

Advancing mungbean productivity: agronomic management practices across a global database
and yield critical period determination

by

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B.S., Maringa State University, 2023

A THESIS

submitted in partial fulfillment of the requirements for the degree

MASTER OF SCIENCE

Department of Agronomy
College of Agriculture

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2025

Approved by:

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Abstract

Legume crops such as mungbean (*Vigna radiata* (L.) R. Wilczek) offer significant nutritional and agronomic benefits, particularly in developing regions. Mungbean is a pulse crop with high protein content (21–33%) and essential micronutrients such as iron and zinc, making it a valuable component of plant-based diets. In addition, its bioactive compounds contribute to various health benefits. Agronomically, mungbean's short life cycle (70-80 days), nitrogen-fixing ability, and positive rotation effects on cereals make it a promising crop for sustainable farming systems. Despite its advantages, optimizing mungbean production is essential to improve yield stability and meet increasing global demand. This study aims to enhance mungbean yield and quality by developing a global dataset to identify high-performing management strategies and fill knowledge gaps. In addition, understanding the physiological processes of the crop is critical to reducing yield variability. Therefore, this research also investigates the critical period for seed yield formation and the key yield components that contribute to yield variation. By integrating agronomic and physiological knowledge, this study provides valuable recommendations for optimizing mungbean production, ultimately contributing to global food security and sustainable agricultural practices.

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Acknowledgments

I would like to acknowledge my appreciation and gratitude to my major advisor, Dr. Ignacio Ciampitti. He has had a profound impact on my life; his mentorship has been an invaluable support as I have learned how to be a better researcher. Most importantly, he makes me believe in my own skills.

My earnest thanks to my committee members, Dr. Vara Prasad and Dr. Timothy Durrett, for their invaluable guidance, kindness, and patience, and for all the advice and knowledge shared.

I would also like to thank the many other faculty members in the department who have supported me and afforded me the opportunity to work and learn alongside them.

Thanks to all the students in Ciampitti's lab from 2022 to 2025; it was a pleasure to share the journey together and create so many good memories.

Thanks to the postdocs with whom I have worked closely and who have taught me so much, especially Ana, Victor, and Federico. Thanks to Dennis Boller, all the visiting scholars and interns I had the pleasure of meeting, who made all this work possible.

I am also grateful for the support and collaboration of my colleagues and staff in the Department of Agronomy. My gratitude also goes to the Kansas Department of Agriculture, which contributed to making these studies possible.

Finally, I am forever grateful to my family for the sacrifices each of them has made along the way to make it possible for me to get here today, and for being my biggest support system. To my fiancée, Leonardo, thank you for your patience, encouragement, and unconditional support. This achievement would not have been possible without all of you.

Dedication

I dedicate this thesis to my family, who have blessed me with unconditional love and support. To my father, who made me always believe in myself. To my mother, whose kindness and happiness have greatly enriched my life, and to my brother, who brought joy and energy into my life. I cannot imagine life without them.

Chapter 1 - General Introduction

Food is a fundamental human right, and agriculture plays a central role in ensuring food availability, but climate change, biotic and abiotic stressors, and socio-economic disparities hinder progress in food production and distribution (Adesogan et al., 2020; Geremew et al., 2020). Currently, the global food supply is based on 30 crops, supplying 95% of our daily caloric intake, of which 60% is provided by just four crops, i.e., rice, wheat, maize, and potatoes (FAOSTAT, 2024). However, minor crops are still important at the local, regional, and national levels. In many cases, these minor crops are staple foods that contribute to food supply and nutritionally balanced diets during certain periods (Hilger et al., 2015).

Mungbean (*Vigna radiata* (L.) R. Wilczek), commonly referred to as green gram, is an ancient, cultivated legume native to Asia (Somta, et al., 2022). It is widely cultivated in Asia, but also in parts of Africa and Australia. Today, almost 90% of mungbean production is in Asia, with India, China, Pakistan and Thailand among the major producers (Lambrides and Godwin 2007). As a pulse crop with multiple nutritional benefits, mungbean is well suited to sustainable farming systems. It is particularly valued for its high protein content, which ranges from 21% to 33% (Ganesan et al., 2018). Additionally, it is a good source of essential micronutrients, including iron (30–60 µg/g) and zinc (20–40 µg/g). Compared to soybean, mungbean has a relatively low phytic acid content, making it a valuable source of dietary iron in plant-based diets, particularly in developing countries (Vijayalakshmi et al., 2003). Its vitamin C content is also higher in sprouted seedlings than in non-germinated dry seeds.

Beyond its nutritional value, mungbean offers numerous health benefits due to the presence of bioactive compounds such as linoleic acid, tocopherol, bioactive peptides,

polysaccharides, and polyphenols (Hussain et al., 1983; World Health Organization, 2004; Institute of Medicine, 2001; Ganesan et al., 2018). In addition, mungbean is a warm-season legume with a short life cycle of about 70-80 days. As a nitrogen-fixing crop, it forms a symbiotic relationship with rhizobia, improving soil quality and reducing the need for nitrogen fertilizer. When grown in rotation with cereals, mungbean increases grain and straw yields due to its residual soil enriching effects (Yaqub et al., 2010).

Given its agronomic and economic advantages, mungbean is a valuable crop for farmers seeking to improve the sustainability and profitability of their farms. With the growing global demand for mungbean, it is essential to optimise its management practices to improve production efficiency and meet market needs. The present study aims to optimize mungbean production. This current Chapter 1 presents the background and objectives of this work. Chapter 2 focuses on the development of a global dataset of agronomic practices for managing seed yield and quality. This dataset helps to identify high performing management strategies that improve seed yield and quality while reducing variability. Additionally, it also enables direct comparisons of different practices, highlight knowledge gaps and guide future research. By making this dataset accessible, the study supports the scientific community in improving the agronomic and environmental performance of mungbean. An effective approach to reducing yield variability and increasing productivity is also to improve our understanding of the physiological processes of a crop. Chapter 3 provides as main goals to: (1) determine the critical period for seed yield formation and its associated yield components in mungbean and (2) identify the key yield components contributing to variations in seed yield. Lastly, Chapter 4 presents an overall conclusions and future research steps.

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Chapter 2 - A global data set on mungbean for managing seed yield and quality

Abstract

Mungbean, a protein- and nutrient-rich legume widely grown in Asian countries, is now expanding to other regions. With increasing global demand for nutritious foods and more sustainable agricultural practices, mungbean represents a valuable opportunity to diversify food systems and improve global nutrition. However, management practices to optimize seed yield and quality (including seed oil and protein concentration) remain largely unexplored due to the recent introduction of this crop in many parts of the world. This study aims to create a global open dataset of key crop management practices and their impact on seed yield parameters and quality. This dataset included 227 studies published between 1984 and 2023, comprising 2,154 observations. It focuses on key agronomic practices, including fertilization, irrigation, row spacing, seeding rate, and planting date. By providing comprehensive insights into mungbean cultivation, this open-access dataset enables researchers and agronomists to optimize management practices, identify research gaps, and enhance seed yield and nutritional quality. It serves as a valuable tool for improving food security and sustainable agriculture.

Introduction

Mungbean (*Vigna radiata* (L.) R. Wilczek) is a summer crop legume, cultivated on about 7 Mha worldwide (Nair and Schreinemachers, 2020). Today, nearly 90% of the mungbean production is found in Asia, where India, China, Pakistan, and Thailand are among the most important producers, but mungbean is also produced in parts of Africa, Australia, North and South America (Lambrides and Godwin, 2007, Nair et al., 2013). This crop has many advantages that make it a good option for inclusion in crop rotations or intercropping systems. It has a short growth cycle (70-95 days), with low-input requirements, and as a legume, it fixes most of its nitrogen (Peoples et al., 2009) allowing growers to increase profitability and sustainability of their farms. Mungbean also plays an important role in nutritional feed. The seeds are rich in easily digestible protein (~24%), fiber, antioxidants, and phytonutrients, and they could be consumed whole, split, ground into flour, or used as sprouts (Tang et al., 2014). This nutritional profile makes mungbean an excellent addition to a balanced diet with cereals, with this legume as a less expensive available source of protein for developing countries (Tharanathan and Mahadevamma, 2003) and for vegetarians. However, mungbean yields are low on a global scale, averaging 0.73 t ha^{-1} , with a great potential to develop better (Kassa et al., 2022).

Understanding the impact of different agronomic practices on mungbean is crucial for developing strategies that enhance both seed yield and quality and reduce seed yield variability. A comprehensive global dataset offers a unique opportunity to analyze the variability in mungbean performance under diverse environmental conditions. This global dataset can help researchers identify high-performing management practices that lead to increased seed yield and quality or reduce seed yield variability. In addition, this global data set provides two important benefits. First, it enables direct comparisons of a wide range of agronomic practices, helping to

identify those most effective in different contexts. Second, it allows researchers to assess current knowledge of practices that affect mungbean yield components and quality, and to identify knowledge gaps in existing research. By highlighting areas where future research is needed, this dataset can guide efforts to further optimize mungbean production. Lastly, by making this dataset available, it supports the broader scientific community in its efforts to evaluate and improve the agronomic and environmental performance of this cash crop.

Material and Methods

Data collection

A comprehensive literature search was conducted in March 2024 across several databases, including Wiley, ScienceDirect, Scopus, and Web of Science, followed by a subsequent search in March 2025 using Google Scholar, to compile data on mungbean cultivation. The search equation was formulated to include key terms related to the crop and its management practices, focusing on the title, abstract, or keywords. The terms used were (“Mungbean” or “Mung bean” or “*Vigna radiata*” or “Green gram”) and (“yield” or “protein” or “oil”) and (“harvest” or “fertilization” or “watering” or “plant density” or “planting date” or “sowing date” or “irrigation” or “row spacing” or “seeding rate” or “fertilizer rate”). The studies on other species such as Black gram or *Vigna mungo* were explicitly excluded.

For the publisher Wiley, the search was restricted to articles within the field of agriculture, resulting in 814 publications. For ScienceDirect, the search was limited to agricultural and biological sciences, including review articles, research articles, and short communications, yielding a total of 667 publications. The search in Scopus, confined to agricultural and biological sciences and English-language articles, reviews, and journals,

resulting in 607 publications. For Web of Science, the search was restricted to areas of Agriculture multidisciplinary, Plant Science agronomy, or Food science and technology, including Articles, early access publications, and Proceedings Papers, also limited to English, resulting in a total of 851 publications. Finally, the bibliographic search was conducted in Google Scholar using the Publish or Perish software (Harzing, 2007). The search equation was employed to search the 2,000 most relevant publications from 1984 to 2025 by title and then by keywords, resulting in a total of 3,415 effective publications. In summary, the initial search across all search engines produced a total of 6,354 published articles (Figure 2-1).

The first screening step involved removing duplicates and articles without DOI, reducing the dataset to 5,135 publications (Figure 2-1). A subsequent abstract screening was conducted to eliminate studies that did not address the specific topics outlined in the search equation, resulting in 1,142 relevant articles. The process of identifying duplicates and conducting the abstract screening was facilitated by the R package devtools (Wickham et al., 2022).

The final screening involved a detailed manual review of the full articles to ensure they reported the effects of key management practices defined in the search equation- on seed yield, protein, and oil concentrations in mungbean. Only studies conducted under field conditions were included, leading to the selection of 227 publications comprising a total of 2,154 individual observations (Figure 2-1).

Data extracted from these articles included plant growth parameters, yield, and seed components, and were recorded manually. In cases where data were presented graphically, figures were digitized using WebPlotDigitizer (<https://automeris.io/WebPlotDigitizer>). In addition, relevant metadata were collected, such as authorship, year of publication, experimental design, information on laboratory methods for determining seed components, soil characteristics

(soil type, texture, and pH), and details about fertilizer application (timing, type), were also gathered to provide context for the observations.

