasing soil organic matter and biological nitrogen fixation, and it can raise yield by 30%~35%, water-use efficiency by 20%~25%, and nutrient-use efficiency by 25%~30% (Akchaya et al., 2025). Long-term rotation studies likewise show that legume-based systems increase soil nutrients, microbial activity, and profitability, with some systems producing 68.97% higher rice-equivalent yield than conventional cereal systems.

Optimization will also require better design of mixed and diversified cropping systems rather than simply adding sword bean to existing rotations. Mixed cropping studies show that seeding ratio and canopy structure strongly affect dry matter yield, crude protein yield, water-use efficiency, radiation-use efficiency, and land-equivalent ratio, with intermediate mixture designs sometimes performing best. On-farm system-optimization studies further show that legume inclusion under zero tillage, residue retention, and improved management can reduce water use and global warming potential while increasing grain yield, energy-use efficiency, and net returns (Radheshyam et al., 2025). The future perspective for sword bean is therefore not only higher yield, but resilient multifunctionality across productivity, quality, soil restoration, and environmental performance. Legume-based systems can maintain crop yields while reducing external inputs and strengthening ecosystem services, but region-specific research and tailored management remain necessary because species choice and local conditions strongly influence outcomes (Liu et al., 2023). Overall, the most promising path for sword bean production is the combination of digital monitoring, systems-level trait integration, and site-specific diversified management that improves growth while sustaining soil, water, and agroecosystem health.

8 Conclusions

Sword bean shows broad agronomic potential because it combines favorable tropical adaptation with comparatively high yield potential among underutilized legumes. Its growth pattern is vigorous but relatively long, with a vegetative phase of about 4-5 months and pod maturation often extending another 5-6 months or more, so management effects accumulate across a long crop cycle. Nitrogen management improves quality more consistently than biomass, since urea treatments produced similar forage yields but altered crude protein and crude fiber, and the 50 kg/ha treatment was considered efficient while preserving rhizobial function. Phosphorus management is more decisive for reproduction, because P fertilization increased yield on acid upland soil, whereas crops without P formed pods but failed to produce seed.

Growth responses also depend strongly on biological and environmental management. VAM inoculation increased nitrogen uptake in sword bean leaves and interacted with rock phosphate to influence phosphorus uptake, showing that nutrient efficiency depends partly on symbiosis rather than fertilizer dose alone. Climatic adaptation is equally important, because under Western Poland conditions only the early cultivar produced viable seed, while the late cultivar remained immature, indicating strong sensitivity to temperature and season length. Field emergence above 60% under those conditions still showed that the crop can establish outside its usual range, but weather remained a crucial determinant of flowering and seed filling. Genotypic diversity adds another management opportunity, since evaluation of 20 native genotypes revealed variation in germination time, pod size, pod weight, and seed weight that breeders can exploit for local adaptation.

The main implication for productivity is that sword bean should be managed as a resource-efficient legume, not as a crop that simply requires high mineral inputs. Evidence from sword bean shows that moderate nitrogen can maintain forage quality efficiently, while broader legume evidence indicates that inclusion of legumes in cropping systems can reduce dependence on synthetic nitrogen through biological fixation. This makes phosphorus availability, root activity, and microbial functioning particularly important targets for management improvement on marginal or acidic soils. In practical terms, productivity gains are likely to come from combining moderate fertilization with inoculation, moisture support, and suitable cultivars rather than from maximizing one input alone.

Productivity improvement also depends on matching sword bean to systems where its ecological functions create added value. The crop grows well in poor or marginal soils and has potential as food, feed, and green-manure material, so its performance should be evaluated at both crop and system level. Reviews of legume intercropping show gains in land productivity, soil health, water-use efficiency, and nutrient-use efficiency, which suggests that sword bean can contribute more through diversified systems than through isolated monoculture evaluation alone. This system perspective is especially relevant for underutilized legumes, whose commercial value often depends on multiple outputs such as seed, forage, soil improvement, and resilience under low-input conditions. Accordingly, improving sword bean productivity means increasing not only yield per hectare, but also stability, nutritional value, and contribution to agroecosystem function.

Future work should focus first on locally adapted agronomic packages for sword bean, because available studies still show large knowledge gaps in cultivation technology, especially for marginal soils and nontraditional environments. Region-specific recommendations are needed for spacing, sowing time, water management, phosphorus strategy, and integrated nutrient use, since sustainability outcomes in legume systems depend strongly on local climate, soil conditions, and field management. Longer-term studies should also test sword bean in intercrops and rotations, because legume-based systems improve soil structure, microbial activity, nutrient cycling, and resilience, but adoption still depends on practical design and economic feasibility. In that context, sword bean is a strong candidate for sustainable intensification because it fits low-input production goals while contributing protein and soil-restorative functions.

A second priority is genetic and physiological improvement linked directly to management needs. Sword bean genotypes already differ substantially in germination and pod traits, and related *Canavalia* improvement studies

show that growth rate, net assimilation rate, and forage yield can be increased through selection and introgression. Mutation-based studies in *Canavalia* also indicate that plant height, leaf area, and dry seed weight can be altered experimentally, although ideal trait combinations remain unresolved. At the same time, sustainable breeding must address anti-nutritional factors, local adaptation, and compatibility with diversified cropping systems rather than pursuing yield alone. Overall, future sustainable cultivation systems for sword bean should integrate adaptive genetics, moderate-input agronomy, and diversified legume-based farming to improve growth performance, productivity, and long-term soil health.