Additionally, annual mean temperature and total precipitation were collected from the studies when reported by the authors. To supplement the weather data, we also included annual mean temperature, total precipitation, annual mean humidity, and total solar radiation from NASA Power (Sparks, 2018) for studies that did not report weather data, as well as for those that did. Thus, the weather data in this database include both observations from the original studies and additional data from NASA Power.

Data Records

The dataset generated from this study is publicly accessible through the Figshare repository, available at <https://doi.org/10.6084/m9.figshare.27111106>. The repository contains the following files:

“Mungbean_dataset.xlsx”: This file includes the comprehensive global dataset.

“Metadata.docx”: This document provides a detailed explanation of the dataset, describing each column and the units of measurement for each variable.

3. “References.docx”: A compilation of all the references from the articles used in this study.

4. “Code.zip”: The scripts used to generate the figures presented in this study.

The “Mungbean_dataset.xlsx” can be divided into three key sections:

First Section: Contains publication-specific details, such as the paper ID, authors, year of publication, URLs, and DOI for each article.

Second Section: Focuses on experimental design and field-related information. This includes the study coordinates, location, year of study, experimental design, number of replications, and descriptors (main, secondary, and additional).

Third Section: Contains the plant growth, yield, and seed quality parameters. This includes metrics such as plant weight, number of leaves per plant, number of branches, number of pods per plant, pod length, number of seeds per pod, seed weight, total seed yield, biological yield (total dry matter produced per plant or unit area), and harvest index (ratio of seed to total above-ground dry matter). Seed components such as protein, oil, starch, and carbohydrates, and the laboratory methods used to determine these components, are also included.

Additionally, the dataset captures relevant soil characteristics, including soil texture, type, pH, bulk density, organic carbon content, and the depth at which these parameters were measured. Weather data, including annual mean temperature, total precipitation, annual mean humidity, and total solar radiation were also recorded. Furthermore, fertilizer-related information was collected, including fertilizer type, time of application, and key nutrients.

The treatments applied in the publications were classified into three main descriptors in the dataset: ‘Fertilization’, ‘Irrigation’, and ‘Other management practices’ (Figure 2-2). The main descriptor corresponds to the management focused on the search theme defined by the authors. ‘Fertilization’ refers to those treatments in which different fertilizer treatments were evaluated. ‘Irrigation’, corresponds to those treatments in which the effect of irrigation was evaluated. ‘Other’ refers to those treatments in which different treatments for planting date, seeding rate, and row spacing were evaluated.

These descriptors are further divided into subcategories (secondary descriptors):

- Fertilization was divided into nitrogen (N), phosphorus (P), potassium (K), and sulfur (S) treatments.
- Irrigation subcategories include sprinkler, furrow, flood, drip, and wick irrigation methods.
- Other management practices were divided into planting date, seeding rate, and row spacing.

‘Nitrogen’, ‘Potassium’, ‘Phosphorus’, and ‘Sulfur’ (N, P, K, and S) are the secondary descriptors for Fertilization, and refer to treatments in which nitrogen, potassium, phosphorus, and sulfur respectively were classified as main nutrient. If more than one nutrient was applied in the treatment, it was classified according to the nutrient with the highest concentration in the formulation.

‘Sprinkler, furrow, flood, drip, or wick’ subcategories, in the secondary descriptor for ‘Irrigation’, correspond to different types of irrigation systems described in each article. The subcategories ‘Planting date’, ‘Seeding rate’, and ‘Row spacing’ into ‘Other management practices’ refer management practices associated with treatments of the same name.

For each secondary descriptor, sub-subcategories, known as ‘Additional descriptors’, were used:

‘N, P, K, and S’ were divided into ‘With fertilization’ and ‘Without fertilization’. In addition, the reported rate of nutrients applied was included along with this classification.

‘Sprinkler’, ‘Furrow’, ‘Flood’, ‘Drip’, and ‘Wick’ was divided into ‘With irrigation’ and ‘Without irrigation’. In addition, the reported amount of water applied, or the timing of application was included along with this classification.

‘Planting date’, ‘Row spacing’, and ‘Seeding rate’ were divided into the date (mm/dd/yy), space (cm), and rate (kg seed ha⁻¹), respectively.

The complete classification (Main, Secondary, and Additional descriptors) is presented in Figure 2-2 to provide a comprehensive overview of the study design and management practices used across the included articles.

Results

Overview of the Dataset

This dataset contains information extracted from papers published between 1984 and 2023 period. Most of these publications originated from countries in South Asia, Middle East, and North Africa, regions most frequently represented in our search criteria (Figure 2-3). The most studied management practices were fertilization and irrigation (together accounting for ~73 % of observations).

Technical Validation

To assess the reliability of the retrieved dataset, a series of quality control measures were conducted. These included visual inspection, box-plot analysis, and detection of potential outliers for the main variables: seed yield and protein concentration (Figure 2-4). The distribution of these variables was analyzed using the first quartile (Q1, the 25th percentile) and the third quartile (Q3, the 75th percentile). The interquartile range (IQR) was calculated as the difference between Q1 and Q3. Seed yield and protein concentration values below the lower threshold ($Q1 - 1.5 * IQR$) or above the upper threshold ($Q3 + 1.5 * IQR$) were identified as mild outliers. Additionally, extreme outliers were determined as those values falling below $Q1 - 3 * IQR$ or above $Q3 + 3 * IQR$. (*Statistical Methods*, 2021).

Eight mild outliers were identified in seed yield for fertilization, exceeding the upper threshold of 1,885 kg ha⁻¹ and the lower threshold of 20.5 kg ha⁻¹ (these observations were collected from IDs 16 and 101, respectively). Furthermore, three extreme outliers were identified in seed yield, with values exceeding 2,585 kg ha⁻¹ (from ID 80). Six mild outliers were detected in seed yield for irrigation, with four observations exceeding the upper threshold of 1,848 kg ha⁻¹ (corresponding to IDs 26, 46, and 52). Only one extreme outlier was identified, with a value of 2,544 kg ha⁻¹ (from ID 46). No mild or extreme outliers were observed in seed protein concentration for either fertilization or irrigation.

Conclusion

This open global dataset is an essential resource for researchers, agronomists, and stakeholders focusing on enhancing mungbean production. This global dataset provides detailed data on seed yield, protein concentration, and various plant growth parameters under different management practices influencing mungbean cultivation. Additionally, this open global dataset can serve to identify scientific knowledge gaps in existing research on key management factors for improving mungbean production and reducing its variability. Addressing these research gaps is critical for optimizing mungbean production and global food security.

Code availability

The global dataset, along with metadata, references, and the R software scripts, are accessible on the Figshare repository (<https://doi.org/10.6084/m9.figshare.27111106>)

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Figures

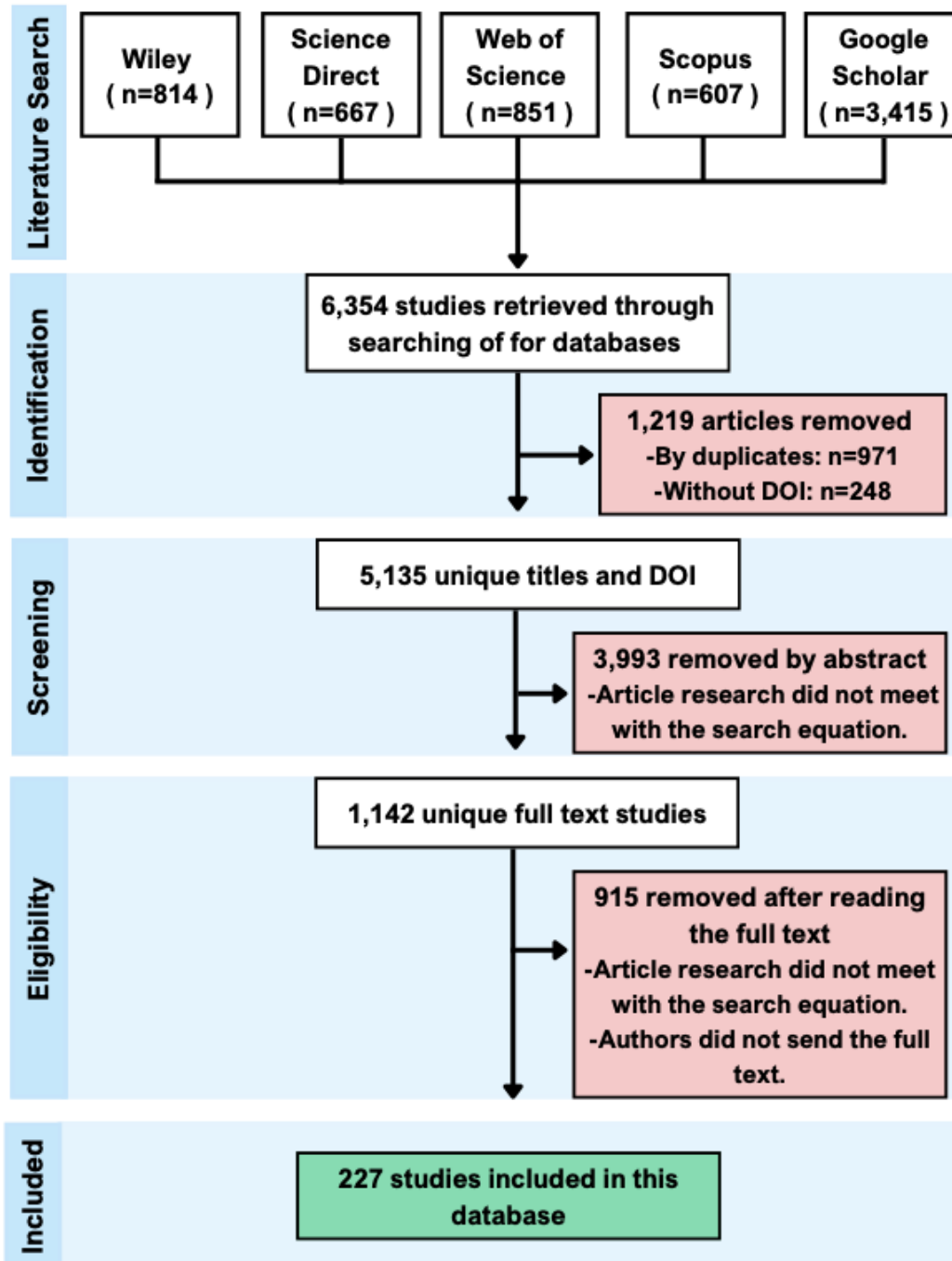


Figure 2-1. PRISMA workflow diagram for the systematic dataset construction, showing the different steps and the number of publications in each step (n).

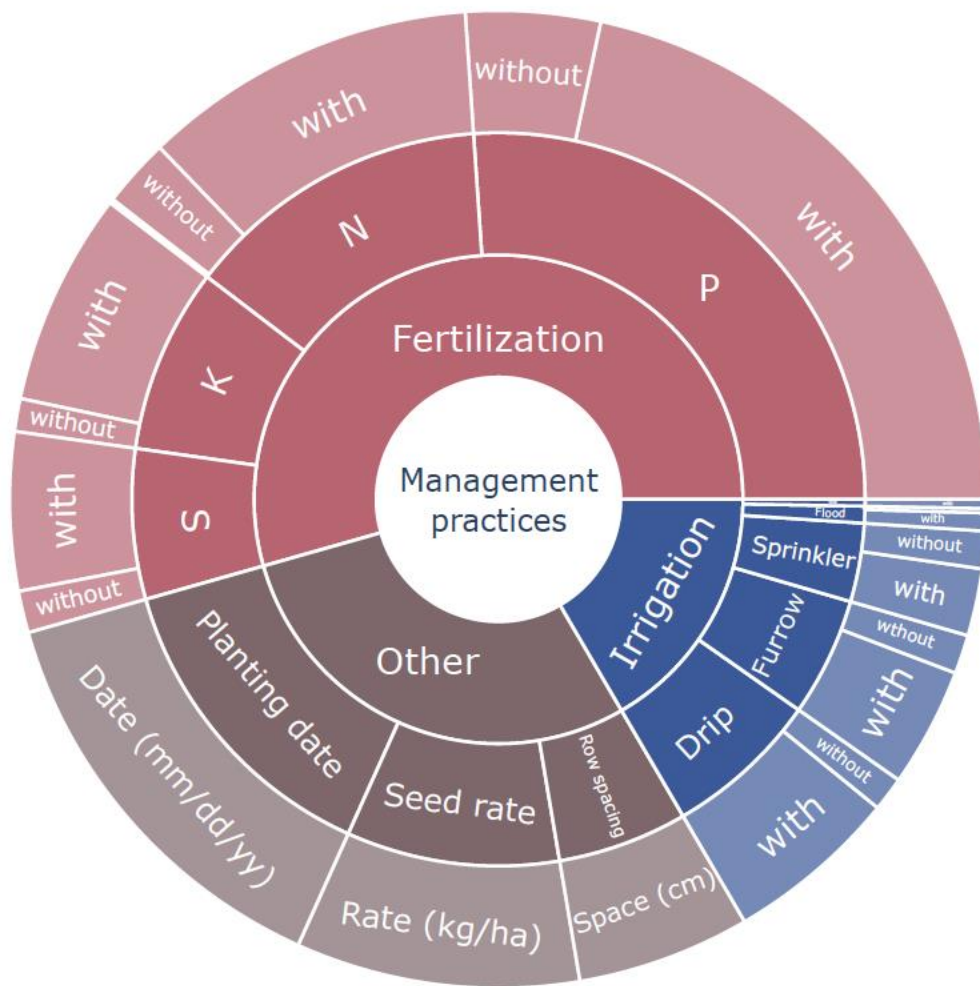


Figure 2-2. Sunburst Diagram of the complete hierarchical structure. At the center, the first layer of information includes the main descriptors, followed by a second layer of information, the secondary descriptors, and lastly, on the outside is the third

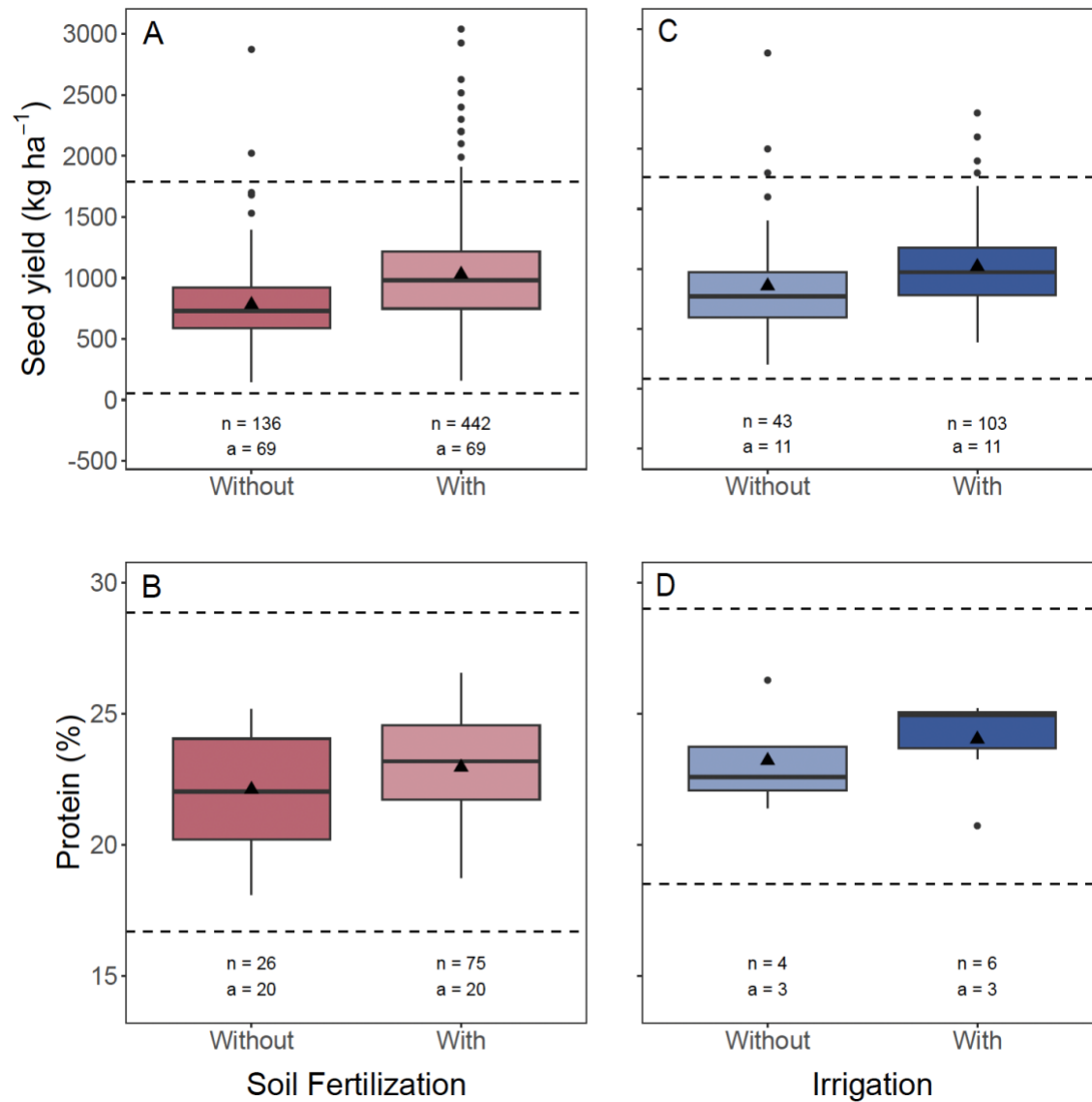


Figure 2-4. Box-plot of seed yield (panels A and C), and seed protein concentration (panels B and D) for Fertilization and Irrigation main descriptors. The solid black line represents the median. The edges of the box correspond to the first (Q1) and third (Q3) quartiles, while the difference between Q1 and Q3 represents the interquartile range (IQR). The whiskers indicate the minimum and maximum value (i.e., $Q1 - 1.5 * IQR$ and $Q3 + 1.5 * IQR$). The dots correspond potential outliers. The triangles correspond to the mean values of seed yield and protein concentration for each level within the treatments. The dashed horizontal lines represent the lower (i.e., $Q1 - 1.5 * IQR$) and upper (i.e., $Q3 + 1.5 * IQR$) limits for mild outliers. 'n' indicates the number of observations, and 'a' indicates the number of studies.

Chapter 3 - Defining the critical period for yield determination in mungbean [*Vigna radiata* (L.) R. Wilczek]

Abstract

Mungbean is a summer legume valued for its high nutritional quality, being rich in protein, essential amino acids, and micronutrients, while also playing a key role in sustainable agriculture through nitrogen fixation and adaptability to diverse cropping systems. However, there is a noticeable gap in knowledge about the critical period of mungbean. For this reason, this study aimed to (i) identify the critical period for seed yield formation and its components in mungbean and (ii) determine the most relevant yield components influencing yield variation. Successive 14-day shading treatments were applied throughout the crop cycle, from emergence to maturity, in field experiments conducted during the 2023 and 2024 growing seasons in Manhattan, Kansas, USA. The critical period was defined as the interval when crop yield was significantly reduced by the shading treatments. The critical period for yield determination was identified between -139.1°C days before flowering (~37 days after emergence) and 427°C days after flowering (~69 days after emergence). Yield reductions ranged from 41% to 68%, with peak sensitivity to shading stress occurring around 100°C days after flowering, corresponding to the beginning of pod formation (R2 stage). Yield losses were primarily driven by reductions in seed number per unit area, with limited compensation from increased seed weight. Pod number per unit area was the strongest determinant of final yield, while seeds per pod had a smaller impact. Defining the critical period for grain yield determination is essential for optimizing mungbean productivity through breeding and management strategies.

Introduction

Mungbean (*Vigna radiata* (L.) R. Wilczek) has gained attention for its nutritional benefits, leading to increased demand (Kim et al., 2015). In addition to its nutritional value, it also offers important advantages to farming systems; these include the possibility of a double crop after a winter crop and the potential to improve soil fertility and cereal yield (Mungbean, 1988; Nair and Schreinemachers, 2020; Pataczek et al., 2018). These characteristics provide farmers with the dual benefits of sustainability and profitability, creating a significant opportunity to invest in this crop and increase production to meet export demand. However, production has not kept pace with demand due to low yields. The average global seed yield of mungbean is relatively low, at just 0.73 Mg ha⁻¹ (Nair and Schreinemachers, 2020). This represents a yield gap of over 100% relative to yields recorded in field experiments (Chauhan et al., 2016; Rachaputi et al., 2019) and those predicted by crop growth models such as the Agricultural Production Systems sIMulator (APSIM), estimated at a potential yield over 2 Mg ha⁻¹ (Chauhan and Williams, 2018; Geetika et al., 2022; Thomas et al., 2004).

To achieve higher average yields, improving our understanding of crop physiology and growth is essential to close the yield gap across production environments. A key starting point for increasing the understanding of crop physiology and growth is the critical period for yield determination, which is defined as the physiological stage in which abiotic stresses have the largest impact on yield determination (Carrera et al., 2024). The concept of a critical developmental period allows us to guide strategies to reduce stress during the most sensitive growth stages (Flohr et al., 2017; Lake et al., 2021). This concept has influenced important agricultural practices, such as optimizing sowing dates and crop cycles (Capristo et al., 2007; Kessler et al., 2020), implement pest and disease management, and enhance irrigation efficiency

(Echarte et al., 2023). All these practices help to avoid exposing plants to stressful conditions in their most sensitive stages.

Sequential shading over a crop lifecycle is commonly used to reduce incident radiation and canopy photosynthesis, thus reducing the source across different phenological stages to identify the critical period for yield determination (Guglielmini et al., 2019; Lake et al., 2021; Mahadevan et al., 2016). This period is well documented for cereals such as oat (*Avena sativa* L.), corn (*Zea mays* L.), barley (*Hordeum vulgare* L.), wheat (*Triticum aestivum* L.), and triticale (*Triticosecale* Wittm) (Arisnabarreta and Miralles, 2008; Cerrudo et al., 2013; Early et al., 1967; Estrada-Campuzano et al., 2008; Fischer, 1985; Mahadevan et al., 2016; Savin and Slafer, 1991). It has also been found in legumes such as chickpea (*Cicer arietinum* L.), lentil (*Lens culinaris* Medik.), soybean (*Glycine max* (L.) Merr.), faba bean (*Vicia faba* L.), lupin (*Lupinus spp.*), and pea (*Pisum sativum* L.) (Kantolic and Slafer, 2001; Lake et al., 2019; Lake and Sadras, 2014; Lake et al., 2021; Monzon et al., 2021; Sandana et al., 2012), as well as other crops such as buckwheat (*Fagopyrum esculentum* Moench) (Guglielmini et al., 2019) and sunflower (*Helianthus annuus* L.) (Cantagallo et al., 1997). However, as far as we know, no studies have been carried out to define the critical period for yield determination in mungbean.

Following the rationale, the aims of this study were to i) determine the critical period for seed yield formation and its yield components in mungbean ii) identify the most relevant yield components accounting for the variation in seed yield and iii) determine the critical period for protein and oil concentration.

Material and methods

Site and management

We conducted four field experiments in 2023 (Experiments 1 and 2) and 2024 (Experiments 3 and 4). All the experiments were carried out at the Experiment Field of Kansas State University in Manhattan, Kansas, United States (39°12'22" N, 96°35'38" W) on a silty clay loam soil. The sowing dates were June 5th (Exp 1) and July 3rd (Exp 2) in 2023, while in 2024, the sowing dates were June 23rd (Exp 3) and July 11th (Exp 4). The seeds were sown mechanically using a drill planter at a depth of 3.8 cm, a plant density of 30 plants m⁻², and a row spacing of 0.38 m. The variety used was Jade-AU. The field was kept free of weeds, which were removed manually when necessary. No pests or diseases were observed in either trial. The plots consisted of four rows of 4.5 m length. Rainfall was supplemented during the growing cycle by a sprinkler system to avoid water stress. Nitrogen fertilization was manually applied as urea (46-0-0) at the R1 (flowering) growth stage at a rate of 180 kg ha⁻¹, supplying a total of 83 kg ha⁻¹ of nitrogen.