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The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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Review Article

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Dynamic Changes in Protein and Oil Contents during Soybean Seed Development

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Abstract Soybean (*Glycine max* L.) is one of the most important global crops, serving as a primary source of plant-based protein and vegetable oil for food, feed, and industrial applications. The accumulation of storage proteins and oils during seed development is a highly dynamic physiological process regulated by genetic programs, metabolic pathways, and environmental conditions. Understanding the temporal patterns and regulatory mechanisms of protein and oil deposition is essential for improving soybean nutritional quality and optimizing breeding strategies. This review systematically summarizes the dynamic changes in protein and oil contents throughout soybean seed development, with emphasis on developmental stages, physiological regulation, and molecular mechanisms underlying storage compound accumulation. During seed filling, protein accumulation is primarily controlled by nitrogen assimilation, amino acid transport, and storage protein biosynthesis, whereas oil accumulation depends on carbon metabolism, fatty acid synthesis, and triacylglycerol assembly. The interaction between carbon and nitrogen metabolism determines the balance between protein and oil contents, resulting in a complex trade-off relationship that influences soybean quality formation. Furthermore, this review discusses the effects of environmental factors, including temperature, water availability, and nutrient management, on seed composition dynamics. Recent advances in multi-omics technologies, high-throughput phenotyping, and machine learning approaches have provided new insights into the prediction and regulation of soybean seed quality. A case study is presented to illustrate how genotype-environment interactions influence protein and oil accumulation patterns under contrasting cultivation conditions. Finally, future perspectives are proposed, focusing on integrating molecular breeding, precision agriculture, and digital technologies to achieve coordinated improvement of soybean yield, protein content, and oil quality. This comprehensive understanding of dynamic storage compound accumulation provides a theoretical foundation for developing high-quality soybean varieties and sustainable production systems.

Keywords Soybean seed development; Protein accumulation; Oil biosynthesis; Carbon-nitrogen metabolism; Seed quality regulation

1 Introduction

Soybean (*Glycine max* L. Merr.) is one of the world's most important crops because it provides both edible oil and high-quality vegetable protein at a scale that strongly influences global food systems and agricultural markets (Messina, 2022). Its seeds typically contain about 18%-22% oil and 36%-42% protein, making soybean unusual among major crops in combining high energy density with substantial protein yield in a single commodity. This dual value underpins its broad use in human foods, animal feed, and industrial applications, including biodiesel and a wide range of processed products (Hamza et al., 2024). Soybean also occupies a strategic position in efforts to improve the sustainability of protein and oil supply, because demand for vegetable oils and plant-derived proteins continues to rise globally. For these reasons, improving soybean seed composition is not only a breeding objective but also an important challenge for food security, industrial raw material supply, and the design of more efficient crop systems (Duan et al., 2023).

The biological importance of soybean seed protein and oil accumulation lies in their central roles as the principal storage reserves that support germination, early seedling growth, and final seed quality. In mature soybean seed, protein and oil together account for almost 60% of total storage matter, and their composition is closely tied to seed size, nutritional value, and commercial worth (Duan et al., 2023). These reserves do not accumulate

randomly; rather, they reflect tightly coordinated developmental programs involving carbon and nitrogen allocation, fatty acid and triacylglycerol biosynthesis, and synthesis of major storage proteins such as β -conglycinin and glycinin. At the same time, oil and protein accumulation are linked by a persistent inverse relationship, indicating competition for shared metabolic precursors during seed development (Niu et al., 2025). Understanding when and how this trade-off is established is therefore essential for clarifying seed developmental physiology and for identifying routes to improve both traits simultaneously.

Research on soybean seed composition dynamics has shown that protein and oil contents change substantially over the course of development rather than appearing only as fixed mature-seed traits (Kambhampati et al., 2021). Early work established that oil percentage rises rapidly during mid-development, while large proportions of total mature protein and oil are synthesized during later filling stages even after percentage values begin to stabilize. Subsequent studies refined this developmental picture by showing that protein content often declines during the first weeks after flowering and then increases gradually, whereas oil accumulates rapidly at earlier stages, and sugars and oligosaccharides follow distinct temporal patterns toward maturity. Stage-based analyses further demonstrated that between reproductive stages R5 and R7, most mature dry weight is accumulated together with marked increases in protein, oil, and sugars, while after R7 moisture declines rapidly and stored-component composition changes relatively little. Collectively, these findings indicate that developmental timing is a major determinant of final seed composition and that the kinetics of reserve deposition must be considered explicitly in studies of soybean quality formation.

Despite substantial progress, important knowledge gaps remain in understanding the regulatory basis of dynamic protein and oil accumulation in soybean seeds. Recent genomic and transcriptomic studies have greatly expanded knowledge of the enzymes, transcription factors, and co-expression modules associated with reserve biosynthesis, especially during late developmental stages when divergence between high-oil and high-protein genotypes becomes most pronounced. Evidence now suggests that late maturation involves antagonistic activation of lipid-centered and nitrogen-centered pathways, providing a systems-level explanation for the oil-protein trade-off (Niu et al., 2025). However, many genetically mapped loci remain functionally unresolved, only a small number of candidate genes have been validated, and technical limitations in soybean transformation continue to slow mechanistic testing of proposed regulators (Duan et al., 2023). In addition, metabolic studies show that mature-seed composition can obscure important temporal shifts, including lipid decline and carbohydrate redistribution during maturation, meaning that endpoint measurements alone are insufficient to explain how seed composition is formed (Kambhampati et al., 2021). Accordingly, a focused analysis of dynamic changes in protein and oil contents during soybean seed development remains necessary to connect developmental stage, metabolic flux, and regulatory control, and to support breeding strategies aimed at improving seed quality without reinforcing the traditional trade-off between these two economically critical reserves.

2 Developmental Stages of Soybean Seeds and Physiological Regulation of Storage Compound Accumulation

2.1 Morphological and physiological characteristics during soybean seed development

Soybean seed development is commonly divided into lag, seed-filling, and maturation phases, and these phases can also be resolved morphologically from cotyledon formation through early maturity, mid-maturity, late maturity, and dry seed stages. Across these stages, seeds enlarge progressively, attain maximum size before desiccation, and then lose water rapidly as they approach physiological maturity, making morphology and water status reliable indicators of developmental progression. Physiologically, the major increase in seed mass and reserve deposition occurs mainly between R5 and R7, when moisture declines gradually but dry weight, protein, oil, and sugars all rise sharply. Cell division is largely completed by R4, whereas the pronounced increase in seed size from R5 to R6 is driven primarily by cell enlargement, during which carbon is partitioned simultaneously into protein, oil, and carbohydrate reserves (Islam et al., 2021).

2.2 Dynamic patterns of protein accumulation during seed development

Protein accumulation during soybean seed development is temporally regulated rather than continuous. Early stages contain relatively higher proportions of low-molecular-weight or nonstorage proteins, whereas the major storage proteins accumulate later as seeds enter active filling and maturation; correspondingly, storage-protein transcripts appear before visible protein deposition, indicating transcriptional control ahead of bulk reserve accumulation. The dominant storage fractions are 7S globulins and 11S glycinin, and their accumulation generally intensifies from mid seed filling toward late filling or maturation, although individual subunits differ in timing. More recent proteomic and compositional studies further show that 7S β -subunit and several 11S glycinin subunits increase steadily across filling stages, globulins remain higher than albumins throughout development, and globulin accumulation often peaks around R6 rather than rising linearly to maturity (Islam et al., 2021; Montanha et al., 2023).

2.3 Dynamic patterns of oil accumulation during seed development

Oil accumulation also shows a marked developmental pattern, beginning later than residual carbohydrate deposition and increasing rapidly during seed filling. A water-relations analysis indicated that residual accumulation starts first, followed by protein and then oil, while classical compositional studies showed that oil percentage rises sharply from about 24 to 40 days after flowering before stabilizing later in development. This rapid lipid deposition is supported by coordinated metabolic reprogramming during developing seed filling. Genes involved in carbon fixation, photosynthesis, glycolysis, and fatty acid biosynthesis are up-regulated during the critical period of oil accumulation, and later developmental transitions are associated with strong activation of carbohydrate degradation, triacylglycerol biosynthesis, and phospholipid signaling pathways, consistent with intensified flux toward storage lipid production in the late filling stages (Niu et al., 2025). Soybean seed development therefore involves a tightly staged transition from morphogenesis to reserve filling and finally desiccation, with protein and oil accumulation following distinct but overlapping temporal programs shaped by developmental state, carbon-nitrogen partitioning, and late-stage metabolic regulation.

3 Molecular Mechanisms Regulating Protein and Oil Biosynthesis in Developing Soybean Seeds

3.1 Genetic regulation of storage protein biosynthesis

Storage protein biosynthesis in developing soybean seeds is controlled by a hierarchical genetic program that integrates seed maturation regulators with structural genes encoding the major storage proteins. The principal storage proteins are β -conglycinin (7S) and glycinin (11S), and their accumulation is regulated not only by the expression of their own gene families but also by upstream AFL-type regulators, including LEC1, LEC2, FUS3, and ABI3, that coordinate the broader maturation state required for reserve deposition (Qi et al., 2026). Genetic mapping further shows that variation in storage protein composition is polygenic, with multiple loci affecting glycinin, β -conglycinin, total storage protein subunits, and the glycinin: β -conglycinin ratio, while polymorphism in the Gy1 promoter is specifically associated with 11S glycinin content (Zhang et al., 2021).

Recent transcriptomic and functional studies indicate that protein accumulation is also regulated through networks linking hormone signaling, nitrogen allocation, and storage protein processing. In contrasting soybean genotypes, candidate pathways associated with seed protein metabolism include photosynthesis, the TCA cycle, and starch and sucrose metabolism, and 40 days after flowering appears to be a critical stage for protein accumulation (Hu et al., 2025). At the gene level, *GmGASA12* acts as a molecular hub: its knockout increases water-soluble protein content, upregulates amino acid transporters and storage protein genes, and modulates the cooperative biosynthesis of β -conglycinin and glycinin through interaction with GmCG-6 (Yang et al., 2025).

3.2 Molecular regulation of oil biosynthesis and fatty acid metabolism

Oil biosynthesis in developing soybean seeds is governed by transcriptional circuits that channel carbon into fatty acid synthesis in plastids and triacylglycerol assembly in the endoplasmic reticulum. WRINKLED1 is a central regulator of this process, directly controlling numerous genes involved in lipid biosynthesis and participating in a positive feedback relationship with LEC1 that promotes the onset and stability of the fatty acid and TAG

accumulation program during seed maturation (Jo et al., 2024). Consistent with this framework, transcriptomic analyses of developing seeds show that rapid oil accumulation is accompanied by coordinated upregulation of carbon fixation, photosynthesis, glycolysis, and fatty acid biosynthesis pathways, indicating that lipid deposition depends on integrated activation of precursor supply and biosynthetic capacity.

Beyond the LEC1-WRI1 axis, soybean oil accumulation is fine-tuned by additional transcription factors and downstream metabolic enzymes. GmZF392 functions as a positive regulator of lipid production by activating lipid biosynthesis genes, acts synergistically with GmZF351, and is positioned downstream of GmNFYA within a three-factor regulatory module that enhances seed oil accumulation (Lu et al., 2021). A second layer of control involves protein-protein cooperation, as GmVOZ1A interacts with GmWRI1a, jointly upregulates GmACBP6a, and thereby promotes TAG accumulation, while broader network analyses in cultivated soybean also identify a BCCP2-SAD-FAD2-OBO/FA9 axis and a PLIP1-dependent pathway linked to enhanced oil biosynthesis (Yang et al., 2024; Niu et al., 2026).

3.3 Coordination between carbon and nitrogen metabolism

The balance between protein and oil accumulation in soybean seeds is shaped by competition for shared carbon skeletons and by developmental regulation of nitrogen assimilation. Sucrose imported into developing seeds is metabolized through glycolysis to produce intermediates such as acetyl-CoA and phosphoenolpyruvate, which support both fatty acid and amino acid biosynthesis, making carbon allocation a central determinant of storage compound partitioning (Qi et al., 2026). This shared metabolic dependence helps explain the widely observed inverse relationship between seed oil and protein, which reflects repartitioning among protein, lipid, and carbohydrate reserves rather than simple independent accumulation of each component (Qi et al., 2026).