Experiment design and shading treatment imposition

To study the effects of shade stress at different growth stages, we applied successive shadings of two weeks each, from emergence (except Exp 1) to physiological maturity (Figure 3-1a). For this purpose, we constructed shade tents using black nylon nets that blocked 90% of the incident radiation. The shade nets were attached to a frame made of polyvinyl chloride (PVC) tubes measuring 2.74 m long, 1.52 m wide, and 0.76 m high, covering an area of 2.1 m². The tents were placed in the center of each plot to minimize boundary effects. The north side of the

tent was left open to ensure regular air movement and to prevent large variations in temperature and relative humidity between the inside and outside of the tent.

The treatments consisted of six different shading times and a control that was left unshaded throughout the growing cycle (S_n ; Figure 3-1a). The treatments were arranged in a completely randomized design with four replicates. The shading treatments were matched to the mungbean phenology based on the phenological scale proposed by the Grains Research and Development Corporation (GRDC) of Australia (GRDC, 2017). Specifically, treatment S1 corresponded approximately to phenologic stages VE-V2, S2 (V3-V6), S3 (V7-V8), S4 (R1-R3), S5 (R4-R5), and S6 (R6-R7). Due to weather conditions, including rain and excessive soil moisture in the field, experiment 1 did not include the S1 treatment, and experiment 2 did not include the S5 treatment. Further details of the shade treatments are given in Table 3-1.

Plant measurements

We recorded crop phenology three times per week following a development scale (GRDC 2017). We defined each developmental stage as the point at which at least 50% of the plants had reached that stage. At maturity, we sampled the aboveground biomass in the two central rows of each plot. We sampled all the plants within 1-meter section measured in each row, totalizing a sampled area of 0.76 m² per plot. We then partitioned the harvested material into pods (containing seeds) and vegetative biomass and dried at 60°C until a constant weight was reached. After counting, we threshed the pods to determine the seed yield per unit area. We counted the total number of seeds to estimate the number of seeds per unit area, while the number of seeds per pod was calculated as the ratio of the number of seeds per unit area to the number of pods per unit area. We calculated seed weight by dividing seed yield by seed number

per unit area and determined harvest index as the ratio of seed yield to total biomass per unit area. Seed yield and its components were expressed on a dry basis for all trials.

Protein, total oil, and fatty acid determination

The determination of seed protein concentration was carried out through dry combustion analysis of nitrogen (N) content, followed by conversion of the nitrogen values to protein using a standard conversion factor, typically 6.25, based on the assumption that protein contains approximately 16% nitrogen. Seed oil concentration and fatty acid profile were quantified using a previously described acid-catalyzed method (Li et al., 2006). Briefly, approximately 20 mg of finely ground grain (particle size of 0.1 mm) from each sample was added to 1.5 mL of toluene, followed by 100 μg of triheptadecanoin as an internal standard. Total lipids were transmethylated by adding 1 mL of 2.5 % (v/v) H_2SO_4 in methanol and heating at 90°C for 1h. The fatty acid methyl esters were extracted from the organic phase after the addition of 1.5 mL of potassium chloride and 2 mL hexane and quantified by gas chromatography using a DB-23 column on Shimadzu GC2100+ gas chromatograph. The oven temperature was initially 200°C for 2 min; then ramped to 240°C at 10°C min⁻¹ and held at that temperature for 4 min. Chromatogram peaks of individual fatty acid methyl esters were identified based by comparing their retention times with those in a standard mixture. Chromatogram peak areas were corrected for flame ionization detector response and oil content was determined as described previously (Li et al., 2006). After obtaining fatty acid concentration in the grain (μg FA mg grain⁻¹), total oil concentration was quantified as the sum of each fatty acid. Thus, individual fatty acid concentration was calculated relative to the total oil concentration and expressed as g fatty acid 100 g oil⁻¹.

Statistical analysis

Seed yield and its components from the shading treatments were normalized to the mean of the control treatment and expressed as a percentage (%) of the unshaded control. Linear fix effects models were performed separately for each of the four experiments, as the number of shading treatments and planting dates varied across the two years. In these models, shading treatment was treated as a fixed effect to evaluate its impact on seed yield and yield components. To examine the effect of shading timing, a one-way analysis of variance (ANOVA) was conducted for each experiment. Pairwise comparisons of all shading treatments with the unshaded control were performed using Tukey's test at a significance level of $P < 0.05$. The relationships between variables were tested using linear regression analysis. All the statistical analyses were performed using the R Core program. Lastly, for each experiment, the thermal time was calculated as growing degree days (GDD, °Cd) from the R1 stage according to the following equation:

$$GDD = \sum_{i=1}^n \left(\frac{Tmax_i + Tmin_i}{2} - Tb \right)$$

where $Tmax_i$ is the daily maximum air temperature on the day i , $Tmin_i$ is the daily minimum air temperature on the day i , and i represents thermal time relative to flowering ($i = 0$ corresponds to flowering, $i < 0$ are days before flowering, and $i > 0$ are days after flowering), and Tb is the base temperature, in this study 7.5 °C (Pasley et al., 2023).

Daily temperature, precipitation, and solar radiation data were retrieved from the Manhattan Kansas Mesonet weather station (<http://mesonet.k-state.edu/>), located about 2 kilometers from the experimental site. 5 (panels B and C) summarizes the weather conditions during the experiments. The mean temperature from sowing to harvest was 25.6°C, 25.3°C,

24.4°C, and 23.5°C in experiments 1, 2, 3, and 4, respectively. The mean maximum and minimum temperatures were 32.3°C and 18.9°C in experiment 1, 32.2°C and 18.3°C in experiment 2, 30.8°C and 18.0°C in experiment 3, and 30.5°C and 16.4°C in experiment 4. The duration of developmental phases varied slightly among experiments. The total crop cycle from sowing to maturity was shorter for experiments 2 and 4, both planted in July (74 days = 1342 °Cd, and 84 days = 1399 °Cd, respectively), compared to experiments 1 and 3, both planted in June (89 days = 1601 °Cd, and 86 days = 1472.5 °Cd, respectively). The mean daily incident radiation from emergence to maturity was 22.9, 21.1, 20.3, and 19.3 MJ m⁻² in experiments 1, 2, 3, and 4, respectively. Total precipitation during the growing season was 199 mm, 132 mm, 217 mm, and 147 mm for experiments 1, 2, 3, and 4, respectively.

Results

The critical period for yield determination and its components

Seed yield

Mean seed yield for the control treatments was 116, 113, 144, and 147 g m⁻² for experiments 1, 2, 3, and 4, respectively (Table 3-2). Yield variation for control treatments within each year was relatively low (3 g m⁻²), with an overall increase of 27% from 2023 to 2024. Shading reduced seed yield in all experiments ($P < 0.05$; Figure 3-2). In 2023, yield reductions ranged from 54% to 65% compared to the control in the treatments S3, S4, and S5. In 2024, the most sensitive treatments were the same as in 2023 (S3, S4, and S5) with yield reductions ranging from 41% to 68% compared to the control. The critical period for yield determination in mungbean was initiated at 139.1 °Cd before flowering (~37 days from emergence) and lasted until 427 °Cd after flowering (~69 days from emergence), on average for the four experiments.

This period ranged from the V8 stage (when the seventh trifoliate leaf at the seventh node is fully expanded) to the R5 stage (when at least one pod on the main stem turns dark brown). The peak sensitivity to shading stress was estimated at ~100 °Cd after flowering, corresponding to the beginning of the pod formation (R2 stage).

Seed number per unit area and seed weight

Mean seed number per unit area (seeds m⁻²) for the control treatment averaged 1696, 1735, 2378, and 2920 for experiments 1, 2, 3, and 4, respectively (Table 3-2). Shading reduced seed number per unit area in all experiments ($P < 0.05$; Figure 3-3a). In 2023, the reduction in seed number ranged from 54% to 59% compared to the control in treatments S3, S4 and S5. In 2024, the most sensitive treatments were S3, S4, and S5 with seed number reductions ranging from 30% to 69% compared to the control. The critical period for seed number determination was initiated at -139.1 °Cd before flowering (~37 days from emergence) and lasted until 427 °Cd after flowering (~69 days from emergence). This period ranged from the V8 stage (when the seventh trifoliate leaf at the seventh node is fully expanded) to the R5 stage (when at least one pod on the main stem turns dark brown). The peak sensitivity to stress was estimated at 184 °Cd after flowering, corresponding to the beginning of the seed formation (R3 stage).

The mean 1000-seed weight for the control treatment was 52.1, 49.8, 46.3, and 47.2 g in experiments 1, 2, 3, and 4, respectively (Table 3-2). The variation in 1000-seed weight within the control (unshaded) treatments each year was relatively low (4.2 g), with an overall decrease of 8% from 2023 to 2024. Shading reduced seed weight in all experiments ($P < 0.05$; Figure 3-3b), except for experiment 2, where an increase was observed. In 2023, seed weight was reduced in the S4 and S5 treatments (23.5% compared to the control, the average of experiments 1 and 2).

In 2024, the reduction in S5 was 16% relative to the control in both experiments. In contrast, seed weight increased in experiment 2, with an observed increase ranging from 11% to 13% in the treatments S1, S2, and S3. The critical period for seed weight determination in mungbean began at 221 °Cd after flowering (~50 days after emergence) and lasted until 427 °Cd after flowering (~69 days after emergence). This period ranged from the R4 stage (when a pod on the top three nodes has constrictions between seeds) to the R5 stage (when at least one pod on the main stem turns dark brown). Peak sensitivity to shade stress was estimated at 336 °Cd after flowering, corresponding to the R4 stage.

Biomass and harvest index

Vegetative biomass was reduced due to shading in three out of the four experiments (Experiments 2, 3, and 4). The most sensitive treatments were before flowering, with the highest biomass reduction in treatment S1 in Experiments 2 and 3, and treatment S3 in Experiment 4. The harvest index (HI) was reduced in 2023 and 2024 ($P < 0.05$). The largest reduction for harvest index was observed for the S3 and S5 treatments in 2023, declining 50% relative to the control (Figure 3-3d), and for the S3 and S5 in 2024, 24% reduction relative to the control. Conversely, the harvest index showed a 31% increase in the S1 treatment for both Experiments 2 and 3.

Integration of yield components and yield

An analysis of yield components with the isolines for seed yield permitted to visualize that shading stress imposed at earlier growth stages (VE-V2 and V3-V6) had a lesser effect on seed weight and number, resulting in relatively stable yields (Figure 3-4). In contrast, when the

stress is applied at reproductive stages between R1-R3 (blue dots) often resulted in a reduction in yield associated with a decrease in grain number per unit area, which was not compensated by the often observed increase in seed weight. Shading stress occurring between the R4 and R5 stages (green dots) resulted in intermediate yield losses associated with a large decrease in seed weight but a milder decrease in seed number. Finally, when stress occurred between the R6 and R7 stages (brown dots), any effect on yield was primarily associated with a reduction in weight per grain.

Relationship between seed yield and pod number and seed number per pod.

Figure 9 shows the relationship between seed yield and the sub-components of seed number per unit area (i.e. pods per unit area and seeds per pod). Seed yield was strongly positively related to the number of pods per m^2 (Figure 3-5a), as 78% ($R^2 = 0.78$) of the variation in seed yield was explained by this sub-component. In contrast, Figure 9B shows a weaker relationship between seed yield and number of seeds per pod, explaining only 35% ($R^2 = 0.35$) of the variation in seed yield. Across all experiments, the number of pods per m^2 ranged from 50 to 350, while the number of seeds per pod varied from 4 to 12. The highest seed yields (above 150 g m^{-2}) were associated with pod numbers above 200 m^{-2} , whereas the number of seeds per pod had a much smaller effect on final yield. Stress applied during the reproductive stages (R1-R5) resulted in the lowest pod numbers and consequently the greatest yield reductions.