Evidence from multi-omics, physiology, and transporter genetics shows that this trade-off is dynamically regulated late in seed development. High-oil and high-protein cultivars diverge mainly during later maturation, when lipid-centric pathways such as TAG synthesis and oil body biogenesis are antagonistically activated against nitrogen-centric pathways including nitrogen assimilation, amino acid metabolism, ABA signaling, and storage protein processing (Niu et al., 2025). Experimental manipulation of maternal carbon supply supports this model: reduced sugar delivery to embryos through disruption of *GmSWEET10a/b* or *GmSUT1* lowers expression of sucrose metabolism, fatty acid biosynthesis, and TAG assembly genes while inducing storage protein genes, shifting final seed composition toward lower oil and higher protein (Sun et al., 2025). In developing soybean seeds, protein and oil biosynthesis are therefore regulated by distinct but interconnected genetic programs, with storage protein accumulation tied closely to maturation and nitrogen-responsive networks, oil accumulation driven by LEC1/WRI1-centered lipid circuits, and the final balance between the two determined by developmental carbon-nitrogen partitioning.

4 Environmental and Agronomic Factors Affecting Protein and Oil Accumulation Dynamics

4.1 Effects of temperature and climate conditions

Temperature during seed filling strongly shifts the balance between soybean seed protein and oil accumulation, although the response is not strictly linear across environments. Meta-analysis indicates that high temperature generally increases final protein concentration, but this increase does not reflect greater absolute protein synthesis; instead, it arises because other seed fractions, especially oil, are reduced more strongly during stressful filling conditions. Controlled-environment studies are consistent with this pattern, showing that exposure to 35°C during seed fill increased seed protein by 4.0 percentage points and decreased oil by 2.6 percentage points relative to 29°C (Figure 1) (Sun et al., 2025).

The climatic control of composition is also modified by the broader thermal regime and by interactions among multiple weather variables. Large-scale sampling in China showed that crude protein was positively associated with accumulated and mean temperature, whereas crude oil showed the opposite trend overall, but oil increased with mean daily temperature when temperatures remained below 19.7°C, indicating a threshold response rather than a simple monotonic one. Developmental analyses likewise showed that high temperature accelerated maturity,

advanced the timing of maximum oil concentration, and increased the rate of late-stage protein accumulation, whereas low temperature prolonged seed growth but reduced growth rate, demonstrating that climate alters both the rate and timing of reserve deposition.

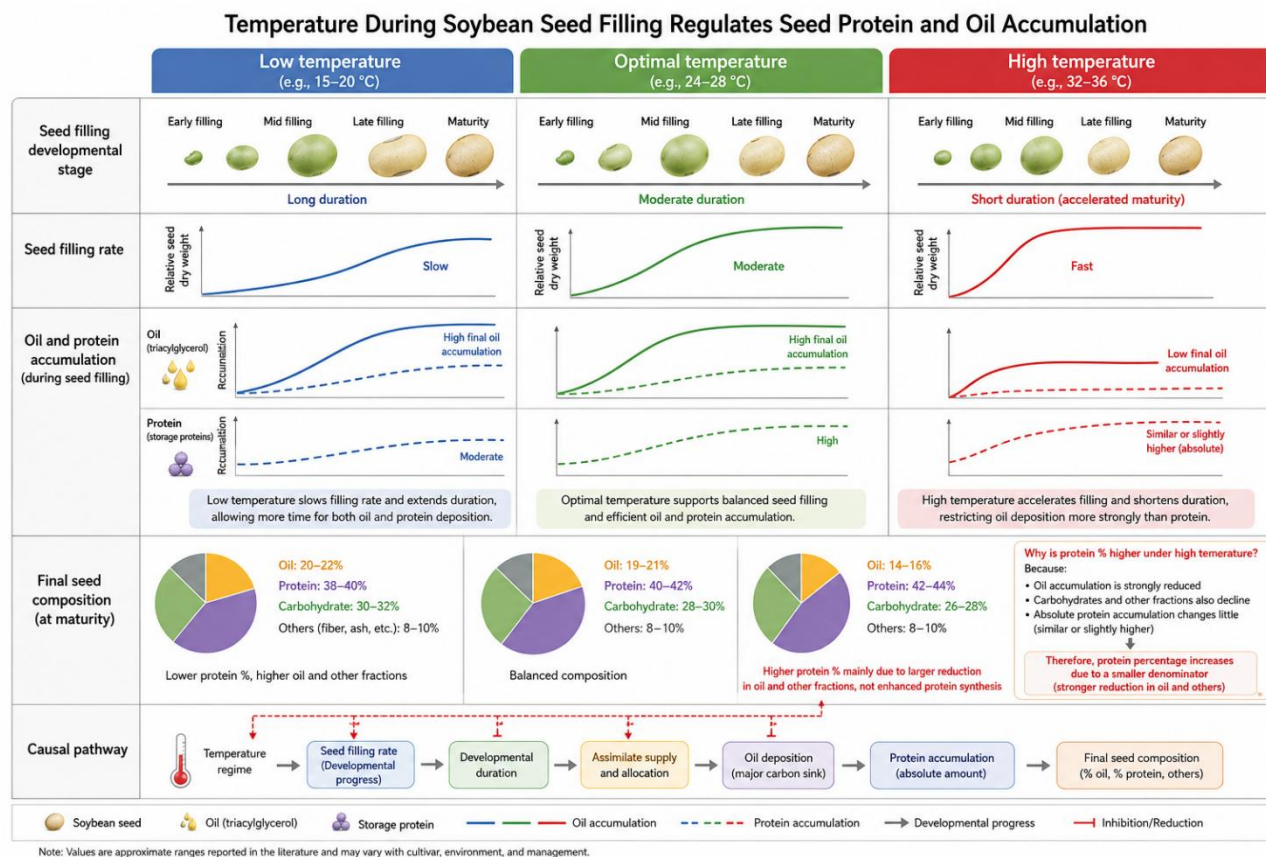


Figure 1 Conceptual framework illustrating the effects of temperature during soybean seed filling on protein and oil accumulation

4.2 Effects of water availability and drought stress

Water limitation during seed development alters both final composition and the temporal pattern of reserve accumulation, but its effect depends strongly on the developmental stage at which stress occurs. A broad meta-analysis found that water stress reduced the absolute content of protein, oil, and residual fractions per seed, yet protein accumulation was less affected than oil accumulation, leading to a higher final protein concentration on a dry-weight basis (Mo et al., 2024). Complementing this general result, mechanistic work showed that drought can change both the rates and durations of component accumulation while maintaining overall seed growth rate, with compensation typically favoring protein because late seed filling can rely more on remobilizable nitrogen whereas oil synthesis depends more heavily on current photosynthesis.

Field studies show that reproductive-stage drought is particularly important for soybean quality because it shifts partitioning away from oil and toward protein while simultaneously reducing yield. In Brazil, water deficit imposed during the reproductive stage consistently produced higher protein and lower oil contents across genotypes, whereas vegetative-stage stress had much weaker compositional effects. However, drought does not act independently of temperature: analyses from Argentine multi-environment trials showed that under stronger water deficit, oil concentration increased with increasing mean temperature whereas protein still increased with temperature but decreased with water deficit, underscoring that climate effects on seed composition should be interpreted as joint heat-water responses rather than isolated factors.

4.3 Effects of nutrient management and cultivation practices

Among agronomic factors, nutrient supply-especially nitrogen-has the most consistent documented effect on seed composition, because nitrogen availability during seed filling directly constrains protein deposition. Across a large

U.S. synthesis, low to moderate fertilizer N inputs increased both protein and oil concentration, although environmental variation still explained most of the total variation in composition. Field experiments in high-yield environments similarly showed that full-season nitrogen supply increased seed protein concentration without increasing oil concentration, while raising both protein and oil yields through higher seed production, indicating that N limitation can restrict both composition and total reserve output.

Management effects beyond nitrogen are real but less uniform, and they often interact with water regime, latitude, and cropping system. Recent field studies showed that late-season N application during seed filling increased protein concentration by 1.2-2.8% with little or no effect on oil concentration, supporting targeted N management as a practical strategy for improving meal quality (Khatri et al., 2026). By contrast, broader management syntheses indicate that delayed planting decreases oil concentration, corn-soybean rotation tends to improve composition and yield, and practices such as no-till, seed treatment, foliar nutrient application, and fungicide produce mixed responses, showing that cultivation practices mainly modify composition indirectly through their effects on crop growth environment and stress exposure.

5 Advanced Technologies for Monitoring and Predicting Protein and Oil Dynamics

5.1 Biochemical and omics approaches for understanding seed composition

Biochemical and omics approaches have become the main tools for dissecting how protein and oil contents change during soybean seed development because they capture regulatory variation across transcripts, proteins, and metabolites rather than only final composition. Integrated transcriptomic, proteomic, and metabolomic studies show that the pathways most consistently linked to protein and oil divergence involve glycolysis and carbon metabolism, while systems-level analyses further indicate that metabolic flux mapping during seed fill is especially useful for connecting developmental gene expression with the biochemical networks that determine mature seed composition (Mo et al., 2024). These datasets also reveal that different omics layers contribute distinct kinds of information, which is important for interpreting developmental dynamics. Joint transcriptome-proteome analysis identified generally poor correspondence between mRNA and protein abundance, while metabolomics studies in contrasting high-protein and high-oil lines detected coordinated shifts in the Calvin cycle, TCA cycle, and glycolysis that favor routing carbon into amino acid and fatty acid synthesis (Mo et al., 2024; Cui et al., 2025).

Proteomics has been particularly valuable for defining the temporal sequence of storage reserve accumulation during seed filling. High-resolution proteome mapping across 2 to 6 weeks after flowering showed a developmental decrease in metabolism-related proteins together with an increase in proteins associated with destination and storage, and more recent TMT-based proteomics further demonstrated that major 7S and 11S storage proteins accumulate steadily from early to late seed filling (Islam et al., 2021). At a broader scale, integrative omics has strengthened gene discovery for seed quality improvement by linking developmental expression patterns to inherited composition loci. Meta-analysis and time-course transcriptomics identified 11 shared meta-QTL hot regions for oil and protein and seven hub genes associated with storage accumulation, while multi-omics comparison among contrasting cultivars detected 22 candidate genes with potential simultaneous negative regulation of protein and oil content (Mo et al., 2024).

5.2 Imaging and phenotyping technologies for seed development monitoring

Non-destructive imaging technologies now allow soybean seed composition and developmental status to be monitored at the single-seed level, which is a major advance over destructive wet-chemistry assays. Near-infrared hyperspectral imaging predicted single-seed protein content with $R^2 = 0.92$ and RMSE of 1.08%, and it also generated chemical maps that visualized within-seed protein distribution for rapid screening of large numbers of samples (Aulia et al., 2022). Hyperspectral approaches are also effective for monitoring oil quality traits that contribute to overall lipid dynamics during development and selection. Reflective hyperspectral imaging classified oleic and linoleic acid contents of single seeds with validation accuracies of 90% and 93.3%, and the study emphasized that single-seed measurement is critical because bulk-seed spectroscopy cannot resolve the composition of individual seeds needed for precision breeding (Fu et al., 2021).