The critical period for seed quality

Protein concentration

Mean protein concentration (%) for the control treatment averaged 25.7, 24.3, 25.0, and 24.7 for experiments 1, 2, 3, and 4, respectively (Table 3-3). Shading increased the protein

concentration in all experiments ($P < 0.05$; Figure 10). In 2023, protein concentration increases ranged from 19.9 % to 29.3% compared to the control in the treatments S4 and S5. In 2024, the most sensitive treatment was S5, with protein increase ranging from 13.4% to 20.4% compared to the control. The increases for protein were initiated at 221 °C days after flowering (~50 days from emergence) and lasted until 427 °C days after flowering (~69 days from emergence). This period ranged from the R3 stage (the beginning of the seed formation) to the R5 stage (when at least one pod on the main stem turns dark brown). Peak sensitivity to shading stress was estimated at 221°C days after flowering, corresponding to the R3 stage (beginning of the seed formation).

Total oil concentration

Mean oil concentration (%) for the control treatment averaged 1.6 to 1.8 for experiments 1 and 2, respectively (Table 3-3). Shading reduced the oil concentration in all experiments ($P < 0.05$; Figure 3-7a). In 2023, oil concentration reduction ranged from 12.1 % to 12.6% compared to the control in the treatments S4 and S5. The decrease in oil concentration was initiated at 221 °C days after flowering (~50 days from emergence) and lasted until 335.7 °C days after flowering (~63 days from emergence). This period ranged from the R3 stage (the beginning of the seed formation) to the R4 stage (when one pod on the top three nodes has constrictions between seeds).

Fatty Acid Composition (g 100 g⁻¹ oil)

Shading significantly influenced fatty acid composition across all experiments ($P < 0.05$; Figure 3-7a), with all these changes occurring from 221 °C days after flowering (~50 days after

emergence) until 335.7 °C days (~63 days after emergence). This period spanned the R3 stage, when seed formation begins, to the R4 stage, when constrictions between seeds appear in pods on the top three nodes. For linoleic acid, the control treatment averaged 42.3 to 41.3 g 100 g⁻¹ oil in experiments 1 and 2, respectively (Table 3-3). Shading caused a reduction of 3.8% to 4.0% in 2023 compared to the control in the treatments S4 and S5. In contrast, palmitic acid showed an increase under shading, with control values averaging 28.5 and 28.0 g 100 g⁻¹ oil in experiments 1 and 2 (Table 3-3). This increase ranged from 2.7% to 6.2% in 2023 compared to the control in the treatments S4 and S5. A similar pattern was observed for linolenic acid, where control concentrations of 15.4 and 14.9 g 100 g⁻¹ oil increased by 2.9% to 5.6% under shading conditions compared to the control in the treatments S4 and S5.

Discussion

Mungbean demand has increased in recent decades, and the crop holds the potential to meet future protein needs (Kumar et al., 2022; Nigam et al., 2021). However, global production remains low and highly variable (Chauhan and Williams, 2018). To the best of our knowledge, our study is the first to identify the critical period for yield determination and the key yield components that contribute to variation in seed yield in mungbean. The yield reduction reported on this study due to shading is similar to the one documented by Islam et al. (1993), who reported a ~64% decrease in seed yield when radiation was reduced by 75% during 16 days following the onset of flowering. In addition, Costa et al. (1999) reported a greater reduction, ~76%, in seed yield due to water limitations during the flowering and seed-filling stages, compared to water limitations during the vegetative stage.

For this study, the critical period ranged from the full expansion of the seventh trifoliate leaf (V8 stage) to the point when at least one pod on the main stem turns dark brown (R5 stage), with the most vulnerable period around 100 °Cd after flowering, corresponding to the beginning of the pod formation. This period coincides with that of other legumes such as lupin, lentil, field pea, faba bean, chickpea and soybean, in which the greatest sensitivity of seed yield occurs after flowering between pod emergence and seed filling (Board and Tan, 1995; Jiang and Egli, 1995; Kantolic and Slafer, 2001; Guilioni et al., 2003; Sandana et al., 2009; Sandaña and Calderini, 2012; Lake and Sadras, 2014; Kirkegaard et al., 2018; Lake et al., 2019, Lake et al., 2021, Cerrudo and Naeve, 2025). Other important crops such as canola and buckwheat coincide with mungbean at the time of occurrence of the critical period (Kirkegaard et al., 2018; Guglielmini et al., 2019). Unlike faba bean (Lake et al., 2019) and chickpea (Lake & Sadras, 2014), where the critical period begins approximately 300 °Cd before flowering, mungbean follows a pattern like that reported by Sandaña and Calderini (2012) in lupin and pea, in which the critical period starts about ten days before R1. On the other hand, for most of the temperate cereals (i.e., barley, oat, triticale, wheat) the critical period occurs mostly after flowering (Fischer, 1985; Fischer et al., 2024; Arisnabarreta and Miralles, 2008; Estrada-Campuzano et al., 2008; Mahadevan et al., 2016). This difference can be attributed to the determinate nature of cereals, as opposed to the indeterminate nature of legumes. In cereals, the subcomponents of kernel number are determined during the developmental stages leading to the onset of grain filling (Carrera et al., 2024). In mungbean, as with other legumes, the period during which seed number components are defined overlaps with seed filling due to the asynchrony in reproductive development (Carrera et al., 2024).

The critical period for mungbean represents around 45% of the crop cycle (566 °Cd). This duration is shorter than in other crops with a longer critical period, such as sunflower, where the critical period spans about 60% of the crop cycle (Cantagallo et al., 1997). Soybean also has a broad critical period, with some studies suggesting that it extends from R1 (beginning of flowering) to R6 (full seed) (Jian and Egli, 1995), or even longer to R7 (beginning of maturity) (Board and Tan, 1995). However, more recent studies suggest that the most sensitive stages during the soybean critical period occur between R3 (Beginning pod) and R6 (full seed) (Monzon et al., 2021; Cerrudo and Naeve, 2025). Other legumes, such as chickpea, lupin and pea, have a critical period duration that is proportionally similar to that of mungbean (Sandaña and Calderini, 2012; Lake and Sadras, 2014). Referring to yield components, the current finding related to the critical period (V8 to R5) aligns to the one documented by Lake et al. (2021) for lentil. However, for seed weight, the critical period was well defined with a small window compared with seed yield and number, around 300 °Cd after flowering. This finding did not match with the output documented by Lake et al. (2021) for lentil, which showed that grain weight was unresponsive to shading effect. For mungbean, seed yield response was primarily driven by a reduction in seed number, while seed weight remained relatively stable, mainly when shading stress occurred before seed filling. This finding is consistent with other studies (Sadras, 2007; Sadras and Slafer, 2012; Slafer et al., 2014; Mahadevan et al., 2016). Shading during the seed filling period reduced both seed number and seed weight, indicating some degree of source-sink colimitation, as demonstrated in soybean by Borrás et al. (2004).

In the present study, the number of pods contributed more to the variation in seed yield than seeds per pod. Several authors (Sandaña and Calderini, 2012; Doré et al., 1998; Ayaz et al., 2004b; Poggio et al., 2005) also reported a close relationship between seed yield and pod number

in lupin, and field pea. However, this was different in canola, where seeds per pod were more responsive to shading than pod number (Kirkegaard et al., 2018). The decrease in seed number was probably related to reduced plant growth rate, as this factor has consistently been a strong predictor of grain number variation in several crops (soybean: Jiang and Egli, 1995; Vega et al., 2001; barley: Arisnabarreta and Miralles, 2008; maize: Andrade et al., 1999; Vega et al., 2001; sunflower: Vega et al., 2001; sorghum: Van Oosterom and Hammer, 2008). Therefore, the source limitations analyzed in this study are likely to have affected seed yield and its components by restricting crop growth rate.

The protein, oil, and fatty acid composition of mungbean were significantly affected by shading. A common phenological stage emerged across all experiments, during which distinct responses in protein, oil, and fatty acids were observed. This stage corresponds to the seed-filling period, similar to what has been reported for stress effects on these traits in crops like sunflower, canola, soybean, olive, and maize (Murphy and Piffanelli, 1998; Echarte et al., 2013; Nacer et al., 2011; Bellaloui and Gillen, 2010; Izquierdo et al., 2009; Rousseaux et al., 2020).

Photosynthesis during the seed-filling period is the primary source of energy for seed growth (Shibles et al., 1987; Wardlaw, 1990) and nitrogen assimilation via nitrate uptake and nitrogen fixation (Harper, 1987). Therefore, reductions in photosynthesis during this period are expected to limit both carbon and nitrogen assimilation, which can impact the biosynthesis of fatty acids and proteins. These compounds typically reach their peak production during seed filling (Diepenbrock and Geisler, 1979). Consequently, shading during the seed-filling period, rather than the flowering period, is likely to have a greater impact on seed oil and/or protein concentrations.

When photosynthesis was reduced due to shading, a decrease in yield was observed, linked to a reduction in seed number due to fewer pods, a decrease in oil concentration, and an increase in protein concentration. Specifically, we found that protein concentration increased under shade during the critical period when seed oil concentration decreased. This indicates a negative correlation between seed oil and protein concentrations, a relationship commonly observed in crops such as canola, soybean, olive, and maize (Rondanini et al., 2014; Murphy and Piffanelli, 1998; Echarte et al., 2013; Nacer et al., 2011; Bellaloui and Gillen, 2010; Izquierdo et al., 2009; Rousseaux et al., 2020). This phenomenon occurs because shading inhibits oil synthesis, leading to a shift in resources toward protein synthesis. As a result, protein concentration increases, while oil concentration decreases during the critical period.

Regarding fatty acids, we observed decreases in stearic and linoleic acids during seed filling. In contrast, palmitic and linolenic acids increased during the critical period in mungbean across all experiments. The observed changes in fatty acid composition in response to shade stress are likely due to different mechanisms. The consistent increase in palmitic and linolenic acids and the decrease in linoleic acid under unshaded conditions suggests that palmitic acid may increase because it is energetically less costly for the plant to produce, requiring fewer carbon molecules (Li et al., 2016, Parchuri et al 2023). This could help the plant maintain membrane fluidity. The decrease in linoleic acid is likely due to the activity of the enzyme ω -3 fatty acid desaturase (FAD3), which converts linoleic acid into linolenic acid. This enzyme is activated under stress conditions to maintain the integrity of thylakoid membranes, serving as a defense mechanism to mitigate stress. (Berestovoy et al., 2020, Batsale et al., 2021)

Conclusion

The critical window for seed yield determination in mungbean ranged from 5 days before R1 to 25 days after R1 (V8 to R5 stages). Seed yield was more linked to both the number of pods and seed number relative to seed weight. The critical period for seed quality was in the seed filling, where protein concentration increased, and oil concentration decreased. This study sheds some light on improving stress management, such as aligning sowing time with cultivar phenology to reduce the risk of severe stress during the critical period. Lastly, the definition of this critical window for yield determination will help breeders improve stress tolerance screening by applying more targeted stress treatments, ultimately facilitating the development of more resilient mungbean varieties.