Imaging-based phenotyping is not limited to chemical traits, because seed architecture and visible phenotype can be quantified at scales that support genetic analysis and breeding decisions. High-throughput image analysis measured approximately 39 065 seeds from 400 lines for morphology and color traits, and the resulting quantitative phenotype data were proposed as useful inputs for GWAS and other gene-discovery efforts (Baek et al., 2020). More broadly, soybean seed monitoring increasingly draws on complementary sensor platforms rather than any single imaging modality. Reviews of soybean seed imaging identify radiography, magnetic resonance imaging, multispectral imaging, chlorophyll fluorescence imaging, infrared thermography, and computerized seedling analysis as viable tools for detecting incomplete maturation, structural injury, and other quality-related changes, while RGB image-based phenotyping has emerged as a practical, lower-cost route for capturing seed traits at phenome scale (Duc et al., 2023; França-Silva et al., 2023).

5.3 Machine learning and modeling approaches for predicting seed quality

Machine learning approaches now make it possible to predict soybean seed protein and oil before harvest by combining field observations with spectral or environmental data. In on-farm prediction using satellite imagery, XGBoost outperformed other algorithms and achieved absolute errors of 1.80% for protein and 1.04% for oil, with the best model timing occurring within one week after the peak of the green chlorophyll vegetation index (Hernández et al., 2023). Deep learning has also shown that time-series crop imagery can recover useful reproductive-stage signals for seed composition, although performance remains trait-dependent. Using PlanetScope imagery, recurrent neural network models identified later reproductive-stage vegetation indices as the most informative features, and the GRU model achieved the best reported performance in that study for protein and oil prediction from standing crops (Sarkar et al., 2023).

For breeding applications, prediction models are moving beyond field-level remote sensing toward integrated genomic, phenomic, and environmental frameworks. Comparative prediction studies found that phenomic prediction outperformed genomic prediction for seed yield, whereas genomic prediction performed better for seed protein and oil, and larger deep-learning frameworks using multi-decadal weather plus genotype and management information showed that pretrained temporal representations from yield data could be transferred to downstream oil and protein prediction tasks (Van Der Laan et al., 2024). An important recent trend is the emphasis on interpretability and efficient feature selection, because predictive accuracy alone is not sufficient for biological insight or breeding utility. In genomic prediction across 1 110 accessions, XGBoost or random forest outperformed deep learning for 13 of 14 prediction tasks and enabled up to 90% marker reduction without loss of performance, while Transformer-based models highlighted influential periods and variables during the growing season through self-attention, improving explainability for seed composition prediction (Gill et al., 2022; Ayanlade et al., 2026).

6 Case Study: Dynamic Changes in Protein and Oil Accumulation under Different Genotypes and Environmental Conditions

6.1 Comparative analysis of protein and oil accumulation among soybean varieties

Comparative studies consistently show that soybean genotypes differ not only in final seed composition but also in the trajectory of reserve deposition during development. In a direct developmental comparison, the high-protein cultivar NPS233 accumulated more protein and less oil than the high-oil cultivar NPS301 at all four sampled stages from 7 to 28 days after flowering, while a broader study of seven specialty genotypes found that although developmental trends were partly shared, substantial genotype-specific differences in protein and oil composition remained evident throughout seed maturation (Xu et al., 2022). This variation extends across diverse germplasm: in 320 resequenced accessions, protein ranged from 37.8% to 46.5% and oil from 16.7% to 22.6%, confirming that soybean varieties span a wide compositional spectrum that provides a practical basis for selecting contrasting developmental phenotypes (Jin et al., 2023).

Genotypic divergence also reflects distinct physiological and molecular allocation strategies rather than simple differences in endpoint composition. Transcriptomic analysis across two high-oil and two high-protein cultivars showed that transcriptional divergence was concentrated in late maturation, when high-oil genotypes activated

lipid-centered pathways and high-protein genotypes activated nitrogen-centered pathways, whereas proteomic comparison of two contrasting varieties indicated that compositional differences were driven mainly by the peripheral proteome, which changed strongly across developmental stages (Huang et al., 2025; Niu et al., 2025). Importantly, this trade-off is not absolute in all materials: under heat and drought stress, several high-protein lines maintained 46%-55% protein, and two lines showed no apparent negative relationship between seed protein and oil contents, indicating that some varieties partially escape the usual antagonism between these traits (Figure 2) (Kakati et al., 2024).