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Figures

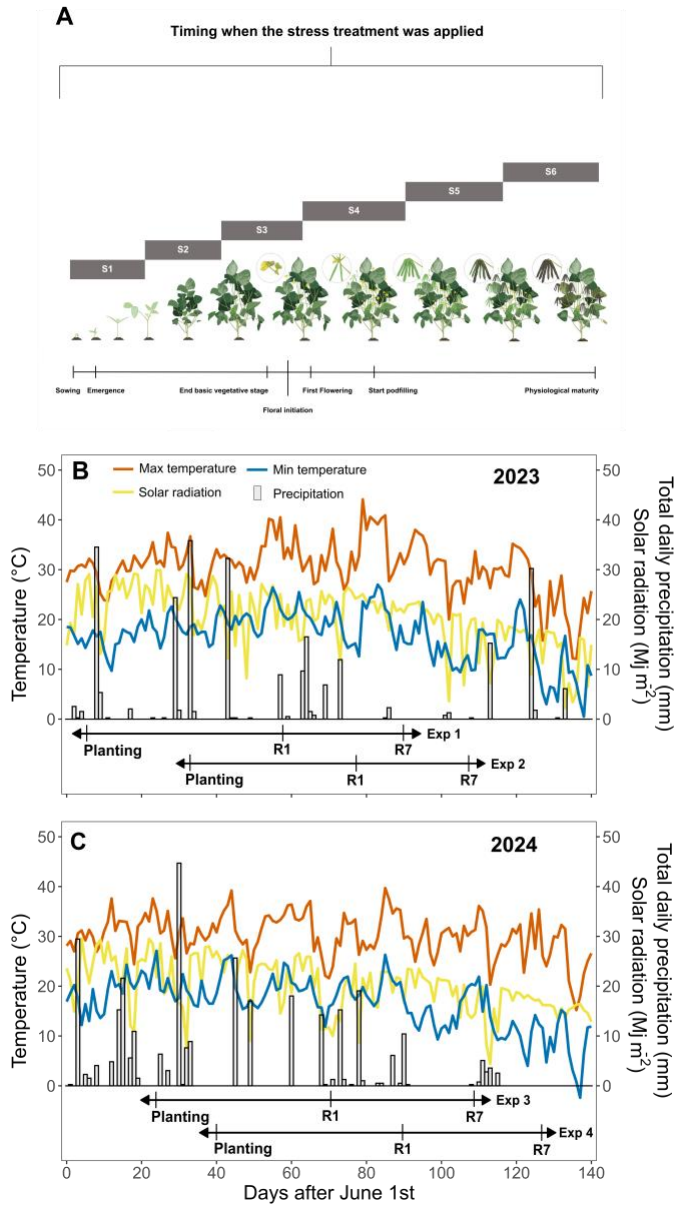


Figure 3-1. Demonstration of shading application throughout the mungbean growth cycle (panel A). Each shading treatment (S_n) was maintained for two weeks per plot, beginning at emergence and concluding at maturity. Figure adapted from Van Haeften et al. (2023). Daily maximum and minimum temperature ($^{\circ}\text{C}$), daily incident radiation ($\text{Rad} - \text{MJ m}^{-2}$), and daily cumulative precipitation (mm) during the mungbean season for the year 2023 (panel B) and 2024 (panel C) for Manhattan, Kansas. Each bar corresponds to daily cumulative rainfall. The horizontal arrow represents the crop cycle, with marks on each experiment's planting date, flowering, and maturity.

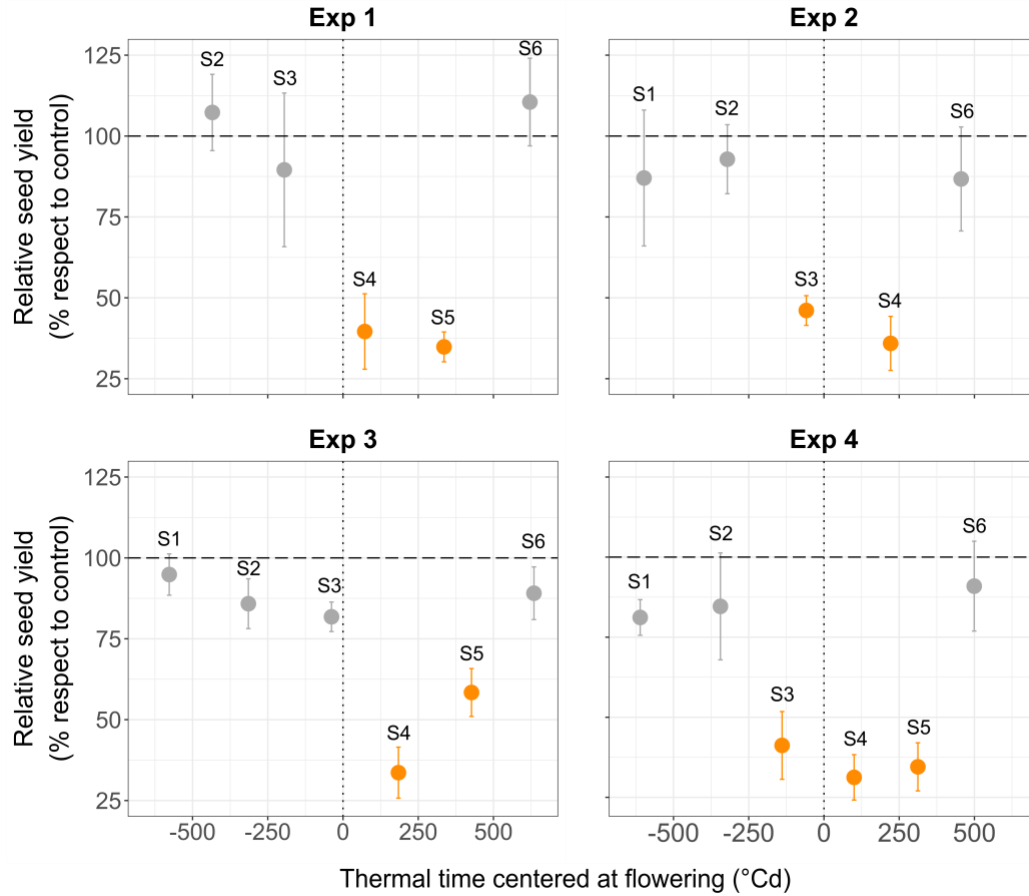


Figure 3-2. Effect of stress imposition on relative seed yield of mungbean for the four experiments conducted during 2023 and 2024. Experiment 1 did not include the S1 treatment, and experiment 2 did not include the S5 treatment. Values are normalized relative to the control plots without the shading imposition (horizontal dashed lines). The midpoint of the shading period was expressed in thermal time (°Cd) from the R1 stage (flowering). Vertical dashed lines represent the thermal time centered at flowering. Gray symbols show no effect of stress imposition relative to the control; orange symbols indicate a reduction due to the stress imposition treatment (P-value < 0.05). Vertical error bars are standard deviations.

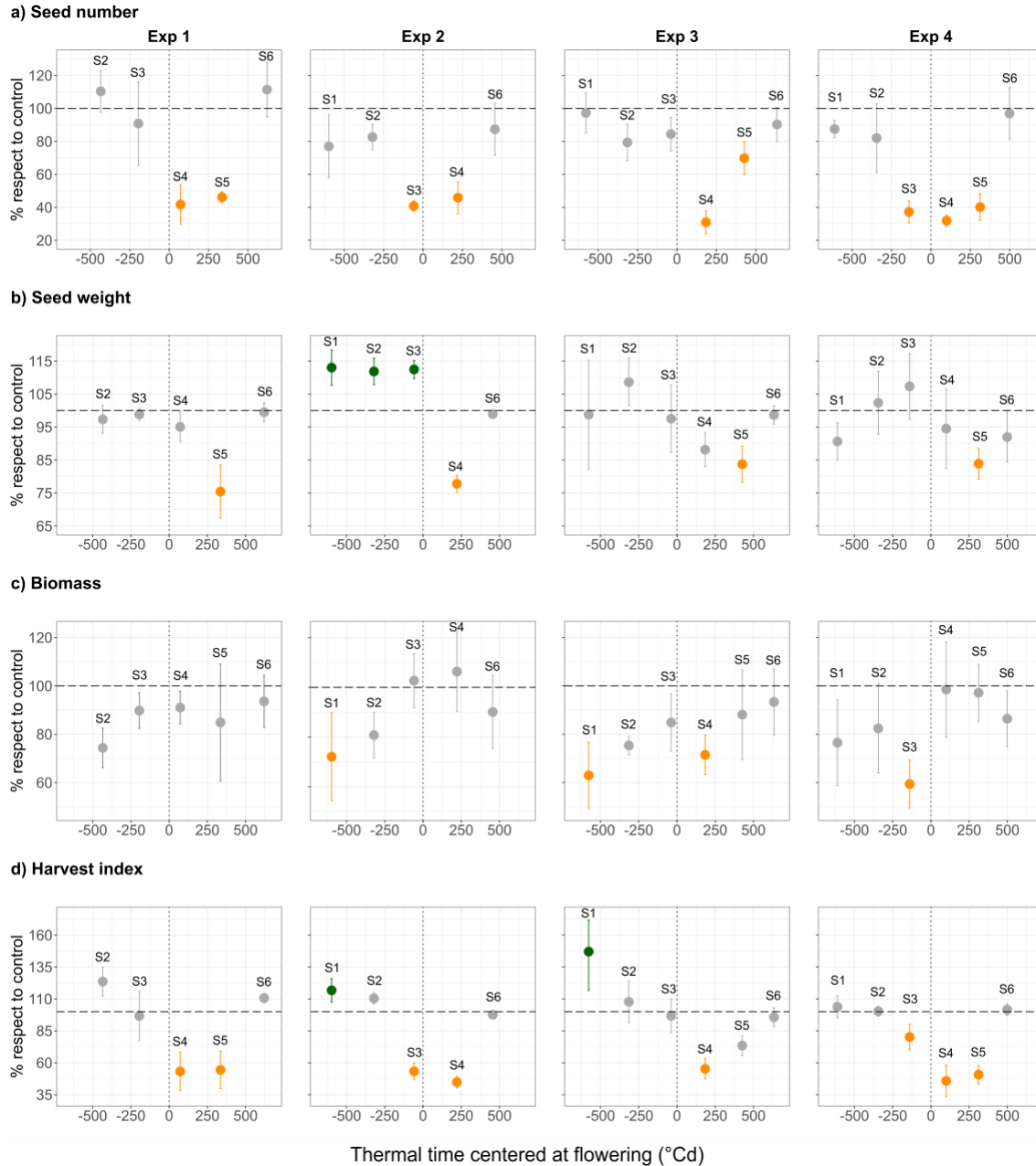


Figure 3-3. Effect of stress imposition on relative seed number m^{-2} (a), relative 1000-seed weight (b), relative vegetative biomass (c), and relative harvest index (d) of mungbean for the four experiments conducted during 2023 and 2024. Experiment 1 did not include the S1 treatment, and experiment 2 did not include the S5 treatment. Values are normalized relative to the control plots without the shading imposition (horizontal dashed lines). Development timing was expressed as the midpoint of the shading period in thermal time ($^{\circ}Cd$) from the R1 stage (flowering). Vertical dashed lines represent the thermal time centered at flowering. Gray symbols show no effect of stress imposition relative to the control; orange symbols indicate a reduction due to the stress imposition treatment ($P < 0.05$); green symbols indicate an increase due to the stress imposition treatment ($P < 0.05$). Vertical error bars are standard deviations and are not shown when they are smaller than the symbol.