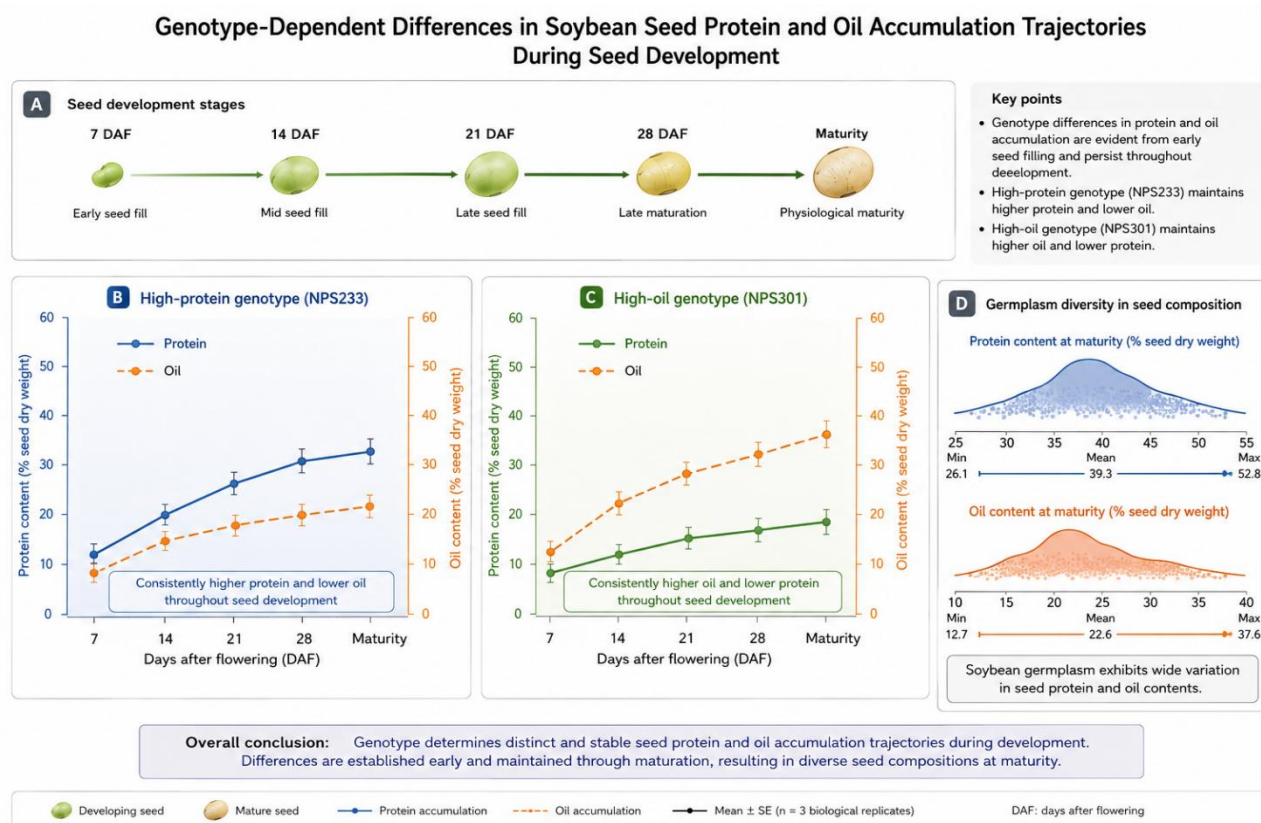


Figure 2 Developmental trajectories of seed protein and oil accumulation in contrasting soybean genotypes

6.2 Effects of environmental stress on seed composition dynamics: a case study

Environmental stress alters the rate and balance of storage compound accumulation, but the direction and magnitude of change depend on the stress scenario and genotype. A meta-analysis found that water stress reduced the absolute accumulation of protein, oil, and residual fractions per seed, yet protein was less affected than oil, which increased final protein concentration on a dry-weight basis; similarly, controlled experiments showed that severe drought increased protein by 4.4 percentage points and decreased oil by 2.9 percentage points during seed fill. Temperature acts in a comparable but not identical way, because high temperature also tends to raise protein concentration without increasing protein synthesis per se, indicating that stress often changes composition through differential suppression of reserve classes rather than through direct stimulation of protein deposition.

Case studies across multiple environments show that these responses are strongly modified by genotype × environment interaction. In Croatia, 32 elite genotypes grown across six dry and eight normal environments showed significant effects of genotype, environment, and their interaction for both traits; drought decreased mean protein by 4.5% and slightly increased oil by 1.2%, and the usual negative protein-oil correlation seen in normal environments disappeared under dry conditions. At larger scale, U.S. synthesis-analysis showed that environment accounted for more than 70% of the variation in seed composition, while management-induced environmental shifts such as delayed planting reduced oil concentration, reinforcing that stress effects on accumulation dynamics emerge from the combined action of weather, timing, and genotype rather than from a single factor alone.

6.3 Integrating multi-omics and phenotyping data to explain seed quality formation

Integrated omics studies now explain varietal differences in seed quality formation by linking developmental phenotypes to coordinated changes in transcripts, metabolites, and candidate regulators. In two contrasting cultivars, combined transcriptomics and metabolomics identified more than 12,000 differentially expressed genes and 315 differential metabolites across seed development, and the authors proposed that high-protein varieties differ from high-oil types through altered sensitivity to desiccation, photomorphogenesis, and senescence timing; in a separate nine-cultivar multi-omics study, more than 1,000 differential metabolites and 7 000 differentially expressed genes were used to define 10 core genes associated with oil content, with *GmADH1* and *GmCrRLK1L34* emerging as hub regulators (Xu et al., 2022). These integrative datasets also converge on central metabolism, because metabolomic analysis of extreme high- and low-protein/oil lines showed enhanced Calvin cycle, TCA cycle, and glycolytic activity that supports carbon entry into amino acid and fatty acid synthesis, helping explain how developmental resource partitioning generates contrasting seed compositions (Cui et al., 2025).

High-resolution phenotyping adds spatial and quantitative context that bulk omics alone cannot provide. In wild soybean, spatial transcriptomics, spatial metabolomics, and single-cell RNA sequencing at mid-maturity showed tissue-level separation between protein- and lipid-associated metabolism and identified *GsMAPK23-4* as a candidate regulator of seed quality, while FT-NIR phenotyping across 191 diverse accessions produced highly accurate protein and oil prediction models with R^2 values above 95%, enabling rapid compositional screening across maturity groups and seed phenotypes. Genetic integration strengthens this framework further: QTL mapping, BSA-seq, and RNA-seq identified 37 QTLs and 12 preliminarily validated candidate genes for protein and oil, showing that multi-omics and phenotyping together can move from descriptive developmental patterns to testable loci and breeding targets (Fang et al., 2025).

7 Breeding Strategies and Future Perspectives for Improving Soybean Protein and Oil Quality

7.1 Genetic improvement of soybean protein and oil traits

Genetic improvement of soybean protein and oil traits still depends on treating these characters as complex quantitative phenotypes shaped by many loci and strong genotype $\times$ environment interaction. QTL mapping, GWAS, and meta-QTL analysis have repeatedly identified stable genomic regions for both traits, and the narrower intervals produced by GWAS now make marker-assisted allele selection more practical for predictable compositional improvement (Kumar et al., 2021).

Breeding strategies are also shifting from locus discovery alone to predictive and design-based selection. Genomic selection achieved cross-validation accuracies of 0.68 for protein and 0.64 for oil, indicating that breeders can identify many top-quartile composition lines before extensive phenotyping (Miller et al., 2023). At the same time, integrative genetics shows that some quality traits can be improved together rather than traded off absolutely, because seed weight and oil content share a positive genetic correlation and candidate genes such as *GmRWOS1* have already been functionally validated for coordinated trait regulation (Yuan et al., 2024).