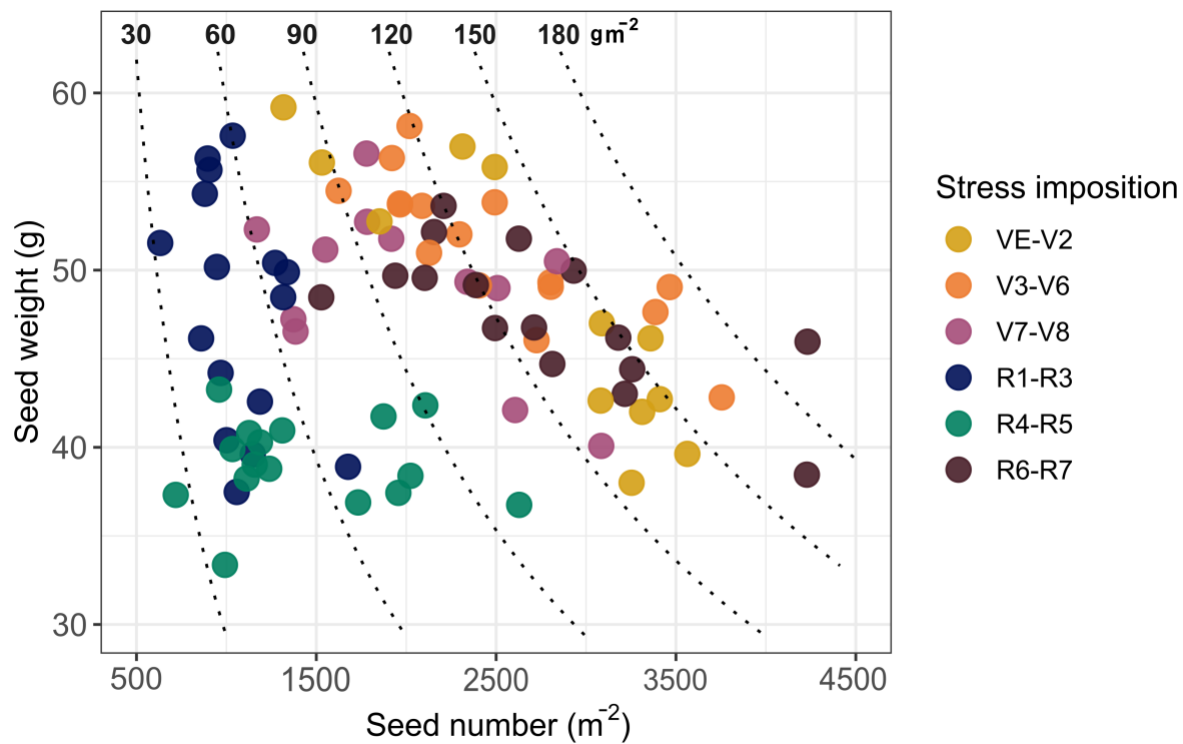


Figure 3-4. Relationship between 1000-seed weight (g) and seed number m⁻² for the four experiments conducted between 2023 and 2024. Symbols represent different stress imposition moments. Black dashed lines connect points with the same yield (g m⁻²).

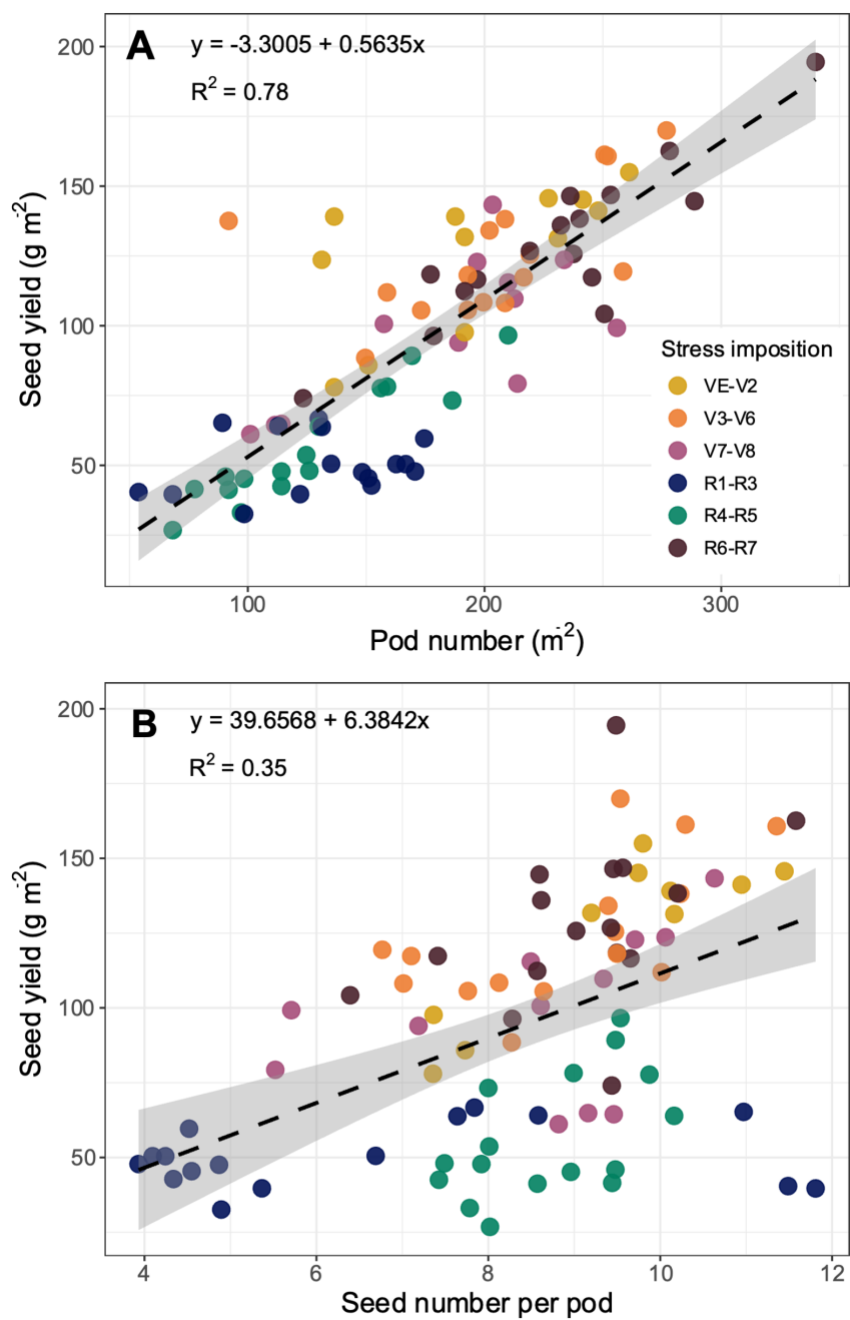


Figure 3-5. Relationship between seed yield (g m^{-2}) and pod number m^{-2} (panel A), seed number per pod (panel B) for the four experiments conducted between 2023 and 2024. Symbols represent the different stress imposition moments.

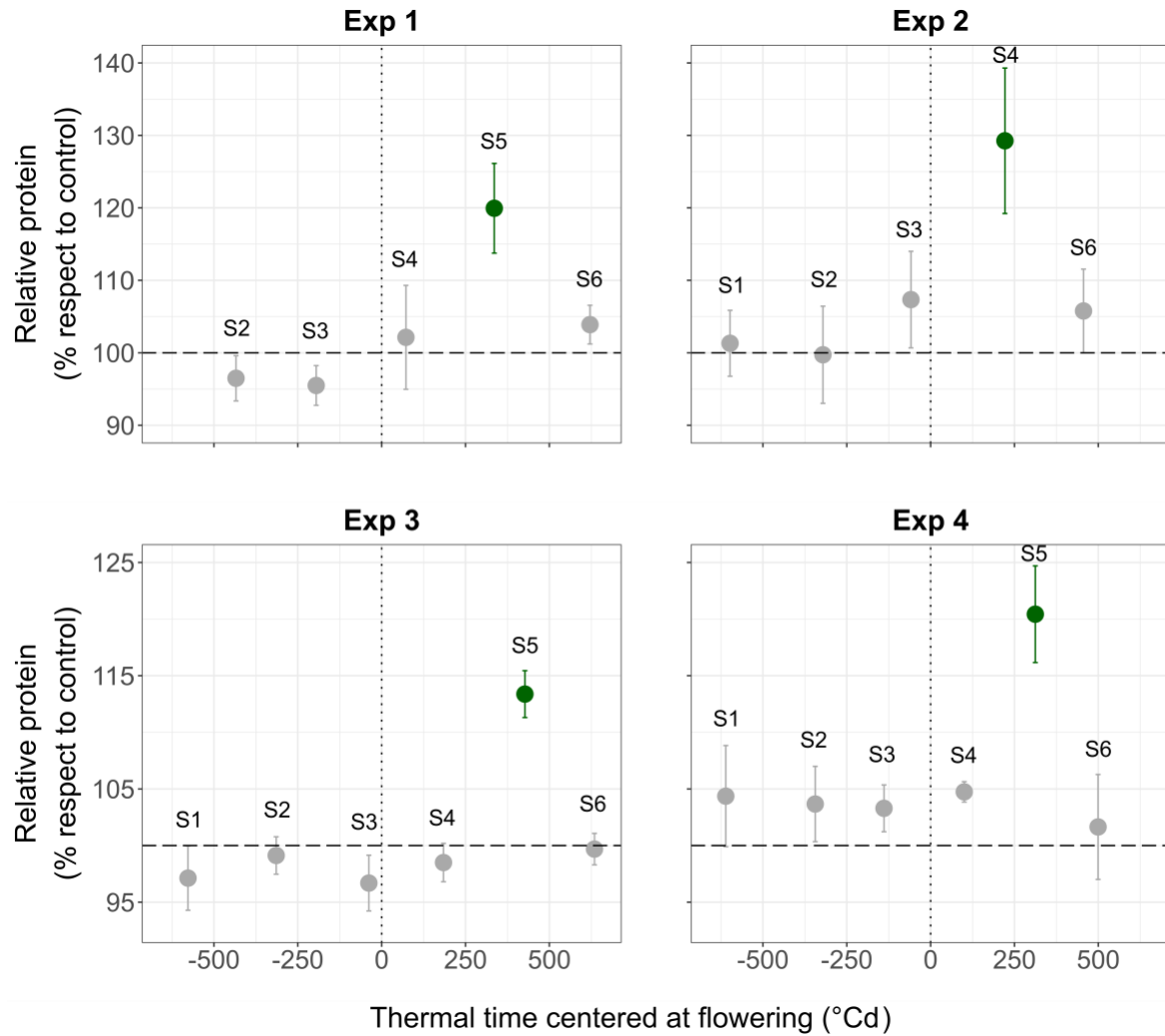


Figure 3-6. Effect of stress imposition on protein concentration of mungbean for the four experiments conducted during 2023 and 2024. Experiment 1 did not include the S1 treatment, and experiment 2 did not include the S5 treatment. Values are normalized relative to the control plots without the shading imposition (horizontal dashed lines). The midpoint of the shading period was expressed in thermal time (°Cd) from the R1 stage (flowering). Vertical dashed lines represent the thermal time centered at flowering. Gray symbols show no effect of stress imposition relative to the control; green symbols indicate an increase due to the stress imposition treatment (P-value < 0.05). Vertical error bars are standard deviations.