7.2 Optimizing agronomic management for enhanced seed quality

Agronomic management can partly buffer quality losses, but environment remains the dominant driver of soybean seed composition across production systems. In a synthesis of 13 574 U.S. data points, site-year explained more than 70% of the variation in protein, oil, and yield, which means management usually works by shifting how crops experience temperature, radiation, water, and nitrogen during seed filling. Within that constraint, delayed planting consistently reduced oil concentration, whereas corn-soybean rotation improved both composition and yield, showing that timing and system context can move quality in useful directions.

More targeted interventions can improve seed quality without necessarily imposing the usual yield penalty. Lower fertilizer N rates increased both oil and protein concentration in the U.S. synthesis, and irrigation in water-limited Nebraska fields increased yield and protein concentration simultaneously in about two-thirds of fields, especially where conditions were not favorable for oil synthesis (Carciochi et al., 2023). Regional field studies further show

that early planting tends to increase oil, late planting tends to increase protein, and improved nutrition at sowing can raise both yield and seed protein concentration, although the response depends on region and field productivity (Di Mauro et al., 2023).

7.3 Future research directions in dynamic regulation of seed composition

Future progress depends on resolving the developmental mechanisms that produce the protein-oil trade-off rather than only selecting around its final outcome. Current reviews argue that breeders need seed development-based studies using mutants, multi-omics, and metabolic flux analysis to explain how soybean seeds rebalance protein, oil, and sucrose during filling (Kumar et al., 2025). This need is reinforced by evidence that only a few soybean-specific oil and protein regulators have been functionally characterized so far, despite the likely existence of many crop-specific transporters, proteases, and transcription factors that are not predictable from Arabidopsis homologs alone.

The most promising future breeding framework combines multi-omics-guided target discovery with precise editing and broader use of untapped diversity. Spatial transcriptomics and metabolomics in wild soybean already show cell-type separation between protein- and lipid-associated metabolism and identify regulators such as *GsMAPK23-4* that alter amino acid and protein accumulation. At the translational end, gene editing now extends beyond natural alleles: DNA-free and AI-assisted editing pipelines are being developed for genotype-independent improvement, and AlphaFold-guided editing of *GmSWEET10a/b* has already increased oil or protein in multi-year, multi-site field trials without reducing yield (Wang et al., 2025; Kim et al., 2026).

8 Conclusions

Protein and oil accumulation in developing soybean seeds follow coordinated but often antagonistic temporal patterns that are shaped by shared metabolic resources and stage-specific regulation. Developmental studies show that the inverse association between mature seed protein and oil reflects cumulative changes across seed filling rather than a single static relationship, and late seed development is especially important because lipid content can decline during maturation while carbohydrates increase as maternal nutrient supply diminishes. Complementing this metabolic view, transcriptomic network analysis across contrasting high-oil and high-protein cultivars indicates that the major transcriptional divergence appears in later developmental stages, when lipid-centered and nitrogen-centered programs become antagonistically activated. These dynamic patterns also help explain why soybean seed composition is difficult to improve through endpoint-based selection alone. Comparative metabolomics of extreme phenotypes identified key intermediates such as glucose, citric acid, and α -ketoglutarate, and showed increased Calvin cycle, TCA cycle, and glycolytic activity in lines with strong protein or oil accumulation, supporting a model in which carbon rerouting underlies reserve deposition. Proteomic analysis further shows that differences in seed oil and protein content arise largely from the peripheral proteome, which fluctuates strongly across seed developmental stages rather than from a fixed constitutive protein set.

For soybean quality improvement, the central implication is that protein and oil should be treated as complex quantitative traits with partially shared but partly separable genetic control. Genome-wide studies have identified many loci affecting seed composition, including 87 chromosomal regions in one diverse panel and additional candidate genes involved in nitrogen fixation, amino acid biosynthesis, and fatty acid metabolism, providing a substantial marker base for breeding. More recent resequencing-based GWAS likewise detected 23 loci for protein and 29 for oil, including multiple new regions and nine candidate genes related to biosynthesis, transport, signaling, and development, reinforcing the feasibility of marker-assisted improvement. At the same time, breeding strategies must account for persistent trade-offs among composition, yield, and adaptation. Historical analyses indicate that selection for yield has reduced seed protein concentration by 0.06% per year while increasing residual low-energy fractions, and century-scale surveys in China found declining protein concentrations with largely stable oil content across decades of cultivar release. Conventional breeding therefore remains constrained by the negative correlation between protein and oil, but newer work suggests that simultaneous improvement is possible when breeders target independent loci, pleiotropic regulators, or specific genomic regions that affect one trait without penalizing the other.

Future research should move beyond descriptive composition analysis toward developmentally resolved, mechanism-based design of soybean seed quality. Reviews of soybean functional genomics emphasize that hundreds of QTLs have already been identified, but relatively few genes have been functionally validated, and progress now depends on integrating genomics, transcriptomics, proteomics, and transformation technologies more effectively. A parallel design-oriented synthesis argues that resolving the protein-oil trade-off will require seed development-focused mutant analysis, multi-omics integration, and isotope-based metabolic flux studies that can capture rebalancing among protein, oil, and sucrose during filling.

Sustainable soybean production will also require linking seed quality improvement with climate resilience and resource efficiency. Soybean already contributes to sustainable agriculture through biological nitrogen fixation, but future breeding must address the fact that abiotic stress disrupts seed filling, shifts the balance among protein, oil, and fatty acids, and reduces protein yield per hectare even when concentration rises under drought or heat. The most promising roadmap combines climate-resilient breeding, optimized source-sink balance and nitrogen fixation, wider use of wild and diverse germplasm, and predictive approaches that incorporate nonlinear environmental effects on seed composition across regions and maturity groups.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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