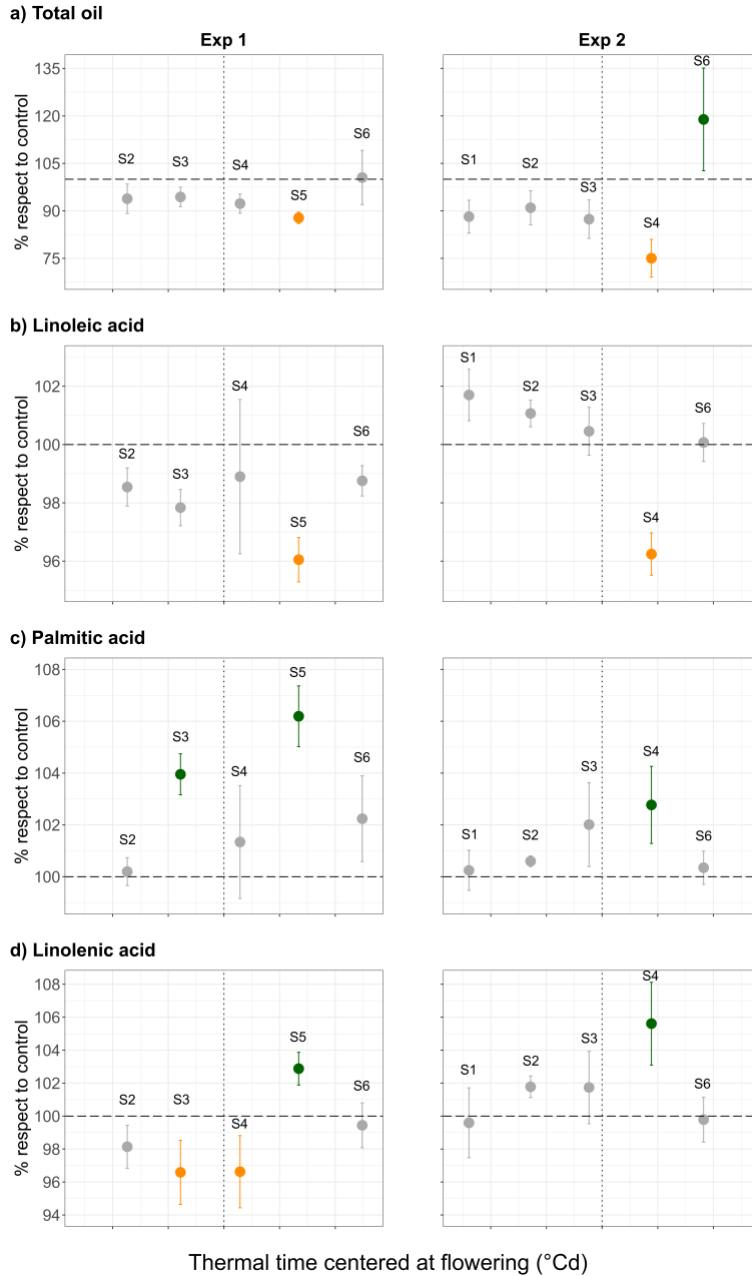


Figure 3-7. Effect of stress imposition on total oil (a), linoleic acid (b), palmitic acid(c), and linolenic acid (d) of mungbean for the four experiments conducted during 2023 and 2024. Experiment 1 did not include the S1 treatment, and experiment 2 did not include the S5 treatment. Values are normalized relative to the control plots without the shading imposition (horizontal dashed lines). Development timing was expressed as the midpoint of the shading period in thermal time (°Cd) from the R1 stage (flowering). Vertical dashed lines represent the thermal time centered at flowering. Gray symbols show no effect of stress imposition relative to the control; orange symbols indicate a reduction due to the stress imposition treatment ($P < 0.05$); green symbols indicate an increase due to the stress imposition treatment ($P < 0.05$). Vertical error bars are standard deviations and are not shown when they are smaller than the symbol.

Tables

Table 3-1. Experiment number along with the information of shading treatment name, shading imposition moment in the phenology, and the thermal time (centered at flowering R1) on which each shade treatment was implemented and removed from the plots.

Experiment	Shading treatment	Moment of stress imposition	Shade starts (°Cd)	Shade ends (°Cd)
1	S2	V3-V6	-564.8	-313.7
	S3	V7-V8	-313.70	-70.8
	S4	R1-R3	-70.8	211.4
	S5	R4-R5	211.4	447.2
	S6	R6-R7	447.2	737.3
2	S1	VE-V2	-727.4	-477.6
	S2	V3-V6	-477.6	-186.2
	S3	V7-V8	-186.2	73.9
	S4	R1-R3	73.9	353.8
	S6	R6-R7	353.8	537.4
3	S1	VE-V2	-694.5	-418.2
	S2	V3-V6	-418.2	-173.8
	S3	V7-V8	-173.8	66.5
	S4	R1-R3	66.5	323.4
	S5	R4-R5	323.4	520.6
	S6	R6-R7	520.6	733.4
4	S1	VE-V2	-722.3	-467.9
	S2	V3-V6	-467.9	-237.2
	S3	V7-V8	-237.2	-20.4
	S4	R1-R3	0	191.3
	S5	R4-R5	191.3	412.9
	S6	R6-R7	412.9	585.3

Table 3-2. Table 2. Mean absolute values for seed yield (g m⁻²), seed number (m⁻²), seed weight (g), vegetative biomass (g m⁻²), and harvest index for the four experiments carried out on the 2023 and 2024 mungbean seasons.

Experiment	Treatment	Yield (g m ⁻²)	Seed number (m ⁻²)	1000-seed weight (g)	Vegetative biomass (g m ⁻²)	Harvest Index
1	Control	116.1 a	1696 a	52.1 a	289.a	0.256 a
	S2	124.6 a	1872 a	50.8 a	215 a	0.317 a
	S3	104 a	1541 a	51.5 a	259 a	0.248 a
	S4	46 b	707 b	49.6 a	263 a	0.136 b
	S5	40.4 b	783 b	39.3 b	245 a	0.140 b
	S6	128.3 a	1890 a	51.9 a	270 a	0.284 a
2	Control	113 a	1735 a	49.8 b	303 a	0.238 b
	S1	98.3 a	1336 a	56.2 a	218 b	0.278 a
	S2	104.9 a	1434 a	55.7 a	244 ab	0.263 ab
	S3	52.1 b	708 b	56 a	311 ab	0.127 c
	S4	40.6 b	795 b	38.7 c	322 a	0.107 c
	S6	98 a	1516 a	49.2 b	273 ab	0.233 b
3	Control	144.2 a	2378 a	46.3 ab	451 a	0.222 bc
	S1	136.7 a	2314 ab	45.7 abc	284 b	0.327 a
	S2	123.8 a	1888 ab	50.3 a	340 ab	0.239 b
	S3	117.9 ab	2008 ab	45.1 abc	383 ab	0.215 bc
	S4	48.5 c	736 c	40.8 bc	322 ab	0.123 d
	S5	84.2 bc	1660 b	38.7 c	397 ab	0.163 cd
	S6	128.4 a	2178 ab	45.7 abc	421 ab	0.212 bc
4	Control	146.6 a	2920 a	47.2 ab	280 a	0.331 a
	S1	143.3 a	2555 ab 2395	42.8 ab	214 ab	0.344 a
	S2	149.4 a	abc	48.3 ab	231 ab	0.332 a
	S3	72.8 b	1087 cd	50.7 a	166 b	0.266 b
	S4	55.2 b	933 d 1173	44.6 ab	276 ab	0.152 c
	S5	61 b	bcd	39.6 b	272 ab	0.168 c
	S6	160.6 a	2830 a	43.4 ab	242 ab	0.336 a

Table 3-3. Mean absolute values for protein, total oil (%), and linoleic acid, palmitic acid and linolenic acid (g 100 g oil⁻¹)

Experiment	Treatment	Protein (%)	Total oil (%)	Linoleic acid	Palmitic acid (g 100g oil ⁻¹)	Linolenic acid
1	Control	25.7 b	1.58 a	42.3 a	28.5 c	15.4 ab
	S2	24.8 b	1.48 ab	41.6 ab	28.5 c	15.2 bc
	S3	24.6 b	1.49 ab	41.3 ab	29.6 ab	14.9 c
	S4	26.3 b	1.46 ab	41.8 a	28.8 bc	14.9 c
	S5	30.9 a	1.39 b	40.6 b	30.2 a	15.9 a
	S6	26.8 b	1.59 a	41.7 ab	29.1 bc	15.4 abc
2	Control	24.3 b	1.81 b	41.3 b	28.0 b	14.9 b
	S1	24.6 b	1.60 bc	42.0 a	28.1 ab	14.8 b
	S2	24.2 b	1.65 bc	41.74 ab	28.2 ab	15.1 b
	S3	26.0 b	1.59 bc	41.48 ab	28.6 ab	15.1 b
	S4	31.3 a	1.36 c	39.75 c	28.8 a	15.7 a
	S6	25.7 b	2.16 a	41.33 ab	28.1 ab	14.8 b
3	Control	25.0 b	-	-	-	-
	S1	24.3 b	-	-	-	-
	S2	24.8 b	-	-	-	-
	S3	24.2 b	-	-	-	-
	S4	24.6 b	-	-	-	-
	S5	28.3 a	-	-	-	-
4	S6	24.9 b	-	-	-	-
	Control	24.7 b	-	-	-	-
	S1	25.8 b	-	-	-	-
	S2	25.6 b	-	-	-	-
	S3	25.5 b	-	-	-	-
	S4	25.9 b	-	-	-	-
	S5	29.8 a	-	-	-	-
	S6	25.1 b	-	-	-	-

Chapter 4 - Conclusion and Future Implications

This research has provided insights into mungbean productivity, focusing on two key aspects: (1) the crop's sensitivity to shading during different moments of the crop phenology and (2) the development of an open global dataset to advance research on agronomic practices influencing mungbean yield and quality. The first study introduces an open global dataset as a valuable resource for researchers, agronomists, and policymakers to analyze the impact of different management practices on mungbean production. This dataset allows direct comparisons under different environmental conditions, helping to identify best practices that optimise seed yield and quality. Furthermore, it serves as a tool for identifying knowledge gaps in current research, facilitating future studies aimed at improving mungbean productivity and sustainability.

The findings from the second study make a significant contribution to the understanding of the critical period for seed yield in mungbean, focusing in particular on the effect of shading during the crop cycle. The data revealed that shading during the critical period for seed yield, which was defined from the V8 stage (when the seventh trifoliate leaf at the seventh node is fully expanded) to the R5 stage (when at least one pod on the main stem turns dark brown), resulted in a significant reduction in seed yield, which fell to 63% compared to unshaded conditions. The reduction in yield was mainly due to a decrease in the number of seeds per unit area, as the increase in individual seed weight was not sufficient to compensate for the losses. Among the yield components, the number of pods per plant was the most influential factor in determining final yield, while the number of seeds per pod played a comparatively minor role. Additionally, vegetative biomass was significantly reduced under shading in three out of four

experiments, with the most pronounced reductions occurring when shading was applied before flowering. The harvest index was also negatively impacted. This yield reduction, however, was accompanied by an increase in protein content and a decrease in oil content, suggesting a shift in the seed composition under stress conditions. The study found that shading during the reproductive stage led to changes in key physiological processes, including photosynthesis and biomass partitioning, which are critical determinants of seed yield. These findings highlight the critical role of light availability in optimizing mungbean biomass accumulation, resource allocation, and overall yield potential.

Together, these studies contribute to a deeper understanding of mungbean productivity, providing a foundation for improved management strategies, data-driven decision-making, and expansion of the crop into new farming systems. This research provides a foundation for advancing mungbean productivity and sustainability, with several key future implications. First, the identification of the reproductive stage (R1–R4) as a critical period for the majority of the variables tested on this study, highlights the need for future breeding programs to develop mungbean varieties with improved tolerance to stress conditions. This could enhance yield stability. In addition, the open global dataset serves as a valuable tool for determining the performance of the crop under different agronomic practices to improve yield and quality.

From a climate adaptation perspective, future studies should explore how mungbean responds to the combined effects of shading, drought, and temperature fluctuations for example. As climate variability increases, understanding how these stressors interact will be crucial for developing climate-smart agricultural practices. Research on optimized, intercropping, and soil health management can further improve mungbean resilience in different agroecological regions. The open global dataset offers an opportunity to analyze large-scale trends and develop region-

specific agronomic recommendations that optimize productivity while minimizing resource use. Mungbean's role in sustainable agriculture can also be expanded. As a nitrogen-fixing legume, mungbean has the potential to enhance soil fertility and improve cereal-based cropping systems. Future studies should evaluate its long-term impact on soil health, nutrient cycling, and overall farm productivity, promoting its adoption in diversified cropping systems.

Beyond agronomic improvements, this research contributes to global discussions on food security. The dataset enables researchers and policy-makers to assess the economic feasibility of mungbean as an alternative protein source, supporting the development of strategies to enhance its production and market potential. Additionally, by making this dataset publicly available, future research can focus on unexplored areas, such as the interactions between agronomic practices, genetic traits, and environmental conditions. Meta-analyses using this dataset can identify global trends, helping researchers prioritize studies on factors that contribute most to yield stability and quality improvements. By integrating these future research directions with ongoing agronomic and breeding advances, mungbean can be positioned as a resilient, high-value crop capable of meeting the challenges of global food security and climate change.